

# Multi-year ecosystem response to hemlock woolly adelgid infestation in southern New England forests

David A. Orwig, Richard C. Cobb, Anthony W. D'Amato, Matthew L. Kizlinski, and David R. Foster

**Abstract:** The introduced hemlock woolly adelgid (HWA) (*Adelges tsugae* Annand) has generated widespread tree decline and substantial mortality of eastern hemlock (*Tsuga canadensis* (L.) Carrière) throughout the eastern United States. To assess the magnitude of ecosystem response to this disturbance, we conducted a multi-year study of forests with and without damage from HWA. Infested forests had significantly higher HWA-induced foliar loss and significantly lower forest floor C:N ratios and soil organic matter than uninfested forests. There were no significant soil temperature differences among stand types, although infested stands did have lower forest floor soil moisture than uninfested stands. Net nitrification and net N mineralization rates were significantly higher in infested versus uninfested forests by the second and third year of this study, respectively. In addition, total N pools and resin bag capture of NH<sub>4</sub> and NO<sub>3</sub> were significantly higher in infested versus uninfested forests throughout this study. Increases in N were likely due to a combination of factors including enhanced decomposition, reduced uptake of water and N by declining trees, sparse understory vegetation, and N-enriched throughfall from infested canopies. These results confirm that invasive pests can initiate substantial changes in ecosystem function soon after infestation occurs, prior to substantial overstory mortality or understory reorganization.

**Résumé :** L'introduction du puceron lanigère de la pruche (*Adelges tsugae* Annand) a entraîné un dépérissement très répandu et une mortalité importante de la pruche du Canada (*Tsuga canadensis* (L.) Carrière) partout dans l'est des États-Unis. Pour évaluer l'ampleur de la réaction de l'écosystème à cette perturbation, nous avons étudié pendant plusieurs années des forêts endommagées ou non par le puceron. Les forêts infestées avaient une perte de feuillage causée par le puceron significativement plus élevée ainsi qu'un rapport C:N dans la couverture morte et un contenu en matière organique dans le sol significativement plus faibles que les forêts non infestées. Il n'y avait aucune différence significative dans la température du sol parmi les types de peuplements mais l'humidité dans la couverture morte était plus faible dans les peuplements infestés que dans les peuplements non infestés. Les taux nets de nitrification et de minéralisation de N étaient significativement plus élevés dans les forêts infestées que dans les forêts non infestées respectivement la deuxième année et la troisième année de cette étude. De plus, les réservoirs de N total et le captage de NH<sub>4</sub> et NO<sub>3</sub> dans les sacs de résine étaient significativement plus élevés dans les forêts infestées que dans les forêts non infestées tout au long de cette étude. Les niveaux élevés de N étaient probablement dus à un ensemble de facteurs incluant une décomposition accrue, une absorption réduite d'eau et de N par les arbres dépérissants, une végétation de sous-bois clairsemée et des précipitations au sol enrichies en N à cause de l'infestation de la canopée. Ces résultats confirment que les ravageurs invasifs peuvent déclencher des changements importants dans le fonctionnement de l'écosystème rapidement après que soit survenue une infestation, avant qu'il y ait une mortalité substantielle dans l'étage dominant ou une réorganisation importante du sous-bois.

[Traduit par la Rédaction]

## Introduction

Infestation by introduced pathogens and pests and the resulting selective decline in dominant species is an important ecological, economic, and evolutionary process that alters ecosystem structure and causes cascading changes in the

function and value of forest ecosystems (Castello et al. 1995; Enserink 1999; Everett 2000). In the northeastern US, insect outbreaks have occurred historically and increasingly in the last century (Castello et al. 1995; Liebhold et al. 1995; Orwig 2002a), causing major reductions in such dominant species as chestnut, elm, and beech (Liebhold et al.

Received 28 February 2007. Accepted 11 October 2007. Published on the NRC Research Press Web site at [cjfr.nrc.ca](http://cjfr.nrc.ca) on 1 April 2008.

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1995; Lovett et al. 2006). Although exotic pests and pathogens may dramatically change ecosystem diversity, forest composition, structure, and microenvironment, their impacts on critical ecosystem processes such as productivity, decomposition, and nutrient cycling and retention are just beginning to be quantified (Vitousek 1986; Schowalter 2000; Lovett et al. 2006).

Herbivory by forest pests may operate similarly to physical disturbances by affecting plant productivity, community dynamics, water and nutrient fluxes, and climate (Schowalter and Lowman 1999). Forest pests that cause canopy defoliation can have a significant impact on soil N cycling by depositing frass, greenfall, insect biomass, and senescent leaf tissue to the forest floor (Mattson and Addy 1975; Hunter 2001). This material is then immobilized and redistributed in the system or mineralized and potentially lost from the system (Lovett et al. 2002). Even short-term (days to weeks) defoliation events in eastern hardwood forests can lead to increased soil N availability (Frost and Hunter 2004). The rate of herbivore-induced changes in soil nutrient cycling varies depending on the mechanisms by which insects affect their host (Hunter 2001). Understanding these changes and the factors that control them will help quantify and predict the various impacts that invasive pests have on forest ecosystems (Parker et al. 1999; Strayer et al. 2006).

The recent spread of hemlock woolly adelgid (HWA) (*Adelges tsugae* Annand), an introduced aphid-like insect from Japan that attacks and kills eastern hemlock (*Tsuga canadensis* (L.) Carrière), provides an opportunity and urgent need to examine the response of insect-induced ecosystem function dynamics as they unfold (Foster 2000). HWA has spread unimpeded across the eastern US since its initial infestation in Richmond, Virginia, in the early 1950s (Souto et al. 1996) and it now occupies 25% of the total range of hemlock (Morin et al. 2005). Its widespread distribution has generated extensive mortality and stimulated logging and preemptive salvage of hemlock (Kizlinski et al. 2002; Orwig et al. 2002; Foster and Orwig 2006). HWA reached southern New England in 1985, produced widespread mortality by 1988, and is currently distributed throughout Connecticut, Rhode Island, and over 40% of Massachusetts (McClure et al. 2000). Tragically, HWA has the potential to cause regional declines or even functional elimination of hemlock from extensive areas of eastern forests over the next several decades (Orwig et al. 2002; Ellison et al. 2005). Hemlock has no apparent resistance to HWA and has not yet shown the ability to recover from chronic infestations (McClure 1995; Orwig and Foster 1998; Orwig 2002b). Given current high rates of adelgid dispersal and hemlock decline, the absence of effective, large-scale biological or chemical control, and hemlock's abundance in New England ( $>3.5 \times 10^9$  cubic feet; 11%–55% of total softwood growing stock; Smith and Sheffield 2000), the potential ecological, economic, and aesthetic losses are enormous.

Because hemlock is one of the most abundant, long-lived, and shade-tolerant trees in the Northeast, it represents a foundation species (cf. Ellison et al. 2005) that plays a unique and dominant role in forest ecosystems. The deep shade and cool, damp microclimates under hemlock trees commonly have low vegetation cover (Daubenmire 1930). Acidic litter, low nutrient availability, and slow rates of de-

composition contribute to slow N cycling in hemlock-dominated forests (Lovett et al. 2004). HWA do not directly consume needles but feed on ray parenchyma cells in hemlock twigs (Young et al. 1995). Over several years, this feeding by HWA populations (twice a year) results in a gradual loss of needles (cf. Stadler et al. 2005). Consequently, progressive decline from HWA often stimulates a period of forest reorganization leading to new, distinct forest types (Orwig and Foster 1998) that may generate profound ecosystem impacts, including altered decomposition, nutrient losses, N export to streams, and erosion (Yorks et al. 2000; Cobb et al. 2006). Hemlock's dominance in wetlands and riparian areas enhances the vulnerability of aquatic ecosystems and their related fauna to these changes (Snyder et al. 2002; Ross et al. 2003). The potential loss of hemlock from forests would also have profound impacts on a variety of wildlife species that rely on this forest type for at least part of their life cycle (Yamasaki et al. 2000; Tingley et al. 2002).

