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Hemlock Woolly Adelgid in New England Forests: Canopy Impacts Transforming Ecosystem Processes and Landscapes

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ABSTRACT

Exotic insect pests may strongly disrupt forest ecosystems and trigger major shifts in nutrient cycling, structure, and composition. We examined the relationship between these diverse effects for the hemlock woolly adelgid (HWA, *Adelges tsugae* Annand) in New England forests by studying its impacts on local canopy processes in stands differing in infestation levels and linking these impacts to shifts in canopy nutrient cycling and stand and landscape effects. HWA initiated major changes in canopy biomass and distribution. Whereas uninfested trees exhibit a significant decline in canopy biomass from the center to the periphery and a positive correlation between total needle litter and estimated biomass, infested trees have significantly less total canopy biomass, produce less new foliage, shed relatively more needles, and exhibit no correlation between litter and canopy biomass. Foliar N content of infested trees was 20%–40% higher than reference trees, with the strongest increase in young foliage supporting the highest densities of HWA. Foliar %C was unaffected by HWA or foliar age. Epiphytic microorganisms on hemlock needles exhibited little variation in abundance within canopies, but colony-forming units of bacteria, yeast, and filamentous fungi were 2–3 orders of magnitude more abundant on medium and heavily infested than uninfested trees. Throughfall chemistry, quantity, and spatial pattern were strongly altered by HWA. Throughfall exhibits a strong gradient beneath uninfested trees, decreasing in volumes from the canopy periphery to the trunk by more than 45%. The amount of throughfall beneath infested trees exhibits no spatial pattern, reaches 80%–90% of the bulk precipitation, and is characterized by significantly higher concentrations of nitrogen compounds, dissolved organic carbon, and cations. Across the southern New England landscape there is a strong south-to-north gradient of decreasing hemlock tree and sapling mortality and understory compositional change that corresponds to the duration of infestation. Regionally, black birch (*Betula lenta* L.) is profiting most from hemlock decline by significantly increasing in density and cover. These findings suggest that it is necessary to study the connections between fast/small-scale processes such as changes in nutrient cycling in tree canopies and slow/integrative processes like shifts in biogeochemieal cycling and compositional changes at forest stands and landscapes to better understand the effects of an exotic pest species like HWA on forest ecosystem structure and function.

Key words: hemlock woolly adelgid; litter; throughfall chemistry; carbon–nitrogen dynamics; forest ecosystems; forest pests.

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INTRODUCTION

The arrival of exotic species in novel environments may severely impact other organisms and ecosystem. Introduced species may develop into major forest pests resulting in extensive environmental and economic damage (Liebhold and others 1995). The most visible direct effects of these pests, including destructive feeding, foliar damage, reduced tree vitality, and widespread mortality, have been studied in numerous contexts (for example, Schowalter and others 1986; Day and Leather 1997; Wilcove and others 1998). Less well understood, however, are the effects of introduced species on local trophic interactions that have been shown to cascade through the system and alter ecosystem processes at local to landscape scales (Seastedt and Crossley 1984; Grimm 1995; Schulze 1995; Schowalter 2000; Crooks 2002). Because these trophic effects have structural and microenvironmental impact to yield the resulting ecosystem effects of the infestation, failure to understand the ways in which insects directly alter canopy structure, leaf chemistry, production, and communities of epiphytic microorganisms may result in an incomplete understanding of pest impacts.

Studies on phytophagous insects, including aphids and lepidoptera larvae, indicate that pests may exert pronounced effects on the abundance and composition of epiphytic microorganisms (Stadler and Müller 1996) and may substantially alter nutrient flows from tree canopies to the forest floor and soil (Stadler and Michalzik 1998; Stadler and others 1998; 2001a). For example, the trophic interactions between honeydew excreted by aphids and communities of bacteria, yeasts, and filamentous fungi significantly decrease the concentrations of inorganic nitrogen (NH_4–N, NO_3N) and increase organic carbon (DOC) and organic nitrogen (DON) concentrations in canopy throughfall (Stadler and others 1998). Inspite of these limited advances, little is known concerning the spatial and temporal variability of these trophic links between phytophagous insects and microorganisms and their ultimate impact on energy and nutrient fluxes within the canopy of trees. However, these inconspicuous consequences of invasive pest behavior could have profound implications for forest and landscape structure and function.

The hemlock woolly adelgid (HWA, *Adelges tsugae* Annand) was introduced from Asia to North America in the 1920s and into the eastern United States in the 1950s where it occurs mainly on eastern hemlock (*Tsuga canadensis* L.) (Souto and others 1996). The ecology of this exotic species in its new environment is well documented (McClure 1989a, 1991; McClure and Cheah 1999, 2002). Its life cycle includes two annual generations with large temporal overlap among all life stages. Adults of the overwintering generation deposit eggs into wax-rich woolly egg sacks from late February to March/April. Hatching commences in April and first instar nymphs (crawlers) begin searching for suitable sites on their host tree or through dispersal by wind, birds, or human activity (McClure 1989b). Two phenotypes occur in this generation. The wingless progrediens initiate a second generation on hemlock, whereas winged sexupare leave hemlock searching for secondary spruce (*Piceae*) hosts but die in eastern North America due to a lack of suitable species. Adult progrediens lay their eggs soon after reaching maturity in June, and hatching nymphs enter an aestival diapause that lasts until October. This second generation feeds and develops through late autumn and matures in late February (McClure and Cheah 1999).

Trees of any age or size can be heavily infested and damaged by HWA, resulting in progressive decline in vitality and eventual mortality within 5–15 years (Orwig and Foster 1998). HWA is currently reported in 15 states in the eastern United States and is spreading about 15–30 km/y (http:/www.fs.fed.us/na/morgantown/fhp/hwa/hwasite.html). Hemlock decline initiates changes in the microenvironment, including increased light reaching the forest floor and higher soil temperatures, and is associated with accelerated nitrate exports (Jenkins and others 1999). The elimination of hemlock is anticipated to have a strong impact on the composition and structure of eastern North American forests, eventually producing a more homogeneous landscape dominated by broadleaved deciduous species (Orwig and Foster 1998; Orwig and others 2002).

A major challenge to understanding the impact of exotic pests on forest ecosystem structure and function is to integrate information on biotic and abiotic changes and interactions initiated by the pest across ecological scales. In this multidisciplinary study we sought to investigate these linkages and their consequences by examining the effect of HWA on (1) local processes in hemlock canopies, including (a) changes in needle litter production, shoot growth, and C and N content, (b) abundance of epiphytic microorganisms on the needle surfaces, and (c) effects of biotic interactions between HWA and microorganisms on canopy C and N cycling, with consideration of the spatial and temporal dynamics of these processes; and (2) stand to landscape effects related to

HWA-induced structural and biogeochemical changes. Figure 1 provides a conceptual overview of how to navigate through the microbial to landscape effects of HWA. Studies were conducted in hemlock stands varying in extent and duration of infestation across a regional transect in southern New England.

