

# Vegetation dynamics in declining eastern hemlock stands: 9 years of forest response to hemlock woolly adelgid infestation

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**Abstract:** Hemlock woolly adelgid (HWA; *Adelges tsugae* Annand) infestations have resulted in the continuing decline of eastern hemlock (*Tsuga canadensis* (L.) Carrière) throughout much of the eastern United States. In 1994 and 2003, we quantified the vegetation composition and structure of two hemlock ravines in the Delaware Water Gap National Recreation Area. This is the first study to use pre-adelgid disturbance data, annual monitoring of infestation severity, and annual records of hemlock health to assess forest response to HWA infestation. In 2003, 25% of monitored hemlock trees were either dead or in severe decline. Measures of hemlock decline (crown vigor, transparency, density, and dieback) were correlated with HWA infestation severity and changes in light availability over the study period. Average percent total transmitted radiation more than doubled at these sites from 5.0% in 1994 to 11.7% in 2003. The total percent cover of vascular plants increased from 3.1% in 1994 to 11.3% in 2003. Species richness increased significantly, and more species were gained (53) than lost (19) from both ravine floras over the 9-year study period. Though exotic invasive plants were absent from these ravines in 1994, our 2003 resurvey found invasive plants in 35% of the permanent vegetation plots.

**Résumé :** Les infestations du puceron lanigère de la pruche (*Adelges tsugae* Annand) sont responsables du dépérissement graduel de la pruche du Canada (*Tsuga canadensis* (L.) Carrière) qui continue à sévir presque partout dans l'est des États-Unis. En 1994 et 2003, nous avons quantifié la structure et la composition de la végétation de deux ravins de la Delaware Water Gap National Recreation Area dominés par la pruche. Il s'agit de la première étude à utiliser des données antérieures à la perturbation par le puceron lanigère, l'évaluation annuelle de la sévérité de l'infestation et des données annuelles sur l'état de santé de la pruche pour évaluer la réaction de la forêt à l'infestation. En 2003, 25 % des tiges de pruche inventoriées étaient soit mortes, soit sévèrement dépéries. Les mesures de dépérissement de la pruche (mort-en-cime, vigueur, transparence et densité de la cime) étaient corrélées avec la sévérité de l'infestation par le puceron lanigère de la pruche et les changements dans la disponibilité de la lumière au cours de la période d'étude. Le pourcentage moyen de radiation totale transmise a plus que doublé dans ces stations, passant de 5,0 % en 1994 à 11,7 % en 2003. Le pourcentage total de couvert de plantes vasculaires a augmenté de 3,1 % en 1994 à 11,3 % en 2003. La richesse en espèces a augmenté significativement et le gain d'espèces (53) a été plus grand que la perte (19) dans la flore des deux ravins pendant la période d'étude de neuf ans. Bien que les plantes exotiques invasives aient été absentes de ces ravins en 1994, notre inventaire de 2003 a relevé la présence de plantes invasives dans 35 % des parcelles permanentes de végétation.

[Traduit par la Rédaction]

## Introduction

Eastern hemlock (*Tsuga canadensis* (L.) Carrière) is currently threatened by the hemlock woolly adelgid (HWA; *Adelges tsugae* Annand) (McClure 1991; Royle and Lathrop

1997; Orwig and Foster 1998). This aphid-like insect was introduced to the eastern United States from Japan. It is currently impacting hemlock forests in 16 states and continues to spread across the range of eastern hemlock (McClure 1996; USDA Forest Service 2004). The adelgid feeds on

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hemlock ray parenchyma cells, causing needle loss and bud mortality (Young et al. 1995), and may cause complete mortality of infested stands within 4 to 6 years (McClure 1991). Eastern hemlock has shown no resistance to HWA, and potential biocontrol agents have yet to prove effective (McClure 2001). Therefore, it appears inevitable that HWA will severely reduce this important species.

Eastern hemlock is a late-successional conifer that exerts strong control over stand microclimate and soil conditions by casting deep shade and depositing acid litter. It is a long-lived, extremely shade-tolerant species that often forms nearly pure stands on certain landscape positions, including stream ravines and north-facing slopes (Braun 1950; Rogers 1978; Burns and Honkala 1990). Uniformly low light availability, low seasonal variability of light levels, relatively small daily temperature fluctuations, and sharply defined borders characterize a hemlock understory (Rogers 1980; Canham et al. 1994). As a result of this modification of the understory environment, it is believed that hemlock strongly influences fundamental community and ecosystem characteristics (Mladenoff 1987; Frelich and Lorimer 1991; Jenkins et al. 1999) and that hemlock mortality may result in ecosystem responses that exceed those resulting from other forest pathogens.

The complete ecological ramifications of hemlock decline remain unclear. Initial efforts to document the immediate consequences of HWA on forest ecosystems suggest significant changes in patterns of species abundance, stand structure, and ecosystem function (Orwig and Foster 1998; Jenkins et al. 1999; Snyder et al. 2002). It has also been suggested that HWA will lead to a significant reduction in landscape-level diversity and structural complexity (Orwig et al. 2002). The impacts of these changes on several wildlife species have been documented, and additional impacts are predicted (Yamasaki et al. 2000; Brooks 2001; Snyder et al. 2002; Tingley et al. 2002; Ross et al. 2004). Paleological studies suggest that the rapid decline in the abundance of eastern hemlock that occurred in the mid-Holocene, likely due to an insect outbreak (Allison et al. 1986; Bhiry and Fillion 1996), had long-term impacts on the species composition of forest (Fuller 1998) and lake (Boucherle et al. 1985; Hall and Smol 1993) communities. This historic decline in hemlock abundance is in many ways analogous to the current HWA-related decline (Orwig and Foster 1998). However, the current hemlock decline is occurring at a time when these forests face a suite of novel stressors, including nitrogen deposition, exotic forest pests and pathogens, elevated white-tailed deer (*Odocoileus virginianus*) populations, and an abundant supply of exotic invasive plants (e.g., Liebhold et al. 1995; Alverson and Walker 1997; Vitousek et al. 1997). The interactions of hemlock decline with these stressors are poorly understood. Though the spread of exotic plant species as a result of hemlock decline has been predicted, it remains largely undocumented (Orwig and Foster 1998; Evans 2002).

Because of its unique aesthetic, recreational, and ecological qualities, eastern hemlock is a highly valued component of reserves and parks in the eastern United States (Evans 1995). In the Delaware Water Gap National Recreation Area (DEWA), it is currently estimated that about 20% of the park's hemlocks are dead, 60% are at various stages of de-

cline, and only 20% are healthy (Evans 2004). In 1994, the National Park Service initiated intensive studies in two hemlock-dominated ravines in DEWA to monitor hemlock health and document baseline ecological conditions prior to HWA disturbance. We established a network of permanent, intensive plots in conjunction with these monitoring sites to document changes in vegetation dynamics in declining hemlock stands. The data set collected at these sites constitutes one of the most complete long-term records of forest response to HWA infestation reported to date. In contrast to previous studies in which the exact timing of HWA infestation was not known, this data set includes annual records of hemlock health and HWA infestation levels dating back to several years prior to infestation. This information allows us to quantify the relationship between hemlock decline and an index of HWA infestation severity and understory light availability. In addition, complete surveys of vegetation and several environmental variables were performed in permanent plots in 1994, prior to HWA infestation, and repeated in 2003.

Insights into the understory plant community response to HWA infestation have been gained from chronosequence studies of hemlock stands that span a range of infestation levels (Orwig and Foster 1998), from studies simulating HWA via girdling hemlock trees (Yorks et al. 2003), and from studies linking canopy gaps in hemlock-dominated forests to the distribution and abundance of understory plants (Rankin and Tramer 2002). However, our understanding of forest response to HWA infestation remains incomplete without longer term studies that include pre-adelgid data and that directly monitor the progression of the infestation. In addition, though much can be inferred from studies of the ecological impacts of hemlock removal via logging or girdling (Brooks 2001; Yorks et al. 2003), the gradual thinning of the hemlock canopy caused by HWA infestation is a novel occurrence in hemlock forests that may result in fundamentally different responses (Kizilinski et al. 2002).

This is the first study to incorporate preinfestation information, annual measures of infestation severity, and annual records of hemlock health into an assessment of forest response to HWA over the long term. Documenting the response of forest ecosystems to the introduction of exotic pests is critical to improve our understanding of the impacts of the decline or elimination of a dominant tree species and to highlight potential issues of management concern. Our main objectives in this study, encompassing 1994 to 2003, were to (1) document the patterns of hemlock decline and mortality, (2) quantify the changes in vascular plant species abundance, richness, composition, and mobility (species losses and gains over time), and (3) examine the relationship between changes in the microenvironment and the response of the understory flora. In addition, we report annual and seasonal fluctuations in the understory vegetation that occurred from 1994 to 1995 to provide a reference for interpreting the changes that occurred over the 9-year study period.