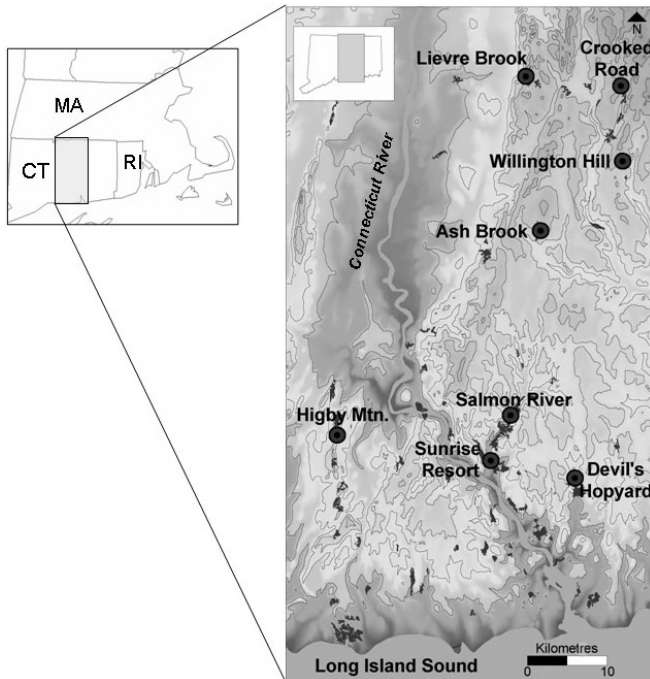
To date, there have been a few studies that investigate how HWA may alter the flow of energy and nutrients from the canopy to soil (Stadler et al. 2005, 2006). Two single-year studies examining the ecosystem response of forests to high HWA-related damage (i.e., 20%–95% overstory hemlock mortality) demonstrated that HWA could affect ecosystem N cycling via direct and indirect pathways (Jenkins et al. 1999; Kizlinski et al. 2002). Questions remaining from this work include the following: What processes drive accelerated N cycling? How long will changes in cycling last? How rapidly and in what manner will ecosystem processes change following initial infestation (cf. Yorks et al. 2000)? Therefore, our goals in this 3-year study of stands undergoing the early phases of infestation are to (i) investigate the microenvironmental changes associated with the initial decline of hemlock due to HWA feeding over several years in southern New England forests, (ii) document trends in N cycling over time, and (iii) examine the potential drivers of these changes as stands naturally deteriorate from HWA.

## Study area

The study area in central Connecticut encompasses the Connecticut River Valley and portions of the eastern uplands (Bell 1985) (Fig. 1). The region encompasses considerable variation in timing of initial HWA infestation (Orwig et al. 2002), and is characterized by a humid, continental climate with long, cool winters and short, mild summers (Hill et al. 1980). Elevations range from 0 to 300 m above sea level and soils are formed primarily from glacial deposits of weathered gneiss, schist, and granite (Reynolds 1979). The region is located at the southern limit of the hemlock – white pine – northern hardwood vegetation type (Nichols 1935) and the northern limit of Braun's (1950) oak–chestnut type.

Eight hemlock-dominated sites (>65% importance value) closely similar in physiography were selected for intensive study in 1997 (Table 1). Only upland sites within the same soil order (i.e., Inceptisols) were selected, because complex interactions between variables such as soil texture, C:N ratios, and N mineralization rates may exist. Since we were interested in examining ecosystem function changes that oc-

**Fig. 1.** Study area with locations of eight eastern hemlock sites examined in southern New England.



cur as hemlock deteriorates with chronic adelgid feeding, we selected sites that initially had moderate to high HWA infestation levels but low levels of overstory mortality.

## Methods

### Field measurements

Vegetation and soil were sampled in three 0.04 ha plots systematically located in the central portions of each stand in spring of 1998. All trees (stems  $\geq 8$  cm diameter at breast height (DBH)) were tallied by species and DBH and assigned a canopy position based on the amount of intercepted light received by the tree crown (Smith 1986). Relative importance values were calculated for each overstory species as: (relative basal area + relative density)/2. Hemlocks that died within the last 2–4 years, identified by retention of fine twigs in the crown (cf. Orwig and Foster 1998), were also tallied to determine hemlock abundance prior to HWA infestation. Foliage in the upper crown was inaccessible at our study sites, so understory trees, recently blown-down trees, and low-hanging foliage at each site were inspected to monitor HWA presence and infestation level. A visual crown loss designation (cf. Orwig and Foster 1998) was assigned to each hemlock tree based on the percentage of dropped foliage (e.g., healthy: 1%–25%, 26%–50%, 51%–75%, 76%–99%, and 100%; or dead). Eight randomly selected trees in each plot were cored at DBH for age determination.

All vascular plant species in each plot were recorded, along with slope, aspect, and topographic position. Saplings (<8 cm DBH and >1.4 m tall) were tallied by species. Ten 1 m<sup>2</sup> subplots were established in each plot at each of the corners and at six additional randomly selected points to assess understory vegetation. In each subplot, percent cover of seedling, herb, and shrub species were estimated using the

Braun–Blanquet scale (Mueller-Dombois and Ellenberg 1974).

### Soil microclimate

Soil temperatures at 1 and 5 cm depths were measured continuously at two subplots in each plot during the growing season. Temperature was recorded every 30 min with Hobo<sup>®</sup> data loggers and averaged daily for each horizon. Soil moisture was determined gravimetrically (105 °C for 48 h) during each net N mineralization measurement. Hemispherical photographs were taken from the center of each sampling plot at the beginning of the study to quantify the understory light environment. Photographs were analyzed with Gap light analyzer software (©1999 Simon Fraser University, Burnaby, British Columbia, Canada and Institute of Ecosystem Studies, Millbrook, New York, USA) to calculate light transmission through forest canopies (Frazer et al. 1999).

### Physical and chemical analyses

Within each study plot, the following properties of soils collected for initial N mineralization analyses (see below) were determined: organic matter by loss on ignition (5.5 h at 550 °C), pH in a soil and CaCl<sub>2</sub> slurry (1:10 organic soil – solution; 1:4 mineral soil – solution), and total C and N content by dry combustion with a Fisons CHN autoanalyzer. Mineral soil texture was determined with a Coulter LS 200 laser diffraction particle size analyzer.

### Nitrogen cycling

#### Net N mineralization

Nitrogen mineralization was measured from May 1998 to May 2001 using a modified core method (cf. Hart et al. 1994; Robertson et al. 1999). At each overstory plot, closed-topped cores were installed in four, 5 m × 5 m subplots at 5-week intervals during each growing season from 1998 to 2000, and with a 23-week over-winter incubation each year. At the beginning of each sampling period, soil was extracted with sharpened polyvinylchloride (PVC) cores (25 cm long) and immediately separated into mineral and organic layers. A second core was incubated in the field for 35 d and then removed and separated by horizon. Cores were installed to a depth of 20 cm, and the bottom 1 cm of each core was removed to prevent root invasion from below in incubated cores, and for consistent volume among samples in initial cores.

