RESEARCH ARTICLE

Stand Dynamics of an Old-Growth Eastern Hemlock-Hardwood Forest in West Virginia

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ABSTRACT: Cathedral State Park (CSP) is a 54-ha, old-growth, eastern hemlock-hardwood forest located in the central Appalachian Mountains of West Virginia. Hemlock woolly adelgid (HWA) (*Adelges tsugae* Annand) is an exotic insect that currently threatens eastern hemlock (*Tsuga canadensis* (L.) Carr.) in its native range, and was found in CSP in 2002. In 2006, field plots established in 2000 were re-measured to assess adelgid-induced changes to forest structure and species composition. The herbaceous plant community was also measured during the 2006 growing season to describe how the ground flora has changed since it was originally surveyed in 1965. In addition, characteristics of snags and downed dead wood in CSP were compared to published data on 25 old-growth hemlock-hardwood stands in the eastern United States. From 2000 to 2006, little HWA-induced change occurred in CSP. Density and basal area of overstory hemlock did not change, while snag density and basal area decreased over time. However, more than 10% of measured overstory hemlock trees were infested with HWA, with plot infestations ranging from 0 to 93% of stems. CSP had 1.5 times the volume of downed dead logs compared to other old-growth hemlock-hardwood stands. This study serves as a reference of forest structure and species composition in CSP prior to HWA-induced mortality.

Index terms: Adelges tsugae, eastern hemlock, forest stand dynamics, hemlock woolly adelgid, old-growth forest, *Tsuga canadensis*

INTRODUCTION

Cathedral State Park (CSP) is a 54-ha, old-growth, eastern hemlock-hardwood forest located in the central Appalachian Mountains of West Virginia. CSP is dominated by eastern hemlock (*Tsuga canadensis* (L.) Carr), with some trees believed to be 400 years old or more (Venable, no date). Trees larger than 100 cm diameter at breast height (dbh) and 35 m tall are common. CSP is an example of the virgin hemlock forests that once flourished in the Appalachian region (Patterson 1988).

The onset of an exotic insect pest, the hemlock woolly adelgid (HWA) (*Adelges tsugae* Annand), currently threatens the fate of hemlocks and the unique habitats they provide. In the eastern United States, both eastern hemlock and Carolina hemlock (*Tsuga caroliniana* Engelm.) are very susceptible to HWA, with all size and age classes at risk (Ward et al. 2004). Since the mid-1980s, HWA has spread at a rate of 20 to 30 km per year (McClure et al. 2001). West Virginia lies within the native range of eastern hemlock and is rapidly being infested by HWA. As of 2008, HWA had been found in 34 counties (62% of state), with HWA discovered in CSP in 2002 (U.S. Forest Service 2009).

The purpose of this study was to document the initial effects of HWA in CSP. In 2000, the U.S. Forest Service established permanent vegetation plots in CSP to record stand conditions prior to the arrival of HWA. In 2006, these plots were re-measured to assess the impact of HWA on overstory, understory, and regeneration strata. In addition, herbaceous vegetation was examined throughout the 2006 growing season and compared to an original flora survey of CSP performed in 1965 (Bieri and Anliot 1965). Finally, the 2006 volume of downed dead wood in CSP was quantified and compared to published data on other old-growth hemlock forests in the eastern United States. The results of this study will provide natural areas managers with an assessment of the changes that can be expected to occur within an old-growth hemlock-hardwood stand prior to and following initial HWA infestation.

STUDY AREA

Cathedral State Park is located in Preston County, West Virginia (39º19.5´N, 79º32.5´W), and is 1.5 km east of Aurora near the Maryland/West Virginia border. Preston County lies within the Allegheny Mountain section of the Appalachian Plateau and has daily minimum and maximum temperatures of –9 ºC and 2 ºC for January and 13 ºC and 29 ºC for July (Core 1966; Baldwin 1973). Mean annual precipitation is 137 cm with an average annual snowfall of 203 cm (Baldwin 1973). The elevation of CSP ranges from 750 to 800 m above sea level. Rhine Creek meanders through CSP and is a tributary of the Youghiogheny River. The soils within the study area are Dekalb loam and Ernest stony silt loam (Patton et al. 1959).

METHODS

2000 Inventory

In 2000, the Forest Service Northern Research Station established thirteen, 0.4-ha circular plots in CSP. The objective was to sample the forest structure prior to HWA infestation. Plot centers were marked with steel rebar, and were positioned on parallel transects in the area best representing the old-growth hemlock-hardwood forest type in CSP.

