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Proceedings: Symposium on Sustainable Management of Hemlock Ecosystems in Eastern North America

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Edited by:
Katherine A. McManus
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Preface

Eastern hemlock (*Tsuga canadensis*) is remarkable because of its extreme tolerance to shade and its long life. Much like the fable of the tortoise and the hare, hemlock can outwait, and outlive, its more aggressive competitors. Although its wood is unremarkable as lumber or fiber compared to other species with which it competes, hemlock has important ecosystem values worth protecting, such as wildlife benefits and aesthetics. Although timber management and cutting practices in eastern North America generally have not favored hemlock reproduction, hemlock has maintained itself on suitable sites. The single most serious concern for the future of eastern hemlock is hemlock woolly adelgid (*Adelges tsugae*), an exotic insect that threatens to decimate eastern and Carolina hemlock over most of their natural range. Pollen records in lake sediments show that hemlock declined, possibly as a result of an insect pest, about 5,000 years ago, but recovered slowly over 1,000 years.

The purpose of this symposium was to bring together researchers and managers to exchange information and foster discussion on managing the extensive ecosystems in which hemlock occurs in eastern North America. The five themes addressed at the symposium included hemlock silviculture, ecology, forest health, wildlife relationships, and marketing and utilization. Thirty-one papers and 20 posters were presented and a field trip demonstrated silviculture, ecology, and wildlife principles and marketing of hemlock wood products. Many of the presentations dealt in some way with hemlock woolly adelgid or probable effects on the ecosystem of large-scale hemlock mortality.

The advances that have been made in understanding the biology of hemlock are rooted in the work of many individuals. Some met at this symposium to share that understanding. The message was not entirely optimistic, and it is hoped that more research will be stimulated as a result. The good news is that hemlock endured a similar decline once before and recovered. The bad news is that recovery took 1,000 years. We hope that the interaction between science and resource management will mitigate the potential effect of the hemlock woolly adelgid and maintain hemlock as a valuable component of the ecosystem.

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Poster Presentations

Hemlock's Future in the Context of its History: An Ecological Perspective

David R. Foster[1]

In October of 1852, Henry David Thoreau went for a stroll through a chestnut forest in Concord, Massachusetts and recorded the following impressions of a vibrant ecosystem:

> "The chestnut leaves already rustle with a great noise as you walk through the woods, as they lie light, firm, and crisp. Now the chestnuts are rattling out. The burs are gaping and showing the plump nuts. They fill the ruts in the road, and are abundant amid the fallen leaves in the midst of the wood. The jays scream, and the red squirrels scold, while you are clubbing and shaking the trees. Now it is true autumn; all things are crisp and ripe".

Thoreau's many writings on chestnut (*Castanea dentata* (Marshall) Borkh.) are diverse and remarkably insightful for modern ecologists who seek to understand the former role of this species in New England forests. For example, his journal observations range from nut dispersal by squirrels and passenger pigeons, to the sprout behavior and growth rate of the trees, to forest structure and dynamics, and on to the many land-use practices associated with the human use of chestnut for wood, fuel, and food (Foster 1999). Thoreau's observations are revealing precisely because they pre-date the arrival of the chestnut blight to eastern North America and, unlike any historical reconstruction that we might attempt today, they are unbiased by the slightest inkling of the fate of the species.

In like fashion, most of the contributors to the symposium *Sustainable Management of Hemlock Ecosystems in Eastern North America* began their research on hemlock (*Tsuga canadensis* (L.) Carriere) forests before the hemlock woolly adelgid (*Adelges tsugae* Annand) became such a clear threat to the forests of eastern North America. Today, however, all hemlock researchers must undertake their studies with the knowledge that the adelgid, which arrived in Virginia in the early 1950s, spread into New England in 1985, and is now widely established across 11 eastern states, is spreading at a rate of 20-30 km per year and is leaving devastated hemlock stands in its wake (Orwig and Foster 1998). As hemlock, one of the most shade-tolerant and long-lived tree species in the Eastern U.S., is succumbing to an introduced pathogen, we find ourselves in the position of chestnut researchers in the early 1900s, questioning the future and fate of a dominant and very important tree species. The adelgid also raises the immediate question as to whether sustainable management of hemlock forests is, itself, a viable concept.

In areas of heavy adelgid infestation hemlock ecosystems are undergoing major changes in structure, composition, and ecosystem function (Orwig and Foster 1998). Interpretation of the long-term consequences of this disturbance and approaches to the management of hemlock forests within and outside the current range of the adelgid, can gain insights from studies of the past dynamics of hemlock. Below, I review these dynamics with the broad objective of highlighting many of hemlock's characteristics and its long-term history in New England. In particular, I focus on the major ecological lessons that emerge from this 10,000 year legacy (Foster and Motzkin 1998).

Post-glacial Migration of Hemlock

Using an array of paleoecological sites across eastern North America it has been possible to determine the history of post-glacial movement of the major tree species upon deglaciation and climate warming (Davis 1981b). By comparing the dynamics of hemlock and other species from northeastern forests, the following observations and important ecological insights emerge: (1) taxa like hemlock, beech (*Fagus grandifolia* Ehrh.), maple (*Acer*), and chestnut, which co-occur in our forests and have strongly overlapping range distributions today, have strikingly different, individualistic histories. These histories include different glacial refugia, contrasting migration rates and pathways, and subtly different modern distributions; (2) co-occurring species also have very different New England histories. For example, whereas chestnut arrived and expanded broadly across the region only within the past 2000 years, hemlock has been present and abundant for more than 8000 years; (3) these differences in species history appear to be driven by ongoing and essentially continuous change in climate and differences in species physiology, population biology, and growth characteristics. Particularly important is the complex nature of climate change, which involves variation in quantity and seasonal distribution of temperature, precipitation, and growing season length, as well as ongoing changes in the earth's atmosphere.

Long-term Dynamics of Hemlock Forests

As background for ecology, conservation, and management, long-term records of local stand dynamics provide essential information (Foster et al. 1996). Unfortunately, such data are impossible to retrieve from standard sampling methods or even long-term records and permanent plots. However, an unusual application of paleoecology, which involves the stratigraphic analysis of sediments in very small basins like vernal pools, small hollows, and confined wetlands, enables us to develop lengthy chronologies at a stand scale. The pollen deposited in these basins, and therefore the vegetation record, derive primarily from within 50-m distance.

In one study using this approach a 9500-yr record was obtained from a mature hemlock forest in the Harvard Forest in Petersham, Massachusetts (Foster and Zebryk 1994). Major results and insights include: (1) hemlock was locally abundant for 8000 years, having invaded sites previously dominated by spruce (*Picea*) and then pine (*Pinus*) and oak (*Quercus*); (2) through time, the relative abundance of

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hemlock and of associated species have changed as the climate changed and as new tree species migrated into the region; (3) major disturbances occurred approximately every 1000 years and included: fire, marked by discrete layers of charcoal, at 7650, 6650, 6150, and 1900 years BP (before present); the hemlock decline at 4700 years BP; and European settlement at 250 years BP; (4) following each disturbance the abundance of hemlock declined abruptly and gradually recovered over a 500+ year period; and (5) the species that replaced hemlock following each disturbance varied through time as a consequence of changes in the species pool: from 8000-2100 BP birch, oak and pine increased as hemlock declined, but since chestnut arrived in the region 2000 years ago it has been the major species increasing after disturbance.

Ecological Consequences of the Mid-Holocene Hemlock Decline

Approximately 5000 years BP hemlock suffered a major decline in abundance across its entire range. Due to the synchronous, widespread, and single-species nature of the decline it has been interpreted as a consequence of outbreak of a pathogen like the eastern hemlock looper (*Lambdina fiscellaria* Gven.), as opposed to climate change (as previously believed) or aboriginal impact (Davis 1981a). Support for this interpretation has been provided by subsequent studies, particularly the identification of large numbers of looper fossils in sediments contemporaneous with, and containing pollen and macrofossil evidence for, the hemlock decline (Bhiry and Filion 1996). Interestingly, the hemlock decline represents the only documented outbreak of a natural pathogen in the paleoecological record.

Detailed paleoecological studies provide interesting insights concerning the nature of the hemlock decline and subsequent ecosystem dynamics (Fuller 1998, Hall and Smol 1993, Foster and Zebryk 1993), including: (1) the decline appears to be a two-stage process in which an initial decrease and temporary recovery was followed by a major, enduring decline; (2) the intensity of the decline and residual abundance of hemlock varied geographically and perhaps on a landscape scale, however, across the range of hemlock the species appears to have survived in small, but widespread, populations; (3) the species replacing hemlock varied geographically and also through time as succession occurred; (4) hemlock abundance after the recovery was oftentimes quite different than before the decline; and (5) the forest disturbance exerted a marked impact on adjoining aquatic ecosystems. In summary, although hemlock showed the potential to recover from, or perhaps evolve resistance to, a major pathogen, the recovery process required 1000 years or more.

Regional Forest Response to Land Use: Interaction of Disturbance and Climate Change

The most rapid change in forest composition in New England during the post-glacial period was initiated by European settlement and land-use activity (Jacobson et al. 1987). Importantly, although this human disturbance initially involved rapid deforestation and increased agricultural activity, over the past 150 years this process has largely been reversed by agricultural decline and natural reforestation (O'Keefe and Foster 1998). Today in New England a largely forested condition prevails in which forest height and tree size are increasing. Among the most important and relevant questions for ecological studies and forest conservation and management in this region are: What are the consequences of this land-use history on forest ecosystems? And, To what extent does modern forest composition parallel pre-European forest composition? To address these questions on a broad scale we examined paleoecological records (<2000 years), historical data, and modern stand characteristics in a region of north-central Massachusetts, extending from the Connecticut Valley Lowland (30-50 m a.s.l.) through the Central Upland (300-400 m a.s.l.) to the Eastern Lowland (< 100 m). Sampling sites are distributed throughout this region, which encompasses a subtle climate gradient.

Findings include: (1) the major compositional dynamic across the region (and much of the northeast) involves a decline in hemlock and beech and increase in birch, oak and red maple since settlement; (2) at the time of European settlement the major forest types and tree species varied geographically: Oak-Hickory forests were abundant in the warmer, lower, southern areas and Northern Hardwoods (maple, beech, birch (*Betula*), maple)-Hemlock forest increased in the cooler, higher and northern areas. However, through time, the history of land use apparently caused a homogenization of the regional vegetation. Today, there is no geographic pattern or statistical relationship between species abundance or forest type and climate (Foster et al. 1998); (3) paleoecological data corroborate these findings but indicate that part of this dynamic, specifically the decline in hemlock and beech, was actually initiated approximately 500 years before present (Fuller et al. 1998). This early forest change was apparently linked to climate change, notably the Little Ice Age, a cooler, drier and more variable period; and (4) consequently, it is potentially misleading to interpret post-settlement forest change in the absence of a thorough understanding of pre-settlement dynamics and environmental change.

Post-settlement Dynamics and the Development of Old-growth Characteristics in Hemlock Forests

Hemlock forests dominated by large trees on sheltered sites represent some of the oldest and most mature stands across southern New England (Foster and O'Keefe 2000). Due to their many old-growth characteristics, lack of recent disturbance, and apparent stability, these forests have been interpreted by many researchers as natural and as possible examples of the pre-settlement vegetation (Nichols 1913, Spurr 1956). Most of these forests occur on sites that were never cleared historically but it is very likely that most were cut once to several times early in the region's history (O'Keefe and Foster 1998). Recently, a number of studies have sought to investigate the history of these stands over the past few hundred years using pollen analysis of the stratigraphic record contained in small hollow or vernal pools (see Long-term Stand Dynamics, above) and organic humus layers in conifer forests.

In studies in north central Massachusetts, Foster *et al.* (1992) and McLachlan *et al.* (1999) analyzed deep (15-25 cm) humus layers in such hemlock forests and revealed a very consistent record of their developmental history: (1) although appearing natural, mature and relatively stable, each of these stands underwent major changes over the last 400 years, generally involving conversion of a pre-settlement forest of mixed hardwoods (beech, birch, oak) and conifer (white pine and hardwood) to a sprout hardwood forest of chestnut or birch upon heavy cutting in the 18th or 19th C. The subsequent development of a hemlock-pine-hardwood forest has occurred through time, low human impact, and the advent of the chestnut blight; (2) these dynamics have resulted in two or three forest types on these sites over time, each with little similarity to each other; and (3) the development of mature forest with many old-growth characteristics has resulted in spite of (and perhaps partly due to) a history of human activity.

Hemlock's Latest Dynamic: Response to the Hemlock Woolly Adelgid

In 1985, the hemlock woolly adelgid crossed Long Island Sound into Connecticut and began to advance northward through New England. Considerable effort and money have been expended in attempts to control the adelgid through chemical and biological means, but surprisingly little work has focussed on the adelgid's ecological impact (however, see articles by York et al. and Orwig and Foster, this volume). In 1994, the Harvard Forest launched a broad program led by Dr. David Orwig to study the progression and ecological consequences of the adelgid in New England. Across a study region extending from Long Island Sound to northern Massachusetts and encompassing the Connecticut River Valley (100 x 250 km), this project seeks to: (1) map all hemlock forests using pre-adelgid air photos; (2) determine the regional pattern of adelgid infestation, assess its impact on the vigor and mortality of hemlock, and interpret these patterns in terms of environmental factors, distance from the Connecticut coast, and time; (3) assess forest ecosystem changes in terms of structure, composition and function (particularly nitrogen dynamics) and interpret these in relationship to changes in the forest environment; and (4) quantify the extent of increased logging of hemlock prompted by adelgid damage and contrast the ecological effects of logging with the "natural" process of mortality generated by adelgid.

Results to-date provide a very sobering view of the state of hemlock in southern New England and an equally pessimistic prognosis for the species throughout its range: (1) the hemlock woolly adelgid is widespread in Connecticut and southern Massachusetts and is continuing to spread at a rate of 20-30 km per year; (2) along the latitudinal and temporal gradients of infestation there is a gradient in mortality and tree vigor, with extensive mortality occurring throughout southern and central Connecticut; (3) no infested hemlock tree or hemlock forest exhibits any sign of recovery, there is no evidence for any site or environmental factors that mitigate mortality, and trees of all size are affected; (4) as hemlock declines in vigor and as understory light levels increase, hardwood species, especially black birch (*Betula lenta* L., establish and grow rapidly; and (5) the major landscape-level consequence of the adelgid is to greatly reduce the complexity and diversity of forest and habitat structure and composition.

Conclusion

Eastern hemlock is very much a species in transition. Whether one's perspective is that of a landowner, forest manager, or conservationist seeking to manage landscapes for multiple sustained purposes, or that of an ecologist interested in interpreting the modern characteristics of ecosystems, it is impossible to consider hemlock forests without some doubt about its long-term viability. Ironically, in an era of extensive concern for global environmental change it is another manifestation of globalization – the movement of exotic organisms – that is changing the southern New England landscape most rapidly. Hemlock mortality and widespread logging of hemlock (more than 4 million board feet of hemlock were cut in Connecticut and Massachusetts in 1998 by Re-Gen, Inc. alone; D. Whitney pers. comm.) are transforming large areas from old, conifer-dominated forest to stands of young, rapidly growing hardwoods. The potential for the adelgid to spread is great and this, in itself, is becoming a strong force encouraging land-use and land-cover changes through "pre-emptive logging" well outside the insect's current range.

The long-term history of hemlock illuminates the discussion of the future of our forests in an adelgid world. Forests are remarkably resilient and the declining and dying hemlock forests will be rapidly replaced by hardwood species such as black birch. The decline will be associated with nutrient pulses to the groundwater and aquatic ecosystems as well as local changes in microenvironment that will have additional repercussions for terrestrial and aquatic ecosystems. For most people, outside those who discover new views or dead landscaping in their backyards or devastated hiking trails and shady ravines, the changes may be largely overlooked. However, the dynamics initiated by the adelgid will be permanent, in human terms. Even if the adelgid could be controlled completely, even if a full restocking of hemlock seedlings could be established, in those stands where the decline is well advanced and mortality is widespread the recovery of hemlock forests will be hundreds of years in the making.

Thus, we should cherish our opportunity to view hemlock in the manner that Henry Thoreau viewed the chestnut, as a vibrant and ecologically unique part of our landscape. Meanwhile, there will be a nagging reminder of hemlock's past and future in the back of our minds.

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Composition, Structure, and Sustainability of Hemlock Ecosystems in Eastern North America

William H. McWilliams[1] *and Thomas L. Schmidt*[2]

Abstract

Across its natural range in North America, eastern hemlock (*Tsuga canadensis* (L.) Carriere) is an important resource for people and wildlife, but it is seriously threatened by the hemlock woolly adelgid (HWA) (*Adelges tsugae* Annand). From 10 to 20 percent of the hemlock resource is found in the Canadian provinces of New Brunswick, Nova Scotia, Ontario, Prince Edward Island, and Quebec. In the United States, hemlock is found across a wide range of forest types and stand conditions. There are 2.3 million acres of hemlock-dominated stands, but this species also is a common associate in many other forest types. The total net volume of live hemlock trees in the United States is 8.4 billion cubic feet, or 2 percent of the total inventory in states within its natural range. The existing hemlock resource is in a mature condition dominated by large-sized stands and trees. Young stands of hemlock are uncommon. Currently, hemlock mortality is low compared to other species within its range, but this would change if the HWA continues to expand. Hemlock is growing at a rate three times faster than it is being removed by harvesting and changes in land use. Long-term sustainability will depend heavily on the degree that hemlock is favored in future management practices, the future spread of the HWA, and the ability of forest managers and policymakers to control the HWA.

Background

Eastern hemlock (*Tsuga canadensis* (L.) Carriere) is an important resource for people and wildlife in North America. Around the turn of the century, hemlock was harvested extensively as a source of tannin for the leather industry. Today, hemlock is used primarily in the manufacture of pulp, paper, and sawlogs. Hemlock provides critical winter habitat for moose, white-tailed deer, ruffed grouse, turkey, songbirds, and other wildlife species. Although not as prevalent as some other tree species, hemlock is highly visible because it frequently grows along streams where high-use hiking trails are located. Recently, the hemlock woolly adelgid (HWA) (*Adelges tsugae* Annand) has emerged as a serious pest across much of hemlock's range (USDA Forest Service 1994).

Source Data

For this analysis, we divided the geographic range of hemlock into five regions: Canada (New Brunswick, Nova Scotia, Ontario, Prince Edward Island, and Quebec), New England (Connecticut, Massachusetts, Maine, New Hampshire, Rhode Island, and Vermont), Lake States (Minnesota, Michigan, and Wisconsin), Mid-Atlantic States (Delaware, Indiana, Maryland, New Jersey, New York, Ohio, Pennsylvania, and West Virginia), and Southern Appalachian States (Alabama, Georgia, Kentucky, North Carolina, South Carolina, Tennessee, and Virginia). Information for Canada is from a recent compendium of national forest statistics (Can. Counc. of For. Minist. 1997). Most of the data for the United States are from the most recent forest inventories conducted by the USDA Forest Service's, Forest Inventory and Analysis (FIA) project (Hansen and others 1992). The Carolina hemlock (*Tsuga caroliniana* Engelm.), a closely related species found on the slopes of the southern Appalachian Mountains, is likely included in the source data. Information on area, volume, and components of inventory change are for hemlock found on "timberland," which is defined as forest land capable of producing merchantable timber crops. This definition excludes public forest land that is reserved from timber harvesting, such as tracts within the Adirondack Park and some unproductive acreage on poor sites.

North America

Hemlock's natural range extends from northeast Minnesota across Wisconsin, northern Michigan, south-central Ontario, extreme southern Quebec, and through New Brunswick and Nova Scotia. This species is found throughout New England, New York, Pennsylvania, and other Mid-Atlantic States; and as far south as northwestern Alabama (Godman and Lancaster 1990). The entire range lies between 33° and 48° N. Hemlock is generally restricted to cool humid climates with adequate moisture. Annual precipitation ranges from 29 inches to more than 50 inches across its natural range.

Within the North American forest mosaic, hemlock occupies a variety of sites, soil types, and climatic conditions. This species is most common at elevations up to 2,400 feet in Canada, New England, and the Lake States, from 1,000 to 3,000 feet in the Mid-Atlantic States, and from 2,000 to 5,000 feet in the southern Appalachians (Fowells 1965). Hemlock prefers moist to very moist soils, but is commonly found growing on drier soils on talus slopes and ridgetops (Braun 1950; Godman and Lancaster 1990). The species is noted as being long-lived, extremely tolerant of shade, and is considered to be a principal cohort of pre-settlement (late successional) forests (Foster 1997). Hemlock's association with other species ranges from occasional membership in diverse broadleaf deciduous systems to a codominant role with a number of northern coniferous species, to a dominant role in relatively pure stands. Although the national inventory data for Canada and the United States are a coarse representation of hemlock's diversity within the regional forest mosaic, they do aid in summarizing composition, structure, and sustainability of the hemlock ecosystem.

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Table 1.—Gross volume of merchantable wood (million cubic feet) on stocked, timber-productive, nonreserved forest land for Canadian provinces within the natural range of eastern hemlock, by province and species group, 1991

Species group	All provinces	Nova Scotia	New Brunswick	Quebec	Ontario
Softwoods					
Spruce	122,965	3,072	7,416	62,189	50,288
Pine	32,737	530	918	9,747	21,542
Fir	38,705	1,519	4,944	25,921	6,321
Hemlock	2,048	212	247	989	600
Other	8,829	71	1,801	3,779	3,178
Total softwoods	205,284	5,404	15,326	102,625	81,929
Hardwoods					
Aspen	36,727	247	1,554	11,371	23,555
Birch	35,738	848	2,048	20,341	12,501
Maple	23,413	2,084	3,108	11,053	7,169
Other	6,851	388	777	2,860	2,825
Total hardwoods	102,729	3,567	7,487	45,625	46,050
All species	308,013	8,971	22,813	148,250	127,979

Canada

In Canada, the national inventory data include estimates of gross merchantable volume for major tree-species groups. Hemlock is found entirely in the provinces of New Brunswick, Nova Scotia, Ontario, Prince Edward Island, and Quebec. Forests in this region are two-thirds coniferous and one-third deciduous (Table 1). The most common species groups are spruce (*Picea* spp. A. Dietr.), fir (*Abies balsamea* (L.) Mill.), aspen (*Populous grandidentata* Michx. and *P. tremuloides* Michx.), birch (*Betula* spp. L.), and assorted pines (mostly jack pine (*Pinus banksiana* Lamb.), red pine (*P. resinosa* Ait.), and white pine (*P. strobus* L.)).

The gross volume of hemlock in Canada is 2.0 billion cubic feet. Differences in compilation procedures and estimation techniques preclude direct comparisons of inventory volume between Canada and the United States; however, Canada likely contributes from 10-20 percent of the hemlock inventory in North America; hemlock volume is less than 1 percent of Canada's total inventory. About half of the hemlock in the five-province region is found along the southern boundary of Quebec. Ontario has 29 percent of the hemlock inventory, nearly all of which is located in the southeast. New Brunswick has 12 percent of Canada's hemlock, or about 1 percent of the total volume. Prince Edward Island contains scant amounts of hemlock (not recorded in Table 2). Nova Scotia contains the rest of Canada's hemlock, or 2 percent of that province's total volume.

United States

Forests of eastern North America support a diverse mix of species and stand structures. One useful measure of composition is FIA's "forest type" variable, which is a classification of timberland based on predominate species. For reporting, it is convenient to combine specific forest types into groups. Oak and maple-beech-birch are the dominant forest-type groups in states within eastern hemlock's natural range, accounting for just over half of the timberland (Table 2). Other important forest-type groups in areas where hemlock is common are aspen-birch, spruce-fir, and white-red-jack pine.

Hemlock is a major component of four forest cover types, a common member of seven types, and a minor species in 18 other types (Godman and Lancaster 1990). The hemlock forest type includes stands where at least half of the stocking is composed of hemlock. The hemlock forest type is included in the white-red-jack pine forest-type group. In states within hemlock's natural range, the hemlock forest type totals 2.4 million acres, or less than 1 percent of the total area of timberland. Hemlock-dominated stands are divided between New England (with 54 percent of the acreage), the Mid-Atlantic States (44 percent), and Southern Appalachian States (2 percent). It should be noted that hemlock-dominated stands are found in the Lake States, but are lumped into the white-red-jack pine group by the North Central FIA project. In the white pine-hemlock forest type, hemlock shares dominance with white pine in varying degrees. There are 0.7 million acres of white pine-hemlock forests in states within hemlock's natural range.

A more complete description of hemlock's role in the composition of eastern forests is gained by examining the volume of hemlock inventory and its distribution by region and forest-type group. The total forest inventory in states within hemlock's range is 382.5 billion cubic feet; this includes the merchantable volume of all live trees at least 5

Table 2.—Area of timberland (thousand acres) by forest-type group, specific forest types within the white-red-jack pine type, and U.S. region, 1999

Forest-type group	All states	New England	Lake States	Mid-Atlantic	Southern Appalachian
White-red-jack pine:					
White pine	4,416.7	2,191.3	488.9	1,319.8	416.7
White pine-hemlock	683.2	224.8	...	273.1	185.3
Hemlock	2,358.2	1,271.5	...	1,046.6	40.1
Other pine	4,132.7	72.6	3,567.2	483.2	9.7
Total	11,590.8	3,760.2	4,056.1	3,122.7	651.8
Spruce-fir	15,640.6	7,363.4	7,570.4	693.7	13.1
Southern pine	36,867.4	178.8	...	1,554.2	35,134.4
Oak	106,851.8	4,122.0	6,033.2	28,819.4	67,877.2
Lowland hardwood	21,801.5	827.9	4,444.9	3,607.0	12,921.7
Maple-beech-birch	48,068.8	12,349.5	13,854.2	20,714.4	1,150.7
Aspen-birch	16,676.5	2,694.1	12,881.8	1,100.6	...
Nontyped	379.5	26.5	199.3	103.9	49.8
Total	257,876.9	31,322.4	49,039.9	59,715.9	117,798.7

Table 3.—Net volume of live hemlock trees (million cubic feet) by forest-type group, specific forest types within the white-red-jack pine type, and U.S. region, 1999

Forest-type group	All states	New England	Lake States	Mid-Atlantic	Southern Appalachian
White-red-jack pine					
White pine	153.7	95.6	6.6	43.9	7.6
White pine-hemlock	387.1	137.4	...	170.0	79.7
Hemlock	2,843.7	1,431.9	...	1,355.5	56.3
Other pine	2.5	...	2.5	...	...
Total	3,387.0	1,664.9	9.1	1,569.4	143.6
Spruce-fir	320.9	245.1	51.2	23.7	0.9
Southern pine	8.7	...	...	0.4	8.3
Oak	1,137.0	230.0	4.1	460.3	442.6
Lowland hardwood	59.6	5.6	43.4	10.0	0.6
Maple-beech-birch	3,439.8	961.3	1,007.0	1,427.6	43.9
Aspen-birch	65.2	33.2	27.9	4.1	...
Total	8,418.2	3,140.1	1,142.7	3,495.5	639.9

inches in diameter. The hemlock inventory is 8.4 billion cubic feet or 2 percent of the volume of all species (Table 3). The Mid-Atlantic States contain 42 percent of the hemlock inventory, followed by New England (37 percent), the Lake States (14 percent), and the Southern Appalachian States (8 percent).

Maple-beech-birch forests contain most of the hemlock volume with 3.4 billion cubic feet or 41 percent of the total. Hemlock is a minor associate in maple-beech-birch forests, but its volume accumulates over vast areas of the type group commonly found in the Lake, Mid-Atlantic, and Southern Appalachian States.

White-red-jack pine contributes 40 percent of the hemlock inventory. The hemlock forest type has 84 percent of the hemlock volume in this type group. The white pine-hemlock and white pine forest types contain nearly all of the remaining hemlock inventory in this group.

The other forest-type group with significant hemlock inventory is the oak group, which is comprised of oak-pine and oak-hickory forests (10 percent). Most of the oak stands containing hemlock are in the Mid-Atlantic and Southern Appalachian States. Hemlock plays a minor role in the other groups, but it is interesting to note that hemlock is found in all the forest-type groups common in the various regions.

The "other private" owner group controls nearly three-fourths of the hemlock inventory in states within its natural range (Table 4). This is roughly equivalent to this group's share of the total inventory for all species. The other private owners are a diverse group, ranging from individuals owning small forest tracts to corporations (other than forest industry) with large tracts. Objectives for owning timberland vary from purely aesthetic to economic, making it difficult to predict future management trends for hemlock. Forest industry owns 10 percent of the hemlock resource. Forest industry owners are defined as individuals or companies that operate a primary wood-using plant. Public owners control the remaining 16 percent of the hemlock inventory. This share is split in roughly equal parts between federal National Forests and other state, county, and municipal owners. The Southern Appalachian states and the Lake States have the largest concentrations of publicly owned hemlock with 35 and 30 percent, respectively. In the Southern Appalachian States, about 90 percent of the publicly owned hemlock is located in National Forests.

Stand structure is a general term describing numbers of trees, tree size, degree of site occupancy, and other vegetative measures. FIA's stand-size variable offers a coarse but useful proxy of stand structure as well as stage of stand development. Stand-size class is assigned to FIA sample locations according to the predominance of stems by size class: seedling-sapling, poletimber, and sawtimber. The limitation of characterizing hemlock using stand-size class is that the species occurs in so many different forest types and type groups that it is most useful for highlighting the hemlock forest type. With this in mind though, the distribution of hemlock-dominated forests by stand-size class has implications for large-scale management and policy issues.

Two dominant trends are apparent in New England and the Mid-Atlantic states where most of the hemlock forest type is found. First, the inventory of hemlock is heavily concentrated in sawtimber-size stands (75 percent) (Table 5). The build-up of hemlock in larger stands is relatively constant across owner groups. Second, there is a general lack of young stands containing hemlock. Only 4 percent of the hemlock inventory is in seedling-sapling stands, primarily in the Mid-Atlantic States, compared to 17 percent of the area of all forest types in New England and the Mid-Atlantic States in seedling-sapling stands.

In the Lake States, the two most recent inventories of Michigan and Wisconsin indicate that the number of small hemlock trees is decreasing (Schmidt and McWilliams 1995). Deer browsing, lack of active management, and damage by forest pests were cited as possible explanations. Inventory data for Mid-Atlantic and New England states does not indicate a shortage of small hemlock trees. Recent inventories of New York, Maine, and New Hampshire show increases in small-diameter hemlock.

Because the health and sustainability of the hemlock resource depends on a wide array of interrelated factors, it is difficult to make blanket statements about hemlock's long-term stability within the eastern forest mosaic. In addition to the composition and structure information, the FIA project's data on mortality, net growth, and removals provide some simple but insightful measures of health and sustainability.

The FIA mortality estimates are expressed on an annual basis to provide information that can be compared among regions and species. The mortality estimates in Table 6 are indexed as a percentage of growing-stock volume. The overall rate of hemlock mortality across its natural range is 0.26 percent. Hemlock's mortality rate is among the lowest of tree species in states within hemlock's natural range. Species with high mortality rates tend to be associated with well-established stressors, such as spruce budworm, *Choristoneura fumiferana* (Clemens), and its impact on spruce and fir (mortality rate of 1.90). The rate for all species combined is 0.86. Thus, it would seem that hemlock is relatively healthy. Rates of hemlock mortality were highest in the Lake and Southern Appalachian States, particularly on publicly owned timberland. Mortality rates were below average in New England and average in Mid-Atlantic States. The current distribution of the HWA extends along the eastern fringe of hemlock's range from northwestern North Carolina to the northern border of Massachusetts (Souto and Shields 1999). Although the HWA has been known to occur in the eastern U.S. since 1951 (Gouger 1971), it's impact was not well publicized until it invaded Connecticut in 1985 (McClure 1987). The effects of the HWA on the hemlock resource will likely increase if the pest spreads to the west. Also, it is expected that the HWA will develop sufficient cold-hardiness to expand its distribution northward (McClure 1996). Monitoring mortality rates as conditions develop will provide a gauge for policies and programs directed at slowing the spread of the HWA.

One measure of hemlock sustainability is the ability of the existing resource to expand in volume. The relationship between FIA's estimates of net growth and removals addresses this question. Table 7 shows average annual net growth-to-removals ratios by owner and region. A ratio of 1.00 indicates a balance between growth and removals. Ratios less than 1.00 indicate overcutting and ratios greater than 1.00 indicate resource expansion. For all owners and regions, the net growth-to-removals ratio is 3.22, which means the hemlock inventory is expanding more than three times faster than it is being harvested or removed by other land uses. The relationships are tightest on forest industry land, particularly in New England. The ratio of 1.03 for New England is driven by conditions in Maine, which accounts for 80 percent of the net growth and 89 percent of the removals of hemlock in this region. Recent outbreaks of spruce budworm and increased demand for fiber during the 1980's and early 1990's had a strong impact as hemlock often was included in the mix of harvested species (McWilliams 1997).

Elsewhere in hemlock's natural range, growth-to-removals ratios are highly favorable for increases in inventory volume. Outside of New England, nearly all the ratios are greater than 2.00. Ratios are highest on publicly owned timberland (4.88 for all owners) and within the Mid-Atlantic States (4.06). The primary reason for high ratios is a relatively low demand for hemlock compared to more valuable species

Table 4.—Net volume of live hemlock trees (million cubic feet) by owner group and U.S. region, 1999

Owner group	All states	New England	Lake States	Mid-Atlantic	Southern Appalachian
Public	1,339.6	306.8	342.0	469.5	221.3
Forest industry	847.8	477.8	204.5	139.5	26.0
Other private	6,230.8	2,355.5	596.2	2,886.5	392.6
All owners	8,418.2	3,140.1	1,142.7	3,495.5	639.9

Table 5.—Area of timberland classified as hemlock forest type (thousand acres) by stand-size class and U.S. region, 1999

Stand-size class	All states	New England	Lake States	Mid-Atlantic	Southern Appalachian
Seedling-sapling	96.9	35.4	...	61.5	...
Poletimber	386.4	254.2	...	132.2	...
Sawtimber	1,874.9	981.9	...	852.9	40.1
Total	2,358.2	1,271.5	...	1,046.6	40.1

Table 6.—Average annual mortality of hemlock growing stock expressed as a percent of inventory volume by owner group and U.S. region, 1999

Owner group	All states	New England	Lake States	Mid-Atlantic	Southern Appalachian
Public	0.33	0.10	0.45	0.33	0.46
Forest industry	0.36	0.32	0.41	0.37	0.39
Other private	0.24	0.15	0.36	0.26	0.34
All owners	0.26	0.18	0.40	0.28	0.38

Table 7.—Ratio of average net growth-to-removals of hemlock growing stock by owner group and U.S. region, 1999

Owner group	All states	New England	Lake States	Mid-Atlantic	Southern Appalachian
Public	4.88	2.67	7.67	6.00	3.81
Forest industry	1.02	0.75	1.16	2.18	...
Other private	2.39	1.08	3.15	4.06	3.00
Total	2.28	1.03	2.66	4.14	3.40

such as white pine, spruce, oak (*Quercus* L.), and aspen. Stumpage prices for hemlock sawtimber are among the lowest for any species. Currently, the hemlock product mix is skewed toward pulp and paper products. Of the total volume of hemlock that is used, 60 percent is used for pulp and paper, and 40 percent is used for lumber. With respect to total timber products output in states within its natural range, hemlock makes up 2 percent of the pulpwood harvest and 1 percent of the sawlog harvest. Hemlock utilization is highest in New England where it accounts for 12 percent of the pulpwood and 7 percent of the sawlog harvest.

Summary

The hemlock resource is in good condition and is increasing in volume across most of its natural range. However, it is important to understand the character of this resource in light of the potential threat posed by the HWA, particularly in the eastern portion of hemlock's range. While the volume of hemlock is increasing, it is doubtful that the area of forest containing this species will expand because sources of new hemlock forests are rare. The existing hemlock resource is in a mature condition dominated by large stands and trees. The short-term expectation for increases in hemlock volume is supported by highly favorable growth-to-removals ratios across most of hemlock's range. The overcutting that developed in Maine during the 1980's and early 1990's has likely subsided. Long-term sustainability will depend heavily on the degree that hemlock is favored in future management practices, the future spread of the HWA, and the ability of forest managers and policymakers to control the HWA.

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Silviculture and Stand Dynamics of Hemlock-dominated Stands in Southern New England: Some Lessons from Early Research

Matthew J. Kelty[1]

Abstract

In the early part of this century, considerable interest existed in the silviculture of hemlock (*Tsuga canadensis* (L.) Carr.) in the southern New England region, where it occurs in mixture with oak (*Quercus* spp.), white pine (*Pinus strobus* L.), birches (*Betula* spp.), and maples (*Acer* spp.). Difficulties encountered with the regeneration of white pine led to the idea that hemlock should be promoted through management as an alternative conifer sawtimber species. Research at forestry institutions in Connecticut and Massachusetts beginning in the 1920's demonstrated the ease with which hemlock-hardwood stands could be converted to pure hemlock by removing the hardwood overstories. However, early attempts to regenerate hemlock in mature hemlock-dominated stands met with difficulties. Shelterwood and group selection methods failed to establish hemlock dependably; problems were ascribed to the deep litter layer, which inhibited establishment of hemlock more than that of some hardwood species, especially black birch (*Betula lenta* L.). Scarification promoted hemlock regeneration, but also promoted the much faster growing black birch. These case studies provide the basis for predicting stand dynamics pathways for hemlock-hardwood stands under different disturbance regimes, both natural and silvicultural.

Introduction

Eastern hemlock has been the subject of increasing interest in forest management both because the species is increasing in abundance in many areas as the forest matures and because it is threatened by the infestation of the hemlock woolly adelgid (*Adelges tsugae* Annand). Hemlock has not generally been as highly valued for timber as a number of associated species, so little silvicultural research has concentrated on it in recent years. However, there was a period in the early part of this century when researchers at the Yale Forestry School, the Harvard Forest, the Connecticut Agricultural Experiment Station, and the Massachusetts College of Agriculture were interested in the prospect of managing hemlock as a timber species, and they conducted a number of studies to determine appropriate silvicultural strategies. These studies took the form of management trials that would fit under the current concept of 'adaptive management'; they were not replicated experiments with controls, but consisted of very careful, quantified observations made at intervals after stand treatments had been carried out. They give useful information about responses to silvicultural treatments, and can also be used to predict vegetation dynamics in unmanaged stands by considering similarities between specific silvicultural and natural disturbances.

These studies were conducted in Massachusetts and Connecticut, and so they relate directly only to southern New England, in which hemlock occurs with oak, red maple (*Acer rubrum* L.), black birch, paper birch (*Betula papyrifera* Marsh.), gray birch (*Betula populifolia* Marsh.), hickory (*Carya* spp.), and white pine—i.e., the transition hardwood-white pine-hemlock type south to the central hardwood-hemlock type according to the classification of Westveld (1956). Some results may apply in a more general way to northern hardwood-hemlock mixtures.

In the 1920's, when much of this research was being conducted, it was understood that hemlock had been markedly reduced from its prevalence in precolonial forests (Merrill and Hawley 1924). Studies of the last remaining uncut virgin stands in the region suggested that hemlock had dominated much of the landscape (Nichols 1913). Compared to most associated species, hemlock had been affected more by cutting and fire, and was slower to become reestablished on former agricultural land. At the time of these studies, hemlock occurred throughout the region in woodlots that may have been cut repeatedly, but had escaped burning or clearing.

Reasons for Favoring Hemlock in the Early Part of the Century

The earliest interest in harvesting products from hemlock in the Northeast was for the tanbark industry, with the old-growth trees usually being felled and bark removed without the wood being used. However, this industry had died out in southern New England long before the beginning of the 20th century. The potential identified in the 1920's was to use hemlock for dimension lumber and railroad ties. The factors behind this interest included the scarcity of old-growth red spruce and white pine lumber from northern regions, the poor timber quality of the local old-field white pine, and the fading hope of growing better quality white pine in new stands (the difficulty of regenerating white pine during the harvest of old-field stands was becoming apparent in early silvicultural trials) (Merrill and Hawley 1924). The problem of poor quality wood in hemlock logs caused by ring shake was well recognized at the time, but it was believed that this was related to tree age, and that second-growth hemlocks would not have the problem. Thus, hemlock was seen as a good alternative to white pine as a source of conifer wood for the timber industry.

Additional support for favoring hemlock in management came from applying the new principles of succession that had been formulated by Clements (1916). One of the early proponents of basing silvicultural treatments on knowledge of the ecology of unmanaged stands was Harold J. Lutz, who proposed that, where possible, silviculture should follow rather than fight against natural successional processes

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(Lutz 1928). He did not favor the creation of the climax forest type as a matter of doctrine, but suggested that successional trends would make it increasingly difficult and costly to establish early and mid-successional stand types during harvesting, if understories of late successional species were already present. Further, he observed that a climax hemlock-hardwood stand "brings about the most complete utilization of the site" in timber production (Lutz 1928, p. 40), because canopy and root layering reduced competition and allowed greater numbers of trees to grow in a given area. Yield studies had shown that hemlock mixed with hardwoods or pine increased total yield compared to pure hardwood or pine stands (Frothingham 1915), and that pure hemlock had greater yields than oak-dominated hardwood stands (although pure pine produced more than any other stand type). In addition, unlike white pine, hemlock was (at the time) free of insect or fungus problems, and its ability to improve the quality of associated white pine by shading off lower branches had been recognized (Tarbox and Reed 1924).

Conversion of Hemlock-hardwoods to Pure Hemlock Stands

Whereas Lutz suggested hemlock-hardwood mixtures as the appropriate silvicultural objective, others favored conversion of these stands to pure hemlock for greater production of conifer timber by taking advantage of the presence of the hemlock understories. The shade tolerance of hemlock was recognized early; seedlings were observed to become established beneath hardwood canopies, but they did not invade open areas in full sun. Marshall (1927) was the first to quantify the ability of hemlock understory trees to respond to release. Working at the Harvard Forest, he examined growth rings of hemlocks in stands that had been partially cut in the mid-1800's, and found that trees that had been suppressed for 10 to 50 years responded with rapid growth after release (a ten-fold diameter growth increase for the decade after overstory cutting, compared to the previous decade). He concluded that hemlock advance growth should be preserved during logging, as the key to developing the next stand.

At the same time, this growth response was being observed in overstory logging in various hardwood-hemlock stands in southern Connecticut (Merrill and Hawley 1924). In one case described, the hardwood overstory was removed in a series of group selection cuttings; the hemlock understory responded to release, with the entire stand gradually being converted to hemlock. The gradual removal of the hardwood overstory was promoted by Merrill and Hawley as a logical timber management treatment, and the idea was taken up by others, at least on a small scale. For example, a set of demonstration plots was established on the school forest of the Massachusetts Agricultural College near Amherst, in which the red oak overstory was removed to create a pure hemlock stand; this allowed comparison of growth and yield between this hemlock plot and an adjacent untreated oak-hemlock plot. However, there are no records that indicate that this idea was applied operationally on a large scale.

Regenerating Hemlock in Hemlock-dominated Stands

The conversion of mixed stands to pure hemlock was quickly understood to be a simple, straightforward task. However, a sustainable management system based on pure hemlock stands required methods to regenerate hemlock in mature stands. It was not as clear how to accomplish this step, because mature hemlock stands characteristically lack advance regeneration of any species. A study at the Harvard Forest, begun in 1924, was designed in part to address this question (Lutz and Cline 1956). Shelterwood, group selection, and strip clearcut methods were applied to a 75-year-old hemlock-white pine stand on an outwash soil. The shelterwood cut left about one-half canopy cover. The problem posed by the deep conifer litter for obtaining hemlock or pine regeneration was recognized, and because the winter logging had not disturbed the seedbed, a harrow was used the spring following the cut to accomplish the task. However, the harrow treatment was judged to be ineffective, so small plots were scarified with hand tools to test the importance of exposing mineral soil. Following the shelterwood cut, hemlock germinated only on particular microsites—on beds of *Polytrichum* moss, in small moist depressions, or on any area where burning of slash piles or scarification treatments had disturbed the forest floor. For the entire cutting area, mean hemlock regeneration density 6 years after cutting was 10,000 stems/acre. However, many hardwoods had also become established, including paper birch, gray birch, black birch, pin cherry (*Prunus pensylvanica* L.), red maple, and red oak (*Quercus rubra* L.). Black birch comprised 70% of the hardwood stems, with 2000 black birch stems/acre greater than 3 ft; only 500 stems/acre of hemlock were taller than 3 ft. Adjacent to the shelterwood cutting, a group selection cutting was made in which all trees were cut within small patches ranging from 0.01 to 0.1 acres in size; cutting was carried out with little disturbance to the forest floor. Again, black birch dominated the hardwoods 6 years later, with heights up to 7 ft; in this case, few hemlocks became established, and nearly all were less that 2 ft tall. The strip clearcuts were 80-, 110-, and 140-ft wide, on a north-south orientation, to allow maximum exposure to the direct sun; little disturbance to the forest floor occurred during logging. Pin cherry, gray birch, and paper birch were the most common hardwood species in the regeneration, but little white pine germinated, and hemlock was almost completely absent from these stands.

In cuttings in hemlock-dominated stands in southern Connecticut, Merrill and Hawley similarly observed that: (1) exposed mineral soil was important to hemlock seedling establishment, and (2) black birch responded prolifically to the same conditions that were favorable for hemlock, and it grew twice as fast (or more) in height as hemlock. They concluded that it would not be practical to attempt weedings of birch and other hardwoods to create pure young hemlock stands. Rather, they proposed a system of growing alternate crops of hardwoods and hemlock. Beginning with a mixed stand, the hardwood overstory would be harvested to release the hemlock; after the hemlock stand reached maturity, the shelterwood method with scarification would be

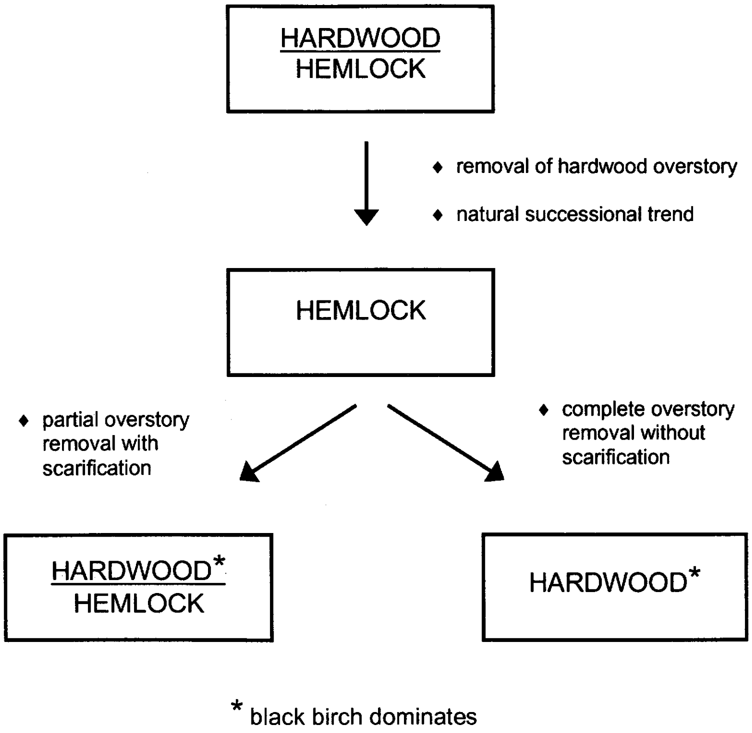

Figure 1.—Diagram of stand dynamics pathways in hemlock-dominated forests in southern New England, as can be inferred from results of early silvicultural studies. See text for further explanation.

carried out to create an even-aged mixed stand with a hardwood upper canopy above a hemlock lower canopy thus completing the cycle.

While this is not necessarily a timber production system to be put into widespread use at present, the stand dynamics pattern it describes (summarized in Fig. 1) is useful as a basis for predicting responses to natural disturbances (e.g., wind damage or mortality from insects) or to specific silvicultural treatments. Especially when questions arise about whether climate change or introduced insect pests such as the hemlock adelgid will bring about entirely new vegetation responses, it is useful to be able to compare current results with patterns of forest dynamics that occurred 75 years ago.

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Natural Regeneration of Eastern Hemlock: A Review

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Abstract

Successful regeneration of eastern hemlock involves a complex biophysical process that commonly spans many years. Critical factors include a reliable source of seed, a suitable seedbed, a partially shaded environment, and several years of favorable moisture. Surface scarification appears critical as a means of site preparation. Even then, young hemlocks grow slowly, and commonly take several years to reach a size suitable for overstory release. Uniform partial cutting, shelterwood method, and patch cutting have all proven effective as strategies for regenerating hemlock. Reserve strip cutting also appears promising.

Silvical Characteristics of Eastern Hemlock *(Tsuga canadensis)*

Eastern hemlock has high shade tolerance (Burns 1923, Graham 1943, Baker 1949, Tubbs 1978, Lancaster 1985, Anderson and Gordon 1994, Tubbs 1996). It regenerates at even 5% of full sunlight (Hough 1960, Anderson and Gordon 1994, Tubbs 1996), and develops in as little as 20-25% light (Hough 1960, Logan 1973, Anderson and Gordon 1994). Saplings may not form growth rings under dense shade (Hough 1960), and those trees show little relationship between diameter and age (Marshall 1927). Due to its high shade tolerance, 50 to 100 year old understory hemlock may only be a few inches in diameter (U.S. For. Serv. 1970).

Hemlock has a shallow root system (Frothingham 1915, Clepper 1934, Lancaster 1985) and can thrive in shallow soil (Frothingham 1915, Clepper 1934), though roots develop down into deep soils as well (Frothingham 1915, Clepper 1934). It develops mycorrhizal associations for nutrient absorption (Harlow 1900). Root respiration may depend on changes in temperature and the rate of photosynthesis (Szaniawski and Adams 1974), and root growth rather than shoot growth may limit survival at low light levels (Anderson and Gordon 1994).

Hemlock grows in a range of soils (Frothingham 1915, Merrill and Hawley 1924, Fowells 1965, U.S. For. Serv. 1970, Godman and Lancaster 1990), and has low mineral nutrition requirements (Hough 1960). Even so, it develops best on wet-mesic to mesic sites (Farr and Tyndall 1992, Kotar 1996), and moist to very moist soils with good drainage (Frothingham 1915, Clepper 1934, Hough 1960, U.S. For. Serv. 1970, Tubbs 1978, Wendel et al. 1983, Godman and Lancaster 1990, Anderson and Gordon 1994, Tubbs 1996). It also occurs on dry, shallow tills (Frothingham 1915, U.S. For. Serv. 1970, Tubbs 1978, Anderson and Gordon 1994); sandy soils (U.S. For. Serv. 1970, Tubbs 1978); interspersed within wet swamps (Anderson and Gordon 1994); on some wet, swampy borders (Anderson and Gordon 1994); acidic soils (Wendel et al. 1983); loams (Frothingham 1915, U.S. For. Serv. 1970); silt loams with neutral soil reaction (Wendel et al. 1983); soils with impeded drainage (Frothingham 1915, Tubbs 1996); and on north or northwest facing rocky slopes (Wendel et al. 1983, Anderson and Gordon 1994).

Hemlock may grow better than hardwoods on dry, sandy, or rocky sites if the trees become established in non-drought years or in moist niches (Nienstaedt and Olson 1955). It is often found on lower slopes and flats, frequently bordering lakes that influence humidity levels over the site (Anderson and Gordon 1994). Hemlock does occur in pure stands (U.S. For. Serv. 1970, Farr and Tyndall 1992), and mixed with other species (U.S. For. Serv. 1970). It grows with eastern white pine *(Pinus strobus* L.*)* in stands originating after fire, windthrow, or other catastrophic disturbances (U.S. For. Serv. 1970). On favorable sites, hemlock usually forms a climax association (U.S. For. Serv. 1970). Yet on sites rich in nutrients, it succumbs to sugar maple (*Acer saccharum* Marsh.) and other associated hardwoods (Kotar 1996). Hemlock may never have dominated those sites in the past, and will not likely become a major component on them in the future (Kotar 1996).

The microclimate under hemlock stands is cooler than under hardwoods (Moore et al. 1924, Tubbs 1996). The soils there also show greater fluctuations in air temperature than those under neighboring stands (Friesner and Potzger 1932), with an average soil temperature slightly lower than under mixtures of American beech *(Fagus grandifolia* Ehrh.*)* and maple (Moore et al. 1924, Daubenmire 1931). Soil surfaces are also drier (Daubenmire 1931, Friesner and Potzger 1932, Friesner and Potzger 1936, Tubbs 1996) due to crown interception of precipitation (Tubbs 1996). As a result, pure hemlock stands seldom have an understory of tree regeneration (Daubenmire 1931, Tubbs 1996). Soils under established stands are also acidic (Fowells 1965, Godman and Lancaster 1990), ranging from pH 3.6 to 4.7.

Seed Development, Dispersal, and Germination

Hemlock is one of the most frequent and abundant cone producers among the eastern conifers (Crow 1996). It produces some seed annually (Ruth 1974), with good crops at 2 to 3 year intervals (Frothingham 1915, Merrill and Hawley 1924, Clepper 1934, Swift 1948, Hough 1960, Fowells 1965, U.S. For. Serv. 1970, Ruth 1974, Anderson and Gordon 1994). Seed production begins between 20 and 40 years of age (Hough 1960, Fowells 1965, Ruth 1974, Wendel et al. 1983, Anderson and Gordon 1994, Crow 1996), but later among trees in the shade (Frothingham 1915, Hough 1960, Fowells 1965, Ruth 1974). In fact, low-vigor trees beneath a dense canopy (Hough 1960, Anderson and Gordon 1994) and shaded portions of crowns (Tubbs 1996) do not produce seeds regardless of age (Hough 1960,

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Fowells 1965, Anderson and Gordon 1994, Tubbs 1996). Mature, dominant trees continue to produce seeds up to 450 or more years old (Hough 1960, Fowells 1965, Crow 1996).

Male and female strobili develop in clusters near the ends of lateral branches (Frothingham 1915, Hough 1960, Ruth 1974). Flowering varies from April to early June (Frothingham 1915, Hough 1960, Fowells 1965, Ruth 1974, Tubbs 1996), depending on the topography and climate (Frothingham 1915, Hough 1960, Fowells 1965). The male (staminate) flower is round, yellow, and approximately ¼-in long (Clepper 1934), becoming well formed by the end of July (Frothingham 1915, Hough 1960, Fowells 1965). Pollen disperses by wind (Frothingham 1915, Hough 1960) approximately 2 weeks following leaf bud burst (Frothingham 1915). It is sensitive to dry weather, a common cause of fertilization failure (Frothingham 1915, Tubbs 1996). Fertilization takes place within roughly 6 weeks following pollination (Frothingham 1915; Nienstaedt and Kriebel 1955; Olson et al. 1959a, 1959b). Then female (pistillate) flowers grow rapidly, and become mature cones by September or October (Frothingham 1915, Clepper 1934, Swift 1948, Hough 1960, Fowells 1965, Ruth 1974).

Cones change from pale green to dark brown during ripening (Frothingham 1915, Clepper 1934, U.S. For. Serv. 1970). They commonly measure between ½- to ¾-in long (Frothingham 1915, Clepper 1934, U.S. For. Serv. 1970), and ½- to ¾-in wide with scales expanded (Frothingham 1915). Cones remain on a tree during the first winter (Clepper 1934). Generally, between 30 and 60% of the seed is viable (Frothingham 1915), with the number per pound reported at 169,800 (Heit and Eliason 1940), 185,000 (U.S. For. Serv. 1970), 190,527 (Toumey and Stevens 1928), 400,000 (Frothingham 1915, Clepper 1934), and 132,000 to 360,000 (Hough 1960). Only about 20 scales in the central part of the cone bear seed (Hough 1960).

Seed dispersal begins during fall following cone maturity (Frothingham 1915, Baldwin 1930, Hough 1960, Fowells 1965, Ruth 1974, Tubbs 1996), and may continue throughout winter (Frothingham 1915, Baldwin 1930, Hough 1960, Fowells 1965, Ruth 1974, Anderson and Gordon 1994, Tubbs 1996). Seeds that remain in the cones over winter are usually sterile (Frothingham 1915; Olson et al. 1959a, 1959b). Cone scales open in dry weather and close when moistened, or in times of high humidity (Frothingham 1915, Clepper 1934, Hough 1960, Fowells 1965, Tubbs 1996). As a consequence, seed disperses only in dry periods (Hough 1960, Fowells 1965, Tubbs 1996) and particularly during dry, windy days (Frothingham 1915; Hough 1960; Fowells 1965; Olson et al. 1959a, 1959b). This alternate opening and closing of the cone scales results in seed dispersal over a protracted period (Clepper 1934, Frothingham 1915). Varying winds distribute the seeds in many different directions (Frothingham 1915, Clepper 1934), and even for up to 1 mile across crusted snow in a strong wind (Frothingham 1915, Fowells 1965, Anderson and Gordon 1994, Crow 1996, Tubbs 1996). Yet most seeds fall within one tree height of the parent (Hough 1960, Tubbs 1996).

Rodents feed on seeds of eastern hemlock (Frothingham 1915, Abbot 1962, Fowels 1965), even rejecting larger ones of other species that contain natural repellants (Abbot 1962). This reduces the supply to some degree. Germination of those that escape predation generally occurs from March to late May (Lloyd 1900, Frothingham 1915, Baldwin 1930, Hough 1960), but as late as June or July at northern latitudes (Hough 1960, Fowells 1965). The germinative capacity is low (Frothingham 1915, Baldwin 1930, Hough 1960, Fowells 1965, La Madeleine 1980, Tubbs 1996) and variable (Stearns and Olson 1958), reportedly ranging from less than 25% (Frothingham 1915, Wendel et al. 1983), 20 to 30% (Hough 1960, Fowells 1965), 30 to 60% (Frothingham 1915), 44% (Toumey and Stevens 1928), and as high as 40 to 60% (Hough 1960).

Germination begins in spring as the temperatures rise (Olson *et al.* 1959a, 1959b), and becomes optimal with a constant temperature of 55-62 °F (Frothingham 1915; Olson et al. 1959a, 1959b; Ruth 1974; Wendel et al. 1983; Crow 1996). A high percentage of germination can occur at 44 to 64°F (Frothingham 1915, Wendel et al. 1983), but constant temperatures below 55°F or above 70°F hinder germination (Olson et al. 1959a, 1959b). Seeds require from 45 to 60 days to reach peak germinative energy (Frothingham 1915, Wendel et al. 1983).

Conditions for Seedling Establishment and Survival

Regeneration failures with hemlock have been attributed to low seed input, poor seedling establishment or limited recruitment among established seedlings (Waller et al. 1996), smothering from hardwood leaf fall (Hough 1960; Fowells 1965; Olson 1954; Olson et al. 1959a, 1959b; Anderson and Gordon 1994; Tubbs 1978, 1996), thick leaf litter (Friesner and Potzger 1932, Tubbs 1978, Anderson and Gordon 1994, Waller et al. 1996), excess moisture (Lloyd 1900, Baldwin 1934, Ward and McCormick 1982), allelopathy (Ward and McCormick 1982), unfavorable soil pH (Ward and McCormick 1982), competition from herbaceous vegetation (Wagner and Joseph 1996) and hardwoods (Lorimer 1996), too much shade (Frothingham 1915, Ward and McCormick 1982, Wendel et al. 1983), and too little shade resulting in sunscald (Frothingham 1915, Hough 1960, Ward and McCormick 1982, Wendel et al. 1983, Crow 1996). Yet even when most of the requisite conditions may seem favorable, only periodically do seedlings establish in large numbers (Lorimer 1996, Tubbs 1996, Waller et al. 1996). Even then, an abundance of seedlings does not necessarily portend a long-term regeneration success (Kotar 1996). Numerous seedlings may appear following favorable germination conditions, only to die during periods of drought within 2 or 3 years (Kotar 1996). In fact, studies indicate that 88% of seedlings may die during the first year, but that the chance of survival increases annually for the first 5 to 6 years.

Seed and seedlings are particularly vulnerable to soil moisture stress (Frothingham 1915; Fowells 1965; Olson and Nienstaedt 1953; Olson et al. 1959a, 1959b; Coffman

1978; Ward and McCormick 1982; Wendel et al. 1983; Lancaster 1985; Anderson and Gordon 1994; Crow 1996, Tubbs 1996; Waller et al. 1996) and establishment depends upon the amount of precipitation received during several successive years following germination (Friesner and Potzger 1944), especially on organic soils (Collins 1990, Anderson and Gordon 1994). In experiments, seeds deliberately dried for between 2 and 6 hours were damaged at rates of 60 to 80%, respectively (Olson et al. 1959a, 1959b). Similarly, seedling mortality and root damage may follow exposure to full sunlight (Lancaster 1985, Tubbs 1996) after excessive release by cutting (Anderson and Gordon 1994) and high evaporation of soil moisture (Lancaster 1985)

Core samples reinforce these observations and indicate that hemlock establishment is sensitive to weather variations (Graham 1943), and particularly periods of drought (Frothingham 1915, Stickel 1933, Clepper 1934, Graham 1943, Hough 1960, Fowells 1965, Lanasa et al. 1996, Lorimer 1996, Tubbs 1978, Wendel et al. 1983, Wagner and Joseph 1996). In fact, establishment occurs in dry areas only during years with greater than normal rainfall (Hough 1960. Fowells 1965). Overall, reproduction of hemlock depends upon a good seed year, followed by a good germinating year, and then several years with favorable moisture conditions (Friesner and Potzger 1944, Waller et al. 1996).

Partial shade favors seed germination (Logan 1973, Nienstaedt and Olson 1955) and enhances seedling survival (Nienstaedt and Olson 1955, Tubbs 1996). Yet available reports disagree whether hemlock regenerates best on warm, moist sites (Frothingham 1915, Crow 1996), or on shaded, moist, cool sites (Hough 1960, Fowells 1965, Anderson and Gordon 1994). Also, reports vary about ideal ground conditions for seedling establishment. Good seedbeds reportedly include: exposed mineral soil (Frothingham 1915, Hough 1960, Davis and Hart 1961, Fowells 1965, Wendel et al. 1983, Lorimer 1996, Tubbs 1996); a mixture of mineral soil and humus (Olson 1954, Davis and Hart 1961, Wendel et al. 1983, Lancaster 1985, Anderson and Gordon 1994); soils rich in organic matter (Lloyd 1900, U.S. For. Serv. 1970); moist and well decomposed litter (Frothingham 1915, Baldwin 1930, Graham 1943, Hough 1960, Fowells 1965, Tubbs 1996, Wendel et al. 1983, Anderson and Gordon 1994); ground covered to some depth with decaying leaves and twigs (Harlow 1900, Frothingham 1915); burned areas (Maissurow 1941, Miles and Smith 1960, Lorimer 1996, Tubbs 1996, Waller et al. 1996); coarse, woody debris (Corinth 1996); moss mats on soil, rocks, and fallen trees (Frothingham 1915, Friesner and Potzger 1932, Olson 1954, Hough 1960, Fowells 1965, Wendel et al. 1983, Collins 1990, Anderson and Gordon 1994, Lorimer 1996); thin litter (Friesner and Potzger 1932, Olson 1954, Collins 1990, Lorimer 1996, Waller et al. 1996); sloping soil where the seeds can lodge and root (Friesner and Potzger 1932); pit and mound topography (Anderson and Gordon 1994); areas free of understory vegetation (Lancaster 1985), such as grass or other tightly growing herbaceous plants (Lloyd 1900); and soils with suitable acidity levels (Potzger and Friesner 1936).

Like other species with a small seed, conditions on undisturbed seedbeds will not commonly lead to establishment of large numbers of seedlings (Godman and Mattson 1976). New germinants grow slowly, with weak radicals that do not develop in unfavorable conditions (Godman and Mattson 1976). Though seed will germinate on rotten wood (Lloyd 1900, Frothingham 1915, Olson 1954, Hough 1960, Fowells 1965, Ward and McCormick 1982, Wendel et al. 1983, Anderson and Gordon 1994, Lorimer 1996, Tubbs 1996), seedlings grow and develop poorly in that medium (Tubbs 1996). Consistent with this, a survey in Wisconsin indicated that most of the reproduction occurred on road cuts, old logging roads, and along lakeshores and rivers (Eckstein 1996). Other evidence indicates that the most consistent regeneration occurs in proximity of a seed-bearing tree (Graham 1958, Anderson and Gordon 1994, Parshall 1995), and particularly in canopy gaps (Eckstein 1996), on shaded sites (Olson and Nienstaedt 1953, Ward and McCormick 1982, Lorimer 1996), along the edges of stands (Lloyd 1900, Ward and McCormick 1982), or under widely spaced or declining older trees (Ward and McCormick 1982).

