Vegetation Composition and Structure in Two Hemlock Stands Threatened by the Hemlock Woolly Adelgid.

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Abstract

We quantified the vegetation composition and structure of two hemlock (*Tsuga canadensis*) ravines in the Delaware Water Gap National Recreation Area threatened by the hemlock woolly adelgid (*Adelges tsugae*). Hemlock accounted for more than 50% of the canopy basal area (ravine mean = 52.3 m^2 ha^{-1}) and more than 75% of the understory trees and saplings (ravine mean = 599 stems ha^{-1}). Other common trees were black birch (*Betula lenta*) and red maple (*Acer rubrum*); white pine (*Pinus strobus*) was abundant at one site. The forest understories were shady with limited cover of vascular plants (ravine mean = 5%). Average understory light levels ranged from 6% of the above-canopy light in the more open stand to only 3% in the more closed-canopy stand. Two ferns, *Dryopteris intermedia* and *Dennstaedtia punctilobula*, were the most abundant herbaceous plants with a patchy distribution. Bryophyte cover averaged 9%; *Mnium hornum* and *Hypnum imponens* were the most abundant mosses.

Birch seedlings were the most frequent vascular plant (>70% of the plots) followed by red maple (> 50% of the plots). Average tree seedling density in 1994 was 3.2 seedlings m^{-2}; seedling density doubled in 1995. The density of woody species germinating from buried seed was < 2 germinants m^{-2}. The dominance of hemlock in both the canopy and subcanopy stratum, the lack of a non-hemlock sapling bank, the absence of a buried seed pool, and the prevalence of black birch and red maple seedlings and adults, all suggest that the initial response to any adelgid caused mortality will be a rapid increase in birch and maple importance in these stands.

Introduction

The hemlock woolly adelgid (*Adelges tsugae* Annand.) is an exotic pest currently threatening hemlock trees (*Tsuga canadensis* (L.) Carr.) in the eastern United States (McClure 1991, Royle and Lathrop 1997, Orwig and Foster 1998). Adelgid infestations have caused rapid defoliation of hemlock trees and can result in complete mortality of all hemlock trees in affected stands within four years (McClure 1991) but the severity of the damage varies among stands (Orwig and Foster 1998). In 1989, the hemlock woolly adelgid was detected on trees at the southern end of the Delaware Water Gap National Recreation Area (DEWA). In response, the National Park Service (NPS) established a program to monitor the adelgid population. However, the NPS is concerned not only about the damage to hemlock trees caused by the adelgid but also about the changes in resource quality and park value that may result from adelgid infestations in hemlock stands at the DEWA (Evans 1995). As part of a larger program to document baseline ecological conditions and to monitor hemlock ravines threatened by the pest, we quantified pre-outbreak vegetation composition and structure in two study ravines. Secondary objectives included identifying the important environmental gradients influencing variation in understory composition and assessing possible vegetation responses to future hemlock decline.

Methods

Study sites

Resource managers at DEWA initiated intensive studies in two forested ravines dominated by eastern hemlock: Adams Creek (Pike County, Pennsylvania) and Van Campens Brook (Sussex and Warren Counties, New Jersey) in order to document baseline ecological conditions. At the start of the study in 1993, neither ravine was infested. By the end of our fieldwork in late summer 1995, adelgid had been detected in both ravines but as of June 1999, there was no sign of decline in resident hemlock trees.

Adams Creek and Van Campens Brook are tributaries to the Delaware River (41° 31' N, 74° 49' W). They are 5.5 km straight-line distance apart. The regional climate is humid continental with 30-yr mean monthly temperature of 10.0°C and median annual precipitation of 74 cm (National Weather Service). 1994 was a wetter than a typical year with total precipitation of 129 cm of rain; 1995 was closer to the norm with 69 cm of rain (National Weather Service). The microclimate of the hemlock ravines tends to be somewhat cooler and more humid than the local average (Rogers 1980).