Soil samples were returned to the laboratory on ice and processed the next day. Forest floor (organic) and mineral soils were passed through a 5.0 mm mesh screen, weighed for total mass, and subsampled for gravimetric moisture and inorganic N. To determine soil NH<sub>4</sub>-N and NO<sub>3</sub>-N concentration, approximately 10 g of forest floor and mineral soil was placed into 100 mL of 1 mol·L<sup>-1</sup> KCl for 48 h. Soil extracts were filtered through a coarse pore filter (0.45–0.6 μm), and inorganic N concentrations were determined colorimetrically with a Lachat AE flow-injection autoanalyzer (Lachat Instruments, Inc., Milwaukee, Wisconsin), using the indophenol-blue (Lachat Instruments, Inc., 1990a) and cadmium reduction methods (Lachat Instruments, Inc., 1990b) for NH<sub>4</sub>-N and NO<sub>3</sub>-N, respectively. Net N mineral-



**Table 1.** Mean vegetation ( $\pm$ SE) and site characteristics at the beginning of year 1 in southern New England eastern hemlock study sites with various levels of hemlock woolly adelgid infestation.

	Salmon River (uninfested)	Crooked Road (uninfested)	Ash Brook (infested)	Lievre Brook (infested)	Willington Hill (infested)	Devil's Hopyard (infested)	Higby Mountain (infested)	Sunrise Resort (infested)
<b>Vegetation</b>								
Average tree age ( $n = 24$ )	68 $\pm$ 3	86 $\pm$ 5	82 $\pm$ 6	81 $\pm$ 5	99 $\pm$ 4	115 $\pm$ 9	116 $\pm$ 11	98 $\pm$ 6
Hemlock relative importance value (%)	74	78	89	82	80	77	69	80
Overstory basal area ( $\text{m}^2 \cdot \text{ha}^{-1}$ )	39	61	62	48	57	57	50	56
Overstory hemlock mortality (%)	0.0	1.0	1.9	2.9	0	2.8	4.2	7.0
Mean hemlock crown foliar loss	1.5 $\pm$ 0.2	1.6 $\pm$ 0.2	3.0 $\pm$ 0.1	2.6 $\pm$ 0.1	2.9 $\pm$ 0.2	2.2 $\pm$ 0.2	3.3 $\pm$ 0.1	3.2 $\pm$ 0.1
Gap light index	5.7 $\pm$ 0.2	4.8 $\pm$ 0.1	8.3 $\pm$ 0.7	5.3 $\pm$ 0.1	5.4 $\pm$ 0.3	12.9 $\pm$ 0.3	20.6 $\pm$ 0.8	12.9 $\pm$ 0.2
<b>Site</b>								
Elevation (m above sea level)	50	259	137	137	190	76	244	15
Aspect(s)	NW-NE	NE-NW	SE	NW	NE	SW-NW	NE	SW
Slope range (%)	3-5	15-26	10-27	15-34	10-15	25-28	22-24	25-75

**Note:** Hemlock relative importance value was calculated as (relative basal area + relative density)/2 derived from three fixed-area plots in each stand. Hemlock crown foliar loss classes were ascribed to each hemlock tree >8 cm DBH based on the amount of dropped foliage: 1, 1%–25%; 2, 26%–50%; 3, 51%–75%; 4, 76%–99%; 5, dead (cf. Orwig and Foster 1998). Gap light index values were calculated from hemispherical photographs taken within each sampling plot using software designed to measure light transmission through forest canopies (Frazer et al. 1999).

ization was calculated as the difference in concentration of inorganic N ( $\text{NH}_4\text{-N} + \text{NO}_3\text{-N}$ ) in incubated cores minus that in initial samples.

### N mobility

An additional assessment of forest floor N availability and mobility was determined at each soil subplot from mixed-bed cation + anion resin bags (IONAC NM-60, Sybron Chemicals Inc., Birmingham, New Jersey; cf. Binkley and Matson 1983). Approximately 10 g of resin was placed in nylon mesh bags and pretreated with 2 mol·L<sup>-1</sup> KCl before deployment for 6-month intervals (growing-season and over winter). Resins were deployed at the forest floor – mineral soil interface at a depth of ~5 cm within 0.5 m from N mineralization incubations. Resins were returned to the laboratory on ice, dried at 105 °C for 24 h, and extracted in 2 mol·L<sup>-1</sup> KCl. Inorganic N was determined by the methods described for soil N extracts.

### Data analyses

Each study site was treated as an experimental unit ( $n = 6$  and 2 for infested and uninfested stands, respectively) and annual values of net nitrification and mineralization, and N pool sizes were summed and compared between infested and uninfested stands using Wilcoxon rank-sum tests. In addition, Wilcoxon rank-sum tests were used to examine the effects of HWA on average annual soil temperature and moisture. Pearson's correlation coefficients were calculated to determine the degree of relationship among HWA canopy impacts, ecosystem properties, and soil temperature and moisture. All statistical analyses were conducted using SAS version 9.1 (SAS Institute Inc. 2004). Significance levels were set at  $\alpha = 0.05$  for all analyses.

## Results

### Stand classification

At the beginning of year 1 of the study, each site was dominated by hemlock trees in all crown classes, with overstory relative importance values between 69% and 89% and trees between 68 and 116 years old (Table 1). Stand compo-

sition included low percentages of hardwood species such as red oak (*Quercus rubra* L.), black birch (*Betula lenta* L.), and red maple (*Acer rubrum* L.). Study sites were classified into two broad categories: uninfested control sites ( $n = 2$ ) and HWA infested sites ( $n = 6$ ). Uninfested control sites contained full, healthy crowns, and low understory light levels at the beginning of the study (Table 1). Infested stands had low but significantly higher overstory mortality levels than uninfested stands (3.1% vs. 0.5%), contained live trees with significantly greater foliar loss (2.9 vs. 1.6 average foliar loss class), and had significantly higher understory light levels (10.9 vs. 5.3 GLI values; paired  $t$  tests,  $P < 0.05$ ). At the beginning of the study in 1998, understory vegetation was sparse in all stands, averaging <1% cover and <1 stems·m<sup>-2</sup> (data not shown). Understory species present in low densities included *A. rubrum*, *B. lenta*, *T. canadensis*, and partridgeberry (*Mitchella repens* L.).

### Site and soil characteristics

Stands were located at elevations of 15–260 m above sea level on predominantly northern aspects and moderate slopes of 5%–30% (Table 1). Sites consisted of sandy loam, silt loam, and loam soils (Table 2). There were significant differences in several soil properties between infested versus uninfested sites. Sites infested with HWA had significantly higher forest floor pH and significantly lower soil C:N and soil organic matter content than uninfested sites (paired  $t$  tests,  $P < 0.05$ ). Mineral soil characteristics were not significantly different between infested and uninfested sites.

