

Vegetation Response Following Hemlock Woolly Adelgid Infestation, Hemlock Decline, and Hemlock Salvage Logging

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Abstract

Ten heavily logged hemlock (*Tsuga canadensis* (L.) Carr.) stands in Connecticut and Massachusetts were examined to compare the vegetation response following intense harvesting with chronic hemlock woolly adelgid (HWA) (*Adelges tsugae* Annand) infestations. All stands were dominated by hemlock, with 66 to 99% of total stand basal area. Salvage or pre-emptive cutting removed more than 50% of overstory stems and more than 65% of the basal area in each stand. Logging generated soil scarification, large accumulations of slash, and more rapid and pronounced microenvironment and vegetation changes than HWA damage. Percent open sky was 25 to 35% in newly cut forests, around 10% in HWA infested forest, and less than 5% in older cuts and healthy stands. A high percentage of residual hemlock and hardwood stems died within several years of logging, presumably due to environmental conditions. Black birch (*Betula lenta* L.) seedling densities and percent cover of brambles (*Rubus* L. spp.), sedges (*Carex* L. spp.) and hay-scented fern (*Dennstaedtia punctilobula* (Michx.) Moore) were significantly higher in cut stands versus HWA damaged and healthy stands. High black birch sapling densities (7,000 ha⁻¹) were common in the oldest cuts but not in adjacent, HWA-damaged portions of these stands. Residual hardwood trees had little influence on the species composition of emerging vegetation in logged sites. Conifer species were virtually absent in the regeneration following logging and HWA infestation, suggesting that silvicultural intervention will be necessary if evergreen species are desired. Results suggest that both the decline associated with HWA feeding and the indirect effects of logging are generating profound changes in structure and composition in these forests.

Keywords:

Vegetation dynamics, salvage logging, hemlock woolly adelgid, hemlock.

Introduction

The introduction of exotic pathogens and pests to forest ecosystems represents a powerful agent of ecological change that may selectively remove dominant tree species, dramatically alter ecosystem structure and function, and increase ecosystem susceptibility to further disturbances, including invasion by exotic plants and animals (Castello et al. 1995; Vitousek et al. 1996; Enserink 1999; Mack et al. 2000). Due to the increasing global movement of organisms and materials, pest and

pathogen outbreaks during the last century in the northeastern United States have led to declines in such dominant species as chestnut (*Castanea dentata* (Marshall) Borkh.) American elm (*Ulmus americana* L.), and beech (*Fagus grandifolia* L.) (Castello et al. 1995; Liebhold et al. 1995). Importantly, pest and pathogen outbreaks often lead to shifts in harvesting strategies of host trees, including increases in both the amount and rate of pre-salvage and salvage logging (Frothingham 1924; Irland et al. 1988; Radeloff et al. 2000).

The recent unimpeded infestation of the hemlock woolly adelgid (HWA) (*Adelges tsugae* Annand) across the northeastern United States (Souto and Shields 2000) provides an unusual opportunity and critical imperative to examine the ecological consequences of the removal of a regionally dominant tree species, eastern hemlock (*Tsuga canadensis* (L.) Carr.), on forest composition, structure, and function. Information from timber harvesters, state agencies, and studies of landscape patterns of hemlock decline in southern New England (Orwig et al. 2002) indicate that HWA is triggering a great increase in salvage and pre-emptive logging of hemlock. Although hemlock was intensively harvested and utilized in the 19th century for the tanning industry in the eastern United States (McMartin 1992; Whitney 1994), very little is known about the stand and ecosystem-level dynamics associated with this removal. Hemlock lumber contains several undesirable wood characteristics that have resulted in historically low demand, utilization, and stumpage prices (Gardner and Diebal 1995; Baumgrass et al. 2000; Howard et al. 2000). Therefore, the recent broad-scale increase in logging associated with HWA is occurring with little ecological assessment and in the absence of scientific background for conservationists, land managers, or policy makers.