MATERIAL AND METHODS

Experimental Sites

Devil's Hopyard State Park (DH) and Selden Neck Preserve (SN) are located in south-central Connecticut within the Windham Hills section of the Eastern Uplands (Bell 1985). The sites experience a humid, continental climate with long, cool winters and short, mild summers (Hill and others 1980). Elevations range from 45 to 60 m a.s.l and soils are predominantly sandy loams formed from weathered gneiss, schist, and granite (Reynolds 1979; Crouch 1983). The region is located at the southern limits of the Central Hardwoods–Hemlock–White Pine vegetation type and the northern extent of the Central Hardwoods–Hemlock type described by Westveld and others (1956). Both sites have been infested with HWA for over 10 years (Orwig and Foster 1998; Bonneau and others 1999). Average HWA infestation on shoots of the previous year was 5–10 egg masses at DH classified below as medium infested site) and 15–25 egg masses at SN (heavily infested site) at the beginning of the experiment. The uninfested reference site was a section of the Prospect Hill (PH) tract of the Harvard Forest, located in north-central Massachusetts at an elevation of 335 m a.s.l. Soils are predominantly acidic, sandy loams that developed in glacial till overlying gneiss and schist. Vegetation is typical of the Transition Hardwoods–White Pine–Hemlock region (Westveld and others 1956).

Canopy Biomass and Shoot Growth

At each of the three sites, four trees were chosen that were approximately 6 m tall and not overtopped by other trees. To estimate biomass above a throughfall sampler (for details see below), a digital photographic image was taken above each funnel at the beginning of the experiment. The central 30% of the image was converted to black and white pixels and analyzed using the Image Tool program (University of Texas Health Science Center at San Antonio, Texas; available at ftp://maxrad6.uthscsa.edu). The number of black pixels provides a standardized (relative) measure of tree canopy biomass above each throughfall sampler. A constant threshold value of 200 was used in the program to convert the images into black and white pixels. Note that such a value is arbitrary for setting the conversion algorithm. However, because we were interested in a relative comparison rather than absolute estimates of canopy biomass in relation to different degrees of infestation, applying the same procedure to every image provides a useful basis for comparing the effects of HWA on canopy biomass. We used only the central part of an image, rather than spherical canopy pictures, because we seek to estimate the biomass of those parts of the crown that most likely affect a particular throughfall sampler. This method is likely to overestimate the absolute biomass of infested canopies because multiple layers of needles are poorly distinguished. However, a broad index is appropriate for the processes addressed in this study, and other approaches like the diffuse light penetration method are generally no more accurate or reliable (Lovett and others 1996) because a number of variables like cloud cover, vertical position of the digital device, or conversion algorithms can profoundly affect the results.

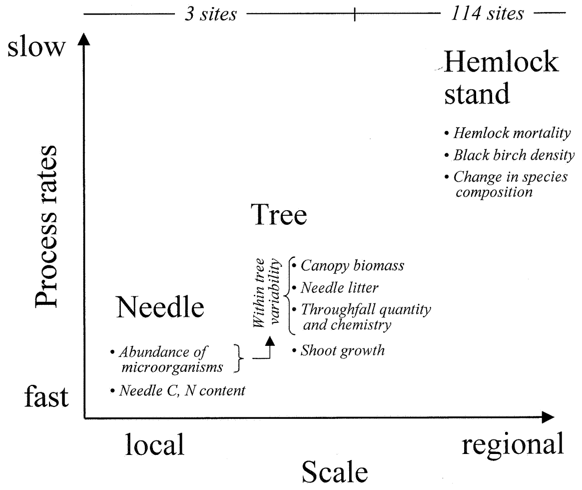

Figure 1. Conceptual overview of the approach used in this study with experiments comprising the scale of needles to the scale of hemlock stands on a north–south gradient from central Massachusetts to southern Connecticut. The time frame of the relevant processes comprises days to weeks at the scale of needles and tree individuals to years at the stand level.

Growth of newly developing shoots was estimated by measuring the length of 20 second-order shoots on each of four trees at each site. Growth was measured at breast height in the periphery of the trees following the aspect to which the samplers were pointing. Measurements were made biweekly at the same time, when throughfall was sampled.

Sampling of Hemlock Shoots to Determine Microbial and HWA Abundance and Foliar N

At three sampling dates (May 22, July 1, and August 31, 2002) shoots were sampled for microbial analysis. These dates cover the different activity periods within the life cycle of HWA: the growth of the first generation from early spring to early summer, the summer aestivation, and the growth of the second generation following the termination of diapause. Four shoots with needle age classes ranging from 0 to 3 y were cut with sterile scissors, transferred into a sterile Stomacher bag, stored in a cooler, and transported to the laboratory where they were frozen until microbial analyses could be completed. The sampled shoots were taken from the lower canopy offset from the throughfall samplers (that is., close to the trunk, close to the canopy periphery, and in between these locations). Shoots and canopy biomass directly above the samplers were kept intact.

To determine HWA infestation intensity and C and N content of needles, an additional three branches were cut from the periphery of each tree during sampling for foliar microbes and were returned to the laboratory on ice. Needles from six randomly selected shoots were detached and processed for C and N analysis and the number of HWA egg masses on the previous year's shoot was counted.

To get a rough estimate on the total number of egg masses in the canopy of medium and heavily infested trees, we counted the number of one-year-old shoots on an entire branch near the base of the tree, multiplied this number by the number of branches on the tree, and then multiplied this number by the average number of egg masses per shoot. Branches at the base develop most new shoots mainly at the periphery and the addition of new growth appears to be similar on branches higher up in the canopy. HWA is fairly evenly distributed in the canopy of hemlock, probably due to crawler dispersal (McClure and others 2001).

Microbiological Analyses

Needles of hemlock were carefully dislodged from the twigs. Three grams of each sample of green needles (all age classes pooled) from the twigs were blended for 2 minutes in 145 mL sterile distilled water using a Stomacher lab blender. Leaf washings were logarithmically diluted in 1/4-strength Ringer's solution and spread-plated onto 1/10-strength Tryptic soy agar (Merck; pH 7.2), supplemented with 0.4 g L^{-1} cycloheximide (Merck), to enumerate the numbers of aerobic heterotrophic bacteria in the sample. Yeasts and filamentous fungi were grown on a Sabouraud-1% dextrose-1% maltose agar (Merck; pH 5.5), to which 0.4 g L^{-1} chloramphenicol (Berlin-Chemie) was added to suppress bacterial growth. All plates were incubated at 25°C for 5 days. Results were expressed as colony forming units (CFU) per gram of needle dry matter.

Throughfall Sampling and Needle Litter Collection

At each site three throughfall samplers were placed beneath each tree, one close to the trunk, one at the periphery, and one midway to capture throughfall across the canopy spatial gradient. Each throughfall sampler covered 162.86 cm^2 and remained in place through the entire experiment. Samplers usually faced to the southwest. The neck of the throughfall funnels was plugged with a nylon filter to prevent the entry of debris and insects, and bottles were wrapped in aluminum foil to protect against light and heat. It is possible that energy-driven microbial reactions within the rain samplers occurred but previous experiments gave no indication that the concentrations of organic and mineral nitrogen was significantly influenced by microbes washed into the throughfall samplers, even when much longer sampling intervals than those used here were used (Michalzik and others 1997). In addition, a relative comparison of throughfall concentrations collected beneath infested and uninfested trees is still valid. At each sampling date the bottles and funnel plugs were replaced with clean ones and the number of hemlock needles in the funnels was counted. Throughfall was collected every two weeks, from May 20 to August 31. In early July the sampling period was three weeks due to low amounts of precipitation. A single rain sampler was installed at each site to collect bulk precipitation for chemical analysis. Precipitation data for each area were also obtained from meteorological stations at Harvard Forest, MA, New Haven, CT, and Middletown, CT.