Seedling Development

Seedlings have a low light requirement, and establish better in shade than full sun (Hough 1960, Logan 1973). Yet in a moist soil and if protected from wind, hemlock saplings thrive in fairly strong light (Hough 1960). Best early height growth occurs at 25-45% light, and dry-matter production of seedlings peaks at 45% light (Logan 1973).

Seedlings form tap roots during the first year (Frothingham 1915, Clepper 1934), and a few laterals (Hough 1960). The former eventually disappear as a lateral root system develops (Frothingham 1915, Clepper 1934, Friesner and Potsger 1944). These shallow roots are sensitive to drying of the surface soil (Frothingham 1915, Friesner and Potzger 1932). So establishment and good early growth depend upon adequate growing season moisture and favorable temperatures (Anderson and Gordon 1994; Friesner and Potzger 1932, 1944; Graham 1941; Hough 1960; U.S. For. Serv. 1970; Wendel *et al.* 1983; Lancaster 1985; Lorimer 1996; Tubbs 1996; Waller et al. 1996).

The young trees develop slowly during the first growing season, reaching 1.0 to 1.5 inches by autumn (Lloyd 1900, Frothingham 1915, Hough 1960, Fowells 1965, Lancaster 1985). Later growth rates vary with exposure to light (Frothingham 1915). Seedlings and saplings may grow as little as 4 inches over a 3 year period in low light (Lloyd 1900), or up to 8 to 12 inches/year in light to moderate shade (Hough 1960). In full sun and with adequate moisture, seedlings may grow at least 18 inches per year (Hough 1960). However, hemlock grows best in full sunlight after the saplings have reached 5 to 10 feet tall (Nienstaedt and Olson 1955, Tubbs 1996).

An abundance of well-developed advance regeneration capable of dominating canopy openings provides the best evidence of a successful regeneration effort (Kotar 1996).

Hemlock trees are considered fully established upon reaching 3 to 5 feet in height (Frothingham 1915), but should be at least 9-10 feet tall to insure development into overstory positions when competing with hardwoods (Kelty 1986). Such well-developed understory saplings commonly respond well to release from overhead competition (Frothingham 1915, Marshall 1927, Graham 1943, Olsen and Nienstaedt 1953, Nienstaedt and Olson 1955, Hough 1960, Fowells 1965, Tubbs 1978, Lancaster 1985, Wendel et al. 1983, Fajvan and Seymour 1993, Anderson and Gordon 1994). Those with live crown ratios of at least 50% respond quickly (Hough 1960, Anderson and Gordon 1994), while others with ratios of less than 30% respond more slowly (Hough 1960, Anderson and Gordon 1994). Further, hemlock growing under a hardwood overstory will respond better to release than those found under a hemlock overstory (Hough 1960). After overstory removal, hemlock saplings may add 4 inches of diameter over a 10 year period (Fowells 1965). The older a sapling when released, the greater its response (Marshall 1927, Lancaster 1985).

Silvicultural Practices

Hemlock has regenerated naturally with minimal site disturbance beneath canopy openings, but success seems related to habitat type, opening size, and presence of advance regeneration (Pubanz 1996). Tenth-acre openings proved successful in areas with at least 75% of the basal area in sawtimber-size hemlock and yellow birch *(Betula alleghaniensis* Britton*)* (Pubanz 1996). Regeneration also occurred after thinning, salvage cuts, or selection cuts implemented over a 20-year period (Brogger 1996). Partial shade from residual overstory trees reduces surface temperatures, and the shading lessens competition from shade-intolerant trees and herbaceous plants (Tubbs 1996). Maintenance of between 70 and 80% canopy cover with scattered gaps should facilitate hemlock regeneration (Lorimer 1996). Hemlock generally succeeds in these small openings, but saplings often become overtopped by faster growing hardwoods in large ones (Lorimer 1996, Parshall 1995). Locating the canopy openings adjacent to seed-bearing hemlock trees helps to insure adequate seed dispersal (Crow 1996). Cuttings should be done in good seed years whenever possible (Davis and Hart 1961). Sixty year rotations have been recommended for free-to-grow hemlock, because older trees decline in growth (Marshall 1927). Advance regeneration should be left in place (Tubbs 1996).

Scarification (Lutz and Cline 1956, Hix and Barnes 1984, Anderson and Gordon 1994, Jordan et al. 1996, Lanasa et al. 1996, Lorimer 1996, Schmidt and McWilliams 1996, Strong 1996, Tubbs 1996), prescribed burning (Frothingham 1915, Hix and Barnes 1984, Anderson and Gordon 1994, Lorimer 1996), other soil disturbance (Crow 1996), and removal of hardwood competition (Davis and Hart 1961, Lorimer 1996, Schmidt and McWilliams 1996, Tubbs 1996) facilitate regeneration. Site preparation should mix the organic and mineral soil, and eliminate understory competition before or immediately after a cut (Frothingham 1915). Removing the humus layers or mixing the humus and mineral soil in shaded areas has provided good seedbeds that lasted for up to 3 years (Wendel et al. 1983). A consistently higher number of eastern hemlock has germinated in scarified plots compared to unscarified ones (Becker et al. 1996), but managers should coordinate site preparation with the occurrence of good seed crops (Godman and Mattson 1976), since successful regeneration depends upon a combination of adequate seed dispersal and favorable climatic and seedbed conditions (Miles and Smith 1960).

Hemlock rarely germinates or becomes established in open areas (Lancaster 1985), and strip cutting has produced varying results. Despite good seed years, hemlock has failed in clearcut strips of different widths, and in ones oriented both north-south and east-west (Lutz and Cline 1956). Some seedlings have developed on burned areas and moss beds, but a thick unscarified litter layer precludes establishment elsewhere (Lutz and Cline 1956). In one experiment, strip cutting worked well in mature stands not previously under management (Lancaster 1985). However, in similar stands, strip widths should not exceed one-half of the dominant tree height, and site preparation should remove competing hardwoods (Lancaster 1985).

In Wisconsin, light selection cutting, shelterwood method, group selection cutting, and cutting large canopy gaps have all been recommended as reproduction methods. So has deferral of any cutting (Eckstein 1996). New stands have successfully established after a combination of two- or three-stage shelterwood method (Anderson and Gordon 1994, Lancaster 1985) with site preparation (Frothingham 1915, Pubanz 1996). This approach is considered the most reliable method for securing hemlock regeneration in the Lake States (Tubbs 1978, Wendel et al. 1983, Lorimer 1996). It compensates for slow seedling development during the first 2 years by reducing moisture stress and inhibiting hardwood establishment (Lancaster 1985). However, the seed cutting should not create openings greater than one-half the height of the main canopy seed trees (Lancaster 1985).

A two-cut shelterwood method works best on poorly to moderately well-drained soil of a sandy loam or finer texture (Tubbs 1978). The seed cut should leave 110 ft^2/ac of basal area in evenly spaced trees, or 50% crown cover of the best dominants (Tubbs 1978, Lancaster 1985). Scarify the site prior to (Tubbs 1978, Wendel et al. 1983, Lanasa et al. 1996) or just following (Wendel et al. 1983, Lanasa et al. 1996) the seed cut, mixing the humus and upper mineral soil on at least 60% of the area (Wendel et al. 1983, Lanasa et al. 1996). Also, control competing hardwood understory trees (Tubbs 1978, Wendel et al. 1983, Lancaster 1985). Schedule a removal cut when the hemlock reproduction becomes well-established (Tubbs 1978), reaching 4 to 5 feet tall (Wendel et al. 1983, Lancaster 1985).

On dry sites and in overmature stands, a three-cut shelterwood method will inhibit grass and brush invasion (Tubbs 1978). Recommended overstory densities vary from 70 to 80% canopy cover following the first cut (Tubbs 1978, Wendel et al. 1983, Lancaster 1985, Anderson and Gordon

1994, Jordan et al. 1996, Lanasa et al. 1996, Strong 1996). Scarify prior to cutting (Tubbs 1978, Wendel et al. 1983, Lanasa et al. 1996), or depend upon logging during the snow-free period to encourage soil disturbance (Lancaster 1985, Anderson and Gordon 1994). Control hardwood competition (Anderson and Gordon 1994, Tubbs 1978, Wendel et al. 1983). After 8 to 12 years (Anderson and Gordon 1994, Tubbs 1978), reduce the crown cover to 50% (Tubbs 1978, Wendel et al. 1983, Anderson and Gordon 1994), again discriminating against hardwoods (Tubbs 1978, Lancaster 1985, Anderson and Gordon 1994). At this point, schedule the logging for winter to protect the regeneration (Lancaster 1985, Anderson and Gordon 1994). After another 10 years, remove the overstory (Anderson and Gordon 1994). Regeneration should have reached 4 to 5 feet tall by this time (Tubbs 1978, Lancaster 1985, Anderson and Gordon 1994). It may be necessary to supplement the cutting with direct seeding (Anderson and Gordon 1994), using a sowing rate of 0.5 lb/ac (Tubbs 1978).

Selection system has been recommended in the east (Anderson and Gordon 1994, Lorimer 1996), but not in the Lake States (Lancaster 1985). While often preferred due to the presence of advance regeneration (Davis and Hart 1961), uneven-aged silviculture seems to speed the replacement of hemlock by hardwoods at upland sites (Lorimer 1996). In mixed stands, single-tree selection cutting has successfully established hemlock regeneration (Lanasa et al. 1996), increased the proportion of hemlock (Wendel et al. 1983, Lanasa et al. 1996), and increased the growth of hemlock regeneration (Wendel et al. 1983). In these cases, schedule the logging for snow-free periods (Davis and Hart 1961, Anderson and Gordon 1994) when the soil is not frozen (Davis and Hart 1961). This will help to break up the soil, mix it with humus, and reduce root competition to some degree (Davis and Hart 1961). Cutting cycles of 10 years are recommended (Anderson and Gordon 1994), with a residual stocking of 130 ft^2/ac in stands with at least 50% hemlock (Lancaster 1985). Leaving 35% of the residual trees in the pole class (5 and 10 inches dbh) and the remainder in larger stems will ensure continuous ingrowth to sawtimber, and encourage regeneration on appropriate seedbeds (Lancaster 1985).

Group selection method has also been recommended (Merrill and Hawley 1924, Marshall 1927). In past trials, some hemlock, and much larger quantities of hardwoods, developed in the group openings (Lutz and Cline 1956), and the hardwoods quickly overtopped the hemlock. Even so, group selection generally proved more successful than the shelterwood method in those trials (Lutz and Cline 1956). When used, the group openings should not likely exceed one-tenth acre, or have a width exceeding one-half the height of adjacent residuals.

Agents Damaging to Regeneration

Regeneration may fail due to browsing by white-tail deer (*Odocoileus virginianus* Miller) (Frothingham 1915; Stoeckler et al. 1957; Graham 1958; Hough 1960; Fowells 1965; Jordan and Sharp 1967; Anderson and Loucks 1979; LaMadeleine 1980; Farr and Tyndall 1992; Anderson and Katz 1993; Abrams and Orwig 1996; Crow 1996; Davis et al. 1996; Lanasa et al. 1996; Lorimer 1996; Schmidt and McWilliams 1996; Tubbs 1978, 1996), even in favorable habitats and stand conditions (Lorimer 1996). In areas with a high deer pressure, few seedlings grow more than 6 inches before being browsed (Swift 1948, Lorimer 1996). Areas receiving deep snow and not used as winter cover by deer often have good regeneration and little evidence of browsing (Anderson and Loucks 1979, Lorimer 1996). Snowshoe hare (*Lepus americanus* Erxleben) also feed on hemlock regeneration (Swift 1948, Sage 1986), and eastern hemlock is highly rated as a food for porcupine (*Erithizon dorsatum* Linnaeus)(Stoeckler 1950).

Hemlock within enclosures has survived and developed better than seedlings on unprotected sample plots (Graham 1958, Sage 1986, Strong 1996, Tighe and Zuidema 1996), because browsing greatly reduces seedling development (Anderson and Loucks 1979). Growth does not differ between seedlings browsed once, and those browsed two or more times (Sage 1986). Within areas of protracted deer browsing, hemlock is more seriously damaged than sugar maple (Anderson and Loucks 1979, Crow 1996), and sugar maple frequently becomes the most important species in the reproduction strata (Anderson and Katz 1993). In such stands, the hemlock component may have a bell-shaped diameter distribution, because deer prevent regeneration and reduce the seedling and sapling age classes (Anderson and Katz 1993). So deer must be controlled for successful regeneration to occur (Anderson and Loucks 1979, Sage 1986), with deer density remaining low for 6-8 years to insure adequate seedling growth (Stoeckler et al. 1957).

Germinating seed and seedlings die from damping-off fungi (Frothingham 1915; Olson 1954; Olson et al. 1959a, 1959b; Hough 1960; Kilpatrick 1985; Ruth 1974; Ward and McCormick 1982; Crow 1996). *Fusarium moniliforme* has been isolated from 10% of the seed examined, and probably contributes to losses (LaMadeleine 1980). Root rot *(Armillaria sp.)* colonizes only overmature trees and those affected by drought (Graham 1943).

Though prescribed fire may help as a site preparation tool in promoting regeneration (Frothingham 1915), fires damage or kill established hemlock seedlings (Frothingham 1915, Merrill and Hawley 1924, Clepper 1934, Graham 1941, Hough 1960, Fowells 1965, Tubbs 1996). Regeneration may be inhibited in areas with a low fire frequency (Lorimer 1996), but fire may also inhibit hemlock regeneration by destroying the organic component of the soil (Frothingham 1915).

Management Implications

Successful regeneration of eastern hemlock involves a complex biophysical process that may span several years. It requires a reliable source of seed with suitable conditions for germination and for early establishment, followed by several years of favorable moisture. Sustained development requires a consistently bright (but partially shaded) and moist environment, and freedom from prolonged intensive browsing. Recurring deficits in these and other requisite factors often interrupt the regeneration process. Good initial seedling density appears important, but many die during early years. Presence of abundant and well-distributed advance seedlings at least 3 feet tall gives a better measure of success. Since hemlock seedlings grow slowly, it may take up to two decades for tall ones to develop.

Available sources provide no consensus about the most suitable reproduction methods. Light partial cutting, creating small openings, and shelterwood seed cutting leaving a uniform cover of upper canopy trees have worked best. Opening widths should not exceed ¾ to 1 times the height of adjacent residual trees. With uniform partial cutting, these openings might cover only one-half the height of adjacent residuals. Following any reproduction method, the residual stand should contain well-distributed hemlock trees of seed-bearing ages.

To enhance the reproduction potential of any cutting, supplemental treatments should include deliberate site preparation to scarify the surface and mix the humus with mineral soil, and to remove any competing broad-leafed woody understory. Though sometimes recommended, relying on skidding to disturb the surface does not appear appropriate, due to the inconsistency of its effects across the stand area, and the potential for uncontrolled skidding to accelerate erosion on slopes. Any cutting plan should include deliberate measures to protect advance hemlock regeneration (e.g., controlling skidding), and to keep it partially shaded until the trees reach at least 5 feet tall (up to 10 feet on sites favorable to hardwoods). Hemlock saplings with a live crown ratio of at least 50% offer the best promise for release, as these develop the best.

Success in regenerating eastern hemlock takes more than casual cutting. It requires deliberate control of residual stand density and spacing to ensure a bright but partially shaded and cool environment, retention of adequate numbers of sexually mature hemlocks to provide good seed dispersion across the regeneration area, appropriate site preparation to create a suitable seedbed and control interfering woody plants, and the good fortune of favorable soil moisture over a long series of consecutive years. The chances for successfully regenerating hemlock seem best at those sites less favorable to hardwoods.

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Eastern Hemlock Response to Even- and Uneven-Age Management in the Acadian Forest: Results from the Penobscot Experimental Forest Long-Term Silviculture Study

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Abstract

Eastern hemlock (*Tsuga canadensis* (L.) Carr.) is an important tree species in the mixed-species conifer forests of northern New England and adjacent Canada. Hemlock is very tolerant of understory conditions; consequently, it responds differently to various silvicultural treatments. In a long-term study at the Penobscot Experimental Forest in east-central Maine, shelterwood silviculture reduced the hemlock component in regenerating stands compared to parent stands, while hemlock increased in abundance and dominance under selection silviculture. On sites where hemlock is common, managers have some control over its prevalence through silviculture.

Introduction

Much of Maine and New Brunswick, as well as Nova Scotia and Prince Edward Island, are within the Acadian Forest Region (Rowe 1972). The region is boreal ecotone with a relatively cool, moist climate. The Acadian and closely related Great Lakes-St. Lawrence Forest Region of southern Quebec are of very mixed species composition; predominately conifers, especially on sites where drainage is impeded. The major conifers of the Acadian Region include spruces, red (*Picea rubens* Sarg.), white (*P. glauca* (Moench) Voss), and to a lesser extent black (*P. mariana* (Mill.) B.S.P.); balsam fir (*Abies balsamea* (L.) Mill.); northern white-cedar (*Thuja occidentalis* L.); eastern white pine (*Pinus strobus* L.) and red pine (*P. resinosa* Ait.); and eastern hemlock (*Tsuga canadensis* (L.) Carr.). Common hardwoods include red maple (*Acer rubrum* L.); paper birch (*Betula papyrifera* Marsh.); gray birch (*B. populifolia* Marsh.); and aspen, both quaking (*Populus tremuloides* Michx.) and bigtooth (*P. grandidentata* Michx.).

In the Acadian Region, stand replacing fires are less frequent than in other boreal and temperate forests (Wein and Moore 1977, 1979). Common natural disturbances are insect epidemics and wind storms that often cause sporadic and partial stand mortality. Such disturbances may occur only once during the life span of the relatively short-lived balsam fir, but several times during the life of spruce, hemlock, northern white-cedar or pine. Expect for the pines, these species are all very shade tolerant and natural regeneration following disturbance is prolific (Baldwin 1977, Piene and Anderson 1987, Brissette 1996). The pattern of natural disturbance and silvics of the commercial species make this forest type amenable to either even- or uneven-age management and most of their associated silvicultural systems.

The Penobscot Experimental Forest (PEF) is located in the towns of Bradley and Eddington, in Penobscot County, Maine. It is 4,000 acres in size and centered at approximately 44°52'N, 68°38'W. The PEF was established in 1950 for the purpose of conducting timber management research in northern conifers. At the time of establishment, the area was a mix of even-aged and apparently uneven-aged stands. Even-aged stands were 60 to 100 years old (Safford et al. 1969). Only a few acres had ever been cleared for agriculture. Cutting was relatively light in the 20 to 40 years before the area became the PEF with some pine, spruce, and hemlock sawlogs harvested. Glacial till is the principal parent material with soil types varying from well-drained loams and sandy loams on low-profile ridges to poorly and very poorly drained loams and silt loams in the flat areas between the ridges.

Between 1952 and 1957, an experiment was established on the PEF to compare the effects of even- and uneven-age management on stand growth, yield, species composition, and value. Even-age management is represented by clearcut and shelterwood silvicultural systems. Some of the shelterwood treatments were also precommercially thinned, or spaced. Uneven-age management is represented by selection silviculture. Diameter-limit cutting is also included in the treatment array. One goal of the experiment is to determine how to increase the component of spruce in stands. Thus, whenever possible for a particular treatment, spruce is left as a seed source or simply to grow and increase in dominance in the stand.

The objective of this paper is to present 40-year results describing how eastern hemlock has responded to shelterwood and selection silviculture in the long-term experiment on the PEF.

Materials and Methods

Treatments were assigned to compartments at random and replicated twice, each replicate or compartment averaging 25 acres. Periodic measurements of stand composition and structure are taken on a series of permanent plots established in each compartment on a grid with a random start. The plots consist of two concentric circles of different sizes with the same plot center. All trees with a dbh $\geq$0.5 in are measured on the interior 1/20 ac plots. All trees with dbh $\geq$4.5 in are measured on the entire 1/5 ac plots. The number of such plots average 18 per compartment. Regeneration inventories are taken on three milacre (0.001 ac) plots located on the circumference of each 1/20 ac plot. Regeneration is defined as a seedling or sprout $\geq$6 in tall but with a dbh <0.5 in. Measurements are taken before and after cutting and at about 5-year intervals between harvests.

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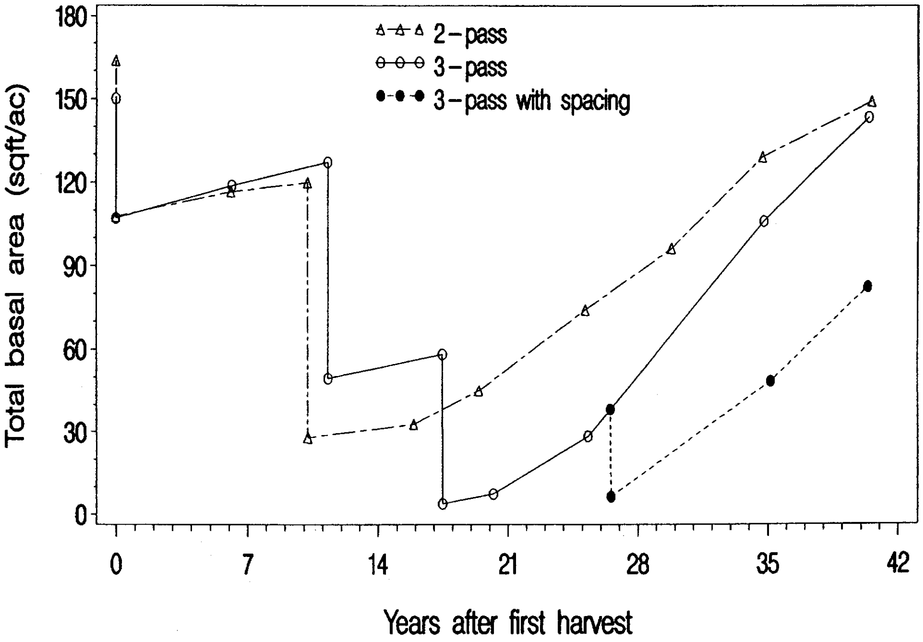

Figure 1.—Harvest and growth history of compartments managed under shelterwood silviculture at the Penobscot Experimental Forest.

In the experiment there are two uniform shelterwood treatments (Figure 1). In one the overstory was removed in two passes or stages. In the other the overstory was harvested in three stages; subsequently these compartments were split, one-half was spaced the other was not. Because advanced regeneration of understory-tolerant species, such as spruce, balsam fir, and hemlock, is usually abundant in the Acadian forest, the principal objective of removing the overstory in stages is to release that regeneration. Shelterwood silviculture also provides a measure of control over species composition in the regenerating stand, primarily by limiting the establishment and growth of intolerant species during the period of overstory removal. Nevertheless, more regeneration is established during the overstory removal phase, and that fact was considered when the shelterwood harvests were planned in this experiment.

Table 1.—Structural goals for compartments under selection management at the Penobscot Experimental Forest.

Cutting cycle	q-factor[1]	Residual basal area	Residual max dbh
		(ft²/ac)	*(in)*
5 years[2]	1.96	115	19
10 years[2]	1.96	100	18
20 years[3]	1.96	80	16

[1] Calculated for 2-in dbh classes, all species combined
Additional constraints:
[2] Harvest <50 percent net periodic growth until optimal structure is achieved
[3] Harvest <75 percent net periodic growth until optimal structure is achieved

Three variations of selection silviculture are represented. All employ a combination of single-tree and group selection cutting, but differ by harvest interval, residual basal area, and maximum diameter goals (Table 1). Target diameter distributions were defined using the BDq method (Guldin 1991).

Results and Discussion

Even-age

Prior to initiating the shelterwood treatments hemlock accounted for over 20 percent of the basal area in the 2-pass compartments (Figure 2) and about 30 percent in the 3-pass compartments (Figure 3). Because spruce was favored as a seed source over all other species during the overstory removal phase, the proportion of hemlock tended to decline during the period under both shelterwood treatments.

A notable difference between the two shelterwood treatments was that under the 2-pass treatment, non-merchantable trees were left during the final overstory removal, while all trees >2 in dbh were cut in the 3-pass treatment. Thus, among trees >0.5 in dbh, there was about 30 ft^2 of basal area per acre following overstory removal in the 2-pass treatment but less than 10 ft^2 in the 3-pass treatment (Figure 1). Following overstory removal in the 2-pass compartments, hemlock accounted for over 3 ft^2 of basal area, almost entirely in residual, unmerchantable trees. There was very little basal area of hemlock following overstory removal in the 3-pass compartments and what was present was advanced regeneration >0.5 in dbh.

After an initial decline in the proportion of hemlock basal area in the 2-pass shelterwood compartments, growth of the residual trees and of advance regeneration returned

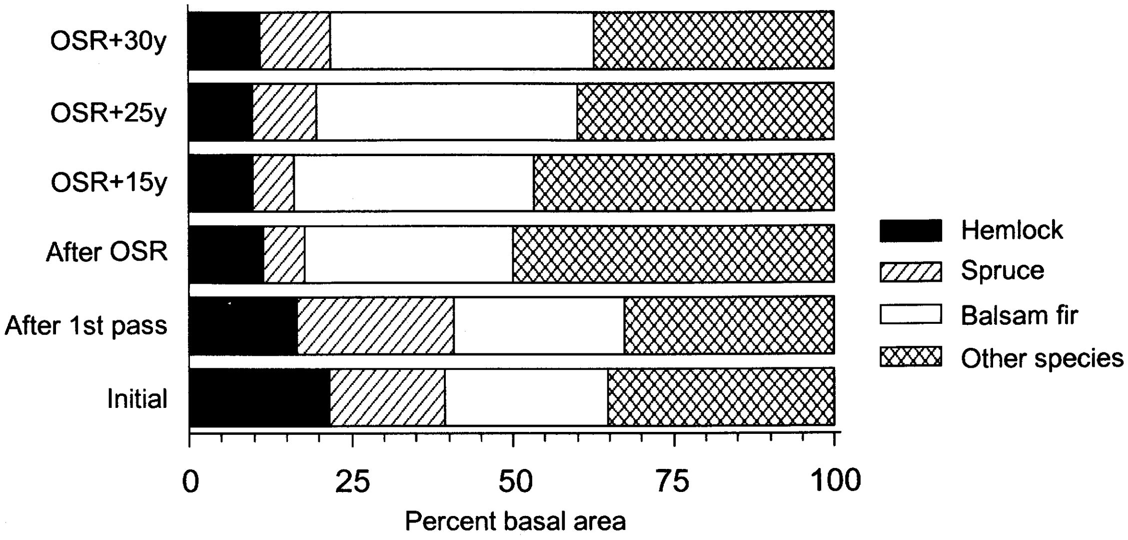

Figure 2.—Species composition history for 2-pass shelterwood compartments at the Penobscot Experimental Forest. OSR = overstory removal.

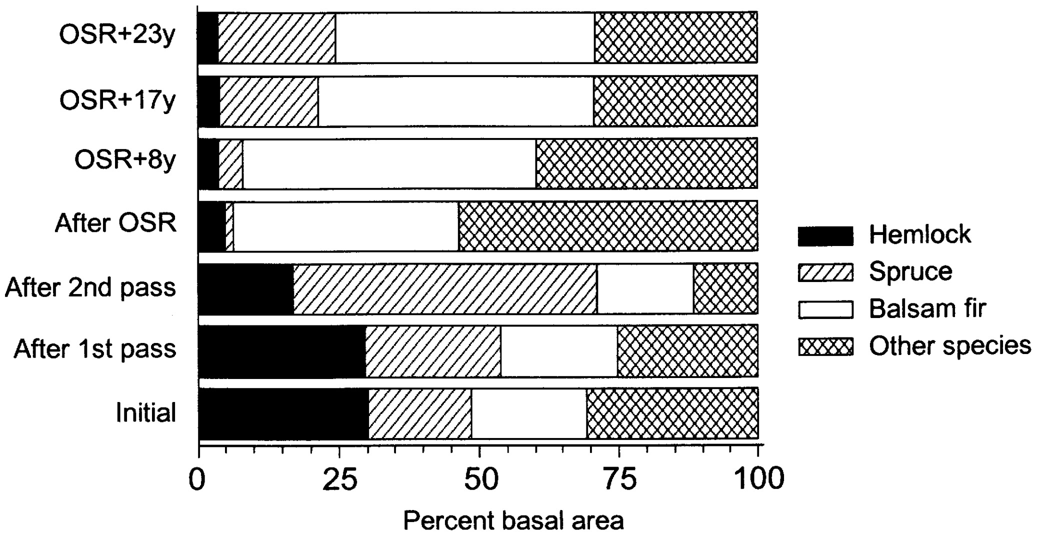

Figure 3.—Species composition history for 3-pass shelterwood compartments (without subsequent spacing) at the Penobscot Experimental Forest. OSR = overstory removal.

hemlock to what it was immediately after the overstory was removed, or about 60 percent of what it was prior to treatment (Figure 2). However, in the 3-pass compartments without spacing, hemlock has not recovered from a similar decline and its proportion has remained constant at about 5 percent (Figure 3). The proportion of hemlock in the spaced stands is even less. Hemlock is very well adapted to understory conditions (Spurr and Barnes 1980); the decline of hemlock after overstory removal is likely due to stress-induced mortality among advance regeneration and, in the 2-pass compartments, suppressed residual trees caused by the relatively sudden opening up of the stands. That stress was greater in the 3-pass compartments than in the 2-pass treatment where some shelter was retained in the residual trees.

At this point in the study, stand basal area of the two treatments is almost the same (Figure 1), even though the regenerating stands under the 2-pass treatment were released about 7 years earlier and had a substantial initial basal area advantage over the 3-pass stands. Clearly, the residual trees have suppressed stand growth. Although the proportion of hemlock is relatively small in both treatments, it is constant or increasing slightly with time. Thus, hemlock is apparently growing at near the average stand growth rate. Without intermediate treatments such as thinning, the proportion of hemlock in both treatments will increase because trees of more light-demanding and shorter-lived species will die as the stands continue to grow and mature.

Uneven-age

A review of the structural development of the PEF selection stands is critical to understanding the behavior of the component species. Without exception, the stands have not yet attained the target structural goals. Pre-cut basal area has been less than the post-cut goal in every entry in the 5-year stands, with only a few pre-cut inventories slightly exceeding the post-cut goal in the 10-year stands (Figure 4). Results from the 20-year cutting cycle show better agreement between target and actual basal area. However, they also reveal a very heavy cut, greater than 50 percent of the total stand basal area, that undoubtedly changed age structure and growth dynamics in these stands.

Evaluation of diameter distributions for all species combined reveals that structural imbalances have developed over the past 40 years under all three cutting cycles. Although the diameter distributions were initially close to the specified goals, surpluses of large trees and deficits in the pole and sapling classes have become apparent. The two most likely explanations for this deviation from the specified target diameter distributions are: (1) past marking practices which removed older trees from the smaller classes while leaving vigorous upper canopy trees, and (2) slow rates of ingrowth into the merchantable classes (Seymour and Kenefic 1998). The former problem appears to be due to poor age-size relationships in the stands, while the latter may result from the rapid closure of single-tree canopy openings.

The diameter distributions of the eastern hemlock component of the selection stands confirm that this species exhibits the stand-level patterns of change described above; that is, the number of trees in the pole classes dropped over time while sawtimber accumulated (Figure 5). Although deficits have developed in the pole classes, abundance and stocking of balsam fir, hemlock, and spruce regeneration far exceed the numbers needed to ensure their presence in the future stands (Brissette 1996). Furthermore, those seedlings are growing into the larger size classes. For example, the number of hemlock saplings in the 1 in dbh class increased over the 40-year period under all cutting cycles (Figure 5). Moreover, the magnitude of this increase is greatest under the longer cutting cycle (lower residual basal area).

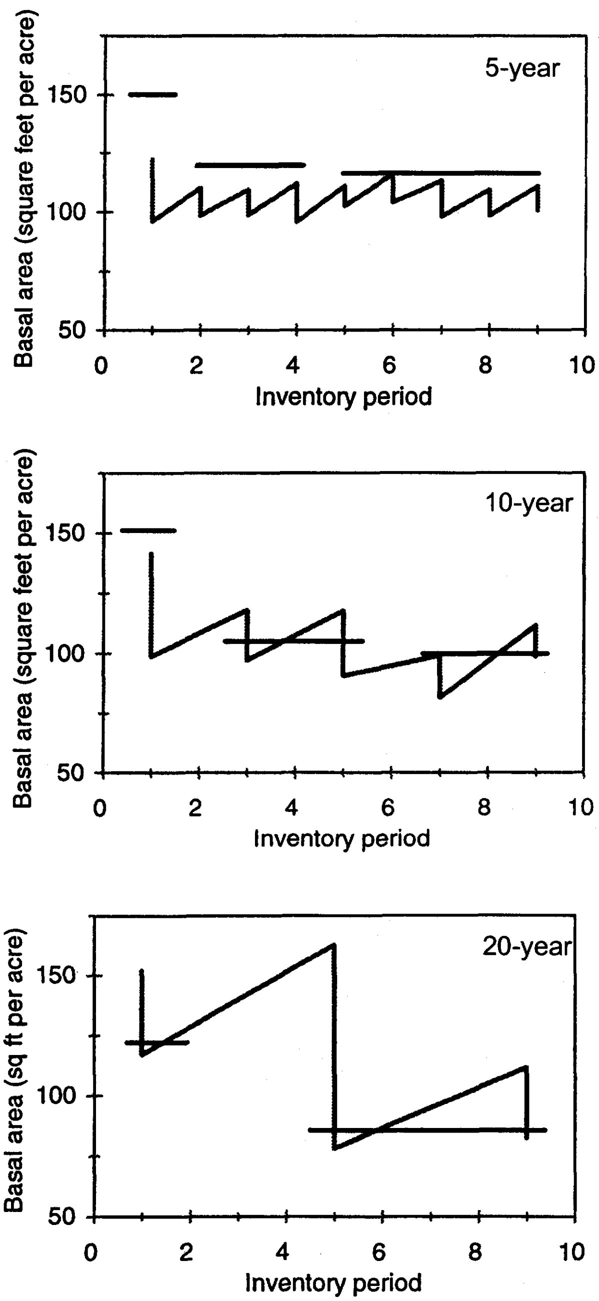

Figure 4.—Harvest and growth history of selection management compartments managed under three cutting cycles at the Penobscot Experimental Forest. (Horizontal lines indicate residual basal area goals.)

In the plan for the long-term study, species compositional goals (expressed as percentage of basal area of trees >0.5 in) were specified with the objective of increasing the proportion of spruce while decreasing hemlock and balsam fir. The goals for hemlock (15-25 percent) and spruce (35-55 percent) led researchers to mark hemlock for harvest and leave spruce where possible. While the spruce component has increased under all cutting cycles, results for hemlock are mixed (Figure 6). Hemlock has flourished under selection cutting on a 5-year cycle, despite repeated attempts to reduce the hemlock component in these stands. Furthermore, analysis of the age structure for the two 5-year stands shows that the hemlock component is extremely uneven-aged, with trees distributed across the range of age classes (Kenefic and Seymour 1999 [see also Kenefic and Seymour in this volume]). Red spruce, on the other hand, is restricted primarily to an age class that originated 100-120 years ago. Thus, as indicated by recruitment across age classes, hemlock exhibits compositional stability but spruce does not.

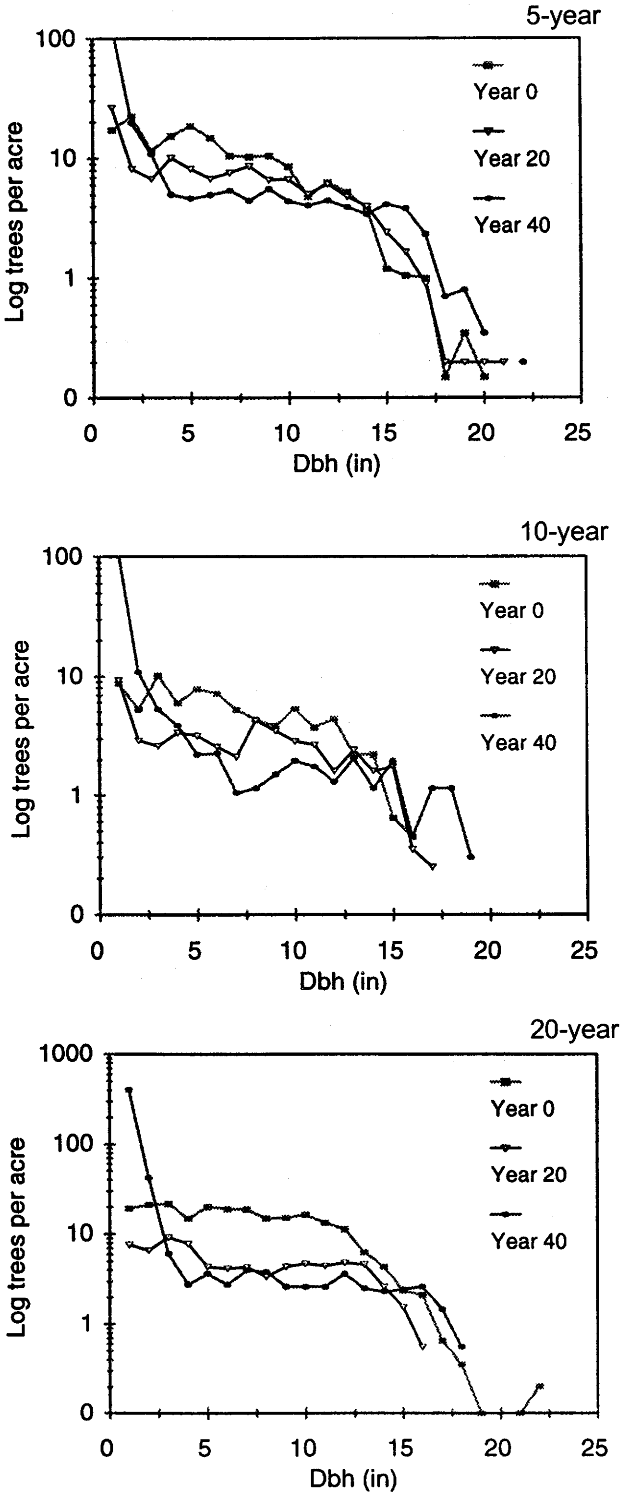

Figure 5.—Diameter distributions for hemlock under selection management with three cutting cycles at the Penobscot Experimental Forest.

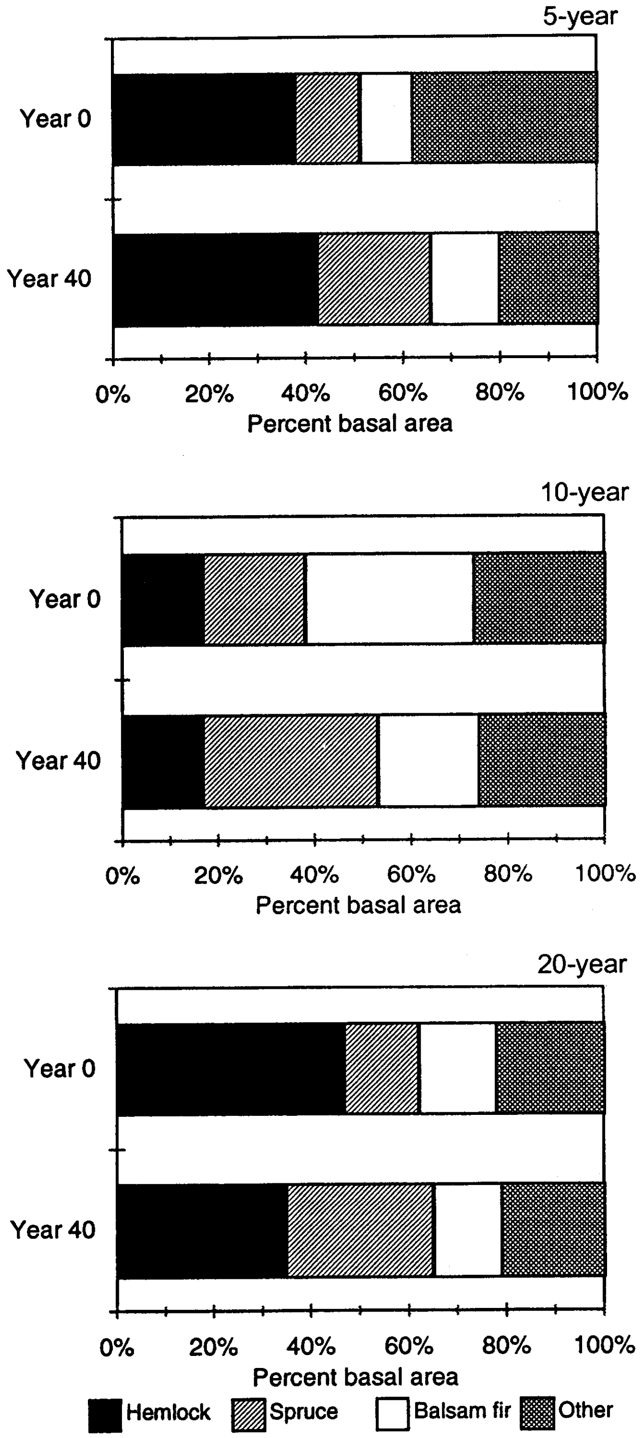

Figure 6.—Species composition history of selection management compartments managed under three cutting cycles at the Penobscot Experimental Forest. (Goals: Eastern hemlock 15-25%, spruce spp. 35-55%, Balsam fir 15-25%.)

Conclusion

Hemlock is well adapted to establish and grow in understory conditions typically found in the Acadia Forest Region. Consequently, it is an important component of many stands. The proportion of hemlock in a stand is determined to a large extent by openings in the overstory, either through natural disturbance or by manipulation during the regeneration phase of forest management. Results of the long-term study on the PEF show that extensive overstory removal, as with shelterwood silviculture or a stand-replacing natural disturbance, results in the regenerating stand having an even-aged structure and a relatively small proportion of hemlock. However, sporadic, small openings in a mature forest canopy leads to uneven-aged structure and favors hemlock to such an extent that it may become the dominant species in the stand. The persistence of eastern hemlock in the PEF selection stands has led us to conclude that this species is well suited to selection cutting in the mixed-species northern conifer forest type. The increase in the proportion of hemlock in the 5-year stands, where small canopy openings and high residual basal area predominate, is particularly noteworthy. Abundant regeneration under all cutting cycles and continuous recruitment of eastern hemlock (as evidenced by the species-specific age structures for the 5-year stands), indicate that this species regenerates prolifically and regeneration patterns suggest that the hemlock component of the PEF selection stands is sustainable, an important consideration when applying uneven-aged silviculture. Clearly, silviculture is a powerful tool managers can use to either limit or increase the proportion of hemlock in stands in the Acadian Forest.

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Growth Patterns of *Tsuga canadensis* in Managed Uneven-aged Northern Conifer Stands

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Abstract

This study reports patterns of regeneration and growth for 100 eastern hemlock (*Tsuga canadensis* (L.) Carr.) up to 20 inches (50 cm) dbh in two mixed-species selection stands on the Penobscot Experimental Forest in east-central Maine. The study stands are part of a U.S.D.A. Forest Service experiment in which eastern hemlock has remained stable over a 40-year period despite efforts to favor other species. Relative to red spruce (*Picea rubens* Sarg.) and balsam fir (*Abies balsamea* (L.) Mill.), eastern hemlock exhibits different growth patterns and canopy structures in response to frequent light partial disturbances. These characteristics, along with frequent and abundant regeneration, make eastern hemlock very well-suited to the selection system in this forest type.

Introduction

Eastern hemlock (*Tsuga canadensis* (L.) Carr.) is an important component of the Acadian Forest of New England, where small-scale natural disturbances and naturally uneven-aged stands predominate. However, little is known about the growth dynamics of eastern hemlock in complex uneven-aged stands. The objective of this paper is to describe eastern hemlock growth dynamics in regulated uneven-aged forest stands in Maine. Comparative information is provided for red spruce (*Picea rubens* Sarg.) and balsam fir (*Abies balsamea* (L.) Mill.), common associates of eastern hemlock in the Acadian Forest.

Study Area

The study stands are located on the Penobscot Experimental Forest in east-central Maine, the site of a long-term U.S.D.A. Forest Service experiment in even- and uneven-aged silviculture. Two replicates of selection cutting on a 5-year cutting cycle were chosen for the eastern hemlock study. These are mixed-species uneven-aged northern conifer stands, dominated by eastern hemlock, red spruce, and balsam fir in mixture with northern white cedar (*Thuja occidentalis* L.), white spruce (*Picea glauca* (Moench) Voss), white pine (*Pinus strobus* L.) and hardwoods including red maple (*Acer rubrum* L.) and paper birch (*Betula papyrifera* Marsh.). The stands were irregularly uneven-aged prior to the onset of Forest Service research. The predominant natural disturbances are windthrow and insect outbreaks, with a low incidence of deer browsing.

There have been nine selection cuttings in the stands to date, with 40 years of mensurational data collected on a 5-year measurement cycle. The structural goals were defined using the BD*q* method, with a residual basal area (BA) goal of 115 ft^2/acre (26 m^2/ha), a residual maximum diameter of 19 inches (48 cm), and a *q*-factor of 1.96 (calculated for 2-inch (5-cm) dbh classes for all species combined) (Seymour and Kenefic 1998). Cuts were very light, averaging 218 ft^3/acre (15 m^3/ha) per entry over the 40-year period.

Methodology

Long-term data (species, dbh, and tree condition) were collected before and after every 5-year cutting by the Forest Service from numbered trees > 0.5 inches (1.3 cm) dbh on fixed-radius nested plots (see Brissette and Kenefic, this volume). These data were used to determine changes in diameter distribution and species composition, as well as stand volume and BA. Additional data were collected for this study from randomly sampled eastern hemlock (n=100), red spruce (n=100), and balsam fir (n=50). Sampling was stratified by 2-inch (5-cm) dbh classes across the range of diameters present in the study stands. Dbh, canopy stratum, crown class, total height, height to the crown, and crown radii were recorded. Increment cores were extracted at breast height, and age at breast height and radial growth were determined using a Velmex measuring system (Velmex, Inc.). Ages of trees smaller than 2.0 inches (5 cm) dbh were determined by counting internodes on the main stem.

Results and Discussion

Species composition

Species composition goals (expressed as percent of BA of all trees > 0.5 inches (1.3 cm) dbh) are used to guide marking in the selection stands. Acceptable ranges were established in the Forest Service study plan as 15-25% for eastern hemlock, 35-55% for spruce spp., and 15-25% for balsam fir. Meeting these goals required an increase in the spruce component and a decrease in eastern hemlock relative to the original species composition (Figure 1, see also Brissette and Kenefic, this volume). Despite preferential marking of hemlock, this species now occupies a greater proportion of stand BA than it did when the study began, far exceeding the compositional goal. As a result, eastern hemlock now comprises more than 40% of the BA, and contributed 46% of the 40-year volume growth for all species combined (49.2 ft^3/acre/year or 3.4 m^3/ha/year) in the 5-year selection stands.

Age structures

Age data for the three dominant species provide insight into the mechanisms responsible for eastern hemlock's proliferation. Age structures for the two replicates are quite

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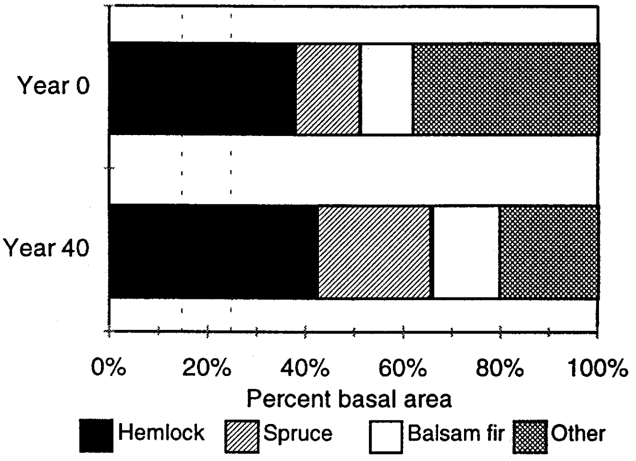


Figure 1.—40-year change in species composition. Vertical dashed lines indicate upper and lower limits of eastern hemlock species composition goal (15-25%).

uneven-aged, with ages ranging from less than 10 to 190 and 210 years, respectively (Figure 2) (Kenefic and Seymour 1999). In both stands, hemlock is represented in almost every age class across the entire age distribution, indicating that this shade-tolerant species has been establishing continuously in the understory. This suggests a compositional and structural stability not evident in red spruce, despite similar silvical properties. The majority of red spruce originated as a single cohort 100-120 years ago. Red spruce is thus more even-aged in character and less likely to remain compositionally stable over time.

Regeneration and release

When managing uneven-aged stands, silviculturists must understand the developmental pathways by which trees are recruited into the canopy. Must trees originate in gaps? Can they remain partially suppressed during the sapling and pole stages? Using Lorimer et al.'s (1988) threshold initial radial growth rate of 1.2 mm/year for gap origin eastern hemlock, we determined that a much smaller percentage (20%) of the hemlock we sampled originated in openings relative to red spruce (49%) (Table 1). In fact, 80% of the eastern hemlock in our sample appear to have originated beneath the canopy, and 11% were never released (release is defined as a > 100% increase in mean annual radial increment between two adjacent 15-year periods (Frelich and Graumlich 1994)). Half of those that were released showed multiple release events.

Table 1.—Percent of sampled trees originating in gaps and beneath the canopy.

	Eastern hemlock n=76	Red spruce n=81
Gap origin	20%	49%
Originated under canopy, never released	11%	12%
Originated under canopy, later released	69%	39%

Of released trees, 50% of eastern hemlock and 32% of red spruce experienced ≥ 2 release events.

These data illustrate the complexity of growth dynamics in the study stands, a result of high canopy closure, stratified stand structures, and overlap within and between canopy layers. Stem mapping (unpublished data) revealed an extremely heterogenous canopy structure, with small trees both within gaps and partially or totally within the crown projection area of larger trees. Many trees exhibit periods of release following dieback or removal of larger trees, as well as long or sporadic periods of suppression. Eastern hemlock's ability to establish beneath an overstory and persist under low levels of light allows it to persist under the canopy conditions associated with selection cutting in the study stands.

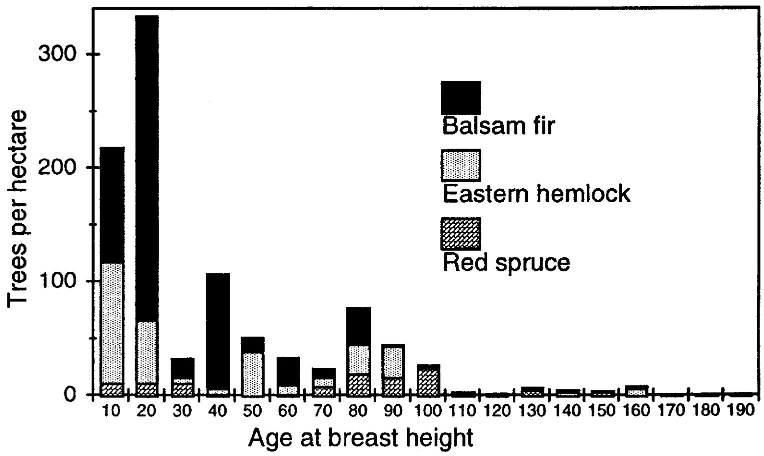
Age-size relationships

In light of the information presented above, it is not surprising that eastern hemlock's age-size relationships are poor (Figure 3) (Seymour and Kenefic 1998). Long or multiple periods of suppression are common, rendering it almost impossible to predict tree age from size or canopy position. Though the mean age of B-stratum codominant and dominant hemlock was 120±6 years, ages varied widely from 55 to 192 years. Thus there are many old and potentially less vigorous trees in the smaller size classes, underscoring the necessity of tending in the midstory to maintain and accelerate growth.

Spruce budworm

Spruce budworm (*Choristoneura fumiferana*) is an important disturbance agent in the Acadian Forest and has a direct effect on radial growth patterns. Defoliation may cause growth reduction, while changes in canopy structure due to mortality of neighboring trees may result in release. Though balsam fir and spruce spp. are the preferred budworm hosts, eastern hemlock also is defoliated by this insect (Irland et al. 1988). Radial growth patterns showing periods of budworm-caused suppression were seen in both eastern hemlock and red spruce in our study (Figure 4). However, our investigation of budworm response reveals that hemlock and spruce are, not surprisingly, affected differently by insect outbreaks. During the severe outbreak ca. 1913-19, for example, a greater percentage of our sampled eastern hemlock show release, while more spruce endured a period of suppression (Figure 5). Though some eastern hemlock were initially defoliated, these trees recovered more quickly than the affected red spruce. Most mature balsam fir were probably killed during the outbreak, and were not available for comparison. Furthermore, the magnitude of response in eastern hemlock and red spruce differs, with a much lower degree of suppression in affected hemlock. This suggests that crown dieback and mortality of the primary budworm hosts have a beneficial effect on eastern hemlock, giving it a competitive advantage in budworm-susceptible stands.

Compartment 9



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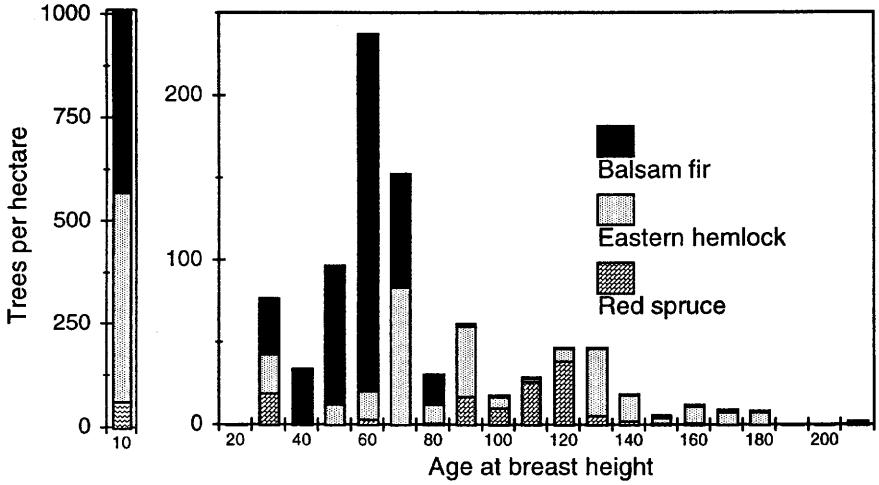

Figure 2.—Age structures for the three dominant species in the Penobscot Experimental Forest 5-year selection stands.

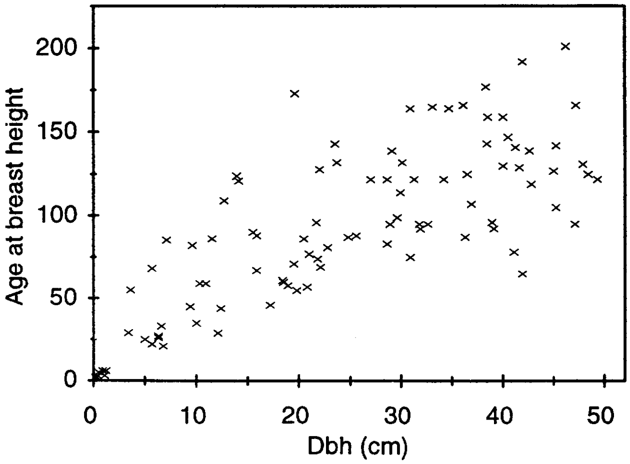

Figure 3.—Eastern hemlock age-size relationship.

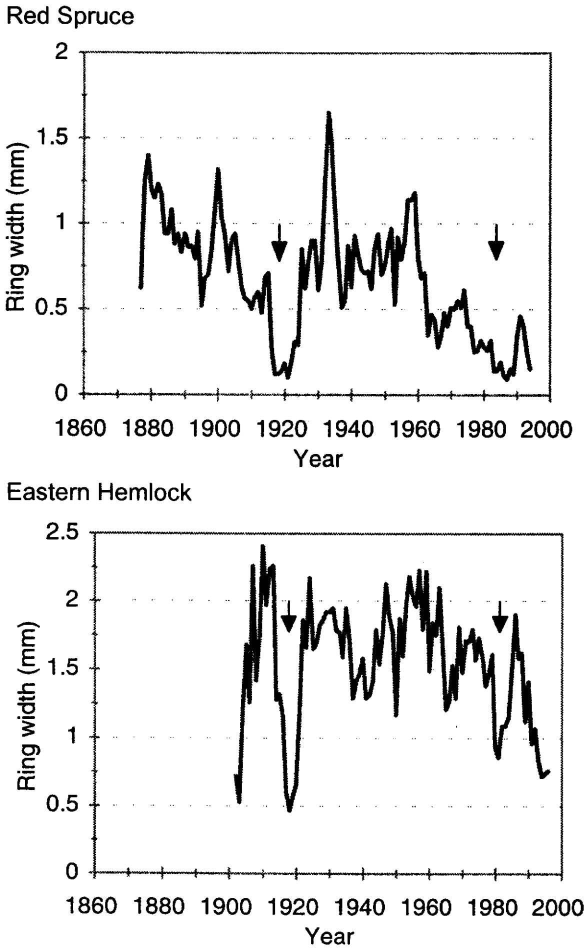

Figure 4.—Examples of individual trees showing budworm suppression.

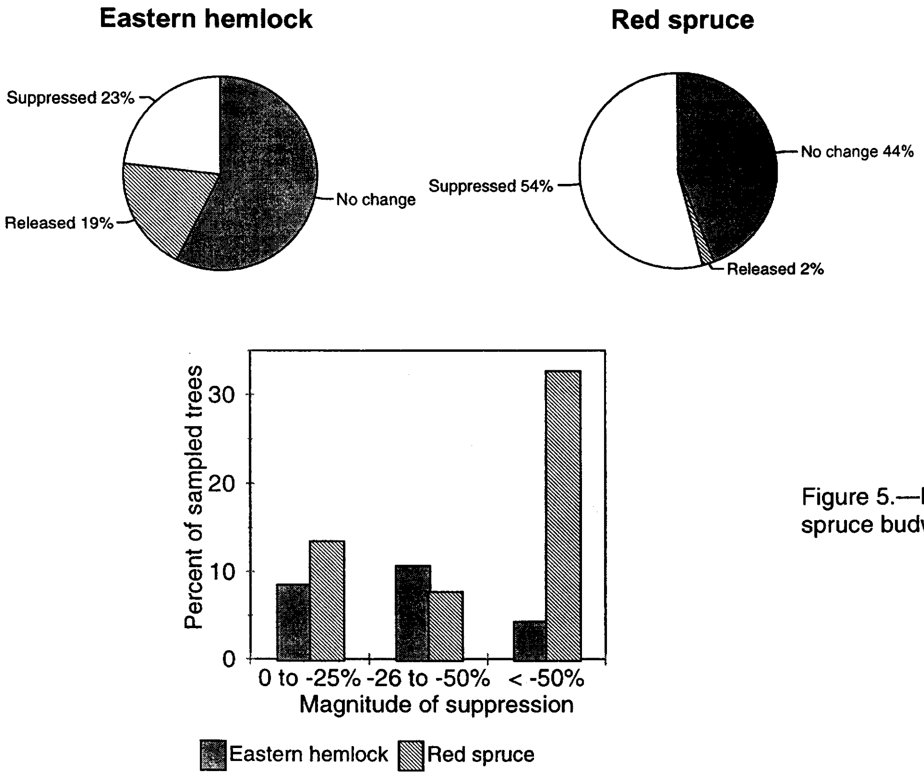

Figure 5.—Radial growth patterns during spruce budworm outbreak ca. 1913-19.

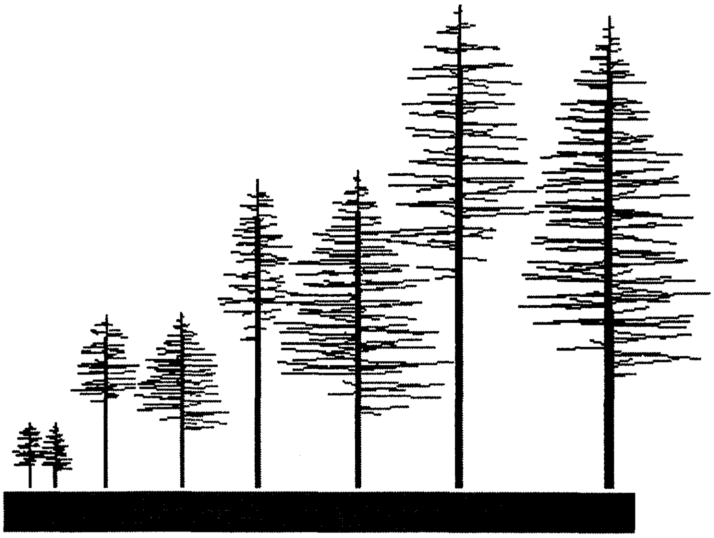

Figure 6.—Crown development of eastern hemlock and red spruce in the Penobscot Experimental Forest 5-year selection stands. Within each stratum, red spruce is shown on the left and eastern hemlock is shown on the right.

Canopy characteristics

The suitability of eastern hemlock for uneven-aged management in the northern conifer type is a direct result of the crown architecture of this species. Average tree height, crown radius, and crown length of eastern hemlock and red spruce in each canopy stratum in the two study stands reveal differences in crown development in these two species (Figure 6). Though total height is similar in each stratum, crown size diverges as the trees move into higher canopy strata. Despite similarities in shade tolerance and longevity, eastern hemlock retains a lower and wider crown base than red spruce in the upper canopy. This difference has implications with regard to growth potential and the ability to occupy available growing space and expand into openings. Clearly, a larger and longer crown allows eastern hemlock to capture a greater proportion of available two-dimensional growing space in the study stands.

Conclusions

Data from a long-term study of uneven-aged silviculture on the Penobscot Experimental Forest in Maine suggest that eastern hemlock is very well-suited to the structural conditions and disturbance regime associated with selection cutting on a 5-year cycle in mixed-species northern conifers. Eastern hemlock exhibits relatively low branch shedding and maintains large crowns, a competitive advantage with regard to two-dimensional growing space occupancy in highly stocked, light-limited stands. This species is able to grow in overlapping canopy arrangements, and can regenerate and persist in suppressed understory positions. Additionally, regeneration has been shown to occur continuously over time, providing a degree of compositional stability. Lastly, radial growth patterns exhibit multiple periods of suppression and release, and a relatively high proportion of release events during spruce budworm outbreaks. All these characteristics support the conclusion that managers can expect eastern hemlock to proliferate in mixed-species stands of the Acadian Forest under light partial disturbances as long as herbivory does not impede seedling establishment. Setting realistic compositional goals that reflect this fact should contribute to sustainable and ecologically sound management of eastern hemlock.

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Downed Wood as Seedbed: Measurement and Management Guidelines

Mark J. Ducey[1] *and Jeffrey H. Gove*[2]

Abstract

Eastern hemlock has exacting germination requirements, and availability of suitable microsites for germination can limit the development of hemlock regeneration. A major contributor to those microsites is coarse woody debris. New methods for quantifying coarse woody debris have recently been developed that are complementary to strategies typically used in timber cruising. We discuss practical issues in estimating the abundance of coarse woody debris and associated germination microsites, and illustrate the techniques with reference to preliminary guidelines for coarse woody debris abundance.

Introduction

Eastern hemlock (*Tsuga canadensis*) does not usually figure as a species of concern when regeneration is considered, at least in the Northeast, although the situation in the Lake States is different (Tubbs 1995). This may be because little economic value is usually attached to the species, despite its clear value for game habitat; perhaps, in part, it is because so many stands show abundant stocking in the seedling and sapling size classes, which conventionally have been taken to represent young age classes. However, the appearance of abundance may be deceiving, since suppressed "seedlings" and saplings may be decades old. An apparent exuberance of regeneration may mask an underlying demographic process of slow and infrequent establishment. Eastern hemlock is one of the more prolific and regular seed producers among the northeastern conifers (Godman and Mattson 1976). However, the seeds themselves are quite small, and viability can be low. Eastern hemlock requires a warm, moist seedbed for successful germination: both the temperature and moisture requirements are exacting (Godman and Lancaster 1990). These factors can combine to limit the establishment of hemlock seedlings and saplings, before other agents such as herbivory can come into play.