Adams Creek is a third order stream which flows southeast off the Pocono Plateau. Elevation 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 consists of approximately 36 ha of hemlock-dominated forest along both sides of Adams Creek. The study area at Adams Creek was never cleared for agriculture; tree cutting was limited to small scale harvests for use on a private estate. A *Pinus strobus* plantation along the northern edge of the ravine was planted by the Civilian Conservation Corps in the mid-1900s (W. Millington, *pers. comm.*). Stand age was estimated from tree cores to be 145 years (Sullivan *et al.* 1998).

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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 Adams Creek and range from 3% to 25% slope. The study area encompasses about 18 ha with most of the hemlock-dominated woods on the north-northwest facing side of the stream. In contrast to Adams Creek, the Van Campens Brook study area was part of an agricultural community in the mid-1800's. The trees were cut for timber and tannin; much of the land was used as pasture (W. Millington, *pers. comm.*). The ravine edge at the upper end of Van Campens is bounded by a series of old backyards from abandoned homesteads. Sullivan *et al.* (1998) reported a stand age of 103 years old.

Alluvial glacial deposits dominate the parent material at both sites. At Adams Creek, the soil on the slopes are classified as a Manilus very rocky silt loam (Taylor 1969). At Van Campens Brook, a Swartswood very stony loam soil predominates (Fletcher 1975, 1979). The soils in the study area are shallow (average depth to obstruction = 7 cm), droughty (average soil water content in mid-summer after 14 days without rain = 29%), and acidic (median pH = 3.8, Battles *et al*. 1997).

Sampling and Analysis

A qualitative survey of all plant species present in the topographic ravines was conducted. The vascular plant survey was completed in 1994 and the bryophyte survey completed in 1995. (Note on terminology: By topographic ravine we mean the concave-sloped terrain surrounding the lengths of the streams under study. The hemlock ravines are those parts of the topographic ravines where hemlock accounts for more than 50% of the canopy basal area.) Over 140 person-hours were spent searching the sites.

To monitor hemlock and adelgid populations, the DEWA managers established a network of plots in the ravines. Random points along each stream were selected and a plot was located at 10 m, 30 m, and 50 m upslope from the stream edge if the adjacent forest was dominated by hemlock trees (basal area > 50%). Each hemlock monitoring plot consists of a 6-m wide belt transect running parallel to slope. Lengths vary to include a sample of ten 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. Initial health and adelgid assessments were completed in 1994. 12 sets of plots (36 plots) were placed in Adams Creek and 8 sets (24 plots) were placed in Van Campens Brook.

Permanent understory points were established in the center of the hemlock monitoring plots. The straight-line distance between the two end trees in the plot 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 (as it existed in Spring 1994) in a line that forms the perpendicular between the 10-m point and the stream bank. To describe the "immediate neighborhood," edge points were also established if a discernible edge (topographic or forest composition) was within 100 m upslope from the 50-m point. These points serve as the fundamental reference for the nested sampling scheme described below.

The vegetation was divided into four categories: canopy trees, subcanopy trees and shrubs, herbs and seedlings, and bryophytes. Canopy trees were defined as trees in dominant or co-dominant crown classes; subcanopy tree were defined as trees in intermediate or suppressed crown class. Shrubs were defined as multistemmed woody plants. Herbs were defined as non-woody vascular plants (i.e., dicots, monocots, ferns, and fern allies). Seedlings were defined as trees < 1 m tall. Bryophytes included mosses and liverworts. These categories represent the vertical stratification and separation of plant life forms in this community. Each category of vegetation was sampled with a scale-appropriate methodology (see below). The basic sampling unit was a 2x4-m quadrat. The quadrat base was set parallel to the streambed and centered on the permanent point (Fig. 1). The quadrat was divided into two 2x2-m subquadrats (upstream and downstream) to facilitate vegetation cover estimates.

