

# Decomposition of green foliage in eastern hemlock forests of southern New England impacted by hemlock woolly adelgid infestations

Richard C. Cobb, David A. Orwig, and Steve Currie

**Abstract:** This study examined the impacts of hemlock woolly adelgid (*Adelges tsugae* Annand) (HWA), a small, invasive insect, on foliar chemistry, forest floor microclimate, and subsequent green foliage decomposition in eastern hemlock (*Tsuga canadensis* (L.) Carrière) forests. We investigated the direct effects of HWA feeding and indirect changes in microclimate on foliar decomposition by incubating HWA-infested and uninfested foliage across eight eastern hemlock dominated stands in southern New England that had different histories of HWA infestation. Infested stands had much poorer average crown health (3.4 versus 1.4 crown loss ratings), higher percent open sky ( $10.9 \pm 2.4$  vs.  $5.3 \pm 0.5$  gap light index), and lower organic soil moisture ( $0.83 \pm 0.02$  g·g<sup>-1</sup> vs.  $1.06 \pm 0.05$  g·g<sup>-1</sup>) than uninfested stands. There were no significant differences in percent C, percent N, or percent lignin for the excised foliage at the start of the study. However, after 120 days, decomposing foliage from infested trees had significantly higher N concentrations ( $1.83\% \pm 0.05\%$  vs.  $1.69\% \pm 0.02\%$ ) and lower C/N ratios ( $29.9 \pm 0.8$  vs.  $31.6 \pm 0.2$ ) than uninfested foliage, suggesting that HWA herbivory resulted in alterations of litter chemistry as decomposition progressed. Mass loss of common uninfested foliage was lower in uninfested hemlock stands than in infested ones ( $30.9\% \pm 0.7\%$  vs.  $34.2\% \pm 0.1\%$ ). These rates of mass loss were significantly correlated with microclimate factors and indicate that organic soil moisture levels are controlling decomposition in HWA-infested forests. Infestation by HWA causes virtually no direct feeding damage to foliage, but it does lead to several indirect and significant ecological and functional changes over the 10- to 20-year course of infestation and stand decline.

**Résumé :** Cette étude examine les impacts du puceron lanigère de la pruche (*Adelges tsugae* Ann.), un petit insecte invasif, sur les propriétés chimiques du feuillage, le microclimat dans la couverture morte et la décomposition subséquente du feuillage vert dans les forêts de pruche du Canada (*Tsuga canadensis* (L.) Carrière). Nous avons étudié les effets directs du puceron lanigère de la pruche et les changements indirects du microclimat sur la décomposition du feuillage en incubant du feuillage sain et du feuillage infesté par le puceron lanigère de la pruche dans huit peuplements dominés par la pruche du Canada dans le sud de la Nouvelle-Angleterre qui avaient différents historiques d'infestation par le puceron lanigère de la pruche. Les peuplements infestés étaient caractérisés par un état de santé des cimes beaucoup plus détérioré (3,4 vs. 1,4 d'indice de perte de cime), un pourcentage plus élevé d'ouverture du couvert ( $10,9 \pm 2,4$  vs.  $5,3 \pm 0,5$  de coefficient de trouées lumineuses) et une humidité du sol organique plus faible ( $0,83 \pm 0,02$  vs.  $1,06 \pm 0,05$  g·g<sup>-1</sup>) que les peuplements sains. Il n'y avait pas de différence significative dans le pourcentage de C, N ou de lignine du feuillage excisé au début de l'étude mais, après 120 jours, le feuillage en décomposition des arbres infestés avait des concentrations significativement plus élevées de N ( $1,83 \pm 0,05$  vs.  $1,69 \pm 0,02\%$ ) et un rapport C/N plus faible ( $29,9 \pm 0,8$  vs.  $31,6 \pm 0,2$ ) que le feuillage sains, ce qui indique que l'herbivorisme du puceron lanigère de la pruche entraîne des modifications des propriétés chimiques de la litière à mesure que la décomposition progresse. La perte de masse du feuillage sain commun était plus faible dans les peuplements de pruche sains que dans les peuplements infestés ( $30,9 \pm 0,7$  vs.  $34,2 \pm 0,1\%$ ). Ces taux de perte de masse étaient significativement corrélés avec les facteurs du microclimat et indiquent que le niveau d'humidité du sol organique contrôle la décomposition dans les forêts infestées par le puceron lanigère de la pruche. Le puceron lanigère de la pruche ne cause pratiquement aucun dommage direct au feuillage en s'alimentant mais entraînent plusieurs changements écologiques et fonctionnels indirects et significatifs pendant la période d'infestation et de dépérissement du peuplement qui dure de 10 à 20 ans.

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## Introduction

Insect outbreaks may alter decomposition and nutrient cycling in forests through several mechanisms, such as herbivory-induced changes to foliar chemistry; altered microclimate, resulting from canopy damage; and shifts in dominant litterfall type (Schowalter et al. 1986; Hunter 2001). Previous studies have developed a general conceptual knowledge that foliar quality, especially lignin concentration, and climate have strong controls on foliar mass loss. Decomposition, when examined at broad spatial scales, has been shown to be strongly influenced by temperature and precipitation (Meentemeyer 1978; Berg et al. 1993). Lignin and foliar phenolic concentrations are thought to control decomposition between regional stand types (Melillo et al. 1982) and sometimes across broad spatial areas for ecosystems with canopy characteristics that moderate year-to-year differences in microclimate (Berg et al. 2000). Foliar herbivory has been shown to increase the concentration of recalcitrant compounds, which subsequently reduce the rates of decomposition (Schultz and Baldwin 1982; Findlay et al. 1996). In other cases, insect herbivory has been shown to increase rates of mass loss by directly increasing litter nitrogen (N) levels (Chapman et al. 2003) and by altering competitive relationships by selecting for plants that produce high-quality litter (Belovsky and Slade 2000). During outbreak conditions significant thinning of the canopy, increased light penetration, and elevated forest floor temperature may alter rates of decomposition. Studies that experimentally increase soil temperature suggest that outbreak-related changes in microclimate will increase mass loss (Hobbie 1996; McHale et al. 1998; Rustad and Fernandez 1998). However, studies of canopy disturbances such as clear-cutting have shown reduced rates of decomposition, as a result of moisture limitation in the forest floor (Blair and Crossley 1988; Prescott et al. 2000). Both initial foliar chemistry and understory microclimate conditions may be impacted by insect outbreaks, but whether these changes increase, decrease, or have no impact on decomposition is likely to vary among insects (Mattson 1980; Schowalter 1981; Hunter 2001).

