

Hemlock woolly adelgid impacts on community structure and N cycling rates in eastern hemlock forests

Jennifer C. Jenkins, John D. Aber, and Charles D. Canham

Abstract: Mortality of dominant tree species caused by introduced pests and pathogens have been among the most pervasive and visible impacts of humans on eastern U.S. forests in the 20th century, yet little is known about the ecosystem-level consequences of these invasions. In this study we quantified the impacts of the introduced hemlock woolly adelgid (*Adelges tsugae* Annand) on community structure and ecosystem processes in eastern hemlock (*Tsuga canadensis* (L.) Carr.) forests in southern New England. Data were collected at six hemlock-dominated sites spanning a continuum from 0 to 99% mortality. Light availability to the understory and seedling regeneration both increased in stands affected by the adelgid. Differences in soil organic matter, total C, and total N pools between infested and noninfested sites were not associated with hemlock decline. Net N mineralization, nitrification, and N turnover increased at sites experiencing hemlock mortality. Inorganic N availability and nitrification rates increased dramatically with adelgid infestation and hemlock mortality, suggesting that nitrate leaching is likely in regions experiencing hemlock mortality. In the longer term, ecosystem processes at infested stands are likely to be driven by the successional dynamics that follow hemlock mortality.

Résumé : La mortalité causée chez les principales espèces d'arbres par des ravageurs et des pathogènes introduits compte parmi les impacts les plus étendus et les plus visibles de l'homme sur les forêts de l'est des États-Unis au cours du vingtième siècle. Pourtant, on connaît peu de choses relativement aux conséquences de ces invasions sur les écosystèmes. Dans le cadre de cette étude, nous avons quantifié les effets du puceron lanigère de la pruche (*Adelges tsugae* Annand) sur la structure des communautés et sur les processus écosystémiques dans des forêts de pruche du Canada (*Tsuga canadensis* (L.) Carr.) du sud de la Nouvelle-Angleterre. Les données ont été récoltées sur six sites dominés par la pruche et où la mortalité variait de façon continue de 0 à 99%. La disponibilité de la lumière, à la fois pour les strates inférieures et la régénération, a augmenté dans les peuplements affectés par le puceron. Les différences en matière organique du sol, en C total et en pool de N total entre les sites infestés et non infestés ne sont pas reliées au dépérissement de la pruche. La minéralisation nette de N, la nitrification et le cyclage de N ont augmenté dans les sites où il y a eu de la mortalité chez la pruche. La disponibilité de N inorganique et les taux de nitrification ont augmenté de façon spectaculaire avec l'infestation du puceron et la mortalité de la pruche, suggérant que les nitrates sont probablement lessivés dans les régions où se manifeste la mortalité de la pruche. À long terme, les processus écosystémiques dans les peuplements infestés seront vraisemblablement contrôlés par la dynamique de la succession qui s'installe après mortalité de la pruche.

[Traduit par la rédaction]

Introduction

Declines in the abundance of dominant tree species due to introduced pests and pathogens such as gypsy moth (*Lymantria dispar* (L.)), chestnut blight (*Cryphonectria* (*Endothia*) *parasitica* (Murr.) Barr.), beech bark disease

(*Cryptococcus fagisuga* Lind. and *Nectria* spp.), and the hemlock woolly adelgid (*Adelges tsugae* Annand) have been among the most visible and pervasive human impacts on eastern U.S. forests in this century. Forest development following invasion by these organisms is fairly well understood (examples include Good 1968; Campbell and Sloan 1977; McCormick and Platt 1980; Huenneke 1983; Twery and Patterson 1984; Orwig and Foster 1998), but relatively little is known about the ecosystem-level consequences of these invasions. This study contributes to a small but growing body of literature on the ecosystem-level consequences of biological invasions in various ecosystem types (e.g., see Grace 1986; Vitousek et al. 1987; Ramakrishnan and Vitousek 1989; Lovett and Tobiessen 1993; Lovett and Ruesink 1995).

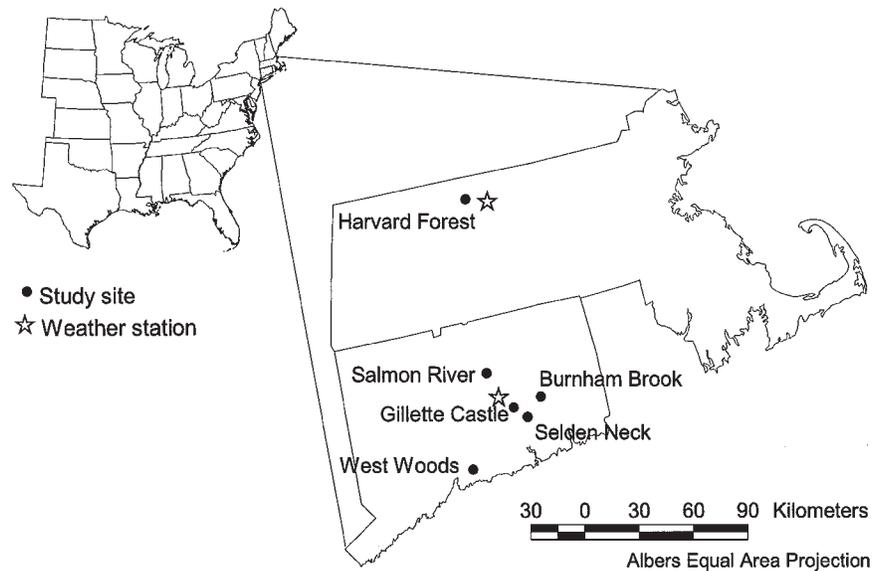
We predicted that changes in forest structure and composition caused by the hemlock woolly adelgid would have measurable impacts on decomposition and N cycling rates within 5–10 years after the onset of hemlock decline. To test

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Fig. 1. Study site locations.

these predictions, we quantified the in situ impact of the hemlock woolly adelgid on forest structure and ecosystem processes in New England eastern hemlock (*Tsuga canadensis* (L.) Carr.) forests.

Adelgid-induced disturbance

The hemlock woolly adelgid has caused significant mortality of eastern hemlock in the eastern United States since the mid-1980s (McClure 1991, Watson 1992, Bonneau and Civco 1996, Royle and Lathrop 1997). A tiny aphid-like insect less than 1 mm long (McClure 1989a), the adelgid is thought to be native to Japan (McClure 1992) and now occurs in the eastern United States from Virginia to Massachusetts.

The insect is spread via birds, deer, wind, and humans (McClure 1989b, 1990), and neither geographic nor physiographic barriers to its distribution appear to have yet been reached. It is prolific in New England, completing two parthenogenetic generations per year (McClure 1989a). The insect colonizes the undersides of the smallest twigs of eastern hemlock and reduces tree vigor by feeding on xylem ray parenchyma cells (Young et al. 1995). Tree mortality can occur in as few as 4 years (McClure 1991).

Unlike other pathogens impacting New England's forests, which have typically caused hardwoods to replace hardwoods, the hemlock woolly adelgid has initiated a rapid shift from a coniferous to a deciduous forest, as seedlings and saplings of red maple (*Acer rubrum* L.), various oaks (*Quercus* spp.), and especially black birch (*Betula lenta* L.) have grown up beneath the dying hemlock canopy (Orwig and Foster 1998). Needle fall from dying hemlock spans several years, and dead trees are left standing. As a result, the gaps created in forests experiencing adelgid infestation are best characterized as "gradual" gaps (Krasny and Whitmore 1992), in contrast to the "sudden" canopy gaps created by well-studied disturbances such as windthrow and logging. The prevalence of eastern hemlock forests in the eastern United States (Dickson and McAfee 1988) suggests the potential for significant regional-scale impacts, making this an especially urgent issue for study.

Materials and methods

Study sites

Study sites were located in central and southern New England (Fig. 1). Four of the six sites (Salmon River, Burnham Brook, Selden Neck, and West Woods) were co-located with those of Orwig and Foster (1998) and the remaining two (Slab City and Gillette Castle) were established for this study. Soils at all sites are mesic typic and lithic Dystrochrepts within the Charlton–Canton–Hollis soil map unit. These are well drained and somewhat excessively drained loamy soils on glacial till uplands (Crouch 1983).

As is nearly always the case with comparative field studies in ecology, it was impossible to control for all site factors. However, to reduce variability between sites, study sites were chosen to be as similar as possible in terms of physical and chemical soil characteristics (Table 1). The basal area (BA) in hemlock before adelgid infestation did not differ significantly among sites, and the six sites spanned a continuum from 0 to 99% hemlock mortality (by BA). Two sites (Salmon River and Slab City) had no evidence of infestation. The exact timing of infestation and hemlock mortality could not be determined, but hemlock decline at all sites began soon after 1990. The four sites co-located with Orwig and Foster (1998) appeared undamaged in 1990 black and white aerial photographs (1 : 12 000 scale) obtained from the Connecticut Department of Environmental Protection (Orwig and Foster 1998). Gillette Castle began to experience visible adelgid damage in 1993–1994 (D. Goss, Gillette Castle State Park Manager, personal communication).

Three square 0.04-ha measurement plots were established well inside stand boundaries at each of the six sites. The plots were gridded at 5-m intervals to create 16 subplots, each 25 m².

Forest structure

Canopy composition

Aboveground forest measurements were taken between June and August of 1995 (Salmon River, Burnham Brook, Selden Neck, and West Woods; Orwig and Foster (1998)) and 1996 (Slab City and Gillette Castle). To quantify canopy characteristics, all trees >8 cm diameter at breast height (DBH) (1.37 m above ground level) were tallied by species and DBH. Standing dead hemlock trees were also tallied to approximate pre-mortality canopy composition. No hemlock stumps or evidence of fallen trees were found on the plots, so we assumed that all trees killed by the adelgid were left

Table 1. Site and soil characteristics.