Within each 0.4-ha overstory plot, all living and standing dead trees ≥ 12.7 cm dbh were recorded by species, dbh, and, for living trees, crown class (dominant, co-dominant, intermediate, or suppressed). Using a clinometer, total heights were measured for approximately 10% of the living trees. Nested within each overstory plot were four understory plots and eight regeneration plots. Understory plots were 0.004-ha circular plots located 15.2 m in each cardinal direction from plot center. Living trees ≥ 2.5 cm dbh and < 12.7 cm dbh were tallied by species, dbh, total height, and crown class. The regeneration plots were 0.0004-ha circular plots located 15.2 m and 30.5 m in each cardinal direction from plot center. Seedlings < 2.5 cm dbh were tallied by species and height class (< 15.2 cm; 15.2 to 30.5 cm; 30.6 to 91.4 cm; 91.5 to 152.0 cm; and >152 cm tall).

2006 Inventory

In summer 2006, each permanent plot established in 2000 was relocated and flagged. The inventory in 2006 followed the same methodology used in 2000. In addition, the presence of HWA on overstory hemlock trees ≥ 12.7 cm dbh was recorded.

Two elements of forest structure not inventoried in 2000 were also examined: herbaceous vegetation and downed dead wood (DDW). Within each overstory plot, eight 1 m^2 herbaceous plots were established. Each regeneration plot center marked the top-left corner of the herbaceous plot when facing north. An herbaceous plant is a plant with no persistent woody tissue occurring above ground. Two non-herbaceous plants were also tallied in the herbaceous plots: blackberry (*Rubus* L. spp.) and greenbrier (*Smilax* L. spp.). These taxa were included because of their similar growth form and competitive relationship within the herbaceous community. All herbaceous plots were visited every fourth week, with three sampling periods occurring from May to July 2006. Within each herbaceous plot, all plants were identified by species, when possible, and percent cover recorded to the nearest five percent class using ocular estimation.

To quantify the characteristics of DDW, one 0.04-ha circular plot was established within each overstory plot. DDW is defined here as downed dead wood ≥ 10 cm at the mid-point diameter and at least 1 m in length. All DDW was tallied as hardwood or softwood, with diameter and log length recorded (Bragg 2004). At each log midpoint, diameter measurements were collected on two sides using tree calipers. Log length was measured end-to-end, and was measured for the dominant stem portion whenever a fork was encountered. The decay class of each downed log was also recorded on a scale of 1 (least decayed) to 5 (most decayed) (Thomas 1979). Using average diameter and log length, volume was calculated using Huber's formula (Avery and Burkhart 2002).

Data Analysis

Changes between 2000 and 2006 in density, relative density, basal area, and relative basal area were examined for overstory and understory species. For the regeneration layer, changes in density and relative density were examined by height class. For each stratum, a Shapiro-Wilk test was conducted to test for normality. A paired t-test was used for species normally distributed, while species not normally distributed were analyzed using a non-parametric, signed rank test. No data transformations were made for non-normal data. All statistical analyses were performed using SAS (2004), with statistical significance for all tests accepted at $\alpha = 0.05$.

Using an average for all three herbaceous sampling periods, relative density and percent cover by species was calculated for each herbaceous plot. To obtain an average for each overstory plot, the average of all herbaceous subplots was determined for relative density and percent cover by species. Importance values were calculated as relative frequency + percent cover /2.

The volume of DDW, snag density, and snag basal area in CSP was compared to other old-growth hemlock-hardwood forests in the eastern United States. Comparable stands were selected using the following criteria: (1) located within the conifer-northern hardwood forest cover type, (2) dominated by eastern hemlock (≥ 40% hemlock basal area), and (3) availability existed for information concerning DDW and snags. Published results from twenty-five old-growth stands were selected from northern Wisconsin and Michigan (Tyrrell and Crow 1994a,b; Tyrrell et al. 1998). Values in CSP for DDW, snag density, and snag basal area were compared to means of the 25 selected stands.