Changes in decomposition during insect outbreaks may lead to additional changes in ecosystem processes. For example, Jenkins et al. (1999) and Kizlinski et al. (2002) showed increased rates of N mineralization in stands experiencing outbreak populations of the exotic hemlock woolly adelgid (*Adelges tsugae* Annand) (HWA). Swank et al. (1981) showed an increased flux of  $\text{NO}_3^-$ -N in oak (*Quercus* spp.) dominated watersheds infested with fall cankerworm (*Alsophila pomataria* Harris), a native pest. Increased N flux in throughfall (Stadler et al. 2001, 2005) and higher N availability as a result of reductions of root N uptake (Kosola et al. 2001) likely contribute to these increases during insect outbreaks. Alternatively, lepidopteran larvae have been shown to increase the lignin content of host foliage, which subsequently reduces rates of decomposition and may act to slow rates of N cycling (Schultz and Baldwin 1982; Hutchens and Benfield 1999; Hättenschwiler and Vitousek 2000). Increased decomposition is often cited as a potential mechanism for increasing N turnover in ecosystems experiencing insect outbreaks. However, few studies have directly investigated the influence of insect herbivory on decomposition (but see Belovsky and Slade 2000; Chapman et al.

2003) or attempted to link decomposition change with change in nutrient cycling (Hunter 2001).

The HWA is an exotic pest of eastern hemlock (*Tsuga canadensis* (L.) Carrière) and has been responsible for considerable declines of the eastern hemlock forest type throughout much of the eastern United States. This insect is now found in 16 eastern states, from Georgia to New Hampshire, and has caused considerable mortality in the mid-Atlantic and southern New England regions (Orwig et al. 2002; Morin et al. 2005). HWA is native to Japan and was first described in the range of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) in the 1920s (Annand 1924). In the western United States, HWA is considered an innocuous forest insect on *Tsuga* species and rarely reaches outbreak levels or results in tree mortality (McClure and Cheah 1999). However, eastern hemlock has no known host resistance, and no effective native predators have been identified in the eastern United States. Once introduced to a stand, HWA populations typically increase rapidly (McClure 1991).

Hemlock stand conditions, community structure, and rates of functional processes are regionally unique and easily distinguished from those of other forest types (Lutz 1928; Rogers 1980; Abrams and Orwig 1996). Eastern hemlock stands are characterized by nearly monospecific canopies, depauperate understories, and deep, acidic forest floors (Daubenmire 1930; Rogers 1978, 1980). Eastern hemlock is extremely shade tolerant and produces acidic litterfall, factors that greatly influence within-stand patterns of tree regeneration and ecosystem processes (Catovsky and Bazzaz 2000; Prescott 2002; Lovett et al. 2004). The rates of litter decomposition and soil N cycling are slower and the soil carbon (C) and N pools are larger in hemlock forests than in regional forests of other types (McClougherty et al. 1985; Elliott et al. 1993; Finzi et al. 1998; Ferrari 1999). Hemlock forest structure and function are rapidly altered by HWA infestation. Understory light levels rapidly increase with hemlock decline and commonly lead to the prolific establishment of hardwood species, such as black birch (*Betula lenta* L.) (Orwig and Foster 1998; Stadler et al. 2005). Infested stands have significant rates of N export, which may subsequently affect stream water quality (Jenkins et al. 1999; Kizlinski et al. 2002; Yorks et al. 2003). However, the mechanisms by which HWA alters ecosystem function are largely unknown, especially during the initial period of hemlock decline prior to widespread overstory mortality.

The objective of this study is to determine the relative direct (change in foliar chemistry) and indirect (microclimate) impacts of HWA on foliar decomposition in eastern hemlock forests of southern New England. We expect HWA herbivory will increase rates of decomposition directly and indirectly. HWA herbivory is expected to increase foliar N, increase forest floor temperatures, and increase rates of decomposition in infested forests.

Decomposition of infested and uninfested excised green foliage was measured across a gradient of stands ranging from uninfested stands with intact canopies to HWA-infested stands with damaged canopies. We also measured stand characteristics, forest floor microclimate, and hemlock foliar chemistry in these stands to contrast the relative influence of direct and indirect impacts across sites. An uninfested common substrate was incubated at each stand so that the effect

of microclimate on decomposition could be quantified without interference from the impacts of HWA herbivory. We also collected foliage at each stand and incubated it locally to quantify the combined effects of microclimate and herbivory across a gradient of HWA-infested forests. Lastly, infested and uninfested green foliage was incubated adjacently at each site to isolate the impacts of HWA herbivory on decomposition.

## Methods

### Study area

The study area in central Connecticut and Massachusetts encompasses the Connecticut River valley and portions of the eastern uplands (Bell 1985). Within the region there is considerable variation in physiography, vegetation, land-use history, and incidence of HWA infestation. HWA is distributed throughout the study area, although there is a gradient of infestation severity, with high mortality and crown loss in the south and progressively better tree health in the north, that coincides with the progression of HWA migration northward in New England (Orwig et al. 2002). 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. Eastern hemlock forms the most prevalent natural conifer-dominated forests in the study region.