Site name	Mean elevation (m)	Aspect	Slope (%)	Texture (%(silt + clay))	Total C (Mg·ha ⁻¹)	
					Organic	Mineral
Slab City	396	W	30	27.5 (1.4) <i>ab</i>	22.1 (1.6) <i>ab</i>	33.7 (1.0) <i>bc</i>
Salmon River	53	N	5	25.6 (2.1) <i>a</i>	31.7 (2.9) <i>b</i>	28.6 (0.5) <i>ab</i>
Gillette Castle	25	W	20	35.2 (3.4) <i>bc</i>	15.8 (1.1) <i>a</i>	35.0 (3.9) <i>c</i>
Selden Neck	23	W-NW	9	45.3 (3.8) <i>d</i>	21.7 (3.6) <i>ab</i>	37.4 (3.4) <i>c</i>
West Woods	20	NW-SE	7	39.5 (0.7) <i>cd</i>	30.4 (1.5) <i>b</i>	28.0 (0.9) <i>a</i>
Burnham Brook	107	NW	15	34.8 (5.3) <i>bc</i>	29.2 (10.0) <i>b</i>	33.6 (1.5) <i>bc</i>

Note: Values are means, with SD given in parentheses, from three plots per site. The Slab City and Salmon River sites have no sign of adelgid infestation. Within a column, values followed by the same letter are not significantly different (ANOVA with the Tukey pairwise mean comparison test ($p < 0.10$)).

Table 2. Selected vegetation characteristics.

Site name	Total pre-mortality BA (m ² ·ha ⁻¹)	Pre-mortality density (stems/ha)	Stand age (years)	Hemlock mortality by BA (%)*	BA dead hemlock (m ² ·ha ⁻¹)	Live BA remaining (m ² ·ha ⁻¹)
Slab City	55.1 (2.3) <i>c</i>	883.3 (112.7) <i>b</i>	96 (7)	2.5 (3.8) <i>a</i>	1.0 (1.6) <i>a</i>	54.0 (3.8) <i>d</i>
Salmon River	40.7 (6.5) <i>ab</i>	566.7 (104.1) <i>ab</i>	68 (3)	4.7 (6.4) <i>ab</i>	2.0 (3.0) <i>ab</i>	38.7 (3.4) <i>c</i>
Gillette Castle	45.2 (7.0) <i>abc</i>	308.3 (38.2) <i>a</i>	97 (5)	26.6 (6.3) <i>abc</i>	8.8 (1.0) <i>bc</i>	36.4 (8.1) <i>bc</i>
Selden Neck	44.3 (5.3) <i>abc</i>	733.3 (194.2) <i>b</i>	85 (6)	48.0 (27.9) <i>cd</i>	10.2 (1.7) <i>c</i>	34.1 (6.8) <i>bc</i>
West Woods	47.5 (3.1) <i>abc</i>	1491.7 (203.6) <i>c</i>	68 (3)	61.2 (15.9) <i>d</i>	22.5 (1.5) <i>d</i>	24.9 (1.7) <i>ab</i>
Burnham Brook	37.3 (6.4) <i>a</i>	666.7 (144.3) <i>b</i>	91 (5)	98.4 (2.7) <i>e</i>	22.9 (6.4) <i>d</i>	14.4 (3.0) <i>a</i>

Note: Values are means, with SD given in parentheses from three plots per site. Species with missing values were not present at the site. BA and density data include only those trees >8 cm DBH. The Slab City and Salmon River sites have no sign of adelgid infestation. Within a column, values followed by the same letter are not significantly different (found using ANOVA with the Tukey pairwise mean comparison test ($p < 0.10$)). Data for Salmon River, Selden Neck, West Woods, and Burnham Brook are from Orwig and Foster (1998). Relative basal area includes only the most common species and may not sum to 100.

*Calculated as [(BA of standing dead hemlock)/(BA of standing dead + live hemlock)] × 100.

standing at sampling time. Based on data from permanent plots in hemlock-hardwood old-growth stands, Tyrrell and Crow (1994) found that hemlock snags were five times more likely to experience no change in any one year as they were to fragment or collapse. Snags of other species were not tallied. We did not quantify coarse woody debris because we did not believe it would contribute to N cycling rates within this short period of time after infestation. Crown vigor was determined for each hemlock stem based on the amount of foliage present; a tree was considered dead only if no live foliage remained. Saplings smaller than 8 cm DBH and taller than 1.37 m were also tallied within each plot. On ten 1-m² subplots randomly located within each plot, percent cover of seedlings, herbs, and shrubs were estimated. Increment cores were taken at breast height from eight randomly selected trees of any species greater than 8 cm DBH within each plot and analyzed for age. General overstory characteristics are described in Table 2.

Leaf litterfall

Leaf litter was collected for 1 year in ten (0.0816-m²) plastic baskets per plot, each placed in a randomly chosen subplot. Baskets were placed in the field in July 1996. Litter collections were made in August, October, and November 1996 and in May and July 1997. Foliage was collected in paper bags, air-dried for no less than 1 week, sorted by species, oven-dried for 48 h at 70°C, and weighed. Total annual litterfall was calculated as the sum of foliage weights over all litter collections for those baskets that were not disturbed at any time during the year. These annual subplot-level values were averaged by plot to find plot-level litterfall values on a per-hectare basis.

Light availability

To estimate light availability to the understory, a gap light index (GLI) (Canham 1988a) was calculated for each plot using hemispherical photography. This method uses predictable relationships between radiative transfer and the geometry of canopy openings to predict the transmission of photosynthetically active radiation (PAR) to points beneath the canopy. (See Canham (1988b) for an in-depth discussion of the technique.) GLI is defined as that percentage of incident PAR transmitted through canopy openings to any particular point in the understory over the course of the growing season. It is calculated as

$$[1] \quad \text{GLI} = [(T_d P_d) + (T_b P_b)] \times 100.0$$

where P_d and P_b are the proportions of incident seasonal PAR received at the top of the canopy as either diffuse sky radiation or direct-beam radiation, respectively, and T_d and T_b are the proportions of diffuse and direct-beam radiation, respectively, that are transmitted through the canopy to a point in the understory. For this study (and on the basis of published data on atmospheric transmission coefficients (Knapp et al. 1980)), P_b and P_d were set equal to 0.5, such that incident radiation was split evenly between diffuse and beam radiation. Transmission of diffuse and direct-beam radiation (T_d and T_b) to the understory was estimated from analysis of hemispherical photos.

To date, this method has been used to create point-level estimates of light availability beneath canopy gaps (Canham 1988b; Canham et al. 1990, 1994). To obtain reliable plot-level GLI estimates given the variable understory light regimes at our plots, a color fisheye (hemispherical) photograph of the forest canopy

Table 1 (concluded).

Total N (Mg·ha ⁻¹)		C/N		Mean pH		Worms present?
Organic	Mineral	Organic	Mineral	Organic	Mineral	
0.84 (0.06) <i>ab</i>	1.34 (0.03) <i>b</i>	26.3 (0.7) <i>b</i>	25.2 (0.3) <i>b</i>	3.11 (0.03) <i>b</i>	3.65 (0.06) <i>a</i>	No
1.20 (0.15) <i>b</i>	1.16 (0.04) <i>b</i>	26.5 (0.9) <i>b</i>	24.6 (0.7) <i>b</i>	2.83 (0.07) <i>a</i>	3.68 (0.07) <i>a</i>	No
0.73 (0.06) <i>a</i>	1.78 (0.11) <i>c</i>	21.6 (0.4) <i>a</i>	19.6 (1.4) <i>a</i>	3.81 (0.04) <i>d</i>	3.96 (0.07) <i>b</i>	Yes
0.94 (0.11) <i>ab</i>	1.80 (0.29) <i>c</i>	22.9 (1.5) <i>a</i>	21.2 (1.8) <i>a</i>	3.38 (0.07) <i>c</i>	3.74 (0.11) <i>ab</i>	No
1.01 (0.08) <i>ab</i>	0.79 (0.02) <i>a</i>	30.4 (0.8) <i>c</i>	35.5 (1.0) <i>d</i>	2.90 (0.04) <i>a</i>	3.51 (0.07) <i>a</i>	No
0.99 (0.32) <i>ab</i>	1.07 (0.05) <i>ab</i>	29.4 (0.6) <i>c</i>	31.4 (0.8) <i>c</i>	2.97 (0.13) <i>ab</i>	3.56 (0.18) <i>a</i>	No

Table 2 (concluded).

Relative basal area by species					
Eastern hemlock (<i>Tsuga canadensis</i> (L.) Carr.)	Black birch (<i>Betula lenta</i> L.)	Black oak (<i>Quercus</i> <i>velutina</i> Lam.)	Red maple (<i>Acer</i> <i>rubrum</i> L.)	GLI	Seedling percent cover
74.6 (4.3) <i>a</i>	7.2 (3.2) <i>ab</i>	— <i>a</i>	10.2 (6.0) <i>a</i>	13.6 (0.9) <i>a</i>	1.0 (0.4) <i>a</i>
81.6 (11.8) <i>a</i>	— <i>a</i>	15.8 (14.8) <i>a</i>	1.4 (6.4) <i>a</i>	13.0 (0.6) <i>a</i>	0.1 (0.1) <i>a</i>
74.7 (4.5) <i>a</i>	15.2 (12.9) <i>bc</i>	10.1 (9.4) <i>a</i>	— <i>a</i>	29.6 (6.4) <i>b</i>	11.5 (3.9) <i>ab</i>
54.6 (15.1) <i>a</i>	22.8 (1.4) <i>c</i>	10.4 (6.5) <i>a</i>	10.1 (17.5) <i>a</i>	20.9 (4.4) <i>ab</i>	0.1 (0.1) <i>a</i>
80.7 (18.4) <i>a</i>	0.8 (1.4) <i>a</i>	— <i>a</i>	5.1 (2.6) <i>a</i>	29.2 (11.6) <i>b</i>	13.9 (11.9) <i>ab</i>
61.5 (8.8) <i>a</i>	2.0 (3.4) <i>ab</i>	3.3 (2.8) <i>a</i>	11.0 (1.4) <i>a</i>	27.0 (4.4) <i>ab</i>	23.4 (13.8) <i>b</i>

was taken at 1.2 m height in the center of each subplot in August–September of 1996. These 16 subplot-level measurements per plot were then averaged to find the plot-level GLI value. Photographs in which understory foliage covered the lens were discarded. The photographs were developed as slides, which were digitized at 840 dpi resolution using a slide scanner (Microtek 35T 24-bit Slide Scanner with a SCSI interface). The digital images were then analyzed for GLI and percent open sky using computer software (GLI/C 2.0, copyright 1995, C.D. Canham) written for that purpose.