In response to the imminent threats posed by HWA, a strategic management plan is being developed by the USDA Forest Service in cooperation with the National Association of State Foresters and the National Plant board (USDA 2001). The plan is designed to develop management strategies to help reduce the impact and slow the spread of this exotic pest. One of the strategies, silvicultural management, is in its infancy but will be critically important as HWA continues to spread and cause widespread decline and mortality. For example, several Connecticut state parks have been recently closed due to falling hemlock trees and limbs associated with years of chronic infestation (Rotting hemlocks prompt State to close part of Guilford Forest. *The Hartford Courant*, November 23, 2001). This has caused management dilemmas and widespread concern of whether to cut down existing trees or let them gradually die and fall on their own (Donnelly 1994; Cox and Mauri 2000). Beyond anecdotal observations, little data exists to help evaluate the consequences of hemlock logging on the residual stand or future stand dynamics. There have been very few studies that have examined the impacts associated with hemlock logging although efforts are underway to examine the wildlife response to such cutting (Brooks 2001).

As part of a larger study examining vegetation and ecosystem response following hemlock logging (Kizlinski 2002), we present vegetation data collected from 10 logged hemlock stands in Connecticut and Massachusetts and compare it with unlogged portions of those stands to address the following objectives: to examine vegetation dynamics associated with intense logging of eastern hemlock, and to compare the magnitude and trajectory of this response with that accompanying HWA infestations.

Methods

Study Area. Ten sites representing five different ages (1, 2, 3, 7, and 13 years since harvest) were studied within an 8,000 km² area extending from southern Connecticut to central Massachusetts and from the Connecticut River lowlands west to the Berkshire Plateau at elevations of 30 to 350 m above sea level. The climate is characterized by cold winters, warm summers, and evenly distributed precipitation of approximately 120 cm yr⁻¹ (Reynolds 1979; Seanu 1995). All sites contained similar loam and fine sandy loam soils formed from shallow glacial till on schist, gneiss, and granite bedrock with moderate slopes (Reynolds 1979; Seanu 1995). Regional vegetation ranges from the Central Hardwoods-Hemlock type in the south to the Transition Hardwoods-White Pine-Hemlock zone in the north (Westveld et al. 1956). Stand composition was dominated by hemlock (> 65% total basal area and > 53% total stem density) (Table 1) with lesser amounts of birch (*Betula lenta* L.), maple (*Acer* L. spp.) and oak (*Quercus* L. spp.). HWA was present in all of the stands studied, but high levels of infestation and hemlock mortality were only observed in the 6 southernmost sites (Table 1). Each site contained at least 1 ha of intensely logged hemlock (i.e., more than 65% basal area removed), and an adjacent unlogged portion of hemlock forest.

Table 1. Stand Characteristics of the 10 Hemlock harvests and Their Adjacent Uncut Hemlock Stands in Southern New England (BA = Basal Area)

Site Name (State)	Harvest Area			Uncut Stand		
	Age of Harvest (Years)	%BA Hemlock ¹	%Total BA Cut	%BA Hemlock	HWA Damage ²	%BA Dead Hemlock
Balsam Acres Tree Farm (MA)	1	90	88	77	low	<1
Penwood State Park (CT)	1	89	87	81	high	18
Cockaponset State Forest (CT)	2	80	65	71	high	36
Stillman Rd. (CT)	2	66	87	66	low	5
MDC Property (CT)	3	68	89	81	low	<1
Wallingford Land Trust (CT)	3	77	75	100	high	8
Gulf Quarry Rd. (CT)	7	82	67	76	high	53
Naugatuck State Forest (CT)	7	99	72	74	high	22
Camp Hazen YMCA (CT)	13	83	69	79	high	79
Mt. Toby (MA)	13	74	100	96	low	3

¹ Basal area of harvested area reconstructed from stump diameters (see text).

² Low = HWA present, but no significant crown loss (0 to 5%); high = HWA present at high densities with significant crown loss of live hemlock (35 to 80%).

Vegetation Sampling. Transects were established in the most heavily cut area and in the nearest unlogged portion of each stand. Vegetation was sampled in five to 10 circular plots (78.5 m²) located every 20 m along these transects. Woody stems 1.5 cm diameter at breast height (dbh) were recorded by species, dbh, and crown position. Pre-harvest basal area was reconstructed allometrically using a regression equation relating stump diameter to dbh ($y = 0.884x + 0.0003$; $r^2=0.995$) from a sample of 215 stems. Species, dbh, and probable mechanism of injury were

noted for dead trees in harvest plots. Sapling (1.5 to 9.9 cm dbh) heights for each species were estimated in each plot. Herb and shrub cover was estimated in three (1 x 1 m) subplots located in random directions 3 m from each plot center. Seedling (< 1.5 cm dbh) densities also were tallied in each subplot.