### Study design

To examine the impacts of HWA on decomposition, we used eight study sites that are part of a long-term study investigating hemlock decline and changes in ecosystem processes (Orwig and Foster 1999; Orwig et al., unpublished data). Vegetation, microclimate, and soil characteristics have been described and monitored continuously since 1998, and many of these data were integrated with the measures of decomposition in this study (Table 1). Three 20 m × 20 m plots were established at each site, and each stem >8 cm diameter at breast height (DBH) was measured for DBH and assigned a crown position. In each stand, a relative importance value was calculated for each species by averaging relative density and relative basal area data. Crown loss was estimated for each hemlock tree on the basis of the amount of retained foliage, with higher values indicating greater foliar loss (see Orwig and Foster 1998). At the beginning of the study, we estimated HWA abundance and assigned a density rating (uninfested; moderate, indicating several ovisacs per 5 cm of twig; or high, indicating ovisacs at the base of most twigs) during May and June by examining several dozen trees at each study site. In May 1998 soil samples were collected, passed through a 2 mm sieve, and analyzed for total C and total N (see Chemical analyses below). Forest floor pH was determined with a CaCl<sub>2</sub> slurry (1:10 organic soil : solution).

### Litter collection

Green foliage has been documented as an important component of early season litterfall in hemlock forests (Ferrari

1999; Stadler et al. 2005), and we commonly observed it falling this time of year. Therefore, hemlock needles were collected from eight trees adjacent to each of our Connecticut study plots in late May and early June 1999. In addition, needles from uninfested trees at Harvard Forest in central Massachusetts were collected to be used as a common substrate in testing for the effects of HWA-induced microclimate. Approximately three fine branches were cut from several trees at the plot margins and returned to the laboratory, where current year foliage was removed and discarded. We removed 1- and 2-year-old green foliage and composited it into a single pool of foliage for each site. Foliage was dried at 45 °C for 96 h to reach a constant mass, and a subsample from each pool was dried at 70 °C for 48 h to back correct for moisture content. We placed 3–3.5 g of foliage into 15 cm × 15 cm (1 mm mesh) bags. In 1999, in mid-June, 24 bags containing foliage from each respective site (in situ) and an additional 24 bags of uninfested foliage collected at Harvard Forest were placed at each site. Six in situ and six Harvard Forest litterbags were collected from each site at four dates: 30, 120, 350, and 500 days following establishment. Per plot values of decomposition were calculated by averaging values from the two Harvard Forest and in situ samples (respectively) collected at each sampling. At the laboratory, each bag was carefully cleaned of soil and plant material, and the contents were removed. Foliage was dried at 70 °C for 48 h, weighed individually, and then composited by plot and ground through a 850 µm stainless steel mesh. Overall, 379 of 384 litterbags were recovered.

### Chemical analyses

Total percent C and total percent N were determined for all excised foliage and soil samples by dry combustion with a CHNOS element analyzer (Fisons, Milan, Italy), with an analysis precision of at least 5%. To determine whether mineral contamination of litterbags occurred during the 30-, 120-, and 500-day measurements, ash content of the initial pools was determined by combustion at 550 °C for 5.5 h. One bag from the Devil's Hopyard site and another from the Sunrise site were contaminated by exogenous soil particles after 500 days and were not included in calculations of decomposition. Total percent lignin was determined for the initial excised foliage pools by near-infrared spectroscopy at the Complex Systems Research Center at the University of New Hampshire (Martin and Aber 1994). Initial foliage pools were scanned two times, and averaged values were reported.

### Microenvironmental analyses

Soil temperature, moisture, and forest floor light levels were examined over the study period. Forest floor soil temperature was monitored every hour at 1 cm with HOBO® data loggers (Onset Corp., Pocasset, Massachusetts) over the course of the 1999 and 2000 growing seasons (May through October). Gravimetric soil moisture of the organic soil was measured every 5 weeks and was calculated as the mass of water per gram dry soil. Forest floor light levels were estimated in fall 1998 using gap light index (GLI) values calculated from six hemispherical photos taken within each sampling plot. The GLI values were calculated with software

**Table 1.** Mean site, overstorey eastern hemlock (*Tsuga canadensis*), soil, and foliar chemistry characteristics of eight hemlock-dominated forests in central Connecticut, United States.

Site	Uninfested sites			Infested sites					
	Harvard Forest <sup>a</sup>	Salmon River	Crooked Road	Ash Brook	Lievre Brook	Devil's Hopyard	Willington Hill	Higby Mountain	Sunrise Resort
Elevation (m a.s.l.)	50	50	259	137	137	76	190	244	15
Slope range (%)	3-5	3-5	15-26	10-27	15-34	25-28	10	22-24	20-60
HWA density	Uninfested	Uninfested	Uninfested	Moderate	Moderate	Moderate	Moderate	High	High
<b><i>Tsuga canadensis</i></b>									
IV (%) <sup>b</sup>	74	74	78	89	82	77	80	69	80
Basal area (m <sup>2</sup> ·ha <sup>-1</sup> )	39	39	61	62	48	57	57	50	56
Mortality (%) <sup>c</sup>	0.0	0.0	1.0	1.9	2.9	2.8	0	4.2	7.0
Crown loss <sup>d</sup>	1.6	1.6	1.1	3.3	3.1	2.6	3.1	4.3	4.2
Gap light index (%)	5.71	5.71	4.81	8.33	5.27	12.9	5.40	20.6	12.9
<b>Soil</b>									
Mineral soil texture		Sandy loam	Silt loam	Silt loam	Loam	Silt loam	Loam	Silt loam	Sandy loam
Forest floor pH		3.73	3.77	4.02	3.93	4.01	4.15	4.46	4.25
Forest floor % N		1.17	1.36	1.45	1.32	1.21	1.01	1.27	0.82
Forest floor C/N		28.4	26.6	22.8	24.2	23.8	22.7	22.2	25.5
<b>Foliar chemistry</b>									
% C	49.85	51.29	49.44	48.79	48.74	48.36	47.34	48.66	50.81
% N	1.14	1.03	1.15	1.08	1.10	1.36	0.93	1.27	1.12
C/N	43.73	49.79	42.99	45.18	44.31	35.56	50.90	38.31	45.36
% lignin	14.13	16.25	14.38	13.80	13.26	14.23	14.50	16.8	14.44

<sup>a</sup>Uninfested foliage collected from Harvard Forest was placed adjacent to locally collected foliage at each stand.