What substrates provide the conditions for hemlock regeneration? The leaf litter layer in mature forests is typically quite thick, and hemlock germinants fare poorly on such a dry, inhospitable substrate (Godman and Lancaster 1990). Tip-up mounds formed by the blowdown of large trees may form an important regeneration microsite in older forests, but tip-up mounds are rarely a significant feature in managed stands. While scarification along skid trails may provide good germination sites in recently cut stands, skid trails should form only a small component of total surface area when harvests are well-planned. Increasing attention to water quality issues, trends toward directional or mechanical felling with widely separated skid trails, and improvements in harvest mechanization have all combined to reduce scarification during harvest in much of hemlock's range. This "accidental" site preparation should not be relied on to stimulate much hemlock regeneration, and deliberate site preparation remains an expensive option. Without site preparation, either accidental or deliberate, the development of hemlock regeneration is usually restricted to downed coarse woody debris, or CWD (Godman and Lancaster 1990, Waller *et al.* 1995). For example, Corinth (1995) found that well-decayed CWD accounted for 57% of the hemlock regeneration in one stand in Wisconsin. Physically, CWD maintains an increased supply of available moisture, while its elevation above the forest floor may increase surface temperature, particularly in the spring germination period when soils are cold (Godman and Lancaster 1990). Tubbs (1995) suggests that hemlock logs may provide a refugium from competition with sugar maple (*Acer saccharum*) and yellow birch (*Betula alleghaniensis*) for young hemlock seedlings. CWD may not be an ideal substrate, but it can be inexpensive to manage. In addition to providing possible regeneration microsites, CWD also contributes to nutrient cycling and wildlife habitat (Hagan and Grove 1999).

It has not been common practice in the Northeast or Lake States to inventory CWD, either for operational or research purposes. Although guidelines have begun to appear (NHFSSWT 1997), they have not addressed the regeneration role of CWD, and baseline information on the abundance of CWD and its relationship to management is largely lacking (Hagan and Grove 1999). Fortunately, recent developments in CWD inventory techniques may reduce the difficulty of obtaining estimates at the stand level. Here, we review four methods of estimating CWD abundance, with particular attention to the variables which are most relevant for assessing regeneration microsites. Then, based on simple principles, we develop a preliminary stocking guide for CWD based on its potential in hemlock establishment. We illustrate how the guide can be used with a straightforward example.

What Aspects of Downed CWD Should be Measured?

Before any attempt at quantification begins, we should consider carefully what constitutes CWD, and what attributes of CWD are important in assessing regeneration potential. Perhaps the only attribute of CWD on which researchers can agree is that it is dead and woody. While studies and guidelines focusing on wildlife habitat attributes have often emphasized the amount of CWD in very large size classes, for example pieces >12" in diameter (NHFSSWT 1997), other studies have considered much smaller material in their definition of CWD. To be functional as a regeneration

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substrate, CWD must have sufficiently large diameter. First, it must be large enough to remain unburied by leaf litter until it has reached an advanced stage of decay. Second, it must still be elevated sufficiently above the surface of the litter layer that the young hemlock seedlings are not at risk of smothering under additional litterfall (Koroleff 1954, Tubbs 1995). Despite these considerations, Corinth (1995) found hemlock seedlings utilizing CWD as small as 4" in diameter. While there is a need for more data to assess these relationships, particularly in the Northeast, it seems that 4" is a reasonable lower diameter cutoff when measuring CWD for regeneration purposes, and it is consistent with previous definitions and procedures (Brown 1974).

A second difficulty lies in deciding what variables (both at the individual piece and the stand level) are important in assessing CWD. In part because most studies of CWD abundance have focused on the role of CWD in wildfire potential or in nutrient cycling, most presentations of inventory methods have stressed evaluating volume (ft^3/acre) or biomass (tons/acre) (Brown 1974, Harmon and Sexton 1996). Unfortunately, these representations of CWD abundance are less useful in assessing regeneration potential. One variable which does seem appropriate is the total ground surface area covered by CWD (ft^2/acre). This measure directly reflects the area upon which hemlock seed rain might fall, and can also be used (with appropriate statistical caution) in evaluating whether regeneration is associated with particular CWD or other surface components. However, as we will show below, surface area may not be the most useful variable in assessing the potential future stocking of hemlock. The total number of pieces (pieces/acre), and total length of pieces (linear ft/acre) may prove more useful.

Finally, it is important to separate CWD in any inventory by stage of decay. Numerous studies have indicated that hemlock regeneration on CWD is confined to pieces in advanced stages of decay. For example, Corinth (1995) found abundant hemlock regeneration only on the two most heavily decayed classes in a 5-class system. This is not surprising, since undecayed material provides little or no rooting environment. The most appropriate scale for evaluating decay in Northeastern forests has been presented by Pyle and Brown (1998); it modifies the traditional 5-class system to account for the peculiarities of decay in some eastern species. Within that system, decay classes IV and V — primarily composed of wood with a soft, friable, or powdery surface — are most important for hemlock regeneration. Pyle and Brown (1999) discuss the heterogeneity of decay classes within pieces, and present a useful table of attributes for judging decay class. Since pieces in advanced stages of decay are less heterogenous than pieces in intermediate stages, using a single "average" decay class for a piece is not likely to pose a problem for the important decay class IV and V logs, at least in operational assessments.

While some authors (e.g. Tubbs 1995) have suggested that the species of CWD may have an influence on species composition of regeneration, those relationships remain speculative. Given the difficulty of obtaining reliable field identification of CWD to species, especially in advanced stages of decay, CWD species is probably not sufficiently important to record in any operational inventory. However, it could be valuable from a research standpoint.

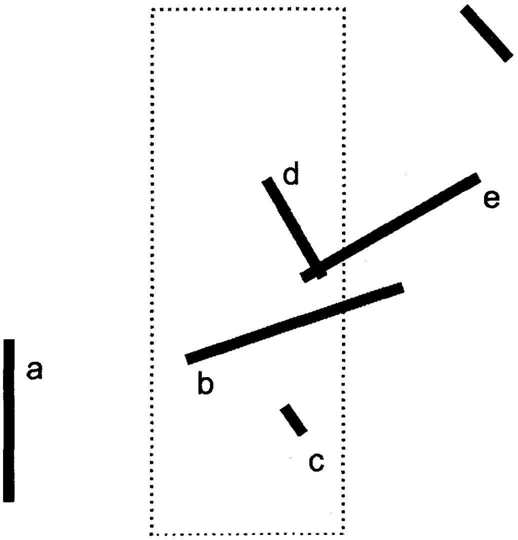

Figure 1.—Sampling CWD using a rectangular plot. Pieces *c* and *d*, which lie completely inside the plot, must be tallied; exactly how pieces such as *b* and *e* are tallied affects the bias of the method.

Methods for Sampling Downed Wood

Fixed-Area Plots

Perhaps the simplest and longest-used method for inventorying CWD is to tally pieces on fixed-area plots. Fixed-area plots are familiar to nearly all foresters and biologists through their use in vegetation assessment. A plot of known area is laid out; all the objects on the plot are tallied; their values for some variables of interest are measured; and the resulting numbers are expanded to per-acre values by multiplying by the reciprocal of plot size (Figure 1). Conceptually, three different approaches to using fixed-area plots for CWD inventory have appeared in the literature. These include:

1) Delineating the plot, then tallying all pieces which lie at least partially within the plot. The entire piece is measured to determine properties such as volume, surface area, or length per acre. Unfortunately, this method is biased; it is analogous to tallying all seedlings or understory plants which overhang the boundaries of a fixed quadrat, regardless of stem location. This approach provides an overestimate of pieces per acre and all derived quantities such as volume per acre and surface area per acre. The estimates of "per piece" quantities, such as the average volume or length of a piece, are also biased.

2) Delineating the plot, then tallying all pieces which lie at least partially within the plot. Only the portion of the piece which falls in the plot is measured to determine properties such as volume, surface area, or length per acre. This method does produce unbiased estimates of derived quantities such as volume and surface area per acre. However, estimates of the number of pieces per acre, as well as "per piece" quantities, are still biased.

3) Delineating the plot, then tallying only those pieces for which some uniquely determined point falls within the plot. The point can be any predetermined place on the log, such as the midpoint, or the location of the pith at the large end, so long as it can be readily and consistently identified in the field. Then, the entire piece is measured to estimate quantities such as volume and surface area per acre. This method provides unbiased estimates of densities, derived quantities, and "per piece" quantities.

An additional source of potential bias may arise when volumes and surface areas of irregular pieces must be measured. For relatively simple pieces, formulas such as Smalian's, Huber's, or Newton's formulas (Avery and Burkhart 1994, p. 55; Husch *et al.* 1982, pp. 99-101) for the volume of a solid of rotation may be used with little bias (Harmon and Sexton 1996). Even for pieces with moderate complexity, the bias introduced by using one of these reasonable approximations is likely to be quite small relative to the sampling error of an operational inventory. For pieces with more complex shapes, or in truly exacting research situations, more sophisticated measurement schemes such as randomized branch sampling (Gregoire *et al.* 1995) may be needed to obtain truly unbiased estimates.

Simplicity is both the greatest strength and the greatest weakness of using fixed area plots to estimate CWD abundance. The method is seemingly simple to implement in the field, but the time cost of locating the plot boundaries accurately, then scouring the area for hidden pieces of debris, can be quite time-consuming. In managed forests, a plot may contain a frustratingly large number of relatively small pieces, all of which must be measured. Once the field work is done, the calculations are relatively straightforward. When the plot itself is the population of interest, as in some research applications, interpretation of the results is easy. However, in the context of an operational inventory, where multiple plots are used to subsample a larger area of interest, the performance of fixed plots can be poor, with confidence limits remaining quite wide even after a significant investment of time and energy.

Line Intersect Sampling

Line intersect sampling is a probability-proportional-to-size technique for estimating the densities of many types of objects, but its most common use in forestry has been in the inventory of logging slash (Warren and Olson 1964), fuel loadings (Van Wagner 1968), and other coarse woody debris. Straightforward introductions to the method can be found in Brown (1974) and Shiver and Borders (1996); more detailed mathematical consideration is given in Kaiser (1983) and de Vries (1986). In practice, a series of sampling lines are laid out in the woods. Every piece which crosses a line is tallied and measured. If a piece crosses multiple lines, or crosses a single line multiple times, it is tallied multiple times (Figure 2). The resulting tally is then converted back into per-acre estimates of the required variables.

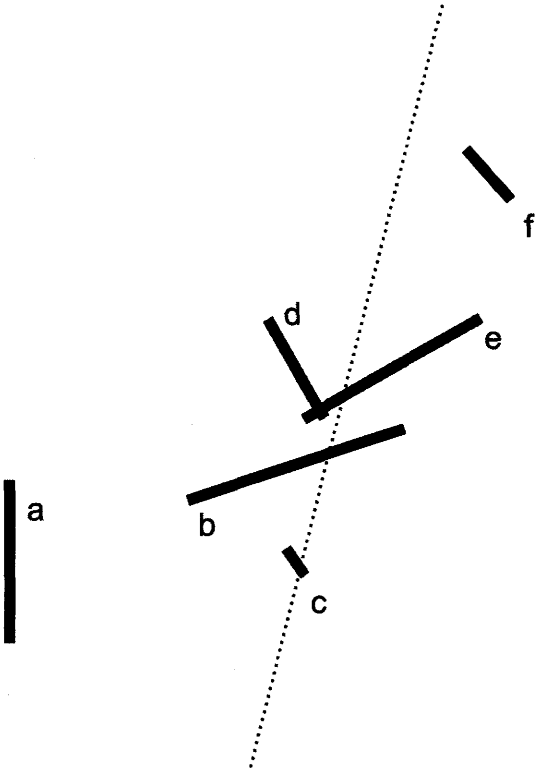

Figure 2.—Sampling CWD using line intersect sampling (LIS). Pieces *b, c,* and *e* will be tallied. Because LIS samples with probability proportional to length, piece *c* will count as more pieces per acre than either *b* or *e*.

The easiest variable to obtain using LIS is the total length (feet/acre) of pieces of CWD. Line intersect sampling selects pieces with probability proportional to length, so each tallied piece on a sampling line counts as a certain amount of length per acre. We can think of this amount of length as being a length factor, directly analogous to the basal area factor in prism cruising. The length factor of a sampling line is

$$F = 43560\pi/(2L)$$

where F is the length factor in feet per acre and L is the length of the sampling line in feet. For example, if we are using a sampling line that is 4 chains or 264 feet long, then $F=43560\pi/[(2)(264)]=259$ feet per acre. Suppose we lay out n sampling lines of equal length in a stand, and score m tallies in total. Then our estimate of the length per acre of CWD is simply mF/n. Confidence limits can be calculated using the standard error of the values calculated from the individual sampling lines, multiplied by the appropriate value of Student's t from a t-table (n-1 degrees of freedom must be used to find the value of t). The formulas to use when lines are of unequal length are detailed in Shiver and Borders (1996).

Estimates for other variables are only slightly more complicated to calculate. Suppose we are interested in some variable X for a stand, and measurement of a tallied piece for that variable is x. For example, if X were the total cubic volume per acre of CWD, then x would be the cubic volume of an individual tallied piece. The amount that the tallied piece contributes to the estimate of X is simply Fx/l, where F is the length factor as before, and l is the length of the piece in feet. To get the estimate of X that a single sampling line provides, we simply sum the values of Fx/l for all the tallies on that line. To combine estimates from multiple lines of equal length, we simply take the mean of the estimates, and confidence limits can be calculated in the usual way.

How does this translate into methods for the CWD variables in which we are interested, specifically volume per acre, surface coverage per acre, length per acre, and number of pieces per acre? For volume per acre, recall that the volume of a piece equals Al, where A is the mean cross-sectional area of the piece in ft^2. Substituting Al for x, we find that the contribution of a piece to the estimate for volume is just FA, or the length factor multiplied by its average cross-sectional area. It turns out that we can use the cross-sectional area at the point where the sampling line crosses the piece instead of A, with no bias and little loss in accuracy (de Vries 1986). So, when a sampling line crosses a piece, we simply measure the diameter of the piece at the intersection using calipers and record the measurement, convert that diameter measurement to cross-sectional area (assuming a circular cross-section; for decaying wood, using two diameter measurements and assuming an ellipse is often more appropriate), and then sum the values of FA for each sampling line. That same measurement of diameter will also give us an estimate of surface area coverage. If diameter, D, is measured in inches, then a fair estimate of the surface area of an individual piece in ft^2 is $Dl/12$. Substituting $Dl/12$ for x, we find that the contribution of a piece to the estimate for surface area coverage should be $FD/12$. If the variable in which we are interested is the length of pieces per acre, then we substitute l for x, and find that the contribution of a piece to the estimate of length is just F – which is why we can estimate length of pieces per acre directly from the number of tallies. Note that for all three of these variables – volume per acre, surface area coverage per acre, and length per acre – the measurement of l has disappeared in the formulas! That means we can estimate all three of these variables using only the number of tallies and the diameter measurements associated with each tallied piece.

Unfortunately, the situation changes slightly when we consider number of pieces per acre as the variable of interest. Here, the value of x for each piece is just 1, since each piece is a single piece of CWD. If we substitute 1 for x, we find that the contribution of a tallied piece to the estimate of pieces per acre should be F/l. This means that we must measure piece length to get estimates of number of pieces per acre in LIS. Measuring piece length is easy when pieces are approximately straight, like logs; however, when pieces form complex shapes like the tops of hardwood trees, obtaining accurate measurements of piece length can be difficult.

Under ideal conditions, LIS is very fast and efficient. Because sampling is with probability proportional to length, little time is spent performing measurements on the numerous small pieces of CWD which seem to pervade the forest floor; time is spent instead on the less frequent but typically more important large pieces. LIS as presented here does make some assumptions, however, and those assumptions must be upheld or corrections will be needed. The first assumption is that the lines are laid out from randomly or systematically located centers in random directions. If the directions of the lines are not random, then the angle of intersection of every piece with the sampling line must also be measured, and additional mathematics are required to obtain the estimates (Kaiser 1983). Second, the pieces are assumed to lie in the horizontal plane. This assumption is frequently violated by fine materials such as those within the tops of downed trees, and will also be violated by coarse material in sloping terrain. In these cases, a simple correction based on the slope of the pieces is required (Brown and Roussopoulos 1974). Harmon and Sexton (1996) note that the correction is always required for fine materials, but rarely for coarse materials; we suggest that the correction should be applied to all sizes of materials whenever the topography includes slopes greater than 30%.

Perhaps the greatest weakness of LIS is the tendency on the part of workers to underestimate the amount of sampling line that is required for good estimates (Harmon and Sexton 1996). Under typical conditions in New England, for example, dozens if not hundreds of chains of sampling line per stand are required to obtain 95% confidence limits of plus or minus 20% on the estimates of most variables. If CWD is being inventoried at the same time as the overstory, this can be accomplished by centering a sampling line perhaps 4-8 chains long on the center of every plot center (in a fixed-area plot cruise) or point (in a prism cruise). Keeping sampling lines straight and of accurate length can be problematic in stands with dense understories or well-developed shrub layers. Thus, while LIS almost certainly represents and improvement over fixed plots in operational inventories of CWD, obtaining good numbers with LIS still requires a considerable time investment.

Transect and Point Relascope Sampling

Two new methods of inventorying CWD based on using an angle gauge may provide improvements over LIS, at least in some circumstances. Transect relascope sampling, or TRS, uses an angle gauge along a line to tally pieces of debris (Ståhl 1998). Point relascope sampling, or PRS, uses the angle gauge around a point, much like prism cruising of the overstory (Gove *et al.* 1999). The term *relascope* in both methods refers to an angle gauge generally, following European usage of the word; the familiar Spiegel-relascope used for overstory sampling uses too narrow an angle to be

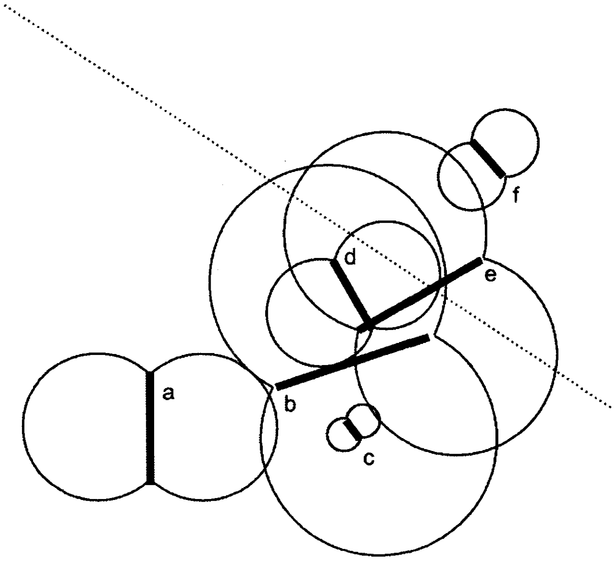

Figure 3.—Sampling pieces using transect relascope sampling (TRS). The inclusion zones are shown around each piece; the inclusion zone is the area within which the piece appears larger than the angle gauge. Pieces *b*, *d*, and *e* are tallied because the sampling line crosses their inclusion zone; the other pieces are not.

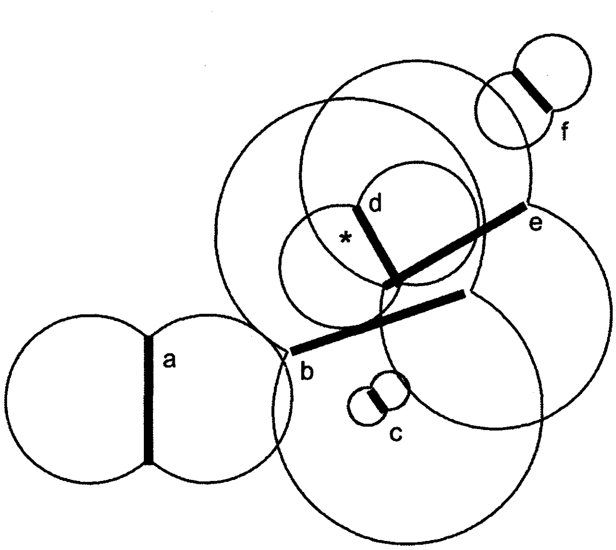

Figure 4.—Sampling pieces using point relascope sampling. The sample point (*) falls within the inclusion zones of pieces *b*, *d*, and *e*; the other pieces are not tallied.

useful for CWD. Typical gauges for TRS and PRS use angles in the range of 20 to 90 degrees.

TRS was developed in Sweden to increase the efficiency of LIS, by tallying more pieces per length of line that must be run (Ståhl 1998). In TRS, sampling lines are laid out from edge to edge in a stand, and every piece which appears larger than the angle gauge from any point on the line is tallied once (Figure 3). This means that in addition to all the pieces which cross the line, pieces which are not on the line will be tallied. However, larger pieces can lie farther from the line and still be tallied, while small pieces must lie close to the line to be tallied. We can envision the process using the concept of an inclusion zone. In prism sampling of the overstory, each tree has an "imaginary circle" located around it. If a sample point falls within the circle, that tree is tallied. In TRS, each piece of CWD has an "imaginary blob" located around it, the shape of which is determined by the angle of the angle gauge. If the gauge has an angle of 90°, the blob will be a circle centered on the midpoint of the piece (Ståhl 1997). If the sample line crosses the blob, the piece is tallied. Like LIS, TRS is sampling with probability proportional to length, so every sampling line is associated with a length factor. Details of calculating the length factor, estimates for different variables, and confidence limits are given by Ståhl (1998).

PRS uses the same sort of angle gauge as TRS, so the inclusion zone of a piece of CWD is exactly the same. However, in PRS the angle gauge is turned around a sample point, just as in prism cruising. So, just as in prism cruising, if a sample point falls within the inclusion zone of a piece, the piece is tallied (Figure 4; Gove *et al.* 1999). PRS samples CWD with probability proportional to the length squared of each piece. The angle of the gauge determines a length squared factor *G*; each tallied piece counts as *G* ft^2 of length squared. Unfortunately, length squared is not a particularly useful variable in itself, and the calculation of *G* is rather involved. Fortunately, once *G* is known, it is easy to obtain estimates of all four main CWD variables: pieces per acre, length per acre, surface area per acre, and volume per acre.

Suppose we are using an angle gauge which uses a 20" wide target held 20" from the user's eye, which is located over the sample point. Such a gauge will have a length squared factor *G* of 20694 ft^2/acre. So, every piece tallied on a point will count as 20694 ft^2/acre of length squared. Now, for every tallied piece, we could measure its length and one or more diameters to determine surface area and volume, just as we would in sampling on a fixed area plot. If we tallied a piece that were 20 ft long, its length squared would be 400 ft^2. That piece would count as 20694/400, or 51.7, toward the estimate of pieces per acre for that point. If the surface area coverage of the piece were 25 ft^2, the piece would count as 51.7´25, or 1293 ft^2/acre, toward the estimate of surface area coverage for that point. If the piece contained 30 ft^3 of volume, then the piece would count as 51.7´30, or 1551 ft^3/acre, toward the estimate of volume per acre for that point. The estimate of any variable for each point is calculated as the sum of the contributions of each of the pieces tallied on the point. Just as in prism cruising, the best estimate of each variable for the stand is simply the mean of the individual point estimates, and calculation of confidence limits is straightforward.

TRS and PRS are new techniques, and their efficiency relative to LIS has not been firmly established. Both simulations (Ståhl 1998) and field studies (Ringvall and Ståhl 1999) suggest that TRS is significantly more efficient, in terms of the relationship of time spent to the width of confidence limits, than LIS. Likewise, early tests of PRS in a variety of stand structures in Maine suggest that PRS is quite competitive with LIS (Brissette *et al.* 1999). PRS has the further advantage of being centered on a sample point, making it complementary to typical strategies for overstory measurements, and therefore easy to combine with them (Gove *et al.* 1999). While these results are promising, further field comparisons would be invaluable in help practitioners choose between methods confidently.

As with the other methods, both TRS and PRS make certain assumptions which must be satisfied or corrected. Like LIS, TRS typically assumes the orientation of the sample lines is random. This assumption is not required for PRS, because the sample unit for PRS (a point) is nondirectional. TRS and PRS also assume that CWD is composed of simple shapes, such as straight logs. If this assumption is violated, additional measurements on each piece may be needed (Gove *et al.* in review). Finally, slope compensation in TRS is somewhat complex, although relatively simple field techniques may alleviate the problem (Ståhl *et al.* in review).

How Much Downed Wood is Enough?

We can quantify the amount of CWD in a stand, but how do measured levels relate to levels we might desire for management? In many ways, this question parallels the traditional distinction between density and stocking as those terms apply to the overstory: density is a quantitative measure of abundance, but stocking is a measure relative to goals and objectives for the stand. As Hagan and Grove (1999) point out, most ecological discussions assume that the more CWD, the better, with some exceptions when fire or other unwanted disturbances are at issue. While many studies have focused on CWD levels in old-growth stands, old-growth levels of CWD should not be considered realistic or normative in younger, managed stands, particularly those in post-agricultural landscapes where few legacies remain from previous rotations. We should expect desired levels of CWD to vary depending on management objectives, much as the desired stocking of the overstory depends on silvicultural objectives. Here, we step through a conceptual pathway based on hemlock regeneration, and develop a preliminary set of guidelines for CWD abundance.

Picture a downed log or similar piece of CWD, well-decayed, and providing a good substrate for hemlock germination and growth. The volume or biomass of that log may be useful for understanding carbon or nutrient cycling, and a log with large volume may be more valuable for hemlock regeneration, but the relationship of volume to regeneration potential is rather indirect. A more direct relationship exists with the surface area of the log. If viable hemlock seeds fall at a certain density in seeds per ft^2, the larger the log, the more seeds it will receive. However, the number of germinants is not really critical, so long as there are enough of them to fully occupy the log in some sense. Just as small plots are usually counted as adequately stocked or unstocked when the substrate is the 2-dimensional ground surface, it is the presence or absence of stocking on segments of the log that are important for the subsequent dynamics of hemlock regeneration. Since hemlock is a prolific seeder (Godman and Mattson 1976), if germination conditions are right, and if neither browse pressure nor competition with other shade-tolerants in the overstory are heavy, it is reasonable to assume that a good substrate will eventually be well-occupied by small hemlocks.

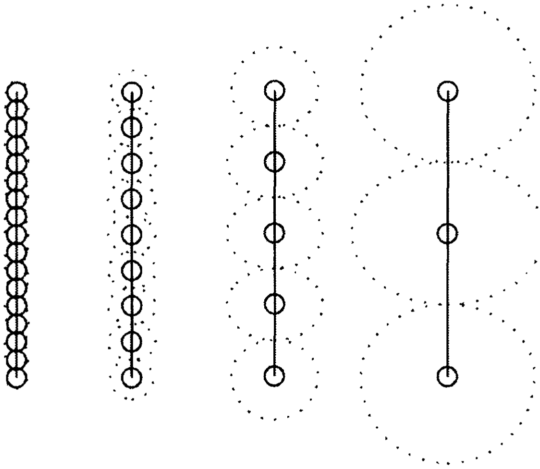

Figure 5.—Conceptual diagram of a cohort of hemlocks self-thinning along a piece, starting from seedlings or saplings on the left and moving toward large trees on the right.

Now, consider how a cohort of small hemlocks would grow and develop along a linear feature such as a downed log (Figure 5). Two things are readily apparent as we move across the figure. First, as the trees grow, their numbers must decline through the usual process of self-thinning, though competition is along a line and not through space. Second, despite the decline in numbers, the amount of crown area occupied by the cohort increases as tree size increases. Therefore, a given log can support a greater crown area of hemlocks as the hemlock cohort grows and develops. This amount depends on how tightly packed the crowns can be; if the crowns can form elliptical rather than circular shapes, more crown area can be supported. The amount of crown area also depends on the length of the log, since the hemlocks at the ends are always free to grow on one side.

If the mean crown area of a hemlock in ft^2 is C, then the amount of crown area that a single log of length l can support is about $C + l\,\text{sqrt}(C)$. That simple formula assumes that the ratio of the short axis through a hemlock crown to the long axis is p/4, or about 78%, which is not unusual for hemlock crown data. How much CWD is required to fill an acre with hemlock crowns? The answer to that question is the formula

$$l_{total} = -\text{sqrt}(C) \times m + 43560/\text{sqrt}(C)$$

where l_{total} is the total length of CWD in feet/acre, and m is the number of pieces per acre. Both are variables which can

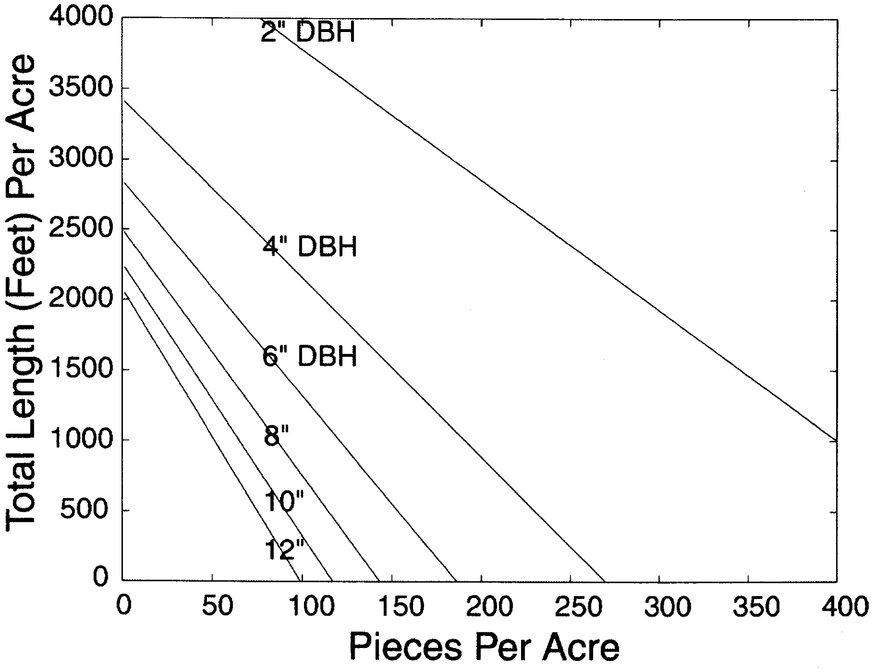

Figure 6.—A preliminary stocking diagram for coarse woody debris, based on the potential for hemlock regeneration. The number per acre and total length per acre of pieces of well-decayed (class IV or V) CWD are used to locate a stand on the diagram; the lines indicate the DBH at which a regenerating cohort of hemlock would be expected to form a closed canopy stratum.

be estimated easily using any of the four sampling methods discussed above. We see that the required amount of total length is a linear function of the number of pieces, with the slope and intercept depending on the mean crown area *C*.

To translate that linear function into stocking guidance for CWD, it is useful to relate *C* back to a more easily measured and visualized number, specifically the DBH of hemlock trees. Based on 24 hemlocks growing in Durham, NH under ordinary conditions, spanning a range of 0.3 to 31.6" DBH, the estimated relationship is

$$\ln(C) = 3.8171 + 0.9136\times\ln(\mathrm{dbh})$$

where ln is the natural logarithm. Using this equation, we can construct a stocking guide which answers the following questions:

1) In a stand with a certain number of pieces per acre and total length per acre of CWD, if that CWD were well stocked with hemlocks, at what DBH would that hemlock cohort form a closed canopy stratum?

2) If a silvicultural goal is to achieve a closed canopy hemlock stratum at a target DBH, how much well-decayed CWD (expressed in possible combinations of number of pieces and total length of pieces) would be required as seedbed?

3) If a silvicultural goal is to achieve a hemlock stratum with some specified percent closure at a target DBH, how much well-decayed CWD (expressed in possible combinations of number of pieces and total length of pieces) would be required as seedbed?

The stocking guide is presented in Figure 6.

As an example of answering the first question, suppose we had performed an inventory of a stand, and found that we had 100 pieces per acre of well-decayed class IV or V CWD, with a total length of 1500 feet/acre. At what DBH would a new cohort of hemlocks be expected to form a closed canopy? Locating the point on the chart corresponding to our data, we find that the stand is just above the 6" DBH line, and well below the 4" DBH line. We would conclude that we have adequate seedbed to form a closed stratum when the hemlocks reach 5.5" DBH.

As an example of answering the second question, suppose we would like to form a closed stratum when the hemlocks reach 8" DBH, to provide initial training trees for a cohort of red oaks, and then provide winter deer yarding habitat late in the rotation. However, an inventory shows our stand has only 50 pieces per acre of well-decayed CWD, totaling only 500 feet/acre in length. It is clear that we do not have enough CWD as seedbed, since our stand is well below the 8" DBH line. If there is enough relatively undecayed (classes I-III) CWD, we may not need to intervene, since our seedbed is already "in the pipeline." However, if not, we might consider inexpensive silvicultural means of creating CWD, such as reducing the utilization of cull trees and tops in a coming thinning.

As an example of answering the final question, suppose instead that we only wish to form a stratum with 60% closure at 12" DBH in the same stand. To answer this question, we must divide our inventory data by 60% or 0.6. So, in the stand above, we would use the values 50/0.6=83 pieces per acre, and 500/0.6=833 pieces per acre. These numbers place our stand above the 12" DBH line, so we conclude that enough seedbed is in place. We can now concentrate on other factors inhibiting hemlock regeneration, such as browsing.

Conclusions

Coarse woody debris is not the best seedbed for eastern hemlock, but it is practically free and easy to manage. Thus, it provides a ready source of seedbed in areas where regenerating hemlock is a silvicultural goal. Continuing improvements in inventory methods for CWD make it possible to obtain estimates of CWD abundance in a reasonable time frame, but it is not always easy to say how much CWD is needed in a stand. In the case of hemlock regeneration, simple geometric assumptions can be translated into a CWD stocking guide which relates the number of pieces and total length per acre of CWD into expected dynamics of a regenerating hemlock cohort. Though rough and preliminary, guidelines such as these should provide reassurance to foresters when their stands are "on track". We stress, however, that guidelines such as these remain largely conceptual; more empirical data would be invaluable in refining them and allowing greater confidence in their use.

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Growth and Stocking of Eastern Hemlock (*Tsuga canadensis*) in New England

Dale S. Solomon and William B. Leak[1]

Abstract

Summarization of the limited growth information in mixed-species stands in New England indicates that eastern hemlock (*Tsuga canadensis*) may be one of the fastest growing species in diameter, second only to white pine. However, on some sites hemlock diameter growth is about equal to that of associated hardwoods. Hemlock grows slowly in height and often endures long periods of suppression, which limits the usefulness of site index curves. Suppressed trees, once released, may grow relatively faster than non-suppressed trees. Hemlock stands attain high basal areas per acre, up to 240 square feet per acre, and recommended residual basal areas after thinning range from 100 to 140 square feet. Volumes may be as high as 4,500 cubic feet in 100-year-old stands, much higher than hardwood stands; however, both hemlock and hardwoods attain similar aboveground dry weights of about 85 tons per acre.

Introduction

Because of eastern hemlock's (*Tsuga canadensis*) moderate timber values, limited research has been conducted on growth and yield of the species, usually as a component of forest stands dominated by more valuable species. Hemlock, while considered a climax species, has both early- and late-successional species characteristics. Lorimer (1995) discussed stand structure of hemlock in association with both northern hardwood and northern conifer stands in the Lake States, indicating that seedling establishment can occur in open areas as well as under a closed canopy. Preferring moist sites, hemlock seedlings establish best in old growth stands and respond similar to shade tolerant species after disturbance in mature stands (Foster 1988). Hemlock averages 5-15 percent in northern hardwood stands and up to 40-60 percent in northern conifer stands (Solomon 1977, Solomon and Frank 1983). Information is available on diameter and height growth of individual trees, as well as basal area, volume growth, and stocking characteristics of stands with hemlock as a significant component. We'll present this information in summary form. Details on study methods and analytical procedures may be found in the cited literature.

Diameter Growth

In the beech-red maple ecological type in New Hampshire, hemlock grows about ¼ inch per year at the lower stand densities of 40-60 square feet per acre (Table 1) and about 1/5 to 1/6 inch per year at densities of 80 to 100 square feet (Solomon 1977). These growth rates are about double the rate of associated hardwoods such as red maple, and 50-100 percent faster than hemlock, spruce, or hardwoods in the hemlock-red spruce ecological type at the Penobscot Experimental Forest in Bradley, Maine (Solomon and Frank 1983). However, the hardwoods in the two areas are growing at similar rates. Possibly, the faster growth rates of hemlock in New Hampshire are due to the different soil/site conditions – well drained, sandy tills in New Hampshire as compared to the somewhat poorly drained soils at the Penobscot. Hemlock in northern hardwood stands is more open and free to grow while more apt to be suppressed in northern conifer stands. Hemlock is well known for its ability to endure long periods of suppression as evidenced by the occurrence of many small annual rings at the center of some trees. These diameter growth rates are comparable to a study at Harvard Forest that showed hemlock when suppressed for periods up to 40 years (and probably longer) and then released made relatively faster diameter growth than unsuppressed trees, and eventually surpassed the unsuppressed stems (Fig. 1) (Marshall 1927).

Regional level Forest Inventory and Analysis (FIA) plots indicate that basal area growth on individual hemlock trees in New England was faster than that of all other species except white pine (Fig. 2), and hemlock increased from 8-10 cm^2 in basal area growth over time from 1950 to 1980 (Hornbeck et al 1988). A larger increase in basal area growth across diameter classes was found on the Bartlett Forest during the period from 1920 to 1980 (Leak 1987a). FIA basal area growth figures for individual states also show an increase from 3-12 cm^2 in all six New England states from 1900 to 1980 (Smith et al 1990). Differences among states were somewhat inconsistent; however, in the last few decades, hemlock growth rates averaged 12 cm^2 in Maine and 9 cm^2 in New Hampshire.

Stand Growth and Stocking

Growth in basal area of spruce-fir-hemlock stands in Maine containing 22 to 55 percent hemlock does not vary greatly among residual density levels (Table 2) partly due to high levels of ingrowth at lower densities (Solomon and Frank 1983). However, survivor growth increases with increasing residual basal area, indicating that softwoods grow better and occupy a site more fully at high stand densities. Hardwood-hemlock stands in New Hampshire contain 6-12 percent hemlock (Solomon 1977). Net growth decreases with increases in residual basal area due to greater mortality, while survivor growth remains somewhat constant. Stocking guides for softwood and mixedwood stands confirm these growth relationships by placing the B-line (suggested residual density after thinning) at about 100-140 square feet of basal area per acre and 90-110 square feet, respectively (Solomon et al 1995, Fig. 3). Maximum average basal areas (A-line) reach 240 to 180 square feet for softwood and mixedwood stands, respectively. These high stocking levels are similar to those found in old-growth softwood/mixedwood stands (Leak 1987b, Table 3).

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Table 1.—Annual diameter growth of hemlock in hemlock-spruce-fir (Penobscot Experimental Forest, ME) and in beech-red maple (Bartlett Experimental Forest, NH) stands related to residual stand density. Ranges of growth are shown (in parentheses) among three cutting cycles (Penobscot) or for three levels of percent sawtimber classes (Bartlett) (Solomon and Frank 1983, Solomon 1977).

	Beech-red maple		Hemlock-spruce-fir		
Density	Hemlock	Red Maple	Hemlock	Spruces	Hardwoods
(ft^2/acre)			*(inches)*		
40	.29 (.23-.35)	.18 (.17-.19)	.14 (.09-.20)	.15 (.12-.19)	.17 (.16-.17)
60	.24 (.23-.24)	.14 (.12-.16)	.14 (.12-.16)	.12 (.11-.13)	.12 (.12-.13)
80	.19 (.18-.20)	.10 (.09-.11)	.13 (.12-.14)	.12 (.11-.13)	.12 (.11-.12)
100	.16 (.14-.19)	.07 (.07-.08)	.12 (.11-.13)	.11 (.11-.11)	.11 (.10-.11)
120	—	—	.10 (.09-.11)	.10 (.09-.11)	.11 (.09-.13)

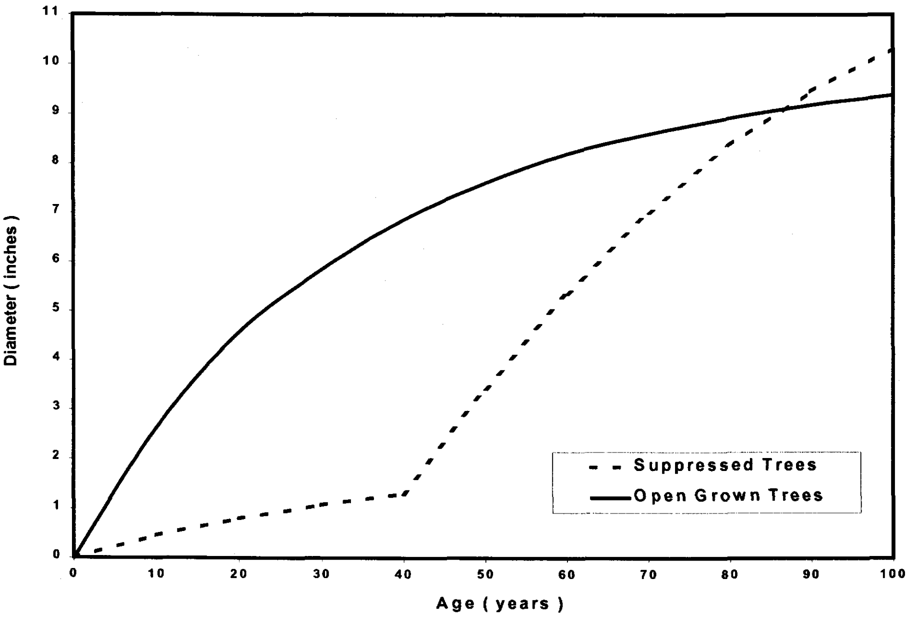

Figure 1.—The average diameter growth of unsuppressed hemlock trees contrasted with trees which were suppressed for 40 years, then released (adapted from Figure 8, Marshall 1927).

Resource managers frequently utilize forest tree models to simulate hemlock's growth and dynamics for different ecological habitats. Hemlock as a component of forest species composition is an essential part of both timber and wildlife management. The forest model FIBER (Solomon et al 1995) provides a reliable basis for simulating hemlock growth and development in both the beech-red maple and hemlock-red spruce ecological habitats (Figs. 4 and 5). A comparison of the measured and predicted basal area growth for softwood and hardwood stands indicate that hemlock development can be modeled through time.

FIA statistics, at a landscape level, indicate that hemlock growth percent based on cubic feet (gross growth minus mortality as a percent of initial volume) ranges from 1.1 percent in New Hampshire to 2.3 percent in Maine (Frieswyk

Table 2.—Net and survivor basal area and estimated volume growth (basal area X 25 ft^3 per acre) by residual basal area for hemlock-spruce-fir stands in Maine contain 22-56 percent hemlock (Solomon and Frank 1983) and northern hardwood stands in New Hampshire contain 6-12 percent hemlock (Solomon 1977).

	Hemlock-spruce fir				Northern hardwoods			
Basal area	Net growth		Survivor growth		Net growth		Survivor growth	
(ft^2/acre)	*(ft^2/acre)*	*(ft^3/acre)*	*(ft^2/acre)*	*(ft^3/acre)*	*(ft^2/acre)*	*(ft^3/acre)*	*(ft^2/acre)*	*(ft^3/acre)*
40	2.66 (1.96-2.86)	66.5	1.98 (1.64-2.19)	49.5	2.02 (1.84-2.22)	50.5	1.82 (1.78-1.90)	45.6
60	2.65 (2.54-2.74)	66.2	2.20 (2.14-2.31)	55.0	2.00 (1.71-2.29)	50.1	1.86 (1.76-1.92)	46.5
80	2.50 (2.38-2.61)	62.5	2.42 (2.36-2.49)	60.5	1.50 (1.15-1.69)	37.6	1.80 (1.62-1.95)	44.9
100	2.62 (2.58-2.70)	65.5	2.56 (2.53-2.59)	64.0	1.29 (0.91-1.74)	32.2	1.85 (1.69-2.02)	46.3
120	2.55 (2.32-2.71)	63.8	2.67 (2.48-2.81)	66.8	—	—	—	—

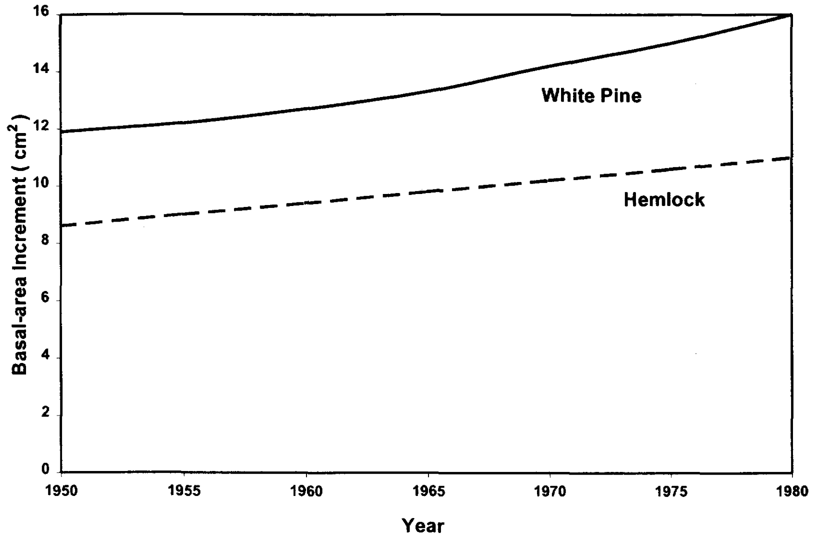

Figure 2.—Regional growth curves for major species in New England forests (adapted from Figure 1, Hornbeck et al 1988).

and Malley 1985, Griffith and Alerich 1996), considerably lower than growth percents of 3 or more commonly attained by white pine (Leak et al 1995). Cubic volumes per acre may reach 3500-4500 cubic feet per acre in 100-year-old mixedwood and softwood stands, considerably higher than volumes in most hardwood stands (Leak 1983, Fig. 6). Except for the poorly drained and enriched sites, biomass per acre appears very similar in both hardwoods and softwoods (Leak 1983, Fig. 7).

Height Growth

Hemlock height growth is relatively slow compared to most other species (Kelty 1986, Hibbs 1982, Fig. 8). Although there are site index curves for hemlock (Carmean et al 1989, Fig. 9), it is difficult to measure site index of this species since many trees are suppressed due to slow height growth. Studies of hemlock suppression demonstrate the ability of hemlock to survive under dense forest stand conditions and respond to release (Fig. 10) (Marshall 1927).

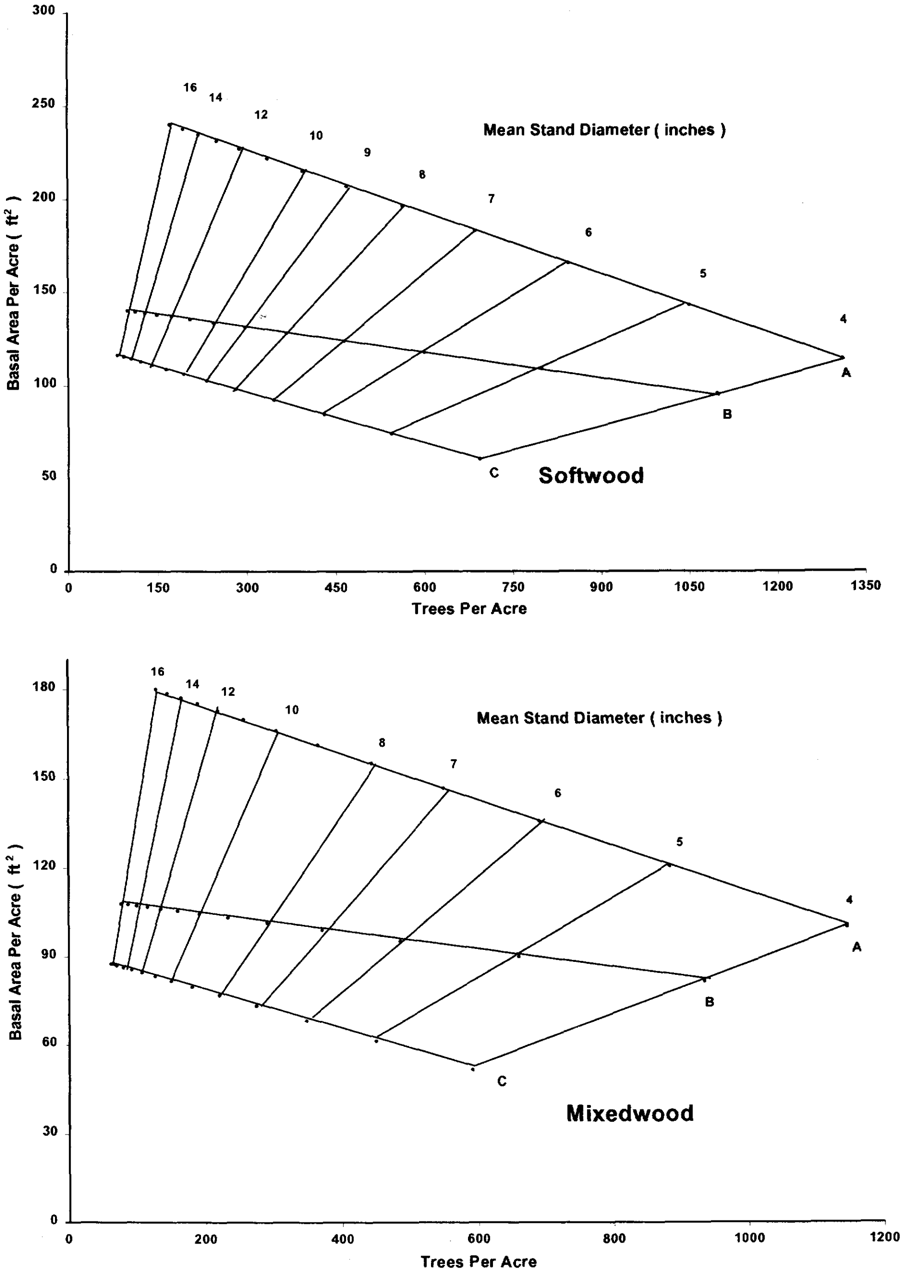

Figure 3a and b.—Stocking charts for softwood and mixedwood stands based on trees in the main crown canopy. The A line is average maximum stocking. The B line is recommended minimum stocking for adequate growth response per acre. The C line defines the minimum amount of acceptable growing stock for a manageable stand (adapted from Figures 3 and 4, Solomon et al 1995).

Table 3.—Basal area per acre by size class and percent hemlock, hardwood, and spruce for two old-growth hemlock/hardwood stands on the Bartlett Experimental Forest, NH (Leak 1987b).

	Diameter Class						Stand Composition		
Area	2-4	6-10	12-14	16-24	26+	All	Hemlock	Hardwood	Spruce
	ft²						*(%)*		
Bartlett Ridge	13.9	55.0	45.0	68.9	3.3	186.7	60	24	16
Bartlett 19	17.1	77.1	51.4	83.6	3.6	232.8	60	28	11

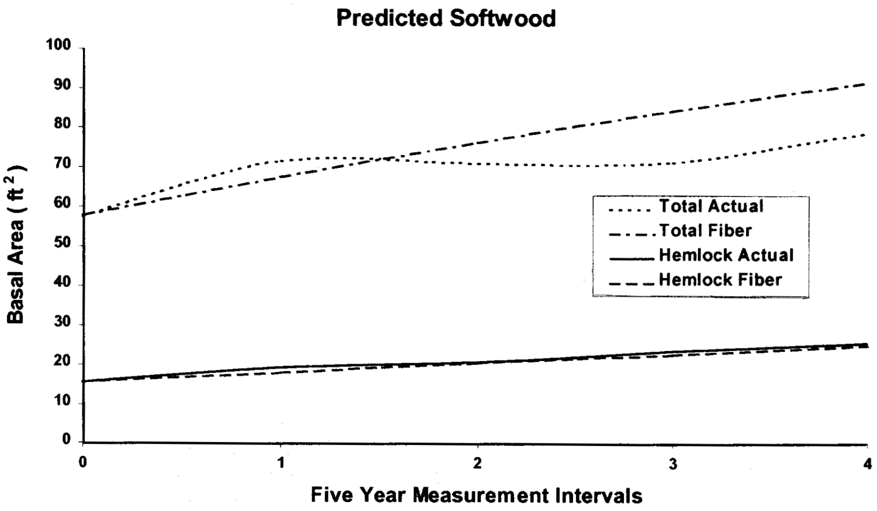

Figure 4.—Measured and FIBER (Solomon et al 1995) predicted softwood stand and hemlock basal area on Plot 32 Compartment 27 of the Penobscot Experimental Forest, Bradley, ME.

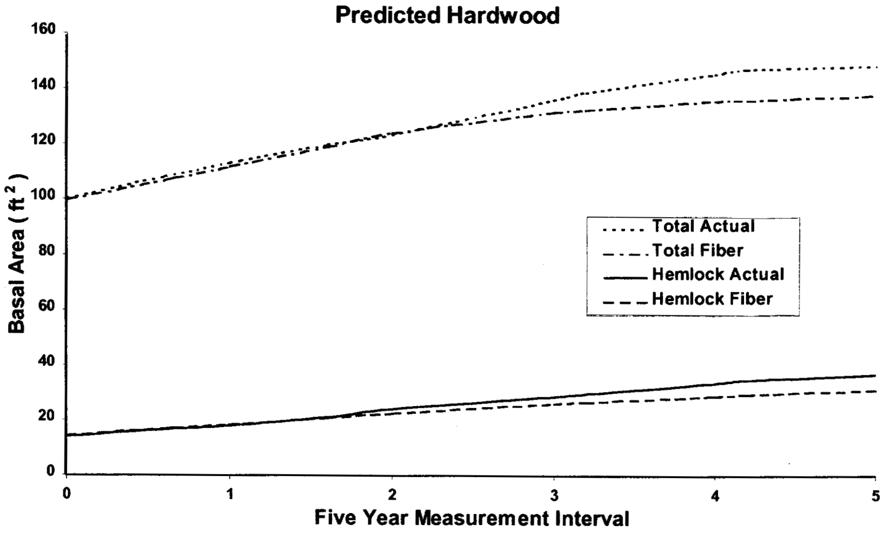

Figure 5.—Measured and FIBER (Solomon et al 1995) predicted hardwood stand and hemlock basal area on Plot 35 of the Bartlett Experimental Forest, NH Density Study.

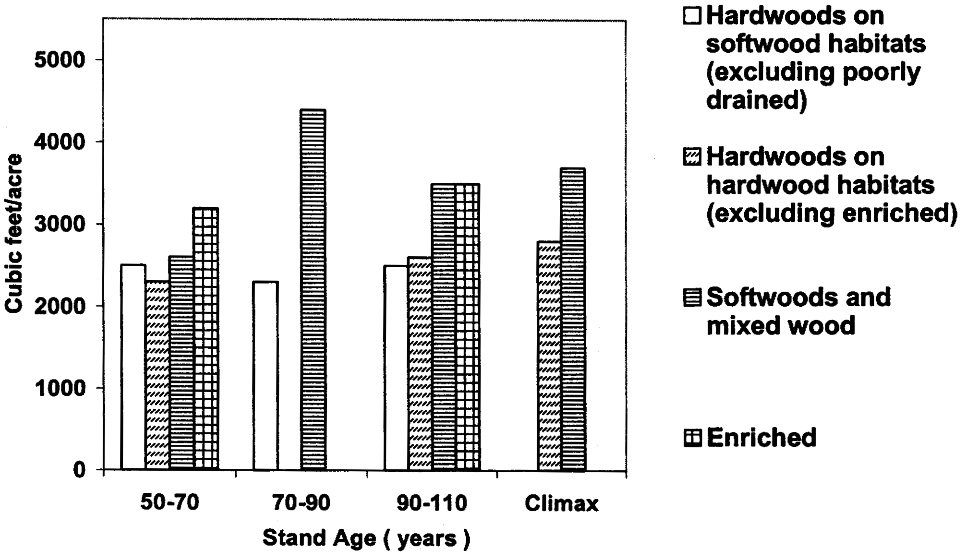

Figure 6.—Average cubic-foot volume per acre by forest habitat groups and stand age (adapted from Figure 13, Leak1983).

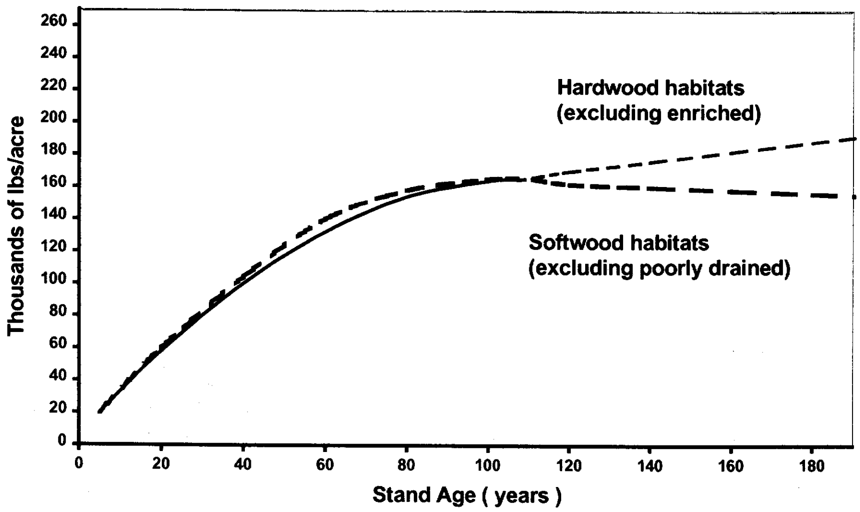

Figure 7.—Aboveground biomass (stems and branches) in dry weight over stand age by forest habitat groups (adapted from Figure 12, Leak 1983).

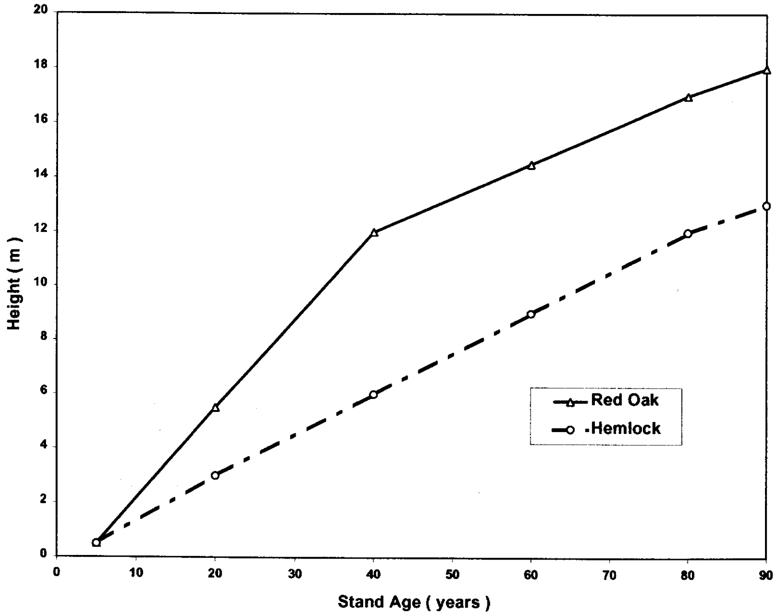

Figure 8.—Average cumulative height growth of Eastern hemlock (adapted from Figure 4a, Kelty 1986).

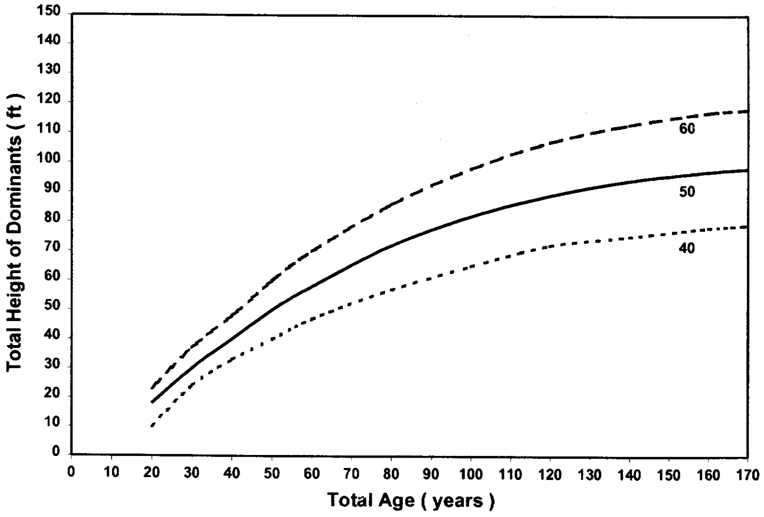

Figure 9.—Site index curves for Eastern hemlock (adapted from Figure 127, Carmean et al 1989).

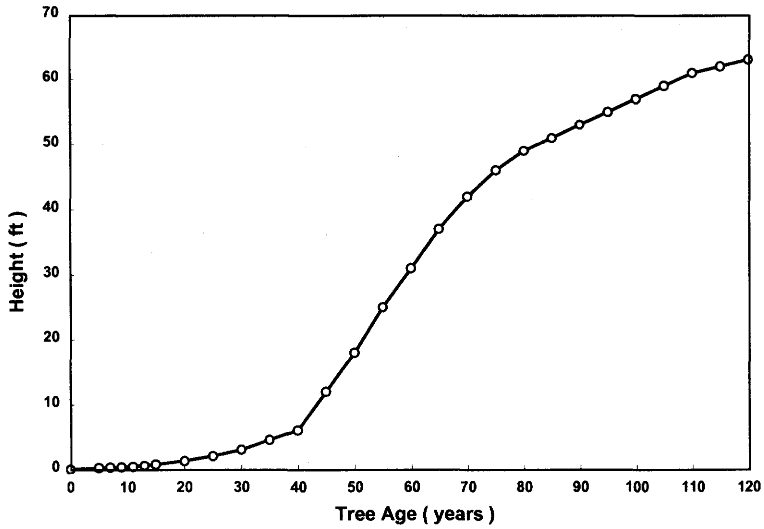

Figure 10.—Hemlock height growth after 40 years of suppression and then released.

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Dynamics of Connecticut Hemlock Stands

Jeffrey S. Ward[1] *and David M. Smith*[2]

Abstract

The stand dynamics and production of two one-acre plots of eastern hemlock (*Tsuga canadensis* L) in Connecticut have been followed for more than six decades. Data were recorded for all individual trees. One plot (Saltonstall) was established in 1924 after the removal of a hardwood overstory. This stand had a nearly pure, almost fully closed understory of hemlock that was subjected to partial cuttings in 1936, 1954, and 1956. The stand was lost to the hemlock woolly adelgid (*Adelges tsugae*) in 1993. The other plot (Perry) was established in 1931 in a nearly pure hemlock stand that had arisen on an abandoned pasture around 1850. This plot had a crop-tree release cutting in 1931 and has not been infested with hemlock woolly adelgid.

Both plots developed a rotated sigmoid diameter distribution, characteristic of uneven-aged forests, after sixty years of management. The 1936 attempt at group-selection cutting in the Saltonstall plot did not maintain the reverse J-shaped diameter distribution that had initially existed. The stand was essentially even-aged and the diameter distribution shifted to a broad bell-shaped form and then to a rotated sigmoid curve when a new age class grew large enough to be included in the tally. The thinning of the Perry plot also turned the initial bell-shaped diameter-distribution curve to the rotated sigmoid form for the same reason. Annual periodic increment (including harvested volumes) was 52 and 50 cubic feet/acre for the Saltonstall and Perry plot, respectively. Annual basal area growth decreased from over 3 ft^2/acre to approximately 2 ft^2/acre on both plots over sixty years. These findings indicate that hemlock is capable of rapid growth with stand management. Implications for managing hemlock forests are discussed.

Introduction

Eastern hemlock is an important component of northeastern and Appalachian forests, often forming nearly pure stands. Although hemlock can be found from ridgetops to swamps, best development in southern New England is on moist, fertile soils with a northern aspect. The dense evergreen cover provided by hemlock is a critical habitat for many species, and is fully as important as wood production.

Hemlock woolly adelgid was first reported in Virginia in 1951, in Connecticut in 1985 and has since spread to at least eleven states (McClure[3], pers. comm.). The unique ecological and esthetic values provided by hemlock stands are lost when these stands are replaced by hardwoods such as red maple and yellow birch. Once an effective biological control for hemlock woolly adelgid is realized, it will be feasible to reestablish hemlock in critical habitats. Thinning stands to accelerate growth should decrease the time required to achieve stand characteristics (biomass, coarse woody debris, canopy cover, etc.) typical of mature stands. This paper will summarize the effects of two long-term thinning studies in nearly pure hemlock stands on biological (diameter and species distribution, basal area) and economic (commercial volumes) attributes.

Study Plots

Detailed records of more than sixty years of development and production by nearly pure stands of eastern hemlock are available from two rather different plots in Connecticut. Stand ages were determined from increment cores. Cubic-foot volumes (Scott 1981) were determined using minimum top diameters (outside bark) of 4 inches. Board-foot volumes (Scott 1981) were determined using minimum top diameters (outside bark) of 7 and 9 inches for conifers and hardwoods, respectively.