RESULTS

Overstory Trees

Fifteen species comprised the overstory vegetation in 2000 and 2006 (Table 1). Four species made up 89% and 88% of total tree density in 2000 and 2006, respectively: eastern hemlock (59% and 61%), red maple (*Acer rubrum* L.) (13% and 11%), sweet birch (*Betula lenta* L.) (11% and 10%), and black cherry (*Prunus serotina* Ehrh.) (6% and 6%). All other species occupied less than 4% relative density. Total tree and hemlock density did not significantly change from 2000 to 2006 (Table 1).

Four species made up 86% and 85% of total basal area in 2000 and 2006, respectively: eastern hemlock (58% and 59%), red maple (12% and 11%), black cherry (9% and 9%), and white oak (*Quercus alba* L.) (7% and 6%) (Table 1). Total overstory basal area was significantly lower ($P = 0.03$) in 2006, decreasing from 43.3 to 41.4 m^2/ha. Hemlock basal area did not change significantly ($P = 0.20$).

Diameter distributions in CSP for 2000 and

Table 1. Comparison of density and basal area of overstory trees (≥ 12.7 cm dbh) at Cathedral State Park in 2000 and 2006 (paired t-test, P < 0.05).

	Density (trees/ha)			Basal Area (m^2/ha)		
Species	**2000**	**2006**	**P-value**	**2000**	**2006**	**P-value**
Acer pensylvanicum	0.4	0.9	0.5	<0.1	<0.1	0.5
Acer rubrum	38.4	33.3	0.06	5	4.6	0.11
Amelanchier arborea	0.8	0.9	1	<0.1	<0.1	1
Betula alleghaniensis	6.6	9.1	0.13	0.6	0.9	0.05
Betula lenta	32.7	30.2	0.27	2.7	2.2	0.22
Fagus grandifolia	6.1	7	0.38	0.7	0.8	0.2
Fraxinus americana	0.2	0	1	<0.1	0	1
Hamamelis virginiana	0.2	0.2	.	<0.1	<0.1	1
Liriodendron tulipifera	0.2	0.2	.	<0.1	<0.1	1
Magnolia acuminata	0.6	0.6	.	<0.1	<0.1	0.25
Nyssa sylvatica	0	0.2	1	0	<0.1	1
Picea rubens	0.4	0.4	.	0.1	0.1	0.5
Prunus serotina	18.8	18.3	0.39	3.8	3.7	0.59
Quercus alba	13.5	12.6	0.13	2.8	2.5	0.43
Quercus rubra	7	6.5	0.75	2.3	2.1	0.7
Tsuga canadensis	180	186.5	0.18	25.2	24.5	0.2
Total	**305.8**	**306.8**	**0.84**	**43.3**	**41.4**	**0.03**

2006 resembled a reverse-J shape characteristic of uneven-aged forests (Figure 1). The majority of larger-sized trees were hemlock. Hardwood species were most abundant in smaller diameter classes. In 2006, the largest hemlock was 150 cm dbh and 43 m tall. Other large trees included a black cherry and American beech (*Fagus grandifolia* Ehrh.) measuring 44 m tall, a northern red oak (*Quercus rubra* L.) with a 91 cm dbh, and a black cherry with a 110 cm dbh.

Understory Trees

Table 2 reveals that six species made up 92% and 95% of total tree density in 2000 and 2006, respectively: eastern hemlock (51% and 35%), great laurel (*Rhododendron maximum* L.) (18% and 33%), black cherry (8% and 11%), sweet birch (7% and 6%), American witchhazel (*Hamamelis virginiana* L.) (5% and 7%), and red maple (3% and 3%). Striped maple (*Acer pensylvanicum* L.) and northern red oak were present in 2000, but were not sampled in 2006. Total understory tree density did not change between the two sampling periods, but there were fewer hemlock (P = 0.03) in 2006. In 2000 and 2006, five species comprised 92% of basal area: hemlock (72% and 64%), great laurel (5% and 11%), black cherry (5% and 8%), sweet birch (6% and 6%), and American witchhazel (4% and 3%). There was no change in total understory basal area from 2000 to 2006, nor was there a change in hemlock basal area (P = 0.09).

Table 2. Comparison of density and basal area of understory trees (≥ 2.5 and < 12.7 cm dbh) at Cathedral State Park in 2000 and 2006 (paired t-test, P < 0.05).