<sup>b</sup>Importance value was calculated as the sum of relative basal area and relative density derived from three fixed-area plots in each stand.

<sup>c</sup>Percent mortality of overstorey trees.

<sup>d</sup>Crown loss classes were ascribed to each hemlock tree on the basis of the amount of retained foliage: 1 = 76%-100%; 2 = 51%-75%; 3 = 26%-50%; 4 = 1%-25%; 5 = dead (Orwig and Foster 1998). The mean for each site is presented.

**Table 2.** Percent mass loss and decomposition constants (*k*) for eastern hemlock foliage decomposed in eight hemlock-dominated stands in central Connecticut, United States.

Incubation (days)	Stand type – foliar type			
	Uninfested		Infested	
	Mass loss (%)	<i>k</i> day <sup>-1</sup>	Mass loss (%)	<i>k</i> day <sup>-1</sup>
<b>Harvard Forest foliage</b>				
30	16.1 (0.6)	0.0058 (0.0002)	13.0 (0.7)*	0.0047 (0.0003)*
120	40.5 (0.7)	0.0038 (0.0001)	34.1 (1.8)*	0.0031 (0.0002)
350	53.4 (0.9)	0.0011 (0.0001)	49.9 (1.1)	0.0012 (0.0001)
500	59.2 (1.2)	0.0009 (0.0002)	57.4 (1.2)	0.0012 (0.0002)
<b>In situ foliage</b>				
30	12.0 (0.8)	0.0043 (0.0003)	10.1 (1.2)	0.0036 (0.0005)
120	36.8 (1.6)	0.0037 (0.0002)	32.9 (2.3)	0.0033 (0.0003)
350	47.8 (1.0)	0.0008 (0.0002)	46.7 (2.0)	0.0010 (0.0001)
500	56.6 (1.2)	0.0012 (0.0003)	56.8 (1.9)	0.0015 (0.0003)
<b>HWA herbivory</b>				
30	13.0 (0.7)	0.0047 (0.0003)	10.1 (1.2)	0.0036 (0.0005)
120	34.1 (1.8)	0.0031 (0.0002)	32.9 (2.3)	0.0033 (0.0003)
350	49.9 (1.1)	0.0012 (0.0001)	46.7 (2.0)	0.0010 (0.0001)
500	57.4 (1.2)	0.0012 (0.0002)	56.8 (1.9)	0.0015 (0.0003)

**Note:** Decomposition of Harvard Forest foliage (a common uninfested substrate) and in situ foliage was compared between sites. The effects of HWA herbivory were examined by comparing adjacently decomposed uninfested Harvard Forest and infested in situ foliage within six HWA-infested stands. Data are means with one standard error in parentheses; \*, significantly different at each respective time step (ANOVA,  $p \leq 0.05$ ).

designed to measure light transmission through forest canopies (Frazer et al. 1999).

### Data analyses

Mass loss was nonlinear, and exponential decay constants (*k*) were calculated for both litter types within each stand by using the model of Olson (1963). Two values of *k* were calculated in our analysis. The first estimated the rates of mass loss between each litter collection and was used to examine rates of litter mass loss over time with a repeated measures analysis of variance (ANOVA):

$$[1] \quad \ln (M_{t2}/M_{t1}) = -kt$$

where  $M_{t2}$  and  $M_{t1}$  are the initial litter masses at the end and at the beginning of each time step, respectively. In these calculations *t* represents the number of days between establishment and first collection (30 days) or between subsequent collections (90, 230, or 150 days) (Table 2). A second calculation of *k* was made for the first complete year of decomposition:

$$[2] \quad \ln (M_t/M_0) = -kt$$

where  $t = 1$  year;  $M_t$  is the percent litter mass remaining after 1 year; and  $M_0$  is the initial litter mass (100%). These values were used in regression analyses of microclimate and litter chemistry variation with *k* rates by site (Table 3).

Regression analysis was used to explore relationships between pre-HWA stand characteristics, such as hemlock importance values and basal area, and factors hypothesized to be affected by HWA, such as overstory mortality, crown loss, and microclimate. Regression was further used to individually explore the relationships of overstory hemlock

mortality and crown loss estimates with forest floor temperature, forest floor percent moisture, and GLI levels. The effects of HWA on initial excised foliar chemistry, microclimate, and site factors were determined with individual one-way ANOVAs, with infestation as the main effect. Moisture, temperature, and light were quantified at different intervals, and therefore all data for an individual parameter were averaged for regression analysis of these factors against year 1 *k* values. Effects of microclimate and microclimate plus herbivory were determined with one-way repeated measures ANOVA of absolute mass loss, incremental *k* values, percent N, and C/N ratios for Harvard Forest and in situ foliage, respectively. Site-level infestation was the main effect for these models. Effects of HWA herbivory on litter decomposition were investigated at the six infested sites by incubating both HWA-infested and uninfested foliage. One-way repeated measures ANOVA of the same factors examined during site-level analysis was used to quantify the effects of HWA herbivory. ANOVA analysis showed significant effects of HWA herbivory on N concentration during decomposition, and therefore a post hoc analysis of the influence of initial foliar chemistry on changes in in situ percent N was undertaken with linear regression. Residuals for each model were examined and transformed to reduce heteroskedastic variance when necessary. All tests were performed with SYSTAT®, with statistical significance considered at  $p \leq 0.05$ .