N cycling rates

Field methods

Net N mineralization and nitrification were measured in situ on all plots for 1 year using the buried bag technique (Eno 1960; Nadelhoffer et al. 1983; Pastor et al. 1984). At each plot, the same four randomly chosen subplots were used for these measurements throughout the study. Undecomposed litter (the Oi layer) was brushed aside, and soil cores were taken to a depth of 10 cm in the mineral soil, split into organic (Oa plus Oe) and mineral horizons, and placed into gas-permeable polyethylene bags. One sample (“initial”) was taken to the laboratory and a subsample was processed for extraction of ammonium and nitrate. The remaining initial soil samples from each collection date were air-dried and stored in paper bags for additional analyses. Three other samples (designated as “incubated”) were put inside bags made of 1-mm mesh nylon window screen material to reduce puncture damage to the polyethylene bags and placed back in the ground. The three in-

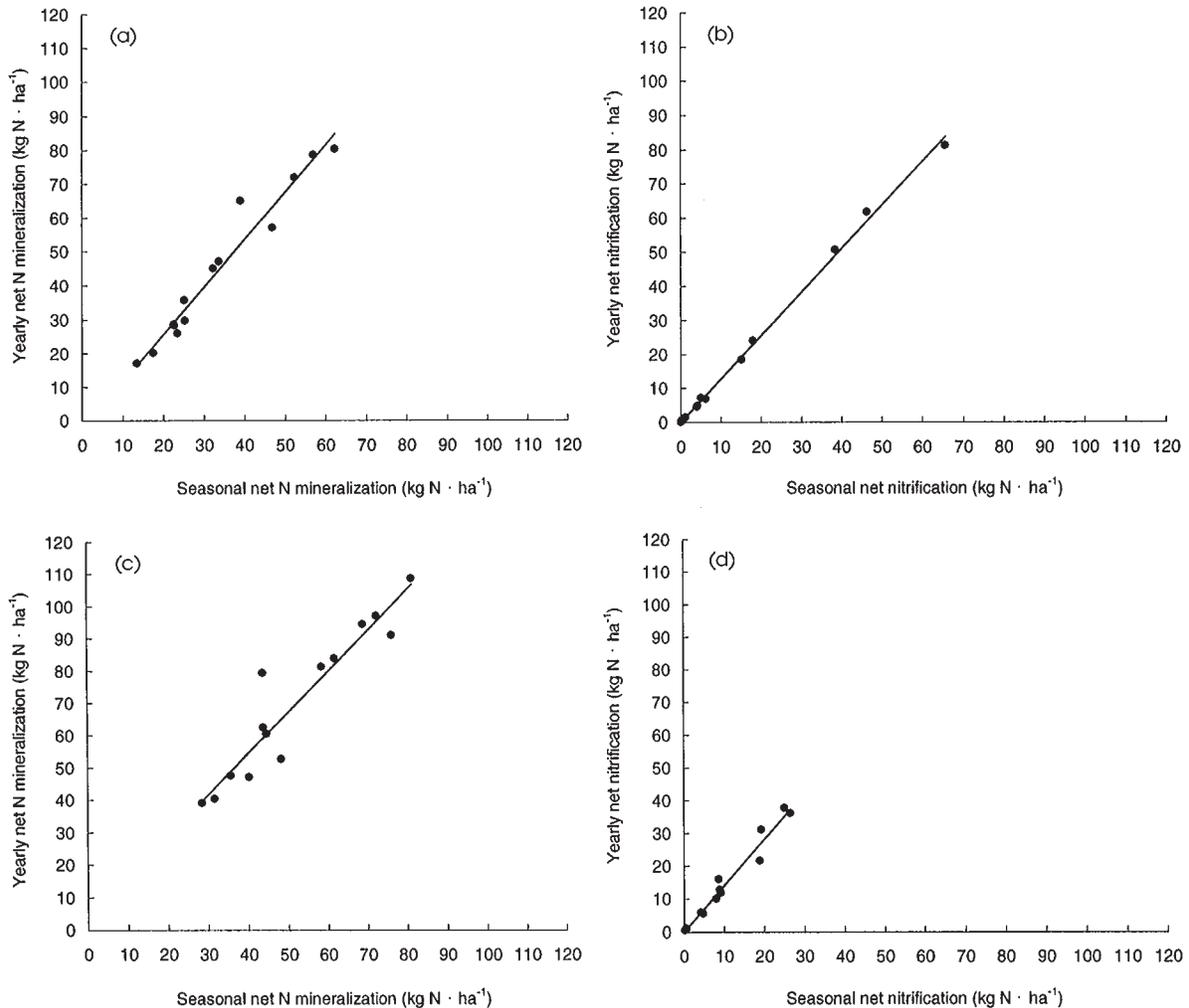
cubated cores at each subplot were composited before analysis to reduce variability among incubated samples. Soil cores were incubated for 4- to 6-week periods from June to October 1996 and from May to June 1997, with one longer overwinter incubation from October 1996 to May 1997. Incubated samples were analyzed for extractable ammonium and nitrate.

Laboratory methods

In the laboratory, soil samples were sieved (2-mm mesh for mineral soil, 5.6-mm mesh for organic soil) to remove roots and rocks and to homogenize the sample. Total soil mass of initial samples was recorded. Subsamples (10–20 g) of initial and incubated soils were oven-dried at 105°C for 48 h to determine moisture content. Percent soil moisture was calculated from the initial subsamples as the ratio of the weight of water driven off during drying (g) to the weight of the soil subsample when dry (g). These soil moisture values were combined to calculate average yearly soil moisture for each plot.

Ammonium and nitrate were extracted by placing approximately 10 g of soil in a glass jar containing 100 mL of 1 M KCl, hand shaking the jar, and extracting for 48 h. Samples were filtered, and the filtrate was frozen until analysis. Thawed extracts were analyzed for NO₃-N and NH₄-N using a Bran & Luebbe TrAAcs 800 autoanalyzer (Technicon Instruments Corp., Tarrytown, N.Y.). Ammonium was determined using Berthelot Reaction chemistry (Technicon Method 780-86T), and nitrate was determined using a hydrazine sulfate reduction technique (Technicon Method 782-86T). The limit of quantitation (LOQ), defined as “the lower limit for precise quantitative measurements” (Miller and Miller 1993)

Fig. 2. Relationships between total annual and “seasonal” net N mineralization and nitrification rates for mineral soil and forest floor (all on a $\text{kg}\cdot\text{ha}^{-1}$ basis). (a) Annual mineral soil net N mineralization = $1.402(\text{seasonal net N mineralization}) - 2.443$, $R^2 = 0.955$, $p < 0.001$ (constant $p < 0.46$). (b) Annual mineral soil nitrification = $1.278(\text{seasonal nitrification}) - 0.42$, $R^2 = 0.998$, $p < 0.001$ (constant $p < 0.92$). (c) Annual forest floor net N mineralization = $1.276(\text{seasonal net N mineralization}) + 3.348$, $R^2 = 0.890$, $p < 0.001$ (constant $p < 0.65$). (d) Annual forest floor nitrification = $1.417(\text{seasonal nitrification}) - 0.086$, $R^2 = 0.971$, $p < 0.001$ (constant $p < 0.928$). Scatterplots show the measured data; regression lines are shown for comparison.



was determined conservatively for each analyte during each half of every autoanalyzer “run” as

$$[2] \quad \text{LOQ} = Y_b + 10S_b$$

where Y_b is the average measured analyte concentration of the four KCl blanks analyzed during that half of the run, and S_b is the standard deviation of those blank values. LOQ values ranged from 0.001 to 0.29 $\text{mg N}\cdot\text{L}^{-1}$.

To eliminate the substantial interference from organic substances in the nitrate analysis, nitrate-N in organic samples was determined using a separate procedure. Each organic sample extract and blank was diluted in a 1:1 ratio with 0.50 $\text{mg}\cdot\text{L}^{-1}$ $\text{NO}_3\text{-N}$ standard, and the dilutions were analyzed for $\text{NO}_3\text{-N}$ using the hydrazine reduction technique. The $\text{NO}_3\text{-N}$ concentrations in the blank samples were averaged and subtracted from the sample values. If the remaining concentration was above the average LOQ for the mineral soil nitrate-N analyses (0.036 $\text{mg NO}_3\text{-N}\cdot\text{L}^{-1}$), it was doubled to account for the dilution, to find the final concentration of $\text{NO}_3\text{-N}$ in the extract. The coefficient of variation (CV) for replicate samples within each sample run for all $\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$

analyses averaged close to 2% and was never greater than 5% for both mineral and organic samples.

Net N mineralization was calculated as the difference between extractable nitrate-N plus ammonium-N in the incubated sample and extractable nitrate-N plus ammonium-N in the initial sample. Net nitrification was calculated as the difference between extractable nitrate-N in the incubated sample and extractable nitrate-N in the initial sample. Annual totals were calculated as the sum of all buried-bag incubations for the year (June 1996 through June 1997).

At 4 of the 18 plots (Salmon River plots 1–3 and Selden Neck plot 1), the overwinter bags were lost when the field vehicle was stolen. To find annual totals for these plots missing overwinter data and to allow for consistency among plots, linear regression equations between “seasonal” (the sum of N mineralization and nitrification rates for June–October 1996 and May–June 1997) and annual total N mineralization rates on a kilogram per hectare basis were found for the 14 plots with both types of data (Fig. 2). These equations were used to determine annual total N mineralization and nitrification rates from the seasonal rates at all 18 plots. For consistency, the predictions from these regression equations were used at all plots for all further analyses. These annual predictions

Table 3. Measured daily air and soil temperatures.

Site name	Mean daily air temperature (°C)	Measured soil temperature (°C)			Difference between mean air and soil temperatures (°C)		
		5-cm depth	10-cm depth	20-cm depth	5-cm depth	10-cm depth	20-cm depth
Slab City ²	9.2	7.6 (0.3)	5.8 (0.2)	4.9 (0.2)	-1.6	-3.4	-4.3
Salmon River ³	10.7	8.7 (0.2)	7.8 (0.1)	7.4 (0.1)	-2.0	-2.9	-3.3
Gillette Castle ⁴	11.6	10.3 (0.4)	10.1 (0.2)	10.0 (0.2)	-1.3	-1.5	-1.6
Selden Neck ⁵	12.0	10.9 (1.0)	10.2 (0.9)	9.5 (0.7)	-1.1	-1.8	-2.5
West Woods ⁶	9.0	11.3 (0.4)	9.2 (0.2)	8.4 (0.2)	+2.3	+0.2	-0.6
Burnham Brook ⁶	9.0	9.0 (1.4)	8.4 (0.9)	7.9 (0.3)	0.0	-0.6	-1.1

Note: Soil temperatures are means, with SD given in parentheses, from three plots per site. The Slab City and Salmon River sites show no sign of adelgid infestation. Mean daily air temperature data are from the Northeast Regional Climate Center, Cornell University, Ithaca, N.Y. Mean daily temperatures for the 24-h periods ending at 08:00 the day of and the day after the soil temperature measurement. Soil temperatures for Slab City, Salmon River, Gillette Castle, and Selden Neck were measured April 30, 1997, May 6, May 14, and May 13, 1997, respectively; West Woods and Burnham Brook were measured April 29, 1997. Air temperature for Slab City was measured at Barre Falls Dam, Barre, Mass; air temperature for the remaining sites was measured at Cockaponset Ranger Station, Haddam, Conn.

are independent of other measured data because they are based solely on measured seasonal rates.