	Density (trees/ha)			Basal Area (m^2/ha)		
Species	**2000**	**2006**	**P-value**	**2000**	**2006**	**P-value**
Acer pensylvanicum	4.7	0	1	<0.1	0	1
Acer rubrum	23.8	23.8	1	<0.1	<0.1	0.75
Amelanchier arborea	14.3	19	1	<0.1	<0.1	0.5
Betula alleghaniensis	14.3	9.5	1	<0.1	<0.1	1
Betula lenta	52.3	47.5	1	0.1	0.1	0.82
Fagus grandifolia	9.5	9.5	.	<0.1	<0.1	0.5
Hamamelis virginiana	33.3	52.3	0.5	0.1	<0.1	1
Ilex montana	9.5	4.7	1	<0.1	<0.1	0.5
Prunus serotina	61.8	85.5	0.75	0.1	0.1	0.56
Quercus rubra	4.7	0	1	<0.1	0	1
Rhododendron maximum	133.1	266.1	0.13	0.1	0.2	0.11
Tsuga canadensis	375.4	280.4	0.03	1.6	1.2	0.09
Total	**736.6**	**798.3**	**0.52**	**2.2**	**1.9**	**0.12**

Tree Regeneration

Among all five height classes, 22 species or species groups were identified in the tree regeneration layer (Table 3). Regeneration totals were significantly different for height classes 1 and 3 from 2000 to 2006. Height class 1 increased (P < 0.01), while height class 3 decreased (P = 0.01). In 2000 and 2006, great laurel was abundant in all height classes and was especially prevalent among stems ≥ 30.5 cm tall. Smaller regeneration (height classes 1 and 2) was predominantly black cherry, red maple, birch (*Betula* L. sp.), great laurel, and hemlock. There were