## Methods

### Study sites

The Delaware Water Gap National Recreation Area (DEWA) is an approximately 27 800 ha park located in

northeastern Pennsylvania and western New Jersey along the Delaware River. Forests occupy 21 885 ha of DEWA and are dominated by *Quercus rubra* L. (red oak), *Acer saccharum* Marsh. (sugar maple), *Quercus prinus* L. (chestnut oak), *Acer rubrum* L. (red maple), *Betula lenta* L. (black birch), *Betula alleghaniensis* Britt. (yellow birch), *Tsuga canadensis*, and *Pinus strobus* L. (eastern white pine). Although historic records suggest that hemlock was much more abundant in DEWA prior to European settlement, stands dominated by hemlock currently account for only about 5% of the forested landscape (Myers and Irish 1981; Young et al. 2002). However, hemlock often accounts for as much as 50%–80% of the basal area in these stands (Sullivan et al. 1998). Hemlock-dominated stands in DEWA occur on shallow soils in spatially patchy, topographically isolated ravines.

In 1994, resource managers at DEWA initiated intensive studies to document pre-adelgid conditions in two hemlock ravines: Adams Creek (AC; Pike County, Pennsylvania) and Van Campens Brook (VC; Sussex and Warren Counties, New Jersey). These sites were selected in conjunction with ongoing hemlock and HWA infestation monitoring. At both sites, hemlock accounted for greater than 50% of canopy basal area. Adams Creek and Van Campens Brook are tributaries to the Delaware River (41°31'N, 74°49'W) and are approximately 18.5 km apart. The regional climate is humid continental with an annual mean monthly temperature of 9.7 °C and mean summer (June, July, August) temperature of 20.8 °C. Mean annual precipitation is 115.5 cm (NOAA 2002, Station 110). During the study period, the region experienced a moderate dry period in the 1995 growing season and a mild dry period from 1999 to 2002 (NCDC 2005).

Adams Creek is a third-order stream that flows southeast off the Pocono Plateau. Elevation in the ravine varies from 120 m at streamside to 280 m at the ravine edge. The ravine sides are steep and range from 12% to 80% slope. The study area encompasses approximately 36 ha of the AC ravine. The bedrock consists of dark gray siltstone and shale with patches of calcareous siltstone (Mahatango formation; Epstein and Epstein 1969; McIntosh and Eister 1981). Slope soils are classified as Manlius very rocky silt loam (Taylor 1969).

Van Campens Brook is a second-order stream formed from the drainage of Long Pine Pond and Blue Mountain Lake and flows southwest into the Delaware River. Elevation ranges from 250 m at streamside to 350 m at the ravine edge. The ravine sides are gentler than those at AC and range from 3% to 25% slope. The study area encompasses about 18 ha of this ravine. The bedrock is red-purple sandstone of the Bloomsburg formation (New Jersey Geological Survey 1989). Ravine slope soils are classified as Swartswood very stony soil and loam (Fletcher 1979).

### Comprehensive plant inventory

In 1994, we conducted a complete qualitative inventory of all vascular plant species present in the AC and VC topographic ravines. Inventories were conducted by a botanist and a park ecologist familiar with the regional flora (140 total person-hours). Voucher specimens were deposited at the Bailey Hortorium, Cornell University. This survey allowed us to quantify how well our understory vegetation sampling

method captured the species diversity present in the ravines. In addition, we were able to document rare and uncommon plants not recorded in the quantitative understory vegetation plots that may be affected by hemlock decline.

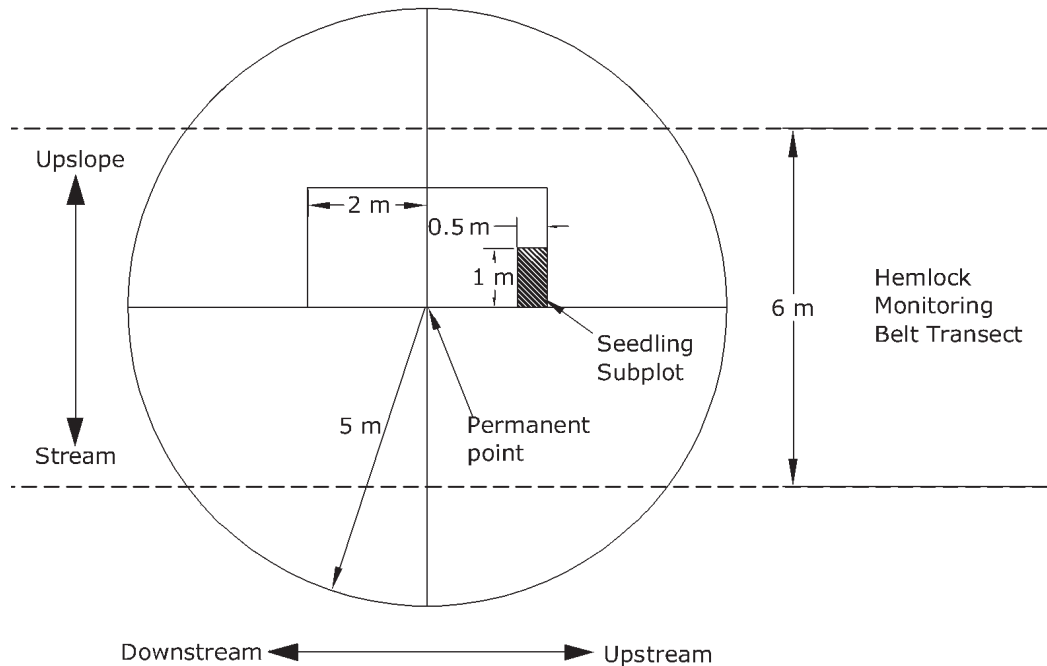
### Establishment of permanent understory plots

In 1993, permanent plots were established in AC and VC to monitor HWA populations and hemlock decline. Random points were selected along each stream using aerial photographs and plots were established 10, 30, and 50 m upslope from the stream edge. Each monitoring plot is a 6 m wide belt transect running parallel to slope. Plot lengths varied to include a sample of 10 hemlock trees with a minimum DBH (diameter at breast height, 1.37 m) of 2 cm and no more than two trees less than 10 cm in DBH (mean plot length = 32.3 m, standard deviation at AC = 10.8 m and at VC = 15.2 m). Twelve sets of hemlock monitoring plots (36 plots) were placed in AC and eight sets (24 plots) were established in VC for a total of 600 monitored hemlock trees.

USDI National Park Service and USDA Forest Service staff assessed hemlock tree health by individually evaluating each of the 10 trees in the hemlock monitoring plot belt transects using the “visual crown rating” methods developed by the Forest Service (USDA Forest Service 1999). These measurements of hemlock tree health were collected annually from 1993 to 2003. Three primary measures of crown health were used: crown density (“fullness” and density of branches and foliage), crown dieback (loss of needles at branch tips), and crown transparency (relative amount of light that passes through tree crown). Measurements were recorded as a percentage relative to an ideal healthy tree, and each hemlock was assigned to one of the following vigor classes based on the amount of foliage retained: healthy (4 = 76%–100%), slight decline (3 = 51%–75%), moderate decline (2 = 26%–50%), severe decline (1 = 1%–25%), or dead (0). In addition, an index of HWA infestation level was recorded in June of each year for permanently marked branches on three trees in each hemlock monitoring plot by counting the proportion of terminals with HWA ovisacs (Evans 1996).

In 1994, permanent understory vegetation plots were established in the center of the hemlock monitoring plots in AC and VC. The straight-line distance between the two end trees in the plot (tree 1 and tree 10) was measured. The midpoint of this distance was marked with a 35 cm tall rebar stake. In addition, near-stream points were located 1 m from the stream edge in a line that forms the perpendicular between the 10 m point and the stream bank. Edge points were also established if a discernible edge of the hemlock-dominated forest was within 100 m perpendicular distance upslope from the 50 m plot. These points serve as the fundamental reference for the nested vegetation sampling scheme described below. Latitude and longitude of all plots were recorded with a geographic positioning device, and corners were marked with rebar to ensure precise relocation. A total of 92 permanent plots were established. Adams Creek has 55 plots: 36 midslope plots, 12 near-stream plots, and 7 edge plots. One AC near-stream plot was completely lost to flooding, and the 2003 data set at this site therefore contains 54 plots with 11 near-stream plots. Van Campens has a total of

**Fig. 1.** Diagram of the quantitative vegetation sampling regime used for the permanent plot survey. All monitored hemlock trees are located within the 6 m wide belt transects that vary in length to include a sample of ten hemlock trees.



37 plots: 24 midslope plots, 8 near-stream plots, and 5 edge plots.

### Quantitative vegetation sampling

Vegetation sampling and environmental measurements were conducted in the established permanent plots in June 1994 and June–July 2003. Ground cover vegetation sampling was also repeated in August 1994 and June 1995 to quantify seasonal and annual changes in the abundance, mobility, and percent cover of seedlings and herbs. Vegetation was sampled in three categories: ground cover (defined as all vascular plants  $\leq 1$  m tall), subcanopy trees and shrubs, and canopy trees (nomenclature follows Rhoads and Block 2000). Composition and percent cover of vascular plants ( $\leq 1$  m tall) were quantified in a  $2 \text{ m} \times 4 \text{ m}$  quadrat set parallel to the streambed at each point (Fig. 1). The quadrat was divided into two  $2 \text{ m} \times 2 \text{ m}$  subquadrats to facilitate plant cover estimates. To further quantify tree seedling abundance, counts of all tree seedlings  $< 1$  m tall were made in a  $1 \text{ m} \times 0.5 \text{ m}$  nested subplot in the lower upstream corner of the  $2 \text{ m} \times 4 \text{ m}$  quadrat (Fig. 1). Percent substrate cover was also recorded in each subquadrat in the following classes: leaf litter, woody debris, rock, bryophytes, and bare mineral soil.