## Results

### Effects of site, microenvironment, and initial foliar chemistry factors on overall decomposition patterns

HWA-infested stands had poorer health as indicated by

**Table 3.** Stand-level regression analysis of first-year decay constants with microclimate, forest floor chemistry, and initial leaf chemistry across eight hemlock-dominated stands in central Connecticut, United States.

	Harvard Forest foliage ( $k \text{ year}^{-1}$ )				In situ foliage ( $k \text{ year}^{-1}$ ) <sup>a</sup>			
	$\beta_0$	$\beta_1$	$r^2$	$p$	$\beta_0$	$\beta_1$	$r^2$	$p$
<b>Microclimate</b>								
Gap light index	0.81	-0.033	0.46	<0.001	2.05	-0.040	0.10	0.130
Temperature	2.54	-0.102	0.50	<0.001	5.13	-0.178	0.23	0.019*
Moisture	0.57	0.211	0.19	0.034*	1.42	0.751	0.35	0.002*
<b>Forest floor chemistry</b>								
pH	1.84	-0.12	0.12	0.092	2.49	-0.139	0.03	0.453
% N <sup>b</sup>	0.57	0.16	0.03	0.464	1.13	0.148	0.08	0.184
C/N	0.44	0.011	0.10	0.142	2.16	-0.009	0.01	0.644
<b>Initial leaf chemistry<sup>c</sup></b>								
% lignin					2.12	-0.015	0.02	0.726
Lignin/N					1.91	0.001	0.00	0.98
% N					2.18	-0.232	0.03	0.689
C/N					1.77	0.003	0.01	0.823

**Note:** Harvard Forest foliage is a common uninfested substrate incubated in each stand. In situ foliage was locally collected and incubated in each stand. \*Significant regression analyses.

<sup>a</sup>Response variable data were exponentially transformed.

<sup>b</sup>Independent variable data were sine transformed.

<sup>c</sup>Harvard Forest foliage was from one site.

significantly higher average crown loss ratings compared with uninfested stands (3.4 vs. 1.4). Additionally, infested stands had significantly greater percent open sky compared with uninfested stands ( $10.9 \pm 2.4$  vs.  $5.3 \pm 0.5$ ). Hemlock importance values ranged from 69% to 89% and were not significantly correlated with the impacts of HWA such as hemlock mortality, crown loss, or GLI of the canopy. However, regression analysis showed significant positive relationships between hemlock mortality, crown loss, and GLI. Forest floor pH was significantly lower in uninfested stands ( $3.75 \pm 0.02$ ) than in infested stands ( $4.14 \pm 0.05$ ) ( $p < 0.001$ ), and forest floor C/N was significantly higher in uninfested stands ( $27.5 \pm 0.7$ ) than in infested stands ( $23.5 \pm 0.4$ ) ( $p < 0.001$ ). Forest floor percent N levels were not significantly different between infested and uninfested stands.

Stand microclimate was significantly affected by HWA infestation (Table 1; Fig. 1). GLI values were 51% higher in infested stands ( $p < 0.05$ ). Overall temperature and moisture levels were considerably different between field seasons: 1999 was relatively warm and dry, and 2000 was cool and wet. HWA infestation did not significantly affect forest floor organic soil temperature. Regression analysis showed a significant positive relationship between GLI and forest floor temperature ( $r^2 = 0.30$ ;  $p = 0.006$ ). Organic soil moisture averaged 0.81 and 1.06  $\text{g}\cdot\text{g}^{-1}$  in infested and uninfested stands, respectively, and was significantly lower in infested stands during the 2000 field season. Regression analysis showed a significant negative relationship between GLI and moisture ( $r^2 = 0.24$ ;  $p = 0.014$ ).

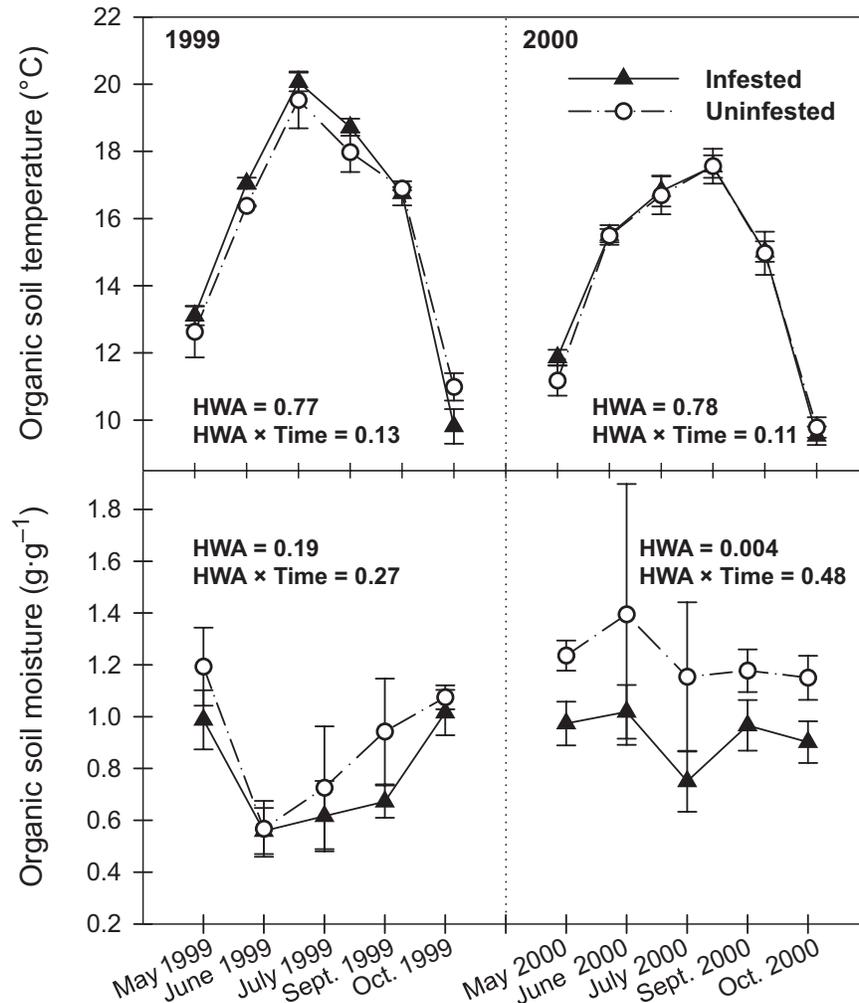
Initial excised foliar chemistry varied between sites; however, there were no significant differences in initial percent C, percent N, or percent lignin between HWA-infested and uninfested foliage (Table 1). Decomposing green hemlock foliage had a greater than twofold increase in percent N dur-