### Microenvironmental trends

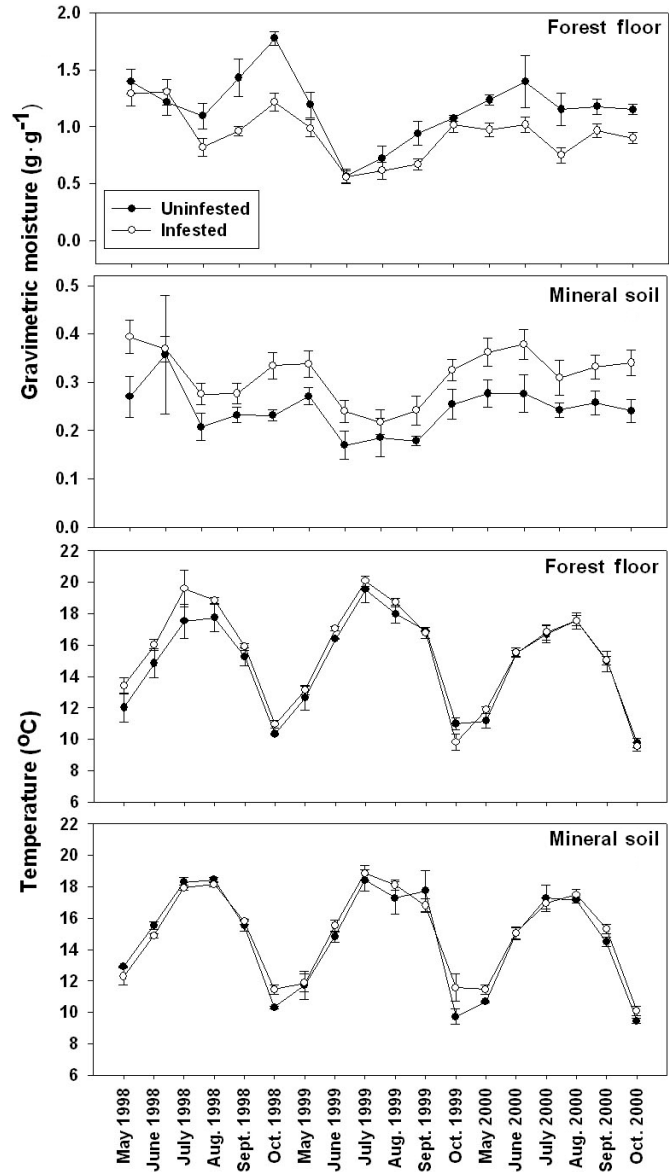
Each of the 3 years of the study differed in overall climatic conditions. The first year, 1998, was generally warm and moist, 1999 was warm and dry, and 2000 was cool and moist. Despite these differences in climatic conditions among study years, we found no significant time effects in ANOVA models used to explore the influence of sample year on our analyses ( $P > 0.05$ ). Initial HWA infestation did not have an effect on forest floor moisture levels; however, infested stands had significantly lower forest floor

**Table 2.** Mean soil characteristics ( $\pm$ SE) at the beginning of year 1 in southern New England eastern hemlock study sites with various levels of hemlock woolly adelgid infestation.

	Salmon River (uninfested)	Crooked Road (uninfested)	Ash Brook (infested)	Lievre Brook (infested)	Wilmington Hill (infested)	Devil's Hopyard (infested)	Higby Mountain (infested)	Sunrise Resort (infested)
Texture	Sandy loam	Silt loam	Silt loam	Loam	Loam	Silt loam	Silt loam	Sandy loam
pH (forest floor)	3.73 $\pm$ 0.03	3.77 $\pm$ 0.02	4.07 $\pm$ 0.11	3.97 $\pm$ 0.02	4.15 $\pm$ 0.06	4.02 $\pm$ 0.08	4.46 $\pm$ 0.19	4.25 $\pm$ 0.06
pH (mineral soil)	4.37 $\pm$ 0.04	4.22 $\pm$ 0.04	4.33 $\pm$ 0.06	4.20 $\pm$ 0.05	4.54 $\pm$ 0.02	4.27 $\pm$ 0.03	4.56 $\pm$ 0.20	4.55 $\pm$ 0.07
C:N (forest floor)	28.4 $\pm$ 0.1	26.6 $\pm$ 1.4	22.8 $\pm$ 0.8	24.2 $\pm$ 0.2	22.7 $\pm$ 0.6	23.8 $\pm$ 1.0	22.2 $\pm$ 0.1	25.5 $\pm$ 1.5
C:N (mineral soil)	23.1 $\pm$ 0.5	27.0 $\pm$ 0.4	21.3 $\pm$ 1.6	26.7 $\pm$ 1.4	21.1 $\pm$ 1.3	22.5 $\pm$ 0.6	20.3 $\pm$ 0.3	23.8 $\pm$ 1.9
SOM (%) (forest floor)	68.7 $\pm$ 6.6	77.6 $\pm$ 4.6	64.1 $\pm$ 2.5	66.5 $\pm$ 3.2	62.2 $\pm$ 2.1	64.0 $\pm$ 7.8	58.8 $\pm$ 5.6	51.7 $\pm$ 4.5
SOM (%) (mineral soil)	6.4 $\pm$ 0.4	9.6 $\pm$ 0.7	10.7 $\pm$ 1.8	7.7 $\pm$ 1.4	8.4 $\pm$ 0.7	9.6 $\pm$ 0.6	14.72 $\pm$ 1.9	6.0 $\pm$ 0.5

Note: SOM, soil organic matter.

**Fig. 2.** Mean gravimetric moisture and soil temperature in the forest floor and mineral soil horizons of hemlock woolly adelgid infested and uninfested eastern hemlock forests by incubation period. Data are means  $\pm$  1 SE ( $n = 6$  and  $2$  for infested and uninfested stands, respectively).

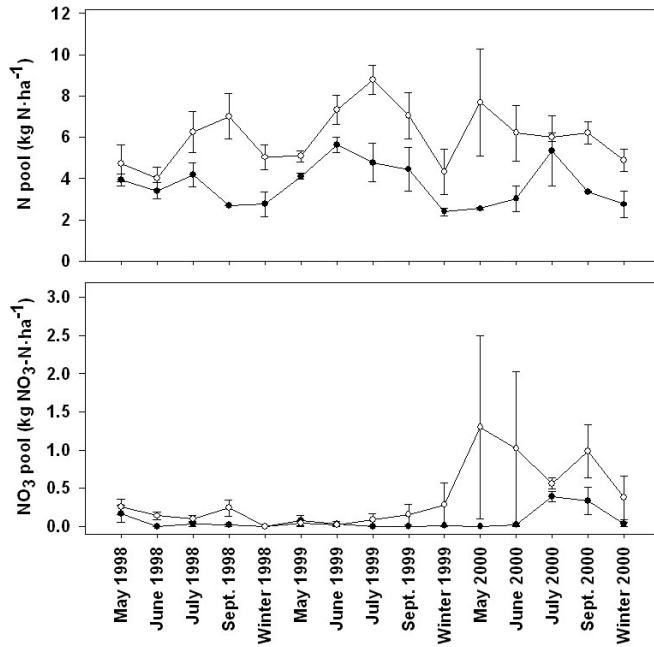


moisture levels than control stands by year 3 of this study (Wilcoxon rank-sum test,  $Z = 1.833$ ,  $P < 0.05$ ) (Fig. 2). In contrast, even though mineral soil moisture levels appeared slightly higher, there was no significant effect of HWA infestation on mineral soil moisture levels (Wilcoxon rank-sum tests,  $P > 0.2$ ) (Fig. 2). Likewise, there were no significant forest floor nor mineral soil temperature differences between infested and uninfested stands (Wilcoxon rank-sum tests,  $P > 0.2$ ) (Fig. 2).