Canopy tree composition was quantified using the point quarter method (with the four quarters delimited by the base of the 2x4-m quadrat and a line perpendicular to the quadrat base (Fig. 4). At stream sites, canopy tree composition was estimated with a 2.5 factor (metric) basal area prism. Canopy height was estimated by measuring the height of the largest tree at each plot. All subcanopy trees and shrubs ≥ 1 m tall and within a 5 m radius of each point were tallied by species (Fig. 1).

Herbs and seedling cover was estimated in 2x4-m quadrat at each point. The presence of all vascular plant species was recorded and visual estimates of percent cover were made for species covering more than 1% of the 2x2-m subquadrat. To further quantify tree seedling abundance, counts of all tree seedlings < 1 m tall were made in a 1x0.5-m nested quadrat in the lower upstream corner of the upstream 2x2-m subquadrat (Fig. 1). Bryophyte composition and abundance was measured using a 1x0.5-m nested quadrat in the lower downstream corner of the downstream 2x2-m subquadrat (Fig. 1).

There are a total of 92 permanent points with their associated plots. Adams Creek has 55 plots: 36 mid-slope plots under hemlock canopy, 12 near-stream plots and 7 edge plots. Van Campens Brook has 37 plots: 24 mid-slope plots, 8 near-stream plots and 5 edge plots.

Three inventories of the herbs and seedlings were conducted: late May-early June 1994 (Spring 1994), early August 1994 (Summer 1994), and August 1995 (Summer 1995). Canopy tree composition and subcanopy tree and shrub composition were measured once in the Spring 1994. During subsequent herb sampling, any major changes in the woody plant composition were noted. Preliminary

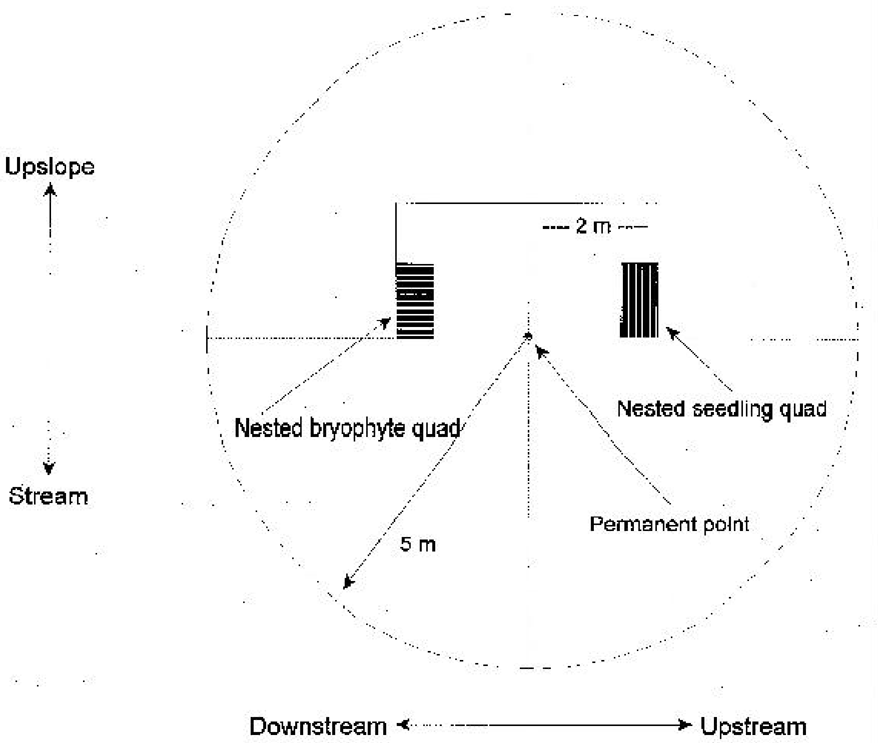

Figure 1.—Diagram of the quantitative vegetation sampling regime used for the permanent point/plot survey.

estimates of bryophyte composition and cover were made in 1994; final estimates were conducted in 1995.