Perry

The older of the two stands was the Perry plot (one acre) established in Tunxis State Forest in East Hartland, Connecticut in 1931. The stand appears to have arisen on a pasture during the 1850s and browsing by sheep or cattle had greatly reduced the hardwood species. In 1931 the stand was predominantly hemlock (74% of basal area) with minor components of maple (15%), birch (9%), and northern red oak (1%). The site is located on a very rocky loam soil, a Lithic Dystrochrepts of the Holyoke series on a gentle to moderate slope.

In 1931, at an estimated age of 81 years, a crop-tree release thinning was done to enhance the growth of residual hemlocks. Selection criteria for crop-trees were not stringent, "the best trees, which promised to make the final crop." Crop-trees trees were banded with blue paint at dbh (4.5 ft). Diameters at were recorded to the nearest 0.1 in and heights were recorded to the nearest 1 ft for all crop-trees. All other trees > 0.5 in dbh were tallied by species in 1 inch classes. Trees that were cut to release crop-trees were also tallied by species and 1 inch classes. The thinning removed 40 ft^2/ac and left a residual stand with 143 ft^2/ac. Measurements were repeated in 1935.

The plot was reestablished in 1994. Original plot corners (iron pipes) were relocated and crop trees were identified by faint paint bands. All trees (> 4 inch dbh) were numbered, mapped. Diameters were measured in 1994 and 1998. Tree heights were measured in 1996 along with sawlog and pulpwood heights. Although the plot was thinned for

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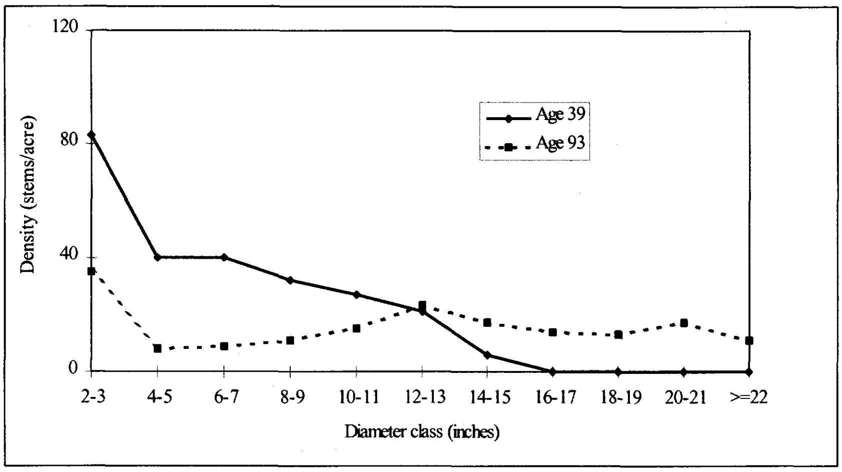

Figure 1.—Diameter distribution of trees Saltonstall hemlock plot in East Haven, Connecticut in 1939 (stand age 59) and 1993 (stand age 113).

fuelwood between 1975-1990 by removing some poles and culls, exact tallies have been lost. Therefore, estimates of volume removed during this period was accomplished by measuring stumps.

Saltonstall

The second plot, Saltonstall, was established in 1924 on an acre of hemlock forest in East Haven, CT. Every tree was numbered and measurements of total height and diameter were recorded. Subsequent measurements were made at intervals of 2-13 years. Hardwoods were not tallied until 1939. The hemlock had been the understory of a stratified mixture that had started from advanced regeneration left by a complete cutting about 1880. Chestnut was killed by the blight in 1913 and virtually all the oak and other hardwoods were harvested in 1923. The stand was on a steep slope below a basalt ridge on a mesic sandy loam soil, a Lithic Dystrochrept of the Holyoke series. During the post-World War I housing boom the prices of hemlock construction lumber had become high. That, and the good volume growth of hemlock, made the conversion to a hemlock monoculture seem desirable. There was also the purpose of testing the view that the previously suppressed hemlock would not die of exposure, but respond vigorously and promptly.

Results and Discussion

Diameter distribution

During the 1930s the concept of the all-aged selection forest was fashionable. Many of its advocates claimed that tree diameter was an effective operational surrogate for age (Meyer 1952). This theory stated that reverse J-shaped distribution curves defined the stand dynamics of a functionally all-aged condition and could be used to guide the management of such stands. Therefore, if one periodically removed trees above some guiding diameter limit and thinned the smaller ones in patterns that preserved the reverse J-shaped curve, subsequent diameter growth would maintain this diameter distribution permanently. It was assumed that large numbers of new seedlings would automatically start after each cutting, grow up to breast height and continually provide the large numbers of saplings needed in smallest DBH classes.

In 1936, the late R.C. Hawley instituted a test of the idea of treating the Saltonstall stand as if it were all-aged because it had a reverse J-shaped curve (Fig. 1). To this end, a group-selection cutting was made in 1936. In this case, none of the postulated developments took place. The small trees, which were supposed to grow fast, died of suppression in large numbers and the larger trees grew rapidly. Enough new hardwoods had developed by the time of the final 1993 measurement that the diameter distribution curve began to shift to the form of the rotated sigmoid curve (Fig. 1).

The Perry plot was initially managed under an even-aged system. Crop-trees were selected in 1931 with a view to maximize growth of existing trees with no provision for regeneration. Perry had a normal diameter distribution typical of even-aged stands in 1931 (Fig. 2). Although unintended, regeneration quickly established in the openings created by thinning, and grew into the smaller diameter classes. The influx of trees in the smaller diameter classes and growth of trees into the largest diameter classes shifted the diameter distribution of the Perry plot towards a rotated sigmoid curve by 1995 (Fig. 2).

Results of this study suggest that a rotated sigmoid curve will develop in partially cut hemlock stands regardless of the initial diameter distribution. Thinning encouraged the development of a rotated sigmoid through two mechanisms. First, thinning created openings where regeneration established and developed. This increased the density of small diameter trees. Second, released hemlocks grew faster in diameter in response to thinning and suppressed growth of other trees. This increased the density of larger diameter, and depressed the density of mid-diameter trees.

Species composition

Some regeneration, mostly of black birch (*Betula lenta*) and red maple (*Acer rubrum*), appeared in the group openings

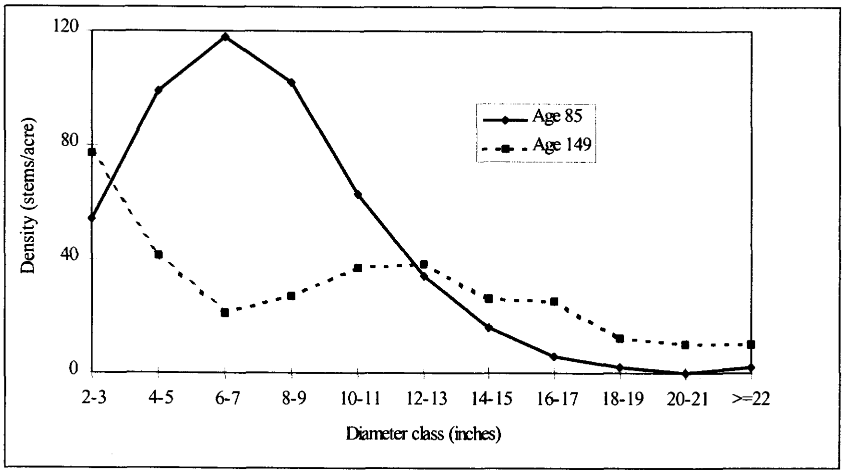

Figure 2.—Diameter distribution of trees in Perry hemlock plot in East Hartland, Connecticut in 1931 (stand age 85) and 1995 (stand age 149).

Table 1.—Species distribution on Saltonstall plot in 1939 (stand age 59) and 1993 (stand age 113) by diameter class (inches). HEM-eastern hemlock, BIR-birch, MAP-maple, OTH-other species.

1939 density (stems/acre)						1993 density (stems/acre)					
Dbh	HEM	BIR	MAP	OTH	Tot	Dbh	HEM	BIR	MAP	OTH	Tot
2-3	29	25	11	18	83	2-3	3	9	3	20	35
4-5	31	3	4	2	40	4-5	1	2	2	3	8
6-7	40	0	0	0	40	6-7	4	3	0	2	9
8-9	32	0	0	0	32	8-9	4	7	0	0	11
10-11	27	0	0	0	27	10-11	5	8	2	0	15
12-13	21	0	0	0	21	12-13	9	10	0	4	23
14-15	6	0	0	0	6	14-15	12	2	1	2	17
16-18	0	0	0	0	0	16-18	11	2	0	1	14
18-19	0	0	0	0	0	18-19	11	0	0	2	13
20-21	0	0	0	0	0	20-21	17	0	0	0	17
>=22	0	0	0	0	0	>=22	11	0	0	0	11
Total	186	28	15	20	249	Total	88	43	8	34	173

on the Saltonstall plot, but only in rather small numbers (Table 1). Those few that began to grow well in height were often bent over and permanently deformed by wet snow sliding off the crowns of the surrounding evergreen hemlocks. There was a small amount of damage to the stand by the 1938 hurricane. The low density of hemlock regeneration prior to the arrival of adelgid is probably due to a very high deer population (~120 deer/mile^2) around Lake Saltonstall. Beech (*Fagus americana*) was the most numerous species in the 2-3 inch diameter class in 1993 and should form part of the future upper canopy.

Unlike the Saltonstall plot, hemlock was the major component of the smaller diameter classes on the Perry plot (Table 2). Density of hemlocks in the 2-3 inch diameter class nearly doubled between 1931 through 1995. The higher hemlock regeneration density relative to Saltonstall is likely due to deer hunting on state forests. As at Saltonstall, black birch, red maple, and beech also colonized the openings created by thinning.

Curiously, several of the hemlocks originally in the smaller diameter classes at Saltonstall survived even until 1993 when adelgid attack caused the stand to be salvaged. These few, standing beneath much larger ones, escaped logging damage and survived with minuscule cambial growth. Root excavations confirmed that these saplings had survived by parasitizing their much larger companions through root-grafts. We also observed hemlock stumps that have callused over on the Perry plot and speculate that they are also surviving by parasitizing neighboring trees.

Basal area

Both stands exhibited rapid basal area growth (Fig. 3). After age 50, annual basal area increments commonly ranged from 2 upwards to 5 ft^2/acre. Basal area growth on both plots increased several years after thinning before begining to decline as stand stocking increased. The trees of the younger Saltonstall plot started rapid diameter growth immediately after the release. This is always the case with

Table 2.—Species distribution on Perry hemlock plot in 1931 (stand age 85) and 1995 (stand age 149) by diameter class (inches). HEM-eastern hemlock, BIR-birch, MAP-maple, OTH-other species.

1939 density (stems/acre)						1993 density (stems/acre)					
Dbh	HEM	BIR	MAP	OTH	Tot	Dbh	HEM	BIR	MAP	OTH	Tot
2-3	28	7	13	6	54	2-3	49	14	9	5	77
4-5	40	20	36	3	99	4-5	23	9	5	4	41
6-7	75	27	14	2	118	6-7	16	3	0	2	21
8-9	80	13	9	0	102	8-9	11	7	9	0	27
10-11	49	3	8	3	63	10-11	16	11	9	1	37
12-13	29	0	5	0	34	12-13	30	4	4	0	38
14-15	13	1	2	0	16	14-15	23	1	2	0	26
16-18	4	0	1	1	6	16-18	24	1	0	0	25
18-19	0	0	2	0	2	18-19	11	0	0	1	12
20-21	0	0	0	0	0	20-21	9	0	0	1	10
>=22	2	0	0	0	2	>=22	8	0	0	2	10
Total	320	71	90	15	496	Total	220	50	38	16	324

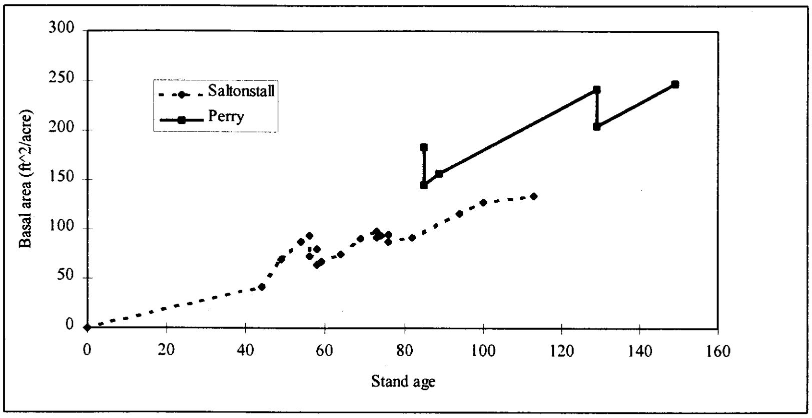

Figure 3.—Basal area (ft²/acre) by stand age on Saltonstall and Perry hemlock plots in Connecticut.

released hemlocks in this part of their range. Although basal area growth gradually declined with age; it is quite remarkable that basal area growth on the Perry plot at 149-years-old was still over 2 ft²/acre/year.

Growth and yield

Wood production per acre of both stands, exclusive of mortality, was determined on the basis of volume tables of Scott (1979, 1981) and the data are shown in Figs. 4 and 5. Wood production on both of these plots is higher than is typical for pure hemlock stands (Godman and Lancaster 1990). The annual production rates of both plots were very similar. Production rates sagged temporarily after each partial cutting, including those that removed some of the larger trees, but recovered and remained stable over remarkably long periods of time. The periodic annual increment (including harvested trees) of the Perry plot was 50 ft³/acre at age 149, and the periodic annual increment of the Saltonstall plot was 52 ft³/acre at age 113. Mean annual growth averaged approximately 80 ft³/acre between ages 60 to 110 for both plots and fell to 60 ft³/acre through age 149 on the Perry plot. The rapid growth decrease on the Saltonstall plot for the final 13 years was probably caused by the adelgid infestation.

In contrast to basal area and cubic-foot growth, board-foot volumes increased faster on the Saltonstall plot after age 40 (~400 b.f./acre/year) than on the Perry plot (300 b.f./acre/year, Fig. 5). The continued relatively high growth rate on the Perry plot through age 149 suggests hemlock can continue acceptable volume increases through at least age 200. Much of this increase is probably due to maintaining a high live crown ratio on residual trees.

Application

Forest managers will want to reestablish hemlock forests as soon as there is an effective biological control for hemlock woolly adelgid. These two cases studies show that eastern

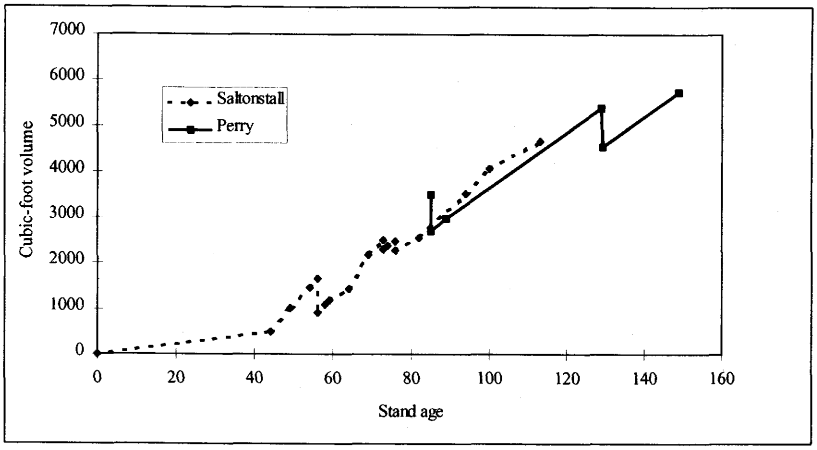

Figure 4.—Cubic-foot volume (ft³/acre) by stand age on Saltonstall and Perry hemlock plots in Connecticut.

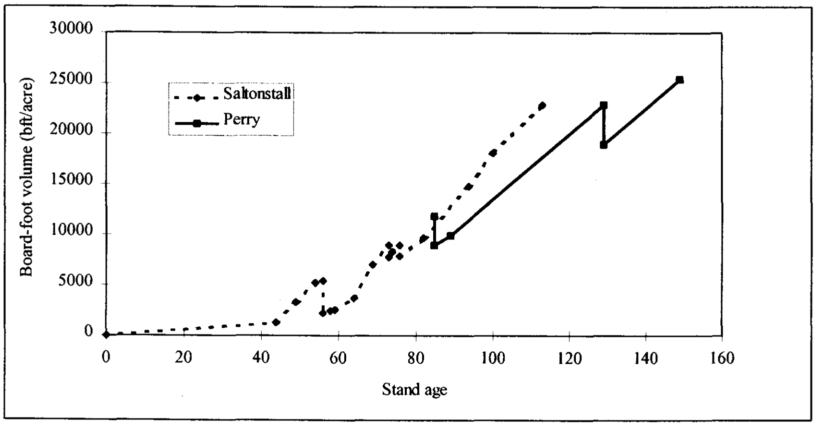

Figure 5.—Board-foot volume (Int. ¼ b.f./acre) by stand age on Saltonstall and Perry hemlock plots in Connecticut.

hemlock can respond vigorously to release even if they were previously oppressed by larger hemlocks. This means that it is possible to prolong the lives of vigorous stands with broad ranges of size classes over long periods of time for multiple purposes of timber, aesthetics, and biological diversity. This does not necessarily mean that old, large hemlocks will not suffer rots and ring-shake, or that single stands can be made into perfect sustained -yield units.

Acknowledgments

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

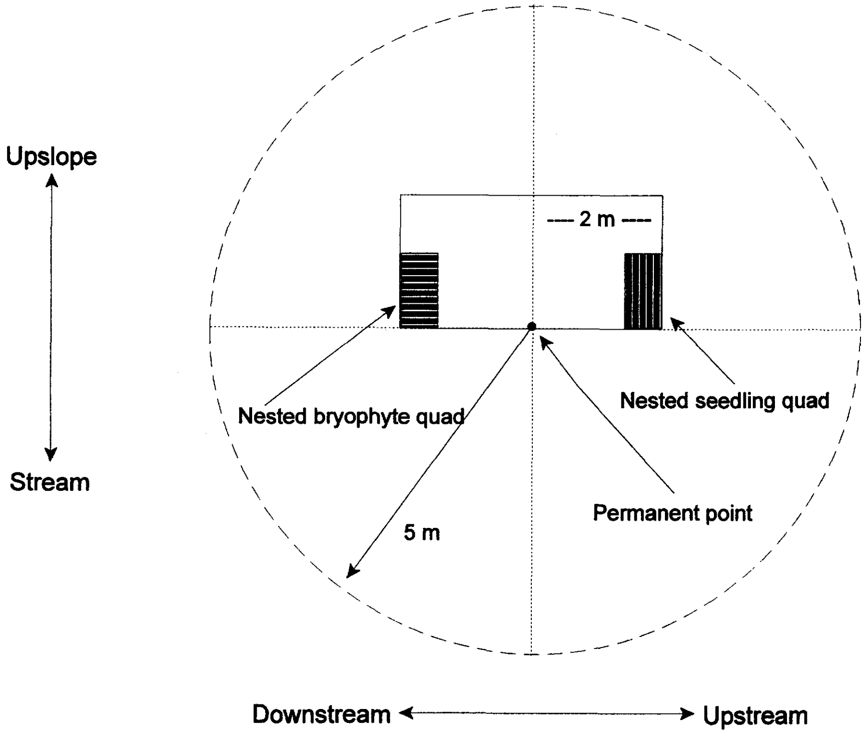

Figure 1.—Diagram of the quantitative vegetation sampling regime used for the permanent point/plot survey.

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 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.

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 (n = 48)	Van Campens (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

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 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.

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 speciesmean	
Hypnum imponens	2
Mnium hornum	1
Leucobryum glaucum	0.8
Tetraphis pellucida	0.6
Brotherella recurvans	0.2

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 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.

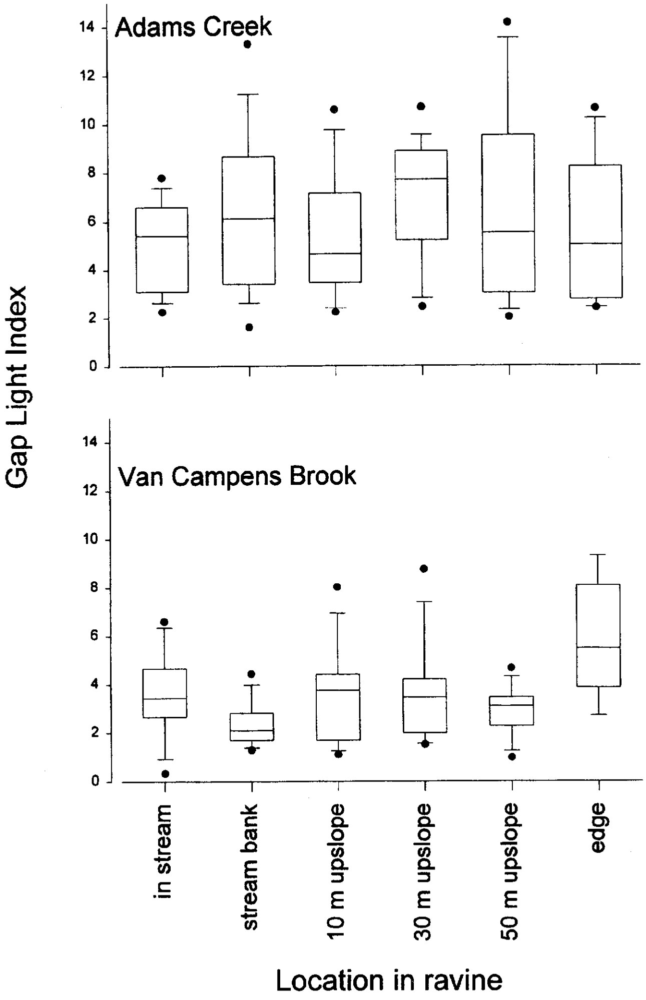

Figure 2.—Box plots of the gap light index by topographic location in the ravine for the two study sites in Delaware Water Gap National Recreation Area. Boxes indicate 10th, 25th, 75th, and 90th percentiles.

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

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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Predicting Long-Term Forest Development Following Hemlock Mortality

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Abstract

The hemlock woolly adelgid (*Adelges tsugae* Annand.), an introduced pest specializing on eastern hemlock (*Tsuga canadensis* (L.) Carr.), threatens to cause widespread hemlock mortality in New England forests. In this study, we used a stem-based model of forest dynamics (SORTIE) to predict forest development in a northeastern forest both with and without eastern hemlock. In all simulations, forest development was explained by species-specific life-history characteristics such as growth, mortality, and recruitment as they relate to light availability. Forest composition after 500 years depended on the relative abundances of late-successional species: eastern hemlock was long-lived but did not easily gain or yield space; American beech (*Fagus grandifolia* Ehrh.) gained dominance quickly and soon comprised nearly all basal area in a stand unless hemlock was present; and yellow birch (*Betula alleghaniensis* Britton) persisted if beech and hemlock were absent. Early-successional species thrived in the forest if late-successional species were not present. We conclude that the long-term impact of the hemlock woolly adelgid on forest composition in northeastern forests will depend both on initial species composition and on the extent of hemlock death. If 50% of the overstory basal area in hemlock is removed by the adelgid, and if the adelgid does not persist at densities high enough to cause extended damage, hemlock stands will continue to be dominated by hemlock. Mixed hemlock - hardwood stands will be dominated by the late-successional species remaining. If hemlock death is near 90% of overstory basal area, hemlock is likely to continue to persist in low densities while the other late-successional species gain dominance. If hemlock death is complete, all stands will be dominated by beech and yellow birch where they are present, no matter what their initial abundances. Hardwood stands will not be affected by the adelgid.

Introduction

Northeastern forests are currently threatened by an outbreak of hemlock woolly adelgid, a defoliating insect pest specializing on eastern hemlock. Because of its extreme virulence, its unusually high fecundity (McClure 1989), and its rapid dispersal via wind and animals (McClure 1990), the adelgid's arrival in a healthy forest stand often foreshadows the death of all hemlock (McClure 1991). Eastern hemlock often grows in pure stands or in mixed stands with deciduous species (Kelty 1986); adelgid infestation in southern New England has thus initiated a rapid shift from mixed and coniferous to deciduous forest (Jenkins et al. 1999, Orwig and Foster 1998). The consequences of hemlock mortality, however, are likely to be visible at a much larger scale, as the selective removal of a dominant forest species is often accompanied by landscape-level reorganization of forest structure (Shugart and West 1977, Twery and Patterson 1984). In this study we used a modeling approach to assess the potential long-term impact of eastern hemlock mortality on forest composition for a small watershed in southern New England.

Methods

SORTIE model

The SORTIE model tracks individual trees on a spatially explicit basis, generating light indices for each stem as a function of its nearest neighbors. In this way, dispersal, growth, mortality, and recruitment rates are based on species-specific responses to resource availability (Canham et al. 1994, Kobe et al. 1995, Pacala et al. 1993, 1996, Ribbens et al. 1994). The model is uniquely appropriate for this study for two reasons: 1) its emphasis on life-history characteristics at the individual tree level allowed us to focus on the effects of selective removal of one species, and 2) SORTIE's species-specific functions were parameterized at the study site in northwestern Connecticut. Nutrient and water limitations are not represented in this version of the model. We do not consider this a limitation of this analysis, as previous field studies have suggested that such limitations are indeed rare at the study site (S. Pacala, pers. comm.).

Study site

The Camp Pond watershed (41°58' N and 73°15' W) encompasses approximately 130 hectares in the northern portion of the Great Mountain Forest in the northwestern corner of Connecticut (Figure 1). Elevation ranges from 420 to 530 meters. Soils are derived from glacial till, range from 10 to about 100 cm thick, and are extremely rocky. The forest lies within the transition hardwood - hemlock - white pine forest vegetation zone (Westveld 1956), though white pine (*Pinus strobus* L.) is absent from the Camp Pond watershed. Most of the forest is between 80 and 100 years old; in parts of the northeast, northwest, and southernmost portions of the watershed, selective harvesting took place within the last 30 years. Hemlock woolly adelgid is not yet present at the site.

Forest survey

We conducted a detailed forest inventory to assess current forest composition by species and 10 cm size class. Sample

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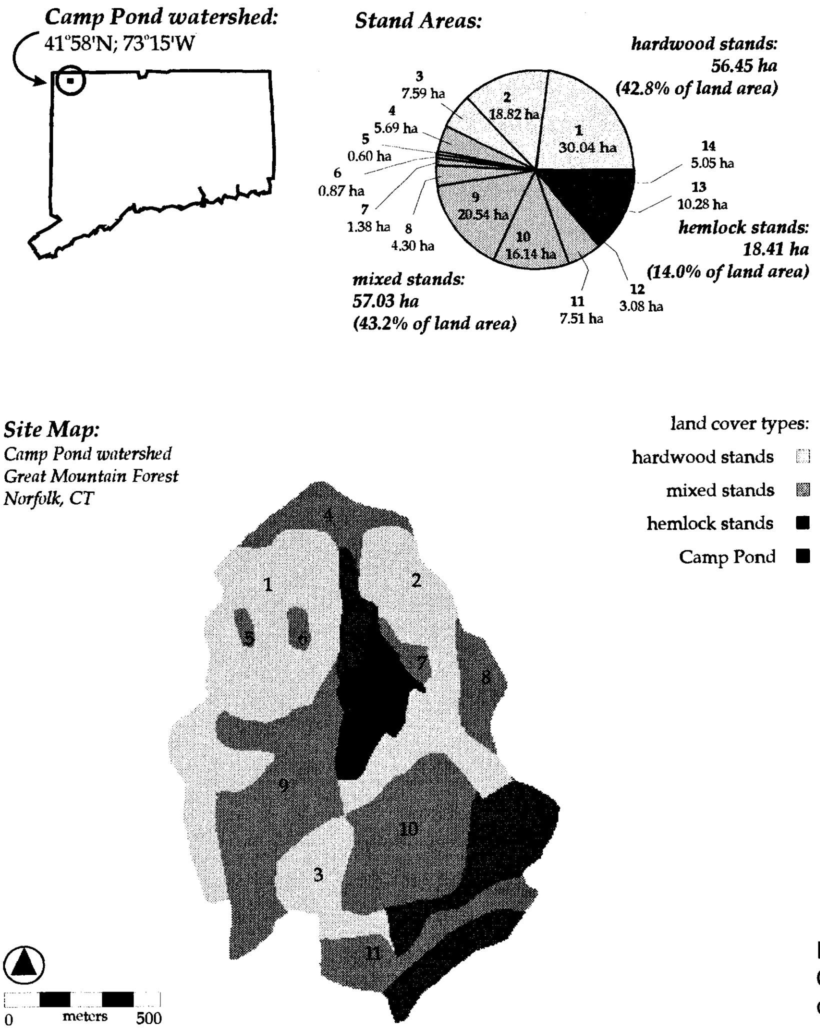

Figure 1.—Site description: location within Connecticut, watershed map, and stand descriptions.

points were located along east-west transects roughly 100 m from each other; transects were established 100 m apart. At each of 124 sample points, variable-radius plots were measured, using a prism with a basal area factor of 2.3 m^2 ha^{-1}. Species and diameter at breast height (dbh) were recorded for each tree counted "in" by the prism. Plots were located with a global positioning system using differential correction (Trimble Pathfinder Basic Plus; 2 to 5 m accuracy). An external antenna was mounted on a 40-foot telescoping stadia rod to alleviate interference from the forest canopy. The Universal Transverse Mercator (UTM) coordinates of each point were registered to a geographic information system (GIS) for further analysis.

Stand delineation

To facilitate modeling forest succession in stands with different species compositions, we used the forest inventory data to divide the watershed into stands. Stands containing less than 10% relative basal area (RBA) in overstory (dbh >= 10 cm) hemlock were classified as hardwood, those containing more than 60% RBA overstory hemlock were classified as hemlock, and stands with 10 to 60% RBA overstory hemlock were classified as mixed hemlock-hardwood stands. Each plot was assigned to one of the three forest cover categories, and stand boundaries were drawn around groups of plots assigned to the same category using the onscreen digitizing function in Idrisi (Eastman 1992). We delineated fourteen stands within the watershed (Figure 1): three hemlock, eight mixed, and three hardwood (Table 1).

Simulations

Each stand was treated separately in the model simulations. In order to initialize the model with current conditions for each stand, we used the forest survey data to calculate the number of trees per hectare in each 10-cm size class for each species, rounded to the nearest integer. Several species were present in the study area but were ignored: striped maple (*Acer pensylvanicum* L.), which made up less than 5% of overstory basal area in the six stands where it occurred; gray birch (*Betula papyrifera* Marsh.), which made up less than 2% of overstory basal area in the three stands where it occurred; and black birch (*Betula lenta* L.), which made up less than 5% of overstory basal area in the five

Table 1.—Current overstory (dbh >= 10 cm) forest composition for 14 stands delineated using plot-based forest inventory of Camp Pond watershed, Great Mountain Forest, Norfolk, CT. See Figure 1 for stand map. Bold values refer to the most abundant species in each stand. Absence of data indicates zero RBA (relative basal area) value. Species abbreviations are as follows: BE, American beech (*Fagus grandifolia* Ehrh.); HM, Eastern hemlock (*Tsuga canadensis* Carr.); SM, sugar maple (*Acer saccharum* Marsh.); YB, yellow birch (*Betula alleghaniensis* Britton); BC, black cherry (*Prunus serotina* Ehrh.); RM, red maple (*Acer rubrum* L.); WA, white ash (*Fraxinus americana* L.); RO, northern red oak (*Quercus rubra* L.).

Stand type		Hardwood			Mixed			
		1	2	3	4	5	6	7
Total BA (m^2 ha^{-1})		**24.13**	**23.16**	**29.77**	**29.77**	**26.06**	**19.27**	**20.04**
RBA values	BE	0.18	**0.29**	**0.30**	0.16			0.06
by species	HM		0.01	0.05	**0.49**	**0.48**	**0.33**	**0.32**
	SM	0.10	0.21	0.10	0.02			0.09
	YB	0.03	0.02	0.11			0.06	0.03
	BC	0.09	0.08	0.11	0.04	0.16	0.11	0.12
	RM	0.14	0.14	0.22	0.17	0.12	0.28	0.25
	WA	0.05	0.05					0.03
	RO	**0.40**	0.19	0.12	0.11	0.24	0.23	0.09

Stand type		Mixed				Hemlock		
		8	9	10	11	12	13	14
Total BA (m^2 ha^{-1})		**36.18**	**28.12**	**33.89**	**30.54**	**21.72**	**31.29**	**32.06**
RBA values	BE	0.10	0.07	0.18	0.22	0.05	0.06	0.14
by species	HM	**0.45**	**0.41**	**0.39**	**0.30**	**0.62**	**0.76**	**0.69**
	SM	0.08	0.03	0.03	0.03	0.05		
	YB	0.02	0.07	0.04	0.11	0.02	0.04	0.02
	BC	0.04	0.06	0.03	0.08		0.02	0.02
	RM	0.27	0.30	0.26	0.20	0.18	0.07	0.01
	WA		0.01	0.02	0.01			
	RO	0.04	0.05	0.04	0.06	0.08	0.04	0.02

stands where it occurred. Black oak (*Quercus velutina* Lam.) occurred in three of the stands and was treated as red oak. All other species had been parameterized in SORTIE and accounted for 100% of the overstory basal area.

While many stands infested with hemlock woolly adelgid have eventually experienced complete hemlock mortality, it is possible that: a) a natural enemy might be found which could be released to keep the population in check (Cheah and McClure 1996, Lyon and Montgomery 1995, McClure 1987, 1995, Montgomery and Lyon 1996); b) the adelgid population would remain too low to cause extensive damage in areas with extremely cold temperatures (but see Parker et al. 1998); c) some localized hemlock trees would prove resistant; or d) site factors would render the pest less virulent in some forests than in others. In these cases, hemlock mortality might be incomplete. To predict the impacts of partial hemlock mortality on northeastern forests, we performed simulations with partial (50% and 90%) hemlock removal in addition to the simulations with complete (100%) mortality. For each of the 11 non-hardwood stands, five 500 year simulations (each using a different random number seed to initialize the stochastic functions in the model) were performed under four sets of conditions: current conditions, 50% hemlock mortality, 90% hemlock mortality, and complete hemlock mortality. We removed hemlock from the community by fixing its initial density at 50%, 10%, or 0% of its current density while holding all other variables constant. We assumed that standing hemlock trees died immediately upon infestation, and that they fell to the forest floor directly after their mortality. This scenario is not truly representative of the "gradual" canopy gaps created in eastern hemlock forests by the adelgid (Jenkins et al. 1999, Krasny and Whitmore 1992), so we may overestimate the light available to understory trees following hemlock mortality. Over the long term, however, we expect that this would have little effect on forest development.

Since hemlock mortality is not likely to alter forest development in hardwood stands, simulations of current forest conditions only were performed for the three stands classified as hardwood. The averages of each species' RBA in the five simulations for each set of species compositions are reported here with their associated standard deviations. In this analysis, we focus on RBA rather than raw basal area (BA) values because a) we were skeptical about the very high raw BA values generated by the model at this stage in model development (subsequent model revisions have addressed this issue), and b) the relative abundance of individual species (and not their absolute BA values) was truly the variable of interest.

Results

Current conditions

In simulations representing future development from existing conditions in the hardwood stands (Table 2), initial RBA of early-successional and shade-intolerant species were replaced by beech, yellow birch, and sugar maple (*Acer saccharum* Marsh.). In simulations representing future development from existing conditions in the hemlock stands (Table 2), the RBA of hemlock remained roughly constant or increased slightly; beech RBA also increased slightly. At the same time, in these stands the RBA of early successional species such as red oak (*Quercus rubra* L.), red maple (*Acer rubrum* L.), and black cherry (*Prunus serotina* Ehrh.) declined. Similar trends were seen in the development of the mixed stands through time (Table 2). In general, where beech, hemlock, and yellow birch were present, they increased dramatically in RBA at the expense of other species, especially red maple and black cherry.

Hemlock removal

When hemlock was completely removed from the three hemlock stands (Table 3), the remaining late-successional species dominated stand development. Beech and yellow birch were present, and they gained dramatically in RBA over time with a concomitant decrease in basal area of early-successional species. When hemlock was removed completely from mixed stands the situation was similar: if beech or yellow birch was present it gained significantly. Under these conditions, though, each species had a greater advantage where it was the only late-successional species present.

When hemlock was partially removed from both hemlock and mixed stands, the remaining late-successional species dominated forest structure at year 500 (Tables 4 and 5). Overall, in simulations representing partial hemlock death, beech made dramatic gains while the remaining hemlock and yellow birch were slower to increase RBA.

Dynamics of late-successional species

The long-term dynamics of succession depended on the initial relative abundances of the species present. In particular, the presence or absence of yellow birch, hemlock, and beech strongly influenced community composition after 500 years of undisturbed succession. When beech was the only species remaining, it dominated by year 50 (Table 3, stand 4); when yellow birch remained alone, it dominated within 300 years (Table 3, stand 6). When hemlock was the only species present of the three (Tables 4 and 5, stand 5), it gained steadily though its RBA increase was not as rapid.

When two of the three species occurred together, dynamics were less predictable. For example, when beech and yellow birch occurred together in the absence of hemlock (Table 3, stands 4-14; Table 2, stand 1), both species were present and had gained RBA in year 500. Beech was quicker to gain basal area, becoming the most abundant in late succession no matter what its initial abundance. In the one case where yellow birch was more abundant than beech at year 500 (Table 5, stand 9), both species were equally abundant initially, suggesting that yellow birch remained competitive in late succession only when its initial abundance was high enough for it to remain competitive with beech. When hemlock occurred with beech but not yellow birch, of course, beech was most likely to be predominant in the stand within 20 years (Tables 2, 4, and 5, stand 4).

More common, however, were simulations in which all three species occurred simultaneously. Under these conditions hemlock was most likely to gain dominance by year 20, but the composition of the remaining forest and the initial abundances of all three late-successional species were better predictors of late-successional outcome.

Dynamics of early-successional species

When none of the three late-successional species were present, early-successional species persisted in the stand through year 500 (Figure 2; Table 3, stand 5). When both types of species were present, however, the trend from year zero was predictable: the early-successional species steadily lost relative basal area while the late-successional species gained (Figure 3).

At year 500, if white ash (*Fraxinus americana* L.) persisted, it was present in very low densities. Black cherry and red oak, while not dominant, were common in the original forest. While they dominated late in succession when no other late-successional species was present (Figure 2), they were largely excluded from late-successional dynamics. Red oak, however, gradually gained basal area in several of the simulations, reaching its peak density between years 100 and 150 (Figure 4) and remaining dominant even in the presence of hemlock in one simulation (Table 5, stand 5). Unlike the early-successional species mentioned so far, red maple was initially common in the forest at Camp Pond. In all of the model simulations, however, red maple steadily lost RBA.

Discussion

Consequences of hemlock mortality

If the current spreading pattern of hemlock woolly adelgid infestation in southern New England reaches Great Mountain Forest, and if a suitable natural enemy or an insecticide practical for forest use does not become available, it is possible that virtually all hemlock in this community will be lost. Forest development after adelgid infestation will depend on the composition of the forest community when the adelgid arrives. The stands that do not currently contain hemlock will continue to develop as predicted, with a gradual decline in early-successional species and an accompanying increase in late-successional species. In predominantly hemlock stands, the loss of hemlock will be accompanied by an increase in yellow birch, a gap-phase species. If beech is present when hemlock dies, the model predicts that beech will increase

Table 2.—Comparisons of current relative basal area (RBA) with RBA predicted by SORTIE after 500 years of undisturbed succession. Initial data are based on 1994 field measurements. Final values refer to the mean (standard deviation) of five 500-year SORTIE simulations. Proportions may not add to 1.00 due to rounding. Bold type indicates the most dominant species. See Figure 1 for stand map. Species are listed in order of decreasing shade tolerance (as described by Canham et al. 1994). Absence of data indicates zero RBA value.

Stand type	Hardwood									Mixed											
	1			2			3			4			5			6			7		
Species	initial	final	(SD)	initial	final	(SD)	initial	final	(SD)	initial	final	(SD)	initial	final	(SD)	initial	final	(SD)	initial	final	(SD)
BE	0.18	**0.83**	(0.06)	**0.29**	**0.72**	(0.06)	**0.30**	**0.72**	(0.12)	0.16	**0.52**	(0.11)							0.06	**0.38**	(0.07)
HM				0.01	0.01	(0.02)	0.05	0.01	(0.03)	**0.49**	0.43	(0.09)	**0.48**	**0.86**	(0.02)	**0.33**	**0.71**	(0.10)	**0.32**	0.35	(0.08)
SM	0.10			0.21	0.18	(0.05)	0.10	0.03	(0.03)	0.02									0.09	0.01	(0.02)
YB	0.03	0.05	(0.05)	0.02	0.03	(0.04)	0.11	0.18	(0.12)							0.06	0.10	(0.10)	0.03	0.13	(0.04)
BC	0.09	0.03	(0.03)	0.08	0.02	(0.03)	0.11	0.01	(0.02)	0.04	0.01	(0.02)	0.16	0.05	(0.05)	0.11	0.07	(0.05)	0.12	0.08	(0.05)
RM	0.14	0.05	(0.03)	0.14	0.02	(0.03)	0.22	0.04	(0.05)	0.17	0.03	(0.03)	0.12	0.03	(0.06)	0.28	0.04	(0.03)	0.25	0.03	(0.03)
WA	0.05	0.01	(0.02)	0.05	0.01	(0.02)													0.03		
RO	**0.40**	0.03	(0.04)	0.19	0.02	(0.04)	0.12			0.11	0.01	(0.02)	0.24	0.05	(0.05)	0.23	0.09	(0.04)	0.09	0.01	(0.01)

Stand type	Mixed												Hemlock								
	8			9			10			11			12			13			14		
Species	initial	final	(SD)	initial	final	(SD)	initial	final	(SD)	initial	final	(SD)	initial	final	(SD)	initial	final	(SD)	initial	final	(SD)
BE	0.10	0.31	(0.11)	0.07	0.15	(0.03)	0.18	0.34	(0.05)	0.22	**0.51**	(0.07)	0.05	0.06	(0.04)	0.06	0.17	(0.09)	0.14	0.25	(0.13)
HM	**0.45**	**0.51**	(0.12)	**0.41**	**0.58**	(0.15)	**0.39**	**0.49**	(0.06)	**0.30**	0.24	(0.13)	**0.62**	**0.88**	(0.07)	**0.76**	**0.78**	(0.08)	**0.69**	**0.67**	(0.10)
SM	0.08	0.05	(0.03)	0.03			0.03			0.03			0.05	0.01	(0.01)						
YB	0.02	0.06	(0.05)	0.07	0.18	(0.15)	0.04	0.1	(0.04)	0.11	0.17	(0.09)	0.02			0.04	0.05	(0.03)	0.02	0.03	(0.03)
BC	0.04			0.06	0.03	(0.04)	0.03	0.01	(0.01)	0.08						0.02			0.02	0.01	(0.03)
RM	0.27	0.06	(0.05)	0.30	0.04	(0.03)	0.26	0.07	(0.07)	0.20	0.03	(0.04)	0.18	0.05	(0.08)	0.07	0.01	(0.01)	0.11	0.03	(0.08)
WA				0.01			0.02			0.01	0.01	(0.02)									
RO	0.04	0.01	(0.02)	0.05	0.02	(0.03)	0.04			0.06	0.04	(0.06)	0.08			0.04	0.01	(0.01)	0.02		

Table 3.—Comparisons of RBA with hypothetical complete eastern hemlock mortality due to woolly adelgid infestation with RBA predicted by SORTIE after 500 years of undisturbed succession following eastern hemlock mortality. Simulations were performed for Mixed and Hemlock stands only (stands 4-14). See Figure 1 for stand map. Initial data are based on 1994 field measurements minus eastern hemlock. Final values refer to the mean (standard deviation) of five 500-year SORTIE simulations. Proportions may not add to 1.00 due to rounding. Bold type indicates the most dominant species; absence of data indicates a zero RBA value. Species are listed in order of decreasing shade tolerance (as described by Canham et al.1994).

Stand type	Mixed											
	4		5		6		7		8		9	
Species	initial	final (SD)	initial	final (SD)	initial	final (SD)	initial	final (SD)	initial	final (SD)	initial	final (SD)
BE	0.32	**0.91** (0.03)					0.09	**0.57** (0.10)	0.18	**0.81** (0.08)	0.12	0.39 (0.11)
HM												
SM	0.04	0.01 (0.02)					0.14	0.03 (0.03)	0.15	0.02 (0.03)	0.05	
YB					0.08	**0.71** (0.07)	0.05	0.23 (0.13)	0.03	0.08 (0.06)	0.12	**0.53** (0.11)
BC	0.08	0.02 (0.04)	0.31	0.32 (0.07)	0.17	0.09 (0.02)	0.17	0.07 (0.04)	0.08	0.05 (0.05)	0.10	0.03 (0.02)
RM	**0.34**	0.05 (0.03)	0.23	0.25 (0.06)	**0.41**	0.06 (0.04)	**0.37**	0.07 (0.03)	**0.48**	0.04 (0.04)	**0.50**	0.05 (0.02)
WA							0.05	0.01 (0.02)				0.02
RO	0.22	0.01 (0.02)	**0.46**	**0.42** (0.08)	0.34	0.14 (0.07)	0.13		0.08			0.09

Stand type	Mixed				Hemlock					
	10		11		12		13		14	
Species	initial	final (SD)	initial	final (SD)	initial	final (SD)	initial	final (SD)	initial	final (SD)
BE	0.30	**0.78** (0.08)	**0.31**	**0.65** (0.08)	0.14	0.37 (0.07)	0.27	**0.59** (0.13)	**0.47**	**0.76** (0.14)
HM										
SM	0.06	0.01 (0.01)	0.04	0.01 (0.02)	0.14	0.20 (0.02)				
YB	0.07	0.09 (0.03)	0.15	0.22 (0.06)	0.05	**0.41** (0.10)	0.17	0.23 (0.08)	0.06	0.13 (0.09)
BC	0.05	0.02 (0.01)	0.12	0.06 (0.02)			0.09	0.02 (0.02)	0.06	0.02 (0.03)
RM	**0.43**	0.09 (0.07)	0.28	0.06 (0.05)	**0.47**	0.12 (0.04)	**0.31**	0.05 (0.04)	0.35	0.08 (0.05)
WA	0.03	0.01 (0.03)	0.01							
RO	0.06		0.09		0.21	0.08 (0.07)	0.16	0.11 (0.08)	0.06	0.01 (0.02)

Table 4.—Comparisons of RBA with hypothetical 50% eastern hemlock mortality due to woolly adelgid infestation with RBA predicted by SORTIE after 500 years of undisturbed succession following 50% eastern hemlock mortality in each 10 cm size class. Simulations were performed for Mixed and Hemlock stands only (stands 4-14). See Figure 1 for stand map. Initial data are based on 1994 field measurements minus 50% of eastern hemlock. Final values refer to the mean (standard deviation) of five 500-year SORTIE simulations. Proportions may not add to 1.00 due to rounding. Bold type indicates the most dominant species; absence of data indicates a zero RBA value. Species are listed in order of decreasing shade tolerance (as described by Canham et al.1994).

Stand type	Mixed											
	4		5		6		7		8		9	
Species	initial	final (SD)	initial	final (SD)	initial	final (SD)	initial	final (SD)	initial	final (SD)	initial	final (SD)
BE	0.21	**0.70** (0.05)					0.08	**0.46** (0.12)	0.13	**0.46** (0.05)	0.09	0.33 (0.05)
HM	**0.33**	0.23 (0.07)	**0.32**	**0.74** (0.08)	0.20	**0.50** (0.04)	0.19	0.19 (0.04)	0.29	**0.46** (0.06)	0.27	**0.37** (0.04)
SM	0.03	0.01 (0.03)					0.11	0.03 (0.03)	0.11		0.03	0.01 (0.01)
YB					0.07	0.30 (0.09)	0.04	0.16 (0.14)	0.02	0.01 (0.01)	0.09	0.21 (0.08)
BC	0.05	0.04 (0.05)	0.21	0.14 (0.06)	0.13	0.08 (0.03)	0.14	0.08 (0.03)	0.06	0.03 (0.03)	0.07	0.03 (0.03)
RM	0.23		0.16	0.06 (0.05)	**0.33**	0.02 (0.02)	**0.30**	0.05 (0.03)	**0.34**	0.02 (0.04)	**0.36**	0.05 (0.04)
WA							0.04				0.01	
RO	0.15	0.02 (0.04)	0.31	0.05 (0.06)	0.27	0.11 (0.09)	0.10	0.01 (0.02)	0.06	0.01 (0.02)	0.06	0.01 (0.02)

Stand type	Mixed				Hemlock					
	10		11		12		13		14	
Species	initial	final (SD)	initial	final (SD)	initial	final (SD)	initial	final (SD)	initial	final (SD)
BE	0.23	**0.51** (0.12)	**0.25**	**0.58** (0.09)	0.08	0.11 (0.04)	0.10	0.23 (0.03)	0.22	0.33 (0.10)
HM	0.22	0.32 (0.13)	0.21	0.16 (0.07)	**0.45**	**0.78** (0.14)	**0.62**	**0.69** (0.03)	**0.54**	**0.48** (0.08)
SM	0.04	0.01 (0.01)	0.03		0.08	0.02 (0.03)				
YB	0.05	0.08 (0.09)	0.12	0.17 (0.06)	0.03	0.03 (0.07)	0.06	0.04 (0.03)	0.03	0.09 (0.03)
BC	0.04	0.02 (0.02)	0.10	0.01 (0.02)			0.03		0.03	0.03 (0.03)
RM	**0.33**	0.04 (0.07)	0.22	0.05 (0.06)	0.26	0.03 (0.03)	0.12	0.03 (0.03)	0.16	0.06 (0.04)
WA	0.03	0.02 (0.04)	0.01							
RO	0.05		0.07	0.02 (0.04)	0.11	0.03 (0.04)	0.06	0.01 (0.02)	0.03	0.01 (0.02)

Table 5.—Comparisons of RBA with hypothetical 90% eastern hemlock mortality due to woolly adelgid infestation with RBA predicted by SORTIE after 500 years of undisturbed succession following 90% eastern hemlock mortality in each 10 cm size class. Simulations were performed for Mixed and Hemlock stands only (stands 4-14). See Figure 1 for stand map. Initial data are based on 1994 field measurements minus 90% of eastern hemlock. Final values refer to the mean (standard deviation) of five 500-year SORTIE simulations. Proportions may not add to 1.00 due to rounding. Bold type indicates the most dominant species; absence of data indicates a zero RBA value. Species are listed in order of decreasing shade tolerance (as described by Canham et al.1994).

Stand type	Mixed																	
	4			5			6			7			8			9		
Species	initial	final	(SD)	initial	final	(SD)	initial	final	(SD)	initial	final	(SD)	initial	final	(SD)	initial	final	(SD)
BE	0.29	**0.81**	(0.06)							0.09	**0.56**	(0.08)	0.17	**0.74**	(0.07)	0.12	0.36	(0.07)
HM	0.09	0.14	(0.08)	0.09	0.28	(0.08)	0.04	0.11	(0.03)	0.07	0.08	(0.02)	0.07	0.07	(0.05)	0.05	0.11	(0.04)
SM	0.04									0.13	0.02	(0.04)	0.14	0.01	(0.02)	0.04		
YB							0.08	**0.63**	(0.05)	0.05	0.15	(0.10)	0.03	0.05	(0.02)	0.12	**0.42**	(0.05)
BC	0.07	0.02	(0.03)	0.28	0.27	(0.09)	0.16	0.06	(0.01)	0.16	0.06	(0.04)	0.07	0.01	(0.01)	0.10	0.06	(0.06)
RM	**0.31**	0.01	(0.03)	0.21	0.14	(0.03)	**0.40**	0.08	(0.02)	**0.35**	0.07	(0.08)	**0.45**	0.10	(0.06)	**0.47**	0.05	(0.02)
WA										0.04	0.01	(0.03)				0.02		
RO	0.20	0.02	(0.03)	**0.41**	**0.30**	(0.12)	0.32	0.12	(0.04)	0.12	0.04	(0.04)	0.08	0.02	(0.03)	0.08		

Stand type	Mixed			Hemlock											
	10			11			12			13			14		
Species	initial	final	(SD)	initial	final	(SD)	initial	final	(SD)	initial	final	(SD)	initialf	inal	(SD)
BE	**0.29**	**0.80**	(0.11)	**0.31**	**0.62**	(0.10)	0.12	0.29	(0.07)	0.21	**0.43**	(0.07)	**0.37**	**0.70**	(0.06)
HM	0.06	0.10	(0.06)	0.03	0.07	(0.04)	0.12	**0.33**	(0.12)	**0.24**	0.32	(0.06)	0.21	0.17	(0.06)
SM	0.05	0.01	(0.01)	0.04			0.12	0.04	(0.04)						
YB	0.06	0.04	(0.03)	0.14	0.25	(0.07)	0.04	0.19	(0.13)	0.13	0.18	(0.08)	0.05	0.08	(0.07)
BC	0.05	0.01	(0.02)	0.12	0.01	(0.02)				0.07	0.03	(0.03)	0.05	0.01	(0.02)
RM	0.40	0.05	(0.07)	0.27	0.03	(0.03)	**0.42**	0.07	(0.07)	0.24			0.27	0.01	(0.03)
WA	0.03			0.01											
RO	0.06			0.08	0.01	(0.02)	0.18	0.08	(0.06)	0.12	0.04	(0.05)	0.05	0.02	(0.02)

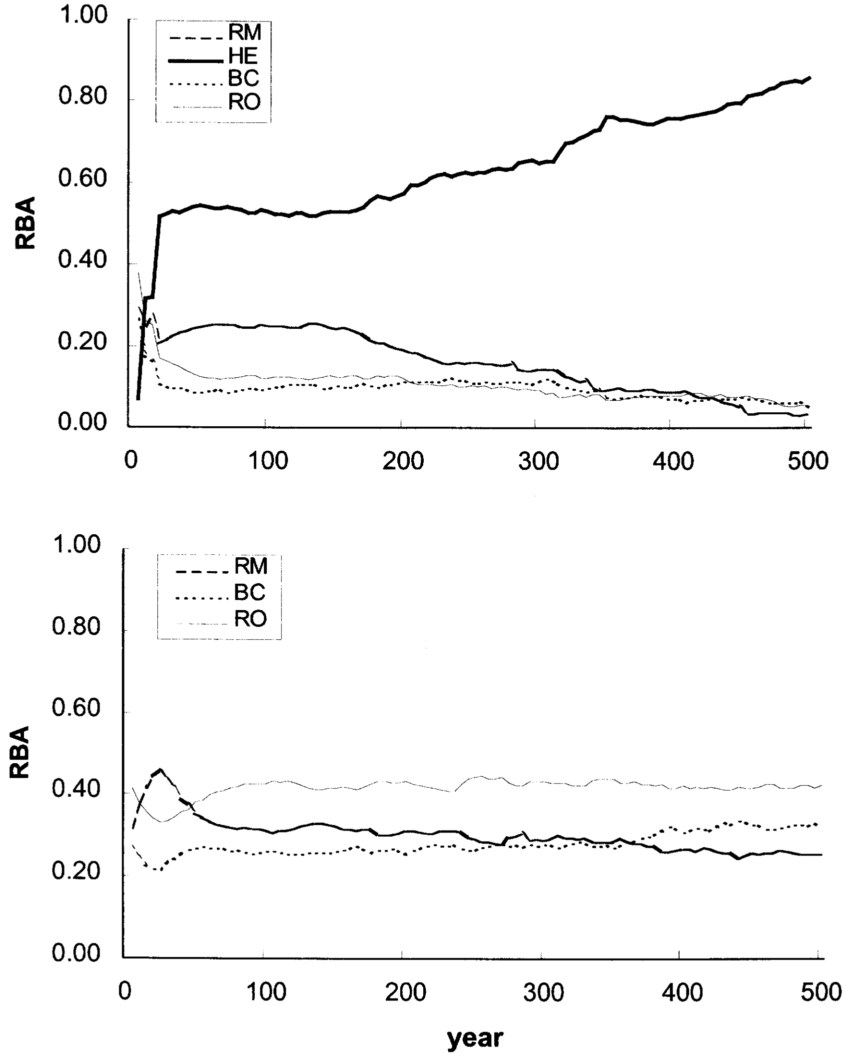

Figure 2.—Predicted effect of complete hemlock mortality in a stand with no other late-successional species (stand 5; see Tables 2, and 3 for initial and final conditions). Top panel shows succession through year 500 with no mortality, and bottom panel shows succession through year 500 with 100 % mortality. Line traces mean RBA values at 5-year time steps. Species abbreviations are as defined in Table 1.

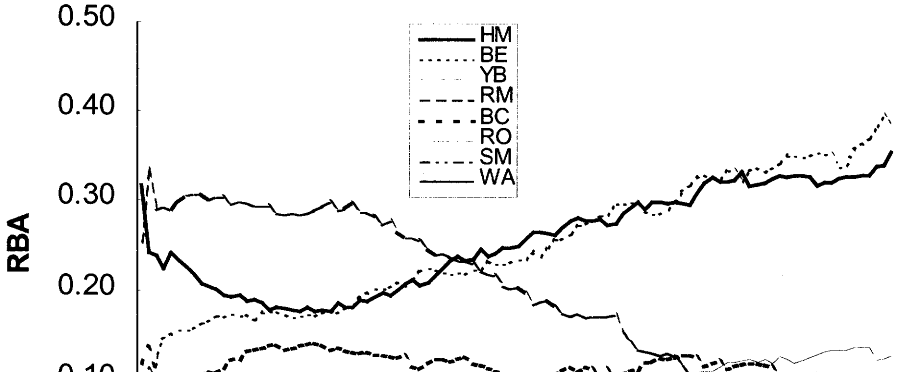

Figure 3.—Typical successional development with all three late-successional species (stand 8; see Table 2 for initial and final conditions). Lines trace RBA values at 5-year time steps. Species abbreviations are as defined in Table 1.

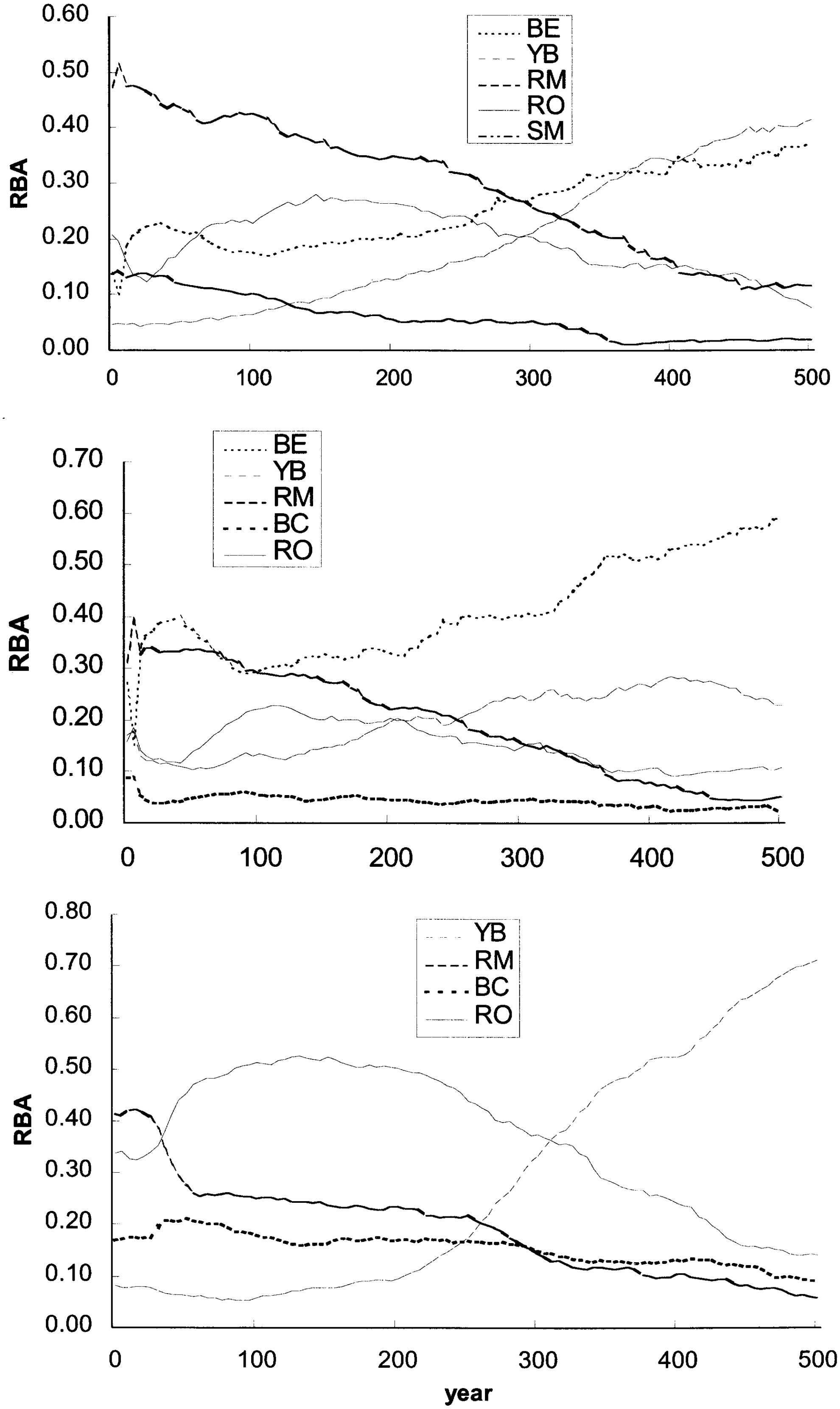

Figure 4.—Typical red oak peak and decline around year 100 (top panel: stand 12, no hemlock; middle panel: stand 13, no hemlock; bottom panel: stand 6, no hemlock; see Table 3 for initial and final RBA values). Lines trace RBA at 5-year time steps. Species abbreviations are as defined in Table 1.

Table 6.—Metrics summarizing interspecific variation among competitive strategies (from Pacala et al. 1996). See Table 1 for species abbreviations.

Species	Years to 3 m height in full sun	Years to 3 m height in 1% sun	Mean dispersal distance (m)	5-year survivorship of a 1 cm sapling in full sun
BE	19.4	55.0	5.9	0.92
HM	15.5	75.3	4.1	0.91
SM	18.4	31.7	8.1	0.69
RM	14.6	92.8	10.6	0.35
YB	13.9	29.3	31.0[1]	0.65
RO	11.9	125.4	8.7	0.38
BC	11.4	49.5	8.0	0.53
WA	11.9	100.6	16.3	0.20

[1] The estimated value was > 65 m; Pacala et al. (1996) chose the lower value based on statistical considerations and because their field plots were not large enough to ensure reliability of estimates this high (see Ribbens et al. 1994).

dramatically and quickly in these stands as well. In mixed stands, the sequence of development will depend upon the initial presence or absence of the other two late-successional species. If beech or yellow birch are present, they will increase in abundance following the loss of hemlock. If neither late-successional species is present, early-successional species will coexist in the undisturbed forest at least to year 500.

If hemlock is not completely lost from the community it is likely to remain at very low densities. In fact, pollen records show that despite the dramatic decline of eastern hemlock in northeastern forests several times throughout history, it has recovered after each decline to be dominant in certain areas of the northeast (Foster and Zebryk 1993).

Late-successional species: life history characteristics

The continued presence of hemlock in forests for sustained periods of time is evidence of its remarkably high survivorship under low-light and low-growth conditions (Canham et al. 1994, Pacala et al. 1996) (Table 6). Hemlock grows relatively quickly when light is plentiful, but it can also survive while suppressed for long periods of time in the understory. Despite this flexibility, it does not produce and disperse recruits as successfully as the other species that comprise this community (Pacala et al. 1996, Ribbens et al. 1994). As a result, hemlock basal area in this study stayed relatively constant: while it did not lose basal area, it did not gain basal area either, especially when present in a community where it had an initially low abundance and competed with other species. However, the recruitment parameters used in the model may affect these results. In SORTIE, all species except beech are assigned the same number of new recruits per 100 cm diameter tree (Pacala et al. 1996). This may bias these simulations toward more hemlock than was realistic because under natural conditions, hemlock seeds experience a 15 to 25% germination rate and hemlock seedlings are extremely susceptible to failure (Godman and Lancaster 1990, Mladenoff and Stearns 1993, Swartley 1984). Because of its low regeneration rate, hemlock in the field may actually take much longer to dominate than it did in these simulations. However, certain site conditions may favor hemlock: for example, hemlock is quite successful in ravines and on rocky slopes (Black and Mack 1976, Rogers 1978, Whitney 1990).