Soil physical and chemical properties

Aliquots of the archived initial soil samples from each collection date were combined for each horizon and ground together. Percentage C and N were determined for organic and mineral horizons from these combined samples for each subplot using a Fisons NA 1500 Series 2 CHN analyzer. Approximately 1 g of the archived soil from each horizon at each subplot from one collection date was combusted in a muffle furnace at 500°C for 5 h, and the ash was weighed to determine percent soil organic matter (SOM). The dry mass of each initial soil sample after sieving (i.e., excluding fragments larger than the sieve size) was divided by its volume to determine soil bulk density. These density values from the initial samples were averaged to calculate bulk density by horizon at each soil collection subplot. Total soil C, N, and SOM were calculated on a per unit area basis (as kg·ha⁻¹) using these density values.

Soil pH was determined for the first and last collections in 1996, in 0.01 M CaCl₂ solution with a ratio of 1 g soil : 10 mL solution (organic) and 1 g soil : 4 mL solution (mineral). The pH values from both soil collections were averaged to give the value reported here. Soil texture was determined for one set of archived mineral soils using the sieve and pipet method as described by Gee and Bauder (1986).

Soil and air temperatures

Soil temperature was measured at 5-, 10-, and 20-cm depths at each soil collection subplot on soil collection days in April and May 1997 using a digital thermometer (Omega HH-25KC; Omega Corp., Stamford, Conn.) fitted with a stainless steel probe. To account for local and temporal variations in temperature, daily maximum and minimum temperature data were obtained from the weather stations closest to the sampling sites (Northeast Regional Climate Center, Cornell University, Ithaca, N.Y.) for the 24-h periods ending at 08:00 on the day before and the day after soil temperatures were measured. Mean daily air temperature for each day was calculated as (minimum + maximum)/2, and these daily values were averaged to find the mean daily air temperature for the 2-day period (Table 3).

Earthworms

Considerable evidence exists that earthworms can increase N cycling rates dramatically (e.g., see Barley and Jennings 1959; Satchell 1963; Anderson et al. 1983; Scheu 1993). Earthworms

were found during 1996 soil sampling at Gillette Castle. To characterize worm populations, in July 1997 we used a vermifuge method to determine worm abundance in one 0.04-ha plot at each site. Four 0.25-m² subplots were established just outside the corners at each of the 0.04-ha plots chosen for worm sampling. At each 0.25-m² subplot, roughly 8 L of a dilute (0.25%) formalin solution were poured onto the soil (Raw 1959; Bohlen et al. 1995). Worms were harvested as they came to the surface and stored in a 5% formalin solution. A separate sample was harvested and stored in 5% formalin for species identification. Worms were stored for several months until they were rinsed, oven-dried at 60°C for 48 h, and weighed.

Statistical analysis

The three plots at each site were sufficiently close together that they could not be considered independent samples for statistical analysis. Instead, plot-level measures from the three plots per site were averaged to obtain one site-level measurement, and these site-level measurements were used for further analysis ($n = 6$). To detect subtle differences among the four infested and two noninfested sites, two-sample hypothesis tests were conducted using t tests with separate variances at the 0.10 significance level (p values are reported in the text). Other analyses were conducted as reported in the text. SYSTAT 7.0 was used for all statistical analyses.

Results

Light, temperature, and soil moisture

Comparing the two groups of sites, gap light index (GLI) was significantly higher at sites experiencing adelgid infestation ($p < 0.001$) (Table 2). Differences in soil temperature between the two groups of sites were not tested statistically because measurements were taken at different times over 15 days (Table 3). Without vegetation cover, soils with intermediate water content and bulk density can be expected to reflect mean daily air temperature to a depth of roughly 12 cm (Campbell 1977). Differences between the soil and air temperatures presented here might therefore be attributed to the influence of canopy cover, soil properties, or temperature differences between the weather station and the study site. The closer relationship between soil and air temperatures at the four infested sites compared with the noninfested sites suggests that soil temperatures may be elevated at sites

Fig. 3. Soil organic matter (SOM) content in mineral soil and forest floor. Error bars are SDs based on three plots per site. Shaded area shows sites with no sign of adelgid infestation. Sites are ordered from least to most mortality by basal area (BA) ($\text{m}^2 \cdot \text{ha}^{-1}$). SC, Slab City; SR, Salmon River; GC, Gillette Castle; SN, Selden Neck; WW, West Woods; BB, Burnham Brook.

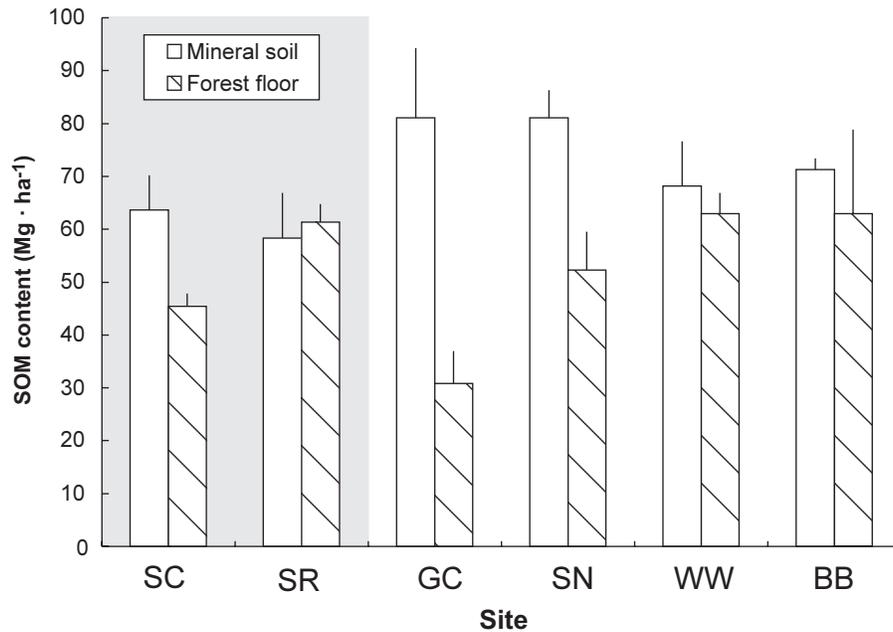
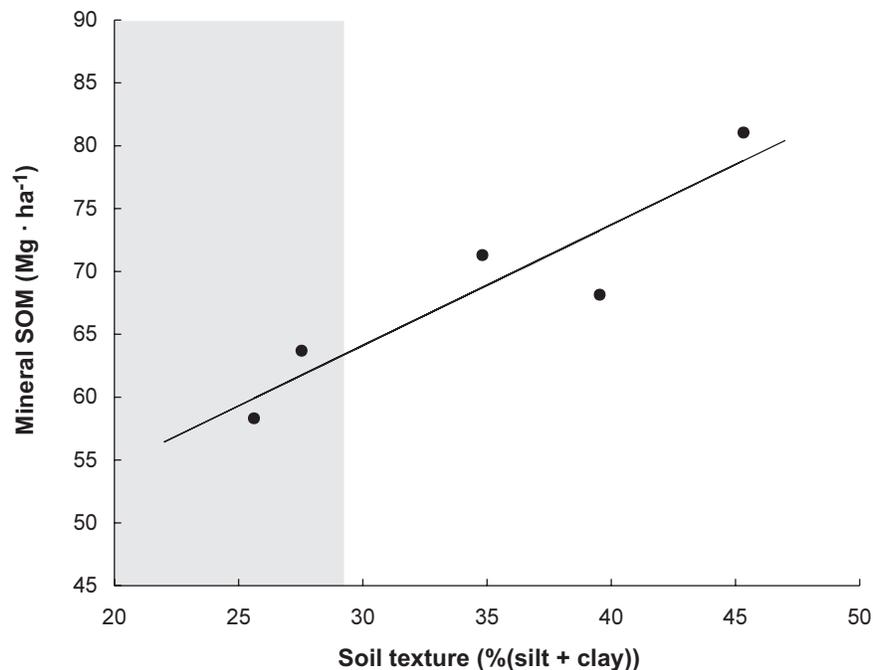


Fig. 4. Mineral soil organic matter (SOM) as a function of soil texture. Regression equation: $\text{SOM} = 0.959(\%(\text{silt} + \text{clay})) + 35.347$, $R^2 = 0.85$, $p < 0.03$ and 0.02 for the coefficient and constant, respectively. Regression was calculated using site-level data, excluding the site with earthworms ($n = 5$). Shaded area shows sites with no sign of adelgid infestation.