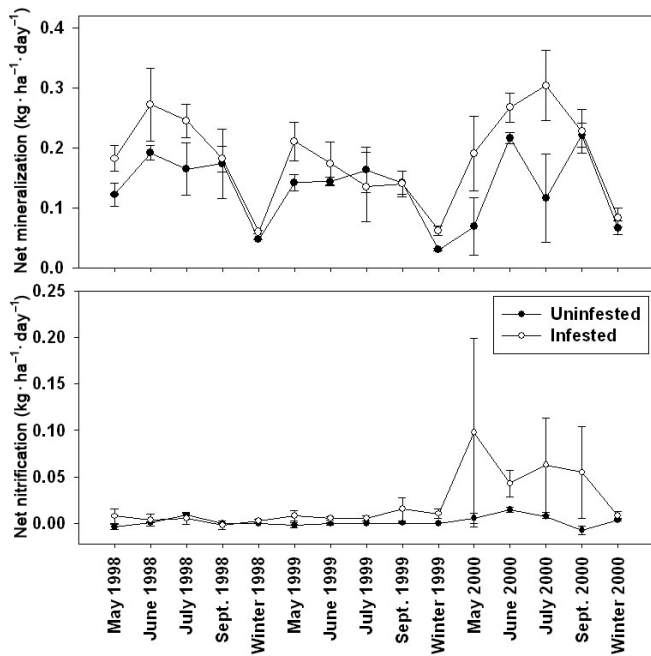
**Inorganic N pools and cycling rates**

There were significant differences in N pool sizes between infested and uninfested stands across the 3 years examined in this study (Wilcoxon rank-sum tests,  $Z = -1.833$ ,  $P < 0.05$ ) (Fig. 3). In particular, total N pool sizes were con-

**Fig. 3.** Mean soil extractable NH<sub>4</sub> and NO<sub>3</sub> pools in hemlock woolly adelgid infested and uninfested eastern hemlock forests by incubation period. Data are means ± 1 SE (*n* = 6 and 2 for infested and uninfested stands, respectively).



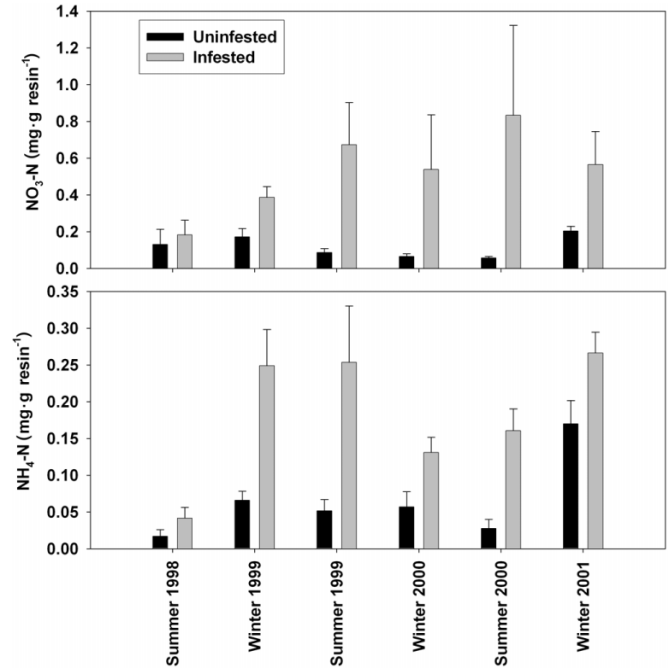
**Fig. 4.** Mean net N mineralization and net nitrification rates in hemlock woolly adelgid infested and uninfested eastern hemlock forests by incubation period. Values of the forest floor and mineral soil horizons are combined. Data are means ± 1 SE (*n* = 6 and 2 for infested and uninfested stands, respectively).



sistently greater in stands infested with HWA. In addition, NO<sub>3</sub>-N pool sizes were greater in infested stands in years 1 and 3 of this study (Wilcoxon rank-sum tests, *Z* = -1.833, *P* < 0.05).

The initial phase of HWA infestation appeared to have little

**Fig. 5.** Mean NH<sub>4</sub> and NO<sub>3</sub> capture on ion exchange resin bags by season. Data are means ± 1 SE (*n* = 6 and 2 for infested and uninfested stands, respectively).



effect on total net N mineralization (ammonification + nitrification) rates, as they did not differ between infested and uninfested stands in year 1 of this study (*P* = 0.08) (Fig. 4). By year 2, net nitrification rates were significantly greater in infested stands (Wilcoxon rank-sum tests, *Z* = -1.833, *P* < 0.05). Similarly, net mineralization rates were greater in infested stands by the third year of this study (Wilcoxon rank-sum tests, *Z* = -1.833, *P* < 0.05).

### Resin bag N capture

Resin bags incubated in the same subplots where soil core measurements took place successfully captured NH<sub>4</sub> and NO<sub>3</sub>, providing an additional index of inorganic N availability. Similar to total net N mineralization, there was no difference in NH<sub>4</sub> and NO<sub>3</sub> capture in year 1 of this study (*P* = 0.12) (Fig. 5). For years 2 and 3, nitrate capture was significantly higher in infested versus uninfested stands, whereas ammonium capture was only significantly higher in year 3 of this study. There was a great deal of variability among resin bag N capture within infested stands (Fig. 5). Overall, more nitrate was captured on resin bags than ammonium. Resin bag N capture appeared to be a very reliable indicator of soil N cycling in this study, as the correlation between resin bag NO<sub>3</sub> capture and soil net nitrification rates was *r* = 0.995, (*P* < 0.05). In addition, resin bag NO<sub>3</sub> and NH<sub>4</sub> capture were significantly correlated with net N mineralization rates (*r* = 0.830 and 0.862, respectively) and total soil N pools (*r* = 0.889 and 0.764, respectively).

### Relationship between soil N and microenvironment

There was a strong relationship with measured forest floor N and soil temperature over the 3-year period of this study (Table 3). Across all sites, forest floor N cycling, total soil

**Table 3.** Pearson's correlation coefficients between ecosystem properties and microclimatic conditions by soil horizon (3-year averages, 1998–2000) within eight southern New England study areas.

	Soil moisture		Soil temperature	
	Forest floor	Mineral soil	Forest floor	Mineral soil
Net nitrification	-0.211	0.541	0.835*	0.637
Net mineralization	-0.095	0.491	0.705*	0.380
Nitrate pool	-0.180	0.544	0.824*	0.596
Total N pool	-0.425	0.552	0.882*	0.640
Resin NO <sub>3</sub> capture	-0.180	0.544	0.824*	0.596
Resin NH <sub>4</sub> capture	-0.027	0.579	0.666	0.371
Gap light index	-0.853*	-0.574	0.864*	0.766*
Overstory hemlock mortality	-0.814*	-0.189	0.734*	0.688
Foliar loss	-0.598	0.292	0.447	0.438
Forest floor moisture	1.000	0.302	-0.517	-0.419
Mineral soil moisture		1.000	0.283	0.118
Forest floor temperature			1.000	0.776*
Mineral soil temperature				1.000

Note: \*Significant at  $P < 0.05$ .

N pools, and NO<sub>3</sub> capture were all significantly and positively correlated with forest floor temperature. There were no significant relationships with mineral soil temperature and soil N cycling or availability. In addition, soil moisture appeared to be less important for soil N cycling or availability, as it was not significantly correlated with any of the measured soil N parameters (Table 3). Gap light index and overstory hemlock mortality were negatively correlated with forest floor moisture content and positively correlated with forest floor temperature.

## Discussion

At the beginning of the study, all stands examined had low overstory mortality levels and a range of crown conditions, from healthy uninfested trees to trees that had lost >50% of their foliage. This low to modest crown damage did lead to increased light levels at some sites (e.g., Higby Mountain, Devil's Hopyard, Sunrise Resort), but had not yet stimulated major changes in understory composition. Average percent cover of understory vegetation was <1 m<sup>-2</sup>, and birch seedlings were only present at densities <1 m<sup>-2</sup>. We have subsequently observed more dramatic vegetation changes at these sites as the crowns have continued to thin (D.A. Orwig et al., unpublished data), and related studies of hemlock stands with more substantial HWA damage have reported dense black birch seedlings (5–10 m<sup>-2</sup>) and saplings (1000–8000 ha<sup>-1</sup>) along with other species like *A. rubrum*, sassafras (*Sassafras albidum* (Nutt.) Nees), and oak (*Quercus*) species (Orwig and Foster 1998; Small et al. 2005; Stadler et al. 2005; Eschtruth et al. 2006).