Chemical Analyses of Throughfall, Nitrogen Content of Needles, and Egg Masses

All throughfall samples were immediately filtered through a 0.45-µm cellulose acetate membrane and frozen until analysis. Dissolved organic carbon (DOC) was determined as CO_2 after persulfate–UV oxidation (Foss Heraeus, Liquid TOC). Ammonium-N (NH_4-N) and nitrate-N (NO_3-N) were measured by ion chromatography (Dionex, Idstein, 2000i-SP). Dissolved organic nitrogen (DON) was calculated from the following relationship: DON = N_{total} − (NH_4–N + NO_3–N). Total nitrogen (N_{total}) was measured as NO_x after thermo oxidation at 700°C (Abimed: TN-05).

To determine the nitrogen content of needles on infested/uninfested shoots and egg mass biomass, needles and egg masses were detached with tweezers and composited for each shoot. In total, 85 needle samples and 32 egg mass samples were analyzed. Foliage and egg masses were dried at 50° C for 48 hours. Foliar material was then ground to pass through a 20–μm screen. Egg sack mass was determined with a fine-scale balance accurate to 0.001 mg. Total C and N content was determined with a Fisons dry combustion CHN autoanalyzer (Milano, Italy). Approximately 20% of foliar samples were analyzed in duplicate.

Change in Stand Structure Due to HWA Infestation

As part of a large study examining landscape patterns of hemlock decline in Connecticut (Orwig and others 2002), 114 hemlock stands were quantitatively sampled for intensity of HWA infestation and stand and site characteristics. Stands were delineated from 1:80,000 scale black and white photographs and were randomly selected across the study region. Overstory and understory vegetation was sampled in one fixed-area (20 × 20 m) plot in a representative portion of each stand. AH trees [stems ≥ 8 cm diameter breast height (dbh)] were tallied by species and dbh and assigned a canopy position based on a visual estimation of the amount of intercepted light received by the tree crown (Smith 1986). Hemlocks that died within the previous 2–4 years, which was determined by extensive retention of fine twigs in the crown, were tallied to determine species composition prior to HWA infestation.

All saplings (<8 cm dbh and >1.4 m tall) were tallied by species. The percent cover of each herb, shrub, and woody seedling species was estimated in each plot using a modified Braun–Blanquet scale (Mueller–Dombois and Ellenberg 1974). Nomenclature follows Gleason and Cronquist (1991).

Data Analyses

Throughfall fluxes were converted to mg m^{-2} 15 $weeks^{-1}$. Because the sites received different amounts of rainfall, it was not useful to compare total fluxes between sites. Instead we restricted the analysis fluxes to the variability *within* the canopies of trees showing different levels of infestation. We used regression analysis to investigate the relationship between the amount of throughfall and the concentrations of specific compounds. In addition, we compared the results of the reference sites with those of the infested sites using GLM analysis of covariance (ANCOVA), with rain volume and infestation as main effects and the index of biomass as a covariable, testing for significant interactions between volume and infestation. The analysis was restricted to throughfall lower than 40 mm per sampling period to account for only the linear part of the relationship between these two variables. Differences in CFUs of microorganisms were tested with one-way analyses of variance (ANOVA) using Bonferroni correction.

Foliar chemistry was analyzed with a two-way repeated–measures ANOVA using infestation and needle age as the main effects. To determine the effects of infestation for any single foliar sampling, we employed a one-way ANOVA with site (infestation level) as the main effect. Recovery of two–year–old needles was inconsistent on infested trees resulting in poor replication for this age class and exclusion from statistical analysis Repeated–measures ANOVAs were also used to test for differences in the spatial variability of litterfall, amount of throughfall, and throughfall fluxes within trees. For the analyses the normality, assumptions of the data were checked and log $x + 1$ transformed when necessary to normalize variances across treatments.

To assess the relative importance of environmental and stand variables in controlling understory vegetation dynamics, we utilized Mantel tests (Mantel 1967; Manly 1997a), which include space (that is, geographic location) as a predictor variable in the analysis. This technique performs a linear regression on distance matrices generated from dependent variables (birch sapling density, birch seedling cover, total understory species richness and herbaceous species richness) and predictor variables (space, latitude, slope, aspect, elevation, and stand size). Prior to analysis, aspect values were transformed from circular variables to a measure relevant to vegetation as aspect = cosin (45 − azimuth degrees) + 1 (Beers and others 1996). Values range from 0 on southwestern slopes commonly exposed to the sun to 2 on the least exposed northeastern slopes. In addition, latitude and longitude were converted to distance measures with the same units (that is, km from the equator or prime meridian, respectively).

The Mantel coefficient of a variable versus location is a measure of the spatial autocorrelation of that variable; a positive value indicates that points close together geographically tend to have similar values and a negative value indicates that points close together tend to have dissimilar values. If there is no spatial autocorrelation, then the value of the observed *r* should not be statistically different from zero. Partial Mantel coefficients were also calculated (for example, birch seedling cover versus elevation controlling for location) to assess the relative contributions of various factors influencing the analysis. Mantel test coefficients and significance levels were calculated with Manly's RT randomization program (Manly 1997b), with 1000 randomizations for each test.

RESULTS

Canopy Biomass, Adelgid Infestation, Egg Mass Biomass, and Shoot Growth

The index for estimated biomass above fhroughfall samplers showed a significant decline from the trunk to the periphery for the uninfested trees ($F_{2,11}$ = 31.674, $P < 0.001$). In contrast, the medium ($F_{2,11}$ = 0.423, $P = 0.668$) and heavily infested ($F_{2,11}$ = 0.690, $P = 0.526$) trees showed no decline as a result of patchy needle loss throughout the canopy (Figure 2a). Overall, biomass in heavily infested trees was significantly lower than in medium infested and uninfested trees ($F_{2,35}$ = 14.903, $P < 0.001$). The estimated number of one-year-old shoots was 139,680 on uninfested trees, 70,920 on medium infested trees, and 24,140 on heavily infested trees. Average shoot density of egg masses was 14.4 ± 2.6 on medium infested and 20.5 ± 10.6 on heavily infested trees. The average dry mass of an egg mass was 0.48 ± 0.04 mg, leading to an estimated total egg mass of 490.2 g on medium infested and 237.5 g on heavily infested trees. Thus, the total egg mass biomass on medium infested trees was approximately 2 times higher than on heavily infested trees despite the fact that the density per shoot was lower.

Elongation of newly developing second-order shoots of hemlock followed a sigmoid growth curve for the uninfested and medium infested trees, peaking at approximately 5 cm in early July (Figure 2b). Heavily infested trees grew much slower and their second-order shoots reached,a maximum length of only 2 cm in early August, presumably due to substantial energy drain by the adelgids.