Data Analysis. Ground level hemispherical photographs taken at each plot center were analyzed using Gap Light Analyzer 2.0 (Frazer et al. 1999) to quantify the light environment incident at the soil surface. Vegetation data was analyzed with a one-way ANOVA with HWA-damage or logging class as the main effects. Data were rank-transformed prior to analyses.

Results

Overstory. Overstory mortality levels varied from 3% in healthy stands to 79% in HWA-damaged stands and the crown vigor in HWA-damaged stands consistently averaged 68% canopy loss (Table 1). Canopy openness in HWA damaged stands was 2.5 times higher than in healthy stands (data not shown). More than two-thirds of the total basal area (Table 1) and between 45 to 100% of the total stem density (data not shown) was removed from cut stands. Composition of residual trees included hemlock (69% of all uncut trees), birch, and a few large oaks. Eighty percent of uncut hemlock and 14% of uncut hardwoods died and many experienced wind damage resulting in snapped boles and tip-up mounds. Light levels in recently logged sites were as high as 38% open sky and decreased with harvest age to 4.5% in the oldest cuts (data not shown).

Seedlings. Healthy stands had significantly lower total seedling densities (1.6 vs. 3.8 m⁻²) than HWA-damaged stands (Table 2). Maple (61%) and hemlock (30%) together composed 91% of seedlings in healthy stands, while maple (50%) and birch (19%) accounted for 69% of the seedlings in HWA-damaged stands. Vegetation that established after logging was more abundant than the understory developing in stands suffering HWA damage, as cuts averaged 6.4 seedlings m⁻² vs. 3.8 m⁻² in HWA-damaged sites. Most seedlings originated immediately after harvest and exceeded 10 m⁻² within several years (data not shown). Seedling composition in logged sites was similar to HWA-infested stands with birch (53%) and maple (21%) accounting for 74% of all seedlings. Species such as oak, sassafras (*Sassafras albidum* (Nutt.) Nees.), and tulip poplar (*Liriodendron tulipifera* L.) were absent in healthy stands and occurred at higher densities in HWA-damaged and cut stands (Table 2). Hemlock seedling densities were low in cut stands and rare in damaged stands (less than 1% of all seedlings sampled). Birch was dominant at all cut ages and the relative proportion of maple seedlings declined with increasing harvest age.

Saplings. Sapling density was significantly higher in HWA-damaged stands (522 ha⁻¹) than in healthy stands (134 ha⁻¹), and hemlock comprised 88 and 95% of the total, respectively (Table 2). The remainder of the saplings consisted mostly of beech and birch. The large number of hemlock saplings in damaged stands resulted from a few dense plots. Hemlock saplings in damaged stands had poorer vigor and twice the mortality level of those in healthy stands (data not shown). Based on size, most hemlock saplings were estimated to have established prior to HWA infestation as advanced regeneration, while hardwood saplings likely originated post-infestation. Saplings were an order of magnitude higher in logged (~ 7600 ha⁻¹) versus damaged stands and were dominated by birch (95%) and a few pin

Table 2. Seedling and Sapling Densities in Healthy, Hemlock Woolly Adelgid (HWA)-Damaged, and Logged Hemlock Stands in Southern New England.

	Seedlings (Number m ⁻² ± SE)		
	Healthy (n=4)	HWA Damaged (n=6)	Logged (n=10)
American Beech	0.1 ± 0.0 a	0.0 ± 0.0 b	0.1 ± 0.1 ab
Birch ³	0.0 ± 0.0 a	0.7 ± 0.2 a	3.4 ± 0.5 b
Hemlock	0.5 ± 0.3 a	0.0 ± 0.0 b	0.1 ± 0.1 b
Maple ⁴	1.0 ± 0.4 a	1.9 ± 0.4 b	1.4 ± 0.2 b
Oak ⁵	0.0 ± 0.0 a	0.4 ± 0.1 b	0.2 ± 0.0 b
Pin Cherry	0.1 ± 0.0 a	0.0 ± 0.0 a	0.3 ± 0.0 b
Quaking Aspen	0.0 ± 0.0 a	0.0 ± 0.0 a	0.1 ± 0.0 b
Sassafras	0.0 ± 0.0 a	0.3 ± 0.1 b	0.2 ± 0.1 b
Tulip Poplar	0.0 ± 0.0 a	0.3 ± 0.1 a	0.4 ± 0.1 b
White Ash	0.0 ± 0.0 a	0.1 ± 0.1 b	0.1 ± 0.0 a
Total	1.6 ± 0.6 a	3.8 ± 0.5 b	6.4 ± 0.6 c