Our multi-year study of lightly damaged forests was designed to investigate the ecosystem function changes associated with HWA infestation as they unfolded. Our findings suggest HWA-induced foliar loss in this study may have already had an influence on forest floor parameters, as C:N and soil organic matter were significantly lower and pH was significantly higher in infested forests compared with uninfested forests.

In addition, as infestation progressed in this study, there were significant increases in net N mineralization and net

nitrification rates in infested versus uninfested forests. Significant correlations among HWA canopy effects, changes in microclimate, and soil N cycling suggest that ecosystem changes documented here are a direct result of HWA infestation. Our findings are consistent with studies examining more extensive hemlock decline and mortality that also resulted in increased nitrification rates (Jenkins et al. 1999; Yorks et al. 2000; Kizlinski et al. 2002). By the third year of our study, net nitrification rates were an order of magnitude higher in infested stands. In addition, total N pool sizes and both NH<sub>4</sub> and NO<sub>3</sub> availability were significantly higher and increased over time at sites with HWA infestation versus uninfested sites, suggesting that the typically "slow" N cycling associated with healthy hemlock forests has already been substantially altered (Lovett et al. 2004).

Jenkins et al. (1999) hypothesized that accelerated cycling was driven by increases in soil moisture and temperatures associated with HWA outbreaks. The modest level of HWA-induced damage observed in this study did lead to drier organic soils in infested forests. Drier organic horizons are consistent with those observed in other heavily HWA-damaged stands because of higher evaporative losses at the soil surface (Kizlinski et al. 2002). Decomposition rates of green foliage placed on the soil surface in these same forests were significantly lower during 1998 and 1999 in infested versus uninfested forests; desiccation at the soil surface was the primary factor influencing these differences (Cobb et al. 2006). However, decomposition of senescent litter may have increased below the soil surface, because of better conditions. A 6-month study using a common cellulose substrate showed significantly faster rates of decay 5 cm below the soil surface than at the soil surface in HWA-infested stands (Cobb and Orwig 2002). It is likely that the combination of enhanced subsurface decomposition, reduced uptake of both water and N by declining trees, and the absence of additional understory vegetative uptake contributed to increases in pool sizes and availability.

An additional factor that likely contributed to enhanced N availability observed in this study is throughfall received by forest soils beneath HWA-infested trees. Throughfall enriched in N from insect frass and (or) leached from foliage



has been observed following pest defoliation events (Hunter et al. 2003), and Stadler et al. (2005, 2006) found that throughfall and litter leachates under HWA-infested crowns were significantly enriched in total N, dissolved organic N (DON), and nitrate N. These higher N fluxes likely contribute to the N captured on soil resin bags in this study, although the amount captured from throughfall is currently unknown.

There were no appreciable differences in soil temperature between infested and uninfested forests in this study. However, temperature appeared to play an important role in nutrient cycling, as it was strongly and positively correlated with N pools, N cycling rates, and N availability for the duration of the study. Thinning crowns and initial hemlock mortality, although low at early stages of infestation examined in this study, were strongly related to forest floor temperature. As predicted by Jenkins et al. (1999) and observed elsewhere (Kizlinski et al. 2002), temperatures should continue to increase in these forests over time with progressive crown deterioration and lead to accelerated N cycling and greater N availability.

Although stands were in an early stage of HWA infestation, we did observe clear evidence that N cycling was altered in these forests. Increases in net N mineralization and nitrification rates, along with increased N pools and available N associated with HWA over the duration of this study, suggest that rates are likely to increase in the future, as HWA will remain and continue to feed in these forests. However, we still do not know the duration or consequences of enhanced N availability, or whether regeneration demand will eventually exceed this. Jenkins et al. (1999) reported significantly higher nitrification rates on infested sites that had substantial understory vegetation establishment, suggesting that seedling demand for inorganic N was exceeded by ammonium-N production and subsequent nitrification. If production of nitrate is not balanced with vegetative uptake, continued hemlock decline could trigger nutrient leaching (Vitousek and Reiners 1975). Outbreaks of native and exotic foliar herbivores have resulted in significant pulses of  $\text{NO}_3$  leached into streams (Swank et al. 1981; Eshleman et al. 1998; Lewis and Likens 2007). Because hemlock forests are often located along streams and in wetlands, N leaching to aquatic systems is possible if HWA-induced declines lead to similar changes in N loss in those systems (Yorks et al. 2000).

Ultimately the impact of HWA on nutrient cycling may last much longer than the period of infestation leading to hemlock mortality, as hemlock is often replaced by deciduous species in these forests, which commonly have greater decomposition and N-cycling rates. Additional long-term studies are needed to adequately document the immediate and long-term impact of hemlock deterioration and loss on both terrestrial and adjacent aquatic systems (cf. Ellison et al. 2005) to adequately forecast the overall impact of this invasive pest.

## Acknowledgements

We thank Bruce Thompson and Sean McVey of the Natural Resources Conservation Service (NRCS) and Jennifer Garrett at the University of Massachusetts, Amherst, for assistance with soil texture data. Steve Currie, Aaron Weiskit-

tel, Spencer Meyer, and Katie Theoharides provided field assistance, while Jessica Brown, Alexis Calvi, Samantha Farrell, and Tawanna Childs provided generous lab support and data entry. We acknowledge the many landowners and managers who granted permission to study their hemlock forests, including The Johnson Family at the Sunrise Resort, The Connecticut Department of Environmental Protection, The Nature Conservancy, and Don Fisco of the Middletown Water Department. We thank A. Ellison for substantial statistical advice. The Harvard Forest Lab group, Heidi Lux, Richard Bowden, and an anonymous reviewer provided critical comments that improved earlier versions of this manuscript. Financial support of this research was provided by the A.W. Mellon Foundation, The Harvard Forest Long Term Ecological Research Program, and the Competitive Grants program of the USDA (Cooperative State Research, Education, and Extension Service (CSREES) agreement No. 9700672).