ing the first 350 days of incubation and then declined slightly (Figs. 2 and 3). The C/N ratio dropped during the first 120 days of incubation and declined more slowly up to the day 350 collection. Total amount of N per gram of foliage increased to 191 % of initial ( $\pm 5.9\%$ ) over the course of the study (data not shown).

#### Indirect (microclimate) impacts of HWA on green foliage decomposition

Analysis of the effects of HWA-altered microclimate on decomposition showed lower rates of mass loss in infested stands. Repeated-measures ANOVA showed significantly lower  $k$  values for Harvard Forest foliage incubated in infested stands than for that incubated in uninfested stands ( $p = 0.037$ ; see Table 2). Uninfested Harvard Forest foliage had significantly greater percent mass remaining in infested stands than in uninfested stands ( $34.2\% \pm 0.1\%$  vs.  $30.9\% \pm 0.7\%$ ) (Fig. 2). The apparent slowing of decomposition rates due to altered microclimate did not extend to our analysis of combined effects of HWA herbivory and changes in microclimate. In situ foliage decomposed at similar rates in infested and uninfested stands (Table 2). Additionally, altered microclimate did not have significant impacts on the chemistry of in situ foliage over time. For both Harvard Forest and in situ foliar types, foliar percent N and C/N values were similar between infested and uninfested stands. Microclimate factors had a significant influence on rates of mass loss for both infested and uninfested foliage. Harvard Forest and in situ foliage  $k$  values were positively correlated with forest floor moisture and negatively correlated with forest floor temperature (Table 3). Additionally, Harvard Forest  $k$  values were negatively correlated with GLI values. The influence of microclimate appears to be independent of site factors such as forest floor percent C, percent N, and pH, as no signifi-

**Fig. 1.** The effects of HWA infestation on forest floor temperature (upper panels) and gravimetric soil moisture (lower panels) in eight eastern hemlock dominated stands in central Connecticut, United States. Data are means with one standard error;  $p$  values are from repeated-measures ANOVAs, with infestation as the main effect.



cant relationships between  $k$  values and these factors were found by regression analysis (Table 3).

### Effects of HWA herbivory

When compared at infested sites, uninfested Harvard Forest foliage and HWA-infested foliage had similar rates of mass loss and similar percent mass remaining during the study (see Table 2; Fig. 3). However, the chemistry of decomposing infested foliage was consistently different from that of uninfested foliage over time. Decomposing infested foliage had significantly higher N concentrations ( $1.83\% \pm 0.05\%$  vs.  $1.69\% \pm 0.02\%$ ) and lower C/N ratios ( $29.9 \pm 0.8$  vs.  $31.6 \pm 0.2$ ) than adjacently incubated Harvard Forest foliage (Fig. 3). Further, these differences resulted in significantly greater absolute amounts of N in infested foliage than in uninfested foliage ( $176\% \pm 4.6\%$  of initial vs.  $161\% \pm 2.7\%$ ;  $p = 0.01$ ). The effects of initial foliar N content on N dynamics were investigated post hoc and were found to be significantly correlated with initial foliar chemistry. Percent N in decomposing foliage was positively correlated with initial percent N ( $r^2 = 0.59$ ;  $p = 0.026$ ). The average C/N ratio

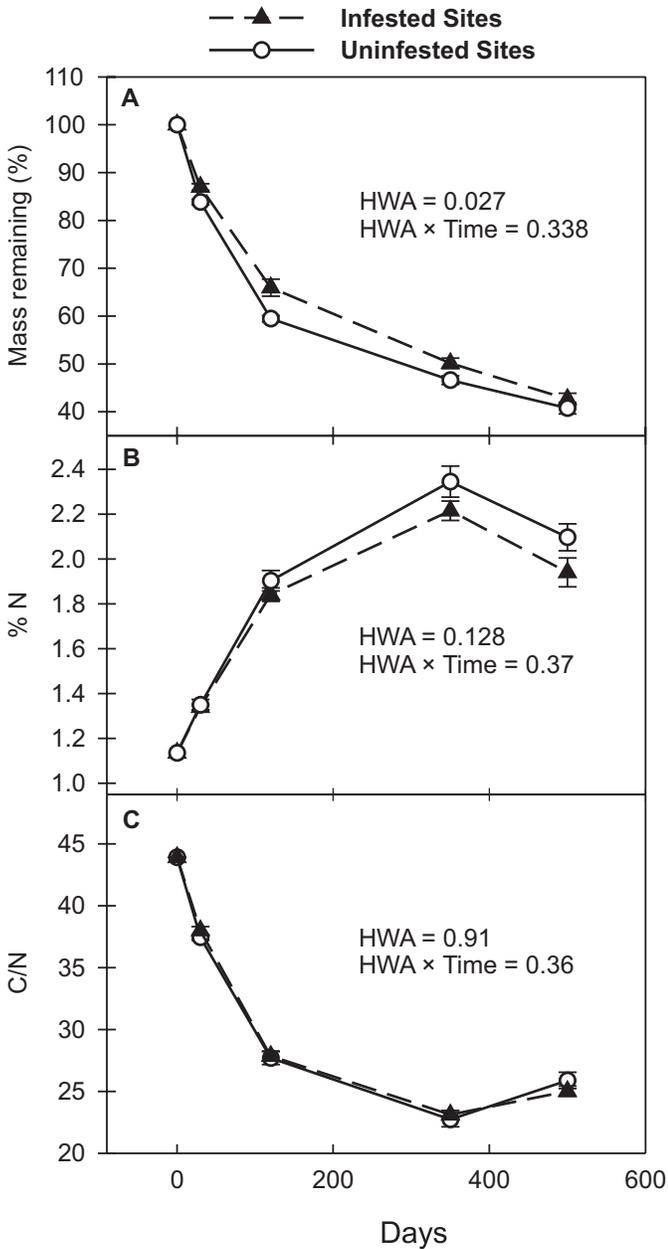
for decomposing foliage was also positively correlated with initial percent N ( $r^2 = 0.69$ ;  $p = 0.011$ ).