In the summer 1996, we evaluated the buried seed pool. We took 10 x 10 cm samples of the forest floor just outside the 4 corners of the mid-slope vegetation plots. We removed the litter and duff (Oi and Oe layers) in order to examine just the buried seeds and to exclude recently dispersed seeds on top of the forest floor. The four samples of humus (Oa) from each plot were mixed together and then spread in flats lined with black mesh. The flats were placed outside in full sun; watered twice daily, and enclosed in a fenced area. All germinants that emerged during a six week test period were tallied and identified.

At each permanent point, slope, aspect, microrelief, and topographic position were recorded. During 1994 available light was estimated 1 m above each point by taking a hemispherical photograph of the canopy and then calculating the percentage of incident photosynthetically active radiation reaching that point during the growing season. We digitized the photograph and used software provided by Canham (1988) to compute the gap light index (GLI) for each image. GLI ranges from 0 for a completely closed canopy to 100 for a completely open site. For details on the GLI methodology see Battles (1999).

Results

In the survey, 316 plant species were found in the understory of the two topographic ravines. This total includes 123 species of bryophytes, 24 species of pteridophytes, 122 species of flowering herbs (common grasses and sedges included), and 47 species of woody plants. The understory flora found under hemlock-dominated parts of the ravines was less species rich than the ravine as a whole (69 species of vascular plants; 50 species of bryophytes).

Adams Creek and Van Campens were similar in that both were mature, closed-canopy forests dominated by large hemlock trees. As is typical for hemlock forests, understory tree densities were low and composed largely of hemlock trees (Table 1). The major differences in tree composition were the high relative basal area of *Pinus strobus* at Adams Creek and the larger component of *Betula lenta* at Van Campens. In terms of canopy structure, the two sites were significantly different. Trees at Adams Creek were taller and had proportionally smaller crown lengths. In addition, twice as much light reached the understory (Table 1, Fig. 2) at Adams Creek (6% vs 3%).

These structural and light differences corresponded to consistent differences in the mean cover of understory vascular plants. In both 1994 and 1995, vascular plant abundance was more than 20 times greater in Adams Creek (Table 2, nested ANOVA $p = 0.08$). Despite the differences in cover, both ravines had relatively low vascular plant cover with the maximum being 10% at Adams Creek in 1995. Plant cover was patchy: 66 quadrants had < 1% cover and 11 had > 10% cover. Two fern species (*Dryopteris intermedia* and *Dennstaedtia punctilobula*) were the most abundant herbaceous plants. These ferns tended to occur in dense groups near canopy

Table 1.—Comparison of stand characteristics between ravine plots in the study ravines at Delaware Water Gap National Recreation Area. Means are reported followed by standard deviations in parentheses. Characteristics followed by * indicate statistically significant differences between sites at the p = 0.05 level.

Stand Characteristics	Adams Creek	Van Campens
	(n = 48)	(n = 32)
Canopy basal area (m^2 ha^{-1})	55.8 (25.9)	47.0 (29.7)
Relative Basal Area (%)		
Tsuga canadensis	53	60
Pinus strobus	20	0
Betula lenta	7	15
Understory density (# ha^{-1})	538 (463)	690 (540)
Relative Density (%)		
T. canadensis	77	91
B. lenta	5	2
Canopy height (m)*	30.2 (3.8)	26.2 (5.1)
Live crown ratio*	0.49	0.53
GLI (%)*	6.4 (3.2)	3.1 (1.8)

[1]Near-stream plots are not included in basal area and density calculations.

Table 2.—Percent cover of the understory vascular plants in the 2x4-m quadrats in two hemlock ravines at the Delaware Water Gap National Recreation Area. The percent cover of the five most abundant vascular plants is also listed. There were 48 quadrats at Adams Creek and 32 quadrats at Van Campens Brook (Edge plots not included). 1994 results based on the second, early August survey. Note: std = standard deviation.