## References

- Bell, M. 1985. The face of Connecticut. Bulletin 110. State Geology and Natural History Survey of Connecticut. Hartford, Conn.
- Binkley, D., and Matson, P. 1983. Ion exchange resin bag method for assessing forest soil nitrogen availability. *Soil Sci. Soc. Am. J.* **47**: 1050–1052.
- Braun, E.L. 1950. Deciduous forests of eastern North America. Macmillan, New York.
- Castello, J.D., Leopold, D.J., and Smallidge, P.J. 1995. Pathogens, patterns, and processes in forest ecosystems. *Bioscience*, **45**: 16–24. doi:10.2307/1312531.
- Cobb, R.C., and Orwig, D.A. 2002. Impact of hemlock woolly adelgid on decomposition: an overview. *In* Proceedings: Hemlock Woolly Adelgid in the Eastern United States Symposium, New Brunswick, N.J., 5–7 February 2002. Edited by R.C. Reardon, B.P. Onken, and J. Lashomb. New Jersey Agricultural Experiment Station Publication, New Brunswick, N.J. pp. 317–322.
- Cobb, R., Orwig, D.A., and Currie, S. 2006. Decomposition of green foliage in eastern hemlock forests of southern New England impacted by hemlock woolly adelgid populations. *Can. J. For. Res.* **36**: 1331–1341. doi:10.1139/X06-012.
- Daubenmire, R.F. 1930. The relationship of certain ecological factors to the inhibition of forest floor herbs under hemlock. *Butler Univ. Bot. Stud.* **1**: 61–76.
- Ellison, A.M., Bank, M.S., Clinton, B.D., Colburn, E.A., Elliott, K., Ford, C.R., Foster, D.R., Kloeppel, B.D., Knoepp, J.D., Lovett, G.M., Mohan, J., Orwig, D.A., Rodenhouse, N.L., Sobczak, W.V., Stinson, K.A., Stone, J.K., Swan, C.M., Thompson, J., Von Holle, B., and Webster, J.R. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Front. Ecol. Environ.* **3**: 479–486. doi:10.1890/1540-9295(2005)003[0479:LOFSCF]2.0.CO;2.
- Enserink, M. 1999. Biological invaders sweep in. *Science*, **285**: 1834–1836. doi:10.1126/science.285.5435.1834.
- Eschtruth, A.K., Cleavitt, N.L., Battles, J.J., Evans, R.A., and Fahney, T.J. 2006. Vegetation dynamics in declining eastern hemlock stands: 9 years of forest response to hemlock woolly adelgid infestation. *Can. J. For. Res.* **36**: 1435–1450. doi:10.1139/X06-050.
- Eshleman, K.N., Morgan, R.P., Webb, J.R., Deviney, F.A., and Galloway, J.N. 1998. Temporal patterns of nitrogen leakage from mid-Appalachian forested watersheds. Role of insect defoliation. *Water Resour. Res.* **34**: 2005–2016. doi:10.1029/98WR01198.
- Everett, R.A. 2000. Patterns and pathways of biological invasions.



- Trends Ecol. Evol. **15**: 177–178. doi:10.1016/S0169-5347(00)01835-8.
- Foster, D.R. 2000. Hemlock's future in the context of its history: an ecological perspective. *In* Proceedings: Symposium on Sustainable Management of Hemlock Ecosystems in Eastern North America, Durham, N.H., 22–24 June 1999. *Edited by* K.A. McManus, K.S. Shields, and D.R. Souto. USDA Gen. Tech. Rep. 267. pp. 1–4.
- Foster, D.R., and Orwig, D.A. 2006. Pre-emptive and salvage harvesting of New England forests: when doing nothing is a viable alternative. *Conserv. Biol.* **20**: 959–970. PMID:16922213.
- Frazier, G.W., Canham, C.D., and Lertzman, K.P. 1999. Gap light analyzer (GLA): Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, users manual and program documentation. Simon Fraser University, Burnaby, British Columbia, and the Institute of Ecosystem Studies, Millbrook, New York.
- Frost, C.J., and Hunter, M.D. 2004. Insect canopy herbivory and frass deposition affect soil nutrient dynamics and export in oak mesocosms. *Ecology*, **85**: 3335–3347. doi:10.1890/04-0003.
- Hart, S.C., Stark, J.M., Davidson, E.A., and Firestone, M.F. 1994. Nitrogen mineralization, immobilization, and nitrification. *In* Methods of soil analysis. Part 2. Microbial and biochemical properties. *Edited by* R.W. Weaver, S. Angle, P. Bottomley, D. Bezdicek, S. Smith, A. Tabatabai, and A. Wollum. Soil Sci. Soc. Am. Inc., Madison, Wisc. pp. 985–1018.
- Hill, D.E., Sautter, E.H., and Gonick, W.N. 1980. Soils of Connecticut. *Bull. Conn. Agric. Exp. Stn.* 787.
- Hunter, M.D. 2001. Insect population dynamics meets ecosystem ecology: effects of herbivory on soil nutrient dynamics. *Agric. For. Entomol.* **3**: 77–84. doi:10.1046/j.1461-9563.2001.00100.x.
- Hunter, M.D., Linnen, C.R., and Reynolds, B.C. 2003. Effects of endemic densities of canopy herbivores on nutrient dynamics along a gradient in elevation in the southern Appalachians. *Pedobiologia (Jena)*, **47**: 231–244. doi:10.1078/0031-4056-00187.
- Jenkins, J.C., Aber, J.D., and Canham, C.D. 1999. Hemlock woolly adelgid impacts on community structure and N cycling rates in eastern hemlock forests. *Can. J. For. Res.* **29**: 630–645. doi:10.1139/cjfr-29-5-630.
- Kizlinski, M.L., Orwig, D.A., Cobb, R.C., and Foster, D.R. 2002. Direct and indirect ecosystem consequences of an invasive pest on forests dominated by eastern hemlock. *J. Biogeogr.* **29**: 1489–1503. doi:10.1046/j.1365-2699.2002.00766.x.
- Lachat Instruments, Inc. 1990a. QuickChem method No. 10-107-06-1-C. Milwaukee, Wisc.
- Lachat Instruments, Inc. 1990b. QuickChem method No. 10-107-04-1-A. Milwaukee, Wisc.
- Lewis, G.P., and Likens, G.E. 2007. Changes in stream chemistry associated with insect defoliation in a Pennsylvania hemlock-hardwoods forest. *For. Ecol. Manage.* **238**: 199–211. doi:10.1016/j.foreco.2006.10.013.
- Liebold, A.M., MacDonald, W.L., Bergdahl, D., and Mastro, V.C. 1995. Invasion by exotic forest pests: a threat to forest ecosystems. *For. Sci. Monogr.* **30**: 1–49.
- Lovett, G.M., Christenson, L.M., Groffman, P.M., Jones, C.G., Hart, J.E., and Mitchell, M.J. 2002. Insect defoliation and nitrogen cycling in forests. *Bioscience*, **52**: 335–341. doi:10.1641/0006-3568(2002)052[0335:IDANCI]2.0.CO;2.
- Lovett, G.M., Weathers, K.C., Arthur, M.A., and Schultz, J.C. 2004. Nitrogen cycling in a northern hardwood forest: do species matter? *Biogeochemistry*, **67**: 289–308. doi:10.1023/B:BIOG.0000015786.65466.f5.
- Lovett, G.M., Canham, C.D., Arthur, M.A., Weathers, K.C., and Fitzhugh, R.D. 2006. Forest ecosystem responses to exotic pests and pathogens in eastern North America. *Bioscience*, **56**: 395–405. doi:10.1641/0006-3568(2006)056[0395:FERTEP]2.0.CO;2.
- Mattson, W.J., and Addy, N.D. 1975. Phytophagous insects as regulators of forest primary productivity. *Science*, **190**: 515–522.
- McClure, M.S. 1995. Managing hemlock woolly adelgid in ornamental landscapes. *Bull. Conn. Agric. Exp. Stn.* 925.
- McClure, M.S., Cheah, C.A.S.-J., and Tigner, T.C. 2000. Is *Pseudotsugus tsugae* the solution to the hemlock woolly adelgid problem?: an early perspective. *In* Proceedings: Symposium on Sustainable Management of Hemlock Ecosystems in Eastern North America, Durham, N.H., 22–24 June 1999. *Edited by* K.A. McManus, K.S. Shields, and D.R. Souto. USDA Gen. Tech. Rep. 267. pp. 89–96.
- Morin, R.S., Liebold, A.M., Luzader, E.R., Lister, A.J., Gottschalk, K.W., and Twardus, D.B. 2005. Mapping host-species abundance of three major exotic forest pests. *USDA For. Serv. Res. Pap. NE-276*.
- Mueller-Dombois, D., and Ellenberg, H. 1974. Aims and methods of vegetation ecology. John Wiley & Sons, New York.
- Nichols, G.E. 1935. The hemlock-white pine-northern hardwood region of eastern North America. *Ecology*, **16**: 403–422. doi:10.2307/1930077.
- Orwig, D.A. 2002a. Ecosystem to regional impacts of introduced pests and pathogens- historical context, questions, and issues. *J. Biogeogr.* **29**: 1471–1474. doi:10.1046/j.1365-2699.2002.00787.x.
- Orwig, D.A. 2002b. Stand dynamics associated with chronic hemlock woolly adelgid infestations in southern New England. *In* Proceedings: Hemlock Woolly Adelgid in the Eastern United States Symposium, 5–7 February 2002. *Edited by* R.C. Reardon, B.P. Onken, and J. Lashomb. New Jersey Agricultural Experiment Station Publication, New Brunswick, N.J. pp. 36–46.
- Orwig, D.A., and Foster, D.R. 1998. Forest response to the introduced hemlock woolly adelgid in southern New England, U.S.A. *J. Torrey Bot. Soc.* **125**: 60–73. doi:10.2307/2997232.
- Orwig, D.A., Foster, D.R., and Mausel, D.L. 2002. Landscape patterns of hemlock decline in New England due to the introduced hemlock woolly adelgid. *J. Biogeogr.* **29**: 1475–1487. doi:10.1046/j.1365-2699.2002.00765.x.
- Parker, I.M., Simberloff, D., Lonsdale, W.M., Goodell, K., Wonham, M., Kareiva, P.M., Williamson, M.H., Von Holle, B., Moyle, P.B., Byers, J.E., and Goldwasser, L. 1999. Impact: toward a framework for understanding the ecological effects of invaders. *Biol. Invasions*, **1**: 3–19. doi:10.1023/A:1010034312781.
- Reynolds, C.A. 1979. Soil survey of Middlesex County, Connecticut. *USDA Soil Conserv. Serv., Storrs, Conn.*
- Robertson, G.P., Wedin, D., Groffman, P.M., Blair, J.M., Holland, E.A., Nadelhoffer, K.J., and Harris, D. 1999. Soil carbon and nitrogen availability: nitrogen mineralization, nitrification, and soil respiration potentials. *In* Standard soil methods for long-term ecological research. *Edited by* G.P. Robertson, D.C. Coleman, C.S. Bledsoe, and P. Sollins. Oxford University Press, New York. pp. 258–288.
- Ross, R.M., Bennett, R.M., Snyder, C.D., Young, J.A., Smith, D.R., and Lemarie, D.P. 2003. Influence of eastern hemlock (*Tsuga canadensis* L.) on fish community structure and function in headwater streams of the Delaware River basin. *Ecol. Freshw. Fish.* **12**: 60–65. doi:10.1034/j.1600-0633.2003.00006.x.
- SAS Institute Inc. 2004. SAS/STAT user's guide, release 9.1. SAS Institute Inc., Cary, N.C.
- Schowalter, T.D. 2000. Insect ecology: an ecosystem approach. Academic Press, San Diego, Calif.
- Schowalter, T.D., and Lowman, M.D. 1999. Forest herbivory by insects. *In* Ecosystems of the world: ecosystems of disturbed