All subcanopy trees and shrubs  $\geq 1$  m tall within a 5 m radius of each permanent point were tallied by species, and DBH was recorded for individuals  $\geq 2$  cm DBH. In addition, the species, height, and abundance of all exotic plant species within the 5 m radius plot were recorded. Canopy tree species composition and density were quantified using the point-quarter method with the four quarters delimited by the base of the  $2 \text{ m} \times 4 \text{ m}$  ground cover quadrat and a line perpendicular to the quadrat base. Canopy trees were defined as trees in dominant or codominant crown classes and subcanopy trees were defined as those in intermediate or sup-

pressed crown classes (Smith 1986). Species, crown class, DBH, crown ratio, and vigor were recorded for each point-quarter tree. Canopy height was recorded for a representative point-quarter tree at each plot. At stream sites, canopy tree composition was estimated with a 2.5 factor (metric) basal area prism.

### Environmental measurements

Understory light availability at each plot was characterized in 1994 and 2003 through use of hemispherical photographs. All photos were taken under diffuse light conditions using scientific grade photographic lenses (Canon 7.5 mm and Nikkor 8 mm). Distortions in the area projections (Herbert 1987) were corrected prior to analysis. We used the Gap Light Analyzer software to compute the fraction of total transmitted radiation reaching each photo point during the growing season (Canham 1988; Frazer et al. 1999). The above-canopy radiation model was based on long-term results from the nearest National Weather Service station (Scranton, Pennsylvania; Knapp et al. 1980). Precision error associated with photographic analyses was less than 5% root mean squared error.

Slope, aspect, elevation, microrelief, soil pH, soil depth, and topographic position in the ravine (i.e., distance from stream) were recorded at each permanent point in 1994. During the 1994 and 1995 growing seasons, indices of gravimetric soil moisture and soil temperature (0 and 10 cm depth) were calculated for each point to assess relative differences within and between sites. Soil temperature was measured with a digital thermometer every 2 weeks during the growing season. The vegetation–environment relationship in the ravines was explored using multivariate analyses. Topographic position and light availability had the best independent correlations with plant composition in 1994 (Battles



et al. 1997). Thus, in the 2003 remeasurement, we focused on these two variables and did not repeat the soil assessment.

### Data analyses

Our data analysis consisted of two main components: (1) before–after analysis of the changes that occurred in all plots over the 9-year study period (June 1994 to June–July 2003) and (2) between site comparisons of these changes. We acknowledge the use of multiple comparisons and therefore set a conservative significance level ( $\alpha = 0.01$ ) throughout. *P* values close to this limit should be interpreted with caution and all effect sizes are reported.

We determined the statistical significance of changes in hemlock crown health (transparency, dieback, and density) by paired *t* tests. To account for the ordinal nature of hemlock crown vigor data, changes in vigor between 1994 and 2003 were analyzed using Wilcoxon signed-rank tests. Monitored trees that died during the study but remained standing were assigned the following values: crown transparency = 90 (sensu Battles and Fahey 2000), crown dieback = 100, and crown density = 0. To account for censored observations (i.e., trees that died during the monitoring period), Kaplan–Meier survival estimates were used to calculate survival curves of time to infestation for hemlock trees in AC and VC (Lee and Wang 2003). In these analyses, a tree was defined as infested when HWA was observed on >5% of terminal branches in order to eliminate annual variation in categorization. The significance of differences in the Kaplan–Meier survival curves at AC and VC was determined by a Mantel–Haenszel test (Lee and Wang 2003).

We determined the statistical significance of changes in understory light availability, percent vegetation cover (total and by species for all species occurring in greater than 10% of plots), substrate cover, and species richness between 1994 and 2003 by paired *t* tests. Sign tests were used to evaluate changes in the frequency of species occurrence over the 9-year study period (Zar 1999). To examine the strength of the relationships between changes in light level and vegetation changes, we calculated Pearson's product moment correlation coefficients. We used single-factor ANOVAs to compare changes in understory light levels, vegetation cover, and hemlock decline by topographic location in each ravine and to examine differences in hemlock decline across size classes (Zar 1999). Lastly, the relationship between invasive species occurrence and light availability was analyzed by logistic regression. The area under the receiver operating characteristic (ROC) curve is reported as a measure of the ability of the model to correctly classify the presence or absence of an invasive species in a given plot (Hosmer and Lemeshow 2000).

Our research design used change in understory light availability to indicate the severity of disturbance caused by hemlock decline. To confirm this relationship between increased light availability and hemlock decline, we calculated the Pearson's product moment correlations between the percent total transmitted radiation and the hemlock crown rating data (crown transparency, crown density, and crown dieback) and between these measures of hemlock crown health and the index of HWA infestation severity. For each plot, the crown rating data and infestation level estimates for the four near-

est trees were included in these calculations (all <9 m from permanent point). To approximate the effect of cumulative load impacts, the average of the infestation levels for all years since initial infestation was used in these comparisons. Variables recorded as percentages were arcsine square-root transformed as needed to meet the assumption of normally distributed residuals.

To examine the spatial patterns of hemlock decline and the changes in understory light availability from 1994 to 2003, we performed Moran's *I* tests for spatial autocorrelation (Dale et al. 2002). The coordinates of each plot center were used for the spatial analyses and mark the exact location of hemispherical photographs. Theoretical distributions with two-tailed *p* values are reported throughout.

To estimate species mobility, turnover rates for understory plants were calculated using several species turnover equations reported in the literature (Palmer and Rusch 2001; Otsus and Zobel 2002; Bakker et al. 2003). However, because these equations substantially undervalue the role of species additions or gains, final reporting includes only the total number of species losses and gains occurring at the plot level. To provide a comparison to annual variability, these calculations are reported for both 1994 to 1995 and for the 1994 to 2003 study period. It is worth noting that calculations for the 1994 to 2003 time period are a more conservative estimate of species mobility because we cannot distinguish between true species persistence and species that have disappeared and reappeared over this longer study period. In addition, we report changes in species composition at the ravine scale as the occurrence of absolute additions or losses of a species in each ravine. Species losses and gains were separated by plot location to examine how changes in species composition were distributed on the landscape.

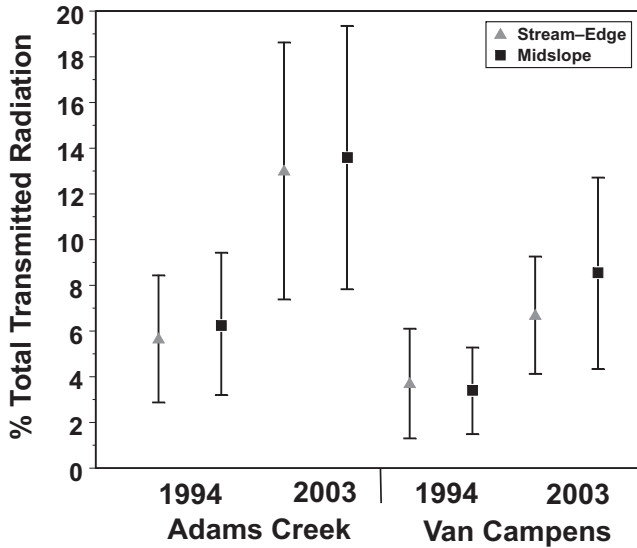
## Results

### Initial conditions: 1994–1995

In 1994, the hemlock forests at AC and VC were characterized by low light levels (Fig. 2) and sparse understory vegetation (Table 1). The comprehensive plant inventories found 316 plant species in the ground cover of the two ravines. This total includes 123 bryophytes, 24 pteridophytes, 122 flowering herbs, and 47 woody plants (for complete species list see Battles et al. 1997). Ground cover flora beneath hemlock-dominated canopy was less species rich than the ravine flora as a whole (69 vascular plant species and 50 bryophyte species). Soils at both sites were shallow (mean depth to obstruction = 7 cm) and acidic (median pH = 3.8).

Hemlock accounted for more than 50% of the canopy basal area and more than 65% of understory trees at both AC and VC (Table 2). Canopy structure differed significantly between the two sites in that trees at AC were taller and had proportionally smaller crown lengths (Table 2). These structural differences were associated with higher understory light availability at AC (Fig. 2). Light levels were consistently low at both ravines with no significant differences in understory light availability related to topographic location (ANOVA,  $p = 0.41$ , Fig. 2). In 1994, vascular plant abundance was more than twice as high at AC (*t* test,  $p = 0.004$ , Table 1). Vascular plant cover did not vary significantly with

**Fig. 2.** Understory light availability at Adams Creek and Van Campens in 1994 and 2003, separated by plot location within each ravine (AC:  $n = 18$  near-stream and edge and 36 midslope plots; VC:  $n = 13$  near-stream and edge and 24 midslope plots). Error bars represent standard deviation.



plot location (ANOVA,  $p = 0.55$ ) but bryophyte cover was greater at near-stream plots (12%, ANOVA,  $p < 0.001$ ).