Beech was quick to gain basal area in this forest. While beech grows more slowly than hemlock in full sun, it grows more quickly than hemlock under low light conditions (Table 6). In addition, it survives well under its own deep canopy while saplings of other species are more severely limited by its shade than by the shade of any other species (Canham et al. 1994). It also disperses over a larger distance, though still largely by sprouts, and has even higher low-light survivorship than hemlock (Table 6). As a result, once it is established beech is likely to continue increasing in basal area until it dominates the stand either by itself or with hemlock. Another reason for the quick increase of beech is its reproduction by root sprouting. In fact, in SORTIE the number of recruits per 100 cm beech tree is lower than the number of recruits per 100 cm tree of all other species in order to compensate for this method of reproduction, which is common at Great Mountain Forest (Pacala et al. 1996). While it is possible that these recruitment parameters actually make beech more prolific in SORTIE than in nature, a lower recruitment rate would simply lengthen the temporal scale of the dynamics. Beech saplings will still survive for an exceptionally long time beneath the shade of their conspecifics regardless of how quickly they colonize available space.

After the simulated loss of a significant amount of hemlock in hemlock stands, yellow birch was quick to occupy the space made available. This gap-phase species grows very quickly in full sun (Table 6). It also grows quickly in low light (Table 6), a trait which makes yellow birch uniquely able to take advantage of a small and short-lived gap. However, yellow birch has a low-growth mortality rate intermediate between those of early- and late-successional species (Pacala et al.

Table 7.—Predicted mortality rate (%/5 years) for sapling of each species under ambient light levels predicted for each canopy species (from Canham et al. 1994). Canopy species are listed horizontally across the top of the table. Species are listed in order of decreasing shade tolerance. See Table 1 for species abbreviations.

Sapling species	BE	HM	SM	YB	BC	RM	WA	RO
BE	2.6	2.5	2.2	2.2	2.1	2.2	2.1	2.1
HM	3.0	1.2	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1
SM	11.8	4.8	0.6	0.6	0.2	0.4	0.2	0.2
YB	20.4	11.2	2.3	2.4	1.0	1.7	1.0	1.0
BC	25.0	8.5	0.1	0.1	<0.1	<0.1	<0.1	<0.1
RM	56.0	34.4	2.7	3.1	0.1	0.1	0.1	0.1
WA	68.1	46.8	5.9	6.5	0.5	2.6	0.5	0.4
RO	76.8	57.3	6.6	7.5	0.1	2.1	0.1	0.1

1996). Mortality rate determined the successional status of yellow birch in these stands: after early-successional species, yellow birch was next to die when light became limiting. And under conditions of full sun, yellow birch RBA was outpaced by the early-successional species because its mortality curve lay above those of the early-successional species (Pacala et al. 1996). In field studies, yellow birch seeds are as likely to travel 1 m as 100 m. Incorporated into SORTIE, this flat dispersal function enables it to colonize distant gaps, thereby preventing the species from disappearing.

Early-successional species: life history characteristics

The early dominance of species such as red maple, black cherry, red oak, and white ash can be attributed to quick growth in full sun while their speedy decline resulted from high rates of mortality in low sun (Table 6). These species disperse well and grow quickly, but late-successional species grow almost as quickly in full sun. The late-successional species cast more shade and have lower mortality and more rapid growth in the low-light conditions they create (Canham et al. 1994). Thus, if even one late-successional tree is established, it will survive and produce recruits until the early-successional species no longer have access to light (Table 7).

Conclusions

While the results from this analysis can be used to predict forest development in other forested watersheds with similar species and size structures, the specific predictions presented here are not directly applicable to every southern New England forest. For example, research in central Connecticut has shown that black birch recruitment is quite common following hemlock mortality (Jenkins et al. 1999, Orwig and Foster 1998). The SORTIE model is not currently parameterized to predict black birch dynamics, and black birch is not common at our study site, so our analysis excludes this early-successional species. Also not considered here is the potential recruitment and migration of species across stand boundaries. Finally, this analysis does not account for the effects of any other disturbance. It is rare that 500 years of autogenic succession would occur without logging, windthrow, or invasion by another forest pest; these events would interrupt the long-term predictions we present here.

Still, this general pattern of succession will follow the mortality of a dominant species in any forest where light is the factor most limiting to growth. Immediately following mortality, shade-intolerant and gap-phase species will experience an increase due to enhanced light in newly-formed gaps. Where late-successional shade-tolerant species are present, they will slowly gain in dominance and continue to persist for years after the disturbance. In essence, selective removal of the dominant species will "restart" succession by increasing the RBA of early-successional shade-intolerant species; over time, late-successional and shade-tolerant species will increase in abundance at the expense of the early-successional species. Because variations in light transmission and shade tolerance can explain growth and mortality of individual tree species, they are excellent predictors of succession (Peet and Christensen 1980, Pickett et al. 1987).

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Overview of Hemlock Health

Dennis R. Souto[1] *and Kathleen S. Shields*[2]

Hemlock is very sensitive to stress—particularly insect defoliation

Although many insects and diseases are associated with hemlock, we will, ironically, draw our first conclusion, that hemlocks are very sensitive to the stress of insect defoliation, from a tale of gypsy moth defoliation. The unprecedented gypsy moth (*Lymantria dispar* L.) outbreak of 1981, when nearly 13 million acres were defoliated in the Northeast (Fig. 1), resulted in hemlock snags throughout the hardwood forest at West Point, New York (and many other locations), in 1986. There were so many larvae in May 1981 that all the preferred hardwood leaves were eaten and the caterpillars still needed more foliage. They turned their hungry attention to the white pine (*Pinus strobus* L.) and eastern hemlock (*Tsuga canadensis* (L.) Carriere) trees that grew in association with the hardwoods and, in many cases, defoliated these conifers completely. Hemlock and white pine responded to this defoliation in very different ways (Stephens 1984). Hemlock trees died within 1 year and most of these were dominant or codominant trees. In contrast, many fewer white pine trees died and the trees that did die succumbed slowly—within 5 years. In addition, these white pine were mostly intermediate or suppressed trees. Stephens (1984) hypothesized that the species impacts were caused by differential bud development patterns and by how much bud (1982 growth) damage each species sustained.

In 1953, a smaller gypsy moth outbreak caused similar damage to white pine and hemlock throughout New England. When House (1960) analyzed the impact of the outbreak on these native conifer species, he found that the results were clear-cut and identical to what Stephens would see decades later. When trees were completely (100%) defoliated, 74% of the canopy hemlocks were dead within 1 year. In contrast, only 28% of the white pine understory trees were dead within 5 years of the defoliation. House noted that the impacts decreased dramatically if defoliation was less than 100%. For example, only 9% of hemlocks that were 90% defoliated died and no hemlocks that were 80% defoliated succumbed. Clearly, 100% defoliation is a critical threshold for severe damage in hemlock.

Multiple stressors have significant effects on hemlock

Our second conclusion, that multiple stressors have significant effects on hemlocks, can be drawn from the image of an entire hillside of dead hemlock trees at Devil's Hopyard State Park in Connecticut. From 1989-1993, hemlock looper (*Lambdina fiscellaria* (Guenee) and *L. athasaria* (Walker) outbreaks occurred throughout the New England states and caused significant damage. For example, Maine's hemlock looper outbreak resulted in statewide defoliation of about 500,000 acres. The Maine Forest Service evaluated this outbreak's impact and found, quite surprisingly, that severe impacts (>30% of canopy hemlock dead or with dead tops) occurred on only 28,319 acres (Trial and Devine 1994). The acreage represented only 6% of the defoliated area. Additionally, the severely damaged areas were widely scattered and in small polygons (5 to 100 acres). Trial and Devine focused on the common denominators in the severely damaged areas and found several variables (Fig. 2). The first three variables are related to site conditions and/or microclimate conditions. The last two variables are related to other stressors besides hemlock looper defoliation. Interestingly, the Pennsylvania Bureau of Forestry found a similar list of other stressors when they investigated severe impacts on state lands associated with gypsy moth defoliation in oak stands in the 1980s (Quimby 1986). In fact, when they overlaid recent shelterwood cuts (partial harvesting on the Maine Forest Service list) with severe oak impacts, the correlation was striking. Similar lists of other stressors are associated with severe impacts for different defoliators and tree species. In the case of Devil's Hopyard State Park, hemlock looper defoliation coincided with the presence of and damage by hemlock woolly adelgid. In other parts of Connecticut, scale insects—elongate [or fiorinia] hemlock scale (*Fiorinia externa* Ferris), and shortneedle evergreen scale (*Nuculaspis tsugae* (Marlatt)—combine with hemlock woolly adelgid and/or looper to cause severe damage.

Hemlock woolly adelgid is the newest, major stressor of hemlock

Our last conclusion is that the hemlock woolly adelgid (*Adelges tsugae* Annand), a native of China and Japan, is the newest major stressor of hemlock. Native hemlock species in both countries are resistant to hemlock woolly adelgid (HWA) damage—they generally support only low population levels and show no growth loss or tree mortality when infested. However, high HWA population levels occasionally are present on heavily stressed trees (Mark McClure, personal communication). HWA was first reported in the United States in the Pacific Northwest in the 1920s. We do not know how it arrived there. However, western hemlocks (*Tsuga heterophylla* (Rafinesque) Sargent and *T. mertensiana* (Bongard) Carriere) were and are resistant to HWA damage. This is difficult to explain because western hemlocks and HWA had no time to co-evolve yet the tree species were already resistant. As a result, even though HWA arrived in North America by the 1920s, it was not yet a problem.

In the spring of 1953 or 1954, HWA was first reported in Virginia (Miller 1988). It was initially observed in a row of

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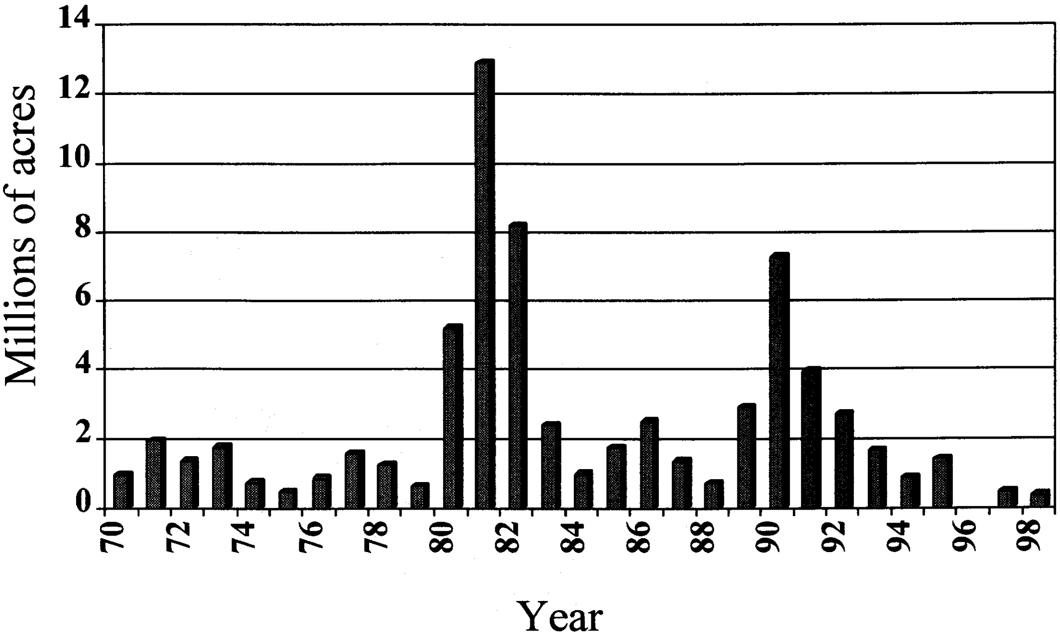

Figure 1.—Gypsy morh defoliated acres, 1970 - 1997.

- DRY SITES WITH EXPOSED LEDGE
- WET, POORLY DRAINED SITES
- CLOSE TO WATER (POINTS AND ISLANDS)
- PARTIAL HARVESTING
- TWO DEFOLIATIONS OR INSECTS

Figure 2.—Other hemlock stressors.

hemlock trees in Maymont Park (a large municipal park) in Richmond. Previously, the park had been the elaborate estate of an avid plant collector who sometime, perhaps early in the century, traveled to many parts of the world. Although the collector may have transported HWA to Virginia, we will never really know. We do know that this was the first report of HWA on the East Coast. Now for the first time, HWA existed in proximity of two hemlock species (*Tsuga canadensis* and *T. caroliniana*) susceptible to its feeding activities (Fig. 3). The HWA moved slowly westward, spreading from ornamental trees to the natural range of hemlocks in the Blue Ridge. Once there, spread and impacts accelerated through the early 1980s.

The year 1985 was a very significant one for HWA. In January, a severe cold wave occurred in Virginia with unprecedented low temperatures. At elevations above 2,000 feet, temperatures of -20 to -28°F were common. Surveys conducted in the spring/summer of 1985 revealed a complete absence of HWA above 2,000 feet (Miller 1988). Below 2,000 feet, HWA was present, but in greatly reduced numbers. Since 1985, HWA populations have slowly but steadily increased, as has its distribution in Virginia. Significant overwintering HWA mortality and subsequent population recovery are themes we would see again in Connecticut after the winter of 1993-1994.

Another significant event in September of 1985 was that Hurricane Gloria might have transported HWA across Long Island Sound to Connecticut. This could explain why Mark McClure first observed and reported HWA in Connecticut in 1986—the first report of HWA in New England. Although HWA had been an East Coast resident for over 30 years, the attention and concern over its impact on our forests and ecosystems began to accelerate with McClure's initial report and subsequent research activities and results.

Currently, Massachusetts is the northernmost state where HWA occurs (Fig. 4). The first report was of an HWA-infested backyard tree adjacent to a large, heavily used municipal

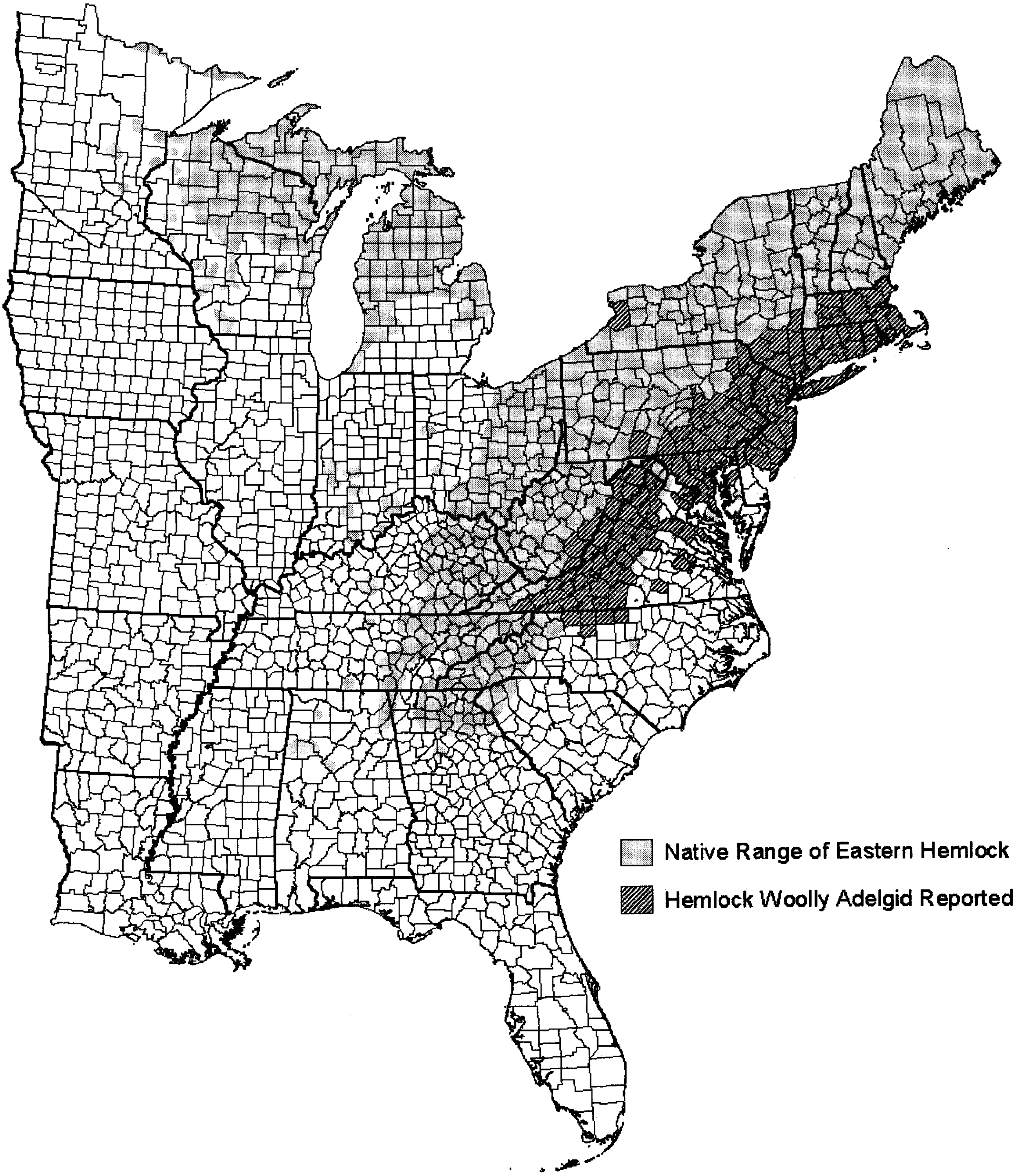

Figure 3.—Native range of eastern hemlock and hemlock woolly adelgid distribution - 1998.

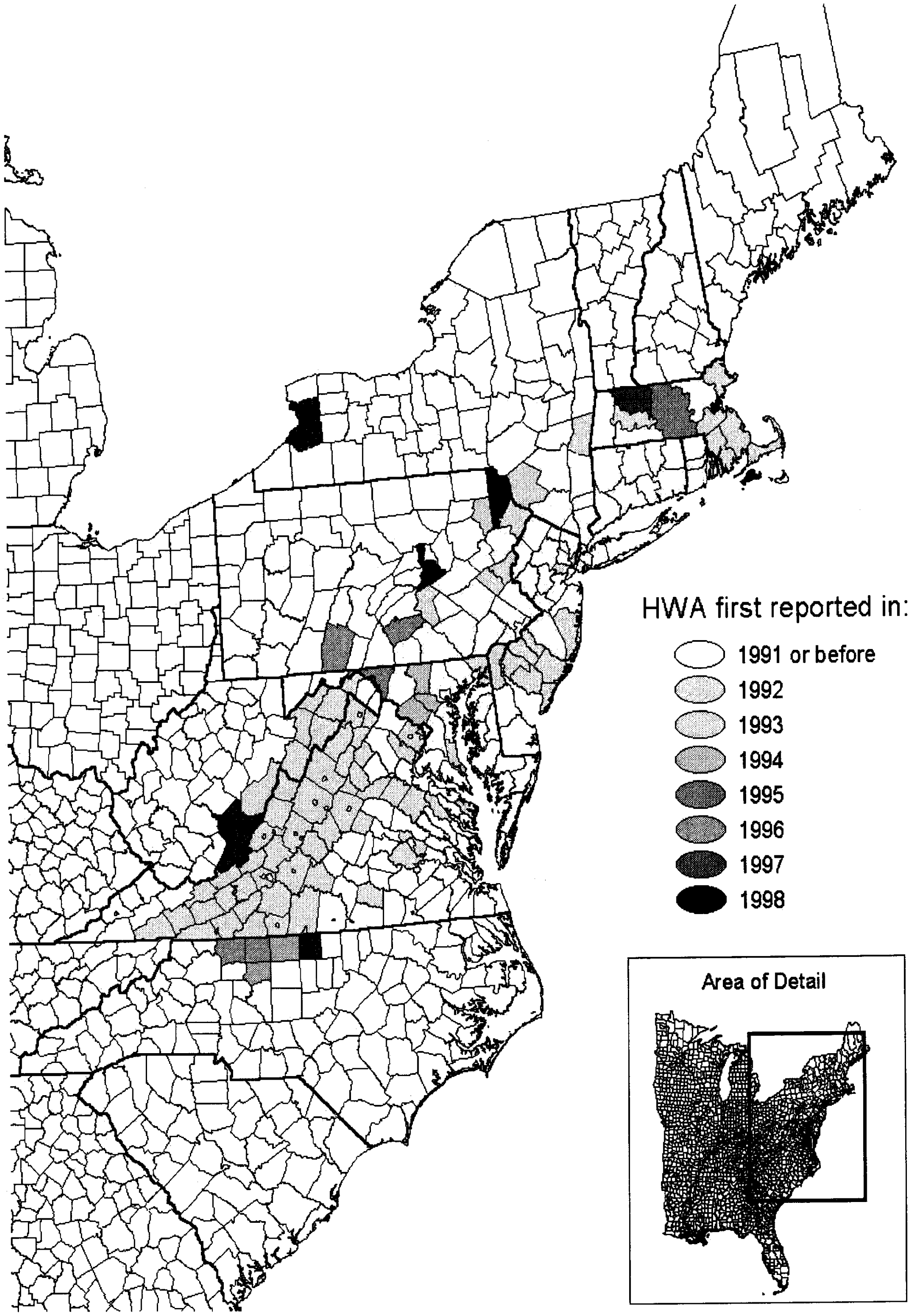

Figure 4.—Hemlock woolly adelgid distribution by year reported 1991-1998.

park (Forest Park) in Springfield. We do not know how HWA arrived there, although some entomologists suspect birds transported it. This initial location (municipal city park) does remind us of the initial observation in Richmond, VA. Massachusetts is a significant case study to observe for those who ask, how many more states and Canadian provinces will become infested by HWA? Or even more importantly, how far north will significant impacts to hemlock health occur and can we predict the location of those impacts?

The northern spread of HWA up the Hudson River Valley in New York has stalled at 42 degrees latitude, near the border of Dutchess and Ulster Counties (Michael Birmingham, personal communication). The most recent, northernmost HWA infestation in this area was reported in 1991. Since then, no new infestations have been discovered farther to the north. What is intriguing is that this same location is the northernmost stopping point for the spread of four other forest insect pests in New York: elongate hemlock scale, shortneedle evergreen scale, red pine scale (*Matsucoccus resinosae* (Bean and Godwin), and red pine adelgid (*Pineus borneri* Annand). We can only hope that this location represents the first geographic limit to HWA's northward spread.

The characteristic that most concerns us about HWA is its chronic nature. For example, both gypsy moth and hemlock looper outbreaks can spectacularly erupt and collapse from one year to the next. Many years can pass between outbreaks allowing trees and stands time to recover, if weather is good and other stressors absent. In general, this is the way most forest pests behave. However, HWA is completely different. Once it arrives, it is there for the duration. With such a chronic stressor present, the likelihood that other stressors will eventually coincide with HWA damage and severely affect hemlock health seems quite probable. This may explain why in New Jersey the greatest impacts on hemlock have occurred in the stands that have had HWA the longest (Mayer et al. 1988).

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The Summer Drought Related Hemlock (*Tsuga canadensis*) Decline in Eastern North America 5,700 to 5,100 Years Ago

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Abstract

High resolution paleoecological analyses from Shepherd Lake, Ontario, Canada, show that 10 to 100 year lake level fluctuations due to climatic change were responsible for alterations in the aquatic biodiversity 5,700 to 5,100 years ago. Thermophilic aquatics such as the Bushy pondweed *Najas flexilis*, charophyte algae and aquatic invertebrates indicate water level fluctuations of several meters, which were likely linked to a warm, dry summer climate. Pollen analysis and radiocarbon dating at Wilcox Lake shows a hemlock decline at 5800 years ago that lasted 1,000 years. Multiple regression analysis indicates that the decline coincides with a drop in mean annual precipitation from 830 to 700 mm. From fossil pollen analysis the impact of these droughts on the upland forest is poorly visible, except for the hemlock decline during the first half of the 6th millennium ago. The two-phased reduction of hemlock from 30% tree cover to less than 5% within centuries is found in large parts of northeastern America. Our results imply drought-weakened hemlock trees and stands, and that drought may have triggered local insect calamities, such as hemlock looper attack. However, this also implies that climatic change and not a pathogen-pest attack was responsible for the synchronous decline of hemlock all over its range in eastern North America. Reconstructing and understanding the hemlock decline is, therefore, of interest to the public and to ecosystem managers when anticipating the effect of pathogen-pest attacks combined with climatic change.

Introduction

Hemlock (*Tsuga canadensis* (L.) Carriere) is a prominent forest tree in the northeastern United States and adjacent Canada. Although hemlock wood is economically unimportant today, hemlock stands have amazing beauty and an important cultural value for humans. However, in the past few years an increasing number of stands have become threatened by the woolly adelgid (*Adelges tsugae* Annand), an introduced insect pest from Asia which has defoliated and killed stands (McClure 1987, Orwig and Foster 1998). It is, therefore of interest to know if similar and comparable large scale hemlock mortality has occurred since its expansion from its ice age refuge to its present range in eastern North America.

Over the past 60 years pollen analysis has revealed forest history of the postglacial period. In southern Ontario, for example, the major expansion of hemlock occurred between 9,000 and 8,000 years ago based on calibrated radiocarbon dates. Pollen studies done within the hemlock range also show that after a rise in importance it had a dramatic and rapid decline, which began 5700 to 5600 years ago (i.e. 4,900 to 4,800 radiocarbon years ago). Thereafter, it took at least a thousand years for it to recover, and at most locations hemlock never became as prominent as it was before its decline. This catastrophic decline from 30% to less than 5% within decades has been known and recognised since the first pollen studies done by Auer (1930) in Canada and by Deevey (1939) in the United States who wrote: "During period C2 conditions in southern Connecticut became slightly more xerophytic, as illustrated by a rise in hickory and the somewhat less striking decline of hemlock". Even if other studies also revealed a hickory maximum during and after the hemlock decline and attributed this to xerothermic conditions in-between two phases of mesic climatic conditions (Niering 1953), the drought hypothesis for the decline was not pursued further at that time; it took another 25 years before Margaret Davis (1981) proposed possible explanations for such a decline. She favoured the hypothesis of a pathogen or pest attack by hemlock looper (*Lambdina fiscellaria*, Lepidoptera), especially when comparing the rapidity of the demise to pathogen attacks occurring during the 20th century, such as the extirpation of chestnut (*Castanea dentata*) due to introduced chestnut blight in eastern North America (Andersen 1974). She pointed out that this explanation was the most probable due to a lack of evidence as to other causes, e.g. climatic change, fire, windstorms and/or prehistoric human activities. First attempts failed to find direct evidence of the pathogen or pest, e.g. the chitinous insect remains (Allison et al. 1986), but some authors of textbooks accepted that hemlock looper was the reason for the decline (e.g. Delcourt and Delcourt 1991). It took several years to get the first evidence of an increased abundance of hemlock insect pests during the decline (Bhiry and Filion 1996). However, until now the question of why a pathogen-pest attack should have occurred around 5,700 years ago and not centuries before or after was not asked. Recently drought, based on sedimentological evidence, was proposed as a triggering mechanism for the potentially explosive but unproven massive presence of hemlock looper in billions of individuals (Yu and McAndrews 1996; Yu et al. 1997). On the other hand, research on the consequences of the reduction in hemlock stands became important during the last few years only, showing that trees such as birch (*Betula* spp.), beech (*Fagus grandifolia*), pine (*Pinus* spp., especially *P. strobus*) and maple (*Acer* spp., especially *A. saccharum*) were filling the canopy gaps formed by dying hemlock (e.g. Fuller 1998) and that the hemlock decline had only a slight effect on lake trophy and biodiversity (Boucherle *et al.* 1986; Hall and Smol 1993). Therefore, and because the hemlock decline was of such importance for prehistoric biodiversity, we here assess mortality-triggering mechanisms by using high-resolution

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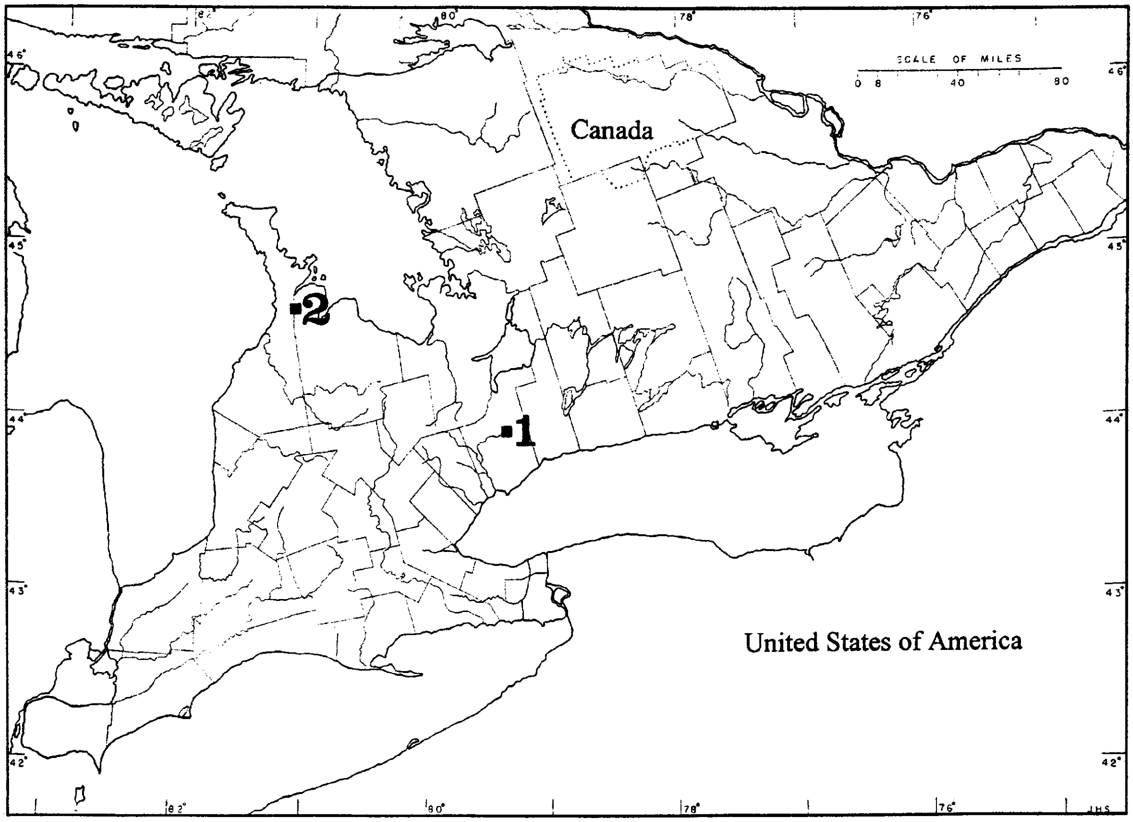

Figure 1.—Location map: Wilcox Lake is at 43°56'24"N, 79°25'58"W, 295 m asl, and Shepherd Lake is at 44°39'30" N, 81°08'30" W, 235 m asl. in southern Ontario, Canada.

pollen and macrofossil data from two sites in southern Ontario. Assessing and clarifying the mechanisms of a near-extinction of hemlock 5,700 to 5,100 years ago may therefore add to our understanding of former forest dynamics and of future threats to hemlock by the woolly adelgid and climatic change.

Materials and Methods

For the present study we chose two lakes: Wilcox Lake is 30 km north of Toronto on the Oak Ridges Moraine and Shepherd Lake is 150 km north-west of Toronto on the Bruce Peninsula (Fig. 1). Wilcox Lake (44 ha) is a kettle lake which formed during the late Pleistocene ca. 15,000 years ago. The cool-temperate climate is typified by the record at Richmond Hill (230 m asl) where the 1951-1980 means were: for January temperature -7.4°C, for July temperature 20.5°C and for annual precipitation 805 mm that is evenly distributed throughout the year (Environment Canada 1982a, b). Judging by remnant woodlots the original mixed forest was dominated by sugar maple (*Acer saccharum*), beech (*F. grandifolia*), red oak (*Quercus rubra*), white oak (*Q. alba*) white ash (*Fraxinus americana*), birch (*Betula papyrifera, B. alleghenienisis*), basswood (*Tilia americana*), ironwood (*Ostrya virginiana*), large toothed aspen (*Populus grandidentata*) and, formerly, white elm (*Ulmus americana*) together with white pine (*Pinus strobus*) and hemlock (*Tsuga canadensis*). Local wetland forest included white cedar (*Thuja occidentalis*), tamarack (*Larix laricina*), red maple (*Acer rubrum*), silver maple (*A. saccharinum*) and black ash (*Fraxinus nigra*).

Shepherd Lake (15 ha) was formed after the retreat of the Glacial Lake Algonquin approximately 11,500 years ago; it lies between low drumlins formed on Silurian dolostone. The lake is surrounded by grazing land and a few cereal crop fields as well as woodlots much like those around Wilcox Lake except that white spruce (*Picea glauca*) and balsam fir (*Abies balsamea*) are prominent. In the lake the Bushy pondweed (*Najas flexilis*), as well as some stonewort algae (*Chara* sp. and *Nitella* sp.) build up dense mats, indicating the lake to be oligotrophic to mesotrophic. The lake has only a very small inlet and outlet indicating rather stagnant water. At the nearby climate station of Wiarton the mean January temperature is -7.1°C, the mean July temperature is 18.5°C and the mean annual precipitation of 965 mm with a peak in November and December (Environment Canada 1982a, b) due to the effect of nearby Lake Huron. A core of uniform calcareous organic gyttja sediment was taken in 1997 from the lake's center in 1.25 m of water depth with a modified Livingston piston sampler (Wright 1967). Ten Radiocarbon dates were measured on terrestrial plant remains at the

Table 1.—Radiocarbon dates from Shepherd Lake, Ontario, performed at the University of Utrecht (The Netherlands).

Depth (cm)	^{14}C-age (BP)	Calibrated age range (years ago)	University of Utrecht No. (UtC)
387	2570 ± 50	2,751-2,715	7154
446	3049 ± 41	3,337-3,173	7215
531	4007 ± 41	4,521-4,414	6129
555.5	4400 ± 110	5,254-4,847	6130 (not used for interpolation)
570.5	4250 ± 170	4,986-4,536	6131
601	4900 ± 70	5,716-5,589	6132
615	5040 ± 60	5,896-5,722	6133
664	5860 ± 50	6,739-6,644	7216
752	7572 ± 100	8,411-8,195	7068
806	8187 ± 47	9,216-8,993	7155

University of Utrecht (The Netherlands), allowing an accurate dating of the sediments and of paleoecological events (Table 1).

For the macrofossil analyses sediment slices of 1 cm thickness representing 15 cc of sediment each were processed following Haas (1996). Sieving of sediment samples was done using 2000, 1000, 500, 250 and 125 mm mesh sieves. Residues were analyzed for plant and animal remains. Pollen samples were prepared following Moore et al. (1991). Pollen determinations were done following McAndrews et al. (1973) and by using the reference collection of the Royal Ontario Museum, Toronto. The pollen sum, generally over 500 per sample, was calculated using total pollen, but by excluding pollen of aquatic plants and spores of bryophytes and ferns.

Results

Figure 2 shows a simplified pollen percentage diagram from Wilcox Lake with the regional zonation since the deglaciation 14,000 years ago (McAndrews 1981). Hemlock migrated from a southern refuge to the upland around Wilcox Lake about 9,000 years ago coincident with climatic warming and moistening. It also indicates an abrupt hemlock decline beginning 5,800 years ago, which is synchronous with other localities in northeastern North America. Canopy gaps formerly occupied by hemlock were filled by maple, pine, and oak. It took a 1,000 years for hemlock to recover, although it never gained the same importance in forests again.

Coincident with the hemlock decline, the annual precipitation dropped from 830 to 700 mm, the sharpest drop since hemlock migrated. At the western limit of hemlock the annual precipitation is 700 to 740 mm. In addition to reconstructing climate using the pollen record we also use local aquatic plants and animals as indicators of climatic change (Haas 1996). Figure 3 shows a selection of plant and animal macrofossils found in Shepherd Lake sediment dating 8,000 to 2,600 years ago. As expected, macrofossils from upland plants such as trees are rare at the center of Shepherd Lake 150 m away from the shore. A few leaves, anthers and cone-scales of hemlock were found.

However, note that the first hemlock macrofossils were present shortly after 7,000 years ago, suggesting that the tree had migrated later to the Bruce Peninsula, which is north of Wilcox Lake (Fig. 1). Hemlock remains between 6,200 and 5,200 years ago indicate trees grew on the nearby drumlins. After 5,200 years ago hemlock fossils are rare, which confirms the near-extinction of hemlock indicated by fossil pollen. In contrast, aquatic plant fossils are more common than remains from upland trees. Bushy pondweed (*N. flexilis*) and charophyte algae dominated the postglacial period. Charophyte data are only partially shown, but the most prominent species was *Chara foliolosa*, a southern species which ranges northward to within 300 km of Shepherd Lake. Both species are typical for shallow water conditions where the water is less than 4 m deep, and thus indicate shallow water at the center of the lake (Haas 1996, Haas et al. 1998) where they were both extremely abundant around 5,700 years ago. *N. flexilis* is an annual plant that reproduces only from seed; it needs warm water conditions of more than 19°C for some days to germinate and to subsequently produce seeds (Haas 1996). This temperature is normally reached in late June to early July where the water is less than 4-m deep, i.e. where there is no thermocline. Such shallow, warm water seems to have prevailed 6,000-5,600 years ago, with a distinctive peak around 5,700 years ago perhaps lasting only a few decades. Given the location in the core and the today's water level this also means that the lake level of Shepherd Lake was at least 2-4 m lower than today. This indicates an extremely warm and dry summer climate.

Several types of animal remains and the northern presence of *C. foliolosa* sustain this reconstruction of summer climate and lake levels, e.g. abundant caddisflies (Trichoptera), freshwater sponges (Porifera), bryozoans, water mites

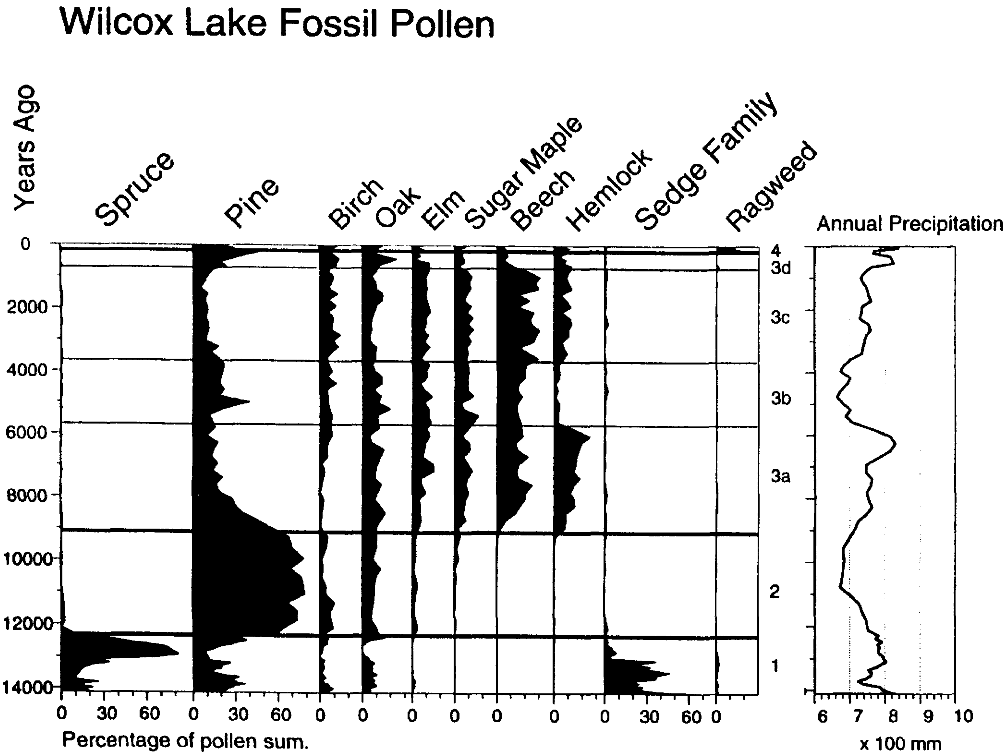

Figure 2.—Pollen percentage diagram from Wilcox Lake, Ontario, showing selected plant taxa. The complete counts are deposited in the North American Pollen Database. The pollen percentage sum is 200 tree pollen grains. Note the hemlock decline at 5,800 years ago. Annual precipitation is plotted as a three-point running mean of values calculated by the multiple regression equation of Bartlein and Whitlock (1993).

(Oribatida), and Ostracodes (Fig. 3). Interestingly, the abundance of charcoal and minerogenic particles does not change significantly in the dry period. This suggests that forest fire was unimportant during the mid-postglacial period at this latitudes, which confirms studies by Anderson et al. (1986) in Maine, and observations in Québec, Canada (C. Carcaillet, pers. communication). Other peaks of *N. flexilis* occurred around 6,300 and 5,300 years ago, and both peaks are paralleled by small peaks of animal remains, especially, Ostracodes. These peaks, spanning a few decades at most, were also the result of low water caused by drought. As *C. foliolosa* is only present in small amounts for this time period, this may point to the fact that such droughts were slightly less severe than the drought around 5,700 years ago.

Fig. 4 shows the corresponding pollen percentage diagram from Shepherd Lake for the period 5,900 to 4,400 years ago. The major event is the hemlock decline and minimum. Note that the total curve of non-arboreal-pollen (NAP, i.e. herbs), do not increase at this time (Fig. 4). Therefore, and because tree pollen did not change, the hemlock decline and succession happens within a dense forest where gaps are filled rapidly.

In detail, the hemlock (*T. canadensis*) decline happened in two phases. The first decline phase from over 35% to 25% occurred 5,700 years ago; it was followed by increased pollen of gap-filling tree species such as pine (*Pinus*) and birch (*Betula*) followed by a short, but intense recovery of hemlock before its second decline started 5,300 years ago. This decline was much stronger and spanned approximately 200 years. Thereafter hemlock did not recover for more than 1,000 years at Shepherd Lake, and in southern Ontario in general. This second decline provoked a succession of different tree species, especially beech (*F. grandifolia*), birch (*Betula*) and elm (*Ulmus*). Note that this change in forest diversity was also accompanied by some small peaks of herbs, such as sedges (Cyperaceae), grasses (Poaceae) and mugwort (*Artemisia*). Forest gaps must have been filled rather rapidly with trees within 10 to 20 years, the limit of stratigraphic resolution.

Discussion

The two hemlock declines at Shepherd Lake occur within seven centuries and coincide with major drought events shown by the macrofossil data. This implicates climate in the hemlock decline in northeastern North America. An insect pest attack could not be documented at Shepherd Lake, where no hemlock looper remains were found, and where insect remains from upland species are rare in general. This does not exclude hemlock looper which may have had a

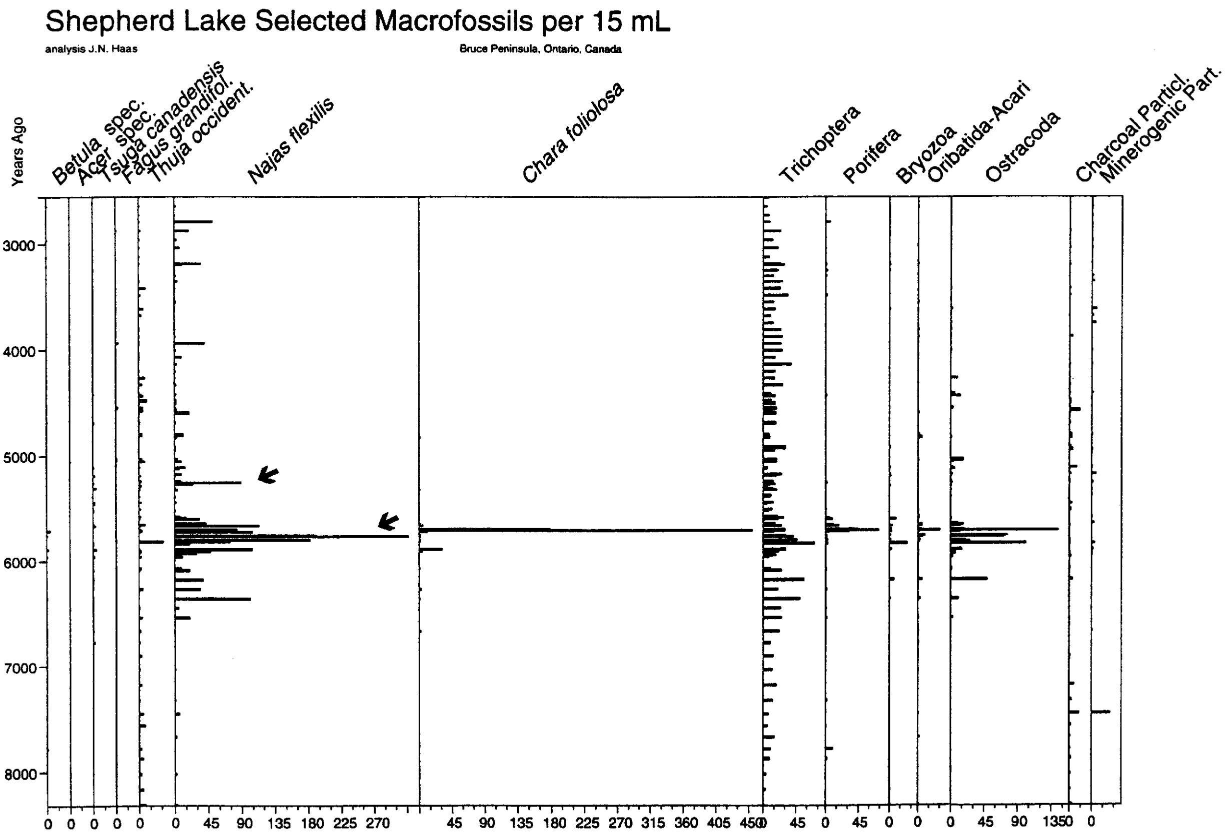

Figure 3.—Macrofossil concentration diagram from Shepherd Lake, Ontario, with selected plant and animal taxa 8,200 to 2,500 years ago. Note the peaks of *Najas flexilis* abundance around 5,800 and 5,300 years ago (arrows), as direct evidence for low lake-levels due to warm-dry summer climate.

destructive defoliation effect at other localities (Bhiry and Filion 1996), but it may indicate that these hemlock looper attacks were only of local importance, as they are in today's forests (Fowells 1965). Such pest attacks would be an indication for drought-weakened and dying hemlock trees. However, a triggering of local hemlock looper populations by climatic change is conceivable and would fit to the today's population behavior of hemlock looper, which never explode more than on a local scale (Fowells 1965). This would also explain why hemlock looper remains are only mentioned and found from a few paleoecological studies (for example Bhiry and Filion 1996, Lavoie et al. 1997).

Of course the droughts were not only present locally at Shepherd Lake or just in southern Ontario. For example, the sediment description of several bogs and lakes analyzed for pollen and macrofossils by Auer (1930) show sediment changes during the hemlock decline suggesting synchronous drought, e.g. from lake mud to bog peat or from fen peat to bog peat. Such records were not discussed in terms of climatic change. However, in recent years some studies indicated a major drought interval in North America during the first half of the 6th millennium ago (Valero-Garcés et al. 1997, Yu et al. 1997), but the resolution and dating quality of most of these studies was low.

To explain such a drought, we must invoke persistence of dry Pacific and/or arctic air masses. In addition, the summer drought events 5,700 to 5,100 years ago fit well to the reconstructed climate in central Europe (Haas et al. 1998) where a warm and dry period was reconstructed for 5,700 - 5,300 years ago within the Alpine arc of Switzerland and northern Italy. So, a general northern hemispheric dry period is indicated.

However, when assessing a climatic nature of the hemlock decline, it is important to assess the ecology of the species. Hemlock is one of the few tree species in North America which has a distinctive shallow rooting system that is susceptible to drought (Fowells 1965). In addition, low atmospheric humidity restricts hemlock growth. Normally the rooting system of seedlings or young trees is confined to the upper 20 cm of soil. A few days of severe summer drought may result in the near-complete mortality of hemlock saplings and populations (Fowells 1965; Godman and Lancaster 1990). It is therefore important to foresters today to keep hemlock litter moist by maintaining shade from adult hemlock trees or other tree and shrub species. Therefore, seedlings and young, immature trees would have suffered from drought periods 5,700-5,100 years ago. Such susceptibility has been described from different places in

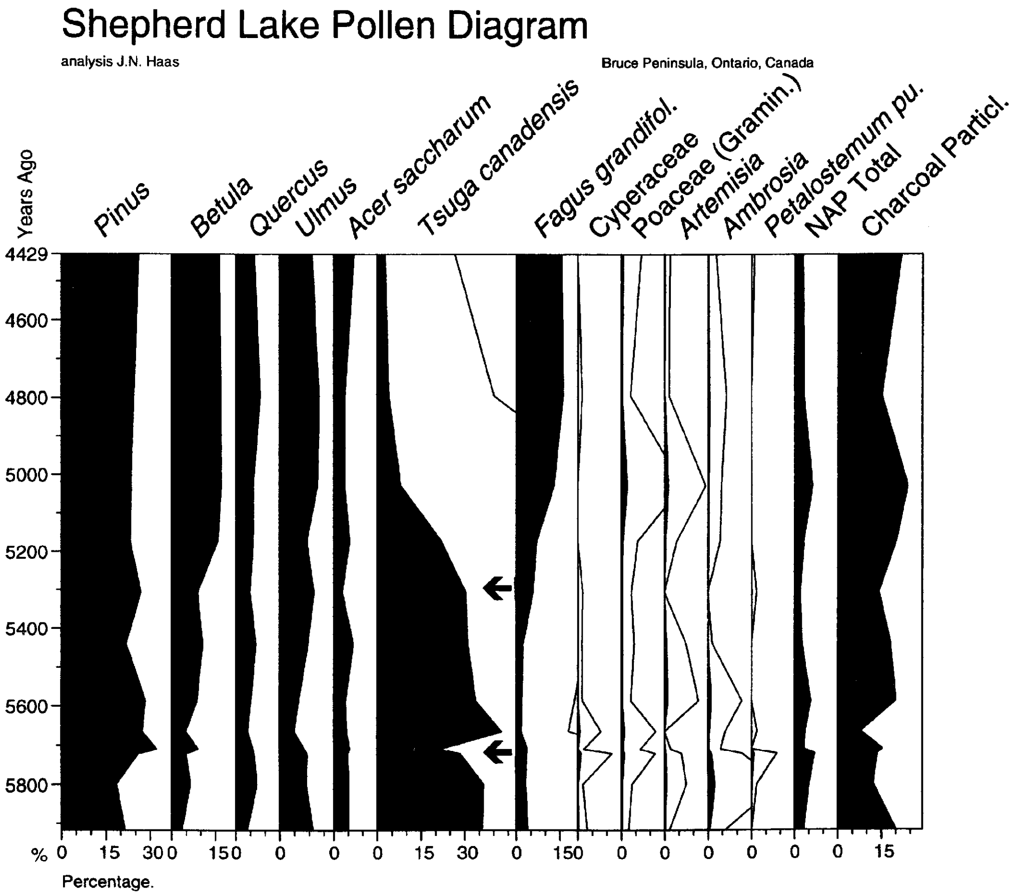

Figure 4.—Pollen percentage diagram from Shepherd Lake, Ontario, with selected plant taxa 5,900 to 4,400 years ago. Note the two-phased hemlock decline around 5,700 years ago, and after 5,300 years ago (arrows). NAP = Non-arboreal-pollen Total (i.e. herbs).

North America (Fowells 1965). Therefore there perhaps was a vicious circle during the 5,700 - 5,100 decline of hemlock: even if large hemlock trees may have survived the drought to be followed by normal mortality, their seedlings would not have survived, allowing other species to grow, which in their turn would have prevented extensive regeneration of hemlock when climate became wetter again. Soil moisture and atmospheric humidity are limiting factors at the natural range limit of hemlock towards the west and the south (Fowells 1965). Hemlock stands on shallow or coarse soils were at risk in former times, as they are today. Shady moist slopes and ravines, on the other hand, would have been places where hemlock survived severe droughts because of reduced, but still available soil moisture. These ecological characteristics of hemlock trees and stands today, therefore, contradict the hypothesis proposed by Filion and Quinty (1993) who attributed the decline to moister climate. Hemlock (Fowells 1965) and our results from Wilcox and Shepherd Lake demonstrate the contrary, and attribute the hemlock decline to drought.

The two-phase hemlock decline over 600 years between 5,700 and 5,100 years ago was also recently noted by Fuller (1998), but her few radiocarbon dates indicate the two declines to be 6,000 and 5,500 years ago, which is slightly too old in comparison with the more accurate dates from Shepherd Lake. Thus the decline of hemlock was a long-term process, provoking different kinds of gap-filling reactions by different tree species depending on the site conditions. It was a synchronous process all over eastern North America linked to drought and perhaps also to local pest attack, but the subsequent forest regeneration and tree population dynamics cannot be seen as a standard process, but were related to time and specific site conditions and geographic location.

Conclusions

Hemlock and hemlock stands were sharply reduced 5,700 to 5,100 years ago because of summer droughts. Seedlings and young hemlock suffered and died because of their shallow rooting system, as soil moisture and atmospheric humidity are the most important limiting factors for hemlock. Larger trees under moisture stress sustained a fatal, but local pathogen-pest attack, perhaps the hemlock looper although not all trees died. Such an attack was triggered by drought, but would not have been the reason itself for the decline of hemlock. Understanding such complex interactions between climate, plants and animals on a long-lasting scale is important when assessing the possible effect of future climatic change. It also shows that major mortality of hemlock populations occurred long before today's attack by pathogens such as the hemlock woolly adelgid. And it also indicates that hemlock survived climatic stress and pathogen attack 5,700 to 5,100 years ago, and that the recovery took more than 1,000 years.

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We thank Thomas Giesecke and Sabine Karg for their help with field work, Christian Mulder for providing specific references, and Peter Del Tredici and Vicente Sánchez for discussions on our results. Greatful acknowledgements go to the Swiss National Science Foundation (Project 823A-046659 to J.N.H.) for general support, to the Royal Ontario Museum Foundation for funding radiocarbon dates, and to the University of Toronto Department of Botany for providing research facilities.

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Is *Pseudoscymnus tsugae* the Solution to the Hemlock Woolly Adelgid Problem?: An Early Perspective

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Abstract

Hemlock woolly adelgid, *Adelges tsugae* Annand (Homoptera: Adelgidae) is native to Japan where it is an innocuous inhabitant of *Tsuga diversifolia* Masters and *T. sieboldii* Carriere. Native populations of this insect are regulated by host resistance and natural enemies. However, introduced populations in eastern North America attain damaging levels on *T. canadensis* (L.) Carriere and *T. caroliniana* Engelmann and are regulated mainly by weather and negative density-dependent feedback mechanisms related to host deterioration. The current hope for suppressing introduced populations of hemlock woolly adelgid in eastern North America lies with the exotic predator, *Pseudoscymnus tsugae* Sasaji and McClure (Coleoptera: Coccinellidae). Extensive laboratory and field studies of the biology and predatory ability of *P. tsugae* revealed that it has great potential for biological control. Nearly 120,000 adults of *P. tsugae* were released in hemlock forests in Connecticut, New Jersey and Virginia from 1995 through mid-June 1999. *P. tsugae* reproduced, dispersed, overwintered, and showed remarkable short-term impact on *A. tsugae* by reducing adelgid densities 47 to 88% in only five months on release branches at the early sites. Spiders, the most important natural enemies of *P. tsugae*, reduced efficacy at some sites. In addition, the recent string of relatively mild winters has been conducive to the survival of *A. tsugae* and of the elongate hemlock scale, *Fiorinia externa* Ferris (Homoptera: Diaspididae) another introduced pest from Japan. Consequently, adelgid and scale populations at some sites have grown and trees have continued to decline despite the presence of *P. tsugae*. Larvae and adults of *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae), a polyphagous predator from Japan, were observed in high numbers from April through September at several study sites, especially those where trees were heavily infested with *A. tsugae*. Considering how rapidly hemlock trees are injured following adelgid attack, *P. tsugae* must establish, reproduce and disperse quickly following a release of relatively few beetles. To become a permanent solution to the hemlock woolly adelgid problem in North America, *P. tsugae* must also be able to consistently maintain adelgid populations below injurious levels. Studies to evaluate the long-term efficacy of releasing 10,000 adults of *P. tsugae* in 5-10 acre infested hemlock forests were initiated in spring 1998 in Connecticut, Virginia and New Jersey and were expanded in 1999 to include additional sites there and others in Maryland, Massachusetts, New York, North Carolina, Pennsylvania, Rhode Island, and West Virginia.

Introduction

Hemlock woolly adelgid, *Adelges tsugae* Annand (Homoptera: Adelgidae) is native to Japan where it is an innocuous inhabitant of *Tsuga diversifolia* Masters and *T. sieboldii* Carriere throughout their natural growing areas. Native populations of *A. tsugae* in Japan are maintained at low densities on hemlock by a combination of host resistance and natural enemies (McClure 1992, 1995a, 1995b). The previously unknown beetle, *Pseudoscymnus tsugae* (Coleoptera: Coccinellidae)(Sasaji and McClure 1997), was the most common and effective insect predator of *A. tsugae* in Japan. It occurred at 24 of 66 infested sites where it killed 86-99% of adelgid eggs (McClure 1995a).

A. tsugae is a destructive introduced pest of *T. canadensis* (L.) Carriere and *T. caroliniana* Engelmann in 11 eastern states from North Carolina to southern New England. Although populations of *A. tsugae* on ornamental hemlocks can be managed successfully using a program that relies heavily on chemical pesticide applications (McClure 1987a, 1995c), adelgid populations in the forest are presently unmanaged and threaten to eliminate *T. canadensis* and *T. caroliniana* throughout much of their natural ranges. Introduced populations of *A. tsugae* are host-destroying and self-annihilating (McClure 1991a). None of the native natural enemies which inhabit hemlock forests in eastern North America are effective biological control agents. Therefore, the dynamics of adelgid populations is driven mainly by weather (McClure 1989, 1996) and the negative density-dependent consequences of host deterioration on adelgid performance (McClure 1991a).

P. tsugae has clearly evolved as a specialized predator-prey system in Japan and appears to be the most promising biological control candidate. Extensive studies in Connecticut on the biology and predatory ability of *P. tsugae* revealed that it possesses many attributes of a successful biological control agent (Cheah and McClure 1996, 1998). In addition, P. *tsugae* is amenable to mass culturing on live *A. tsugae* collected from the field and three or more generations can be reared each year in the laboratory under controlled temperature conditions (McClure and Cheah 1998). This paper evaluates the performance of *P. tsugae* during its first three years in the field and provides an early perspective on whether or not this predator will be a solution to the hemlock woolly adelgid problem in eastern North America

Materials and Methods:

Field releases of *P. tsugae*

During the past five years we have released more than 120,000 adults of *P. tsugae* at 14 sites in Connecticut, one in New Jersey and two in Virginia (Table 1). The 14 release

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Table 1.—Location and description of hemlock forests where we released *Pseudoscymnus tsugae* between 1995 and 1999 in Connecticut (CT), New Jersey (NJ), and Virginia (VA). Infestation levels for hemlock woolly adelgid (HWA) and elongate hemlock scale (EHS) when *P. tsugae* was first released are: None (N) present; Low (L) = most trees and branches not infested and without injury; Moderate (M) = about half the trees and branches infested and some injured; High (H) = most trees and branches infested and injured, Very High (V) = all trees and branches infested and greatly injured. See also Fig. 1.

					Infestation		*P. tsugae*	
Site	State	County	Town	Elevation (ft)	HWA	EHS	Year first released	Total released to date
1.	CT	Fairfield	New Fairfield	700	V	V	1997	2,100
2.	CT	Litchfield	New Hartford	600	L	M	1996	10,505
3.	CT	"	Washington	776	L	H	1998	10,500
4.	CT	"	"	580	L	L	1999	5,000
5.	CT	Hartford	Bloomfield	500	M	M	1996	10,760
6.	CT	"	Granby	780	L	N	1999	10,000
7.	CT	"	Suffield	570	M	N	1999	10,000
8.	CT	"	Windsor	150	M	M	1995	3,125
9.	CT	Middlesex	East Haddam	210	M	L	1999	6,086
10.	CT	New Haven	Cheshire	260	H	M	1995	100
11.	CT	"	Hamden	250	H	H	1997	3,600
12.	CT	New London	Voluntown	390	M	N	1999	3,000
13.	CT	Tolland	Union	920	L	N	1999	10,000
14.	CT	Windham	Pomfret	270	M	N	1998	5,084
15.	NJ	Sussex	Vernon	1,235	H	H	1998	10,000
16.	VA	Albemarle	Charlottesville	400	M	N	1998	10,500
17.	VA	Rockbridge	Montebello	3,200	M	N	1997	10,100

sites in Connecticut represent all eight counties and include sites in the southern part of the state where *A. tsugae* has been present for more than 10 years and where many hemlocks have been killed or severely weakened, sites in the central and north-central parts where adelgid infestations are 5-10 years old and where trees are in varying levels of decline, and sites in the northeast and northwest towns where adelgid infestations are patchy and light and where trees are mostly unaffected (Fig. 1).

Between 100 and 10,760 adults of *P. tsugae* (~1:1 sex ratio) were released at study sites in the spring by placing beetles directly on trees. The number of beetles released initially and in subsequent years and the pattern of their release within the site were determined by the nature of the study. In early studies 2,000-3,000 beetles were released onto relatively few trees to investigate local impacts of *P. tsugae*. To enhance the establishment of *P. tsugae*, some of these sites were later augmented to achieve release densities of at least 10,000 beetles. A minimum of 5,000 beetles were released at other new sites in an effort to establish *P. tsugae* throughout Connecticut. Later studies to evaluate dispersal and long-term impacts involved the release of at least 10,000 adult beetles over a larger area. Observations were made at sites prior to and periodically following release of *P. tsugae* to monitor hemlock health, abundance of nymphs and adults of *A. tsugae*, overwintering ability of *P. tsugae*, and the presence of any other arthropod pests of hemlock or their natural enemies.

Evaluating the efficacy of *P. tsugae*

1995 Experiment: The first field release of *P. tsugae* in North America was made in 1995 in a forest of eastern hemlock, white pine, and mixed hardwood species in Windsor (Table 1 & Fig. 1, Site #8). Hemlock woolly adelgid was prevalent in the forest, but hemlock trees had not yet suffered significant decline. Five hemlocks with full crowns and ranging in height from 10-20m and from 25-55cm dbh were selected for the study. On June 15, four infested branches located at the four cardinal directions of the lower crown of each tree were tapped three times to dislodge any native natural enemies and were then enclosed within 0.5x 0.25m nylon mesh sleeve cages to protect adelgids from *P. tsugae*. Four other infested branches located at the four cardinal directions of the lower crown of each tree were marked and were not caged. Between June 16-20, 50 adults of *P. tsugae* (1:1 sex ratio) were released onto each of the four marked branches giving a total of 200 adults released per tree. On May 1, 1996 the sleeve cages were removed and the four previously caged and the four marked, non-caged branches were removed from each tree and returned to the laboratory for examination. The number of adelgids present on 2cm lengths (measured from the base of the tip outwards and viewed from the underside only) of each of 20 youngest tips per branch were counted. This number included living and dead individuals of the overwintering generation and represents those that survived attack by predators during 1995.

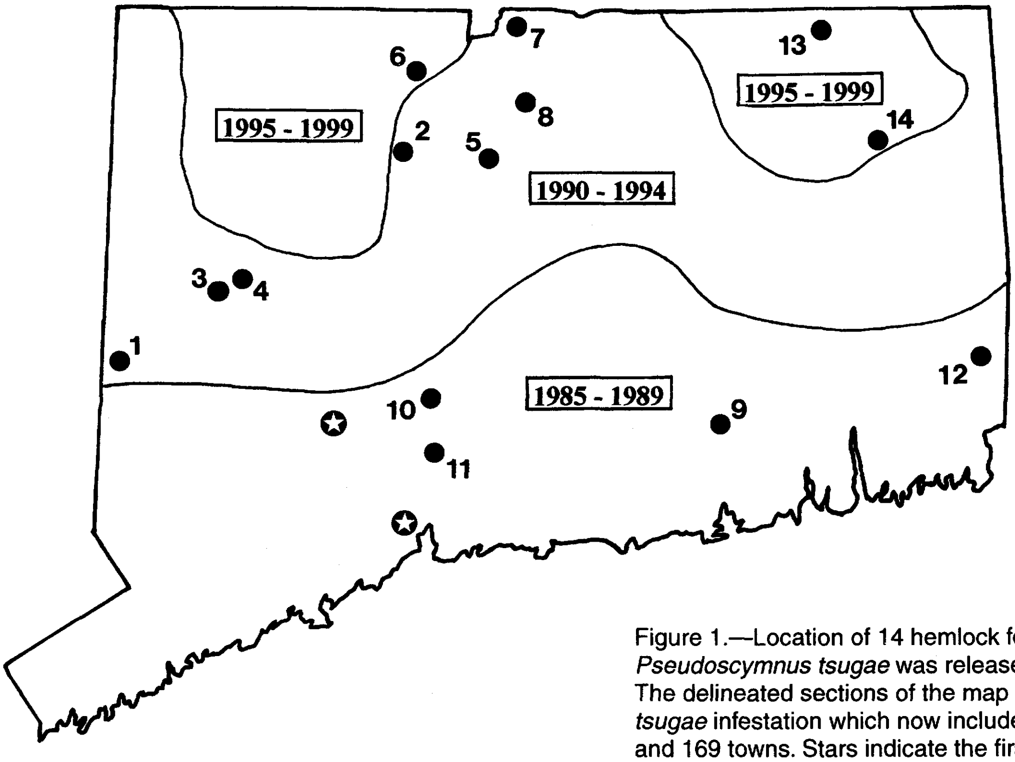

Figure 1.—Location of 14 hemlock forests in Connecticut where *Pseudoscymnus tsugae* was released between 1995 and 1999. The delineated sections of the map show the history of the *Adelges tsugae* infestation which now includes all of the state's 8 counties and 169 towns. Stars indicate the first and only known adelgid infestations recorded in 1985 in Middlebury and New Haven (both in New Haven County). See Table 1 for description of release sites.