	Saplings (number ha ⁻¹ ± SE)		
	Healthy (n=4)	HWA Damage (n=6)	Logged (n=4)
Birch	6 ± 6 a	25 ± 15 a	6997 ± 638 b
Cherry, Fire	0 ± 0 a	0 ± 0 a	220 ± 57 b
Hemlock	127 ± 29 a	459 ± 102 b	5 ± 5 c
Maple ⁴	0 ± 0 a	25 ± 15 a	167 ± 111 b
Oak ⁵	0 ± 0 a	8 ± 6 a	103 ± 40 b
Total	134 ± 34 a	522 ± 109 b	7614 ± 638 c

¹Sapling values from only 7- and 13- year-old cuts with only the most common species are listed.

²Significant differences between sites are indicated by different letters ($p < 0.05$).

³ Black, gray, yellow.

⁴ Red and sugar.

⁵ Black, chestnut, red.

cherry (*Prunus pennsylvanica* L.f.), maples, and oaks. Sapling heights after harvest were 4 to 5 m within 7 years and exceeded 7 m within 13 years. Unlike HWA-infested stands, hemlock saplings were rare in cut sites.

Shrub and Herb Cover. Shrub cover was virtually absent in healthy stands (0.05%), and low (0.82%) but significantly higher in HWA-damaged stands. Several species such as blackberry (*Rubus allegheniensis* T.C. Porter), red raspberry (*R. idaeus* L.), and black raspberry (*R. occidentalis* L.), exhibited significantly higher cover in cut versus HWA-damaged stands (Figure 1). Total shrub cover peaked at 28% in the 3-year-old cuts and was less than 10% in older cuts, apparently due to reduced light levels associated with dense birch cover. Average herbaceous

cover in HWA-damaged stands was nearly twice that of healthy stands (3.4 versus 1.8%) and consisted primarily of sedge (*Carex* L. spp.), Canada mayflower (*Maianthemum canadense* Wiggers), sarsaparilla (*Aralia* L. spp.), and pokeweed (*Phytolacca americana* L.). Following cutting, average herb cover was significantly higher than in HWA-damaged stands, ranging from 9.0 to 21.1% and consisting of light demanding species such as sedge, hay-scented fern (*Dennstaedtia*