Few significant differences were observed in the comparisons of seasonal (June 1994 and August 1994) or annual (June 1994 and June 1995) vegetation sampling. No significant changes in percent cover were observed across seasons or years, though a slight increase in the cover of *Dryopteris intermedia* was recorded from June to August as a result of further expansion of emerging fronds. Fluctuation in the abundance of tree seedlings was significant between years (paired  $t$  test,  $p < 0.001$ , Table 1) but not between June and August (paired  $t$  test,  $p = 0.37$ , Table 1). Species composition did not change between 1994 and 1995, and much of the increase in seedling density was due to recruitment of *Betula* spp. seedlings (includes *Betula lenta* and *Betula alleghaniensis*; Table 1). The only change in species composition between June and August was the addition of *Monotropa uniflora* L. (indian-pipe) and *Epifagus virginiana* (L.) Bartram (beechdrops), both late-blooming parasitic species, to the August survey.

**Canopy changes: 1994–2003**

From 1994 to 2003, no significant change occurred in total basal area ( $t$  test, AC  $p = 0.56$ , VC  $p = 0.52$ , Table 2) or in the relative dominance of hemlock ( $t$  test,  $p = 0.57$ , Table 2). However, hemlock tree vigor declined significantly (Wilcoxon signed-rank test,  $p < 0.001$ , Fig. 3), and changes in the transparency, dieback, and density of hemlock crowns all indicate significant decline (paired  $t$  test, all  $p < 0.001$ , Fig. 4). No trees met the definition of infestation (HWA on >5% of terminals) for several years following initial HWA detection at AC and VC. From 1999 to 2003, the number of infested trees increased annually with the most dramatic change occurring in 1999 and 2000 (Fig. 5). The mean adelgid infestation severity at each plot was strongly correlated with estimates of the annual change in crown transpar-

**Table 1.** Summary of vegetation cover, seedling densities, and species richness (plot and ravine scale) in permanent plots at each sampling period.

	Adams Creek ( $n = 54$ )				Van Campens ( $n = 37$ )				$p$ value	$p$ value
	June 1994	August 1994	June 1995	June 2003	June 1994	August 1994	June 1995	June 2003		
Vegetation cover (%)	4.2 (5.0)	4.4 (5.3)	7.9 (13.2)	16.6 (24.2)	1.6 (1.5)	1.5 (1.7)	2.5 (3.8)	3.4 (3.9)	<0.001	0.002
Total seedling density (seedlings·m <sup>-2</sup> ) <sup>a</sup>	1.9 (3.4)	2.5 (3.1)	5.3 (12)	8.4 (9.0)	2.8 (3.9)	3.2 (5.1)	4.9 (10.7)	6.7 (7.4)	<0.001	<0.001
Relative seedling density (%)										
<i>Acer rubrum</i>	25.1	22.9	41.7	12.6	10.7	22.1	37.9	18.4		
<i>Acer saccharum</i>	34.2	30.6	15.8	2.1	22.3	26.0	33.6	0.95		
<i>Betula</i> spp.	33.0	35.0	27.4	69.8	52.2	34.7	16.8	71.9		
<i>Tsuga canadensis</i>	7.7	8.2	5.6	14.9	3.1	5.1	8.2	5.3		
Plot species richness	5.04 (3.76)	5.1 (3.91)	6.18 (4.37)	7.25 (4.25)	4.18 (2.88)	3.97 (2.69)	4.62 (3.42)	5.38 (4.04)		
Ravine-scale richness	69	71	70	79	35	36	39	59		

**Note:** Values reported at the plot scale are means (standard deviation) and those at the ravine scale are total species counts by site.  $P$  values are reported for all significant paired  $t$  test (two-tailed) comparisons between: June 1994 and August 1994 (seasonal), June 1994 and June 1995 (annual), and June 1994 and 2003; values are shown in the column next to the latter sampling period.

<sup>a</sup>Seedling (trees <1 m tall) densities calculated from 1 m × 0.5 m subplots.

**Table 2.** Summary of stand and site characteristics at Adams Creek and Van Campens ravines in 1994 and 2003.

	Adams Creek ( <i>n</i> = 54) <sup>a</sup>			Van Campens ( <i>n</i> = 37) <sup>a</sup>		
	1994	2003	<i>p</i> value	1994	2003	<i>p</i> value
Canopy basal area (m <sup>2</sup> ·ha <sup>-1</sup> )	52.1 (18.3)	55.2 (20.5)	0.557	44.9 (19.9)	48.8 (24.0)	0.519
Relative basal area (%) <sup>b</sup>						
<i>Acer saccharum</i>	5.1	5.1		0.2	1.4	
<i>Betula lenta</i>	6.8	8.6		14.6	14.4	
<i>Pinus strobus</i>	17.0	15.1		—	—	
<i>Quercus alba</i>	6.2	6.9		8.6	8.8	
<i>Quercus prinus</i>	4.9	5.4		2.3	2.1	
<i>Tsuga canadensis</i>	51.4	53.5		55.2	57.4	
Understory density (stems·ha <sup>-1</sup> )	877 (526)	1063 (706)	0.002	1032 (621)	742 (457)	0.006
Relative understory density (%) <sup>b</sup>						
<i>Acer rubrum</i>	3.6	2.8		7.3	5.4	
<i>Betula lenta</i>	8.6	10.4		9.2	11.6	
<i>Fagus grandifolia</i>	4.1	18.3		2.6	2.1	
<i>Tsuga canadensis</i>	66.3	36.0		69.3	69.0	
Canopy height (m)	30.2 (3.8)	29.5 (4.0)		26.2 (5.1)	27.0 (5.7)	
Live crown ratio	0.50	0.45		0.53	0.52	
Substrate cover (%)						
Mineral soil	0.23 (1.0)	0.85(3.1)	0.158	0.07 (0.41)	0.26 (1.1)	0.160
Bryophyte	5.1 (11.6)	5.3 (10.8)	0.852	1.4 (4.2)	3.9 (10.0)	0.033
Woody debris	2.3 (4.2)	5.1 (6.4)	0.004	3.6 (5.2)	3.5 (4.4)	0.935
Leaf litter	88.0 (15.0)	84.0 (17.5)	0.007	87.3(14.2)	85.6 (17.9)	0.198

**Note:** Values reported are means (standard deviation). Significance of 1994 to 2003 comparisons based on *t* tests (two-tailed) are given.

<sup>a</sup>Near-stream plots are not included in basal area and density calculations (AC, *n* = 43; VC, *n* = 29).

<sup>b</sup>All species with >5% relative basal area or relative density in one or both sites or time periods are reported.

ency ( $r = 0.818, p < 0.001$ ) and crown dieback ( $r = 0.687, p < 0.001$ ) and had a weaker relationship with the change in crown density ( $r = 0.275, p = 0.03$ ). Between 1995 and 2003, the average annual mortality rate for canopy hemlocks was 2.0% (2.7% at AC and 1.3% at VC, calculated as recommended in Sheil and May 1996). In 2003, 25% of the 600 monitored hemlock trees were either dead or in severe decline (Fig. 3).

Though hemlock decline was evident at both sites, all the metrics used to quantify decline show that AC has been more severely impacted by HWA than VC. From 1994 to 2003, 19% of measured hemlock trees at AC declined from a vigor rating of healthy to severe decline, and 13% declined from healthy to dead. At VC, only 2% of monitored hemlocks declined from healthy to severe decline, and 7% declined from healthy to dead. In 2003, 34% of monitored hemlock trees at AC were either dead or in severe decline compared with only 9% of monitored trees at VC. Vigor data from AC show substantial decline (Wilcoxon signed-rank test,  $p < 0.0001$ , Fig. 3); transparency increased by 45%, density decreased by 12%, and dieback increased by 38% (paired *t* test, all  $p < 0.0001$ , Fig. 4). At VC, the change in density was not significant (4%, paired *t* test,  $p = 0.09$ ), transparency increased more gradually by about 16%, dieback increased by 19% (paired *t* test, both  $p < 0.0001$ , Fig. 4), and vigor declined significantly but remained relatively high (Wilcoxon signed-rank test,  $p < 0.0001$ , Fig. 3). These trends in decline were consistent with the rate of infestation spread in each ravine. The proportion of trees with HWA infestation increased more rapidly at AC than at VC (Mantel–Haenszel,  $p < 0.0001$ , Fig. 5). Although the median time to HWA infestation for trees at AC (6 years) and VC