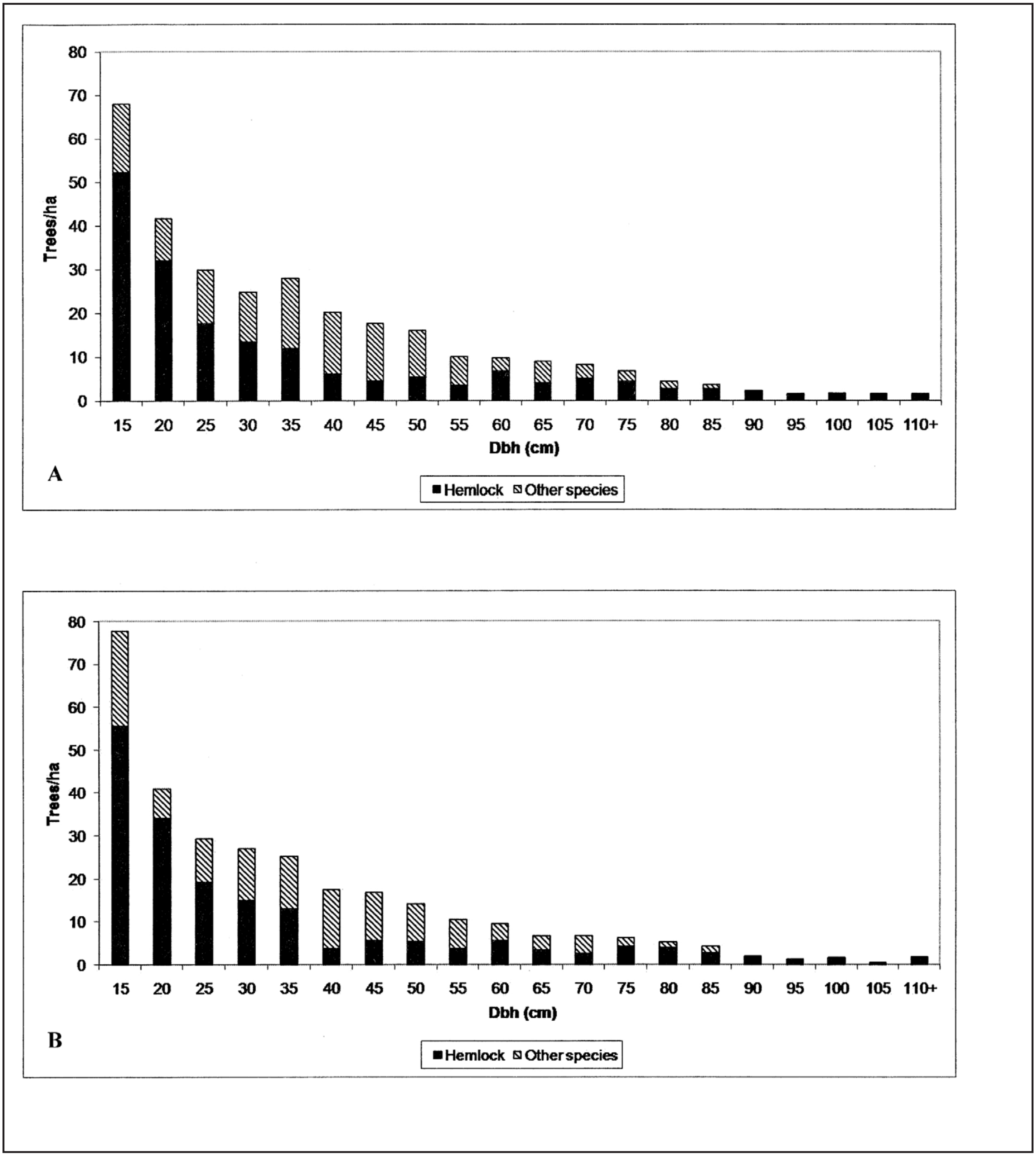

Figure 1. Diameter distributions for overstory trees ≥ 12.7 cm dbh in 2000 (A) and 2006 (B) at Cathedral State Park, West Virginia.

Table 3. Comparison of tree regeneration density (seedlings/ha < 2.5 cm dbh) by height class at Cathedral State Park in 2000 and 2006 (paired t-test, P < 0.05).

	Height Class 1 < 15.2 cm			Height Class 2 15.2 - 30.5 cm			Height Class 3 30.6 – 91.4 cm			Height Class 4 91.5 – 152 cm			Height Class 5 > 152 cm		
Species	**2000**	**2006**	**P-value**	**2000**	**2006**	**P-value**	**2000**	**2006**	**P-value**	**2000**	**2006**	**P-value**	**2000**	**2006**	**P-value**
Acer pensylvanicum	190	166	1	190	71	0.5	333	24	0.75	71	0	1	0	0	.
Acer rubrum	20672	29439	0.17	570	737	0.92	95	71	1	0	0	.	24	0	1
Amelanchier arborea	499	24	0.05	309	0	0.03	0	0	.	0	0	.	0	0	.
Betula spp.	2732	7770	0.01	1188	2495	0.13	2210	380	0.06	24	48	1	71	0	0.5
Carya spp.	0	0	.	0	24	1	0	0	.	0	0	.	0	0	.
Cornus alternifolia	0	0	.	0	24	1	0	48	1	0	0	.	0	0	.
Crataegus spp.	0	190	0.5	119	24	1	0	24	1	24	0	1	0	24	1
Fagus grandifolia	0	119	1	143	95	1	261	238	1	0	48	0.5	0	0	.
Hamamelis virginiana	356	594	0.28	71	24	0.5	143	48	1	0	0	.	71	48	1
Ilex montana	903	950	0.79	546	214	0.06	451	95	0.03	0	0	.	0	0	.
Kalmia latifolia	0	0	.	24	0	1	0	0	.	0	0	.	24	0	1
Liriodendron tulipifera	24	0	1	0	0	.	0	0	.	0	0	.	0	0	.
Nyssa sylvatica	0	48	1	0	0	.	0	0	.	0	0	.	0	0	.
Picea rubens	0	24	1	24	0	1	0	0	.	0	0	.	0	0	.
Prunus pensylvanica	0	0	.	24	0	1	0	0	.	0	0	.	0	0	.
Prunus serotina	14137	31435	< 0.01	1164	855	0.51	618	166	0.03	0	0	.	0	0	.
Quercus rubra	0	285	0.03	0	0	.	0	0	.	0	0	.	0	0	.
Rhododendron maximum	3350	4324	0.98	3113	903	0.09	4039	261	0.03	2305	190	0.06	1901	1164	0.19

continued

Table 3. Comparison of tree regeneration density (seedlings/ha < 2.5 cm dbh) by height class at Cathedral State Park in 2000 and 2006 (paired t-test, P < 0.05).