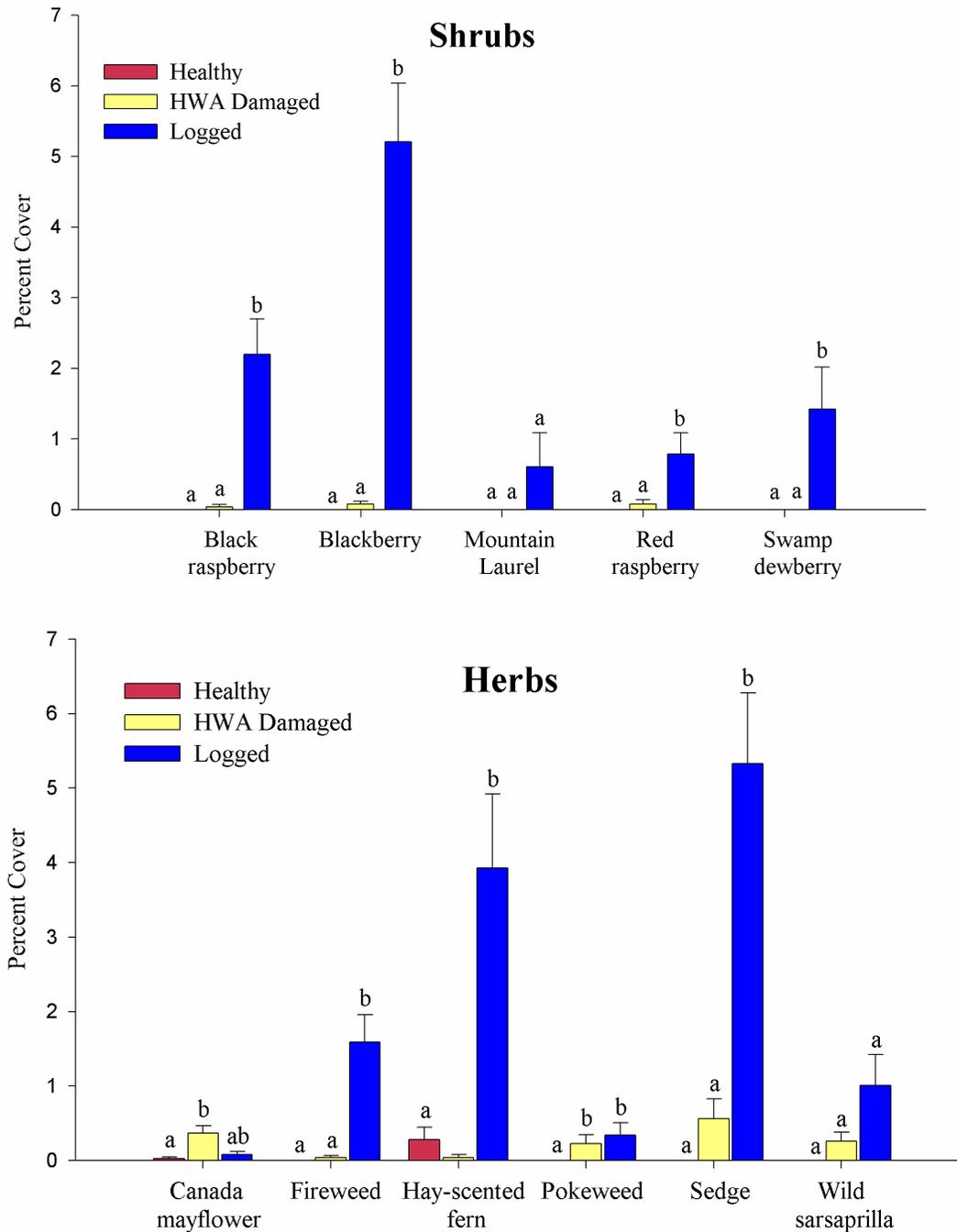


Figure 1. Percent shrub and herb cover in healthy (n=4), HWA-damaged (n=6), and logged (n=10) hemlock stands in southern New England. Values are based on square meter subplots. Significant cover differences between sites are indicated by different letters ($p < 0.05$).

punctilobula ((Michx.) Moore), and fireweed (*Erechtites hieracifolia* Raf.). Herb cover was less abundant in older cuts with taller vegetation and reduced light levels. The only herbs common to all harvested sites were sedges that occurred in 70% of cut plots with the highest average cover.

Discussion

There have been many studies examining vegetation dynamics following either logging (Hix and Barnes 1984; Mou et al. 1993; Wang and Nyland 1993; Smith and Ashton 1993) or pest and pathogen outbreaks (Korstian and Stickel 1927; Huenneke 1983; Twery and Patterson 1984; Witter and Ragenvich 1986). However, despite the tremendous impact that HWA has had on eastern hemlock forests, few studies have investigated vegetation patterns following HWA infestation (Orwig and Foster 1998; Orwig this volume) and none have compared the vegetation dynamics associated with species removal by both HWA and associated logging. This study successfully compared the dynamics resulting from the direct impacts of HWA infestation with the indirect effects of pre-emptive and salvage logging.

Given the recent increase in hemlock harvesting within and outside the zone of HWA infestation, the ecological consequences of this activity should be of major interest to wildlife managers, conservationists, and forest policymakers. While both logging and chronic HWA infestation resulted in the near complete mortality of hemlock, logging altered forest structure and subsequent environmental conditions more abruptly and severely by rapidly removing hemlock across a sharply defined area. In contrast, hemlock decline from HWA occurs more gradually over 4 to 10 years or more (McClure 1991; Orwig this volume), resulting in a larger number of snags. In addition, logging introduced additional variables such as scarification, soil compaction, and a more clumped distribution of slash that does not accompany chronic HWA infestation, and that may be important in post-harvest vegetation and ecosystem recovery.