1996 Experiment: A second study was conducted in another area of the Windsor forest during 1996 to evaluate the impact of *P. tsugae* on *A. tsugae* without using cages to exclude predators. Four mature, well-infested hemlocks with full crowns were selected for the study. On June 5, six infested branches (~ 0.5m long) in the lower portion of the crown of each tree were marked and the number of adelgid egg masses on newest growth on each branch was counted. Then 40 adults of *P. tsugae* (1:1 sex ratio) were released onto each of four adjacent marked branches on each tree (160 beetles per tree); no beetles were released onto the remaining two branches per tree which were located together as far away from the other four branches as possible. On December 5, 1996 and again on May 15, 1997 marked branches were reexamined for the presence of living adelgids on newest growth. Adelgid densities on release and non-release branches were compared.

1997 Experiment: Field evaluations of the efficacy of *P. tsugae* against *A. tsugae* were expanded to three additional forests in Connecticut and one in Virginia in 1997. The three new Connecticut study sites were located in Bloomfield (Table 1 and Fig. 1, Site # 5), New Hartford (Site # 2), and Hamden (Site # 11); the Virginia site was located near Montebello (Table 1, Site # 17). Each of these sites was a mixed conifer-hardwood forest in which eastern hemlock was well represented in the overstory and understory. The adelgid infestation was light to moderate at Bloomfield, New Hartford and Montebello and heavier and more widely distributed at Hamden. Each area was sufficiently large to identify distinct release and control areas that were very similar in terms of habitat, hemlock size, age, condition, and level of adelgid infestation, and yet the areas were separated by a distance of at least 500m. A minimum of 40 and 13 infested hemlock branches were marked within the release and control areas, respectively, at each site. No more than four branches were selected from any single tree. The number of adelgid egg masses present on 30cm of newest growth (measured from the base of the tip outwards and viewed from the underside of the branch only) on each marked branch was counted. At the New Hartford and Montebello sites an additional 10 branches within the release area were marked, examined for number of adelgids present, and then enclosed within nylon mesh sleeve cages, described previously, to exclude *P. tsugae.* Between April 29 and June 19, 2,400 adult beetles (1:1 sex ratio) were released at each site by placing 60 adults on each of the 40 non-caged, marked branches in each release area. Hemlocks in the release and control areas were examined periodically during the spring and summer and the presence of *P. tsugae* larvae and adults was recorded. In October each of the previously marked branches in the release and control areas, including those within cages were reexamined and the density of adelgid on each branch was determined as before. Overwintering ability was evaluated in late winter 1998 as described below.

Overwintering ability

The ability of *P. tsugae* to survive the first winter (1995-96) at Windsor was determined by hanging yellow sticky traps, which are attractive to both male and female adults, in late winter in the hemlock forest. Subsequently it was deemed more suitable to sample for beetles in late winter using beating sheets or by visually inspecting branches and foliage for beetles. Minimum daily temperatures for the overwintering period were obtained from published data from the nearest official weather station. In later studies, temperature data recorders were deployed in the field at some sites in Connecticut, New Jersey and Virginia during the overwintering period.

Statistical methods

Data were analyzed using parametric and non-parametric, 2-sample or paired sample t-tests according to normality of data and equal variance assumptions with the Number Cruncher Statistical System (Hintze 1995). For normal data with equal variances, the equal variance t-test was used, while data with non-equal variances were analyzed using the Aspin-Welch Test. Data with different distributions were analysed using the Komolgorov-Smirnov test for non-normal data with unequal variances while non-normal data with equal variances were tested using the Wilcoxon Rank-Sum Test. For multiple comparisons of non-normal data, the Kruskal-Wallis procedure was used.

Results and Discussion

Field releases of *P. tsugae*

P. tsugae has established, reproduced, spread and has shown remarkable short-term impact on *A. tsugae* at several release sites. Unfortunately however, adelgid populations have increased dramatically in recent years not only at the release sites, but also throughout the eastern United States, probably due in part to a series of relatively mild winters that have been conducive to adelgid survival. Indeed, *A. tsugae* is spreading at an alarming rate and infested hemlocks are experiencing rapid decline. Coincident with this recent proliferation of *A. tsugae* has been the increased presence on adelgid-infested hemlocks of *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) (McClure and Cheah 1998), a polyphagous predator that was introduced from Asia. Larvae and adults of *H. axyridis* were observed from April through September at several study sites, especially those where trees were heavily infested with *A. tsugae* (Table 2). Preliminary observations suggest that *H. axyridis* can complete its development on *A. tsugae* (McClure and Cheah 1998). The potential of this opportunistic predator as a biological control agent for hemlock woolly adelgid is currently being investigated.

The elongate hemlock scale, *F. externa* Ferris (Homoptera: Diaspididae) occurred at more than half of the *P. tsugae* release sites in Connecticut and at the New Jersey release site (Table 1). This scale, which is also native to Japan, attains damaging levels on *T. canadensis* and *T. caroliniana* throughout the eastern United States, despite the presence of its principal natural enemy from Japan, *Aspidiotiphagus citrinus* Craw (Hymenoptera: Aphelinidae)(McClure 1986) and several predators, mainly Chilocorus spp. (Coleoptera: Coccinellidae)(McClure 1977). Like *A. tsugae*, populations of *F. externa* are affected mainly by weather and negative density-dependent feedback mechanisms related to host deterioration (McClure 1980, 1986) and have probably been encouraged in recent years by mild winter weather. Although *F. externa* is less destructive than *A. tsugae*, probably because it feeds on needles rather than on twigs (McClure 1991b), it is also capable of severely weakening and killing trees (McClure 1980). Simultaneous feeding by both insects hastens the decline of hemlock, but *A. tsugae* suppresses populations of *F. externa* in mixed infestations through competition (McClure 1991b). Hundreds of hours of laboratory and field observations revealed that *P. tsugae* does not attack *F. externa*. Consequently, the selective predation of the adelgid by *P. tsugae* would stimulate scale population growth and thereby continue the decline of hemlock even if biological control of *A. tsugae* were effective. The continued presence and high abundance of various developmental stages of *Chilocorus* spp. at several of the *P. tsugae* release sites (Table 2) suggests scale population growth. Therefore the presence of *F. externa* should be considered when selecting beetle release sites and when evaluating the efficacy of *P. tsugae* on the basis of hemlock health.

Evaluating the efficacy of *P. tsugae*

1995 Experiment: Adelgids were 79% less abundant on branches that had been exposed to *P. tsugae* than on ones which had been caged to protect adelgids from beetles which suggests that *P. tsugae* had significantly reduced adelgid numbers in a single growing season. Mean density of adelgids was 0.78 ± 0.32 (n=18) individuals per cm of newest growth on exposed branches and 3.79 ± 2.25 (n=20) on caged branches. These differences were significant ($p < 0.05$, Komolgorov-Smirnov test, Dmn = 0.85). Unfortunately, the 1995 experiment could not rule out the possibility that the cages themselves had somehow enhanced adelgid survival, for example by excluding incidental native predators or by favorably moderating the microclimate of the branch. The 1996 and 1997 experiments addressed this issue.

1996 Experiment: Fall adelgid densities on release and non-release branches were compared using Komolgorov-Smirnov test and found not to be significantly different ($p > 0.05$), particularly, as the available data for non-release branches were highly variable (Table 3). A paired comparison made between initial spring pre-release egg mass counts and December nymph counts using the Wilcoxon Rank-Sum test, was however, highly significant ($Z = 3.4651$; $p < 0.001$) for release branches but not for non-release branches ($p > 0.05$). This suggests that the impact of a small initial release of *P. tsugae* in one season, though marked, is rather localized on the same release tree.

A further comparison between counts in 1996 and 1997 indicated the importance of overwintering mortality and

Table 2.—Occurrence of larvae (L), pupae (P), and adults (A) of the two coccinellid beetles, *Harmonia axyridis* and *Chilocorus* spp. at *Pseudoscymnus tsugae* release sites in Connecticut.

Stages of *Harmonia axyridis*	Date of observation	Location (CT)	Stages of *Chilocorus* spp.	Date of observation	Location (CT)
L	6/8/95	Ashford	A	5/28/96	Windsor
L	4/9/96	Hadlyme	A	9/15/96	"
L	5/7/96	"	A, P, L	7/15/97	Hamden
A	5/5/96	Windsor	A	9/9/97	Bloomfield
L	7/15/97	Hamden	A	9/10/97	New Hartford
A	5/7/98	New Fairfield	A	9/16/97	Hamden
A, L	5/19/98	Hamden	A, L	6/2/98	New Hartford
L	6/2/98	New Hartford	A	"	Bloomfield
L	"	Bloomfield	A, L	6/17/98	Washington
A, L	6/9/98	New Hartford	A, P, L	7/13/98	"
L	6/10/98	Windsor	A , L	9/1/98	Bloomfield
L	6/18/98	Hadlyme	A, L	9/1/98	New Hartford
A, L	6/24/98	Windsor	A, L	9/2/98	Washington
L	7/13/98	Washington	A	9/14/98	Hamden
L	9/1/98	Bloomfield	A	10/22/98	New Hartford
L	9/8/98	Pomfret	A	11/25/98	"
L	6/10/99	Washington	A	"	Washington
A, L	6/16/99	Pomfret	A	4/3/99	"
			A, L	6/10/99	"

Table 3.—Density and mortality of *Adelges tsugae* on release and non-release branches in the Windsor hemlock forest in spring 1996, prior to the release of *Pseudoscymnus tsugae* and in fall 1996 and spring 1997 following release.

Windsor	1996 spring No. of egg masses/branch	1996 fall No. of nymphs /branch	Overwintering + negative feedback mortality	1997 spring No. of egg masses/branch
Release	136.7 ± 9.8 *a* (n=15)	36.9 ± 44.5 *b* (n=16)	69.2 ± 18.8 *e* (n=12)	10.7 ± 13.2 (n=15)
Non-Release	114.1 ± 22.2 *c* (n=7)	170.4 ± 176.2 *c* (n=7)	59.4 ± 24.5 *e* (n=7)	49.1 ± 47.9 (n=7)

Means followed by different letter significantly different at $p < 0.01$; means followed by the same letter not significantly different ($p > 0.05$).

reduced survival due to density-dependent negative feedback. Differences between fall nymph counts in 1996 and spring egg mass counts in 1997 were calculated for % mortality per branch. Percentage mortality on non-release and release branches were not significantly different (equal variance t-test; $p > 0.05$) and the overall mean overwintering mortality was 66.1 ± 19.5 % for 1996-1997. Again the data were highly variable due to small sample size and although reductions of 93.5 ± 8.1% on release branches and 61.0 ± 30.5% on non-release branches were recorded, this was clearly a combined result of predation, negative feedback and overwintering mortality.

1997 Experiment: Table 4 summarizes the fall density counts of nymphs for release, caged controls and control area tips. Data were analyzed separately for new growth tips and older tips to account for density-dependent negative feedback effects. As much of the data were not normal, appropriate non-parametric t-tests were used in analysis (Hintze 1995). Overall, in all four sites, adelgid densities on release tips were significantly lower than densities on either caged branches or in the control area ($p< 0.05$ - $p < 0.001$). Concurrently, comparison of densities in caged controls with densities in control areas for Montebello and New Hartford showed no significant differences ($p > 0.05$), indicating the minor role of native predators and cage effects in adelgid survival.

Table 4.—Density of *Adelges tsugae* on new and older hemlock tips on caged and uncaged branches in the release and control areas five months after the release 2,400 adults of *Pseudoscymnus tsugae* in spring 1997 at each of four sites in Connecticut and Virginia.

1997 Sites	Release area New tips		Release area Older tips		Control area	
	Caged	Uncaged	Caged	Uncaged	New tips	Older tips
Montebello VA	5.8 ± 2.3 *a* (n=5)	2.6 ± 2.1 *b* (n=38) *e*	2.8 ± 1.7 *c* (n=6)	1.3 ± 0.6 *d* (n=5)	5.3 ± 3.0 (n=11) *f*	5.1 ± 3.1 (n=3)
New Hartford CT	9.6 ± 1.6 *a* (n=10)	2.8 ± 2.8 *b* (n=36) *e*	6.3 ± 3.5 *c* (n=6)	0.9 ± 1.1 *d* (n=22) *h*	8.9 ± 4.7 (n=21) *f*	6.7 ± 5.2 (n=8) *g*
Bloomfield CT	-	5.0 ± 4.2 (n=33) *a*	-	1.3 ± 1.4 *c* (n=28)	9.4 ± 3.7 (n=24) *b*	4.5 ±3.2 *d* (n=16)
Hamden, CT	-	2.1 ± 1.5 (n=37) *a*	-	0.7 ± 0.9 *c* (n=19)	12.5 ± 4.6 (n=24) *b*	2.0 ±2.0 *d* (n=16)

Significance levels of comparisons of fall adelgid densities:

Montebello	*a,b *; c,d *; e,f **
New Hartford	*a,b ***; c,d ***; e,f ***; h,g **
Bloomfield	*a,b ***; c,d *
Hamden	*a,b ***; c,d *

Table 5.—Mean percent reduction in the density of *Adelges tsugae* from spring to fall 1997 on new and older tips using comparisons between release tips and (1) control tips and (2) tips enclosed in sleeve cages in the release area for four sites in Connecticut and Virginia where 2,400 adults of *Pseudoscymnus tsugae* were released in spring 1997.

1997 Sites	No. of nymphs/cm (new tips)	No. of nymphs/cm (older tips)
Bloomfield, CT	47.0 % ↓	70.0% ↓
New Hartford, CT	69.2 % ↓	86.6 % ↓
New Hartford (caged)	70.8 % ↓	85.6 % ↓
Hamden, CT	82.8 % ↓	62.8 % ↓
Montebello, VA	52.9 % ↓	78.1 % ↓
Montebello, VA (caged)	57.5 % ↓	48.1 % ↓

Results from the 1997 studies in Bloomfield, Hamden, and New Hartford, Connecticut and near Montibello, Virginia reveal remarkable short term impact by *P. tsugae* on *A. tsugae* (Table 5). Comparison between caged and uncaged branches within release areas and between uncaged branches in the release areas and those in the control areas at least 500m away revealed that adelgid densities had been reduced 47.0-82.8% on new tips and 48.1-86.6% on old tips in only 5 months by a starting population of only 2,400 to 3,600 adult beetles (Table 5).

Overwintering ability

Several adults of *P. tsugae* were captured at the Windsor release site on sticky traps during April, 1996 which documented its overwintering ability in North America for the first time. That winter was one of the coldest and snowiest on record in Connecticut with minimum temperatures in January and February, 1996 reaching -20°C or lower (Table 6). Each of the following three winters were relatively mild and dry (Table 6). In the later part of each of these three winters, adults of *P. tsugae* were easily observed on hemlock branches at six of the eight release sites in Connecticut. Only at the New Fairfield and Cheshire sites where relatively few beetles were released (Table 1) has overwintering ability not been documented. *P. tsugae* also survived each of the past two winters in Virginia and the past one in New Jersey.

Natural threats to the establishment of *P. tsugae*

Several adults of *Homalotylus* sp. (Hymenoptera: Encyrtidae), an Asian parasitoid with no close relatives in North America, emerged during the quarantine period from larvae of *P. tsugae* that were shipped from Japan in 1994.

However, since then there have been no parasitoids observed among the thousands of beetles either reared in the laboratory or examined in the field. As was noted earlier, *H. axyridis* sometimes occurs in high numbers on hemlocks that are heavily infested with *A. tsugae*. Although this beetle is often aggressive and cannibalistic in laboratory colonies and when food is in short supply (McClure 1987b), direct contact between it and *P. tsugae* in the field has not been observed. The direct interaction between these two predators, as competitors or mutual enemies, is currently being investigated. Spiders, which frequent hemlock trees throughout the growing season, represent the greatest threat to the establishment of *P. tsugae*. Spiders were especially evident at the Windsor site where fewer beetles than expected were recovered following each year of release. Webs were present on many branch tips at this site and beetles were sometimes seen entangled in webs and in the grasp of spiders. In an effort to explain the slow population increase of *P. tsugae* in Windsor compared to three other areas, we surveyed the population density of spiders at each of the four sites in July, 1997. Fifteen trees at each site were sampled by tapping a branch and collecting spiders on a 1m square sheet held beneath.

Table 6.—Minimum daily temperature recorded in Windsor between December and March from 1995 through 1999, a period during which nearly 40,000 adults of *P. tsugae* were released in Connecticut.

	Minimum temperature per month (°C)			
Year	December	January	February	March
1995-1996	-13.0	-20.0	-21.7	-15.0
1996-1997	- 9.4	-18.3	- 9.4	- 7.8
1997-1998	-10.6	-14.4	-11.1	-11.1
1998-1999	-12.2	-16.7	-13.3	-10.6

The densities of spiders at Windsor were significantly higher than at any of the other sites ($p < 0.05$; Kruskal-Wallis 1-Way ANOVA). There were 9.7 (± 2.9) spiders per m^2 of branch in Windsor which was nearly three times more than in Hamden (3.7 ± 1.6) and nearly five times more than in Bloomfield (2.1 ± 2.1), New Hartford (1.9 ± 1.2), and Montebello (1.8 ± 1.6). Fortunately the high population density of spiders at Windsor was more the exception than the rule, and was probably due to the proximity of the site (within 50m) to a vast old field with abandoned barns that provided exceptional food and breeding and overwintering sites for spiders.

Summary

Laboratory studies have revealed that *P. tsugae,* possesses many important qualities of a successful biological control agent (Cheah and McClure 1998). It is relatively host specific, is multivoltine, and has a biology that is highly compatible with its prey. Furthermore, results of the initial release experiments reveal remarkable short-term impact on adelgid densities on release branches by *P. tsugae*. However, even though *P. tsugae* has established and increased its numbers in these release areas, trees have generally continued to decline. The recent string of relatively mild winters, which has been conducive to the survival and growth of adelgid and scale populations, as well as the explosive population increase of *F. externa* at some release sites have compounded the problem. Considering the lag time following the release of a successful biological control agent that is often required before control is achieved and the rapid rate of decline of hemlock trees that often occurs following adelgid attack (McClure 1991a), we are clearly in a race against time that we may not win. Indeed we are expecting more from *P. tsugae* in North America than in Japan where *A. tsugae* and *F. externa* do not injure their host.

Whether or not *P. tsugae* will become a permanent solution to the hemlock woolly adelgid problem in North America will depend upon its ability to establish, quickly increase its numbers, disperse, and consistently maintain adelgid populations below injurious levels following the initial release of relatively few adult beetles. Studies to evaluate the long-term efficacy of *P. tsugae* were initiated in spring 1998 in three relatively isolated, 10-15 acre stands of recently infested hemlock in Connecticut, Virginia and New Jersey. At each site, adelgid egg masses were counted on the release tree and on trees at 50m intervals along 200m transects prior to releasing 10,000 adult beetles. Establishment, reproduction and distribution of *P. tsugae*, tree health, and changes in adelgid population density along the transects were monitored in 1998 and will continue to be monitored in subsequent seasons. Studies in 1999 were expanded to include releases of 10,000 beetles in 10 eastern states (Connecticut, Maryland, Massachusetts, New Jersey, New York, North Carolina, Pennsylvania, Rhode Island, Virginia, and West Virginia) using a slightly revised protocol.

Should *P. tsugae* prove to be a successful long-term biological control agent for hemlock woolly adelgid, natural resource managers could then utilize this predator and the knowledge gained through these studies as a forest management tool. For example, early results indicate that *P. tsugae* may be more successful in recently infested forests at the fringe of the infestation where adelgid populations are low and trees are uninjured. Therefore, resource managers could play a prominent role by identifying new infestations of *A. tsugae*, releasing beetles in strategic locations throughout the forest, subsequently monitoring the changes in forest health, and implementing appropriate resource management strategies as needed. Our preliminary studies have also revealed that *P. tsugae* attacks and develops from egg to adult on other important adelgid pests as well including the balsam woolly adelgid and the Cooley spruce gall adelgid. These and other alternate adelgid hosts could serve to enhance the establishment and survival of *P. tsugae* in the conifer forests of eastern North America and increase its efficacy against *A. tsugae* and these other adelgid pests as well.

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Chinese Coccinellidae for Biological Control of the Hemlock Woolly Adelgid: Description of Native Habitat

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Abstract

The hemlock woolly adelgid, *Adelges tsugae* Annand, is generally believed to be native to Asia and is known to occur in India, Japan, and China. In China, there are approximately four species of hemlock that grow in 14 provinces. We explored regions of the Southwestern Plateau in Yunnan, Sichuan, and Shaanxi Provinces for the adelgid and its natural enemies. The montane- forests of this region are largely in their natural state and noted for their biological diversity. We found the hemlock woolly adelgid in all three provinces and on each hemlock species examined (*Tsuga dumosa* (D. Don) Eichler, *T. forrestii* Downii, and *T. chinensis* (Franch.) Pritz.). More than 9 families of natural enemies were found in association with *A. tsugae* in China. One family, the Coccinellidae, is exceptionally diverse and seems to have an important role in maintaining the adelgid at low population densities. Of the 50+ species of lady beetles found on hemlock, at least 25 are new to science. Nine species are known to feed on HWA and three have been imported for further evaluation as biological control agents. The biodiversity of the lady beetles is discussed in relation to the habitat and climate of their native range compared with potential release sites in the United States.

Introduction

The hemlock woolly adelgid, *Adelges tsugae* Annand, is a non-native invasive pest of hemlock in the eastern United States. The adelgid is native to Asia and has been found in India, Japan, and China, including the island of Taiwan (Blackman and Eastop 1994). Its first recognition as a species was based on specimens from Oregon and British Columbia (Annand 1928).

The first reports of *A. tsugae* in the eastern United States was in Virginia in the 1950s. By the mid-1980s it had spread to the eight mid-Atlantic states from Virginia to Rhode Island, and had become a serious forest pest (Souto et al. 1995).

The hemlock woolly adelgid is considered a pest only on the hemlocks that grow in eastern North America—*Tsuga canadensis* L. (Carrière) and *T. caroliniana* Engleman. The vulnerability of eastern hemlock to *A. tsugae* is probably the consequence of a lack of natural enemies and an intolerance to adelgid feeding (McClure 1987). There are only a few native and introduced predators that attack the hemlock woolly adelgid in the eastern United States (Montgomery and Lyon 1996) and these do not have significant impact on *A. tsugae.* In Japan, McClure (1995) found five predators that killed 96 percent of *A. tsugae* in forest sites. One of these, an orabatid mite, did not feed directly on the adelgid but destroyed up to 91 percent of the adelgid eggs by dislodging them from the egg mass. Insects preying on *A. tsugae* in Japan were a lady beetle, a green lacewing, a midge fly, and a flower fly. Both the mite and lady beetle were imported and released in the United States and the lady beetle, *Pseudoscymnus tsugae* Sasaji and McClure (1997) has demonstrated good potential as a biological control agent of *A. tsugae* (Cheah and McClure 1996).

Extensive field exploration in China from 1996 to 1998 of hemlock forests in Yunnan, Sichuan, and Shaanxi Provinces found predaceous insects in eleven families that are potential natural enemies of *A. tsugae* (Wang et al. 1997). The families are Coccinellidae, Cecidomyciidae, Syrphidae, Hemerobiidae, Chrysopidae, Derodontidae, Anthocoridae, Miridae, Inocellidae, Staphylinidae, and Labaiduridae. The coccinellids (lady beetles) seem especially promising for biological control of hemlock woolly adelgid.

This report discusses the environment in China in which these lady beetles were found. The objective is to increase understanding of the habitat and climate of an area where an extraordinary diversity of lady beetles associated with *A. tsugae* occurs. This information will facilitate establishment of effective biological control of the adelgid in the eastern United States.

Description of Habitat

Forests in China

Forests in China are similar to those in the United States in many respects. The land area of China is slightly greater than that of the U.S., including Alaska. The forests are more concentrated in the eastern half of the country and much of the western part is grassland, desert, or mountains above timberline. There are six major types of natural forest in China that are organized in broad latitudinal bands or narrow altitudinal gradients (Wang 1961). The forest types from north to south are: (1) boreal coniferous; (2) mixed northern hardwood; (3) temperate, deciduous broad-leaved; (4) mixed mesophytic; (5) sclerophyllous, evergreen broad-leaved; and (6) rain forest. These extant types originally formed a remarkably unbroken expanse of forest from the Arctic to below the Tropic of Cancer (Wang 1961). Extensive land clearing for agriculture and establishment of secondary forests of pine and, to a lesser extent, poplar, have disrupted the continuity and little of the lowland natural forest remains. Because of their ruggedness and isolation, the forests in the mountains of southwestern China are in a remarkably intact, natural condition. In a day's journey from 800 m to 4,000 m, the forest can change from rainforest to evergreen

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Table 1. Species and varieties of *Tsuga* occurring in China

Species/Variety	Cheng 1983			Fargon 1990		
	Sp.	Var.	Syn.	Sp.	Var.	Syn.
T. chinensis (Franchet) Pritzel in Diels	x			x		
T. oblongisquamata (Cheng et Fu) Cheng et Fu	x				x	
T. chinenesis var. *robusta* Cheng et Fu		x			x	
T tchekiangensis Flous	x					x
T. formosana Hayata	x					x
T. forrestii Downie	x			x		
T. dumosa (D. Don) Eichler	x			x		
T. yunnanensis (Franchet) Pritzel			x			x
T. longibracteata Cheng	x					x*

* placed in a new genus as *Nothotsuga longibracteata* (Cheng) Hu ex C.N. Page

sclerophyllus broad-leaved, to deciduous broad-leaved, to montane coniferous, to alpine scrub. In this area, the montane-boreal forests often occur as isolated "islands" (Wang 1961). Hemlock is common at the lower elevations in the fog belt where boreal coniferous forest merges with broad-leaved forest.

Hemlocks in China

There are approximately 20 previously described species of hemlock in China, but no more than 7 are considered valid species by modern authorities (Table 1). Only 3 of the 7 species of *Tsuga* in C[Z]heng (1983) are listed as true species by Fargon (1990).One of the species, *T. longibracteata* Cheng, has been placed in a distinct new genus, *Nothotsuga* (Page 1988). The common name of this species, bristlecone hemlock, refers to the unusually large and bristly cones that distinguish it from *Tsuga* species. The classification of the *T. chinensis* group varies among authorities with the Chinese maintaining more species than Western botanists (see following discussion about *T. chinensis*. The nomenclature in Table 2 is not meant to be authoritative to but provide an identity meaningful to both Chinese and North American entomologists for the various "hemlocks" found in China. All of the taxons in Table 2 except *Tsuga dumosa* (D. Don) Eich. occur only in China.

Tsuga dumosa occurs in a relatively narrow range of latitude across the southern Himalayan Mountain Range from northeastern Pakistan, northern Myanmar (Burma), to northwestern Yunnan and southwestern Sichuan in China. It is a common species in the transition zone between boreal coniferous forests and deciduous hardwoods. Chinese specimens in herbariums and local usage are often called *T. yunnanensis* (Franchet) Pritzel, but both Chinese and Western authorities (Cheng and Fu 1978, Fargon 1990) regard it and *T. dumosa* as the same species. Its common name is Himalayan hemlock, but it is called Yunnan tieshan in Chinese. In Yunnan, *T. dumosa* usually is found at elevations between 2,600 and 3,000 m. Precipitation is over 1,000 mm/yr, with most falling during the growing season.

Tsuga chinensis (Franch.) Pritzel, is the most widely distributed hemlock species in China occurring from eastern Xizang (Tibet) west to the island of Taiwan, and from Gansu south to Yunnan. The species is often divided into several varities, but there is not a concensus on the varities or whether some species are distinct from *T. chinensis.* An earlier publication (Cheng and Fu 1978) classified *T. oblongisquamata* Cheng et Fu and *T. tchekiangensis* Flous as varieties of *T. chinensis* (Franch.) Pritz. Only the variety *T. chinensis* var. *robusta* seems to be universally recogized. A hemlock restricted to Taiwan, *T. formosa* Hayata, is considered a species by Cheng and Fu (1978), but Fargon (1990) believes that it does not have sufficient consistent differences to regard it as a variety of *T. chinensis. Tsuga chinensis*, including its varieties, usually occurs at elevations of 1,200 to 3,200 m. Soils may be red, yellow, or podzols (Fargon 1990). Climate usually is temperate and relatively moist. It occurs in mixed mesophytic forests and montane boreal forests. The common name is Chinese hemlock and in Chinese it is simply hemlock (tieshan).

Tsuga forrestii Downie is a species with morphological characteristics intermediate between *T. dumosa* and *T. chinensis* (Fargon 1990). Some authorities consider it a subspecies of *T. dumosa*, others a subspecies of *T. chinensis.* The range of *T. forrestii* is limited to the mountains near the border of northwestern Yunnan and southwestern Sichuan where the two former species meet. *Tsuga forrestii* is known as a high mountain species occurring between 2,000 and 3,500 m. The Chinese name for this species, Lijiang tieshan, reflects its principal locality. We found *T. forrestii* above 2,800 m in close proximity to *T. dumosa* when collecting lady beetles in Lijiang Prefecture, Yunnan, and could easily distinguish them.

The Chinese species tend to have broader, more flat crowns than the North American species. They have pendulous leaders and branch tips, similar to *T. heterophylla* (Raf.) Sargent. Like the North American species, the Chinese hemlocks are usually the most shade tolerant and oldest species in a forest. The largest hemlock we observed was almost 40 m tall with a diameter greater than 3 m.

Table 2. Distribution of hemlocks in China

	Province														
Taxon	**Xizang**	**Gansu**	**Yunnan**	**Sichuan**	**Shaanxi**	**Guizhou**	**Guangxi**	**Hunan**	**Hubei**	**Henan**	**Guangdong**	**Jiangxi**	**Anhui**	**Fujian**	**Taiwan**
Tsuga dumosa (D. Don) Eich.	x		x	x											
T. forrestii Downie			x	x											
T. chinensis (Franch.) E. Pritz.	x	x	x	x	x	x			x	x					
T. c. oblongisquamata Cheng et Fu				x					x						
T. c. tchekiangensis (Flous) Cheng et Fu	x						x	x			x	x	x	x	
T. c. robusta Cheng et Fu				x					x						
T. c. formosana Hayata															x
Nothotsuga longibracteata (Cheng) ex page						x	x	x			x	x		x	

General Characteristics of the Hemlock Forest

In China, *Tsuga* species usually are a minor component of the forest (Wang 1961). They usually are scattered among other species and are more abundant on steep, north-facing slopes at lower altitudes and south slopes at higher altitudes. Hemlock forest is a transitional zone between the montane coniferous forest and the hardwood forest zones. In the upper Yangtze Valley it is the upper limit of the mixed mesophytic forest.No tree species dominates this forest. What is most striking is the extraordinary diversity of tree species. Besides Tsuga, there are species in the genera Abies, *Aesculus, Carpinus, Cercis, Chamaecyparis, Clethra, Corylus, Ilex, Juglans, Juniperus, Lindera, Magnolia, Malus, Prunus, Picea, Pinus, Pseudotsuga, Sorbus, Taxus, Tilia, and Ulmus*. There are also species in other genera not present in North America such as *Castanopsis, Cercidiphyllum, Schima, Cunninghamia*, and *Keteleeria*. This assemblage of a large number of tree species with the crown layer shared by several species with no species or groups predominate is a characteristic of the mixed mesophytic forest type. This forest type is extensive in the hilly country of the Yangtze River Basin and also occurs in the Southern Appalachians of eastern North America.

The areas we explored for natural enemies of the hemlock woolly adelgid are located in northwestern Yunnan, southwestern Sichuan, and southern Shaanxi (Fig. 1). We examined hemlockgrowing between between 2,500 and 3,000 m altitude in forestwith deciduous broad-leaved species with intrusions of montane-boreal conifers from higher altitudes , and evergreen sclerophyllus broad-leaved species from lower altitudes. The areas where we made collections were reminiscent of the forest where hemlock occurs in Great Smoky Mountain National Park, USA, an area also noted for its biodiversity. The most common fir and spruce species in the areas where we found the hemlock woolly adelgid were *Abies fabri* (Masters) Craib, *A. delavayi* Franch., *A. forrestii* C. Coltm Rodgers, *Picea brachtyla* (Franch.) Pritz., and *P. likiangensis* (Franch.) Pritz. Other conifers present, besides hemlock, include *Pinus armandii* Franch., *P. yunnanensis* Franch., *Keteleeri evelyniana* Masters, *Cunninghamia lanceolata* (Lamb.) Hook, *Larix* potaninii Batalin and *Taxus chinensis* (Pilg.) Reg. Among the deciduoushardwood trees, species of *Acer, Alnus, Betula,* and *Populus* were most common. Evergreen oaks were common in Yunnan. *Rhododendron* spp. were prevalent in the understory in all areas. Mountain bamboo, *Arundinaria* spp., was common in the understory in Sichuan.

The montane-coniferous forests of the region have about 24 species and varieties of *Abies* and *Picea* (Wang 1961), although the taxonomic status of many of these is unclear. There are 3 species of hemlock with one species found nowhere else. It seems that speciation in many tree genera in the region remains active; both polymorphic species and incipient genera are not uncommon.

Climate

All areas where hemlock occurs in China are very moist during the growing season. Monsoon rains extend to the collection area in northwestern Yunnan and influence the weather further north. The narrow band of altitude where hemlock grows is a fog belt. The tree trunks in this forest are covered with mosses and lichens and long strands of the lichen, *Usnea longessima*, hang from the crowns.

The Perfecture of Lijiang, in Yunnan Province, was the most southerly and highest in elevation of the three collecting

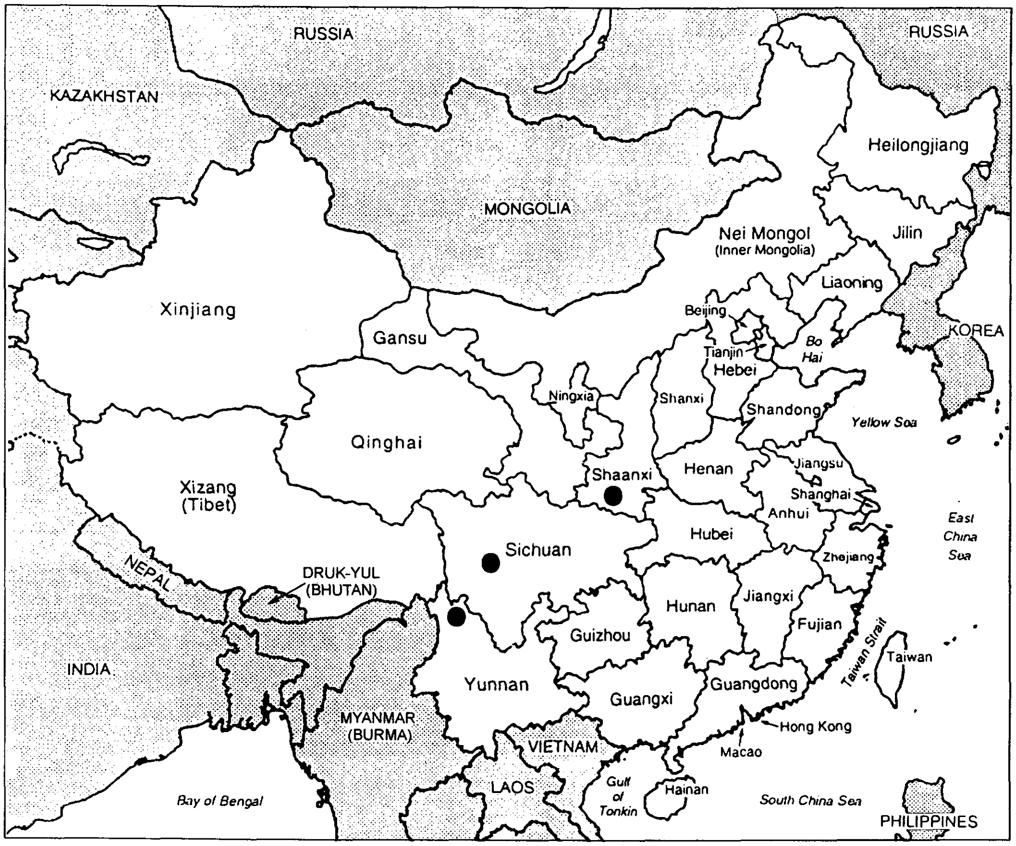

Figure 1.—Map of the provinces of China showing the areas explored (solid circles) for natural enemies of the hemlock woolly adelgid.

areas. Monthly temperature and precipitation means for Lijiang are compared to Shenandoah National Park, Virginia, U.S.A. (Fig. 2). The weather station in Lijiang is located near the city at an altitude of 2,400 m. We adjusted these temperatures to 2,800 m, where the hemlock grows, by applying a lapse rate of 0.5°C per 100 m (Yoshino 1975). The weather station in Shenandoah National Park is at 1,100 m and 38.5°N latitude. The longitude of Lijiang is 27.1°N; this is about the same as Miami, Florida (Lijiang is much colder because it is 8,000 ft higher in elevation).

Although the climate in Lijiang is mild, temperatures frequently drop to -10°C during the winter. Snowfall is heavy, especially in early winter and late spring. We experienced a >5 cm snowfall at 2,900 m during the afternoon in late April.

The Chinese hemlocks, like most *Tsuga* species, grow where the humidity is high and the soil is moist throughout the growing season. They do not extend in altitude to the tree line and are not as cold tolerant as spruce and fir. The temperature range for *T. diversifolia* in Japan, *T. heterophylla* in western North America, and *T. dumosa* in China are similar; not below -10°C or above 20°C, January and July monthly means, respectively (Fargon 1990). It appears that all the Asian species exist in climates that are warmer than the extremes at which the North American species, *T. canadensis* and *T. mertensiana* (Bong.) Carrière can occur.

Lady beetles on Chinese hemlocks

To date, we have collected 54 species of lady beetles from hemlocks in China. Most species were found in Yunnan (45), whereas only 11 and 5 species were found in Sichuan and Yunnan, respectively. Only eight of the species were found in more than one location and no species was found in all three locations. A listing of the 54 species collected from hemlock, including descriptions for 20 new species, can be found in Yu et al. (in press).

There are several reasons why more species of lady beetles were collected in Yunnan; some are logistical and others are habitat related. Much more collecting effort was made in Yunnan. A greater diversity of accessible hemlock habitats existed near our base in Lijiang City, Yunnan. Extensive stands of both *T. dumosa* and *T. forrestii* were within a one-half day drive. *Pinus armandii* was more prevalent in our collecting areas in Lijiang than in the other two provinces. This 5-needle white pine was infested by an undetermined adelgid in the genus *Pineus*. Several of the lady beetles, including those that were most abundant, were collected also from the white pine.

The majority of lady beetles we collected from hemlock in China are in the tribe Scymnii. Members of this tribe are predators of homopterous insects, mostly aphids, adelgids, and scales (Pang and Gordon 1986). Of the nine species we

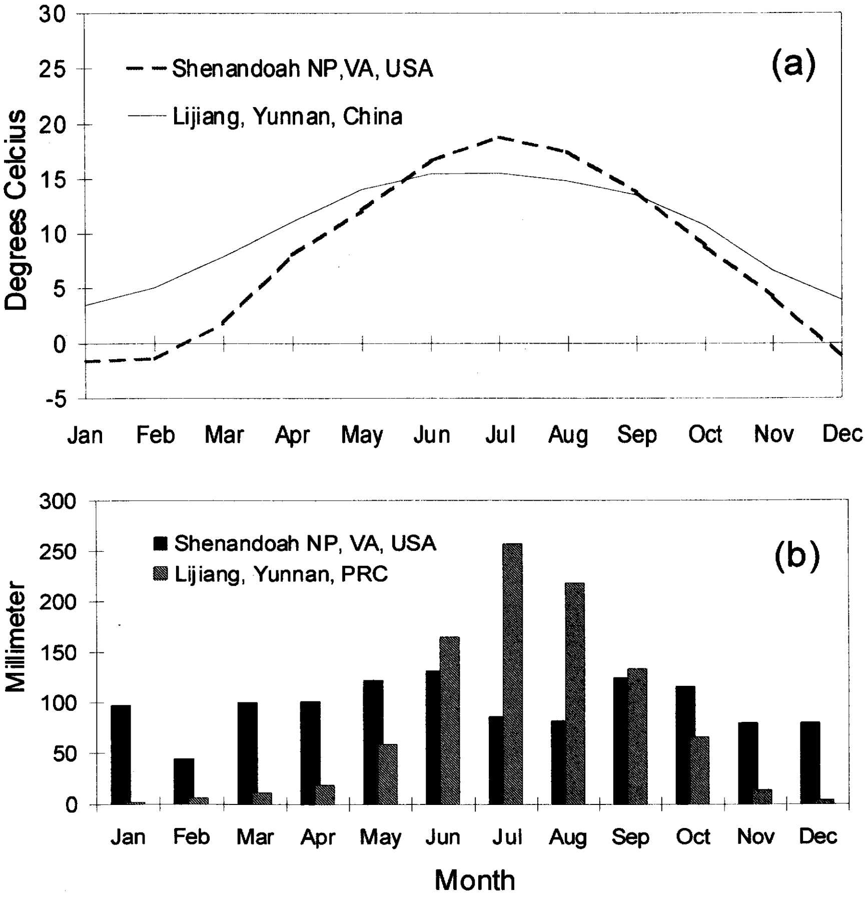

Figure 2.—Comparison of monthly mean temperature (a) and precipitation (b) between growing sites of hemlock in southwestern China and southeastern United States.

Table 3.—Number and percent of the total of lady beetles in different sites in Lijiang County, Yunnan Province

Species of beetle	Wenbi Shan Temple		Yulong, Snow Mountain		Heyuan Forest Farm	
Scymnus (Neopullus) sinuanodulus	67	65%	21	22%	11	16%
Scymnus (Neopullus) camptodromus	2	2%	71	74%	18	27%
Other *Scymnus* spp.	15	15%	5	6%	26	39%
All other	19	18%	1	1%	12	18%

confirmed to feed on *A. tsugae*, five are in the genus *Scymnus* (Yu et al., in press). Three of the others (*Oenopia billieti* (Mulsant), *Adalbia conglomerata* (L.), and *Calvia championorum* Booth) are widespread and feed on other Homoptera besides adelgids. The genus *Scymnus* is the largest genus in the family Coccinellidae and has been divided into five subgenera.

Whenever we made collections, we found a member of the subgenus *Scymnus (Neopullus)* to be the most common lady beetle on hemlock infested with *A. tsugae. Scymnus (Neopullus) camptodromus* Yu et Liu was the only member of the subfamily found in more than one province. The relative distribution of members of the subfamily varied among collecting areas in the same country (Table 3). The elevation of the Yulong site is 2,900 m, 200 m higher than the other two sites. *Tsuga dumosa* was at each site, but Heyuan also had *T. forrestii.*

End Remarks

As with the tree species, the lady beetles in the hemlock forests of southwestern China are exceptionally diverse. The steep, broken mountains where hemlock is most abundant in China may have fostered speciation of the hemlock and other trees, their pests, and the natural enemies of the pests. The *Scymnus* lady beetles especially are diverse, with many localized species. It has, historically, been difficult to grow Chinese hemlocks in North America. It may be equally difficult to transplant the lady beetles that feed on *A. tsugae* in China.Attempts to establish lady beetles should give special care to climate matching.

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[1] The preferred spelling is Zheng, C. J. in Pinyin, the system adopted in 1979 by PRC for transliterating Chinese ideograms into the Latin alphabet. Cheng is used here to maintain consistency with the nomenclature author of some Tsuga species.

The Effects of Site Factors on the Rate of Hemlock Decline: A Case Study in New Jersey

Denise Royle and Richard Lathrop[1]

Abstract

The rate of decline of hemlock (*Tsuga canadensis*) trees infested with hemlock woolly adelgid (*Adelges tsugae*) appears to be highly variable and site dependent. Rates of hemlock forest decline have not been quantified at the landscape scale and reasons for observed variations in the rate of decline remain unknown. Others have suggested that site characteristics and/or landscape features, hemlock woolly adelgid (HWA) dispersal patterns, weather and climate, genetic variation, and a host of other factors may play a role in structuring this apparent variation in the rate of decline. In this paper, we: 1) report the results of a preliminary investigation in which we quantify the rate of change in hemlock forest canopy across the Highlands landscape of northern New Jersey using multiple dates of remotely sensed data and change detection techniques; 2) summarize patterns in the rate of change in hemlock forest canopy; and 3) explore the effects of site factors on the rate of change.

The study area consists of the New Jersey Highlands, a 2,340 km^2 (900 mi^2) area of rugged, forested terrain, containing about half of the state's estimated 10,690 ha (26,000 ac) of hemlock forest. The remotely sensed data consist of four scenes of leaf-off (November or December) Landsat TM imagery: 1984, 1992, 1996, and 1998, (30m pixel resolution). All scenes were terrain-corrected and georeferenced, converted to radiance values, and normalized to remove atmospheric differences.

Hemlock forest was delineated using a digital map produced by New Jersey Department of Environmental Protection forestry personnel from air photos. Although hemlocks do occur in wetlands such as cedar swamps, they comprise a small percentage of the canopy, and were thus excluded from analysis. Therefore, only upland hemlock forest pixels representing cloud- and snow-free sites in all image dates were retained for analysis, representing about 5,527 ha (13,657 ac) of hemlock-mixed hardwoods forest type The Normalized Difference Vegetation Index (NDVI), derived from near infrared and visible red reflectance values ((NIR - red)/(NIR + red)) was obtained for each hemlock pixel in each image. A neighborhood value was calculated for each hemlock pixel to diminish the effects of any minor, inherent misregistration of the images on the change detection. This neighborhood value represented the average NDVI for that pixel and its eight hemlock neighbors (four adjacent and four diagonal). An increase in the NDVI from Time 1 to Time 2 represents an increase in the amount of hemlock foliage present on a site (pixel), while a decrease in the NDVI represents a loss of hemlock foliage. By simply subtracting the Time 2 data from the Time 1 data, the change in the NDVI can be quantified.

We calculated the rate of change in NDVI for each time interval by subtracting the images in sequence: 1992-1984, 1996-1992, 1998-1996, and dividing the change in NDVI by the number of years in that time interval, e.g., (1992-1984)/8). During the first time interval before 1992, 90% of the NJ Highlands hemlock forests showed no change, but there were areas of severe defoliation comprising 8% of the hemlock forests. During the second time interval (1992 to 1996), the majority (52%) of the hemlock forests showed no change, while 21% showed a decline, and 27% increased in NDVI. During the third time interval (1996 to 1998), the majority (65%) of the Highlands hemlock forests decreased in NDVI, while 25% showed no change and 10% increased in NDVI.

Analysis focused on those site factors related to site moisture, directly or indirectly. The hypothesis is that hemlocks stressed by a moisture deficit decline at a faster rate. As part of the initial data exploration, we conducted a multiple regression analysis to determine the extent to which site variables correlated with the rate of change. We selected 5,000 hemlock sites at random for analysis. The dependent variable was the rate of change in NDVI, and the independent variables were: elevation in meters above mean sea level; slope in degrees; aspect represented as northness; a brightness index representing site illumination levels; a land form index representing convexity and concavity. All of these site variables were derived from a digital elevation model (DEM) of the area (30m resolution). The independent variables were standardized to prevent varying scales of measurement from influencing the analysis.

In general, all of the site variables except aspect were highly significant ($P < 0.0001$). However, site characteristics explained a relatively small amount of the overall variation in the rate of change in NDVI (R^2 varied per time period and ranged from 0.09 to 0.25). Slope was significant during the first two time intervals, but not during the last interval. Though weak, the results suggest that: 1) during the early years (before 1992), the rate of change was greatest at low elevation, concave sites; 2) during the second time interval, the rate of change was greatest at high elevation, bright, convex sites; and 3) during the third time interval, rate of change was again greatest at low elevation, concave sites. Only during the second time period does the decline appear to be related to site moisture deficit (i.e., exposed ridge tops). The results for the first and third periods run counter to our original hypothesis.

No simple, clear cut relationship is evident from this analysis, and explaining the rate of decline may require additional variables. To incorporate the observed coarse-scale pattern in HWA dispersal across the region over the entire time period, latitude and longitude will be included. Future work will explore the inclusion of weather records, alternative sampling schemes, and statistical techniques to further investigate the relationship between site and landscape factors and the rate of hemlock decline.

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Field Surveys and Evaluation of Native Predators of the Hemlock Woolly Adelgid (Homoptera: Adelgidae) in the Southeastern United States

Matthew S. Wallace and Fred P. Hain[1]

Abstract

There has been little research conducted on native enemy effects on the hemlock woolly adelgid, *Adelges tsugae* Annand. This two-year study examined the relationship between native predators and *A. tsugae* in the southeastern United States utilizing field surveys and cage exclusion experiments. Predators were collected in very low densities in 1997 and 1998. *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae), lacewings (Neuroptera: Chrysopidae and Hemerobiidae), and gall gnats (Diptera: Cecidomyiidae) represented 81% of the total predators collected in 1998. Cage exclusion experiments revealed no significant predator effects at all three sites in 1997 and 1998. It is unlikely native predators are exhibiting any significant control on adelgid populations due to the low densities of predators collected at a time when adelgids were abundant. Therefore, controlled releases of exotic predators into these sites should be considered. It is important for scientists and resource managers to continue to recognize the importance for pre-release surveys of native natural enemies prior to mass releases of foreign predators.

Introduction

The hemlock woolly adelgid, *Adelges tsugae* Annand, is an exotic pest of eastern hemlock, *Tsuga canadensis* (L.) Carriere, and Carolina hemlock, *Tsuga caroliniana* Engelm., in the eastern United States from north-central North Carolina to northern Massachusetts. This destructive homopteran was accidentally imported from Japan and was first discovered in the eastern United States near Richmond, Virginia in 1951 and in the western U.S. in the early 1920's (McClure 1989 and 1991). *Adelges tsugae* exploits the valuable hemlock tree by depleting storage cells, or parenchyma cells, located in the xylem tissue (Shields et al. 1996). Heavy infestations of the adelgid can result in the premature drop of foliage, bud abortion, and in extreme cases, mortality within 4 years of infestation (McClure 1991). *A. tsugae* undergoes a polymorphic life cycle where a certain portion of the winter generation (sistens) progeny become wingless progrediens that remain on hemlock while the remaining portion become winged sexuparae which migrate to spruce and subsequently die. Both the sexuparae and progrediens mature in the spring (McClure 1989).

Due to the ineffectiveness of insecticides and the lack of natural enemies of *A. tsugae* in the eastern United States, classical biological control, or the importation of natural enemies from an exotic pest's original location, has become the most researched and promising control option. Classical biological control is the most feasible control method because *A. tsugae* is kept at innocuous densities in Japan by a combination of natural enemies and host resistance. Recently, a small coccinellid beetle, *Pseudoscymnus tsugae* sp. nov., was described as an important predator of *A. tsugae* in Japan (Sasaji and McClure 1997). Experiments in the northeastern United States have shown that this beetle is a very promising biological control agent for *A. tsugae* (Cheah and McClure 1996).

One of the most important first steps in biological control is to survey for and evaluate the effect of native enemies on pest populations before any type of release of exotic enemies is implemented. Evaluation is important because it scientifically examines the values and weaknesses of native natural enemies. It also allows for more educated decisions on the introductions of exotic enemies and the necessity or lack thereof to modify the environment to assist incumbent enemies (DeBach et al. 1976). If an exotic predator is to be considered for release into the southeast in the future, an intensive survey of natural enemies and their effects on adelgid survivorship is needed. The primary objective of this two-year study was to identify natural enemies of *A. tsugae* in North Carolina and Virginia and their degree of synchronization with *A. tsugae* in the field. The second objective was to determine the effects of predation on adelgid survivorship using predator exclusion cages.

Materials and Methods

Field Surveys

All research was conducted at three field sites: Hanging Rock State Park (HR), Stokes County, North Carolina; North Creek (NCR), Jefferson National Forest, Botetourt County, Virginia; and Cave Mountain Lake (CML), Jefferson National Forest, Rockbridge County, Virginia. All trees in all sites were selected for study based on high degrees of adelgid infestation. Arthropod collections were performed in two ways: shaking hemlock branches in the lower canopy of hemlock trees into a 0.45 square meter beat net (Montgomery and Lyon 1996) and probing for arthropods in infested twig samples with the aid of a light microscope. The distal 0.5 meter of 5 infested branches was sampled on every tree and one sample consisted of 5 branches per tree. Twig sampling was conducted only in 1998 and began in late March. It was added to the sampling scheme in order to learn more about microscopic immature predators. Three twigs per tree were clipped with twig cutters from selected trees at every site. Sampling during both years of the study was conducted in the spring and summer months at all three sites.

Most predatory taxa were identified by comparing recently collected individuals with specimens that had been determined by taxonomy specialists. Predators identified in table 1 have either been observed feeding on adelgids given

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to them in the laboratory or been observed feeding on adelgids from infested twigs collected in the field. Voucher specimens have been deposited in the North Carolina State University Insect Collection, Raleigh, NC, and the National Museum of Natural History, Washington D.C.

Cage exclusion experiments

Each tree at each site was randomly assigned three caged treatments (closed-cage, open-cage, no-cage) in the lower canopy. The closed-cage treatment monitored cage and other effects on adelgid survivorship; the open-cage monitored cage effects, predator effects, and other effects; and the no-cage treatment monitored predation effects and other effects on adelgid survivorship. During both study years, experiments were conducted in late-May and June. The spring generation of *A. tsugae* (progrediens) was chosen as the most appropriate life stage to evaluate. We believed that predators would be most abundant during this spring period due to the large number of adult adelgids. This was considered a critical period for predator evaluation because if predators were most abundant at this time, they could hypothetically have the most profound effect on adelgid survivorship by feeding on adults and preventing their entire clutch from being laid. At all sites, appropriate twigs were selected from cage treatments for before and after counts of the number of live progrediens per 10 cm of infested twig. The difference between the number of live progrediens between the before and after counts was then analyzed in all treatments. If there was a significant before/after effect in the no-cage treatment or open-cage treatment compared to the closed-cage treatment, then predation was considered as the cause.

Table 1.—Percentage of total predators collected from twig samples and beat samples combined in all three sites, 1998.

Taxon	HR	NCR	CML
Coleoptera: Coccinellidae (*H. axyridis*)	28.92	38.00	40.50
Coleoptera: Derodontidae (*L. rubidus*)	2.41	2.00	3.31
Diptera: Cecidomyiidae (*Aphidoletes* sp., *Lestodiplosis* sp.)	0.00	20.00	30.58
Diptera: Chamaemyiidae) (*Leucopis* sp.)	0.00	2.00	6.61
Diptera: Syrphidae	25.30	8.00	5.79
Neuroptera: Chrysopidae and Hemerobiidae	43.37	30.00	13.22

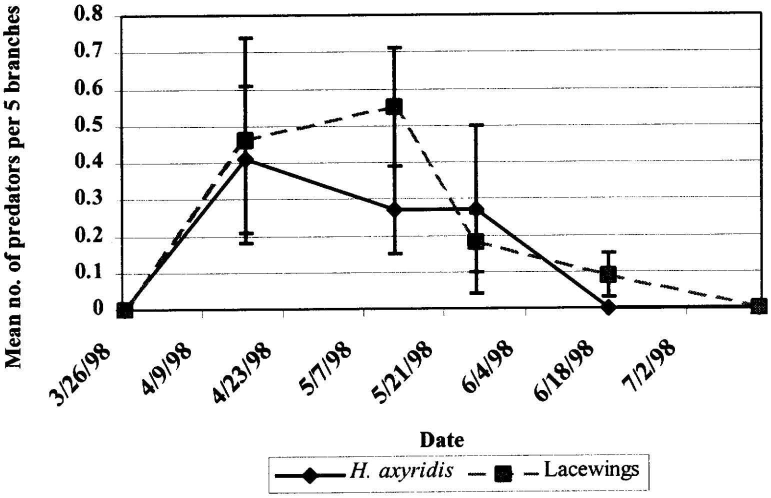

Figure 1.—Densities (mean ± SE) of the most abundant predators in beat samples at Hanging Rock State Park, NC, in 1998.

Results

Field Surveys

Overall in 1997, 22 predators were collected from the beat samples at all three sites combined. The 3 species collected were Asian-multicolored lady beetles, *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae); green lacewings, most likely *Chrysoperla harrisii* (Fitch) (Neuroptera: Chrysopidae); and brown lacewings, most likely *Hemerobius humulinus* L. (Neuroptera: Hemerobiidae). Densities in 1997 were so low and sampling dates were conducted so late in the field season that it was difficult to make any definite conclusions about predator phenology. Sixty-eight immature predators from the family Cecidomyiidae were collected on 24 June 1997 from the no-cage twig samples during the cage exclusion experiments at the Virginia sites. Four of the 68 were identified as *Aphidoletes abietis* Kieffer.

A total of 254 predators was collected from 1998 beat samples and twig samples combined at all three sites. In the 1998 twig samples and beat samples combined, *H. axyridis*, lacewings (Neuroptera: Chrysopidae and Hemerobiidae), and gall gnats (Diptera: Cecidomyiidae) comprised 81% of all individuals collected in all three sites. Table 1 gives a complete listing of the predators collected in 1998. At all sites, overall predator densities in both beat and twig samples were very low in 1998. Predators collected in the beat samples were most abundant in April and May while the greatest abundance of predators collected in the twig samples was observed in late-March and late-June. Figures 1-5 illustrate predator densities over time at all sites.

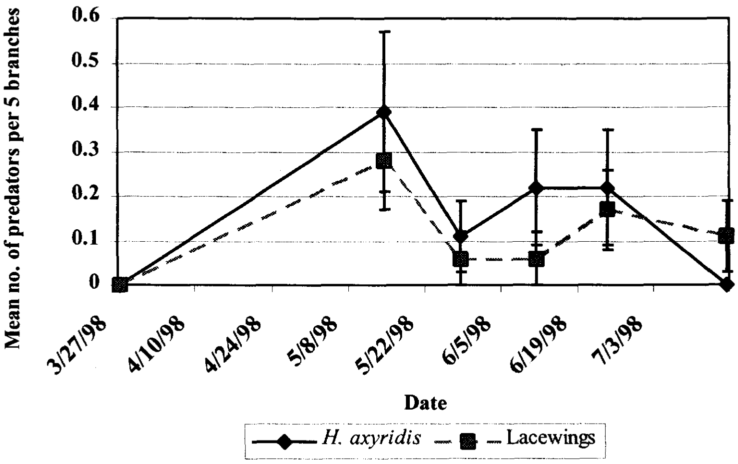

Figure 2.—Densities (mean + SE) of the most abundant predators in beat samples at North Creek, VA, in 1998.

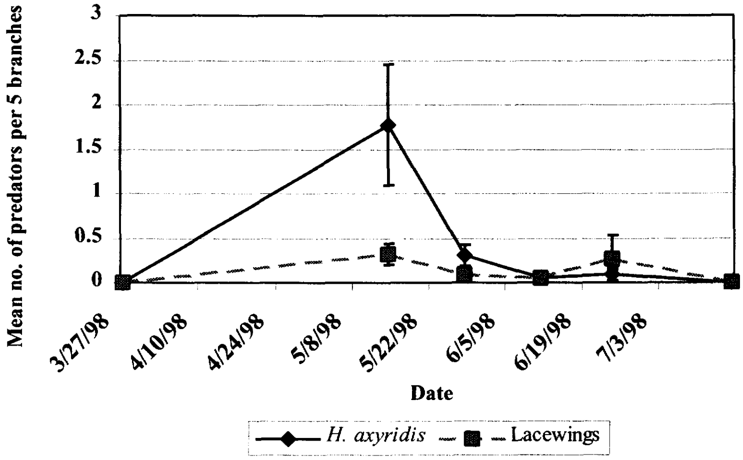

Figure 3.—Densities (mean ± SE) of the most abundant predators in beat samples at Cave Mountain Lake, VA, in 1998.

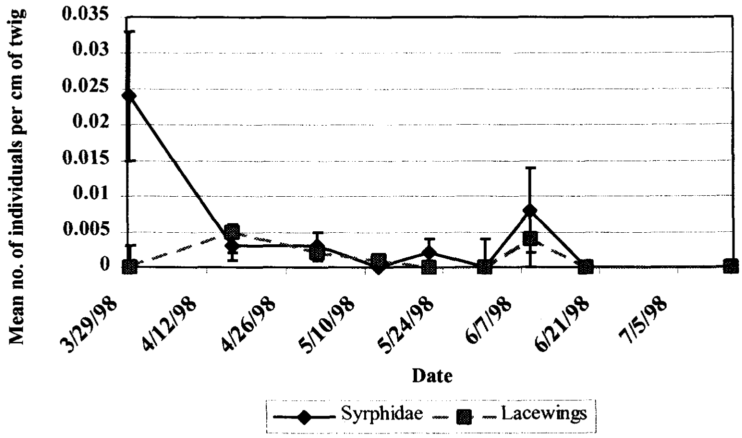

Figure 4.—Densities (mean ± SE) of the most abundant predators in twig samples at Hanging Rock State Park, NC, in 1998.

Cage exclusion experiments

Figures 6 and 7 show the results of the 1997 and 1998 cage exclusion experiments respectively. Results from the statistical analysis revealed significant before/after effects in every treatment at every site in 1997. However, there were no significant differences between the no-cage treatment and other treatments in the change from the before to after count at any site. These results show that there was no difference between treatments in adelgid survivorship in 1997 at any site and no evidence of predator effects.

Results from 1998 revealed no before/after effects in any treatment at either Cave Mountain Lake or North Creek.

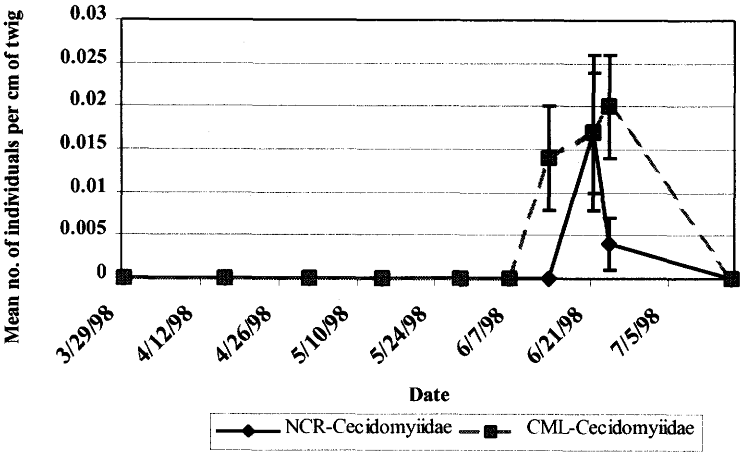

Figure 5.—Densities (mean ± SE) of the most abundant predators in twig samples at the Virginia sites, 1998; NCR, North Creek; CML, Cave Mountain Lake.