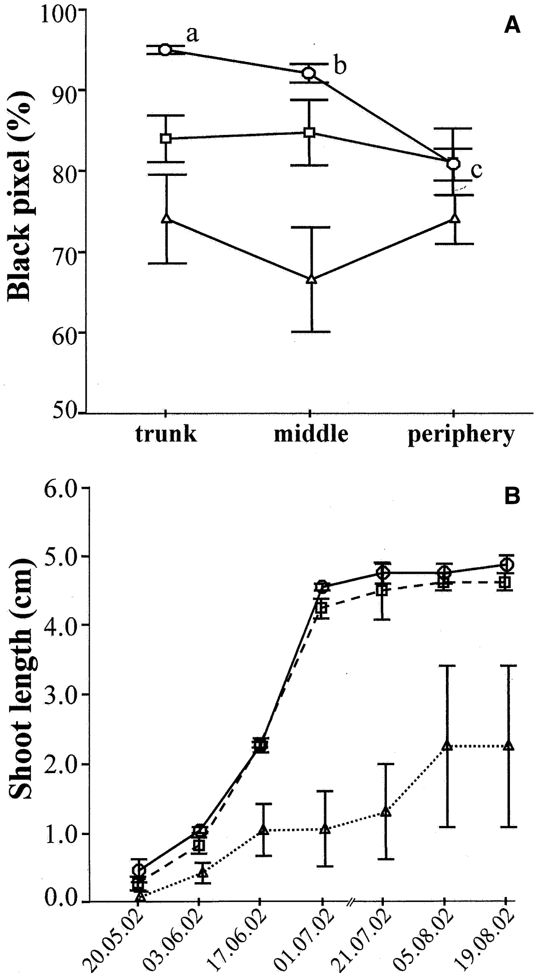

Figure 2. **a** Within canopy index of biomass estimated as the proportion of black pixels in a digital picture taken directly above the throughfall samplers, separated for different positions and levels of HWA infestation (mean ± 1 SE). Different letters indicate significant differences in this biomass index along a vertical gradient within a hemlock tree. (○) Reference, (□) medium infested trees, (△) heavily infested trees, **b** Cumulative growth of second-order shoot of uninfested (continuous line), medium infested (dashed line), and heavily infested trees (dotted line).

Needle Litter, Needle C and N Content, and Abundance of Epiphytic Microorgnisms

The total number of needles collected in the throughfall funnels over the 15-week period showed a significant positive relationship with the biomass index for the reference trees (r_p = 559, $P = 0.029$, $n = 12$), but not so for the medium and heavily infested trees (medium: $r_p = 0.418$, $P = 0.088$, $n = 12$; heavily: $r_p = 0.017$ $P = 0.479$, $n = 12$) *(*Figure 3). This suggests that the biomass in

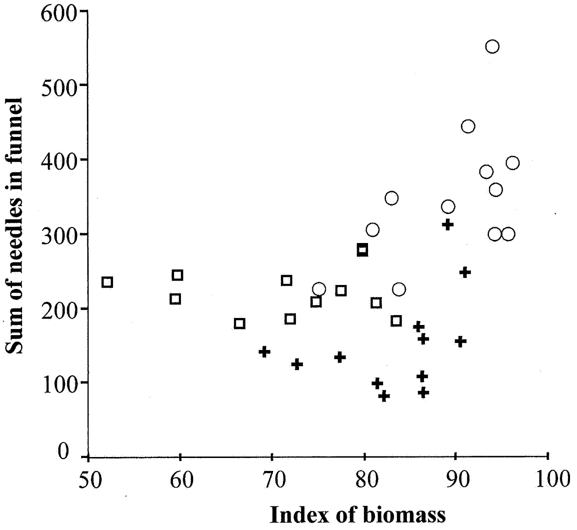

Figure 3. Relationship between the biomass index and the total number of needles collected in the throughfall funnels beneath a tree during the complete experimental period (mean ± 1 SE). (○) uninfested; (+) medium infested; (□) heavily infested. Only reference trees had a significant relationship between these variables.

infested tree canopies is largely wood. The highest number and dry mass of needles was shed from reference trees (149.1 g/m^2), followed by heavily infested (94.6 g/m^2) and medium infested trees (63.9 g/m^2; Table 1). Thus, in spite of their relatively low needle biomass, heavily infested trees shed relatively large quantities of needles. Spatial variability in needles falling to the ground was relatively small, especially beneath infested trees (PH: $F_{2,12} = 1.591$, $P = 0.256$; DH: $F_{2,11} = 0.790$, $P = 0.483$; SN: $F_{2,12} = 0.252$, $P = 0.783$) (Table 1), whereas seasonal variability in needle fall was high, especially from uninfested trees (data not shown).

In May and July, foliar nitrogen was significantly higher at sites infested by HWA (Table 2), with the highest levels usually found at Selden Neck, the heavily infested study site. Needle age class also had a strong effect on foliar N levels ($F_{2,76} = 45.5$, $P < 0.001$). Nitrogen content varied among foliage age classes: current year > one-year-old foliage > two-year-old foliage. Foliar N differences between infested and uninfested trees also declined through the growing season. Foliar carbon content showed little response to different degrees of infestation. Foliar C increased over the course of the growing season ($F_{2,76} = 45.5$, $P < 0.001$) all sites and for all age classes (Table 2). Needle age class did not significantly affect foliar C ($F_{2,76} = 0.01$, $P = 0.920$).

The growth of epiphytic microorganisms followed a consistent pattern and therefore we present data for one sampling date only (1 July 2002). In all cases microorganisms in all groups (bacteria, yeasts, and filamentous fungi) living on needles of infested trees thrived significantly better than those on uninfested trees, and microorganisms on heavily infested hemlock produced significantly more CFU than those on medium infested or reference trees (Figure 4). For bacteria on medium infested trees ($F_{2,11} = 7.413$, $P = 0.013$) and for filamentous fungi on reference trees ($F_{2,11} = 6.942$, $P = 0.015$), there was a statistically significant difference between the number of microorganisms collected close to the trunk versus the middle and periphery of the canopy. Otherwise there was no spatial gradient in microorganism abundance. Overall, within tree canopies microbes on heavily infested trees displayed less variability in abundance across the canopy gradient than those on medium and uninfested trees, perhaps due to the homogeneous canopy structure of damaged trees.

Throughfall Quantity and Chemistry

Amounts of bulk precipitation and throughfall varied considerably among the three sites (Figure 5), as most precipitation resulted from thunderstorms. There was strong spatial variation in throughfall amounts during all sampling intervals beneath uninfested trees, as higher needle biomass significantly intercepted more rain toward the tree interior (PH: $F_{2,12} = 9.292$, $P = 0.006$). Little spatial variability (DH: $F_{2,12} = 1.052$, $P = 0.389$; SN: $F_{2,12} = 0.454$, $P = 0.649$) and greater total amounts of throughfall were recorded beneath infested trees (Table 1).

Total bulk precipitation was 311 mm at Harvard Forest, 262 mm at Devil's Hopyard, and 206 mm at Selden Neck. Because of the differences in precipitation a direct comparison of fluxes is not suitable for particular sampling intervals. Instead, GLM ANCOVA was used to compare the slopes of the regression lines for different infestation levels and for comparable ranges of precipitation. For example, 72.5% of all samples had less than 40 mm of throughfall solution. The concentrations of ammonium nitrogen were not significantly different beneath trees showing different degrees of infestation (no significant interaction between throughfall infestation) (Figure 6a and Table 3). In contrast, nitrate nitrogen, total nitrogen, and dissolved organic nitrogen concentrations were significantly higher in throughfall solutions from infested compared to uninfested trees (significant throughfall × infestation interaction) (Figure 6b–d and Table 3). For NO_3–N, however, higher concentrations were found only beneath medium

Table 1. Averaged Total Number of Needles and Throughfall (mm) Collected Beneath Hemlock Trees at Different Sites during the Complete Sampling Period

	Position	**Prospect Hill (reference site)**		**Devil's** Hopyard (medium infested)		**Selden Neck (heavily infested)**	
Collected needles	**Trunk**	**385**	**37.9%**	**163**	**36.0%**	**218**	**32.6%**
	Middle	355	35.0%	174	38.6%	233	34.9%
	Periphery	275	27.1%	115	25.4%	216	32.5%
Collected throughfall	Trunk	131.6	42.3%	207.9	79.3%	162.0	78.8%
	Middle	202.3	65.0%	211.5	80.7%	159.3	77.5%
	Periphery	287.8	92.5%	235.7	89.9%	178.4	86.7%

Values are means from four trees at each site per sampling date subsequently summed over the seven sampling intervals, Sampling area for needle litter and throughfall was 163 cm^2 beneath each tree and for each position. Percentages of throughfall refer to the collected volumes relative to the bulk precipitation at the respective sites (PH: 311.2 mm, DH: 262.1 mm, SN: 205.7 mm).