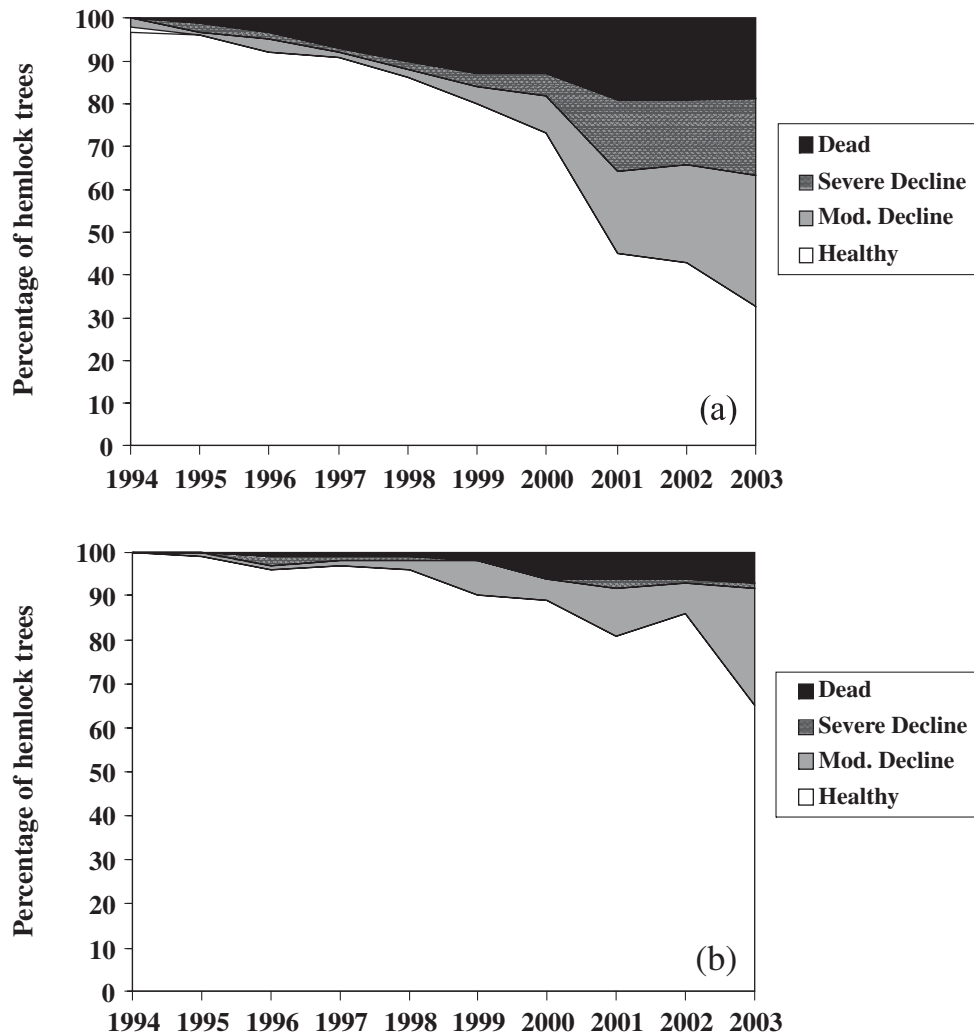
(7 years) differed by only 1 year, the percentage of infested trees at AC in 2003 was 95.6% compared with 67.6% at VC (Fig. 5).

Although hemlock vigor at AC declined more than at VC, the condition of individual hemlock trees in each ravine ranged from healthy to dead. In 2003, approximately 75% of the hemlock monitoring plots contained at least one dead tree, and all plots had trees with only slight decline. There was no apparent relationship between hemlock decline (transparency, dieback, density) and topographic location or distance from stream (ANOVA, all  $p > 0.50$ ). In addition, no spatial autocorrelation was observed in the pattern of hemlock decline based on crown vigor, transparency, dieback, or density (Moran's *I*, all  $p > 0.65$ ). At both sites, canopy class was a significant factor in hemlock decline. Greater hemlock decline and mortality occurred in intermediate and suppressed trees (ANOVA,  $p < 0.005$ ). Understory hemlock density declined from 581 to 383 stems·ha<sup>-1</sup> at AC and from 715 to 511 stems·ha<sup>-1</sup> at VC over the 9-year study period (paired *t* test, both  $p < 0.0006$ , Table 2).

**Response to canopy change**

Understory light availability increased significantly from 1994 to 2003 in both ravines (paired *t* tests, both  $p < 0.001$ , Fig. 2). Between site comparisons showed that average light levels increased significantly more at AC (7.8%) than at VC (4.2%, *t* test,  $p = 0.006$ ). Changes in light availability did not vary significantly among topographic locations (i.e., near-stream, midslope, or ravine edge plots; ANOVA,  $p = 0.35$ ). In addition, no spatial autocorrelation was observed for understory light availability (Moran's *I*, both  $p = 0.82$ ) or changes in light availability over the study period (Moran's

**Fig. 3.** Percentage of hemlock trees in each crown vigor class at (a) Adams Creek (AC,  $n = 360$ ) and (b) Van Campens (VC,  $n = 240$ ) from 1994 to 2003. Vigor classes are based on the amount of foliage retained: healthy (in this figure, included trees in slight decline, 51%–100%), moderate decline (26%–50%), severe decline (1%–25%), or dead (0).



$I$ , AC  $p = 0.83$  and VC  $p = 0.32$ ). Light availability at each plot was strongly correlated with measures of crown density ( $r = -0.676$ ), transparency ( $r = 0.697$ ), and dieback ( $r = 0.822$ ) from adjacent hemlock trees (all  $p < 0.001$ , Fig. 6).

Changes in substrate composition at AC included a 4.0% decrease in litter cover (paired  $t$  test,  $p = 0.007$ ) and a 2.8% increase in woody debris (paired  $t$  test,  $p = 0.004$ , Table 2). No significant change in substrate cover occurred at VC (Table 2). The only significant difference between sites was the greater increase in woody debris at AC ( $t$  test,  $p = 0.009$ ). Bryophyte cover remained significantly higher in near-stream plots (12%,  $p < 0.002$ ), and there were no differences in substrate change among plot locations (ANOVA, all  $p > 0.10$ ).

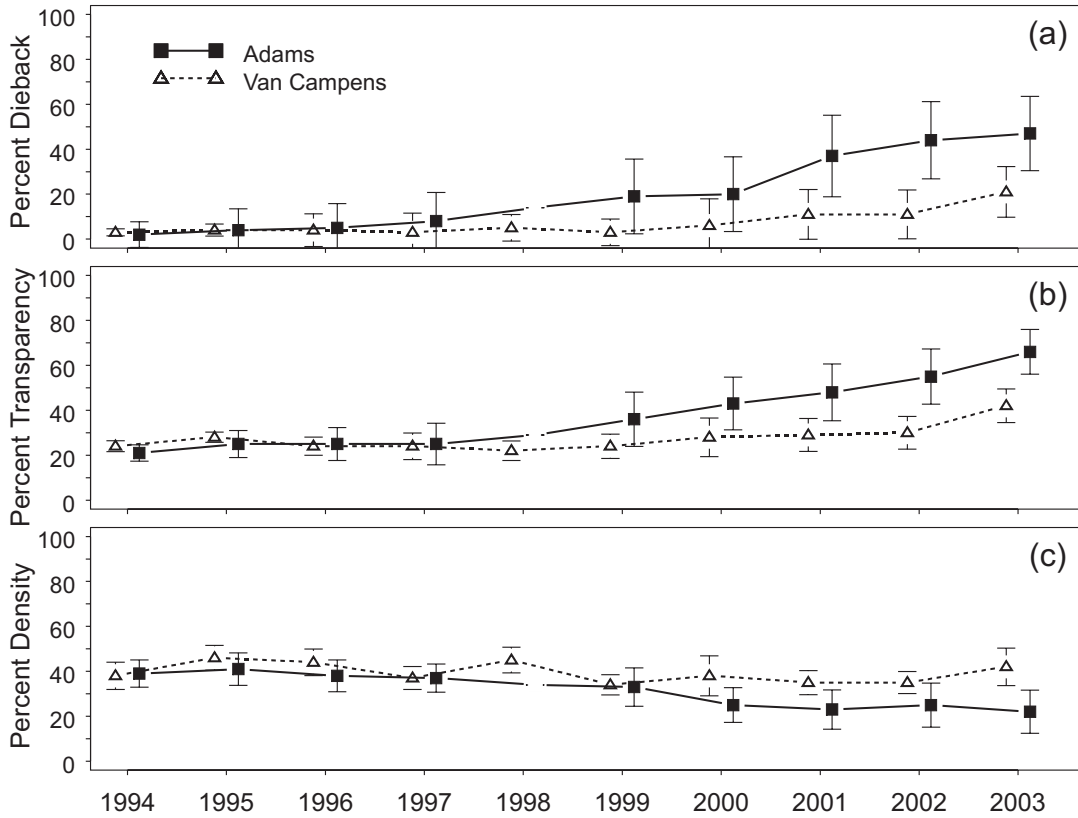
Although understory hemlock density declined at both sites, the density of all understory trees increased at AC and decreased at VC ( $t$  test, all  $p < 0.006$ , Table 2). At AC, significant increases in the density of *Fagus grandifolia* Ehrh. (American beech) and *Betula* countered the decline of the hemlock understory, and hemlock relative density was reduced (Table 2). In contrast, no species experienced a significant increase in understory density at VC, and hemlock

relative density did not change (Table 2). Average tree seedling densities were four times higher in 2003 with a significantly greater increase in seedling density occurring at AC ( $t$  test,  $p < 0.001$ , Table 1).