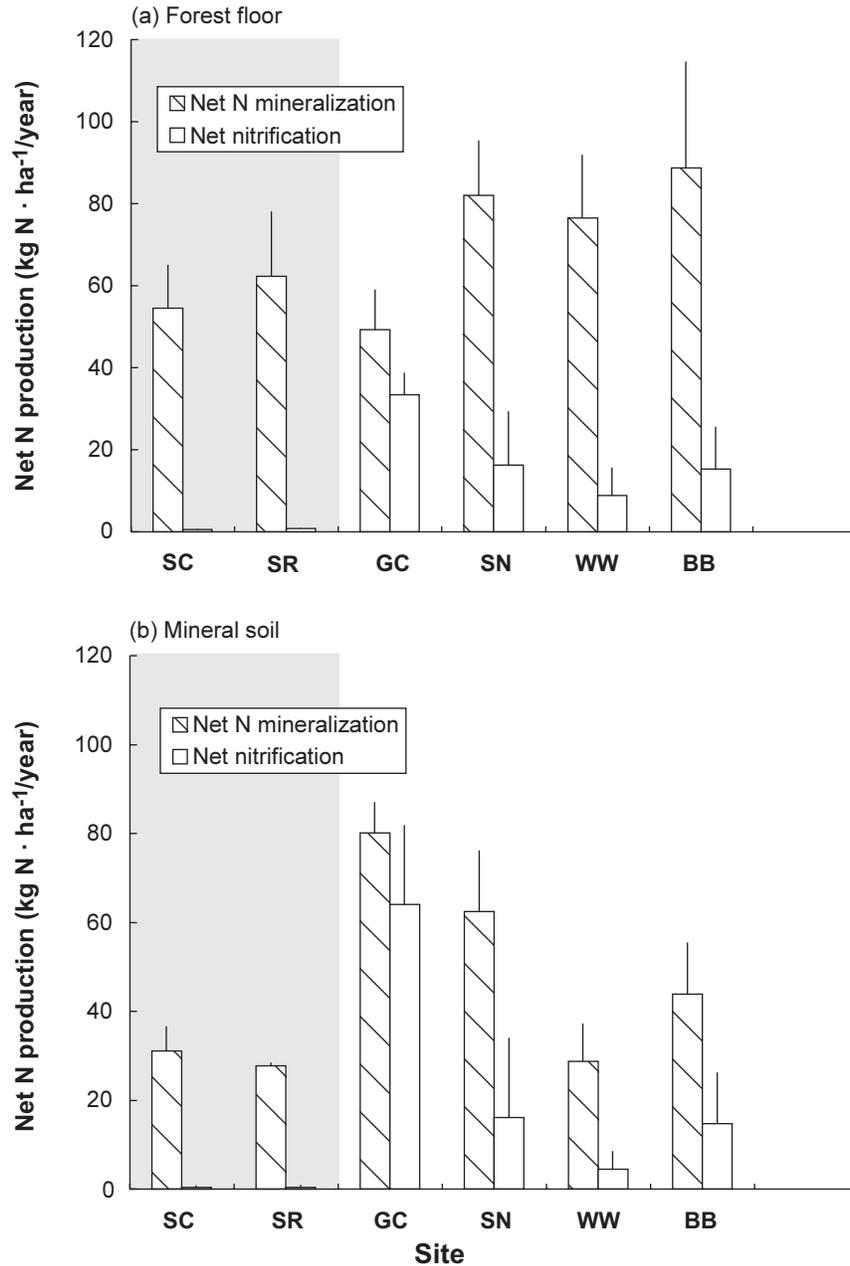


experiencing additional solar radiation resulting from hemlock mortality, although more detailed monitoring of soil and air temperatures would be needed to confirm this. No difference in soil moisture existed between infested and noninfested sites.

Seedling regeneration and litterfall

Comparing the two groups of sites, total percent cover of seedlings was greater at sites experiencing adelgid infestation ($p < 0.09$) (Table 2). Between 42 and 93% of the seedling cover at all sites with adelgid infestation was black

Fig. 5. Annual net N mineralization and nitrification rates for forest floor (a) and mineral soil (b). Error bars represent standard deviation from three plots per site. Shaded area shows the two sites with no sign of adelgid infestation. Sites are ordered from least to most hemlock mortality by basal area (BA) ($\text{m}^2\cdot\text{ha}^{-1}$), and site abbreviations are as in Fig. 3.



birch, with red maple and oak contributing the remainder. Seedling regeneration increased with GLI, and was not related to overstory composition. No relationship existed among non-hemlock overstory BA and seedling percent cover. No hemlock seedlings were found at infested sites.

Annual litterfall at sites experiencing adelgid infestation averaged $3.5 \text{ Mg}\cdot\text{ha}^{-1}$ per year and was significantly higher than litterfall at healthy sites, which averaged $2.5 \text{ Mg}\cdot\text{ha}^{-1}$ per year ($p < 0.05$). Gillette Castle, the site with earthworms, experienced the highest annual litterfall at $4.2 \text{ Mg}\cdot\text{ha}^{-1}$ per year. Hemlock was a minor contributor to litterfall mass at all sites, with $0.12 \text{ Mg}\cdot\text{ha}^{-1}$ per year of hemlock needles produced at sites experiencing infestation and $0.21 \text{ Mg}\cdot\text{ha}^{-1}$ per

year at sites with no adelgid. No strong relationships existed among seedling percent cover and litterfall.

Soil organic matter (SOM)

The Gillette Castle site was not included in statistical analyses of SOM or N cycling rates for the forest floor or mineral soil because considerable evidence exists that worms change both SOM distribution and N cycling regimes (Edwards and Bohlen 1996). Data from that site appears in the figures only for comparison.

No significant difference in forest floor SOM ($\text{Mg}\cdot\text{ha}^{-1}$) existed between sites with and without adelgid (Fig. 3), and forest floor SOM did not vary strongly with litterfall or

Fig. 6. N turnover rate as a function of gap light index (GLI) in mineral soil (○) and forest floor (●). Regression line is shown for mineral soil data: $N \text{ turnover} = 1.096(\text{GLI}) + 9.573$, $R^2 = 0.89$, $p < 0.005$ and 0.10 for the coefficient and constant, respectively. Shaded area shows the two sites with no sign of adelgid infestation.

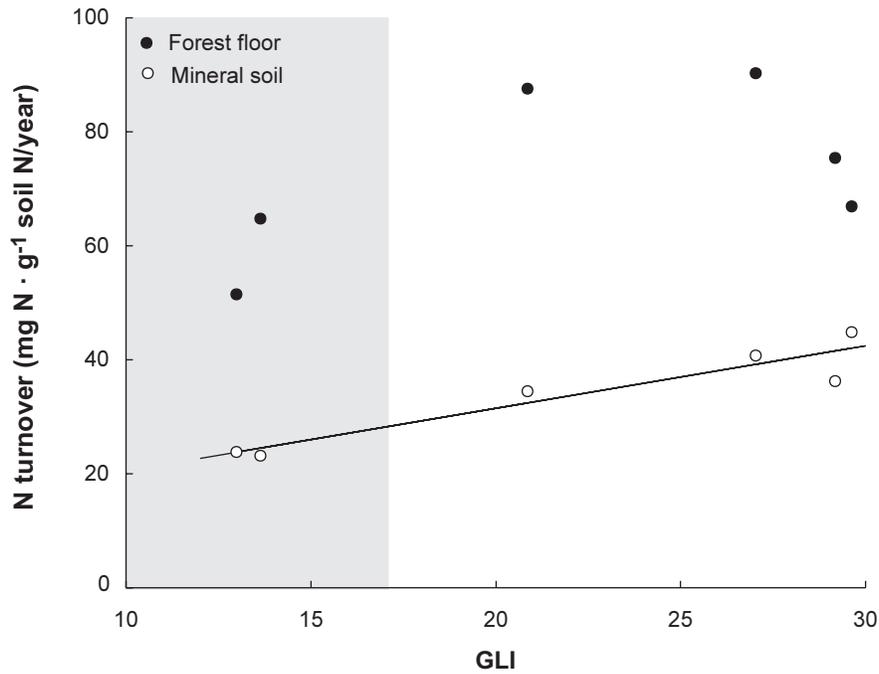
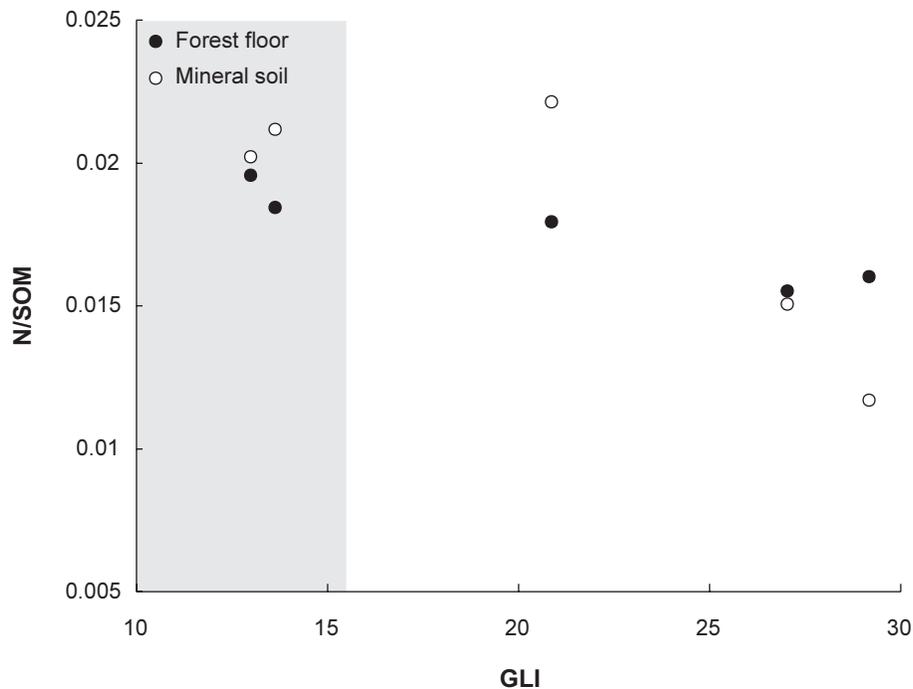


Fig. 7. Ratio of N to soil organic matter (N/SOM) as a function of gap light index (GLI) in mineral soil (○) and forest floor (●). Shaded area shows the two sites with no sign of adelgid infestation.



hemlock mortality. Mineral SOM was higher at those sites experiencing adelgid infestation ($p < 0.08$) (Fig. 3) but also did not vary with litterfall or hemlock mortality. Instead, mineral SOM was most strongly related to soil texture (Fig. 4). The two sites with no sign of adelgid had both the

coarsest soil texture and the least SOM. Soil texture is thus a potentially confounding variable. However, soil texture was not related as strongly to any other measured variable in this study, suggesting either that (i) the impact of soil texture on N cycling rates was smaller than the impact of adelgid

Fig. 8. Net nitrification rate as a function of extractable ammonium-N for mineral soil and forest floor, excluding the site with earthworms. Linear regression equations: mineral soil net nitrification rate ($\text{kg}\cdot\text{ha}^{-1}$ per year) = $4.435(\text{extractable ammonium-N (kg}\cdot\text{ha}^{-1}) - 10.75$, $R^2 = 0.97$, $p < 0.002$ and 0.02 on coefficient and constant, respectively; forest floor net nitrification rate ($\text{kg N}\cdot\text{ha}^{-1}$ per year) = $5.245(\text{extractable ammonium-N (kg}\cdot\text{ha}^{-1}) - 13.61$, $R^2 = 0.92$, $p < 0.01$ and 0.04 for the coefficient and constant, respectively. Shaded area shows the two sites with no sign of adelgid infestation.