1994	mean	std
Adams Creek	7	16
Van Campens Brook	0.3	0.2
Both sites	4	13
Both sites by species		
Dryopteris intermedia	2	9
Dennstaedtia punctilobula	1	3
Betula seedlings	0.2	0.8
Aster divaricatus	0.2	0.9
Polystichum acrostichoides	0.1	1
1995	**mean**	**std**
Adams Creek	10	20
Van Campens Brook	0.4	0.6
Both sites	6	16
Both sites by species		
Dryopteris intermedia	3	10
Dennstaedtia punctilobula	1	8
Betula seedlings	0.4	1
Mitchella repens	0.2	0.8
Aster divaricatus	0.2	1

openings. The most frequently occurring understory vascular plants were the tree seedlings. In both years, *Betula* seedlings were found in > 70% of the plots and *Acer rubrum* seedlings in > 50% of the plots.

Bryophyte cover was greater than or equal to vascular plant cover (Table 3). There was less of a difference in bryophyte abundance between the two ravines (nested ANOVA, p = 0.12). Like the vascular plants, a few common species (*Mnium hornum* and *Hypnum imponens*, and at Adams Creek, *Thuidium delicatulum*) accounted for most of the bryophyte cover.

There were no significant differences in understory light availability related to topographic location in the ravines (Fig. 2). Even in the middle of the stream and on the edges, light levels remained low and consistent throughout each study site. The outliers with higher than average understory radiation occurred under or near canopy gaps. There was also no differences in vascular plant cover with location in the ravines (nested ANOVA, p = 0.55) but moss cover was significantly greater at near-stream plots (22%) than the other four plot locations (nested ANOVA, p < 0.001).

Woody plant composition of the edge plots also varied between sites. At Adams Creek, *Pinus strobus* and *Betula lenta* were the most important canopy species, but together, the four common species of oaks (*Quercus* spp) had the greatest importance in the edge plots (30%). Along the edges of Van Campens, hemlock was still the dominant canopy tree with *Acer rubrum* second in importance. Three common oaks contributed 23% of canopy importance at Van Campens (Table 4). The dominant woody plants in the understory edge of Adams were blueberries (*Vaccinium* spp.) followed by roughly equal contributions of *P. strobus, B. lenta*, and hemlock. At Van Campens, *B. lenta* and *A. rubrum* shared dominance in the understory edge (Table 5).

There was a significant annual difference in tree seedling density (Table 6). There were twice as many seedlings present in 1995 compared to 1994 (paired t-test, p = 0.02). We tested for within-year differences in 1994 and while there were slightly more seedlings present later in the growing season, the increase was not significant (p = 0.24, Table 6). Much of the increase in 1995 was due to recruitment of *Betula* seedlings. *Betula* spp. and *A. rubrum* were the two most abundant species in the seedling layer. In Summer 1994, 51% of the seedlings were *Betula* and 16% *A. rubrum*; in Summer 1995, 65% of the seedling were *Betula* and 11% *A. rubrum*. There was a depauperate buried seed pool. At Adams Creek, average density of vascular plant

Table 3.—Percent cover in 1995 of bryophytes in the 0.5x1-m nested quadrats in two hemlock ravines at the Delaware Water Gap National Recreation Area. At each site the mean cover of the five most abundant species is listed. There were 55 quadrats at Adams Creek and 37 quadrats at Van Campens Brook. Note: std= standard deviation.

Total cover	mean	std
Adams Creek	10	16
Van Campens Brook	6	12
Both sites	9	15
Adams Creek by species	**mean**	
Thuidium delicatulum	3	
Mnium hornum	2	
Brotherella recurvans	1	
Leucobryum glaucum	1	
Hypnum imponens	0.9	
Van Campens Brook by species	**mean**	
Hypnum imponens	2	
Mnium hornum	1	
Leucobryum glaucum	0.8	
Tetraphis pellucida	0.6	
Brotherella recurvans	0.2	

germinants was 2.3 germinants m^{-2}; at Van Campens, the average germination rates of vascular plants was 11.2 germinants m^{-2}. For woody species only, average density was 0.6 germinants m^{-2} at Adams and 1.7 germinants m^{-2} at Van Campens.