HWA and Vegetation. Due to low densities of HWA, healthy stands examined in this study showed little evidence of decline and had vegetation and understory characteristics typical of healthy hemlock forests such as very low light infiltration; cool and moist soils with thick, acidic forest floors; scattered hemlock seedlings; and few herbs or shrub species (Rogers 1980). In contrast, HWA-damaged hemlock stands had higher seedling densities and percent cover of shrub and herb species due to high hemlock mortality and resulting increased light levels. Understory vegetation was similar in composition to other HWA-damaged sites and consisted mostly of birch and red maple seedlings (Orwig and Foster 1998, Jenkins et al. 1999; Orwig this volume). The rate and pattern of this vegetation response was temporally variable, poorly correlated with the duration of infestation, and affected by the size and extent of canopy opening and composition of the surrounding forest. Despite this variability, it is quite clear that black birch and red maple have responded most favorably to the HWA-induced hemlock decline.

Logging and Vegetation. Post-harvest vegetation composition was similar to HWA-damaged stands, but contained significantly higher densities of seedlings and saplings and percent cover of shrub and herb species. Rapid birch seedling establishment followed logging at most sites, regardless of residual tree composition, and resulted in tall, dense sapling thickets within 7 years of harvest. Based on its

potential longevity and current overstory abundance in Connecticut (Ward and Stephens 1996; Orwig et al. 2002), we predict that birch will continue to dominate these sites for decades.

Hemlock seedlings were sparse in cut and damaged stands and are unlikely to regain dominance following logging, even in areas lacking HWA. Hemlock regeneration is affected by a myriad of problems (Mladenoff and Stearns 1993) and is greatly reduced by limited seed production from any remaining trees, low seed viability (Frothingham 1915), retarded germination of remaining seeds in highlight environments (Duchesne et al. 1999), and, where present, the continued infestation of HWA. In addition, most residual hemlocks died following logging, either from wind exposure, continued HWA attack, or unknown causes. Consequently, even outside the distribution of HWA, hardwood dominance after logging will lead to a long-term decrease in hemlock (Hibbs 1983; Kelty 1986; Smith and Ashton 1993).

Sharp increases in blackberry, black raspberry, hay-scented fern and sedge occurred immediately after logging, followed by gradual declines with time as they became shaded. Increases in these species are commonly observed following logging (Smith and Ashton 1993; Archambault et al. 1998; Iseman et al. 1999), but, with the exception of hay-scented fern, are not common following hemlock decline from HWA (Orwig and Foster 1998; Orwig this volume).

The vegetation response observed in southern New England may differ as HWA infestation and salvage logging continue to spread northward into regions with different species assemblages and environmental conditions. American beech, sugar maple (*Acer saccharum* Marshall), and yellow birch (*B. alleghaniensis* Britton) become the dominant hardwoods, and white pine (*Pinus strobus* L.) commonly grows with hemlock in a more diverse conifer component (Westveld et al. 1956). How these species will respond to the removal of hemlock is still largely unknown. While this study focused on the near complete removal of hemlock, less intensive hemlock logging also is occurring across the New England landscape (Orwig et al. 2002) and will likely lead to a more diverse regeneration component due to the increased shade and seed source provided by residual hardwood trees. Additional research is needed to examine the various successional pathways that accompany different levels of hemlock harvesting.

Conclusions

While our goal was not to determine whether infested stands should be cut or not, our results can be used to help inform decision making on this management dilemma. Vegetation patterns that accompany HWA infestation or logging were broadly similar in species composition but occurred at different temporal and spatial scales. Logging abruptly altered microenvironmental conditions by rapidly removing overstory stems, while chronic HWA infestation led to a gradually thinning canopy with abundant, scattered snags. In each case, black birch and other hardwoods replaced hemlock and there was no indication that hemlock will regain a presence in these forests in the near future. Vegetation re-establishment following logging contained a larger pulse of shade-intolerant seedlings, herbs, and shrubs. Due to the scarcity of conifer regeneration on these sites, it is likely that silvicultural intervention in the form of plantings and hardwood thinnings will be required if evergreen species are desired, although the cost of these operations would have to be carefully considered.