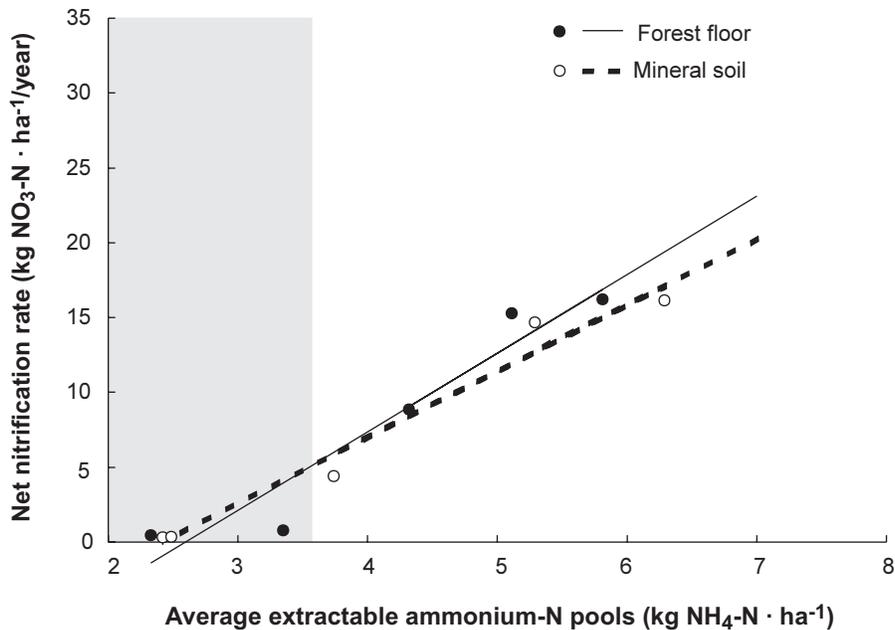
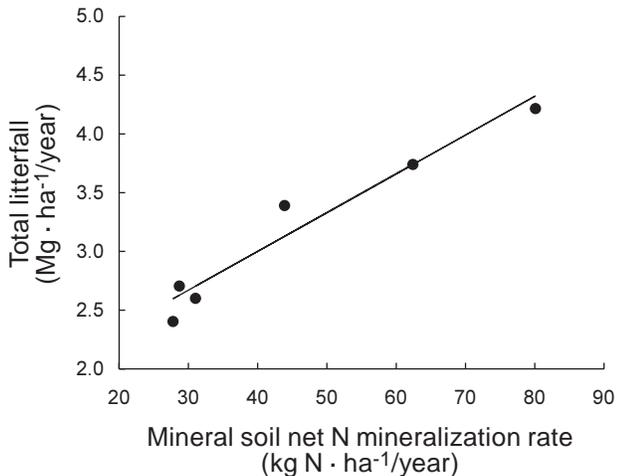


Fig. 9. Relationship between annual litter production and annual mineral soil net N mineralization. Regression line is shown: Annual litterfall = $0.033(\text{mineral soil net N mineralization (kg}\cdot\text{ha}^{-1}$ per year) + 1.68 , $R^2 = 0.95$, $p < 0.001$ for both coefficient and constant.



infestation and hemlock mortality or (ii) adelgid infestation and hemlock mortality occurs preferentially on sites with coarse soil texture. The second possibility cannot be ruled out based on the results from this study; further research at the regional scale will be needed to determine the factors predisposing certain sites to adelgid attack.

Soil C and N

While some variability from site to site was evident (Table 1), no significant differences existed between the four

infested and two noninfested sites in total C pools, total N pools, or C:N in the total soil profile, forest floor, or mineral soil. This was true whether or not the site with earthworms was included in the analysis.

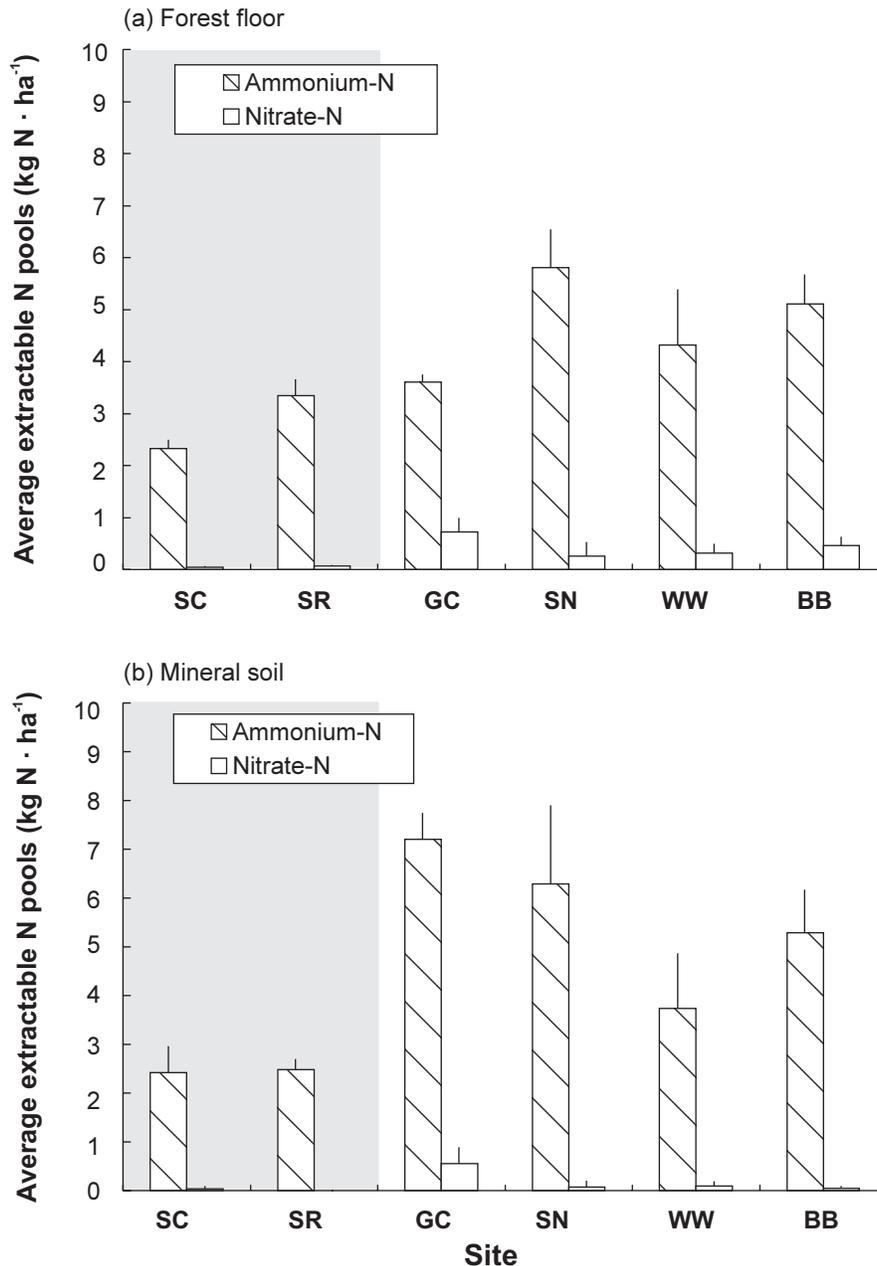
N cycling rates

Adding together N production in the forest floor and mineral soil, annual net N mineralization and nitrification ($\text{kg N}\cdot\text{ha}^{-1}$ per year) were both higher at the four sites with adelgid infestation ($p < 0.08$ and 0.06 for mineralization and nitrification, respectively).

Forest floor net N mineralization and nitrification rates (on a $\text{kg N}\cdot\text{ha}^{-1}$ per year basis) were significantly higher at infested sites ($p < 0.03$ and 0.04 for mineralization and nitrification, respectively) (Fig. 5). Forest floor N turnover (expressed as milligrams N mineralized per gram soil N) was related positively to GLI at low light levels but declined at the highest GLI levels (Fig. 6). Overall, forest floor N turnover rate was significantly higher at those sites experiencing adelgid infestation ($p < 0.09$). Measured as milligrams N per gram SOM, net N mineralization in the forest floor did not increase at those sites experiencing mortality. However, forest floor N/SOM declined at high GLI levels (Fig. 7), suggesting that the accelerated N turnover at infested sites is changing the composition of forest floor SOM.

In the mineral soil, net N mineralization (as $\text{kg N}\cdot\text{ha}^{-1}$ per year) did not change with adelgid infestation, but net nitrification increased ($p < 0.10$) (Fig. 5). Controlling for site-level variability in available N pools, mineral soil N turnover rate (expressed as milligrams N mineralized per gram soil N per year) increased slightly with GLI (Fig. 6) and was significantly different between infested and noninfested sites ($p < 0.02$). As with the forest floor, net N mineralization

Fig. 10. Average extractable soil N pools for forest floor (a) and mineral soil (b). Error bars are SDs of the average soil N pools from the three plots per site. Sites are arranged in order of hemlock mortality by basal area (BA) ($\text{m}^2 \cdot \text{ha}^{-1}$); site abbreviations are as in Fig. 3. Shaded area shows the two sites with no sign of adelgid infestation.



expressed per unit SOM in the mineral soil did not change at those sites experiencing mortality. While a trend toward lower mineral soil N/SOM at high GLI was apparent (Fig. 7), no significant difference in N:SOM existed among infested and noninfested sites.

Both mineral soil and forest floor nitrification were linear functions of extractable ammonium-N, again excluding the site with earthworms (Fig. 8). Overall nitrification rates were as high as $32 \text{ kg} \cdot \text{ha}^{-1}$ per year at infested sites without earthworms; the site with earthworms (Gillette Castle) experienced a nitrification rate of $97 \text{ kg} \cdot \text{ha}^{-1}$ per year.