Table 2. Eastern Hemlock Foliar % Nitrogen (N) and % Carbon (C) at Sites with Different Levels of HWA Infestation

	Foliar %N			**Foliar %C**		
Site	**May**	**July**	**August**	**May**	**July**	**August**
Current year						
Prospect Hill	1.93 (0.01) a	1.48 (0.11) a	1.65 (0.02)	48.0 (0.1)	50.0 (0.2)	50.0 (0.1)
Devil's Hopyard	2.65 (0.13) b	1.93 (0.06) b	2.27 (0.37)	48.4 (0.1)	49.0 (0.1)	50.2 (0.2)
Selden Neck	2.76 (0.07) b	2.20 (0.14) b	1.88 (0.18)	48.5 (0.2)	49.0 (0.2)	50.2 (0.2)
One year old						
Prospect Hill	1.04 (0.04) a	1.10 (0.04) a	1.17 (0.04)	48.3 (0.4)	49.9 (0.2) ab	50.4 (0.1)
Devil's Hopyard	1.40 (0.05) b	1.40 (0.02) b	1.73 (0.30)	47.1 (0.4)	50.6 (0.2) b	51.4 (0.8)
Selden Neck	1.74 (0.10) c	1.64 (0.07) c	1.66 (0.12)	47.7 (0.2)	49.2 (0.2) a	50.0 (0.3)
Two year old						
Prospect Hill	0.93 (0.00)	0.93 (0.07)	1.03 (0.07)	48.2 (0.1)	48.0 (1.3)	49.5 (1.5)
Devil's Hopyard	nm[a]	1.16 (0.01)	0.98 (0.24)	nm[a]	51.1 (1.1)	50.9 (0.4)
Selden Neck	1.25 (0.08)	1.40 (0.10)	1.14 (0.18)	47.1 (0.2)	48.9 (1.5)	50.0 (0.3)

[a]nm = age class not measured. Data are means from four trees per site with one standard error in parenthesis. Different letters indicate statistically significant differences between trees with different levels of HWA infestation (ANOVA, Bonferroni multiple comparison, P < 0.05), Prospect Hill, uninfested; Devil's Hopyard, medium infested; Selden Neck, heavily infested. The two-year-old age class was not included in statistical analysis due to poor recovery at infested sites (see text).

infested trees. Concentrations of DOC, K, and Mn were also higher in throughfall beneath infested trees and had significant interactions with throughfall volume (Figure 7a–c and Table 3). There was no significant correlation between throughfall volumes and DOC concentrations for the medium infested sites ($r_p = 0.237$, $P = 0.081$, $n = 55$, 2-sided), indicating an increasing supply of DOC with increasing precipitation. Only Mg concentrations were not significantly different beneath infested and uninfested trees (Figure 7d). This implies that for a particular amount of throughfall higher quantities of most compounds are reaching the forest floor beneath infested trees. Rain water concentrations were on average 0.97 mg/L for total nitrogen and 4.12 mg/L for DOC and differed little among sites.

Over the complete sampling period, strong declines in organic carbon and organic nitrogen fluxes were observed from the trunk to the periphery beneath medium infested trees (DOC: $F_{2,12} = 0.912$, $P = 0.003$; DON: ($F_{2,12} = 2.104$, $P = 0.001$), but not beneath heavily infested (DOC: $F_{2,12} = 0.342$, $P = 0.719$; DON: $F_{2,12} = 0.861$, $P = 0.455$) and uninfested (DOC: $F_{2,12} = 0.209$, $P = 0.816$; DON: $F_{2,12} = 0.208$, $P = 0.816$) trees (Table 4). Total nitrogen fluxes did not differ with the position beneath a tree. The consistency in the total fluxes of DOC, DON, and N_{total} from different parts of the canopy of uninfested trees results from high nutrient concentrations but low throughfall volumes observed near the center of trees, whereas in the periphery the contrary was true (see Figure 5). Despite the fact that infested trees had a lower

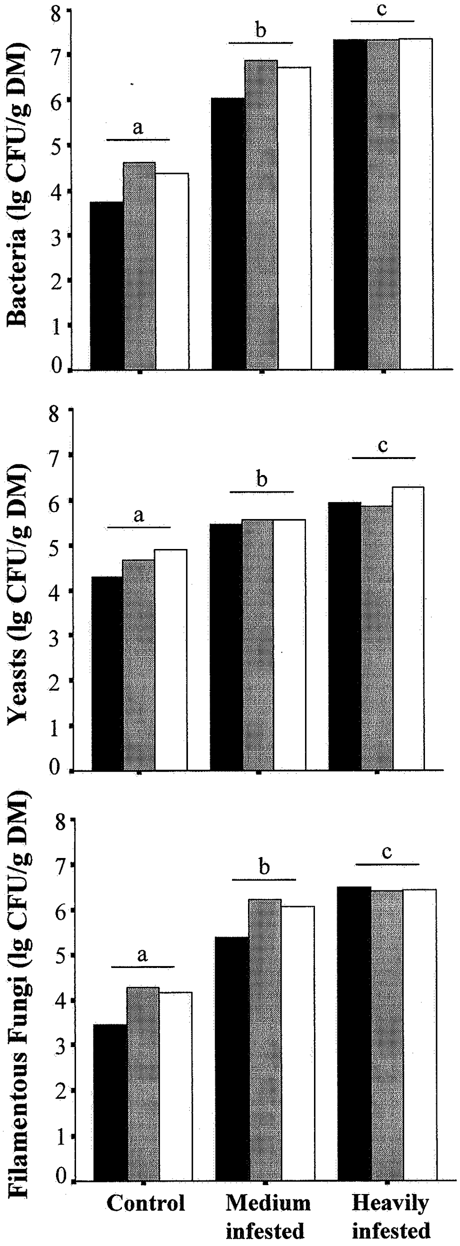

Figure 4. Number of colony forming units (CFUs) of epiphytic bacteria, yeasts, and filamentous fungi per gram needle dry mass (DM) separated for different degrees of infestation. Only data for one sampling date are shown (1 July 2002) because the results were consistent with those taken in early July and late August. Different letters indicate significant differences in CFUs on needles of trees with different levels of infestation (ANOVA, Bonferroni multiple comparison, $P \leq 0.05$). Position where samples have been taken: black column = close to the trunk, gray column = middle, open column = periphery.

needle biomass and received 15.8% (medium infested site) and 33.9% (heavily infested site) less rainfall compared to the reference site, total fluxes