Discussion

The hemlock forests at Adams Creek and Van Campens Brook aptly fit Rogers' (1978, 1980) description of a typical hemlock-dominated ecosystem. These places are characterized by low light levels, thin and infertile soils, microclimates cooler and damper than nearby hardwood forests, and sparse understory vegetation. As noted by Rogers (1980), ferns are the only herbaceous vascular plants able to achieve patchy high coverage under hemlock canopies. Bryophyte cover exceeded vascular plant cover in the understory. The two hemlock ravines were dominated by a small assemblage of bryophytes adapted to the low light and high moisture conditions (Cleavitt and Fahey 1996). As a long-lived, very shade tolerant species, hemlock thrives on environmental constancy and is not well-adapted to disturbance (Rogers 1978). This constancy is apparent in the lack of variation in understory light levels in the ravines.

Both Adams Creek and Van Campens represent the mature phase of hemlock forest development. However differences in their past land-use history and age since major disturbance were related to significant differences in forest structure and understory vegetation. Adams was an older stand with taller more massive canopy trees. More light reached the understory. The vascular flora was more abundant and more diverse (Battles *et al.* 1997) at Adams compared to Van Campens.

Both ravines seem relatively "well-buffered" against invasive plant species in their immediate neighborhoods. Woody plant composition of the near-edge consisted of species present in the hemlock ravines that achieved greater abundance in the edge environment. The only abundant "edge" species not present in the hemlock ravines were blueberry bushes (*Vaccinium* spp.) at Adams. Buried seeds were not a major source of potential colonists. The long time since the last major disturbance (50+ years) may explain the depleted pool of viable buried seeds (Tierney and Fahey 1998).

The immediate vegetation response to any adelgid-caused decline in hemlock most likely would be increases in fern cover followed by prolific establishment of *B. lenta* and *A. rubrum*. *B. lenta* can establish on intact

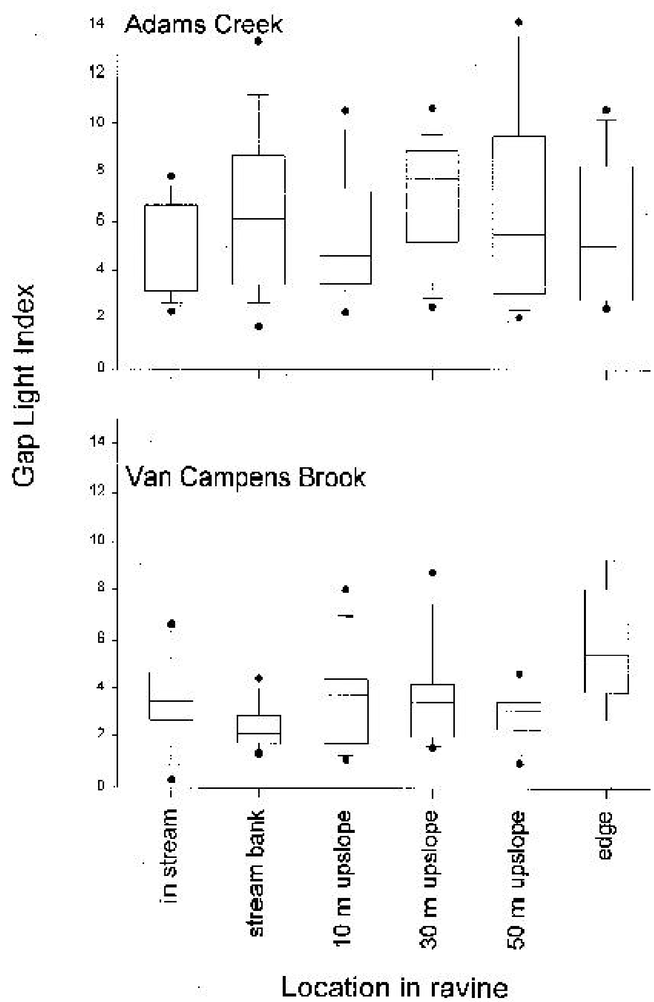

Figure 2.—Box plots of the gap light index by topographic location in the ravine for the two study sites in Delaware Water Gap National Recreation Area. Boxes indicate 10th, 25th, 75th, and 90th percentiles.