Other researchers have noted a relationship between aboveground productivity and N mineralization rate (Pastor

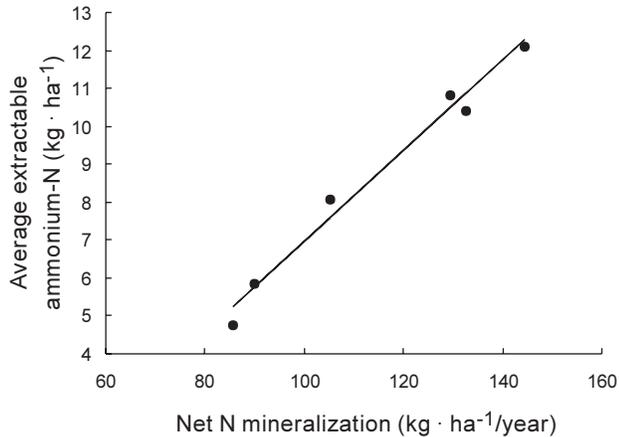
et al. 1984, Reich et al. 1997). Litter production varied with mineral soil net N mineralization rate in this study as well (Fig. 9).

Excluding the site with earthworms, average total extractable ammonium-N and nitrate-N pools in the soil solum were significantly higher at infested sites ($p < 0.04$ and 0.02 for ammonium-N and nitrate-N, respectively) (Fig. 10). Average extractable ammonium-N ($\text{kg} \cdot \text{ha}^{-1}$) varied positively with N mineralization rate (Fig. 11).

Earthworms

Earthworm abundance at Gillette Castle was $13 \text{ individuals} \cdot \text{m}^2$, and the dry biomass of those worms was $29.8 \text{ kg} \cdot \text{ha}^{-1}$.

Fig. 11. Average extractable ammonium-N ($\text{kg}\cdot\text{ha}^{-1}$) as a function of net N mineralization rate ($\text{kg}\cdot\text{ha}^{-1}$ per year) for mineral soil and forest floor together. Regression line is shown: extractable ammonium-N ($\text{kg}\cdot\text{ha}^{-1}$) = $0.12(\text{net N mineralization rate (kg}\cdot\text{ha}^{-1}$ per year)) - 5.03, $R^2 = 0.98$, $p < 0.000$ and 0.006 for the coefficient and constant, respectively.



The worms were identified as a mixture of lumbricid species (*Lumbricus rubellus* Hoffmeister and *Lumbricus castaneus* (Savigny)) native to Europe (P. Bohlen, Institute of Ecosystem Studies, Millbrook, NY, personal communication). Mineral SOM mass was higher and forest floor SOM mass was lower at Gillette Castle than at any other site (Fig. 3), suggesting a mixing effect due to worms.

Discussion

With adelgid-induced hemlock mortality, we hypothesized that the thinning hemlock canopy would transmit more light to the understory, enabling rapid seedling regeneration (Fig. 12). In this study, both GLI and seedling percent cover were higher at sites experiencing adelgid infestation. This is similar to results reported by Orwig and Foster (1998), who also found a significant increase in light availability to the understory in stands affected by the adelgid. An increase in birch abundance following hemlock decline is not unprecedented: after the rapid and synchronous pathogen-induced decline in hemlock abundance around 4850–4700 years BP in the New England region (Davis 1981; Allison et al. 1986; Foster and Zebryk 1993), a short-lived increase in birch pollen was characteristic. More recently, Perkins et al. (1988) noted increased birch regeneration associated with changes in light availability beneath declining red spruce (*Picea rubens* Sarg.) canopies in the 1980s.

Hemlock forests are noted for their dense canopies, which typically result in cool understory microclimates (Adams and Loucks 1971). An increase in light availability to the understory due to hemlock decline might be expected to change the understory microclimate (Fig. 12), and our results suggest that elevated soil temperature could be one result of adelgid infestation. Disturbance-induced changes in soil temperature have been noted by other researchers. For example, in a comparison of conditions beneath hemlock forest and treefall gaps, Mladenoff (1987) reported midsummer temperature increases of up to 10°C in the forest floor due to treefall gap formation. Matson and Vitousek (1981)

noted increases of 2°C following clear-cutting in Indiana and larger increases in soil temperature due to disturbance caused by laminated root rot (*Phellinus (Poria) weirii* (Murr.) Gilbertson) in Oregon (Matson and Boone 1984). Perkins et al. (1987) found increased soil temperature beneath declining red spruce canopies and attributed the change to higher solar gain due to changes in canopy density.

Variation in total C, total N, and SOM content among our study sites was not associated with adelgid infestation. While we had predicted a change in SOM with disturbance (Fig. 12), our results were confounded by site-to-site variability in soil texture. Without physical disturbance, however, it is likely that measurable organic C, organic N, and SOM accumulation or decline at these sites will take at least a decade. In fact, Johnson (1995) found fewer changes in soil C, N, and SOM pools than expected at Hubbard Brook, New Hampshire, 8 years after clear-cutting. Covington (1981) and Federer (1984) report sequences of forest floor SOM decline and recovery following clear-cutting, with the lowest forest floor masses (close to 50% declines) occurring roughly 15 years after disturbance.

We hypothesized an increase in N mineralization rates facilitated by adelgid-induced disturbance (Fig. 12), and we did find that net N mineralization and nitrification rates (expressed as kilograms N per hectare per year) were higher at sites experiencing infestation. Accelerations of N cycling rates have been noted in response to other disturbances as well. For example, Matson and Boone (1984) reported that root rot doubled N mineralization rates and attributed the increase to a combination of increased temperature and altered substrate quality. Mladenoff (1987) reported increased N mineralization and doubled nitrification rates in hemlock treefall gaps. Disturbances such as defoliation, gap formation, and clear-cutting have also increased available N pools, N mineralization and nitrification rates, and N leaching (Swank et al. 1981; Waide et al. 1988; Kim et al. 1995).

Increased N cycling and N turnover rates at sites experiencing hemlock mortality cannot be attributed to changes in pool sizes of C, N, or SOM. We suggest that, instead, accelerated N cycling rates may be attributable to a short-term (within 6 years) shift in microclimate induced by changes in canopy structure. This suggestion is based on the following lines of evidence: (i) the measured increase in GLI (leading inevitably to an increase in solar gain at infested sites), (ii) the apparent trend toward increased soil temperature at infested sites, (iii) evidence from other studies of cooler air temperatures within hemlock stands compared with adjacent stands of other species, and (iv) results from previous studies in which disturbances causing thinning forest canopies have induced temperature shifts. More detailed monitoring of soil moisture and temperature throughout the growing season will be required to confirm this. David Orwig and David Foster (Harvard Forest, Petersham, Mass.) continue to monitor hemlock stands throughout central New England as part of a comprehensive study designed in part to address these issues.

The increased N cycling rates appear to have induced a decrease in forest floor and mineral soil N/SOM, suggesting that organic matter quality has begun to decline at sites experiencing adelgid infestation. This result is surprising because one would expect an increase in forest floor N/SOM

earthworms (at densities approaching “field numbers”) can increase N mineralization rates by as much as 90 kg N·ha⁻¹ per year (Willems et al. 1996), and that they enhance leaf, stem, and root production by *Betula pendula* Roth (Haimi and Einbork 1992; Haimi et al. 1992).

Future stand development

Ultimately, the extent of change in ecosystem processes following hemlock mortality will depend on the differences between hemlock and its successors in terms of their influence on ecosystem function. For example, if hemlock and American beech (*Fagus grandifolia* Ehrh.) share dominance on a site, then one might expect that little change in ecosystem processes would occur resulting from hemlock mortality, given the similarity between beech and hemlock in terms of their impacts on N cycling rates (Finzi et al. 1998). On the other hand, on base-rich sites where hemlock shares dominance with sugar maple (*Acer saccharum* Marsh.) (van Breemen et al. 1997), the shift to a maple-dominated stand would be expected to lead to more dramatic changes in rates of C and N cycling.

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References

- Adams, M.S., and Loucks, O.L. 1971. Summer air temperatures as a factor affecting net photosynthesis and distribution of eastern hemlock (*Tsuga canadensis* L. (Carriere)) in southwestern Wisconsin. *Am. Midl. Nat.* **85**: 1–10.
- Allison, T.D., Moeller, R.E., and Davis, M.B. 1986. Pollen in laminated sediments provides evidence for a mid-Holocene forest pathogen outbreak. *Ecology*, **67**: 1101–1105.
- Anderson, J.M., Ineson, P., and Huish, S.A. 1983. Nitrogen and cation mobilization by soil fauna feeding on leaf litter and soil organic matter from deciduous woodlands. *Soil Biol. Biochem.* **15**: 463–467.
- Barley, K.P., and Jennings, A.C. 1959. Earthworms and soil fertility III. The influence of earthworms on the availability of nitrogen. *Aust. J. Agric. Res.* **10**: 364–370.
- Bohlen, P.J., Parmelee, R.W., Blair, J.M., Edwards, C.A., and Stinner, B.R. 1995. Efficacy of methods for manipulating earthworm populations in large-scale field experiments in agroecosystems. *Soil Biol. Biochem.* **27**: 993–999.
- Bonneau, L.R., and Civco, D.L. 1996. The use of remote sensing and GIS to detect and evaluate hemlock woolly adelgid impacts at the landscape level. *In Proceedings of the First Hemlock Woolly Adelgid Review*, 12 Oct. 1995, Charlottesville, Va. Edited by S.M. Salom, T.C. Tigner, and R.C. Reardon. USDA Forest Service Forest Health Technology Enterprise Team, Morgantown, W.V. pp. 67–74.
- Campbell, G.S. 1977. An introduction to environmental biophysics. Springer-Verlag, New York.
- Campbell, R.M., and Sloan, R.J. 1977. Forest stand responses to defoliation by the gypsy moth. *For. Sci. Monogr.* No. 19.
- Canham, C.D. 1988a. An index for understory light levels in and around canopy gaps. *Ecology*, **69**: 1634–1638.
- Canham, C.D. 1988b. Growth and architecture of shade-tolerant trees: response to canopy gaps. *Ecology*, **69**: 786–795.
- Canham, C.D., Denslow, J.S., Platt, W.J., Runkle, J.R., Spies, T.A., and White, P.S. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Can. J. For. Res.* **20**: 620–631.
- Canham, C.D., Finzi, A.C., Pacala, S.W., and Burbank, D.H. 1994. Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees. *Can. J. For. Res.* **24**: 337–349.
- Covington, W.W. 1981. Changes in forest floor organic matter and nutrient content following clearcutting in northern hardwoods. *Ecology*, **62**: 41–48.
- Crouch, M.H. 1983. Soil Survey of New London County, Connecticut. U.S. Department of Agriculture, Soil Conservation Service in cooperation with the Connecticut Agricultural Experiment Station and the Storrs Agricultural Experiment Station, Storrs Conn.
- Davis, M.B. 1981. Outbreaks of forest pathogens in Quaternary history. *In Proceedings of the 4th International Palynological Conference (1976–1977)*. Vol. 3. Birbal Sahni Institute of Paleobotany, Lucknow, India. pp. 216–227.
- Dickson, D.R., and McAfee, C.L. 1988. Forest statistics for Connecticut—1972 and 1985. USDA For. Serv. Res. Bull. No. NE-105.
- Edwards, C.A., and Bohlen, P.J. 1996. Biology and ecology of earthworms. Chapman & Hall, London.
- Eno, C.F. 1960. Nitrate production in the field by incubating the soil in polyethylene bags. *Soil Sci. Soc. Proc.* **24**: 277–279.
- Federer, C.A. 1984. Organic matter and nitrogen content of the forest floor in even-aged northern hardwoods. *Can. J. For. Res.* **14**: 763–767.
- Ferrari, J.B., and Sugita, S. 1996. A spatially explicit model of leaf litterfall in hemlock–hardwood forests. *Can. J. For. Res.* **26**: 1905–1913.
- Finzi, A.C., van Breemen, N., and Canham, C.D. 1998. Canopy tree – soil interactions within temperate forests: species effects on carbon and nitrogen. *Ecol. Appl.* **8**: 440–446.
- Foster, D.R., and Zebryk, T.M. 1993. Long-term vegetation dynamics and disturbance history of a *Tsuga*-dominated forest in New England. *Ecology*, **74**: 982–998.
- Gee, G.W., and Bauder, J.W. 1986. Particle-size analysis. *In Methods of soil analysis. Part I. Physical and mineralogical*