	Height Class 1 < 15.2 cm			Height Class 2 15.2 - 30.5 cm			Height Class 3 30.6 – 91.4 cm			Height Class 4 91.5 – 152 cm			Height Class 5 > 152 cm		
Species	**2000**	**2006**	**P-value**	**2000**	**2006**	**P-value**	**2000**	**2006**	**P-value**	**2000**	**2006**	**P-value**	**2000**	**2006**	**P-value**
Sambucus nigra	95	24	0.5	24	24	1	0	0	.	0	0	.	0	0	.
Tsuga canadensis	3136	7128	0.05	309	499	0.19	24	238	0.13	48	48	1	0	95	1
Viburnum spp.	0	48	1	0	24	.	0	24	.	0	0	.	0	0	.
Unknown	428	0	0.25	71	0	0.33	71	0	1	0	0	.	0	0	.
Total	**46,523**	**82,568**	**< 0.01**	**7,888**	**6,011**	**0.34**	**8,244**	**1,616**	**0.01**	**2,471**	**333**	**0.09**	**2,091**	**1,331**	**0.24**

more hemlock seedlings < 15.2 cm tall in 2006 than in 2000 (P = 0.05).

Herbaceous Vegetation

Fifty-six herbaceous species, within 29 families, were sampled throughout the 2006 growing season (Table 4). While some plots lacked any herbaceous cover, other plots contained as many as 16 herb species. Woodfern (*Dryopteris Adans.*, nom. conserv. spp.), partridgeberry (Mitchella repens L.), and Canada mayflower (*Maianthemum canadense* Desf.) were the most common herbs encountered, representing the top three species for percent cover, relative frequency, and importance. These three herbs accounted for more than 50% of the overall herb species importance. Jack-in-the-pulpit (*Arisaema Martius*. spp.) ranked among the top five species for frequency and importance value but not for percent cover. Eastern hayscented fern (*Dennstaedtia punctilobula* (Michx.)) ranked among the top three species for percent cover, but did not rank within the top five for frequency or importance value.

Snags and Downed Dead Wood

Snag density and snag basal area decreased from 2000 to 2006. Snag density declined (P < 0.01) from 57.0 to 35.3 snags/ha, while snag basal area decreased (P = 0.02) from 8.3 to 5.8 m2/ha. In 2006, eastern hemlock accounted for 57% of snag density and 61% of snag basal area, while in 2000, hemlock accounted for 42% of snag density and 41% of snag basal area.

In 2006, total density and volume of DDW in CSP was 682.4 logs/ha and 122.9 m3/ha, respectively. Hemlock made up 84% and 88% of total density and volume, respectively. Using mid-point diameter, 83% of all DDW was 20 cm. Hemlock comprised 89% of logs 20 cm. Decay class 1 (least decayed) was the only class in which species other than hemlock were dominant.

Comparisons of DDW and snags to other old-growth stands showed that CSP had 1.5 times more log volume of DDW logs ≥ 20 cm mid-point diameter (Table 5). Comparisons of snag basal area (≥ 12.7 cm dbh in CSP and ≥ 10 cm dbh from comparable stands) were similar. However, less than half the snag density was found in CSP compared to the other old-growth stands.

Hemlock Woolly Adelgid Assessment

Of the 982 hemlocks measured in 2006 within the overstory stratum, 12% were infested with HWA. HWA was found in six of the 13 (46%) overstory plots. With one exception, all HWA-infested plots were situated in the northwest portion of CSP. In two plots, more than 90% of hemlocks were infested with HWA. The majority (81%) of HWA-infested trees were within the dominant and co-dominant canopy classes.

DISCUSSION

Overstory and understory structure at CSP changed little from 2000 to 2006. Although there is a strong presence of HWA in CSP, there was no change in overstory hemlock density, basal area, and volume, or in understory hemlock basal area. Also, snag density and basal area were lower in 2006 than in 2000, indicating no recent increase in tree mortality.

The herbaceous vegetation in 2006 was similar to that reported over 40 years ago by Bieri and Anliot (1965). The major herbaceous species in 1965 and 2006 were: wood fern, partridgeberry, Canada mayflower, wood-sorrel (*Oxalis* L. sp.), Jack-in-the-pulpit, violet (*Viola* L. sp.), eastern hayscented fern, blackberry, shining clubmoss (*Huperzia lucidula* (Michx.) Trevisan), and small enchanter's nightshade (*Circaea alpina* L.). Herbaceous vegetation differences between sampling dates include an increase in Canada mayflower and a decrease in Indian cucumber (*Medeola virginiana* L.) from 1965 to 2006.