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References

- Archambault, L., J. Morissette, and M. Bernier-Cardou. 1998. Forest succession over a 20-year period following clearcutting in balsam fir-yellow birch ecosystems of eastern Québec, Canada. *Forest Ecology Management* 102: 61-74.
- Baumgras, J.E., P.E. Sendak, and D.L. Sonderman. 2000. Ring shake in eastern hemlock: frequency and relationship to tree attributes. pp. 156-160. In McManus, K.A., K.S.Shields, D.R. Souto (eds.). *Proceedings of the Symposium on Sustainable Management of Hemlock Ecosystems in Eastern North America, 22-24 June 1999, Durham, New Hampshire*. General Technical Report 267. U.S. Department of Agriculture, Forest Service, Newtown Square, Pennsylvania.
- Brooks, R.T. 2001. Effects of the removal of overstory hemlock from hemlock-dominated forests on eastern redback salamanders. *Forest Ecology and Management* 149: 197-204.
- Castello, J.D., D.J. Leopold, and P.J. Smallidge. 1995. Pathogens, patterns, and processes in forest ecosystems. *Bioscience* 45: 16-24.
- Cox, G. and M. Mauri. 2000. Practical Management: The hemlock dilemma. *Woodland Steward* 30: 3-5.
- Donnelly, C. 1994. Attack on Connecticut hemlock presents challenges and opportunities. *The Northern Logger and Timber Processer*: October 1994.
- Duchesne, L.C., C. Mueller-Rowat, L.M. Clark, and F. Pinto. 1999. Effect of organic matter removal, ashes, and shading on Eastern Hemlock, *Tsuga canadensis*, seedling emergence from soil monoliths under greenhouse conditions. *Canadian Field Naturalist* 113: 264-268.
- Enserink, M. 1999. Biological Invaders Sweep In. *Science*. 285: 1834-1836.

- Frazer, G.W., C.D. Canham, and K.P. Lertzman. 1999. Gap Light Analyzer (GLA): Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, users manual and program documentation. Simon Fraser University, Burnaby, British Columbia, and the Institute of Ecosystems Studies, Millbrook, New York.
- Frothingham, E.H. 1915. *The Eastern Hemlock*. U.S. Department of Agriculture. Bulletin 152.
- Gardner, D.J. and J.F. Diebal. 1995. Eastern hemlock (*Tsuga canadensis*) uses and properties. pp. In Mroz, G. and J. Martin (eds.). *Proceedings on Hemlock Ecology and Management Conference*. University of Wisconsin, Madison, Wisconsin.
- Hibbs, D.E. 1983. Forty years of forest succession in central New England. *Ecology* 64: 1394-1401.
- Hix, D.M. and B.V. Barnes. 1984. Effects of clear-cutting on the vegetation and soil of an eastern hemlock dominated ecosystem, western Upper Michigan. *Canadian Journal of Forest Research* 14: 914-923.
- Howard, T., P. Sendak, and C. Codrescu. 2000. Eastern hemlock: a market perspective. pp. 161-166. In McManus, K.A., K.S. Shields, D.R. Souto (eds.). *Proceedings of the Symposium on Sustainable Management of Hemlock Ecosystems in Eastern North America*, 22-24 June 1999, Durham, New Hampshire. General Technical Report 267. U.S. Department of Agriculture, Forest Service, Newtown Square, Pennsylvania.
- Huenneke, L.F. 1983. Understory response to gaps caused by the death of *Ulmus americana* in central New York. *Bulletin of the Torrey Botanical Club* 110: 170-175.
- Ireland, L.C., J.B. Dimond, J.L. Stone, J. Falk, and E. Baum. 1988. *The spruce budworm outbreak in Maine in the 1970's- assessment and directions for the future*. Maine Agricultural Experiment Station Bulletin 819.
- Iseman, T.M., D.R. Zak, W.E. Holmes, and A.G. Merrill. 1999. Revegetation and nitrate leaching from lake states northern hardwood forests following harvest. *Soil Science Society of America Journal* 63: 1424-1429.
- Jenkins, J.C., J.D. Aber, and C.D. Canham. 1999. Hemlock woolly adelgid impacts on community structure and N cycling rates in eastern hemlock forests. *Canadian Journal of Forest Research* 29: 630-645.
- Kelty, M.J. 1986. Development patterns in two hemlock-hardwood stands in southern New England. *Canadian Journal of Forest Research*. 16: 885-891.
- Kizlinski, M.L. 2002. Vegetation and ecosystem response to eastern hemlock decline and logging: direct and indirect consequences of the hemlock woolly adelgid. M.S. dissertation, Harvard University, Cambridge, Massachusetts.