### Discussion

#### Changes in foliar chemistry

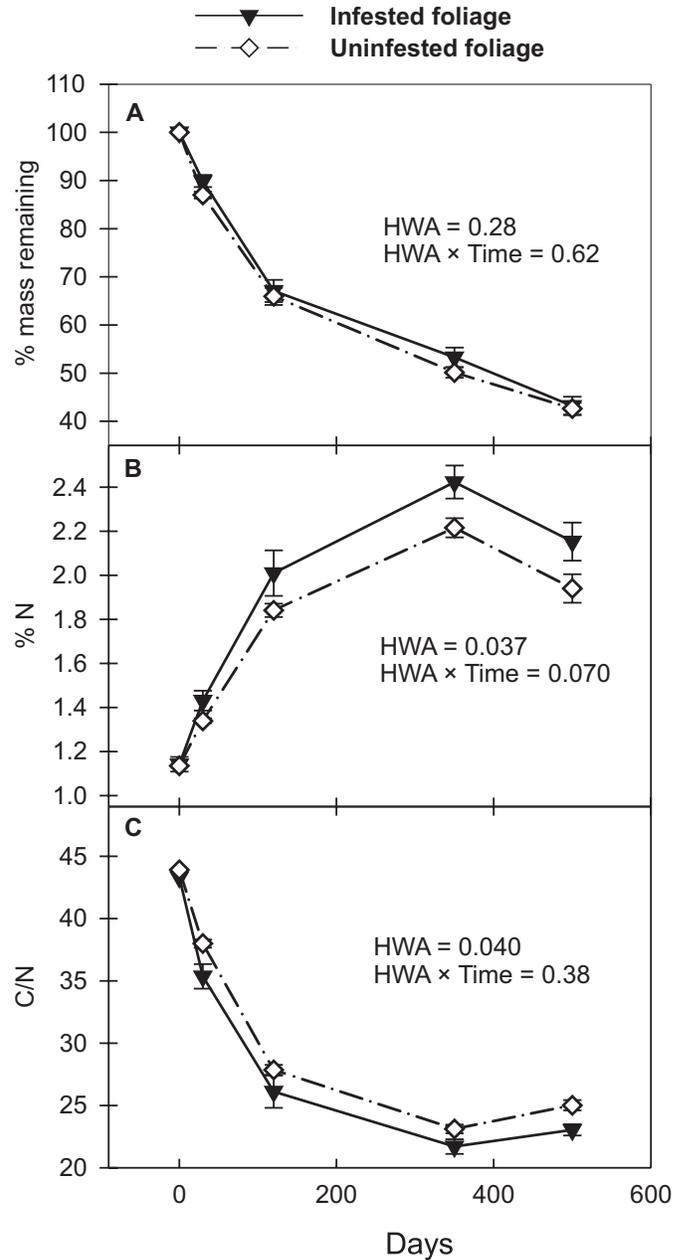
This study investigated changes in decomposition during the early period of hemlock decline following initial HWA infestation through significant canopy damage but prior to extensive overstory mortality or dominant species change. During the early to middle stages of infestation, HWA populations are often at their highest densities on individual trees (Stadler et al. 2005), and we therefore hypothesized that the direct effects of herbivory would be greatest during these stages. Further, we expected herbivory to increase foliar N levels and increase forest floor temperature, leading to an expected increase in rates of foliar decomposition and N release. However, no differences were found in rates of mass loss or initial foliar chemistry in infested foliage versus those in uninfested foliage, a result that may reflect the low amount of foliar damage during HWA feeding. Other re-

**Fig. 2.** Indirect effects (altered microclimate) of HWA infestation on physical (A) and chemical (B and C) changes during decomposition. Data are from a common substrate of uninfested green foliage from the Harvard Forest stand that decomposed in infested and uninfested hemlock-dominated stands in Connecticut, United States. Data are means with one standard error.



searchers have found higher levels of foliar N in HWA-infested trees. Pontius et al. (2002) reported slightly higher levels of foliar N in infested foliage than in uninfested foliage and no differences in percent lignin in a survey of 60 eastern hemlock stands with varying levels of HWA canopy damage. Stadler et al. (2005) also reported small but significantly higher foliar N levels in infested hemlock trees than in uninfested ones. A follow-up sampling of senescent and fresh foliage in 2001 at the hemlock stands used in this study also revealed significantly higher percent N in infested foliage than in uninfested foliage (S. Meyer, unpublished

**Fig. 3.** Direct effects of HWA herbivory on physical (A) and chemical (B and C) dynamics of green foliage decomposition in six HWA-infested, hemlock-dominated stands in central Connecticut, United States. Infested foliage was collected locally at each stand and decomposed adjacent to uninfested foliage collected at the Harvard Forest study site, located north of the HWA infestation front. Data are means with one standard error.



data). Foliar age-class is also an important factor affecting N concentration in HWA-infested foliage (Stadler et al. 2005; S. Meyer, unpublished data), and the combining of 1- and 2-year-old foliage in this study may have further reduced our ability to detect differences in initial foliar N levels.