The two primary plant communities described by Bieri and Anliot (1965) – hemlock-fern and hemlock-rhododendron – are still prominent within CSP. The hemlock-fern community is easily identified by its two-layered structure and a dense herbaceous layer of eastern hayscented fern and wood fern. Field observations suggest the dense fern layer and closed canopy can prevent successful establishment of tree regeneration. The hemlock-rhododendron community still occurs primarily in areas of poor drainage, especially adjacent to Rhine Creek. This community has a two-layered structure of hemlock and great laurel, with sweet birch and scattered northern red oak in the overstory. The majority of birch and hemlock seedlings appear to use DDW as sites for establishment as has been noted previously at CSP (Bieri and Anliot 1965) and elsewhere (Lorimer 1996; Loucks and Nighswander 1999).

The three smaller communities described by Bieri and Anliot (1965) were also observed in 2006. The most common herbaceous plants in the hemlock-fern/hemlock-rhododendron ecotone were wood fern, partridgeberry, Jack-in-the-pulpit, Canada mayflower, and Indian cucumber. The hemlock duff community is a unique area in which the herbaceous and regeneration layers are not well developed, although rare occurrences of partridgeberry, wood fern, and Canada mayflower were identified. Bieri and Anliot (1965) speculated these characteristics were due to the "very dense canopy" of overstory trees. The maple-cherry-birch community still exists in extremely poorly-drained areas of the stand.

During the 2006 census, no hemlock mortality in CSP could be directly attributed to HWA. However, the future of hemlocks in CSP is likely bleak, and a change in overstory structure seems inevitable. Other hemlock-dominated stands in the northeast have been dramatically altered following HWA infestation. Orwig and Foster (1998) examined seven stands with HWA in southern New England, with two stands suffering more than 95% mortality in overstory hemlock density.

Unless more efficient means of adelgid control on a stand-level are found, the death of some hemlocks in CSP will likely occur in the next few years (McClure 2001). Mortality will probably occur in overstory hemlocks which already show

Table 4. Relative frequency (%), percent cover (%), and importance values (%) for herbaceous plant species at Cathedral State Park in 2006.

Species	Relative Frequency	Percent Cover	Importance Value
Ageratina altissima	0.1	0.1	0.12
Alliaria petiolata	0.3	0	0.13
Arisaema sp.	7.6	3.1	5.35
Bellis perennis	0.1	<0.1	0.07
Bidens sp.	0.3	<0.1	0.15
Brachyelytrum erectum	1.1	1.7	1.41
Carex folliculata	0.1	<0.1	0.07
Carex spp.	0.7	0.5	0.6
Chelone glabra	0.8	0.1	0.44
Circaea alpina	2	0.3	1.18
Claytonia caroliniana	0.1	0	0.06
Danthonia compressa	1.2	1.3	1.24
Dennstaedtia punctilobula	3.9	5.5	4.7
Dryopteris sp.	18.8	41.8	30.29
Eupatorium perfoliatum	0.1	<0.1	0.07
Eupatorium purpureum	0.1	0.1	0.1
Eurybia divaricata	0.1	0	0.06
Galium sp.	0.7	0.1	0.4
Glyceria striata	0.3	0.1	0.18
Huperzia lucidula	2.5	2.1	2.3
Hydrocotyle americana	1.1	0.6	0.9
Hypericum punctatum	0.1	<0.1	0.07
Impatiens capensis	1.8	1.5	1.64
Iris pseudacorus	0.6	0.4	0.53
Laportea canadensis	0.6	0.1	0.35
Lycopodium digitatum	0.7	0.6	0.69
Lycopus uniflorus	0.5	<0.1	0.29
Maianthemum canadense	10.9	9.7	10.27
Medeola virginiana	1	0.5	0.73
Mitchella repens	13.4	10	11.72
Monotropa uniflora	0.3	<0.1	0.19
Myosotis scorpioides	0.6	0.5	0.57
Osmunda cinnamomea	0.6	1.9	1.27
Oxalis sp.	7.8	2.7	5.26

continued

Table 4. Relative frequency (%), percent cover (%), and importance values (%) for herbaceous plant species at Cathedral State Park in 2006.