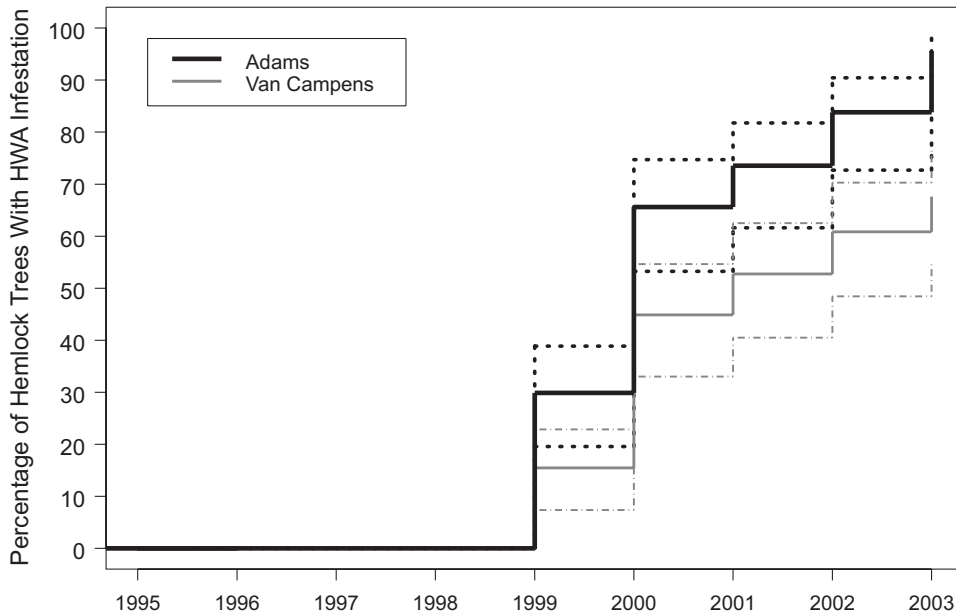
The percent vegetation cover increased significantly at both AC and VC from 1994 to 2003 (paired  $t$  test, both  $p < 0.002$ , Table 1). However, a between-site comparison showed that the increase in percent cover at AC (12.4%) was significantly greater than the increase at VC (1.8%,  $t$  test,  $p = 0.003$ , Table 1). The percent cover of *Betula* spp., *Tsuga canadensis*, *Dryopteris intermedia*, *Dennstaedtia punctilobula*, and *Mitchella repens* L. (partridgeberry) increased significantly at AC, while only *Betula* spp. and *Sassafras albidum* (Nutt.) Nees (sassafras) cover increased significantly in VC (paired  $t$  test, all  $p < 0.001$ , Fig. 7). When plots from both sites are combined, small but significant increases in the percent cover of *Liriodendron tulipifera* L. (tulip tree) and *Nyssa sylvatica* Marsh. (black gum) were also observed (paired  $t$  test, all  $p < 0.001$ ). No species experienced a significant decline in percent cover at either site. No change was detected in the percent cover of other common species such as *Fagus grandifolia*, *Maianthemum canadense* Desf.



**Fig. 4.** Change in the (a) dieback (loss of needles at branch tips), (b) transparency (relative amount of light that passes through tree crown), and (c) density (“fullness” and density of branches and foliage) of hemlock crowns at Adams Creek (AC,  $n = 360$ ) and Van Campens (VC,  $n = 240$ ) from 1994 to 2003 (no data for AC in 1998). Error bars represent standard deviation.



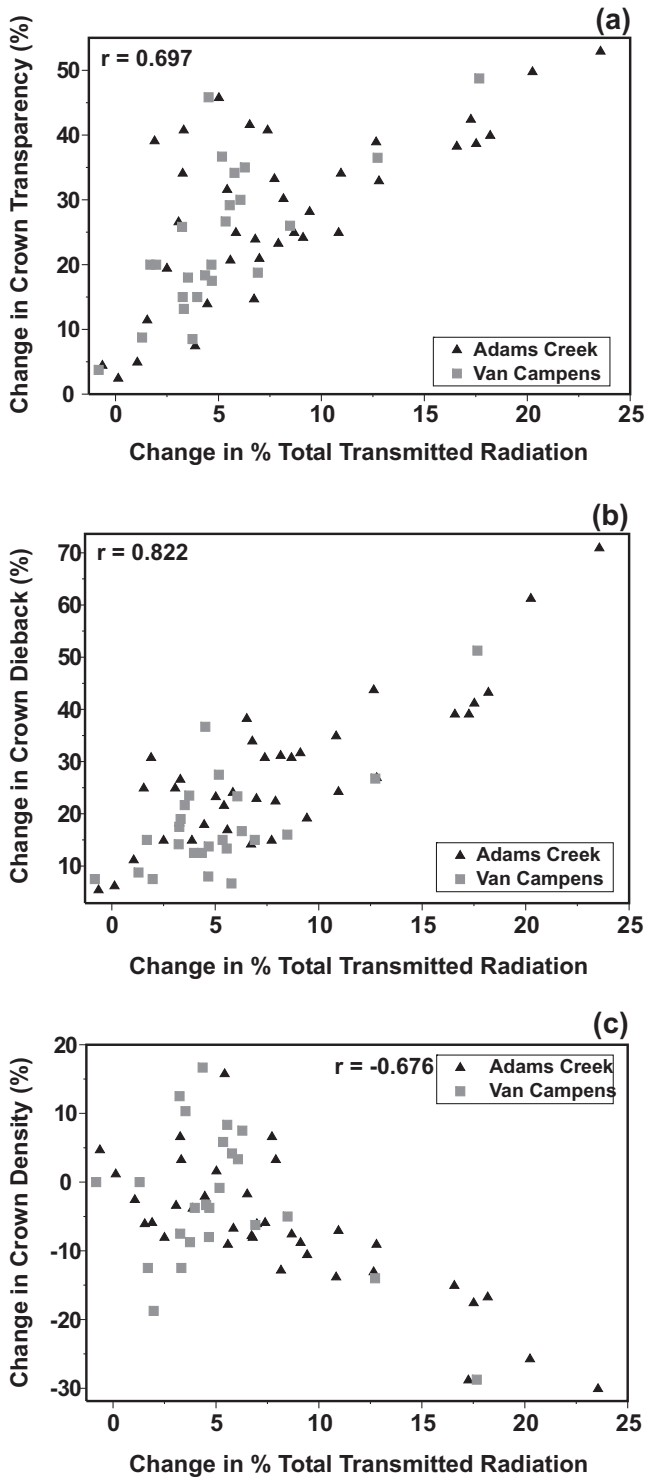
**Fig. 5.** Kaplan–Meier survival curves of time until infestation for hemlock trees at Adams Creek and Van Campens with 95% confidence intervals ( $n = 174$ ). For this analysis, monitored hemlock trees were categorized as infested when HWA was observed on >5% of terminal branches. Although HWA was present in the ravines in 1995, no monitored hemlock trees met this definition of infestation until 1999.



(Canada mayflower), or *Acer rubrum* (paired  $t$  test, all  $p > 0.01$ , Fig. 7). *Dryopteris intermedia* and *Dennstaedtia punctilobula* exhibited the greatest increases in percent

cover from 1994 to 2003 (Fig. 7). There was no significant relationship between topographic location and total plant cover or change in cover (ANOVA, both  $p > 0.55$ ). Change

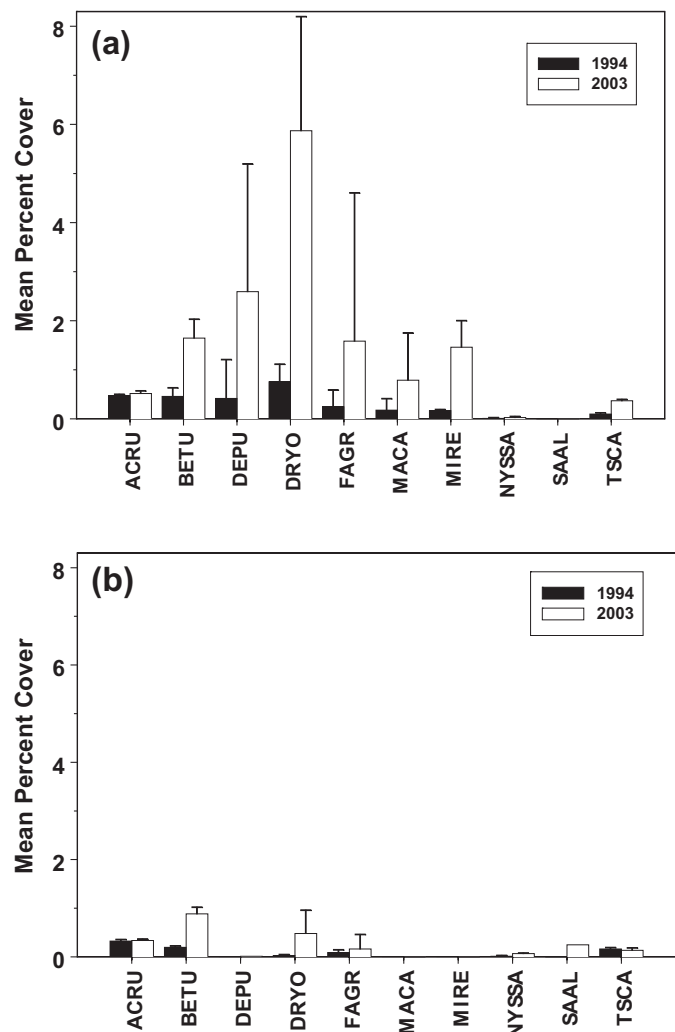
**Fig. 6.** Relationships between changes in light availability and changes in crown rating measures at Adams Creek and Van Campens from 1994 to 2003. Change in hemlock crown (a) transparency, (b) dieback, and (c) density (all  $n = 60$ ).



in plant cover was positively correlated with change in understory light availability ( $r = 0.644$ ,  $p < 0.001$ ).