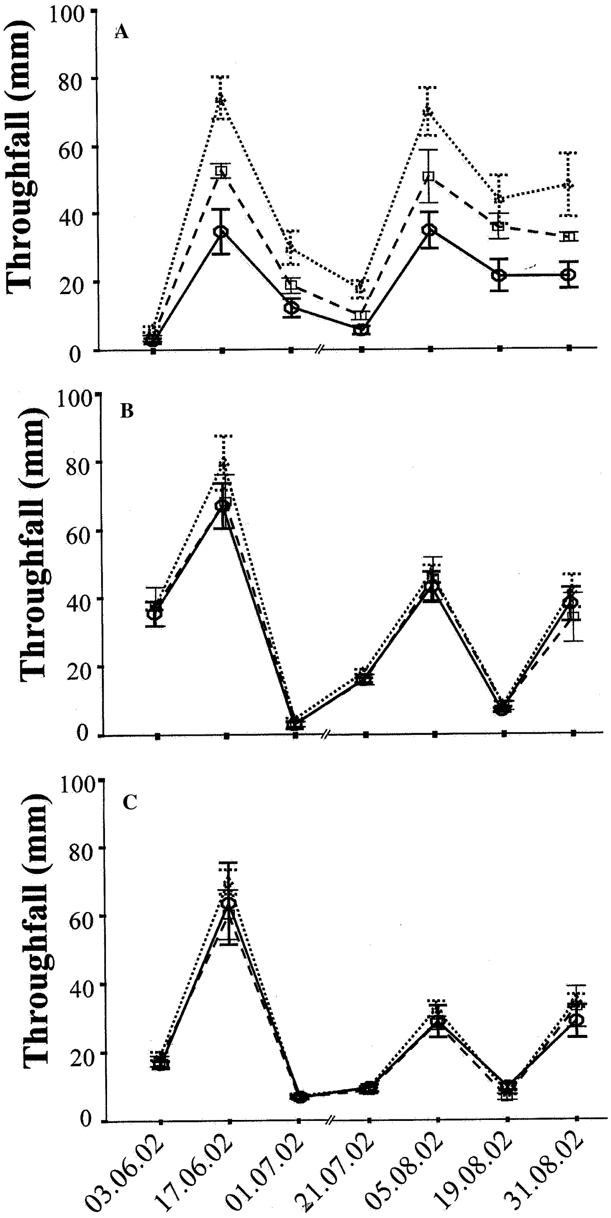

Figure 5. Throughfall (mm) collected at three positions beneath hemlock trees. (**a**) Prospect Hill = uninfested control, (**b**) Devil's Hopyard = medium infested, (**c**) Selden Neck = heavily infested with hemlock woolly adelgid. Position of the throughfall samplers: solid line = trunk, dashed line = middle, dotted line = periphery (mean ± 1 SE).

of DOC increased by 44.4% and 19.6% respectively, these sites (Table 4).

Change in Stand Structure Along a Gradient of Differently Infested Sites

A broad geographic pattern of overstory and understory hemlock mortality was observed across the Connecticut study area, with higher mortality

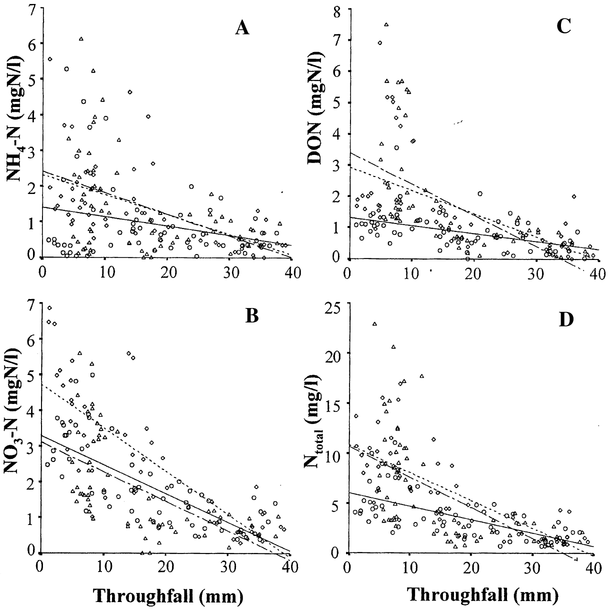

Figure 6. Relationships between different nitrogenous compounds collected in throughfall samplers beneath hemlock trees. The position of the samplers beneath a tree is implicit in the *x*-axes, with lower amounts of throughfall usually collected closer to the trunk, for example, beneath uninfested trees. Data and regression lines were separated for different levels of infestation: (○) uninfested, continuous line; (◇) medium infested, dotted line; (△) heavily infested, dashed line. Only data for throughfall lower than 40 mm per sampling interval were plotted because larger volumes of rainfall usually generated very low concentrations of most compounds.

in southern stands (Figure 8a and b). The most abundant understory species was black birch (*Betula lenta* L.) (Figure 8c), although red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.), black cherry (*Prunus serotma* Ehrh.), and red oak (*Quercus rubra* L.) were common at low cover. Understory cover, herbaceous species richness, and birch sapling cover and abundance exhibited no significant spatial autocorrelation and were not significantly correlated with latitude, slope, elevation, or aspect. Birch abundance was highest in the south, where 8 stands had sapling densities exceeding 200 ha^{-1}, and 14 stands had 10% or greater seedling cover (Figure 8d). Birch seedling cover was significantly correlated ($r = 0.227$, $P = 0.038$) with stand size, even when other variables were controlled for.

DISCUSSION

The hemlock woolly adelgid is exerting effects on hemlock forest ecosystems in the eastern United

Table 3. GLM ANCOVA for Different Compounds (mg/L) Collected in Throughfall Samplers Beneath Hemlock

	N_{total}			DON			NH_4–N			NO_3–N			DOC			K			Mg			Mn		
Factor	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*
Throughfall volume	1,180	122.02	*<0.001*	1,172	94.89	*<0.001*	1,182	33.05	*<0.001*	1,174	187.08	*<0.001*	1,179	53.12	*<0.001*	1,182	108.77	*<0.001*	1,182	169.10	*<0.001*	1,182	102.45	*<0.001*
Infestation	2,180	13.19	*<0.001*	2,172	13.57	*<0.001*	2,182	2.89	0.058	2,174	13.63	*<0.001*	2,179	11.74	*<0.001*	2,182	14.98	*<0.001*	2,182	10.73	*<0.001*	2,182	31.20	*<0.001*
Interaction	2,180	6.61	*0.002*	2,172	7.84	*0.001*	2,182	1.94	0.146	2,174	4.45	*0.013*	2,179	3.92	*0.022*	2,182	3.06	*0.049*	2,182	2.83	0.062	2,182	48.27	*<0.001*

Throughfall volumes and different degrees of infestation were main factors and the index of biomass was used as covariate. Analyses were restricted to throughfall lower than 40 mm. Significant effects are in italics.