- ground. *Edited by* L.R. Walker. Elsevier, Amsterdam, Netherlands. pp. 269–285.
- Small, M.J., Small, C.J., and Dreyer, G.D. 2005. Changes in a hemlock-dominated forest following woolly adelgid infestation in southern New England. *J. Torrey Bot. Soc.* **132**: 458–470. doi:10.3159/1095-5674(2005)132[458:CIAHFF]2.0.CO;2.
- Smith, D.M. 1986. *The practice of silviculture*. John Wiley & Sons, New York.
- Smith, W.D., and Sheffield, R.S. 2000. A brief overview of the forest resources of the United States, 1997. USDA Forest Service Forest Inventory and Analysis, Washington, D.C., and Asheville, N.C.
- Snyder, C.D., Young, J.A., Lemarié, D.P., and Smith, D.R. 2002. Influence of eastern hemlock (*Tsuga canadensis*) forests on aquatic invertebrate assemblages in headwater streams. *Can. J. Fish. Aquat. Sci.* **59**: 262–275. doi:10.1139/f02-003.
- Souto, D., Luther, T., and Chianese, B. 1996. Past and current status of HWA in eastern and Carolina hemlock stands. *In* Proceedings of the First Hemlock Woolly Adelgid Review, Charlottesville, Va., 12 October 1995. *Edited by* S.M. Salom, T.C. Tignor, and R.C. Reardon. USDA Forest Service, Morgantown, W.Va. pp. 9–15.
- Stadler, B., Müller, T., Orwig, D.A., and Cobb, R.C. 2005. Hemlock woolly adelgid: canopy impacts transforming ecosystem processes and landscapes in New England forests. *Ecosystems* (N.Y. Print), **8**: 233–247. doi:10.1007/s10021-003-0092-5.
- Stadler, B., Muller, T., and Orwig, D. 2006. The ecology of energy and nutrient fluxes in hemlock forests invaded by the hemlock woolly adelgid. *Ecology*, **87**: 1792–1804. doi:10.1890/0012-9658(2006)87[1792:TEOEAN]2.0.CO;2. PMID:16922328.
- Strayer, D.L., Eviner, V.T., Jeschke, J.M., and Pace, M.L. 2006. Understanding the long-term effects of species invasions. *Trends Ecol. Evol.* **21**: 645–651. doi:10.1016/j.tree.2006.07.007. PMID:16859805.
- Swank, W.T., Waide, J.B., Crossley, D.A., Jr., and Todd, R.L. 1981. Insect defoliation enhances nitrate export from forest ecosystems. *Oecologia* (Berl.), **51**: 297–299. doi:10.1007/BF00540897.
- Tingley, M.W., Orwig, D.A., Motzkin, G., Foster, D.R., and Field, R. 2002. Avian response to removal of a forest dominant: consequences of hemlock woolly adelgid infestations. *J. Biogeogr.* **29**: 1505–1516. doi:10.1046/j.1365-2699.2002.00789.x.
- Vitousek, P.M. 1986. Biological invasions and ecosystem properties: can species make a difference? *In* Ecology of biological invasions of North America and Hawaii. *Edited by* H.A. Mooney and J.A. Drake. Springer-Verlag, New York.
- Vitousek, P.M., and Reiners, W.A. 1975. Ecosystem succession and nutrient retention: a hypothesis. *Bioscience*, **25**: 376–381. doi:10.2307/1297148.
- Yamasaki, M., DeGraaf, W.B., and Lanier, J.W. 2000. Wildlife habitat associations in Eastern Hemlock – birds, smaller mammals and forest carnivores. *In* Proceedings: Symposium on Sustainable Management of Hemlock Ecosystems in Eastern North America, Durham, N.H., 22–24 June 1999. *Edited by* K.A. McManus, K.S. Shields, and D.R. Souto. USDA Gen. Tech. Rep. 267. pp. 135–143.
- Yorks, T.E., Jenkins, J.C., Leopold, D.J., Raynal, D.J., and Orwig, D.A. 2000. Influences of eastern hemlock mortality on nutrient cycling. *In* Proceedings: Symposium on Sustainable Management of Hemlock Ecosystems in Eastern North America, Durham, N.H., 22–24 June 1999. *Edited by* K.A. McManus, K.S. Shields, and D.R. Souto. USDA Gen. Tech. Rep. 267. pp. 126–133.
- 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.