Despite statistically similar initial percent N levels, decomposing infested foliage in this study had significantly higher percent N than uninfested foliage. These increases, combined with equivalent amounts of mass loss between fo-

liar types, resulted in significantly higher total amounts of N in infested foliage. The mechanism driving these differences is unclear. Throughfall N levels have been shown to be greater under HWA-infested hemlock trees (Stadler et al. 2005), but any effects of exogenous N can be ruled out in our study because infested foliage decomposed adjacent to uninfested foliage at each site, and thus both types were equally affected by HWA-altered throughfall. Although no significant differences in initial foliar N levels were detected in this study, post hoc regression analysis suggests that HWA herbivory is likely to increase N content in decomposing foliage. Another potential source of increased N in decomposing foliage is initial microbial populations on senescing needles. Significantly higher populations of yeast, bacteria, and epiphytic fungi have been documented on hemlock foliage infested by HWA (Stadler et al. 2005). Higher initial epiphytic microbe populations on infested foliage may have resulted in a more suitable substrate for rapid colonization by the fungi and bacteria that ultimately decomposed the litter (T. Müller, personal communication). More rapid colonization by decomposers would likely lead to the increased rates of N accumulation observed in HWA-infested foliage.

#### **Indirect effect of HWA (microclimate) on decomposition**

HWA significantly alters the microclimate of eastern hemlock forests (Orwig and Foster 1998; Jenkins et al. 1999). Because HWA infestation lasts for years, the gradual crown loss results in drier forest floor conditions. The positive correlation between mass loss and forest floor microclimate suggests that moisture limitation plays a role in year-to-year variation of decomposition in infested forests. Although this result is counter to our initial expectation that higher forest floor temperatures would increase rates of decomposition, it is in agreement with the findings of other studies that have shown a strong control of moisture availability on mass loss following major canopy disturbances (Whitford et al. 1981; Prescott et al. 2000; Kizlinski et al. 2002). Prescott et al. (2000) documented lower rates of litter decomposition in the 2 years following clear-cutting than in unharvested stands in coniferous forests in British Columbia, and Kizlinski et al. (2002) documented reduced mass loss of cellulose paper in recently harvested eastern hemlock forests (1–3 years following cutting). A previous study by Berg et al. (2000) in Norway spruce (*Picea abies* (L.) Karst.) forests can be considered an appropriate baseline for comparison of pre-HWA-infested hemlock forests. In its native range Norway spruce forms dense, dark, monospecific stands with generally slow rates of decomposition and nutrient cycling relative to those of other regional forest types (Berg et al. 2000). In these forests rates of decomposition are controlled predominantly by initial foliar chemistry, and the same effect can be seen when the rates are compared across a regional-scale climate gradient (Berg et al. 2000). In our study, microclimate played a more important role than initial foliar chemistry in controlling litter decomposition and suggests that HWA infestation has altered short-term decomposition rates in eastern hemlock forests.

Elevated rates of nitrification have been documented in HWA-infested stands (Jenkins et al. 1999) and following

harvesting in eastern hemlock forests (Kizlinski et al. 2002). Additionally, in a recent study in which Yorks et al. (2003) simulated HWA infestation by girdling a hemlock stand, the authors observed an increased  $\text{NO}_3^-$ -N flux for 4 years following treatment application. Lower  $k$  values observed in our study do not directly support the hypothesis that higher rates of decomposition are responsible for the changes in nitrification observed in other studies (Jenkins et al. 1999; Kizlinski et al. 2002). Increased  $\text{NO}_3^-$ -N turnover may result from C limitation to microorganisms following reduction of litter inputs from the canopy (Hart et al. 1994). Hemlock root N uptake is likely to decrease as canopy crown loss and mortality increase (Kosola et al. 2001). Additionally, higher percent N may retard long-term rates of decomposition through chemical stabilization of lignin (Berg 1986). Observations that included both herbivory and microclimatic effects showed no overall changes in percent N or in C/N ratios for decomposing foliage at infested sites in comparison with control sites. These results suggest that moisture limitation to decomposition in infested forests may be tempering the effects of herbivory (chemical changes) in decomposing foliage at this stage of infestation. However, accumulation of N in the forest floor resulting from herbivory has the potential to increase rates of N mineralization at later stages of infestation by lowering C/N ratios for the forest floor (see Finzi et al. 1998). Changes in the amounts and quality of litterfall as a result of hemlock mortality and replacement of hemlock by black birch are also very likely to increase decomposition at later stages of infestation and stand decline.

#### **Conclusions**

The HWA is an exotic, damaging pest that is rapidly altering eastern hemlock forests throughout the mid-Atlantic and southern New England regions. Hemlock mortality due to HWA occurs over a 10- to 20-year period and leads to several indirect but significant ecological and functional changes in these ecosystems. This study demonstrates the effects of HWA infestation on decomposition of excised foliage in eastern hemlock forests and represents an additional example of how invasive insects may influence ecosystem function. HWA slowed rates of mass loss primarily by reducing the amount of moisture in the forest floor. Altered microclimatic conditions have the potential to persist for many years as the species composition of infested forests changes gradually over time. Herbivory by this insect did not significantly increase initial foliar N or lignin levels. However, herbivory resulted in increased rates of N accumulation in decomposing foliage. But herbivory did not result in significantly higher amounts of N in infested stands, because of the overall slower rates of decomposition stemming from an apparent moisture limitation to decomposers. This study suggests that changes due to herbivory and altered microclimate at early stages of infestation, prior to dramatic changes in canopy structure or establishment of understory vegetation, may not contribute to the increased rates of N cycling observed elsewhere. HWA herbivory is likely to lower C/N ratios in the forest floor over time and lead to increases in N cycling at later stages of infestation.

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