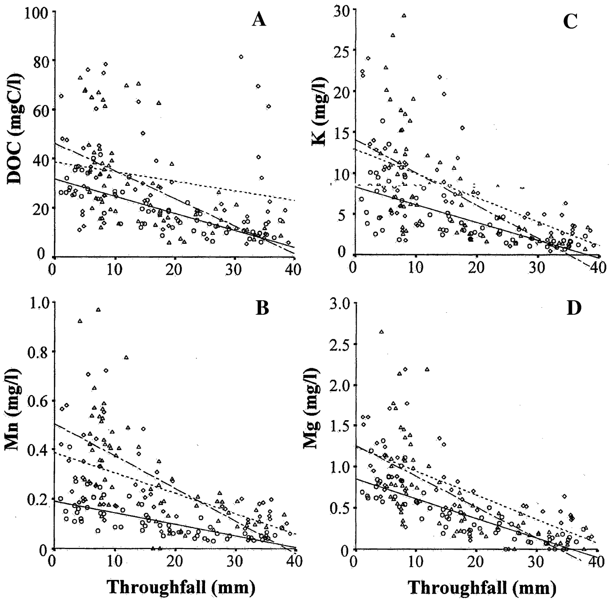

Figure 7. Relationships between dissolved organic carbon (DOC) and different ions with the amount of throughfall collected beneath hemlock trees. Data and regression lines were separated for different levels of infestation/sampling sites: (○) uninfested, continuous line; (◇) medium infested, dotted line; (△) heavily infested, dashed line.

States that equal or exceed those of major lepidopteran pest species. Our results suggest that in addition to the obvious direct damage to hemlock and resulting effects on forest environment, stand structure, and composition, HWA is initiating subtle but important changes in needle development, production, and chemistry that generate significant changes in the abundance of epiphytic microorganisms, which will eventually alter the nature of throughfall chemistry and litter quality. These changes may initiate fundamental transformations in forest biogeochemistry that will generate feedbacks to forest productivity and composition at stand to regional scales. In the following we highlight the sequence of processes from the scale of needles to the scale of landscapes by describing the impact HWA exerts on canopy features, forest environments, and eventually on forest floor characteristics.

Infested trees support lower needle densities and biomass in a more even canopy distribution than in uninfested trees, and they shed relatively more needles. Trees infested with few to medium numbers of adelgids supported fewer current-year shoots than uninfested trees but experienced little or no reduction in shoot growth (Figure 2b). However, heavily infested trees developed little new foliage and often exhibited no new growth, indicating a heavy drain of resources.

Bacteria, yeasts, and filamentous fungi thrived significantly better on medium and especially on heavily infested shoots (Figure 4). Although the actual mechanism of egg sac wax metabolism by these organisms is poorly understood, it is likely that increased exposure to sunlight and rain promotes the breakdown of wax into more readily usable components. Eventually, the volume of the egg mass declines during the course of the season. Contrary to honeydew excreted by aphids in the canopy of trees (Stadler and Michalzik 1998), which is easily washed off from needles and leaves, HWA wax wool seems to be washed out of the canopy at a lower rate, providing a fairly continuous source of energy and a less impulse-driven environment for microbes.

One could argue that many of the small-scale processes reported here are driven by site-specific weather conditions. For example, higher precipitation in central Massachusetts compared to southern Connecticut should be more favorable for microorganismic growth. However, because microbial numbers were highest on infested trees which were exposed to lower amounts of precipitation, the effect of HWA is likely to override potential differences in local abiotic conditions and overall the results presented here may be regarded as conservative.

Throughfall volumes and spatial patterns were strongly disrupted by adelgid infestation. Whereas only 66.6% of bulk precipitation was collected beneath uninfested trees, more than 80% was collected beneath infested trees. Throughfall exhibited a strong spatial gradient beneath reference trees but no spatial variation under infested trees (Figure 5). Greater quantities of nutrient-rich throughfall and reduced uptake of water due to declining vigor and leaf area of the infested trees suggests the potential for significant nutrient loss or leaching from these stands. Currently, however, we are not aware of any studies that quantified the effects of HWA on nutrient export at the catchment scale.

A recent study of soil N cycling in southern Connecticut demonstrated higher N availability and nitrification rates in soils of HWA-infested stands, which were attributed to increased soil temperature and decomposition rates (Jenkins and others 1999). Our study suggests that an additional set of factors may be operative, namely, that the forest floor beneath infested trees receives higher nutrient inputs than uninfested stands. Over the extended period of time during which hemlock trees decline from HWA infestation these inputs

Table 4. Total Fluxes of Dissolved Organic Carbon (DOC), Dissolved Organic Nitrogen (DON), and Total Nitrogen (N_{total}) (mg m^{-2} 15 $weeks^{-1}$) Collected Beneath Hemlock Trees at Different Sites during the Complete Sampling Period (20 May–31 August)

	Position	Prospect Hill (reference site)		Devil's Hopyard (medium infested)		Selden Neck (heavily infested)	
DOC	**Trunk**	**554.5**	**31.7%**	**1296.0**	**41.2%**	**815,9**	**37.5%**
	Middle	624.9	35.7%	1012.4	32.1%	648.0	29.8%
	Periphery	571.9	32.6%	840.0	26.7%	713.3	32.7%
DON	Trunk	24.5	31.4%	52.7	39.5%	52.6	38.7%
	Middle	26.9	34.5%	48.0	36.0%	42.9	31.5%
	Periphery	26.6	34.1%	32.6	24.5%	40.6	29.8%
N_{total}	Trunk	103.4	34.6%	131.9	36.8%	112.1	36.2%
	Middle	102.8	34.3%	124.6	34.7%	101.6	32.8%
	Periphery	93.1	31.1%	102.3	28.5%	96.1	31.0%

Throughfall fluxes at a particular position beneath a tree are given as percentage of the total flux beneath a tree.

may help to alter biogeochemical cycles in ways that affect forest development as the hemlock succumb. For example, DON and total nitrogen concentrations increased significantly below 30 mm of throughfall beneath infested trees (Figure 6c). These increases are paralleled by (a) increased nitrogen content of infested needles that leach into throughfall and (b) enhanced growth and abundance of microorganisms in the canopy that are eventually washed off the needles onto the ground (Figure 4 and Table 2). Higher nitrogen content in leaves at the time of leaf fall should also affect decomposition and carbon sequestration in humus layers (Berg and others 2001). In similar fashion enhanced concentration of foliar nitrogen in leaf fall was correlated with the standing crop of the sycamore aphid, *Drepanosiphum platanoidis* (Schr.), on leaves of *Acer pseudoplatanus* (L.) (Dixon 1971).

In spite of the contrasting abundance of HWA on medium and heavily infested trees, throughfall nitrogen concentrations were similar. Thus, it appears that high HWA densities but low total numbers on damaged trees generate the same effect as medium HWA densities but large absolute numbers (Figure 6a–d). However, large numbers of adelgids on medium infested trees result in greater absolute production of waxes, which eventually break down and are washed from the canopy in increasing quantities as precipitation increases (Figure 7a). As a consequence, DOC concentrations exhibited a negative correlation with throughfall beneath uninfested and heavily infested trees, but not so beneath medium infested trees. Interestingly, our previous studies on aphids and lepidopterous larvae (For example, Stadler and others 2001a) also showed increased carbon fluxes but lower nitrogen fluxes in throughfall beneath infested trees. The difference in the HWA-mediated N chemistry reported here is likely due to the chemical nature of honeydew and frass pellets of caterpillar excrements which are largely composed of labile carbon (mostly mono- and disaccharides) readily available for microbial N immobilization. Wax wool, in contrast, which is hydrophobic and takes longer to break down, probably is more difficult to use by microorganisms. In addition, aphids like *Elatobium abietinum* (Walker) or *O. brumata* do not increase foliar nitrogen content as adelgids do (Day and Leather 1997). Clearly, detailed knowledge of the ecology and physiological impacts of pest species on host plants is critical in the evaluation of the overall impact of pests on ecosystem processes.