In both 1994 and 2003, the most frequently occurring understory vascular plants at both sites were *Acer rubrum* and *Betula* spp. seedlings (Table 3). *Betula* spp. had the largest increase in frequency from 1994 to 2003, while *Acer*

**Fig. 7.** Mean percent cover of 10 common (found in  $\geq 10\%$  of plots) ground cover plant species in 1994 and 2003 for (a) Adams Creek and (b) Van Campens. Error bars represent standard error of the mean. Species are abbreviated as follows: ACRU, *Acer rubrum*; BETU, *Betula* spp.; DEPU, *Denstaedia punctilobula*; DRYO, *Dryopteris intermedia*; FAGR, *Fagus grandifolia*; MACA, *Maianthemum canadense*; MIRE, *Mitchella repens*; NYSSA, *Nyssa sylvatica*; SAAL, *Sassafras albidum*; TSCA, *Tsuga canadensis*.



*rubrum* frequency did not change (Table 3). Although several species increased in frequency, the only species with significant reductions in plot occurrence were *Fagus grandifolia* and *Streptopus amplexifolius* (L.) DC. (twisted-stalk; sign tests, both  $p < 0.005$ , Table 3). The occurrence of *Tsuga canadensis* seedlings increased significantly at AC but declined somewhat at VC (Table 3). For species such as *Liriodendron tulipifera*, *Nyssa sylvatica*, *Sassafras albidum*, and *Tsuga canadensis* the increase in frequency largely explains the increase in cover (sign tests, all  $p < 0.001$ , Table 3), and the size of individuals did not increase significantly. However, the percent cover of other common species such as *Mitchella repens*, *Dryopteris intermedia*, and

**Table 3.** Changes in species frequency at Adams Creek and Van Campens from 1994 to 2003.

	Adams Creek ( <i>n</i> = 54)			Van Campens ( <i>n</i> = 37)		
	Frequency 1994	Frequency 2003	<i>p</i> value	Frequency 1994	Frequency 2003	<i>p</i> value
<i>Acer rubrum</i>	42	43	0.754	29	31	0.754
<i>Acer saccharum</i>	6	13	0.118	3	3	—
<i>Aster divaricatus</i> *	1	12	<0.001	0	2	0.50
<i>Betula</i> spp.*	29	49	<0.001	21	30	0.004
<i>Carex</i> spp.	2	5	0.250	3	7	0.219
<i>Carya glabra</i>	0	5	0.063	0	0	—
<i>Circaea alpina</i> *	0	8	0.008	0	0	—
<i>Dennstaedtia punctilobula</i>	5	7	0.50	2	2	—
<i>Dryopteris intermedia</i>	18	23	0.063	4	7	0.375
<i>Fagus grandifolia</i> †	8	4	0.031	6	5	0.250
<i>Liriodendron tulipifera</i> *	0	2	0.50	0	8	0.008
<i>Maianthemum canadense</i>	7	11	0.125	1	0	0.891
<i>Mitchella repens</i>	25	30	0.125	1	0	0.891
<i>Nyssa sylvatica</i> *	2	5	0.375	2	10	0.008
<i>Pinus strobus</i>	10	10	—	0	0	—
<i>Polystichum acrostichoides</i>	7	6	0.691	0	2	0.50
<i>Prunus serotina</i>	0	4	0.125	0	3	0.250
<i>Quercus alba</i>	1	6	0.125	0	2	0.50
<i>Sassafras albidum</i> *	0	0	—	0	9	0.004
<i>Streptopus amplexifolius</i> †	5	0	0.0625	3	0	0.250
<i>Tsuga canadensis</i> *	14	32	<0.001	17	12	0.125

**Note:** List includes species found in  $\geq 9\%$  of plots and seedling species new to the ravine floras in 2003. Values are numbers of 2 m  $\times$  4 m plots in which the species occurred. *P* values indicate the significance of 1994 to 2003 comparisons by ravine (sign tests). \* indicates significant increase and † indicates significant decrease (all  $p < 0.007$ ) in species frequency between 1994 and 2003 when plots from both sites combined.

*Dennstaedtia punctilobula* increased dramatically but with no significant change in frequency (Fig. 7, Table 3). Fern species occurred in dense patches under canopy openings and therefore had highly variable distributions (coefficient of variation >500%).

Species richness increased overall, though this increase was only significant at AC (*t* test, AC  $p < 0.001$ , VC  $p = 0.021$ , Table 1). The change in species richness in the midslope plots was positively correlated with change in light availability from 1994 to 2003 ( $r = 0.81$ ,  $p < 0.002$ ). In both ravines, species gains made up the largest component of plot-level species mobility followed by species persistence and then losses (Table 4). At the plot level, species gains were significantly higher at AC (Table 4). Seedlings and herb species contributed equally to plot-level species mobility. A similar pattern was seen in the absolute losses and gains of species at the ravine scale (Table 4). The number of new species added to the ravine flora between 1994 and 2003 was greater than the number of species lost. However, at the ravine scale more species were gained at VC than at AC (Table 4). Notable species additions included several early-successional or higher light demanding species such as *Sassafras albidum* (9 plots), *Carya glabra* (Mill.) Sweet (pignut hickory; 5 plots), *Parthenocissus quinquefolia* (L.) Planch (Virginia-creeper; 5 plots), and *Prunus serotina* Ehrh. (black cherry; 7 plots) (Burns and Honkala 1990; Rhoads and Block 2000).

The comprehensive plant inventories conducted in 1994 found no invasive plants at AC or VC despite the existence of reproducing populations along ravine edges (Battles et al. 1997). However, resurveys of these plots conducted in 2003

show that nearly 35% of the 5 m radius plots contained at least one invasive plant species and 5% of these plots contained two or more. AC had more than 70% of the invasive plant occurrences: *Ailanthus altissima* (Mill.) Swingle (tree-of-heaven; 1 plot), *Alliaria petiolata* (M. Bieb.) Cavara (garlic mustard; 4 plots), *Berberis thunbergii* DC. (Japanese barberry; 13 plots), *Microstegium vimineum* (Trin.) A. Camus (Japanese stiltgrass; 6 plots), and *Rosa multiflora* Thunb. ex Murray (multiflora rose; 2 plots). Only *Berberis thunbergii* (3 plots) and *Microstegium vimineum* (7 plots) were found at VC. Spatial patterns of invasion differed between the two ravines in that all invasive plants at VC were in the near-stream and 10 m plot locations, whereas invasive plants at AC were evenly distributed among all plot locations. Invasive plant species occurrence was not significantly related to light availability at these sites (Wald  $Z = 1.76$ ,  $p = 0.079$ , area under ROC = 0.579).

## Discussion

Introduced pests and pathogens are among the most serious threats to the integrity of forest ecosystems. The frequency of exotic pest and pathogen outbreaks has continued to increase throughout the past century, resulting in widespread and dramatic shifts in forest structure and function (Castello et al. 1995; Liebhold et al. 1995). The importance of understanding the consequences of forest pest outbreaks is magnified for species such as hemlock that exert strong control over stand microclimate and ecosystem processes. The continuing decline of hemlock caused by HWA provided a unique opportunity to examine forest response to the

**Table 4.** Summary of species mobility at Adams Creek and Van Campens at plot and ravine scales from 1994 to 1995 and from 1994 to 2003.

Plot scale	1994 to 1995					1994 to 2003				
	Total loss	Total gain	Persisted	Species richness		Total loss	Total gain	Persisted	Species richness	
				1994	1995				1994	2003
Adams Creek	58	97	197	5.0 (3.8)	6.2 (4.4)	84	236	149	5.0 (3.8)	7.3 (4.3)
Van Campens	38	75	86	4.2 (2.9)	4.6 (3.4)	53	116	74	4.2 (2.9)	5.4 (4.0)
Ravine scale										
Adams Creek	1	2	68	69	70	14	24	55	69	79
Van Campens	0	4	35	35	39	5	29	30	35	59

**Note:** Plot-scale losses = the number of times a species occurred in a plot in 1994 and was absent in the resurvey (1995 or 2003). Plot-scale gains = the number of times a species occurred in a plot in the latter survey (1995 or 2003) that had not been recorded in that plot in 1994. Ravine-scale values reflect absolute changes in species richness at each site (all plots combined AC 54 plots, VC 37 plots). *P* values indicate the significance of paired *t* test (two-tailed) comparisons between time periods.

selective decline of a dominant tree species. This study documented dramatic changes in understory light availability and vegetation patterns and highlighted potential issues of management concern such as the invasion of exotic plants.

Although hemlock decline was more severe at AC than VC, we found no spatial pattern in hemlock decline at the scale of these plots, and hemlock conditions at both sites ranged from healthy to dead. Despite significant mortality of hemlock at these sites, basal area did not change significantly and was not a good indicator of hemlock decline. Though it has been suggested that hemlock decline is correlated with site factors such as slope, slope shape, aspect, and soil moisture (Royle and Lathrop 2002; Young and Morton 2002), we found no significant difference in hemlock decline at varying topographic positions or distance from streams. Consistent with previous findings (Orwig and Foster 1998), canopy position was a significant factor in hemlock decline at these sites, with greater decline and mortality for suppressed and intermediate trees.