- methods. *Edited by* A. Klute. American Society of Agronomy, Inc., Madison, Wis. pp. 383–411.
- Good, N.F. 1968. A study of natural replacement of chestnut in six stands on the highlands of New Jersey. *Bull. Torrey Bot. Club*, **95**: 940–953.
- Grace, J.R. 1986. The influence of gypsy moth on the composition and nutrient content of litter fall in a Pennsylvania oak forest. *For. Sci.* **32**: 855–870.
- Haimi, J., and Einbork, M. 1992. Effects of endogeic earthworms on soil processes and plant growth in coniferous forest soil. *Biol. Fertil. Soils*, **13**: 6–10.
- Haimi, J., Huhta, V., and Boucelham, M. 1992. Growth increase of birch seedling under the influence of earthworms—a laboratory study. *Soil Biol. Biochem.* **24**: 1525–1528.
- Huenneke, L.F. 1983. Understorey response to gaps caused by the death of *Ulmus americana* in central New York. *Bull. Torrey Bot. Club*, **110**: 170–175.
- Johnson, C.E. 1995. Soil nitrogen status 8 years after whole-tree clear-cutting. *Can. J. For. Res.* **25**: 1346–1355.
- Kim, C., Sharik, T.L., and Jurgensen, M.F. 1995. Canopy cover effects on soil nitrogen mineralization in northern red oak (*Quercus rubra*) stands in northern Lower Michigan. *For. Ecol. Manage.* **76**: 21–28.
- Knapp, C.L., Stoffel, T.L., and Whitaker, S.D. 1980. Insolation data manual: long term monthly averages of solar radiation, temperature, degree-days and global Kt for 248 National Weather Service Stations. Solar Energy Research Institute, Washington, D.C.
- Krasny, M.E., and Whitmore, M.C. 1992. Gradual and sudden forest canopy gaps in Allegheny northern hardwood forests. *Can. J. For. Res.* **22**: 139–143.
- Lovett, G.M., and Ruesink, A.E. 1995. Carbon and nitrogen mineralization from decomposing gypsy moth frass. *Oecologia*, **104**: 133–138.
- Lovett, G.M., and Tobiessen, P. 1993. Carbon and nitrogen assimilation in red oaks (*Quercus rubra* L.) subject to defoliation and nitrogen stress. *Tree Physiol.* **12**: 259–269.
- Marks, P.C. 1974. The role of pin cherry (*Prunus pennsylvanica* L.) in the maintenance of stability in northern hardwood ecosystems. *Ecol. Monogr.* **44**: 73–88.
- Matson, P.A., and Boone, R.D. 1984. Natural disturbance and nitrogen mineralization: waveform dieback of mountain hemlock in the Oregon Cascades. *Ecology*, **65**: 1511–1516.
- Matson, P.A., and Vitousek, P.M. 1981. Nitrogen mineralization and nitrification potentials following clearcutting in the Hoosier National Forest, Indiana. *For. Sci.* **27**: 781–791.
- McClure, M.S. 1989a. Evidence of a polymorphic life cycle in the hemlock woolly adelgid, *Adelges tsugae* (Homoptera: Adelgidae). *Ann. Entomol. Soc. Am.* **82**: 50–54.
- McClure, M.S. 1989b. Importance of weather to the distribution and abundance of introduced adelgid and scale insects. *Agric. For. Meteorol.* **47**: 291–302.
- McClure, M.S. 1990. Role of wind, birds, deer, and humans in the dispersal of hemlock woolly adelgid (Homoptera: Adelgidae). *Environ. Entomol.* **19**: 36–43.
- McClure, M.S. 1991. Density-dependent feedback and population cycles in *Adelges tsugae* (Homoptera: Adelgidae) on *Tsuga canadensis*. *Environ. Entomol.* **20**: 258–264.
- McClure, M.S. 1992. Hemlock woolly adelgid. *Am. Nurseryman*, **176**: 82–89.
- McCormick, J.F., and Platt, R.B. 1980. Recovery of an Appalachian forest following the chestnut blight, or, Catherine Keever—you were right! *Am. Midl. Nat.* **104**: 264–273.
- Miller, J.C., and Miller, J.N. 1993. *Statistics for analytical chemistry*. Ellis Horwood PTR Prentice Hall, New York.
- Mladenoff, D.J. 1987. Dynamics of nitrogen mineralization and nitrification in hemlock and hardwood treefall gaps. *Ecology*, **68**: 1171–1180.
- Nadelhoffer, K.J., Aber, J.D., and Melillo, J.M. 1983. Leaf-litter production and soil organic matter dynamics along a nitrogen-availability gradient in southern Wisconsin. *Can. J. For. Res.* **13**: 12–21.
- Orwig, D.A., and Foster, D.R. 1998. Forest response to the introduced hemlock woolly adelgid in southern New England, USA. *Bull. Torrey Bot. Club*, **125**: 60–73.
- Pastor, J., Aber, J.D., McClaugherty, C.A., and Melillo, J.M. 1984. Aboveground production and N and P cycling along a nitrogen mineralization gradient on Blackhawk Island, Wisconsin. *Ecol. Monogr.* **65**: 256–268.
- Perkins, T., Vogelmann, H., and Klein, R. 1987. Changes in light intensity and soil temperature as a result of forest decline on Camels Hump, Vermont. *Can. J. For. Res.* **17**: 565–568.
- Perkins, T.D., Klein, R.M., Vogelmann, H.W., and Badger, G.J. 1988. *Betula* seedling establishment in response to forest decline induced canopy degeneration. *Eur. J. For. Pathol.* **18**: 250–252.
- Ramakrishnan, P.S., and Vitousek, P.M. 1989. Ecosystem-level processes and the consequences of biological invasions. *In* Biological invasions: a global perspective. *Edited by* J.A. Drake. John Wiley & Sons, Ltd., London. pp. 281–300.
- Raw, F. 1959. Estimating earthworm populations by using formalin. *Nature (London)*, **184**: 1661.
- Reich, P.B., Grigal, D.F., Aber, J.D., and Gower, S.T. 1997. Nitrogen mineralization and productivity in 50 hardwood and conifer stands on diverse soils. *Ecology*, **78**: 335–347.
- Royle, D.D., and Lathrop, R.G. 1997. Monitoring hemlock forest health in New Jersey using Landsat TM data and change detection techniques. *For. Sci.* **43**: 327–335.
- Satchell, J.E. 1963. Nitrogen turnover by a woodland population of *Lumbricus terrestris*. *In* Soil organisms. *Edited by* J. Doekens and J. van der Drift. North Holland, Amsterdam. pp. 60–66.
- Scheu, S. 1993. There is an earthworm mobilizable nitrogen pool in soil. *Pedobiologia*, **37**: 243–249.
- Swank, W.T., Waide, J.B., Crossley, D.A., and Todd, R.L. 1981. Insect defoliation enhances nitrate export from forest ecosystems. *Oecologia*, **51**: 297–299.
- Twery, M.J., and Patterson, W.A., III. 1984. Variations in beech bark disease and its effects on species composition and structure of northern hardwood stands in central New England. *Can. J. For. Res.* **14**: 565–574.
- Tyrrill, L.E., and Crow, T.R. 1994. Dynamics of dead wood in old-growth hemlock-hardwood forests of northern Wisconsin and northern Michigan. *Can. J. For. Res.* **24**: 1672–1683.
- van Breemen, N., Finzi, A.C., and Canham, C.D. 1997. Canopy tree – soil interactions within temperate forests: effect of soil elemental composition and texture on species distributions. *Can. J. For. Res.* **27**: 1110–1116.
- Vitousek, P.M., and Reiners, W.A. 1975. Ecosystem succession and nutrient retention: a hypothesis. *BioScience*, **25**: 376–381.
- Vitousek, P.M., Walker, L.R., Whiteaker, L.D., Mueller-Dombois, D., and Matson, P.A. 1987. Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. *Science (Washington, D.C.)*, **238**: 802–804.
- Waide, J.B., Caskey, W.H., Todd, R.L., and Boring, L.R. 1988. Changes in soil nitrogen pools and transformations following forest clearcutting. *Ecol. Stud. No. 66*. pp. 221–232.
- Watson, J.K. 1992. Hemlock woolly adelgid threatens eastern hemlock in Shenandoah National Park. *Park Sci.* **12**: 9–11.

- Whitney, G.G. 1990. The history and status of the hemlock–hardwood forests of the Allegheny Plateau. *J. Ecol.* **78**: 443–457.
- Willemms, J.J., Marinissen, J.C.Y., and Blair, J. 1996. Effects of earthworms on nitrogen mineralization. *Biol. Fertil. Soils*, **23**: 57–63.
- Young, R.F., Shields, K.S., and Berlyn, G.P. 1995. Hemlock woolly adelgid (Homoptera: Adelgidae): stylet bundle insertion and feeding sites. *Ann. Entomol. Soc. Am.* **88**: 827–835.