Species	Relative Frequency	Percent Cover	Importance Value
Phlox paniculata	0.2	0.3	0.28
Pilea pumila	0.2	0.3	0.27
Poa. sp.	0.1	<0.1	0.07
Podophyllum peltatum	0.2	<0.1	0.13
Polygonatum pubescens	0.8	0.1	0.47
Polygonum sp.	0.9	0.3	0.62
Ranunculus hispidus	0.5	0.1	0.31
Rubus sp.	2.5	3.9	3.23
Rumex obtusifolius	0.6	1.1	0.86
Sanicula odorata	0.2	<0.1	0.14
Scutellaria lateriflora	0.3	<0.1	0.15
Smilax sp.	0.6	0.1	0.35
Symphyotrichum prenanthoides	0.5	1	0.73
Symplocarpus foetidus	1	1.2	1.08
Taraxacum officinale	0.1	<0.1	0.09
Thalictrum pubescens	0.1	<0.1	0.08
Thelypteris noveboracensis	1.2	0.8	0.98
Trillium undulatum	1	0.1	0.53
Unknown Compositae	0.2	0.1	0.18
Unknown Gramineae	1.6	1.5	1.53
Unknown sp.	1.1	0.3	0.66
Viola sp.	4.6	3.2	3.86

initial symptoms of HWA infestation, including chlorotic foliage and needle and branch dieback. In CSP, the most damaged hemlocks occur in the north-west corner of the park. This area is dominated by larger, overstory hemlock, a sparse understory, and a dense herbaceous layer consisting primarily of eastern hayscented fern. This area is likely targeted by HWA because of the healthy (i.e., more nutritious) foliage available from canopies receiving full sunlight and the ease of adelgid dispersal among tall, overstory hemlocks.

As large overstory hemlocks die, the canopy gaps they create will likely allow for the establishment of shade-intolerant tree species that previously have not been able to successfully establish. Tree species most likely to advance to the overstory in CSP are sweet birch, black cherry, and perhaps red maple based on 2006 understory dominance (Table 2). Orwig and Foster (1998) and Eschtruth et al. (2006) reported the prolific establishment of sweet birch seedlings in HWA-infested stands, especially in those with a higher percentage of hemlock mortality. In contrast, understory hemlock that escapes the HWA infestation is slow-growing and extremely shade-tolerant (Godman and Lancaster 1990), and may not be able to compete successfully if large canopy gaps are created by tree mortality.

With large canopy gaps created, great laurel should remain important in the areas where it already thrives. This will create a major hindrance to future advance tree regeneration. The increased likelihood of invasive plant species will also be a management concern following hemlock mortality (Orwig and Foster 1998). Species such as tree-of-heaven (*Ailanthus altissima* (P. Mill.) Swingle) and Japanese stilt grass (*Microstegium vimineum* (Trin.) A. Camus) may pose a major threat to regeneration of native tree species, although neither species was found in 2000 or 2006.

Structural characteristics of the CSP forest will likely change in the next few decades following HWA spread. The level of change will depend on several factors, including fluctuations in seasonal HWA populations, success of stand-level control methods, browsing pressure by white-tailed deer (*Odocoileus virginianus* Zimmerman), and the percentage of overstory occupied by hardwood species (Orwig and Foster 1998). If successful control methods are discovered, hemlock recovery may be possible if a reliable seed source is still present. In contrast, if the forest becomes dominated by shade-intolerant hardwood species following HWA-induced mortality, return to a hemlock-dominated forest may take decades or centuries, or may never occur.

Areas like CSP serve as a living history of what forest composition and structure were like prior to the extensive logging that occurred throughout much of the Appalachian region. This study documents the characteristics of a relic old-growth eastern hemlock-hardwood forest prior to and during the initial stage of HWA infestation. The abundance of large snags and DDW demonstrate the uniqueness of this old-growth forest. Understanding the dynamics of old-growth forests like CSP provides both a template for the management of younger stands that lack old-growth characteristics and a quantitative reference of a forest that may be lost forever if the HWA infestation follows well-established patterns.

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Table 5. Comparisons of downed dead wood (DDW) and snags at Cathedral State Park in 2006 to 25 hemlock-hardwood old-growth stands from the eastern United States (based on data from Tyrrell and Crow 1994a; Tyrrell et al. 1998).

Variable	Cathedral State Park	Other Old-Growth Stands
DDW Volume (m^3/ha)	81.9 ± 13.0	54.7 ± 5.4
Snag Density (trees/ha)	35.4 ± 3.5	79.6 ± 7.2
Snag Basal Area (m^2/ha)	5.7 ± 0.6	5.9 ± 0.5

One significant digit is preferred for these wood metrics.

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