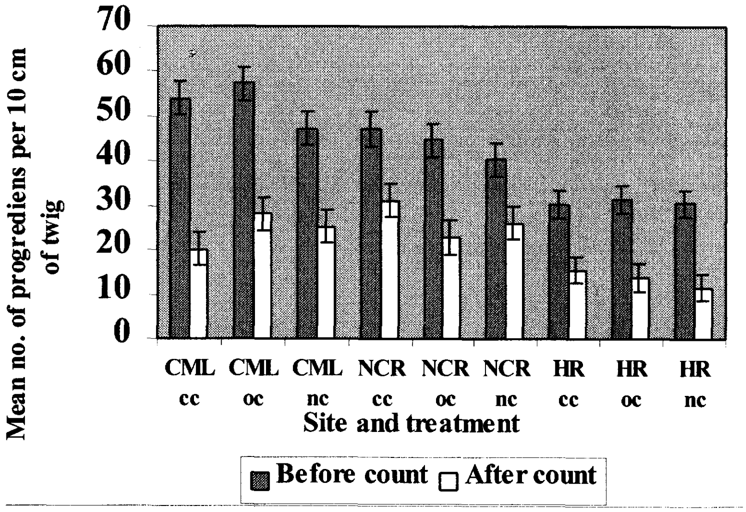

Figure 6.—Mean number of progrediens per 10 centimeters of infested twig ± SE in before and after counts of three caged treatments at all three sites in 1997. CML, Cave Mountain Lake; NCR, North Creek; HR, Hanging Rock; CC, closed-cage; OC, open-cage; NC, no-cage.

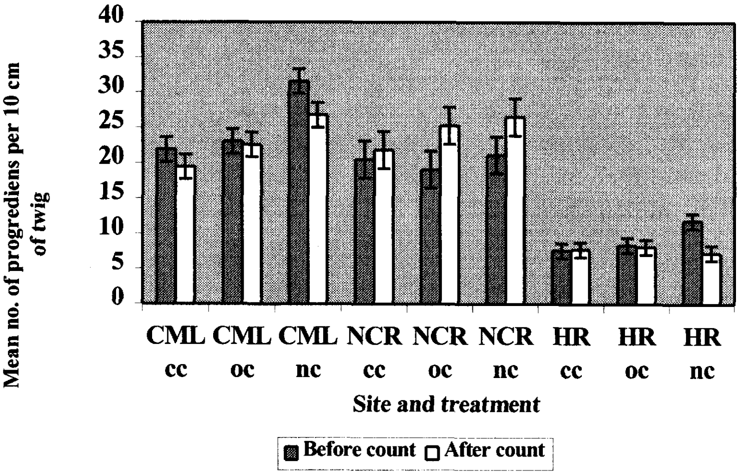

Figure 7.—Mean number of progrediens per 10 centimeters of infested twig in before and after counts of three caged treatments at all three sites in 1998. CML, Cave Mountain Lake; NCR, North Creek; HR, Hanging Rock; CC, closed-cage; OC, open-cage; NC, no-cage.

There were also no significant differences between the no-cage treatment and other treatments in the difference from the before to after count. Therefore, there was no difference in adelgid survivorship between treatments over time and no suggestion of predator effects. At Hanging Rock, results showed a significant before/after effect in the no-cage treatment only. This change from the before to after count was significantly different than the changes from the before to after count in the closed-cage and open-cage treatments. However, this effect probably doesn't have any biological significance due to the lack of predators sampled at the time of the after counts.

Discussion

Results from the 1997 and 1998 field surveys indicate the existence of a small native predator complex associated with *Adelges tsugae* in the southeastern United States. Many of the predators collected in this survey have been found before to be associated with *A. tsugae*. In surveys of predators of *A. tsugae* in Connecticut, representatives from the families Cecidomyiidae, Syrphidae, and Chrysopidae were collected (McClure 1987). *Laricobius rubidus* was also found in surveys of hemlock in Connecticut (Montgomery and Lyon 1996). The most important predators found in this study in terms of abundance were *Harmonia axyridis*, cecidomyids, and lacewings in the families Chrysopidae and Hemerobiidae. Representatives of these groups and many of the individuals collected in this study are known predators of the family Adelgidae (Wilson 1938, Smith and Coppel 1957, Amman 1966, Harris 1973, Tedders and Schaefer 1994).

Even though predators of *A. tsugae* have been documented in this study, results from the cage exclusion studies and field surveys strongly suggest that they are not abundant enough to effectively control *A. tsugae* or prevent tree mortality. Other surveys have found similar predatory taxa associated with *A. tsugae* that were in densities too low to impact adelgid populations (McClure 1987). Predators were collected in very low densities during both years of the study but they were moderately well synchronized with the adelgid life cycle. Figures 1-3 show that the highest abundance of predators in the beat samples (mid-April to mid-May) was observed at a time when sistens adults were beginning to die off but progrediens eggs and nymphs were abundant. This suggests that these predators likely have preferred sources of prey since their populations did not respond with any numerical increase to the abundant numbers of adelgids available to them.

The high densities of cecidomyids observed in late June of 1997 and 1998 (Figure 5) had little impact on adelgid survivorship because they were feeding at a time when adelgids had already laid most of their eggs and adults were dying off. If they and other adelgid specific predators such as *Leucopis* sp. were in high densities from mid-April to early-June when adelgid eggs, nymphs, or adults were most abundant, they may have had more of an effect on adelgid survivorship.

Due to the low densities of predators and their lack of ability to control adelgid populations in these three sites, the release of a foreign specific predator such as *Pseudoscymnus tsugae* should be considered. Such a release should not proceed without caution however. Native predator densities were low in these sites but it is difficult to make an accurate statement of the predator/prey relationship in a two-year study. Low predator numbers could easily be attributed to normal yearly population fluctuations. It should also be noted that *Harmonia axyridis* was one of the more common predators. This generalist predator, which will feed on a large number of organisms and may feed on other predators, could pose a problem for the establishment of an exotic predator.

Even though predators were collected in low densities in this study, it is still important for scientists and resource managers to understand the importance of conducting native enemy evaluations prior to mass releases of an exotic natural enemy. The baseline information gathered in these studies lays the groundwork for future studies with exotic enemies and in some cases may show that incumbent natural enemies serve an important role in pest control. Future research should more closely examine the relationships between exotic predators such as *Pseudoscymnus tsugae* and incumbent predators of these sites.

Acknowledgments

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Host Suitability and Preference of *Laricobius nigrinus* (Fender) (Coleoptera: Derodontidae): A Predatory Beetle for Potential Biological Control of *Adelges tsugae* (Annand) (Homoptera: Adelgidae)

Gabriella Zilahi-Balogh, Scott M. Salom, and L.T. Kok[1]

Abstract

Laricobius nigrinus (Coleoptera: Derodontidae) is being evaluated as a potential biological control agent of hemlock woolly adelgid (HWA), *Adelges tsugae* (Homoptera: Adelgidae) Annand in eastern North America. HWA is not considered a pest on western species of hemlock (McClure *et al.* 1996). A combination of natural enemies and host resistance likely play an important role in maintaining levels of HWA below economic thresholds. We are studying *L. nigrinus* because it may play a role in regulating HWA abundance.

L. nigrinus develops and reproduces successfully on a diet of HWA. Host preference tests are being conducted. In no choice tests, *L. nigrinus* lay significantly more eggs on *A. tsugae* than on *Pineus strobi* or *A. lariciatus.* In paired choice tests, *L.nigrinus* lay significantly more eggs on *A. tsugae* than on *P. strobi.* The expected results from these studies will indicate host range of *L. nigrinus* which is a key requirement for determining its suitability for release in the eastern U.S.

Biology of *L. nigrinus* has not been previously reported in the literature. Our laboratory studies indicate that mating occurs readily between February and April. Males lie lateral to females when copulating. Females lay eggs singly within the woolly ovisacs of HWA. The beginning of egg laying by *L. nigrinus* appears to be synchronized with egg laying by HWA in the spring. This is being confirmed with our field sampling. The eggs appear to be deposited with a sticky secretion on the surface to aid in adhering to the wool. Eggs are bright yellow when first laid, oblong in shape and smooth surfaced. The egg undergoes a color change as it develops, changing from bright yellow to pale greenish-yellow. A few days before hatch, black compound eyes can be seen through the chorion. The ovipositional period lasts from February to late April. Four instars were determined from head capsule measurements. All life stages of *L. nigrinus* feed on HWA. Early instars feed within the woolly sacs and can only be found by picking open the wool. Later instars feed within the wool but are also active on the stem in search of prey. Larvae appear to have well developed mandibles, which they use to grasp prey and suck out body fluids. Mature fourth instars migrate to the soil and remain in a prepupal state for about 10 days before pupating. Pupation period is between 10 and 14 days. Mean development time (± SD) from egg hatch to adult is 56.8 ± 2.61 and 44.2 ± 2.55 at 15 and 18°C, respectively. Emergent adults remain in the soil and aestivate, resuming activity in early October.

Biology of *L. nigrinus* described from laboratory observations is similar to biology described by Franz (1958) for *L. erichsonii*, a European species. However, Franz (1958) reports that emergent adults feed prior to undergoing aestivation from August to October. This was not observed for *L. nigrinus* under laboratory conditions. Aestivation for *L. nigrinus* occurred from May to October in the laboratory.

We are currently sampling *L. nigrinus* and HWA in western hemlock seed orchards in western North America (where *L. nigrinus* is native) to determine its seasonal abundance and synchrony with HWA. Temperature requirements are also being determined to compare HWA phenology and to help streamline our rearing efforts.

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Hemlock Resources at Risk in the Great Smoky Mountains National Park

Kristine D. Johnson[1], *Fred P. Hain*[2], *Katherine S. Johnson*[3], *and Felton Hastings*[4]

Introduction

Eastern hemlock (*Tsuga canadensis* (L.) Carr) is the dominant species in a variety of sites in Great Smoky Mountains National Park. Hemlock covers approximately 3820 acres (1528 hectares) or one percent of the Park, which at 524,856 acres is the largest area managed as wilderness in the eastern United States. Since timber was never harvested in about 20% of the Park, many of the hemlock areas are virgin forests containing trees exceeding 400 years of age. From 1992-1995, Park resource managers began to identify, map, and gather baseline information on hemlock forests. Approaching infestations of hemlock woolly adelgid provided some urgency for this inventory. In addition, the fauna of hemlock forests are virtually unknown. In 1996, the Park began a cooperative project with NC State University to develop survey methods for arthropods associated with hemlock. Knowledge of species present, seasonal abundance, natural variations in abundance and locations of rare species will be fundamental in decisions regarding the use of insecticides or biological controls against HWA. Baseline information gathered prior to infestation will assist Park managers in evaluating changes in the ecosystem and potential restoration efforts.

Objectives

1) Determine the location and size of hemlock - dominated forests throughout the Park
2) Determine the species composition, ages, and disturbance history of these forests before the arrival of hemlock woolly adelgid
3) Develop survey methods for hemlock fauna
4) Determine seasonal abundance and distribution of selected arthropod species associated with hemlock

Methods

Potential hemlock stands were located using Great Smoky Mountains National Park's Geographic Information Systems data (Pyle, 1985) and 1982 winter aerial photographs (scale 1:34000). Minimum stand size was 5 hectares. Winter photos gave the benefit of leaf-off condition for hardwoods and weather conditions may make one set of photos better than another for distinguishing hemlock from white pine (*Pinus strobus* L.). Once located on the aerial photos, the larger potential areas of hemlock were field checked to verify the forest cover type, to obtain species composition and age data, and to note visual signs of past disturbance. The two forest type classifications used for hemlock delineation were "hemlock/cove hardwood" and "hemlock/northern hardwood." These were determined by the species association with the highest representation of stems in the upper canopy layers. To verify overall forest type and species composition, a minimum of two canopy tree tallies were conducted in each stand, using approximated 1/10-ha circular "plots." For each of the tallies, a center point was arbitrarily selected, and within a visually estimated 20m radius, trees greater than 10 cm DBH were tallied by species, crown class, and presence/absence of regeneration. To determine tree ages and to gain an idea of tree sizes within the stand, increment cores and diameter were taken at breast height from a minimum of two trees per tally site. Any visual signs of disturbance such as (but not limited to) selective logging, fire, or chestnut blight (Cryphonectria parasitica (Murrill) Barr), were noted on the field data sheets.

For the arthropod monitoring component of the study, research plots were established in two old growth stands (Inadu Knob and Cataloochee) and two secondary growth stands (Elkmont and Cosby). Within each stand, 16 monitoring stations were located at sites representative of the plot. Each station was a 0.1-acre circular plot. Approximately 20 meters separated the stations. The study had a total of 64 monitoring stations (32 in old growth and 32 in secondary growth stands). The design allowed for sampling all 64 stations within one week. Several sampling techniques were used, with light traps and pit-falls producing the most specimens. On successive nights, one UV light trap was placed in each of the four hemlock stands to capture nocturnal aerial insects. For approximately one hour after sunset, insects attracted to the light trap were captured with an aerial net.; a white sheet hung near the light facilitated this operation. The light trap was powered by a portable battery pack and remained the entire night, with insects being captured in soapy water.

Ground dwelling arthropods were captured in pit-fall traps that were open 24 hours. The center of each sampling station had five traps placed in an X-pattern. Surveys were conducted in the weeks of June 5, 1995, July 17, 1995, September 4, 1995 and April 22, 1996.

Results

Hemlock forests are widely distributed in the Park with elevations ranging from 1,500 to 5,700 ft. At lower sites, stands are found along streams and north-facing slopes, while higher sites are along ridges. In addition to the contiguous stands delineated in this study, hemlock are a frequent component of cove hardwood and northern hardwood forests and are sometimes mixed with pine or spruce. The hemlock stands were heavily logged before the Park was established: Thirty three million board ft. were removed from the Smokemont drainages alone, and one billion board ft. from the Little River area (Stupka, 1964). While the Park has the current national champion tree (a

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specimen 165 ft tall) many of the oldest trees are growing on poorer sites inaccessible to loggers and may be rather small. For example, one 20-inch DBH tree cut for a trail footlog was 535 years old. Average ages were around 220 years. Forty-nine stands were delineated, with a total of 87 ha (2,169 acres). Most of this was old growth, with some areas showing signs of selective logging and occasional fires. At present, 57% of the Park's photo-delineated stands have been ground checked, with the priority placed on the largest contiguous areas. A rough estimate of the Park's hemlock coverage stands at approximately 4,000 acres.

One of the reasons for delineating the hemlock stands was to facilitate research in inventory and monitoring of species associated with these ecosystems. Specimens from one of the first studies, the NC State arthropod study, are still being processed and identified. The total number of specimens caught in light traps were numerous and considering that most were microlepidopterans and even smaller insects, these numbers are probably in the order of five to six thousand. Where aerial nets were used to selectively sample insects coming to the light traps, 668 quality specimens were collected. Approximately 50 percent of these have been identified to species. In the old growth stands, 260 were collected at Cataloochee and 57 at Inadu; for the secondary growth stands, 184 were collected at Cosby and 195 at Elkmont. In addition to the 668 specimens taken with aerial nets, light traps yielded 614 specimens from Cataloochee and 461 from Inadu; for Cosby the number was 793 and for Elkmont, 579. All these specimens are pinned and identified to family. The results of the pitfall traps clearly show distinctive differences in insect diversity between the old growth and secondary growth forests. The old sites yielded only 172 insects (Cataloochee 116 and Inadu 56), but the secondary growth sites totaled 1133 (Cosby 259 and Elkmont 874). The diversity in these terrestrial insects is striking when expressed in terms of family. The old growth had 27 families while the secondary growth had 63 families. There were 13 families that were common to each of the different forest sites.

In 1998 the Park began an "All Taxa Biodiversity Inventory" with the goals of completing a comprehensive checklist of all life forms in the Park, along with range maps, habitat and natural history information, and relative abundance. Priority is placed on ecosystems at risk, and hemlock is certainly among these. The Park invites researchers to assist in this project.

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Relationships Between Environmental Factors and Hemlock Distribution at Mt. Ascutney, Vermont

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Abstract

In order to quantify relationships between environmental factors and the distribution of eastern hemlock (*Tsuga canadensis* (L.) Carr.) and other tree species, sites were established every 100 m along four contour lines, lying at 455 m (1500'), 610 m (2000'), 760 m (2500') and 915 m (3000') on Mt. Ascutney, a monadnock in the Connecticut River valley of eastern Vermont that rises to 960 m (3150'). At each site, basal areas of all trees were determined with a 2.5 BAF metric prism. Dominance, or relative basal area per hectare, of each species was then calculated. At each site, slope, aspect and topographic position were recorded. Fuzzy set ordination was then used to find relationships between these environmental factors and hemlock distribution. Overall, hemlock was the most dominant species at 455 m, the lowest elevation (it was not found at the two higher ones). Hemlock was an important codominant at 610 m. At 455 m, hemlock was a significant component at all aspects, but was most dominant on northwest aspects. At 610 m, it was most important on west aspects. It was also most dominant at intermediate topographic positions (e.g. slopes), with little difference between elevations. Although hemlock is often considered to be important in cool, dark, wet stream bottoms, the results of this study indicate that hemlock is also important at more well-drained upland sites.

Introduction

Eastern hemlock (*Tsuga canadensis* (L.) Carr.) is an important species in the northeastern forest. The hemlock woolly adelgid (*Adelges tsugae* Annand), a tiny sucking insect thought to be introduced from Japan (McClure 1992), has caused significant mortality of hemlock in New England since its introduction in the mid-1980s (McClure 1991, Watson 1992, Bonneau and Civco 1996, Royle and Lathrop 1997). The adelgid is currently not found in most of northern New England, but is expected to spread across the entire range of hemlock (McClure 1989, 1990).

The effects of hemlock mortality are well-studied in southern New England (Orwig and Foster 1998, Jenkins et al. 1999). However, while hemlock remains an important part of the northern New England forest, the associated species change. For example, black birch (*Betula lenta* L.), which is one of the most important successional species after adelgid-induced mortality in southern New England (Orwig and Foster 1998), is not present in most of northern New England. Thus, the pattern of succession after hemlock mortality in northern New England may differ from that seen so far in southern New England. Therefore, the object of this study was first to find where hemlock is distributed at an upland site in the upper Connecticut River valley of Vermont and New Hampshire. Based on the current locations and tree species associations found at sites where hemlock is now found, an attempt was then made to predict which species will take over after hemlock mortality occurs.

Methods

Data were collected from Mt. Ascutney (43°27' N, 72°27' W), a monadnock in the Connecticut River valley of eastern Vermont, that rises to an elevation of 960 m (3150'). Sites were established every 100 m along four contour lines, lying at 455 m (1500'), 610 m (2000'), 760 m (2500') and 915 m (3000'), so as to circumnavigate the entire mountain. At each site, basal areas per hectare of trees were determined with a 2.5 BAF metric prism (Avery and Burkhart 1983). Slope and aspect were also recorded. Dominance of each species at each site was calculated as its basal area per hectare divided by site total basal area per hectare and ranged from 0 to 1. Aspect values were calculated as (cos(q-30°)+1)/2 (Roberts 1986), where q is the aspect, so that plots on northeast aspects would have values near 1, while plots with southwest aspects would have values near zero. Slope was expressed as the "percent" slope = tan (slope (°)). Topographic position was recorded subjectively and coded from 1 to 3, with a 1 indicating a ridge top and a 3 indicating a stream bottom. Both total basal area per hectare and relative basal area (dominance) of each species at each elevation were calculated. Mean basal areas of each species at each elevation were also determined. A total of 383 sites were included from all four elevations; of this number, 154 sites were at 455 m and 130 were at 610 m.

The distribution of sites with hemlock at the lower two elevations (hemlock was not found above 610 m) was also examined in detail. Circular plots showing site aspect and dominance were generated. Mean angles of hemlock-dominance-weighted aspects and angular dispersions were calculated (Zar 1984). The Moore nonparametric modification of the Rayleigh test for significant direction using aspect angles weighted by hemlock dominance was also applied to both elevations (Zar 1984). Those sites with hemlock present were assigned to one of four aspect classes: NE (>0-90°), SE (>90-180°), SW (>180-270°) and NW (>270-360°). At each aspect class and elevation, other tree species with a mean dominance greater than 0.10 were noted. Each aspect class was then further divided into four classes based on hemlock dominance (<0-0.25, <0.25-0.50, <0.50-0.75, and >0.75-1). The two associated species with the largest dominances were then noted (three species were listed if the second and third largest were similar).

Fuzzy set ordination (FSO), as described in Boyce (1998), was performed to examine relationships between tree species and site factors. FSO is a technique introduced by Roberts (1986), who has shown it to be a general technique

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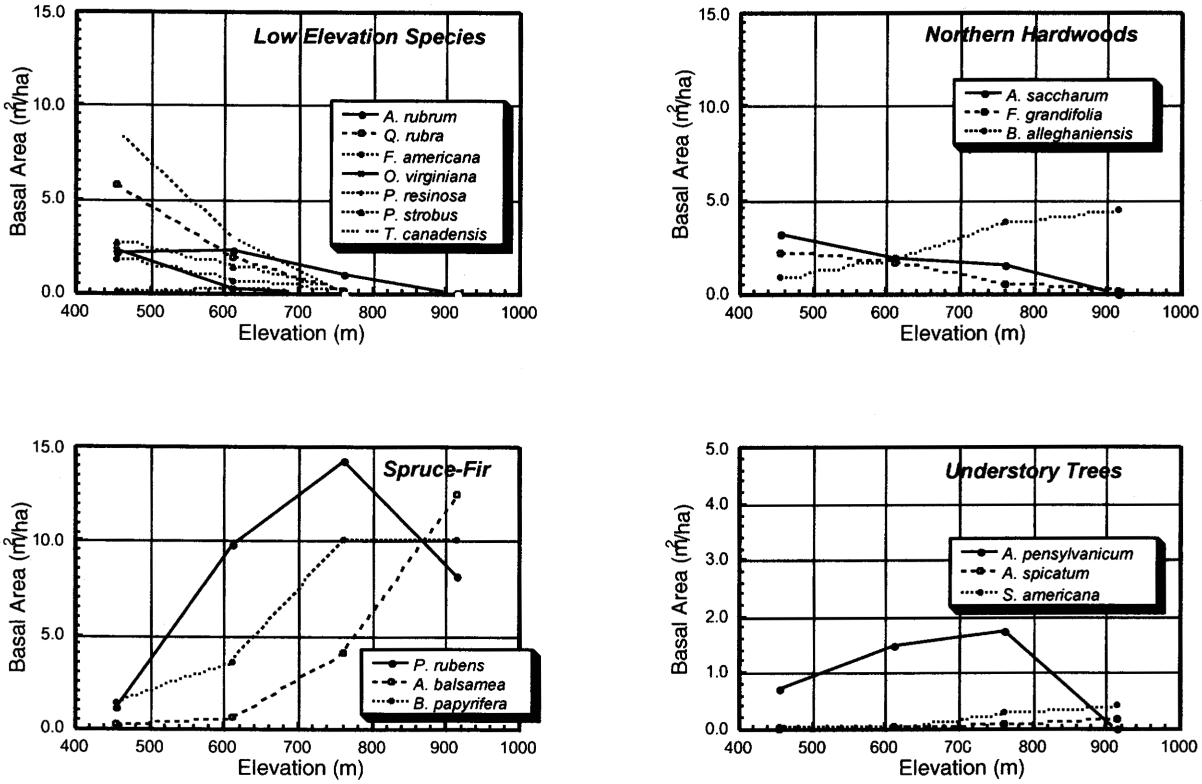

Figure 1.—Mean basal area per hectare of each species at each actual elevation.

that includes direct gradient analysis (Whittaker 1967), Bray-Curtis ordination (Bray and Curtis 1957) and environmental scalars ordination (Loucks 1962). An investigator using fuzzy set ordination must hypothesize a relationship between the environment and the vegetation before performing the ordination. Sites are assigned values that can range from 0 to 1 that denote their membership in a set. For example, the values of site in a fuzzy set of "high elevations" would range from 0 (the lowest site) to 1 (the highest site). One very useful operator in vegetation analysis is the anticommutative difference (Roberts 1986), which can be understood as "while not." This can be used, for example, to construct a fuzzy set that includes the membership of sites that are similar in composition to high elevation sites while not similar to low elevation sites. This is referred to as "apparent elevation" and shows the elevation of a site based on its composition. Thus, a spruce-fir stand would have a higher apparent elevation than an oak-pine stand found at the same elevation. Details of the ordination procedure are given in Boyce (1998). After FSO was performed, species dominance was plotted against apparent elevation to determine which species were associated with high and low apparent elevations. Mean site attributes (topographic position, slope and aspect values) of each species, weighted by dominance, were determined for each elevation.

Results

In terms of mean basal area, forests at 455 m were dominated by hemlock and red oak (*Quercus rubra* L.) (Fig. 1). A number of other hardwood and conifer species were also found in small amounts. By 610 m, however, red spruce (*Picea rubens* Sarg.) had become the dominant species, with white birch (*Betula papyrifera* Marsh.) and hemlock as important codominants. At 760 m, red spruce and white birch were the most dominant species, while balsam fir (*Abies balsamea* (L.) Mill.) had become an important component. Red spruce basal area peaked at 760 m and the basal area of white birch leveled off, but the dominance of balsam fir increased so that it had become the dominant species at 915 m, followed by white birch and red spruce. At no elevation was the "Northern Hardwood" forest type, consisting of sugar maple (*Acer saccharum* Marsh.), beech (*Fagus grandifolia* Ehrh.) and yellow birch (*Betula alleghaniensis* Britton), ever dominant. Among understory trees, striped maple (*A. pensylvanicum* L.) achieved its greatest dominance at 760 m, while mountain maple (*A. spicatum* Lam.) and mountain-ash (*Sorbus americana* Marsh.) were most dominant at 915 m.

Plots with low apparent elevations were dominated by red oak and hemlock (Fig. 2), and were found on sites with south-facing aspects and steep slopes. Sites with the

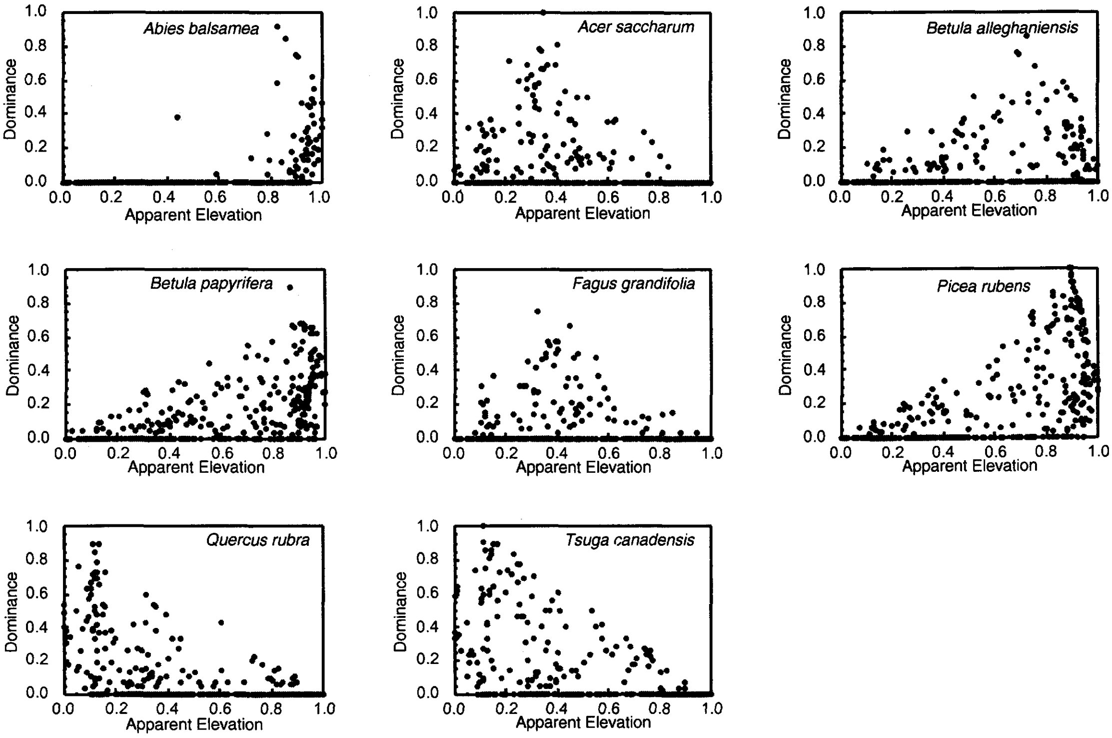

Figure 2.—Plots of dominance (relative basal area) vs. apparent elevations for important species on Mt. Ascutney.

highest apparent elevations were dominated by balsam fir, red spruce and white birch (Fig. 2). Hemlock was generally found on midslopes at both 455 and 610 m, rather than on ridgetops or stream bottoms; there was little variation in topographic position with elevation (Fig. 3). Hemlock sites had one of the higher mean percent slopes of those species found at both elevations, although there was a good degree of variation (Fig. 4). Hemlock mean aspect values were approximately 0.6, indicating a preponderance of sites that faced a bit north of true east and west, but the variation was quite large, indicating that hemlock was widely distributed at many different aspects (Fig. 5).

Analysis of actual aspect weighted by dominance showed a mean northwest aspect at both elevations (Fig. 6). At 455 m, mean aspect was 340°, with an angular deviation of 70°, while at 610 m, mean aspect was 307° and angular deviation was 57°. Despite high angular deviations, both directions were statistically significant (Fig. 6). At 455 m, the most important associated species was red oak at all aspects except the northeast, where sugar maple and beech were important (Table 1). White pine and beech were also important on the southwest and southeast aspects, respectively. As hemlock increased in dominance, however, red spruce became increasingly important, except on southwest aspects, where red oak and white pine were the most important associates. Yellow and white birch were important associates on northeast and northwest aspects as hemlock increased in dominance. At 610 m, red spruce was the most important associate (Table 1). Yellow and white birch were also important on the northern aspects, while white pine was also important on the southern aspects. At this elevation, there was little difference in associates among dominance classes.

Both red oak and hemlock reached their maximum dominance at or below the lowest apparent elevation examined in this study (Fig. 7). Both species are capable of completely dominating a stand at low apparent elevations. Although northern hardwoods are not at present a very important component of the forests on Mt. Ascutney, Figure 7 shows that they are capable of becoming the dominant species at lower-middle apparent elevations. Yellow birch actually reached its peak of dominance at higher apparent elevations than the other two "Northern Hardwood" species. Red spruce was found at all apparent elevations, but it reached its greatest dominance at or above the highest apparent elevations, where it could completely dominate a site. Balsam fir could also completely dominate high apparent elevations but was not found at lower apparent elevations. White birch achieved its maximum dominance at the highest apparent elevations, but it never completely dominated a stand like the two conifer species did. Among understory trees, only striped maple was able to reach high levels of maximum dominance, which occurred at middle apparent elevations. Both mountain maple and mountain-ash attained low levels of maximum dominance at high apparent elevations. Among other tree species, only white

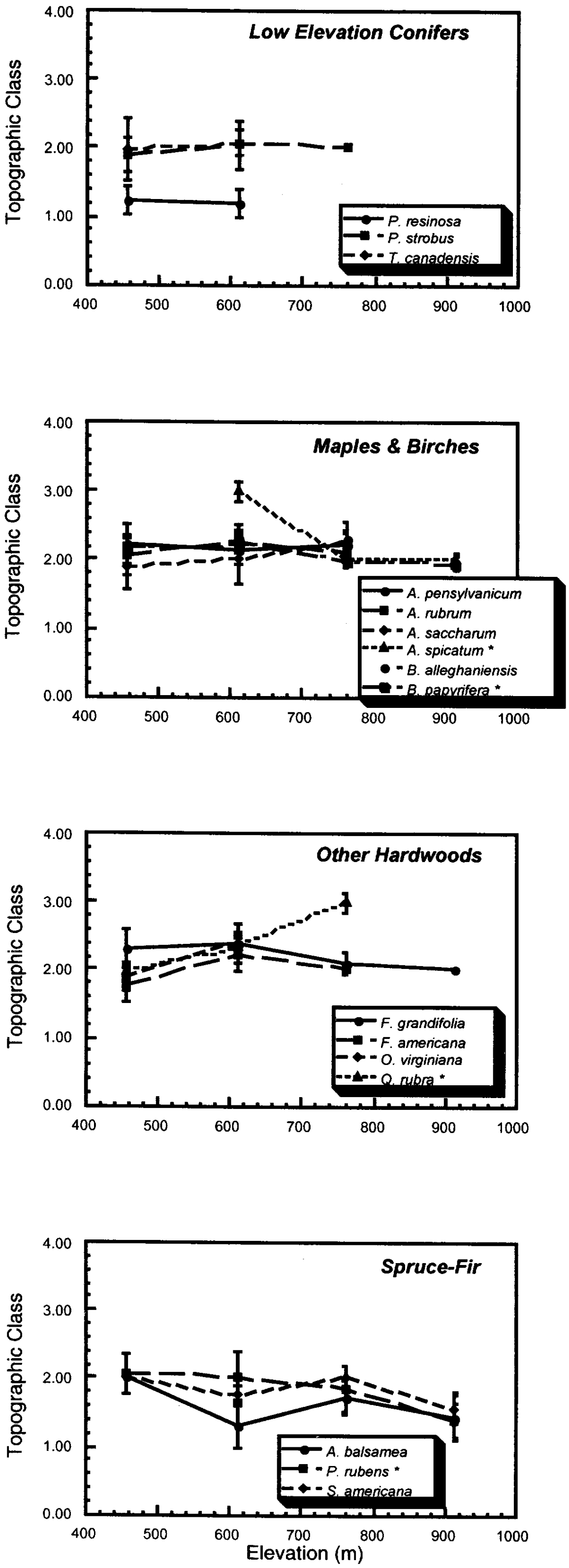

Figure 3.—Mean topographic position (1=ridgetop, 2=intermediate position (slope), 3=stream bottom) of each species at each elevation, weighted by dominance of the species at each site, vs. actual elevation. Species with statistically significant linear increases or decreases with elevation (P<0.05, F-test) are indicated with a star. Error bars are standard deviations.

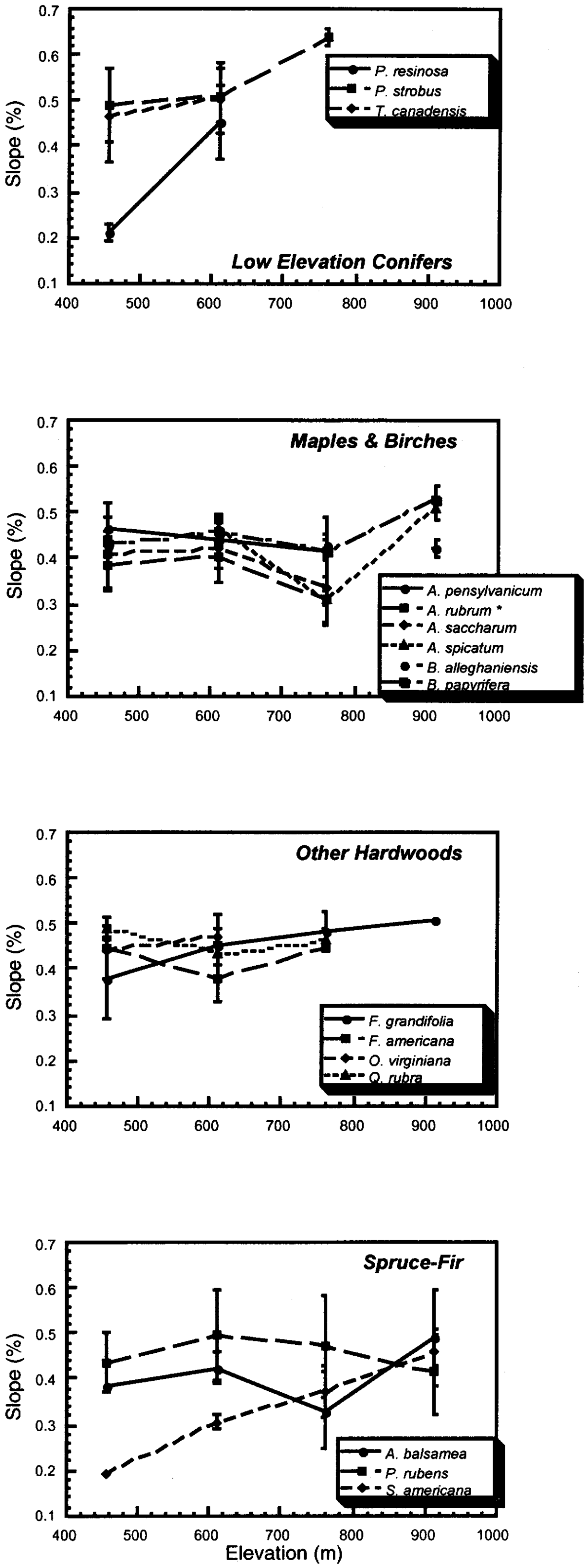

Figure 4.—Mean slope of each species, weighted by dominance of the species at each site, vs. actual elevation. Species with statistically significant linear increases or decreases with elevation (P<0.05, F-test) are indicated with a star. Error bars are standard deviations.

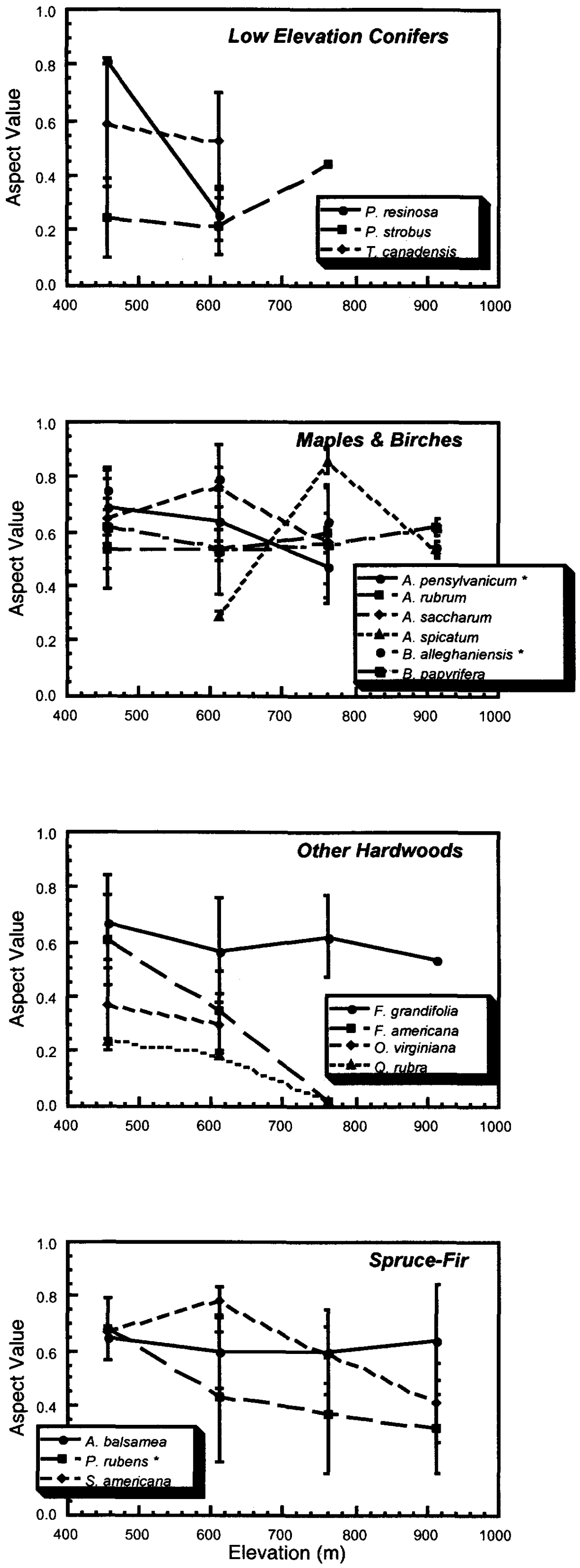

Figure 5.—Mean aspect value of each species, weighted by dominance of the species at each site, vs. actual elevation. Note than an aspect of 30° has an aspect value of 1, while an aspect of 210° has an aspect value of 0. Species with statistically significant linear increases or decreases with elevation (P<0.05, F-test) are indicated with a star. Error bars are standard deviations.

pine (*Pinus strobus* L.) showed the potential to almost completely dominate a stand. Red maple (*Acer rubrum* L.) was widely distributed across apparent elevations but appeared incapable of attaining more than codominant status. Hophornbeam (*Ostrya virginiana* (Mill.) K. Koch) is usually an uncommon understory or subcanopy tree (Burns and Honkala 1990), but there were stands at lower apparent elevations on Mt. Ascutney where it appeared capable of making up more than 50% of relative basal area.

Discussion

Hemlock is currently an extremely important species on Mt. Ascutney, with the highest basal area at 455 m and an important codominant at 510 m. Boyce (1998) asserted that it has the potential to dominate many sites at 455 m and in fact does; however, analysis of the upper bounds of dominance indicates that it probably reaches its most importance at elevations below those sampled in this study. Hemlock is widely distributed on the lower reaches of this mountain. While there is a significant trend toward greater hemlock dominance at northwest aspects, especially at 610 m, the species is clearly widely distributed. Figure 6 shows that hemlock is less prevalent on the southeast aspects at 610 m. This may be due in part to the hurricane of 1938, which strongly affected the southeast-facing slopes of Mt. Ascutney (ATA 1992); indeed, the southeastern side of Mt. Ascutney has noticeably fewer conifers that other aspects (R. Boyce, personal observation). This effect may be enhanced at higher elevations because of increasing wind speeds.

At the upland sites sampled here, hemlock is found mainly on slopes. This species is typically found to occupy stream bottoms (e.g. Burns and Honkala 1990). Why is this not the case at the upland sites sampled here? There appears to be a parallel response to elevation of both hemlock and red spruce. Boyce (1998) found that red spruce was restricted to stream bottoms at the lower elevations on Mt. Ascutney. However, it moved to slopes and ridges at higher elevations, which may be due to the increasing moisture that is available at all topographic positions at higher elevations (Boyce 1998). Hemlock appears to exhibit a similar trend, albeit at lower elevations than spruce.

A wide variety of species associate with hemlock at both elevations. At 455, red oak is the most dominant hemlock associate (Table 2). On sites with northeast aspects, however, sugar maple and beech are the most important. However, in stands at this elevation dominated by hemlock (more than 75% of the basal area), red spruce is the most important associate. At 610 m, red spruce is by far the most important associate overall and at most of the different levels of hemlock dominance as well.

So what does this imply for these upland hemlock stands when they are attacked by hemlock woolly adelgid? Studies in southern New England have shown that the adelgid causes a rapid shift from a coniferous to a deciduous forest, with the most common colonizers being red maple, oaks (*Quercus* spp.) and black birch (Orwig and Foster 1998).

Table 1.—Dominance of hemlock and associated species by aspect class at 455 m and 610 m, along with total number of sites with hemlock. Each aspect class is also divided into four hemlock dominance classes; the two most important asociated species are listed for each dominance class, along with the number of sites for each dominance class (e.g. n^{25} is the number of sites in the 0-.25 class).

Aspect	N	Species	Mean dominance	n^{25}	0-.25	n^{50}	.25-.50	n^{75}	.50-.75	n^{100}	.75-1.0
455 m											
NW	23	Hemlock Red oak	0.50 0.13	7	Red oak Sugar maple	4	Yellow birch Red oak	8	White birch Red oak	4	Red spruce
NE	35	Hemlock Sugar maple Beech	0.38 0.12 0.10	15	Sugar maple Beech	9	Red spruce White birch	6	Sugar maple White birch	5	Yellow birch Red spruce
SE	13	Hemlock Red oak Beech	0.42 0.19 0.11	4	Red oak Hophornbeam Beech	4	Red oak White pine	3	Beech Red oak	2	Red spruce Striped maple
SW	16	Hemlock Red oak White pine	0.33 0.30 0.11	6	Red oak White pine	6	Red oak White pine	4	Red oak White pine	—	
610 m											
NW	15	Hemlock Red spruce White birch	0.30 0.31 0.12	8	Red spruce White birch	4	Red spruce White pine White birch	3	Red spruce Striped maple	—	
NE	10	Hemlock Red spruce White birch Yellow birch	0.24 0.33 0.12 0.11	7	Red spruce Yellow birch White birch	2	Red spruce White birch	1	Yellow birch Sugar maple Beech	—	
SE	1	Hemlock Red spruce White pine	0.26 0.35 0.17	—		1	Red spruce White pine	—		—	
SW	15	Hemlock Red spruce White birch	0.24 0.31 0.15	9	Red spruce White birch	6	Red spruce White pine	—		—	

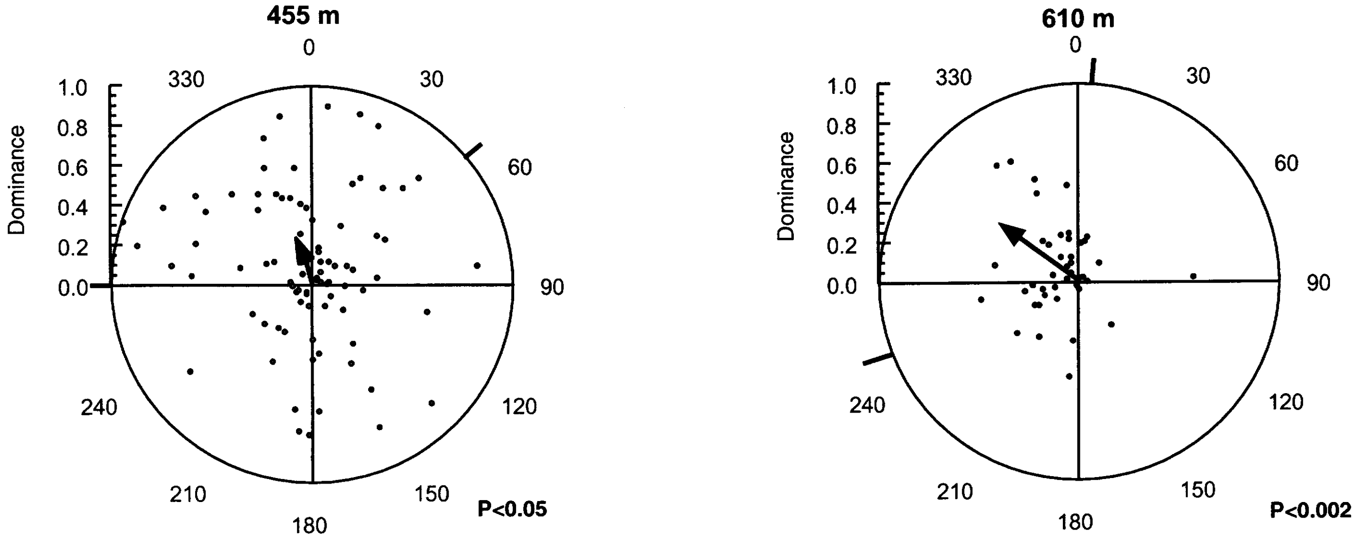

Figure 6.—Aspect and dominance of sites with hemlock present at 455 and 610 m. Mean vector length and directions (Zar 1984), weighted by hemlock dominance, are shown for each elevation by an arrow with its base at the origin. Angular dispersions are denoted by marks on the periphery of the circle. The mean vector length, direction and angular dispersion for 455 m are 0.26, 340° and 70°, respectively. The mean vector length, direction and angular dispersion for 610 m are 0.51, 307° and 57°, respectively. The Moore nonparametric modification of the Rayleigh test for significant direction, using aspect angles weighted by hemlock dominance, rejected the null hypothesis of no significant directionality at both elevations (455 m: R'=1.19, P<0.05; 610 m: R'=1.62, P<0.002).

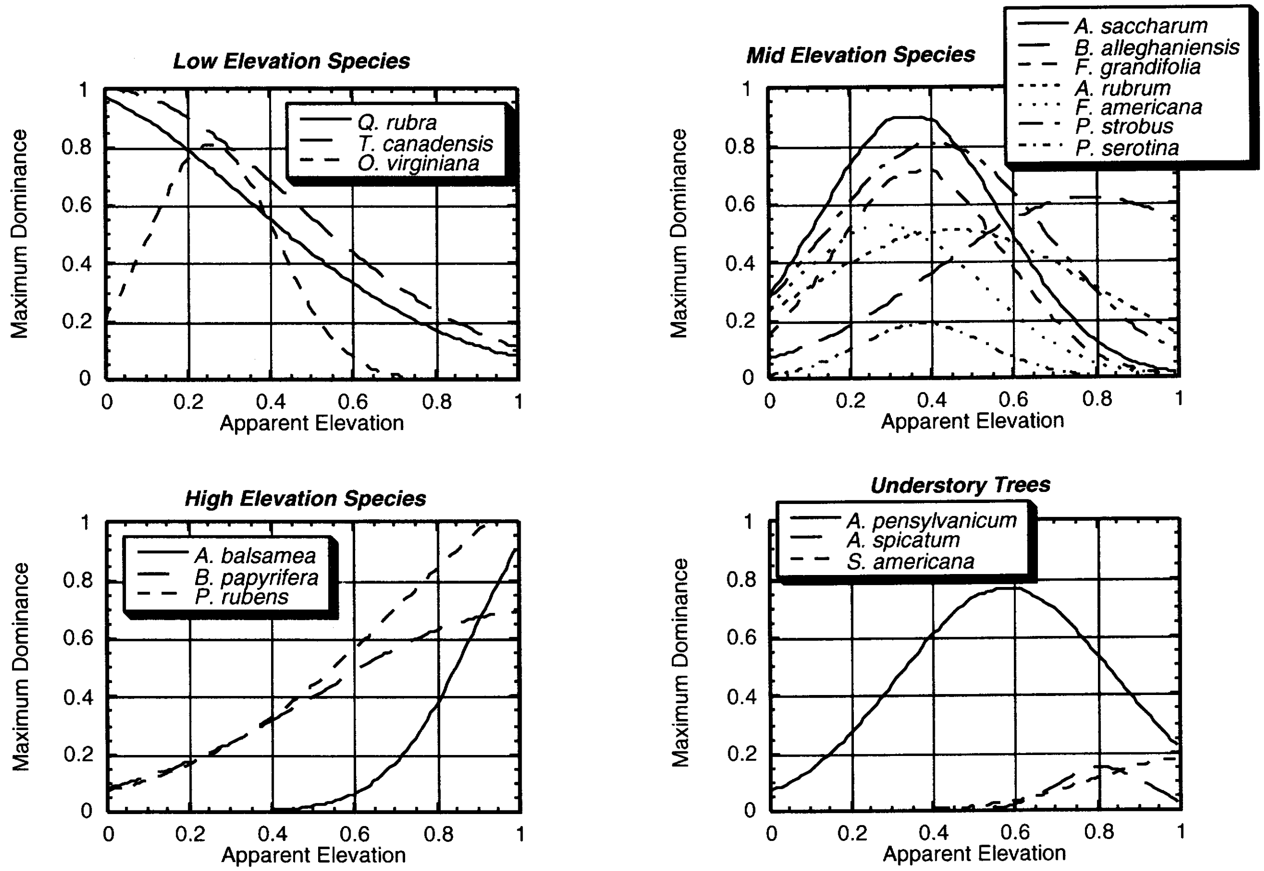

Figure 7.—Upper bounds of dominance of each species vs. apparent elevation. Upper bounds were derived from the data in Fig. 2, using the procedure described in Boyce (1998).

Thus, those hemlock sites with red oak, maples, and birches as associates are likely to be replaced by those species. However, red spruce is an important component in hemlock-dominant stands at 455 m and most stands at 610 m. Red spruce is generally considered a late-successional species that responds slowly to disturbance. However, the "gradual" gaps (sensu Krasny and Whitmore 1992) caused by hemlock decline may allow red spruce to take over what are currently hemlock-dominated stands. If the decline is more rapid, however, yellow or white birch-dominated stands may be more likely. Also, red spruce is in decline in New England (Peart et al. 1992), though not noticeably at Mt. Ascutney (R. Boyce, personal observation). Perkins et al. (1988) noted that yellow and white birches rapidly colonized areas impacted by spruce decline in northern New England; since these species are often important in stands with hemlock, they may also colonize stands with adelgid-induced hemlock mortality.

Because of Mt. Ascutney's proximity to the Connecticut River, the lower elevations lie in Westveld's (1956) "Transition Hardwoods" region, which is shown by the importance of species such as red oak and hophornbeam (Fig. 4). The typical "Northern Hardwoods" forest (sugar maple, beech and yellow birch), which dominates nearby sites in the White and Green Mountains between 610 and 760 m (Bormann et al. 1970, Siccama 1974), is not as important at this site. This mountain is already highly disturbed; within the last 100 years, Mt. Ascutney has experienced logging, fires, granite quarrying and a hurricane (ATA 1992). Disturbance is a likely explanation for the relative importance of white birch at low elevations, as well as the importance of striped maple, which generally requires disturbance to reach the tree stratum (Fig. 7). Thus there are already an abundance of pioneer species present. While the hemlock woolly adelgid is expected to drastically decrease hemlock abundance, the forest is likely to recover quickly. There is likely to be an initial conversion to hardwood stands, particularly birch. While stands currently dominated by oaks may remain that way, stands that are colonized by birch may eventually convert to red spruce, especially at 610 m, provided spruce is not itself in decline.

Acknowledgments

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Changes in the Genetic Diversity of Eastern Hemlock as a Result of Different Forest Management Practices

Gary J. Hawley[1], Donald H. DeHayes[1], and John C. Brissette[2]

Abstract

Loss of populations and individuals within species to human-induced selective forces can result in loss of specific genes and overall genetic diversity upon which productivity, ecosystem stability, long-term survival, and evolution depend. This is particularly true for long-lived organisms, such as forest trees, because genetic diversity confers adaptability necessary for trees to persist across temporally and spatially variable environments. Forest management is an anthropogenic force by which forest managers selectively remove individual trees from a population leaving a residual stand to provide the gene pool for future generations. Very little is known about the influence of forest management and silvicultural practices on the genetic diversity within forest ecosystems. The goal of this research was to evaluate the impacts of forest management on genetic diversity of forest ecosystems.

Genetic diversity assessments were conducted on hemlock trees in stands that have resulted from long-term, active silvicultural experiments established between 1952 and 1957 on the Penobscot Experimental Forest in east-central Maine. In those experiments treatments include fixed diameter limit cuts, and selection cuts. Diameter limit cuts were imposed in 1952, 1973, and 1994 and trees 24 cm or larger were removed each year. For selection cuts, phenotypically superior trees were favored and inferior, unmerchantable and poor risk trees were removed in both 1957 and 1977. Stand-level genetic diversity estimates were obtained for stands representing each silvicultural treatment using starch-gel electrophoresis. These estimates was compared to genetic diversity and inbreeding estimates of an unmanaged control stand to determine genetic changes resulting from these long-term forest management experiments.

Our data indicate that eastern hemlock is low in genetic diversity relative to many north temperate conifer species. Compared to genetic estimates in unmanaged control stand, a series of selection cuts have had limited impact on the level of genetic diversity in the residual stand. Selection cuts did however result in a loss of rare alleles that may be valuable for future evolution. Trees remaining after repeated diameter-limit cuts, leaving only the very worst trees in terms of size and form, had significantly higher levels of heterozygosity, polymorphic loci, and effective number of alleles per locus. These counter-intuitive results reflect an apparent association between rare alleles and defective phenotypes in eastern hemlock. Several alleles that occurred at very low frequencies ($p < 0.03$) in the natural unmanaged stand occurred at much higher frequencies in the diameter limit cut because the defective residual trees preferentially possessed these rare alleles. That is, rare alleles conferred a negative fitness impact on eastern hemlock trees. In fact, 68% and 24% of the residual trees from the diameter limit cut possessed at least one or two rare alleles, respectively, compared to 26% and 6% and 32% and 2% for the unmanaged and selection cut stands, respectively. If rare alleles are disadvantageous, there may be a loss of fitness in the diameter limit cut stand compared to the unmanaged control stand. Because residual trees in the selection cut stand contained fewer rare alleles than the control stand, there may be increase in fitness resulting from repeated selection cuts, at least in the short term. However, in the long term this loss of rare alleles in the selection cut stand compared to the control stand may come at an evolutionary cost because rare alleles are the raw material for evolutionary change.

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Stand, Landscape, and Ecosystem Analyses of Hemlock Woolly Adelgid Outbreaks in Southern New England: An Overview

David A. Orwig and David R. Foster[1]

Abstract

Hemlock woolly adelgid (HWA) (*Adelges tsugae*), an introduced aphid-like insect from Asia, is expanding across the northeastern United States through the range of eastern hemlock (*Tsuga canadensis* (L.) Carr.) and has the potential to severely reduce or eliminate this important late-successional species. While infestation and unimpeded migration of HWA presents a tremendous management problem, it also has provided an unusual opportunity to examine the impacts of an introduced pest as it spreads. In order to develop insights into these management issues, we have developed a multi-faceted research effort that examines various forest responses to HWA outbreaks in Connecticut including stand and community reorganization dynamics, landscape patterns of HWA infestation, damage, and hemlock mortality, microenvironmental changes and their impact on ecosystem processes, and the effect of cutting infested forests on successional and ecosystem dynamics. This paper presents an overview of this research, conducted by Harvard Forest scientists.

Introduction

Hemlock woolly adelgid (HWA; *Adelges tsugae* Annand), an introduced aphid-like insect from Asia, is expanding across the northeastern United States through the range of eastern hemlock and has the potential to severely reduce or eliminate this important late-successional species (McClure 1995a; Orwig and Foster 1998). Despite the growing knowledge about the biology of HWA (McClure 1987, 1989,1990,1991, 1995a; Salom et al. 1996; Young et al. 1995) and increasing efforts to find, raise and release natural or exotic biological controls (Gouli et al. 1997; McClure 1995b; McClure and Cheah 1998; Sasaji and McClure 1997; Others, this volume), we still know very little about how HWA infestation will affect forest and ecosystem processes. Therefore, this paper will present results from past and current research by Harvard Forest scientists on the various forest responses to HWA outbreaks in southern New England.

Research Approaches

Stand-level Dynamics

As part of a large study investigating stand to landscape level forest dynamics resulting from HWA infestation, we examined the initial community response of hemlock stands varying in mortality levels in south-central Connecticut (Orwig and Foster 1998). Since 1995, mortality of overstory and understory hemlock has risen to over 60% in half of the stands and continues to increase 5 to 15% per year. The health and vigor of remaining trees has deteriorated in all stands, with the majority of trees containing less than 25% of their foliage. We have observed no sign of tree recovery on these sites over the last 4 years and predict that all sampled trees will die within the next few years. A rapid recolonization of these forests with seedlings of black birch (*Betula lenta* L.), red maple (*Acer rubrum* L.), and oak (*Quercus*) as well as opportunistic herbaceous species has continued to occur following additional hemlock mortality. Seedling densities have increased in moderately damaged sites and have thinned but increased in cover in heavily damaged areas. We will continue to examine the ongoing dynamics in these forests to gain detailed information on the mechanisms and rate of vegetation recovery.

Landscape-level dynamics

Data and observations from these original eight stands were limited to southern Connecticut and we were interested in how representative the results were compared to a much broader study region. To meet this objective we established a 5900 km^2 transect surrounding the Connecticut River Valley extending from Long Island Sound north to the Massachusetts border (Orwig et al. unpublished data). Within the transect we mapped hemlock stands from aerial photographs and then visited and compiled information on stand composition and structure, presence of HWA, degree of overstory and understory mortality, seedling densities, and site characteristics from 114 stands. HWA presence was observed in nearly 90% of all stands visited and hemlock sapling and overstory trees have experienced much higher rates of mortality (20 to 100%) in the southern part of the state compared to rates in the northern part of the state (0 to 15%). Hemlock mortality exceeded 20% on most topographic aspects, not just the drier southwest or west facing slopes. The health of remaining trees exhibits a pattern similar to mortality, with healthier trees located in the northern part of the transect. These data suggest that except latitude, site factors play little, if any role in the susceptibility of forests to adelgid, and that most stands will suffer heavy or complete mortality following infestation.

Forest composition data from infested stands is useful in predicting the species that will eventually replace hemlock. Currently, black birch, red oak (*Quercus rubra* L.), and red maple are present in the overstory of most stands and are starting to become established in the understory. We have found that most forests contained few hemlock seedlings but modest to high densities of hemlock saplings (200 to 800 ha^{-1}). However, saplings are currently experiencing high levels of adelgid infestation and mortality and seeds do not remain viable for more than a year or two. Therefore, we predict a complete change in cover type from hemlock to hardwood-dominated forests across broad geographical areas.

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Ecosystem-level Impacts

Results from prior ecosystem-level research conducted on sites we have been following for several years (Jenkins et al. 1999; Yorks et al. this volume) suggest that HWA infestation can lead to dramatic changes in nitrogen cycling. Jenkins et al. (1999) found large increases in N mineralization and nitrification rates in infested versus healthy hemlock forests. However, we still do not know how rapidly these changes occur, how long they persist, or to what degree changes in soil temperature or biotic uptake affect nutrient cycling. In order to answer these questions, we have initiated a study examining N availability, mineralization, and nitrification rates in a subset of Connecticut sites that are infested with HWA but have experienced little to no hemlock mortality (Orwig et al. unpublished data). These measurements will continue for at least 3 years to investigate the temporal dynamics and potential mechanisms driving the changes. Additional soil analyses including pH, moisture, carbon to nitrogen ratios, texture, and total soil organic matter have been completed on these 8 sites and we will be quantifying macronutrients such as Ca, Mg, P, and K.

To complement the ongoing ecosystem study, R. Cobb et al. (unpublished data) have initiated a 2-year project examining the effect of HWA infestation on hemlock foliar decomposition rates. We predict that rates will increase with thinning hemlock canopies, although the magnitude of increase may, in turn, be mediated by foliar quality, which may be affected by HWA infestation. To elucidate these potentially interacting factors, hemlock foliage from eight infested stands in Connecticut and from uninfested forests at Harvard Forest in Petersham, MA will be examined for total C, N and C:N ratios and then analyzed *in situ* over time for relative decomposition rates. To investigate what role microenvironmental changes have on nutrient cycling and decomposition rates, organic-layer and mineral-layer soil temperatures are being recorded and hemispherical photographs are being examined to quantify increases in light reaching the forest floor.

Logging impacts

While sampling forests for the landscape-level study, we observed hemlock being cut on over 20% of the stands visited. These observations and others throughout Connecticut, Rhode Island and Massachusetts suggest that hemlock logging is increasing in frequency as a management option in infested stands. However, we do not know how cutting infested hemlock stands will affect regeneration composition or ecosystem processes. Newly initiated research by M. Kizlinski (unpublished data) is examining the effect of hemlock logging on revegetation and ecosystem processes that will complement ongoing research efforts in uncut stands and will shed insight on whether continued cutting will have any adverse impact on hemlock ecosystems.

Conclusions

The future of hemlock forests in New England is bleak. HWA continues to migrate northward apparently unimpeded by any site or meteorological characteristics except extremely cold winter temperatures (Parker et al. 1998). In currently infested stands, trees continue to deteriorate over time and observations from hundreds of stands suggest there is little chance of recovery. Unless an effective biological or chemical control is found that can be released or used on a massive scale that coincides with the range of HWA, hemlock may be eliminated across broad portions of its range in a few decades. By investigating the various forest and ecosystem responses to adelgid infestation as it progresses, however, we can be armed with predictions and pertinent information on how best to manage these lands in the future.

Acknowledgements

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Influences of Eastern Hemlock Mortality on Nutrient Cycling

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Abstract

Mortality of eastern hemlock (*Tsuga canadensis* (L.) Carriere) may be caused by a variety of agents, but hemlock trees of all sizes over a large geographic area are currently threatened by an outbreak of the hemlock woolly adelgid (HWA: *Adelges tsugae* Annand) in the eastern United States. In this paper, we review what is currently known about changes in nutrient cycling due to hemlock mortality, identify gaps in current knowledge, and describe research being conducted to better understand the influences of hemlock mortality on nutrient cycling. Recent research clearly demonstrates that hemlock mortality can strongly influence nutrient cycling rates. Jenkins et al. (1999a) concluded that hemlock mortality due to HWA infestation is likely to result in accelerated nitrogen (N) mineralization and nitrification rates. Yorks, Leopold, and Raynal have observed elevated nitrate and cation (e.g. ammonium, Al, Ca, Mg) leaching in soil water during hemlock decline and mortality. Such nutrient losses can result in reductions in site nutrient capital and future forest productivity. Nitrate and cation leaching is also likely to cause reductions in surface water quality near impacted sites. Despite significant progress regarding our understanding of hemlock mortality and nutrient cycling, several important questions remain. For example: 1) What processes drive the accelerated N cycling rates found at infested hemlock stands?; and 2) How long will changes in nutrient cycling (e.g. elevated nutrient losses to soil water) continue after hemlock mortality? To further understand relationships between hemlock decline and nutrient cycling rates, our current research includes a search for relationships between soil and foliar nutrient status and susceptibility to HWA damage, continued soil water sampling in healthy and dying hemlock stands, stream water sampling from watersheds with a wide range of hemlock abundance, and measurement of soil characteristics in HWA-infested stands.