Results from these study plots and other hemlock monitoring at DEWA (Evans 2004) suggest a more gradual rate of hemlock decline than has been reported for other locations. McClure (1991) reported that feeding by HWA can kill hemlock stands within 4 years. Orwig et al. (2002) found that mortality in moderately damaged stands increased by 5%–15% per year but that trees on some sites seemed to survive more than 10 years of infestation. After 8 years of HWA infestation in our study sites, hemlock decline has been significant but only 15% of hemlock trees have died. Although this varying temporal response to HWA infestation has been documented, the factors contributing to the observed variations in the rate of hemlock decline remain unclear. The recorded rate of decline at DEWA may be lower because of site characteristics, climatic influence, genetic factors, rate of HWA dispersal, or success of biocontrol agents. It is also possible that the lower observed rate of decline at DEWA was caused by underestimation of the timing of initial HWA infestation in previous studies. Given the slow initial rates of hemlock decline (Fig. 3) and HWA infestation spread (Fig. 5), it is likely that HWA presence at AC and VC would have gone undetected for several years if not for DEWA's ongoing monitoring program. Accurate information on the rate of HWA-caused hemlock decline is valuable in that variation in this rate could have important impacts on forest understory response. For instance, in a comparison of forest response to hemlock canopy removal from HWA damage and from logging, Kizlinski et al. (2002) found significant differences in the abundance and composition of understory vegetation and the size of inorganic nitrogen pools.

Previous studies have found that hemlock regeneration following HWA infestation is largely absent and often shows signs of adelgid presence (Orwig and Foster 1998; Yorks et al. 2000; Orwig 2002). In contrast, we observed a significant increase in the overall frequency and cover of hemlock seedlings. In addition, a related study similarly conducted in 10 DEWA hemlock ravines in various stages of decline found that few hemlock seedlings had signs of HWA infestation (14% of the 110 plots with hemlock seedlings, A.K. Eschtruth, unpublished data). However, the distribution of hemlock cover values suggests that the increase in hemlock



seedling cover is largely due to an increase in the frequency and not the size of individuals. It is also interesting to note that while the overall frequency of hemlock seedlings increased, the frequency decreased somewhat at VC, the site less impacted by HWA. Additionally, hemlock seedling density changed significantly over both the 9-year study period and from 1994 to 1995. This suggests that seedling abundance may not be a good criterion for monitoring purposes, as it reflects annual variation in seed production and predation, herbivory, weather, and germination rather than establishment success. The presence of hemlock regeneration and slower rate of overstory hemlock decline at DEWA suggest a slightly more optimistic outcome; however, HWA has spread to nearly all hemlock stands in DEWA, the canopy monitoring data suggest a continuing decline, and no infested tree has shown any sign of recovery.

Measures of hemlock crown health and HWA infestation levels provided a means of quantifying the strength of the relationship between understory light availability and the extent of hemlock decline. The high correlations between HWA infestation severity and hemlock decline in these plots allow us to attribute much of the decline observed over this study period to HWA infestation. However, additional factors may have contributed to this decline including summer drought in 1997 and 2001, chronic nitrogen deposition (NADP 2005), and damage from other forest pests such as hemlock scales (*Fiorinia externa* and *Nuculaspis tsugae*) and the hemlock borer beetle (*Melanophila fulvoguttata*) (Evans et al. 1996). The sensitivity of hemlock to drought stress (Burns and Honkala 1990) and the benefits of available nitrogen (McClure 1992) and mild winters (Parker et al. 1998; Skinner et al. 2003) for HWA populations have been documented and clearly play a role in regulating HWA population levels and hemlock health. However, the extent and role of these interacting factors in contributing to HWA susceptibility and hemlock decline remain poorly understood (Evans et al. 1996). Despite these contributing stressors, the evidence from these sites suggests that HWA was the dominant factor in this decline.

Owing to the absence of a reference ravine at DEWA that has not been infested with HWA, it is not possible to conclusively attribute all observed changes in hemlock health to HWA. However, evidence from several noninfested hemlock stands during the same time period can provide baseline information for changes due to factors other than HWA. In 1998, long-term monitoring plots were established in hemlock stands (mean hemlock relative abundance = 51.2%) in the New River Gorge National River and Gauley River National Recreation Area in West Virginia (Wood 1999). HWA was not found in these stands until 2004. Annual mortality rates for hemlock trees ( $\geq 8$  cm DBH,  $n = 482$ ) from 1998 to 2003 were 0.25%, and the percentage of trees in moderate to severe decline increased from 0% in 1998 to 3% in 2003 (Wood 1999, J.H. Perez, unpublished data). Similarly, annual mortality rates for hemlock ( $>10$  cm DBH,  $n = 642$ ) in long-term monitoring plots in the Arnot Forest (mean hemlock relative basal area = 17.2%) in south central New York from 1993 to 2000 were 0.22% (Fain et al. 1994; T.J. Fahey, unpublished data). In the Hubbard Brook Experimental Forest in New Hampshire, hemlock annual mortality rates of 0.20% ( $>10$  cm DBH,  $n = 51$ ) were observed in permanent

plots monitored from 1995 to 2005 (mean hemlock relative basal area = 15.4%, Schwarz et al. 2003; J.J. Battles, T.J. Fahey, and T.G. Siccama, unpublished data). Data from these forests indicate that in the absence of HWA, hemlock mortality and decline were not elevated during the time period of our study.

The varying severity of HWA damage at AC and VC allowed us to compare understory response to different degrees of disturbance. The greater decline at AC was associated with higher light levels, a larger increase in the abundance and frequency of vascular plant species, greater woody debris substrate cover, a dramatic increase in fern cover, higher numbers of early-successional plant species, and may have contributed to the greater frequency of invasive plants. At both sites, change in ground cover included an increase in species richness. This change was largely due to an increase in the frequency of common species such as *Betula* spp. and *Tsuga canadensis* and, to a lesser extent, the addition of new species and increase in the frequency of early-successional species. The low rate of new species occurrences in these ravines may be due, in part, to the absence of a buried seed pool (Battles et al. 2000).

While species composition did not change significantly at either ravine, many early-successional species were added to the ravine floras and few species were completely lost. Species losses may increase as some hemlock-associated species are out competed as a result of a more complete conversion of the hemlock canopy. Interestingly, more new species occurrences were seen at VC despite the lower increase in light. This may be due to the fact that the range of light levels occurring in these forests in 1994 was significantly lower at VC. These low light levels may have excluded many species that were able to establish after a small threshold increase in understory light level. Although several species were lost from these ravines over the study period, most were relatively low in frequency and therefore did not exhibit a significant negative response. However, some of these losses are of potential concern. For instance, *Streptopus amplexifolius* is a state-listed endangered species in both New Jersey and Pennsylvania (Table 3).

Understory species did not respond uniformly to changes in light availability. Most common species at AC experienced an increase in percent cover. *Mitchella repens*, *Dryopteris intermedia*, and *Dennstaedtia punctilobula* had dramatic increases in percent cover but were not found in significantly more plots in 2003. Whereas for species such as *Liriodendron tulipifera*, *Nyssa sylvatica*, *Sassafras albidum*, and *Tsuga canadensis* the main response was an increase in frequency that was great enough to be detected as a significant increase in cover. The decline in occurrence of *Fagus grandifolia* in the ground cover was unexpected, as seedlings are abundant in nearby forests and *Fagus grandifolia* increased significantly in the understory ( $>1$  m in height).

Although many forest ecosystems are currently experiencing unprecedented levels of novel disturbances, ecologists do not fully understand the role of disturbance in influencing community susceptibility to invasion. This long-term data set with baseline vegetation and environmental measurements can provide insights into the patterns and mechanisms of invasive species entry into disturbed systems. Hemlock

decline may contribute to the spread of invasive plant species both directly through disturbance impacts and indirectly by removing dispersal barriers. Historically, hemlock canopy recruitment occurred largely via replacement in fine-scale tree-fall gaps (Frellich and Lorimer 1991), and the abundance of vascular plants was limited by the understory environment (Rogers 1978). The gradual thinning of the canopy caused by HWA infestation is a novel occurrence in hemlock forests that may have fundamentally different consequences for exotic plant invasion than the process of gap formation and species replacement. Severe hemlock decline appears to have contributed to the significant increase in exotic plant species invasions at these sites; however, the mechanism for this increase remains unclear. Presence of invasive plant species at these sites was not well explained by changes in light availability, and the historical absence of invasives at AC and VC suggests that propagule pressure may be a more limiting factor than light in the early stage of invasion. The spatial patterns of invasion of exotic plant species at these sites further indicate the importance of propagule pressure. Further studies at these sites will investigate the role of propagule pressure in influencing the spread of exotic plants in response to hemlock decline.

Through periodic remeasurement of permanent plots with detailed baseline vegetation and environmental data, this study contributes to our understanding of the changes in forest structure and composition resulting from an introduced forest pest. Evidence from this and other studies indicates that hemlock decline will result in dramatic changes in understory vegetation, light availability, and inputs of coarse woody debris, and will likely result in complete hemlock canopy mortality and transition to hardwood stands in many areas. Long-term documentation of forest ecosystem response is essential to identify the risks associated with the introduction of exotic pests. In an age where forests face a suite of novel stressors, it is critical that we improve our understanding of the relative roles of these stressors and the consequences of their interaction in determining forest response.

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