Table 4.—Comparison of canopy tree composition between mid-slope plots and edge plots in the study ravines at Delaware Water Gap National Recreation Area. Composition expressed as relative importance value (relative basal area/2 + relative density/2). Number in parentheses is the number of point-quarter samples.

Species	Adams Creek		Van Campens Brook	
	Mid-slope (36)	Edge (7)	Mid-slope (24)	Edge (5)
Tsuga canadensis	53	10	52	44
Pinus strobus	14	26	absent	absent
Fagus grandifolia	4	absent	3	absent
Acer rubrum	<1	6	4	16
Acer saccharum	5	2	<1	absent
Betula alleghaniensis	<1	absent	10	absent
Betula lenta	9	19	17	9
Quercus alba	6	7	6	10
Quercus prinus	5	9	4	4
Quercus rubra	<1	4	1	9
Quercus velutina	absent	10	absent	absent

Other canopy trees present: *Amelanchia laevis, Carya ovalis, Carya ovata, Fraxinus americana, Liriodendron tulipifera, Nyssa sylvatica, Pinus resinosa,* and *Populus grandidentata*.

Table 5.—Comparison of subcanopy tree and shrub composition between mid-slope plots and edge plots in the study ravines at Delaware Water Gap National Recreation Area. Composition expressed as relative density (%). Number in parentheses is the number of 5-m radius plots.

Species	Adams Creek		Van Campens Brook	
	Mid-slope (36)	Edge (7)	Mid-slope (24)	Edge (5)
Tsuga canadensis	77	16	91	22
Betula lenta	5	16	2	28
Pinus strobus	2	14	absent	absent
Acer rubrum	1	7	absent	28
Other canopy tree species[1]	12	16	7	16
Vaccinium spp.	3	30	absent	absent
Hamamelis virginiana	3	absent	absent	5

[1]Includes all the other tree species listed in Table 4.

Table 6.—Seedling density (trees < 1-m tall) in the 1x0.5-m nested quadrats in two hemlock ravines at the Delaware Water Gap National Recreation Area. Seedling density is expressed in seedlings m^{-2}. Note: std = standard deviation.

	Spring 1994		Summer 1994		Summer 1995	
	mean	std	mean	std	mean	std
Total	2.4	3.9	3.2	5.2	6.3	12
Adams Creek	1.9	3.4	2.5	3.1	5.3	12
Van Campens	3.1	4.4	4.2	7.1	7.9	12

forest floor without soil scarification and grows rapidly in high light (Orwig and Foster 1998). Annual variation in seed production, seed germination and seedling survival will influence the specific course and rate of response to hemlock deterioration. Two exotic woody plants present in the topographic ravines, *Ailanthus altissima* (tree-of-heaven) and *Berberis thunbergii* (barberry), could become aggressive competitors.

Hemlock trees have recovered from declines in the mid-Holocene (Fuller 1998) and more recently from human agricultural practices (Abrams and Orwig 1996). However several novel factors exist now that may inhibit another hemlock recovery even if the adelgid is eventually controlled (*sensu* Foster *et al.* 1998). They include: 1) the presence of exotic plant competitors, 2) high densities of herbivores, 3) chronic atmospheric nitrogen pollution, and 4) a rapidly changing climate. These disturbances all bode poorly for a species like hemlock that thrives on constancy. However, individual hemlock trees in the two study ravines have remained healthy despite low to moderate levels of adelgid infestation during the last five years.

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