Cations, including potassium, displayed increased throughfall concentrations (Figure 7b–d), corroborating studies of other phytophagous insects (Seastedt and Crossley 1984; Schowalter and others 1991; Stadler and others 2001b). The higher nutrient and ion inputs beneath infested trees are pronounced despite the fact that total needle biomass was significantly lower. Further studies need to examine the temporal dynamics of these changes in foliar chemistry through the infestation sequence to better identify the mechanisms underlying these processes.

Although many factors affect canopy throughfall fluxes and chemistry, the most prominent appear to be precipitation and leaf area (for example, Tukey 1970; Knops and others 1996; Lovett and others 1996). However, trophic interactions between host plants, phytophagous insects, and epiphytic microorganisms clearly influence the nature and magnitude of these exchange processes in profound ways, even at endemic levels of infesta-

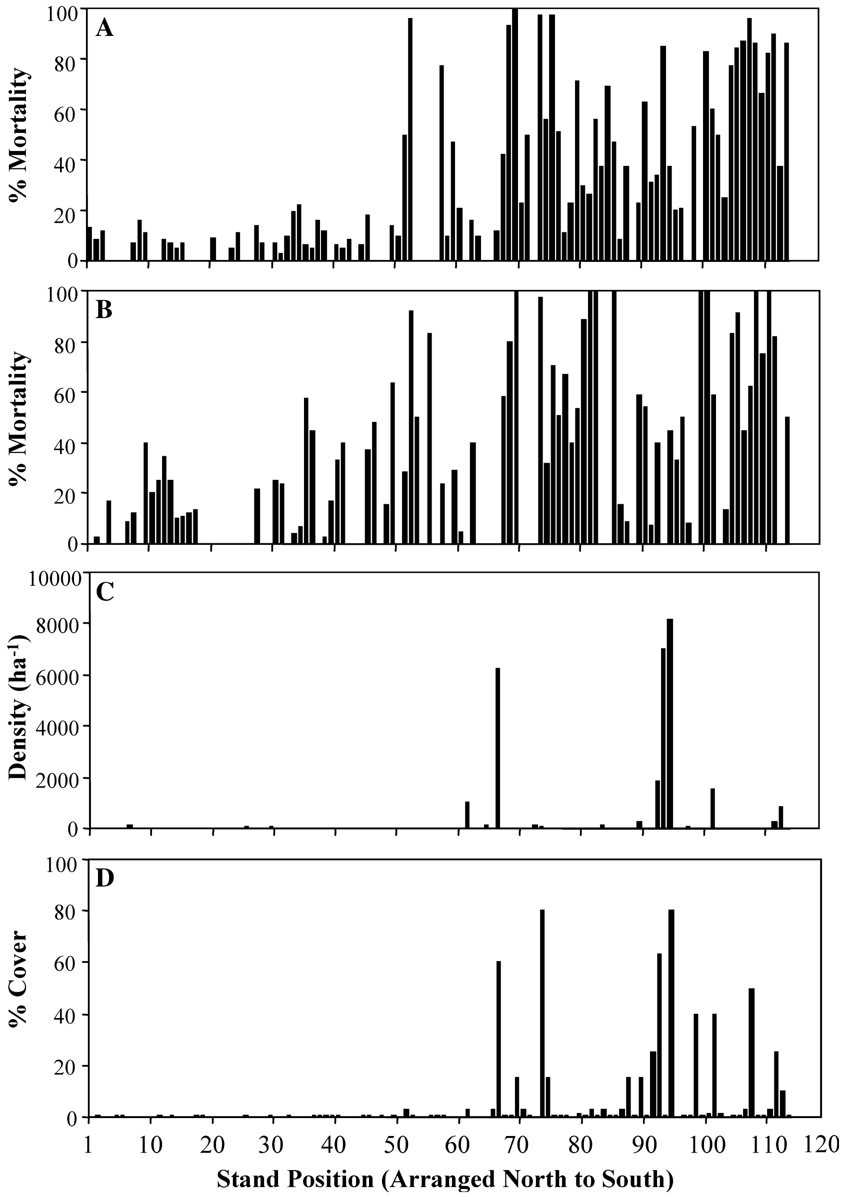

Figure 8. Impact of hemlock woolly adelgid on (**a**) overstory and (**b**) sapling hemlock mortality, and understory black birch (**c**) sapling densities and (**d**) seedling cover in 114 stands in central Connecticut. The study area extends from the Connecticut–Massachusetts border in the North (site 1) to Long Island Sound in the south (site 114). The latitudinal pattern of damage corresponds to duration of HWA infestation and northerly migration of the insect.

tion (Carlisle and others 1966; Stadler and others 2001a). Hemlock stands in which HWA has appeared relatively recently (medium infestation) are likely to show pronounced shifts in ecosystem processes at multiple spatial scales. For example, increased inputs of labile carbon (Figure 7a) and nitrogen (for example, Figure 6d) with throughfall (see also Carlisle and others 1966; Swank and others 1981; Hunter 2001) may lead to increased soil respiration, accelerated decomposition, and nitrate exports (Schowalter and others 1991; Lovett and Ruesink 1995; Michalzik and others 1999; Michalzik and Stadler 2000; Reynolds and Hunter 2001; Aber and others 2002) as well as significant shifts in resources that may affect plant performance and competitive interactions in hemlock stands (Catovsky and Bazzaz 2002).

In particular, black birch is known to capitalize on a high nitrogen environment and to outcompete co-occurring species in New England forests (Crabtree and Bazzaz 1992, 1993). These shifts in soil nutrient availability may be an important factor explaining the great abundance and success of black birch in declining hemlock stands across southern New England. Across a regional transect of infested stands, birch seedling cover was unrelated to site characteristics, but strongly associated with larger stands and hemlock mortality (Orwig and others 2002). We hypothesize that the dramatic structural, microenvironmental, and biogeochemical changes occurring with infestation facilitate rapid birch establishment, growth, and success in dominating the canopy of the developing stand (Figure 8a–d).

CONCLUSIONS

The effects of exotic pests like the hemlock woolly adelgid are generally overlooked until severe damage is visible on infested trees. Even in intense studies of pest effects, it is often assumed that ecological impacts progress in parallel with observed damage and corresponding changes in stand microenvironment and tree performance. However, this study underscores the fact that major changes in tree physiology, stand level nutrient cycling and water relations, and forest microbiology may be initiated well in advance of either heavy infestation by the pest or the appearance of severe damage to the trees. Shifts in leaf chemistry, ion fluxes, and microbiology may initiate profound changes in ecosystem function and may have an important effect on the subsequent structure and composition of the succeeding forest. In the case of the hemlock woolly adelgid, the result appears to be a gradual development of extensive and relatively homogeneous stands of an uncommon forest type that is dominated by black birch, which is a nitrophilous species.

We do not suggest a simple scaling-up approach from fast/small scale to slow/regional scale processes because of the growing errors that are involved. Rather we believe that there is a clear need to identify and understand the chain of mechanisms that link the different types and scales of ecological processes involved in ecosystem dynamics related to pest infestation (see Figure 1). This requires a concerted multidisciplinary/multiscale approach. Studies of infestation that ignore these subtle processes and treat the impact solely as physical disturbance (that is, a defoliation and mortality event) will fail to gain complete insight into the quality of ecosystem disruption and the mechanisms responsible for explaining resulting ecosystem dynamics.

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