- Korstian, C.F. and P.W. Stickel. 1927. The natural replacement of blight-killed chestnut in the hardwood forests of the Northeast. *Journal of Agricultural Research* 34: 631-648.
- Liebholt, A.M., W.L. MacDonald, D. Bergdahl, and V.C. Mastro. 1995. Invasion by exotic forest pests: A threat to forest ecosystems. *Forest Science Monograph* 30: 1-49.
- Mack, R.N., D.S. Simberloff, W.M. Lonsdale, H. Evans, M. Clout, and F.A. Bazzaz. 2000. Biotic invasions: Causes epidemiology, global consequences, and control. *Ecological Applications* 10: 689-710.
- McClure, M.S. 1991. Density dependant feedback and population cycles in *Adelges tsugae* (Homoptera: Adelgidae) on *Tsuga canadensis*. *Environmental Entomology* 20:258-264.
- McMartin, B. 1992. Hides, hemlocks, and Adirondack history. North Country Books, Utica, New York.
- Mou, P., T.J. Fahey, and J.W. Hughes. 1993. Effects of soil disturbance on vegetation recovery and nutrient accumulation following whole-tree harvest of a northern hardwood ecosystem. *Journal of Applied Ecology* 30: 661-675.
- Orwig, D.A. 2002. Stand Dynamics Associated with Chronic Hemlock Woolly Adelgid Infestations in Southern New England. (this volume).
- Orwig, D.A. and D.R. Foster. 1998. Forest response to the introduced hemlock woolly adelgid in southern New England, USA. *Journal of the Torrey Botanical Society* 125: 60-73.
- Orwig, D.A., D.R. Foster, and D.L. Mauseel. 2002. Landscape Patterns of Hemlock Decline in New England Due to the Introduced Hemlock Woolly Adelgid. *Journal of Biogeography*. (in press).
- Radeloff, V.C., D.J. Mladenoff, and M.S. Boyce. 2000. Effects of interacting disturbances on landscape patterns: budworm defoliation and salvage logging. *Ecological Applications* 10: 233-247.
- Reynolds, C.A. 1979. Soil Survey of Middlesex County, Connecticut. U.S. Department of Agriculture, Natural Resource Conservation Service, Washington, DC.
- Rogers, R.S. 1980. Hemlock stands from Wisconsin to Nova Scotia: Transitions in understory composition along a floristic gradient. *Ecology* 61: 178-193.
- Seanu, R.J. 1995. Soil Survey of Hampden and Hampshire Counties, Western Part, Massachusetts. U.S. Department of Agriculture, Washington, DC.
- Smith, D.M. and P.M. Ashton. 1993. Early dominance of pioneer hardwood after clearcutting and removal of advanced regeneration. *Northern Journal of Applied Forestry* 10: 14-19.

- Souto, D., and K. S. Shields. 2000. Overview of hemlock health. pp. 76-80. In McManus, K.A., K.S.Shields, D.R. Souto (eds.). *Proceedings of the Symposium on Sustainable Management of Hemlock Ecosystems in Eastern North America, 22-24 June 1999*, Durham, New Hampshire. General Technical Report 267. U.S. Department of Agriculture, Forest Service, Newtown Square, Pennsylvania.
- Twery, M.J. and W.A. Patterson III. 1984. Variations in beech bark disease and its effects on species composition and structure of northern hardwood stands in central New England. *Canadian Journal of Forest Research*. 14: 565-574.
- U.S. Department of Agriculture. 2001. Research and technology development needs assessment for management of hemlock woolly adelgid in the eastern United States (draft). Morgantown, West Virginia.
- Vitousek, P.M., C.M. D'Antonio, L.L. Loope, and R. Westbrooks. 1996. Biological invasions as global environmental change. *American Scientist* 84: 468-478.
- Wang, Z. and R.D. Nyland. 1993. Tree species richness increased by clearcutting of northern hardwoods in central New York. *Forest Ecology and Management* 57: 71-84.
- Ward, J.S. and G.R. Stephens. 1996. Influence of crown class on survival and development of *Betula lenta* in Connecticut, U.S.A. *Canadian Journal of Forest Research* 26: 277-288.
- Westveld, M.V., and Committee on Silviculture, New England Section, Society of American Foresters. 1956. Natural forest vegetation zones of New England. *Journal of Forestry* 54: 332-338.
- Whitney, G. G. 1994. *From Coastal Wilderness to Fruited Plain*. Cambridge University Press, Cambridge, Massachusetts.
- Witter, J.A. and I.R. Ragenovich. 1986. Regeneration of Fraser fir at Mt. Mitchell, North Carolina, after depredations by the balsam woolly adelgid. *Forest Science* 32: 585-594.