Introduction

Mortality of eastern hemlock may be caused by a variety of agents, including drought (Stickel 1933, Secrest et al. 1941, Rogers 1978) and pest insects such as hemlock looper (*Lambdina fiscellaria* Guen.), gypsy moth (*Lymantria dispar* L.), and hemlock woolly adelgid (HWA). In this paper, we review what is presently known about the biogeochemical consequences of hemlock mortality, identify gaps in knowledge and propose some relevant hypotheses, and describe current research being conducted to further our understanding of hemlock mortality effects on nutrient cycling. Although other factors may cause hemlock mortality, we will focus on mortality due to the HWA. The HWA is a relatively new but significant forest pest on eastern hemlock; many stands from North Carolina to Massachusetts are currently infested, and the insect may spread into new areas at a rate of 10-15 miles per year (Souto et al. 1996). The HWA is a small piercing and sucking insect that feeds on sap in young twigs and branches, usually near the point of needle attachment (Young et al. 1995). Feeding by the HWA retards and/or prevents new growth and can kill all hemlocks in an infested stand within four years (McClure 1991). Hemlocks killed by HWA lose their needles and create canopy gaps over a period of several years. This mortality directly reduces plant nutrient uptake, reduces evapotranspiration, and opens the overstory canopy which increases the amount of light reaching understory vegetation and the forest floor. Consequently, the HWA has strong potential to alter nutrient dynamics in affected stands.

It is well-documented that tree mortality due to harvesting (e.g. clearcutting) can have dramatic effects on nutrient losses to soil and stream water. For example, studies at the Hubbard Brook Experimental Forest in New Hampshire and elsewhere have illustrated elevated losses of nutrients in stream water for several years after clearcutting (see Martin et al. 1985, Hornbeck et al. 1986). However, other causes of mortality (e.g. diseases, insects) and their effects on nutrient cycling have not received nearly as much attention, despite the fact that pathogen-induced tree mortality is a critical component of ecosystem function (see Castello et al. 1995). A few studies have documented increases in stream water nutrient concentrations in association with insect defoliation (e.g. Swank et al. 1981, Eshleman et al. 1998), but little is known about the effects of insect- or disease-induced tree mortality on nutrient cycling. Some researchers have girdled trees to simulate individual tree mortality due to insects or disease and studied the subsequent effects on nutrient cycling. However, findings have ranged from little or no effect of mortality (e.g., Knight et al. 1991: 60% mortality of lodgepole pine [*Pinus contorta* Dougl. ex. Loud.]) to large increases in leaching and transformation rates (e.g., Edwards and Ross-Todd 1979, Johnson and Edwards 1979: 100% mortality of yellow-poplar [*Liriodendron tulipifera* L.] dominated mixed deciduous forest). Because the effects of tree mortality on nutrient cycling are poorly understood, particularly the impacts of HWA infestation on stands dominated by hemlock, several studies have been completed or are underway to determine the effects of hemlock mortality on nutrient cycling.

Importance of Hemlock Mortality to Nutrient Cycling

Although hemlock is not generally considered to be a commercially important species, it is dominant in many eastern US forests. For example, hemlock and white pine

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(*Pinus strobus* L.)/hemlock forests cover more than 300,000 ha in New York (Alerich and Drake 1995), and hemlock is among the eight most abundant species in northern New England as measured by biomass (Wharton et al. 1985, Frieswyk and Malley 1986a, 1986b). Where hemlock is the dominant overstory tree species, few or no other trees or shrubs may occur in the understory and the herbaceous layer may be sparse (Braun 1950, Lewin 1974). Hemlock is commonly dominant on sites with shallow and/or nutrient-poor soils that are reliably moist (Rogers 1978). In stands where this species is dominant, hemlock mortality can have dramatic effects on nutrient cycling rates and may result in nutrient leaching from soil and nutrient loadings to stream water (Jenkins et al. 1999a). Changes in nutrient cycling due to hemlock mortality are important because elevated nutrient losses may lead to site nutrient capital reduction, increased nutrient loadings to stream water, and acidification of soil and stream water. Elevated ion concentrations in soil and stream water are of concern because leaching of nitrate and other anions (e.g. sulfate) is associated with nutrient cation leaching (e.g. Ca, Mg), mobilization of potentially toxic metals (e.g. Al), and contributes to the acidification of soil and surface water (Reuss and Johnson 1986, Stoddard 1994). Increased nutrient loads to stream water may decrease surface water quality and affect the management of watersheds providing municipal water supplies. Hemlock mortality is likely to contribute substantially to stream water degradation given its tendency to grow near streams and in ravines (Lewin 1974, Whitney 1991).

Conclusions from Previous Research

Specific tree species, including eastern hemlock, are known to affect soil characteristics. These effects can result in significant changes in ecosystem function, especially when a coniferous species such as hemlock is replaced by deciduous hardwood species (Jenkins et al. 1999a). In a study of soil characteristics beneath five hardwood species and hemlock, Finzi et al. (1998a) found soil pH to be lowest and exchangeable Al and Fe to be highest under hemlock trees. Messenger (1975) reported similar findings for a successional sequence from hemlock/white pine-dominated systems to northern hardwoods, attributing the changes in soil characteristics to differences in foliar quality. Finzi et al. (1998b) found forest floor mass, carbon, and nitrogen pools to be greatest under hemlock. Additionally, soil C:N ratios were relatively high, and net N mineralization rates were relatively low under hemlock trees. Similarly, Mladenoff (1987) found lower N mineralization and nitrification rates under intact hemlock forest than under maple forest, while nitrification rates were doubled in hemlock gaps compared to the intact forest. These interspecies differences suggest that replacement of hemlock by hardwood species is likely to result in increases in pH and N turnover rates, reductions in forest floor carbon and nitrogen, and reductions in exchangeable cations.

Most of what we currently know regarding hemlock mortality and nutrient cycling is derived from a recently published study (Jenkins et al. 1999a) and unpublished data (e.g. Yorks, Leopold, and Raynal). In terms of its impacts on nutrient cycling, hemlock mortality due to HWA (or other insects or diseases) may be expected to be similar to timber harvesting since nutrient uptake by overstory trees is likely to be dramatically reduced and understory light levels and temperatures will probably increase. However, in contrast to harvesting, mortality due to HWA occurs over a much longer time period (e.g. several years) and dead trees are left standing. Although it seems likely that there should be some similarities between timber harvesting and HWA-induced mortality regarding changes in nutrient cycling, important differences between these two types of disturbances (e.g. temporal extent, level of soil disturbance) do not allow us to make such assumptions. Any disturbance that reduces or eliminates tree growth also reduces the rate of nutrient uptake, potentially allowing nutrients to be leached from the system in soil and stream water. Reductions in evapotranspiration due to mortality result in higher soil moisture, and increases in the amount of sunlight reaching the forest floor probably lead to increased soil temperature, though recruitment by young seedlings may modulate these expected changes in temperature and moisture status. Still, it has been hypothesized that the combination of increased soil moisture and temperature may be associated with increases in nitrogen mineralization and nitrification (Jenkins et al. 1999a).

To examine the *in situ* impacts of adelgid-induced hemlock mortality on forest community structure and nutrient cycling rates, Jenkins et al. (1999a) established a set of six sites spanning a continuum from 0% to 99% mortality at hemlock-dominated sites in Connecticut and Massachusetts. At these sites, we sought to test a series of hypotheses (Fig. 1) related to the interactions between hemlock mortality and variables thought to control N cycling rates at infested stands. Nitrogen transformation rates were quantified using the buried bag technique (Eno 1960), light availability was quantified using fisheye photography (Canham 1988), and factors thought to drive N cycling rates (e.g. soil temperature, soil moisture, soil texture, soil C and N capital, soil pH) were measured using standard techniques.

Jenkins et al. (1999a) found that net N mineralization and N turnover rates accelerated in sites experiencing HWA infestation (Fig. 2), and we suggest that those changes are attributable to changes in microclimate induced by increased light availability. One of the most significant results of this investigation, however, was the dramatic increase in net nitrification rates at infested sites. In essence, regeneration of birch seedlings beneath dying hemlock canopies was not sufficient to take up inorganic N being produced by accelerated root decomposition and microbial activity. This suggests strongly that nitrate leaching will be a result of HWA infestation and hemlock mortality, at least until the new forest canopy becomes established and begins taking up the additional inorganic N. While this study showed that HWA-induced hemlock mortality is likely to have significant impacts on N cycling rates in soil, we were not able to establish clearly the drivers of change in this correlative study. Ongoing studies by Yorks et al. and Orwig et al. are designed in part to investigate and quantify the variables potentially driving the changed N transformations.

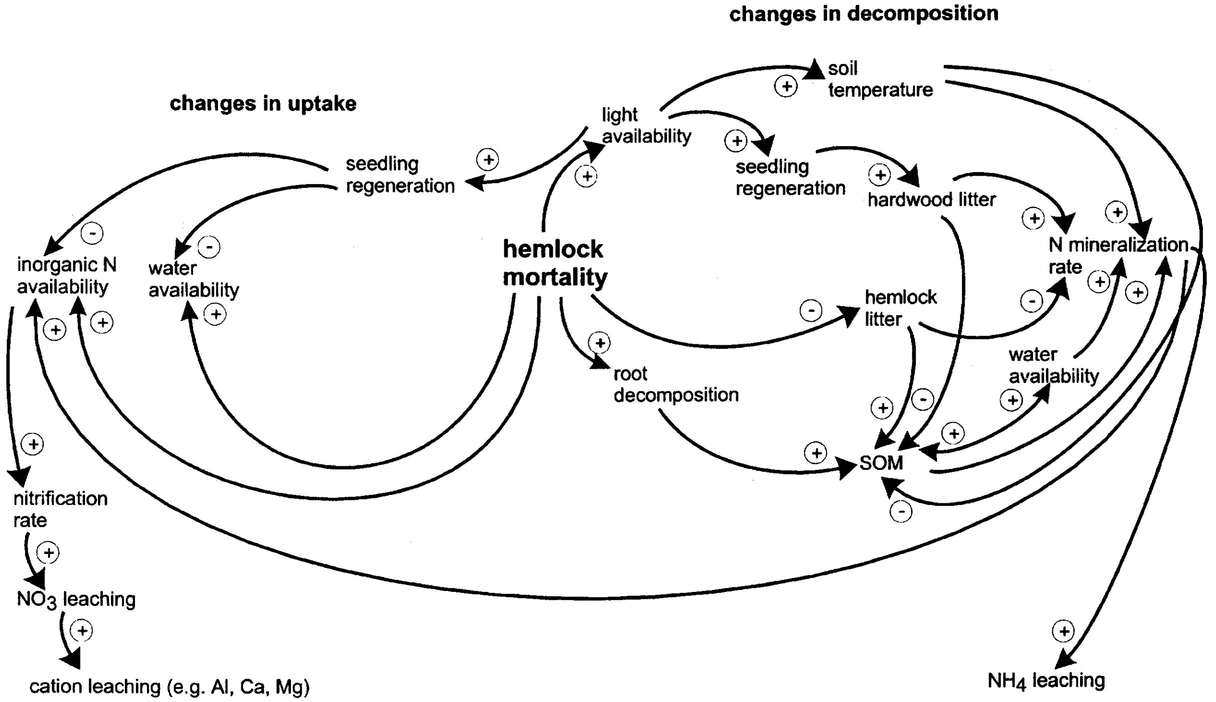


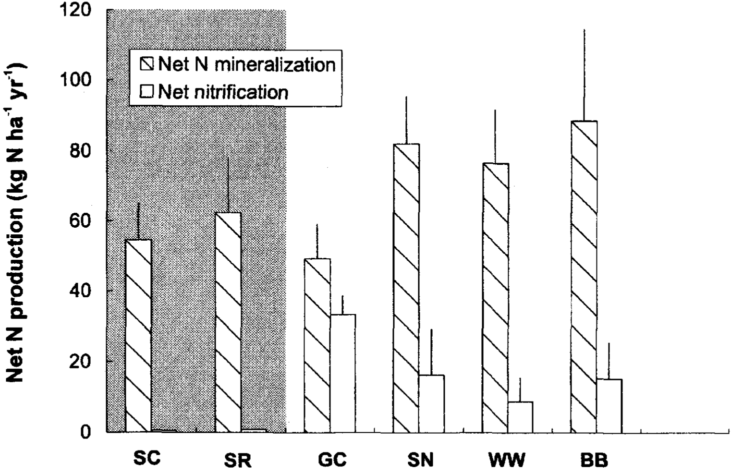
Figure 1.—Hypothesized relationships among forest community structure and N cycling rates with hemlock woolly adelgid infestation and hemlock mortality (from Jenkins et al. 1999 with the addition of "cation leaching" and "NH_4 leaching"). Positive relationships (i.e. an increase in one variable will cause an increase in the next) are designated by (+), and negative relationships (i.e. an increase in one will cause a decline in the next) are designated by (-).

Yorks, Leopold, and Raynal are currently studying the effects of hemlock mortality on soil water chemistry in hemlock-dominated stands (basal area estimates of 38-50 $m^2\ ha^{-1}$, 67-87% hemlock) in the Catskill Mountains of New York. Within each of four small (<1 ha) stands, eight tension lysimeters were installed at each of two depths (15 and 50 cm) in August 1996 (total of 16 lysimeters per plot). Soil water has been collected monthly since October 1996 by evacuating lysimeters to a tension of 38 cm Hg and collecting samples 24-30 hours later. Samples are analyzed for major anions (Cl^-, NO_3^-, SO_4^{2-}), cations (Al, Ca^{2+}, H^+, K^+, Mg^{2+}, Na^+, NH_4^+), and total N. All eastern hemlock trees in two of the plots were girdled (i.e. bark and cambium severed around the base of the bole) in July 1997 to simulate mortality due to the HWA.

By initiating this study in healthy hemlock stands and collecting data for almost a year before simulating mortality due to HWA, Yorks et al. were able to characterize variability in soil water chemistry among hemlock stands prior to mortality, and establish a basis for future comparison. Initially, girdling elevated concentrations of NO_3^- and NH_4^+ in the fall of 1997 (Fig. 3 and 4). These increases were most likely attributable to fine root mortality, decomposition, and mineralization processes. Concentrations returned to baseline levels during the winter of 1997-1998 when low temperatures restricted biological transformations and nutrient turnover in soil. Very high N leaching losses were observed in the summer of 1998 and continued through the fall and early winter (Fig. 3 and 4), presumably due to the elimination of nutrient uptake by hemlock trees and continued root mortality, decomposition, and mineralization. Elevated NO_3^- losses were accompanied by cation leaching as indicated by the positive relationship between NO_3^- and cation (e.g. Al, Ca^{2+}, and Mg^{2+}) concentrations in the summer and fall of 1998 (Fig. 5). These data demonstrate that hemlock mortality can lead to NO_3^-, NH_4^+, and cation leaching (Fig. 1) even in the absence of the soil disturbance and rapid overstory removal associated with timber harvesting. Total nutrient losses would be even greater than indicated by elevated soil water nutrient concentrations since evapotranspiration is reduced after tree mortality, and higher volumes of soil water leach from sites with hemlock mortality. Over the long term, these changes may lead to shifts in forest floor and mineral soil nutrient status; these shifts may have lasting effects on forest productivity at impacted sites.

The recovery of pre-mortality nutrient cycling rates (e.g. reduced nitrification and nutrient concentrations in soil water) will be strongly influenced by the rate of woody species regeneration. Rapid growth and nutrient uptake by regeneration use nutrients that might otherwise be lost from sites with hemlock mortality. Furthermore, canopy closure by the regenerating stand reduces the amount of light reaching the forest floor and increases evapotranspiration. Orwig and

(a) Forest floor



(b) Mineral soil

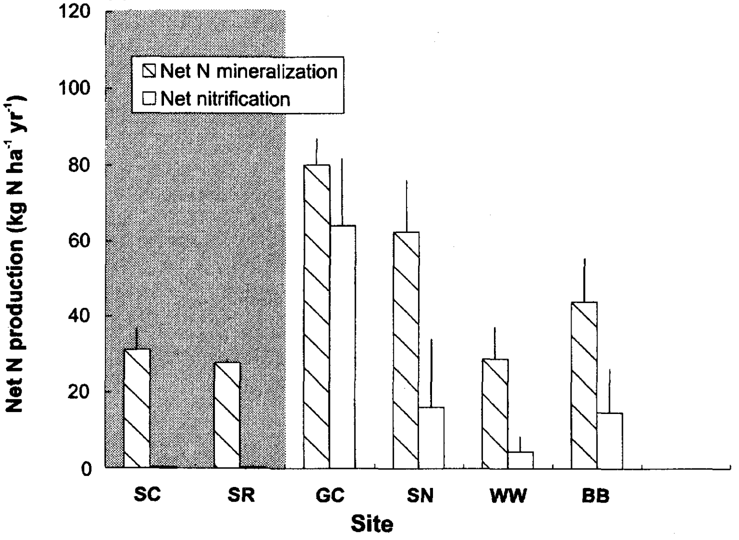


Figure 2.—Annual net N mineralization and nitrification rates for (a) forest floor and (b) mineral soil (from Jenkins et al. 1999). Error bars represent standard deviation from three plots per site. Shaded area denotes two sites with no sign of HWA infestation. Sites are ordered from least to most hemlock mortality by basal area (BA) (m^2 ha^{-1}).

Foster (1998) and Jenkins et al. (1999a) reported a positive relationship between percent hemlock mortality and the amount of light reaching the understory. These increases in forest floor light resulted in rapid growth of understory vegetation, especially regeneration of black birch (*Betula lenta* L.) seedlings. Yorks et al. (1999a, 1999b) also found high potential for replacement of hemlock by yellow birch (*B. alleghaniensis* Britton) after hemlock mortality (also see Mladenoff 1990). Birch species may be very important in the regeneration of many hemlock stands in the event of hemlock mortality. However, even with prolific seedling regeneration, availability of inorganic N (NO_3^- and NH_4^+) and other nutrients may exceed biological demand and result in the loss of these nutrients from the system (see Jenkins et al. 1999a).

Questions Remaining

Although significant progress has been made in understanding potential effects of hemlock mortality on nutrient cycling, additional important questions need to be answered. For example, 1) What processes drive the accelerated N cycling rates found at infested hemlock stands? These processes probably include root decomposition, increased mineralization as a result of increased soil temperatures, and/or increased water availability (Jenkins et al. 1999a, see Fig. 1) but the relative contribution of each process to accelerated N cycling is unknown. 2) How long will changes in nutrient cycling (e.g. elevated nutrient losses to soil water) continue after hemlock mortality? Jenkins et al. (1999a) demonstrated that elevated nitrification rates may be observed for at least several years after HWA infestation and the onset of hemlock decline, but it is still unclear how long nutrient cycling may be affected by hemlock mortality. 3) What is the minimum proportion of hemlock trees that must be killed, and how quickly must they die to cause significant alterations in nutrient cycling? Monospecific hemlock stands subject to rapid decline and mortality due to the HWA are most likely to exhibit dramatic changes in nutrient dynamics. However, hemlock mortality in stands where this species is not dominant (e.g. northern hardwood-hemlock forests) may not result in significant changes in nutrient cycling rates since surviving trees may quickly fill canopy gaps and maintain rapid nutrient uptake. Similarly, if hemlocks within a stand are killed over a prolonged period of time (e.g. 10 yr), lateral growth of surviving trees and regeneration may compensate for gradual reductions in nutrient uptake by hemlock and buffer the stand from elevated nutrient losses. 4) How large are total losses of site nutrient capital likely to be? This question may be answered by monitoring stands from the onset of hemlock decline through the recovery of pre-mortality nutrient cycling rates. 5) How does heavy deer browsing, common in many stands in the northeastern US, affect replacement of hemlock and subsequent nutrient losses? If regeneration on HWA-infested sites is delayed or prevented by excessive deer browsing, nutrient losses will probably be greater than on sites with rapidly aggrading regeneration. Other questions include: 6) How will salvage logging and associated soil disturbance and inputs of coarse woody debris affect nutrient cycling?; and 7) How will changes in overstory species composition (i.e. replacement of hemlock by hardwoods) affect long-term (e.g. several decades) changes in nutrient cycling (see Finzi et al. 1998a, 1998b, Jenkins et al. 1999b)?

Current Research

We are currently studying ecosystem response to adelgid infestation and hemlock mortality in a number of stands across the eastern US. By using a variety of methods and by studying stands all over the region, we hope to gain a more

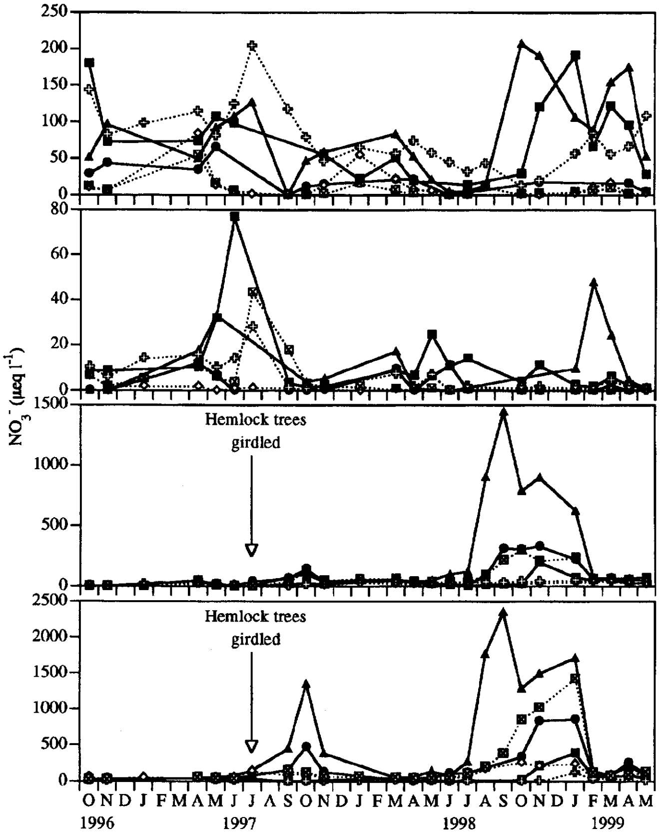


Figure 3.—Nitrate concentrations in soil water from three shallow (solid lines and symbols) and three deep (dashed lines, open symbols) lysimeters with the most complete soil water chemistry record in each stand.

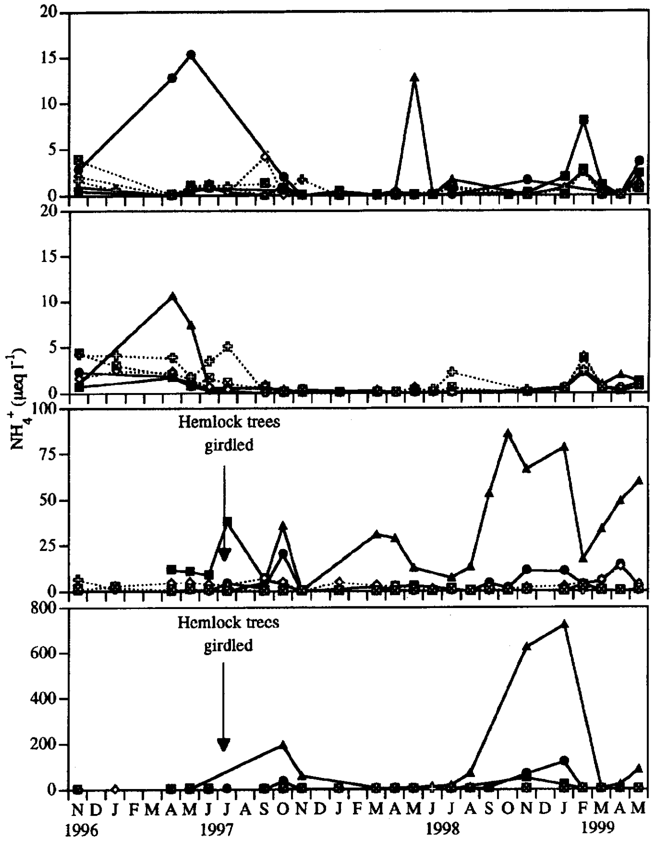


Figure 4.— Ammonium concentrations in soil water from three shallow (solid lines and symbols) and three deep (dashed lines, open symbols) lysimeters with the most complete soil water chemistry record in each stand.

complete understanding of ecosystem response to hemlock mortality and answer several of the questions proposed in the previous section.

Jenkins and R. Hallett (USDA Forest Service) have initiated chemical analyses on archived soil and litter samples collected from sites established by Orwig and studied by Jenkins et al. (1999a). We are interested in potential links between soil and foliar calcium status, hemlock susceptibility to HWA infestation, and/or the severity of HWA infestation. Calcium is of particular interest since previous studies have illustrated relationships between sugar maple decline and calcium status at a regional scale, and because we suspect that there may be a link between insect proliferation, host plant vigor, and calcium status. We plan to establish additional study sites if data suggest potential relationships between calcium and HWA damage.

Yorks, Leopold, and Raynal are continuing to collect and analyze soil water samples from healthy and dying hemlock stands in the Catskill Mountains of New York. It is unknown how long elevated nutrient losses will continue, but the high magnitude of 1998 ion concentrations from girdled plots indicates that elevated leaching losses could persist several additional years. Continued sampling will allow us to determine how long elevated nutrient concentrations continue after hemlock mortality and estimate total nutrient losses per unit area (e.g. kg of nutrients/ha/yr) due to mortality.

Yorks et al. also recently began analysis of water samples from streams draining forested watersheds in the Delaware Water Gap National Recreation Area (Pennsylvania and New Jersey) in cooperation with R.A. Evans of the National Park Service. Fourteen pairs of topographically similar streams draining sites with contrasting species compositions (hardwood sites vs. sites with substantial hemlock abundance) were identified in a previous study of hemlock influences on aquatic biodiversity (see Snyder et al. 1998, LeMarie et al. 1999). Samples are being collected monthly and analyzed for major anions, cations, dissolved organic nitrogen, and dissolved organic carbon. One of our short-term objectives is to determine if species composition of these sites and/or watersheds is related to stream water quality. We are specifically interested in whether abundance of hemlock may be negatively related to stream water concentrations of nitrate and associated cations under non-infested conditions. These stream water chemistry data will also be available for comparison if and when the HWA or other agents begin to cause significant hemlock mortality on these sites. We predict that watersheds with high abundances of hemlock will exhibit elevated nutrient concentrations in stream water if large proportions of hemlocks are killed within a few years.

Orwig et al. are examining the timing and magnitude of N cycling changes in HWA infested stands in Connecticut as they deteriorate. A combination of closed-topped soil cores and ion-exchange resin bags is being used to evaluate the temporal availability of N. Resin bags located outside of hemlock plots are also being used to evaluate the potential for nitrate export as hemlock trees decline. At each stand, organic-layer and mineral-layer soil temperatures are being recorded and hemispherical photographs are being examined to quantify overstory light environments and crown thinning. Soil pH, texture, carbon to nitrogen ratios, soil organic matter, gravimetric moisture, and macronutrients (e.g. Ca, K, Mg, P) are being quantified at each site as well. We predict that as hemlock stands deteriorate, increased light and soil temperature will lead to enhanced decomposition rates, N cycling rates, and nitrate leaching that will last for several years following complete mortality. In addition, M.L. Kizlinski (Harvard Forest) has initiated a project examining the effect of hemlock logging on ecosystem processes (e.g. N cycling) that will complement ongoing research efforts in uncut stands.

Management Implications

There is clearly a strong potential for significant losses of N and nutrient cations to soil water in hemlock stands with high mortality. These losses reduce site nutrient capital and may affect future productivity, especially on sites that were nutrient-poor prior to hemlock mortality. Nutrient losses to soil water may also lead to declines in surface water quality (i.e. increases in nutrient concentrations) in areas with significant proportions of hemlock and where hemlock is typically dominant in ravines and on steep slopes. Such effects on surface water quality will be particularly important to those managing forested watersheds that provide a domestic water supply. Even in regions where hemlock is not the dominant species overall (e.g. Catskills Mountains of New York), mortality of this species and subsequent changes in nutrient cycling must be considered within the larger forest landscape and its management.

Although site nutrient losses will probably be unavoidable during and after hemlock mortality, these losses might be reduced somewhat by promoting rapid regeneration of tree species. Management practices that encourage regeneration and growth of woody species also increase nutrient uptake and storage by vegetation. Such activities may include soil scarification to enhance germination and survival of tree seedlings and control of white-tailed deer densities to reduce browsing. As the use of salvage logging increases as a management option in dead and declining hemlock stands, the effect of this practice on ecosystem processes will be increasingly important. Preliminary data (Kizlinski, unpubl.) indicate that logging may increase regeneration relative to uncut, naturally deteriorating stands.

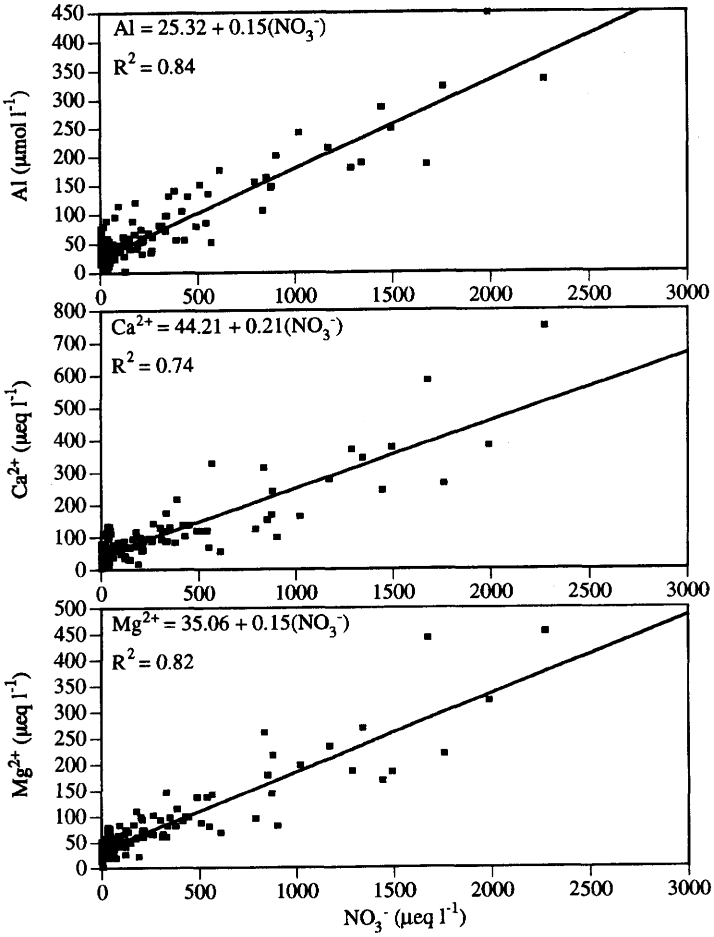


Figure 5.—Relationships between nitrate and cation concentrations in soil water collected from four hemlock stands from July to November 1998 (n=176). For each soil water sample, a point represents its nitrate and cation concentration (aluminum, calcium, or magnesium) in each of the three graphs. Simple linear regression analyses indicated highly significant positive relationships between nitrate and all three cations (P<0.0001)

Acknowledgments

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Assessment of Landscape Correlates of Eastern Hemlock Decline Due to Hemlock Woolly Adelgid

John Young[1], *Craig Snyder*[1], *James Akerson*[2], *and Gary Hunt*[2]

Eastern hemlock (*Tsuga canadensis*) is in decline throughout its range in the eastern US due to infestation by an exotic insect pest, the hemlock woolly adelgid (*Adelges tsugae*). In Shenandoah National Park, the hemlock woolly adelgid (HWA) rapidly killed many stands of hemlock after first appearing in the late-1980's, while having only minor impact in other stands. At present, few investigators have examined the mechanisms that produce this discontinuous impact, although landscape factors are predicted to play a major role (Orwig and Foster, 1998: Perry 1988). In an effort to address possible landscape correlates to hemlock decline, we conducted a preliminary analysis of 5 years of hemlock health estimates in comparison to measures of terrain, stand isolation, and potential dispersal corridors at the stand level. We found that elevation, slope, light conditions, and distance to streams all exhibited relatively strong correlation with hemlock decline, although the relationship varied by year. In addition, there appears to be some evidence of spatial autocorrelation in decline, suggesting that similar environmental conditions are either controlling the adelgid or making hemlock stands more susceptible to HWA. We are using the results of this preliminary analysis to guide more detailed efforts aimed at modeling hemlock stand vulnerability as a result of site, landscape, and regional factors.

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Wildlife Habitat Associations in Eastern Hemlock — Birds, Smaller Mammals, and Forest Carnivores

Mariko Yamasaki[1], *Richard M. DeGraaf*[2], *and John W. Lanier*[3]

Abstract

Ninety-six bird and forty-seven mammal species are associated with the hemlock type in the northeastern United States. Of these species eight bird and ten mammal species are strongly associated with the hemlock type though none of these species are limited to it. Hemlock species richness appears to be lower than in other conifer or hardwood types. Avian habitat considerations include the distribution and variety of structural habitat features throughout managed and unmanaged stands in sustainable patterns. Sawtimber hemlock stands support significantly higher bird communities than young stands. Smaller mammal habitat considerations include dense patches of coniferous regeneration, hard mast-producing inclusions, cavity trees, coarse woody debris, and wetland seeps and inclusions. Forest carnivore habitat considerations include the availability and distribution of predictable prey and suitable cover opportunities (cavity trees, coarse woody debris, wetland seeps and inclusions, and rocky ledge and well-drained den sites). Differences of ten or more inches of annual precipitation distinguish most northern New England landscapes from the majority of landscapes in the western Great Lakes region. Northern New England landscape level habitat elements include lower slope positions and imperfectly drained, excessively drained, or shallow to bedrock sites.

Introduction

Though eastern hemlock (*Tsuga canadensis*) is a well-documented habitat element in winter deer range management throughout the northeastern United States and eastern Canada (Mattfeld 1984; Huot et al. 1984; Blouch 1984; Crawford 1984; Reay et al. 1990), limited research has been conducted specifically on bird and mammal communities in hemlock stands. Roughly 96 avian and 47 mammalian species have been documented using the hemlock type in New England (DeGraaf and Rudis 1986; DeGraaf et al. 1992). Appendix 1 lists eight bird and 10 mammal species strongly associated with the hemlock type.

We review some of the more important landscape and habitat considerations regarding the hemlock type and provide some examples of avian and mammalian habitat associations in the northeastern United States and eastern Canada for birds, small mammals, and forest carnivores.

Landscape Level Habitat Elements

Eastern hemlock occurs from the Maritime Provinces in eastern Canada to northern Georgia and west into northeastern Minnesota (Godman and Lancaster 1990). Average annual precipitation in New England ranges from 30-50 inches compared to 21-36 inches in the upper Lakes States (McNab and Avers 1994). Average annual snowfall in New England ranges from 40 to 160 inches compared to 40 to 70 inches and in some sections upwards of 250 to 400 inches along the Lake Superior shoreline (McNab and Avers 1994). This has tended to generally produce abundant hemlock regeneration on coniferous sites in New England in contrast to the difficulties faced by forest managers in the upper Lakes States to regenerate hemlock in the face of significant deer densities (Anderson and Loucks 1979; Alverson et al. 1988; Godman and Lancaster 1990; Mladenoff and Stearns 1993).

Hemlock grows on both imperfectly drained and shallow to bedrock sites as well as excessively drained sites as described by Leak (1982). Secondary successional processes on the Bartlett Experimental Forest in the White Mountains of New Hampshire continue to increase the percentage of hemlock basal area on both managed and unmanaged stands on deciduous as well as coniferous land types occurring on lower slope positions (Figure 1) (Leak and Smith 1996). Extrapolating this information across northern New England land types means there are more opportunities to manage hemlock in distinct stands, mixedwood stands, and coniferous inclusions than in the western Great Lakes region.

Hemlock volume in the northeastern United States is considerably greater in New England than the western Great Lakes region (Table 1) (Powell et al. 1993). New Hampshire timberland acreage in hemlock has increased slightly over the last 25 years from 3.2 to 3.7 percent of the total timberland acreage or 148.3 to 165.7 M acres (Cullen, personal communication). Current size-class distribution of hemlock timberland acreage is concentrated in the sawtimber size-class (120.1 M acres) and pole size-class (45.6 M acres), with almost no discernible seedling-sapling size-class acreage. New Hampshire sawtimber volume has increased over the last 25 years from 1508.3 to 2534.1 MMBF, as has growing stock volume from 596.7 to 832.9 MMCF. These numbers suggest that the hemlock resource is distributed across the New England landscape in much different patterns compared to the patterns seen in the western Great Lakes region.

Potential impacts of an expanding hemlock woolly adelgid (*Adelges tsugae*) population concern forest and wildlife managers over the possible loss of significant sources of winter thermal cover in a variety of site types and slope positions (Evans et al. 1996).

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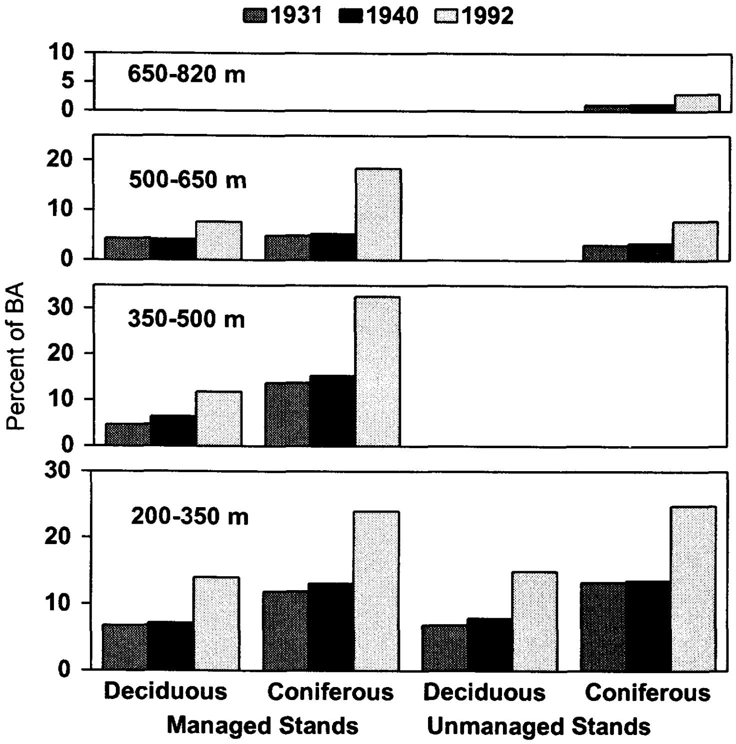

Figure 1.—Percent of hemlock basal area by deciduous and coniferous land types in managed and unmanaged stands and elevation for Bartlett Experimental Forest, New Hampshire (from Leak and Smith 1996).

Table 1.—Eastern hemlock growing stock in million of cubic feet (MMCF), board foot volume in million board feet (MMBF) and acreage of timberland in thousand acres (M acres) in the northeastern United States (from Powell et al. 1992).

Region State	Net Volume	Board Foot Volume	Timberland Acres
	(MMCF)	*(MMBF)*	*(M Acres)*
Northeast			
Maine	1397	3920	16987
New Hampshire	586	1594	4760
Vermont	294	1618	4429
Massachusetts	403	1157	2960
Connecticut	231	838	1768
Rhode Island	-	-	371
Totals	2912	9127	31275
North Central			
Michigan	644	2726	17442
Minnesota	-	-	14773
Wisconsin	321	1353	14921
Totals	965	4079	47136

Avian Habitat Examples

Forest habitat selection by breeding birds is mostly a function of vegetative structure (Anderson and Shugart 1974). Forest cover-type and stand size-class have been useful terms in describing the relationship of some cover type obligate species (e.g. boreal chickadee, white-winged crossbill) and size-class obligate species (e.g. magnolia warbler, blackburnian warbler), as well as species that prefer combinations of cover type and size-class (e.g. winter wren, solitary vireo) (DeGraaf and Chadwick 1987). Breeding season bird abundance in forested habitats is also strongly influenced by forest structure (e.g. structural habitat features) not necessarily well-described by forest cover type or size-class designations (DeGraaf et al. 1992; DeGraaf et al. 1998).

Structural habitat features are largely determined by the variability in canopy closure and the resulting effects on the vegetative layers beneath the forest canopy. Structural habitat features include the overstory inclusions that differ from the dominant canopy component (e.g. hardwood or mast-producing tree inclusions in a coniferous canopy), the resultant midstory and understory woody vegetation, and finally the effects of increasing light levels on the herbaceous component usually found under fairly dark ground conditions within hemlock stands. Habitat components such as cavity trees, coarse woody debris, seeps and wetland inclusions, and dry well-drained den sites are other elements influenced by overstory manipulation. Having said this, few studies describe avian use of hemlock stands in the northeastern US and eastern Canada (DeGraaf and Chadwick 1987; DeGraaf et al. 1998; Benzinger 1994a, b; Martin 1960).

Several points become very clear from these studies. Species richness (Table 2) was significantly higher in sawlog or mature stands of hemlock, northern hardwoods, and red maple than in young or pole stands of the same types (DeGraaf and Chadwick 1987). Hemlock type species richness tended to be lower than in the three other coniferous types studied (balsam fir, spruce-fir, and white pine), despite an intermediate tree dbh, low tree density, and the highest shrub density of all the forest types studied (DeGraaf and Chadwick 1987).

Several bird species, black-throated green warbler (see scientific names in Appendix 2) and winter wren, attained the highest numbers of singing males in hemlock relative to any other coniferous, hardwood, or mixedwood type or size-class. Three species, black-throated green warbler, ovenbird, and blackburnian warbler composed 27.5 percent of the total number of singing males in hemlock stands (all size-classes) in 1979-1980 survey period in the White Mountains; and composed 33.7 percent of the total in

Table 2.—Comparison of breeding bird species composition among young (pole) and mature (sawtimber) stands, White Mountains of New Hampshire and Maine, 1979-1980 (DeGraaf and Chadwick 1987).

	Hardwoods					Softwoods			
Birds	Aspen	Paper Birch	Northern Hwds	Swamp Hwds	Oak-Pine	Balsam Fir	White Pine	Spruce-Fir	Eastern Hemlock
Young stands [a]									
No. Individuals	174	144	123	122	-	124	204	148	101
No. Species	30	22	13	21	-	27	40	32	27
Mature stands [b]									
No. Individuals	-	164	167	187	177	131	165	176	169
No. Species	-	23	27	32	31	35	38	35	32

[a] Live softwoods 4-8.9 inches or live hardwoods 4-11.9 inches dbh.
[b] Live softwoods ≥ 9 inches or live hardwoods ≥ 12 inches dbh.

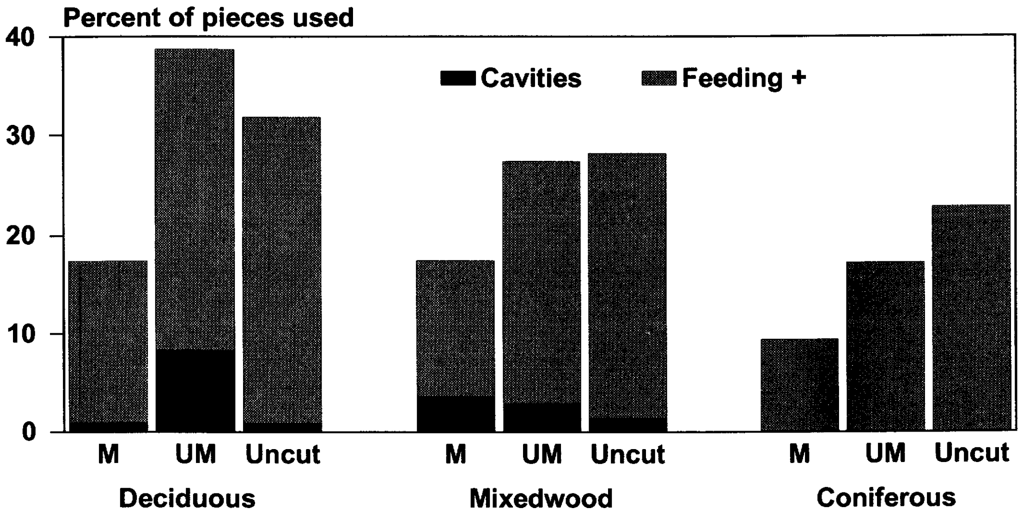

Figure 2.—Percentage of woodpecker usage in coarse woody debris by management type (M = managed, UM = unmanaged, and uncut stands), overstory composition, Bartlett Experimental Forest, New Hampshire (Yamasaki, unpublished data).

1991-1992 survey period. The five most abundant species (the above three species plus black-capped chickadee and solitary vireo) composed 38.3 percent of the total number of singing males in hemlock stands in the 1979-1980 survey period; and composed 46.4 percent of the total in the 1991-1992 survey period (DeGraaf, unpublished data). Similarly black-throated green warbler, blackburnian warbler, solitary vireo, winter wren plus the red-breasted nuthatch showed significant associations with hemlock in New Hampshire, New Jersey, the western Great Lakes region, and southeastern Ontario (Holmes and Robinson 1981; Benzinger 1994a, b; Howe and Mossman 1995; Martin 1960).

During the non-breeding season and throughout winter, eastern hemlock, as individual trees, inclusions, and stands, provide an important seed source for pine siskin, goldfinch, red crossbill, white-winged crossbill, evening grosbeak, as well as for numerous small mammals like red squirrel (DeGraaf and Rudis 1986; Howe and Mossman 1995).

Other important avian hemlock habitat associations include ruffed grouse, yellow-bellied sapsucker, great horned owl, and a number of overwintering forest birds for a variety of reasons. Ruffed grouse habitat management guidelines often addressed the importance of hemlock stands, inclusions, and single trees as high quality fall and winter roosting locations (Edminster 1947; Jordan and Sharp 1967). Conversely, the importance of residual conifers in providing goshawk and great horned owl hunting perches in regenerating hardwood and aspen stands was recognized in the western Great Lakes region by Gullion and Svoboda (1972).

Affinities for hemlock tree boles by foraging and cavity dwelling primary excavators like the yellow-bellied sapsucker and pileated woodpecker have been recognized by Rushmore (1969) and others. The relationship between yellow-bellied sapsuckers, hemlock ring shake, and the proximity of suitable aspen nesting trees has been recognized Shigo (1963; personal communication). Hemlock tends to be long-lived, develops a number of potential cavity sites and perhaps a higher level of cavity-dwelling and foraging use by an array of woodpeckers, smaller mammals, and forest carnivores. Coarse woody debris found under mixedwood (e.g. mostly hardwood-hemlock) overstory conditions on the Bartlett Experimental Forest shows a higher percentage of woodpecker use than coarse woody debris under more coniferous (e.g. red spruce and balsam fir) overstory conditions (Figure 2) (Yamasaki, unpublished data).

Hemlock in hardwood and mixedwood, as well as in mixed conifer stands can influence usage of these stands by raptors such as the great horned owl, long-eared owl, and barred owl (DeGraaf and Rudis 1986). Great horned owls were observed using larger forested stands with scattered hemlocks more than red-tailed hawks in central New York (Hagar 1957).

Smaller Mammal Habitat Examples

Of the 32 species of insectivores, hares, and rodents that inhabit northeastern forest habitats, roughly 23 species use the hemlock type (DeGraaf et al. 1992). Five species having some preference for hemlock include snowshoe hare, red squirrel, deer mouse, southern red-backed vole, and porcupine (DeGraaf et al. 1991). Limited information exists on any of the nine forest bat species use of the hemlock type.

The deer mouse and southern red-backed vole are two of six species (including masked shrew, short-tailed shrew, white-footed mouse, and woodland jumping mouse) that comprise 92 percent or more of the annual sampling effort in the White Mountains (Yamasaki, unpublished data). Annual small mammal abundance and species richness can fluctuate dramatically due to food availability (e.g. prior year's mast crop) and winter severity (e.g. frozen ground with no snow cover) among other variables. Important structural habitat features to smaller mammal communities include a range of overstory canopy closures. The resulting effects on the midcanopy and shrub layers, and perhaps the patterns of coarse woody debris contribute to the subsequent accessibility of prey by both avian and mammalian predators such as northern goshawk, barred and great horned owls, and typical forest carnivores like fisher, raccoon, red fox, and bobcat (DeGraaf et al. 1992; Powell et al. 1997a, b).

Other important structural habitat features include the overstory inclusions that differ from the dominant canopy component (e.g. mast-producing tree inclusions in a coniferous canopy), patches of regenerating and midstory hemlock and other woody regeneration, and finally the effects of increasing light levels on the herbaceous component usually found under fairly dark ground conditions within hemlock stands. Preliminary data inspection for relationships between the most commonly trapped small mammal species in the White Mountains and increasing coniferous basal area suggests a positive relationship for southern red-backed vole and perhaps white-footed mouse, an inverse relationship for woodland jumping mouse and short-tailed shrew, and no apparent relationship for deer mouse and masked shrew (Yamasaki, unpublished data). Cavity trees, both live and dead, provide summer roosting opportunities for forest bats; the hoary bat is known to roost in coniferous foliage (DeGraaf and Rudis 1986).

Snowshoe hare use very dense coniferous (including hemlock) understories in winter (O'Donoghue 1983; Litvaitis 1985; Monthey 1986) that are often found in regenerating patches in mixedwood and coniferous stands. Significant snowshoe hare predators include fisher, bobcat, and northern goshawk.

Species like gray squirrel, eastern chipmunk, and northern flying squirrel also use hemlock stands and inclusions, especially when hard mast-producing trees such as beech (*Fagus grandifolia*) and oak (*Quercus* spp.) are present in the overstory even though hemlock is not their preferred habitat (DeGraaf et al. 1992).

The porcupine-hemlock habitat relationship is a complex one. Porcupines often find suitable foraging sites and denning sites in both large diameter cavity trees and large down hollow logs, and rocky ledges in hemlock stands and inclusions often in wintering deer areas (Dodge 1982; Griesemer et al. 1994). Porcupines cut branches from the tops of the trees; the branches fall to the ground and often are consumed by deer. White-tailed deer and porcupine seem to have a symbiotic relationship with mature hemlock in the winter.

Forest Carnivore Habitat Examples

Thirteen of 14 wide-ranging carnivore species that inhabit forest habitats in New England use the hemlock type (DeGraaf et al. 1992). Four species, red fox, black bear, marten, and bobcat appear to have some seasonal preference for the hemlock type (Harrison et al. 1989; Elowe 1984; Strickland and Douglas 1987; DeGraaf and Rudis 1986). For red fox this may be partly attributed to the spatial relationship of hemlock and other softwoods to lower slope positions and riparian (e.g. lakeshore, stream, and river) habitats, as well as coyote avoidance (Voigt and Earle 1983).

Black bear are known to forage in wetland seeps, swales, and riparian drainages in the spring for ephemeral herbaceous forage (e.g. skunk cabbage, various sedges, grasses, and tubers) present in these habitat conditions (Elowe 1984). Female black bear use softwood riparian areas in Maine when hard mast crops are marginal (Schooley 1990). Vander Haegen and DeGraaf (1996) found black bear travelling softwood tributary buffer zones between forested watersheds. Coarse woody debris is a source of grubs and ants especially in the spring and large hollow trees and logs, and slash piles can be winter den sites (DeGraaf and Rudis 1986).

Fisher use the hemlock type extensively in New England (Kelly 1977). Hemlock and mixedwood stands and inclusions were selected by female fishers as spring-early summer den sites at greater rates than hemlock was available in central New England (Powell et al. 1997a). This seasonal pattern of use is similar but not as strong as winter fisher use of available hemlock in the western Great Lakes region (Thomasma et al. 1994). This may be due in part, to the diffuse pattern of hemlock and other softwood occurrence and distribution in New England.

Fisher and bobcat are opportunistic foragers, hunting in regenerating and mature mixedwood and softwood areas with abundant prey bases (e.g. snowshoe hare, cottontails, red, gray, and flying squirrels, voles and mice, and even raccoon and dead deer) (Giuliano et al. 1989; Arthur et al. 1989; Powell et al. 1997b; Litvaitis et al 1986). Some speculate that female fisher also select denning sites in areas supporting wintering deer populations, as reliable sources of food (e.g. deer carcasses) during kit rearing activities (Kelly 1977). Female fisher can move their kits up to four times per litter (Powell et al. 1997a), so higher densities of maternal den trees in hemlock and other coniferous stands and inclusions may be warranted for fisher, raccoon, marten, and other mammal cavity-dwellers, as well as a significant coarse woody debris component. Talus piles, rocky ledge sites, and well-drained den sites used by bobcat also are often found in places where the hemlock type occurs (McCord and Cardoza 1982).

Summary

Hemlock seems to be an important component of the habitat requirements of a number of avian and mammalian species. As we have seen from the many adelgid-related presentations in this symposium, concerns over the future of eastern hemlock habitat in New England pose many more questions on the potential effects to a broader range of wildlife species than just for white-tailed deer. A disruption of the patterns of hemlock cover through the region could have some significant effects on future species occurrence and distribution patterns.

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Appendix 1.

Bird and mammal species strongly associated with eastern hemlock habitats in the northeastern United States (adapted from DeGraaf et al. 1992).

	Structural Habitat Features								
Species	Closed conifer canopy	Dens / tree cavities	Dense understory / thickets	Wetland inclusions / seeps	Down woody debris	Mast	Rock ledges/ talus	Well-drained den sites	Forest clearings nearby
Birds									
Great Horned Owl		X							
Long-eared Owl	X		X	X					X
Northern Saw-whet Owl		X							X
Blue-headed or Solitary Vireo	X								
Blue Jay						X			
Red-breasted Nuthatch		X							
Hermit Thrush			X						
Black-throated Green Warbler			X						
Mammals									
Snowshoe Hare			X						
Red Squirrel	X								
Deer Mouse					X	X			
Southern Red-backed Vole				X	X	X			
Porcupine		X					X		
Red Fox								X	X
Black Bear				X	X	X	X		
Marten		X			X				
Bobcat			X				X		
White-tailed Deer	X		X			X			

Appendix 2.

Common and Scientific Names of Bird and Mammal Species Using Hemlock Mentioned in this Paper.

Common Name	Scientific Name
Birds	
Northern Goshawk	*Accipiter gentilis*
Red-tailed Hawk	*Buteo jamaicensis*
Ruffed Grouse	*Bonasa umbellus*
Great Horned Owl	*Bubo virginianus*
Barred Owl	*Strix varia*
Long-eared Owl	*Asio otus*
Northern Saw-whet Owl	*Aegolius acadicus*
Yellow-bellied Sapsucker	*Sphyrapicus varius*
Pileated Woodpecker	*Dryocopus pileatus*
Blue-headed or Solitary Vireo	*Vireo solitarius*
Blue Jay	*Cyanocitta cristata*
Black-capped Chickadee	*Poecile atricapillus*
Red-breasted Nuthatch	*Sitta canadensis*
Winter Wren	*Troglodytes troglodytes*
Golden-crowned Kinglet	*Regulus satrapa*
Ruby-crowned Kinglet	*Regulus calendula*
Hermit Thrush	*Catharus guttatus*
Magnolia Warbler	*Dendroica magnolia*
Black-throated Green Warbler	*Dendroica virens*
Blackburnian Warbler	*Dendroica fusca*
Ovenbird	*Seiurus aurocapillus*
Red Crossbill	*Loxia curvirostra*
White-winged Crossbill	*Loxia leucoptera*
Pine Siskin	*Carduelis pinus*
American Goldfinch	*Carduelis tristis*
Evening Grosbeak	*Coccothraustes vespertinus*
Mammals	
Masked Shrew	*Sorex cinereus*
Short-tailed Shrew	*Blarina brevicauda*
Hoary Bat	*Lasiurus cinereus*
Cottontails	*Sylvilagus* sp.
Snowshoe Hare	*Lepus americanus*
Eastern Chipmunk	*Tamias striatus*
Gray Squirrel	*Sciurus carolinensis*
Red Squirrel	*Tamiasciurus hudsonicus*
Northern Flying Squirrel	*Glaucomys sabrinus*
Deer Mouse	*Peromyscus maniculatus*
White-footed Mouse	*Peromyscus leucopus*
Southern Red-backed Vole	*Clethrionomys gapperi*
Woodland Jumping Mouse	*Napaeozapus insignis*
Porcupine	*Erethizon dorsatum*
Coyote	*Canis latrans*
Red Fox	*Vulpes vulpes*
Black Bear	*Ursus americanus*
Raccoon	*Procyon lotor*
Marten	*Martes americana*
Fisher	*Martes pennanti*
Bobcat	*Lynx rufus*
White-tailed Deer	*Odocoileus virginianus*

Management of Eastern Hemlock for Deer Wintering Areas

Russell S. Reay[1]

Abstract

Hemlock stands provide superior winter cover for white-tailed deer. When a site is suitable for the support of a hemlock community, a decision to undertake active management is appropriate, however the difficulty of securing adequate hemlock regeneration must guide and govern the timber management plan. The need to maintain deer wintering areas creates some limitations to the optimum application of silvicultural guides. Stand diversity caused by site quality variation, management history, or species composition can be exploited to improve quality of cover or to expand a wintering area. Up to 30 % of the main canopy can be non-hemlock, high value timber. A wintering area should be managed by area regulation to assure that at least 50 % of the area is in functional cover at all times. Uneven-age management using small group selection techniques maintains tree vigor and stocking levels for periodic timber yield, while also maintaining adequate winter cover for deer. Single tree selection is not recommended, because it does not adequately stimulate regeneration. Even-age regeneration practices are appropriate only when the stand is large enough to retain the required area of functional cover . Where the wintering area is comprised of large sawtimber with few stems available to replace a harvested component, or where the stand acreage is too small to afford winter cover following a partial harvest, a no-cut prescription is appropriate.

Introduction

Of all the softwood species which provide winter shelter for whitetail deer (*Odocoileus virginianus*), hemlock stands afford the best.

For many years the designation of deer wintering area as a forest management objective has been made because the stand is currently a deer wintering area, and because wintering area management practices take priority over timber management practices. For some landowners with very strong wildlife interests, current use by deer is not a prerequisite. They will manage their hemlock as a deer yard secure in the knowledge that good winter shelter is available when the deer find it. The priority issue has been, and continues to be, determined by personal desires, institutional objectives, or political expedience.

We must now recognize the need to make a third, and more fundamental determination of whether the subject stand is growing on a hemlock site. Natural communities research which has been lead by Bill Leak for several years portrays a favorable future for hemlock stands. His studies show that many hardwood stands with an agricultural or active timber harvesting history will, in fact, yield to hemlock dominance in time (Leak, 1998,Thompson, 1999).

An active wintering area which is a product of a successional stand can be sustained only as long as human perseverance can hold back the inevitable. In some circumstances that decision can be justified, but the challenge must be acknowledged. A stand which is determined to be a hemlock community is worth the investment in time and effort to assess stand condition, and prescribe and implement management practices. The prospects for wintering area expansion will be good, and the liklihood of regeneration success will be strong.

Deer Wintering Area Requirements

Deer wintering areas have only two significant components-dense softwood stands for shelter, and a supply of browse close by. Published literature and recommendations of wildlife biologists identify the following general guidelines for wintering area management:

1) within every wintering area there is a nucleus of high canopy, dense softwood which affords the best shelter during stressful periods. This is often referred to as 'functional cover'. In Vermont functional cover is defined as softwood greater than 35 feet in height, and greater than 70 % crown closure.

2) travel lanes consisting of undisturbed bands of softwood cover at least one chain wide should be preserved in every stand treatment. The travel lanes connect numerous small pockets of cover in large wintering areas, and provide routes to facilitate deer movement out of the nucleus for feeding during good weather.

3) no more than 50 % of the area of winter shelter should be disturbed in each entry

4) some diversity of age classes is necessary if a landowner plans to undertake active management, or if sudden loss of the shelter is to be avoided.

5) adequate supplies of nutritious browse close to the preferred cover must be assured.

Hemlock Management

The initial choice between even-age and uneven-age management should be quickly resolved in favor of an uneven-age regime. The only exception is in the case of a large wintering area, say 50 acres or more, which is not currently used to its capacity. Some publications, notably Lancaster's 'Managing Eastern Hemlock, A Preliminary Guide'(Lancaster, 1985), and others written in the 1980s, recommend even-age management, not uneven-age. A careful reading reveals that the distinction between even-

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and uneven-age management is often based on scale, with clearcut and shelterwood regeneration practices defining even-age, and single tree selection defining uneven-age management. I favor group selection managment, and feel that it is legimately an uneven-age practice at the stand level, and even-age at the group level. There is broad agreement that single tree selection cutting is not an appropriate management regime, because it will not secure enough regeneration.

A managed deer yard should feature three types of softwood stand stucture-functional cover, thinned areas and regenerating areas. The functional cover is the area which must be capable of providing the necessary winter shelter, and this should be at least 50% of the wintering area. The 50% standard is based on the recognition that the short-term loss of half of the best winter shelter is tolerable, because active management will maintain or enhance stand health and vigor, prolong the useful life of the entire wintering area, and that the thinned areas have some shelter value, though diminished. The distribution of the functional cover throughout the wintering area can vary with stand size and terrain. A large stand could be divided in half , and treatments scheduled half a cutting cycle apart. In such a case the need to identify travel lanes would be minimized. Frequently, steep terrain or the presence of watercourses limit operating options, and subdivision of stands must depart from theoretical ideals. If travel lanes are evident, and there are no opportunities to replace or move them, there may be no choices of which areas to treat. In small stands the ability to undertake reasonable management practices often rests with the ability to enlarge the area of softwood cover.

The area to be regenerated requires the most careful planning and execution. If the area regenerated exceeds the ideal, the next entry may need to be delayed, or the area of functional cover may be reduced too much. If regeneration patches are too small or too few, successful regeneration may not become established, or the age and size of the main canopy may grow beyond the point of good merchantability. Regeneration needs can be calculated using the formula

Cutting interval / rotation age = area to be regenerated.

Regeneration patch size has been recommended to be no larger than one-half the height of the dominant trees (Reay, 1990), however a little larger patch size is probably acceptable. Due to the uncertainty of regeneration success, and the need to limit the reduction in shelter value of the adjacent stand, error on the side of caution is preferred. A very significant component of site preparation for hemlock regeneration is soil scarification to mix organic matter with mineral soil (Burns, 1990, Lancaster, 1985). This mixture is necessary for moisture retention to allow seedling survival after germination. If seedlings regeneration is successful, they are considered fully established at 3 to 5 feet in height, and can be released. In a wintering area, the real challenge is for seedlings to escape destructive browsing, and reach 5 feet in height.

Thinning

Thinning should be undertaken in the treated area not identified for regeneration. This is expressed in the formula

50% of wintering area - area to be regenerated
= area to be thinned

The purpose of thinning is primarily for timber objectives, and the long term vitality of the wintering area. In the short term thinning reduces the shelter value of the canopy, and the forest manager must recognize the trade-offs. Thinning should be to the B line on the hemlock stocking chart (Lancaster, 1985). Note that the hemlock stocking chart has a B line and a B' line. The B' line applies to stands with less than 30% hemlock, and such stands are not suitable wintering areas. It is worth noting, however, that a comparison of Bill Leak's (1983) percent crown cover tables and this stocking chart, shows that thinning a pure hemlock stand to the B' level will still maintain more than 70% crown cover.

Cutting Cycle

The first cut in a previously unmanaged wintering area is fairly straightforward to prescribe as previously outlined. Subsequent entries must be scheduled based on regeneration success, and recovery of crown closure in thinned areas. It is imperative that 50% of the total wintering area be retained in functional cover at all times. A cutting cycle of twenty years is recommended as a starting point for site-specific determinations. A vigorous stand on a good site will recover faster than a less vigorous stand or one on a poorer site. Also the irregular composition and structure of many hemlock stands may allow for shorter cutting cycles if the hemlock shelter is not reduced.

Discussion

The ideal conditions described above are rarely encountered, making the treatments difficult to apply if the forest manager tries to use the recommendations like a cookbook. In reality, most hemlock stands are irregular in stocking, structure and species composition. This irregularity is a distinct advantage for the forest manager, because the silvicultural demands and opportunities of the stand are readily apparent. In his study of Canadian deer yards, Telfer (1973) found that a high degree of crown closure in a dense stand was not as valuable as a more irregular stand with a substantial volume of softwood crown between ten and twenty feet above ground (Fig. 1). The high dense cover is effective at retarding snow depths, but the lower softwood crown component is valuable for moderating wind velocity. Although Telfer's work was done in spruce and fir deer yards, this diagram is typical of a patchy hemlock stand.

Unlike northern hardwoods or spruce and fir which respond relatively predictably to carefully prescribed treatments, hemlock stand dynamics include certain features which must be taken into account on a case by case basis. The first challenge is to obtain adequate regeneration, and culture it to a height and stem density where it can be factored into a schedule of stand treatments. In forest conditions hemlock seedlings grow very slowly. The three to

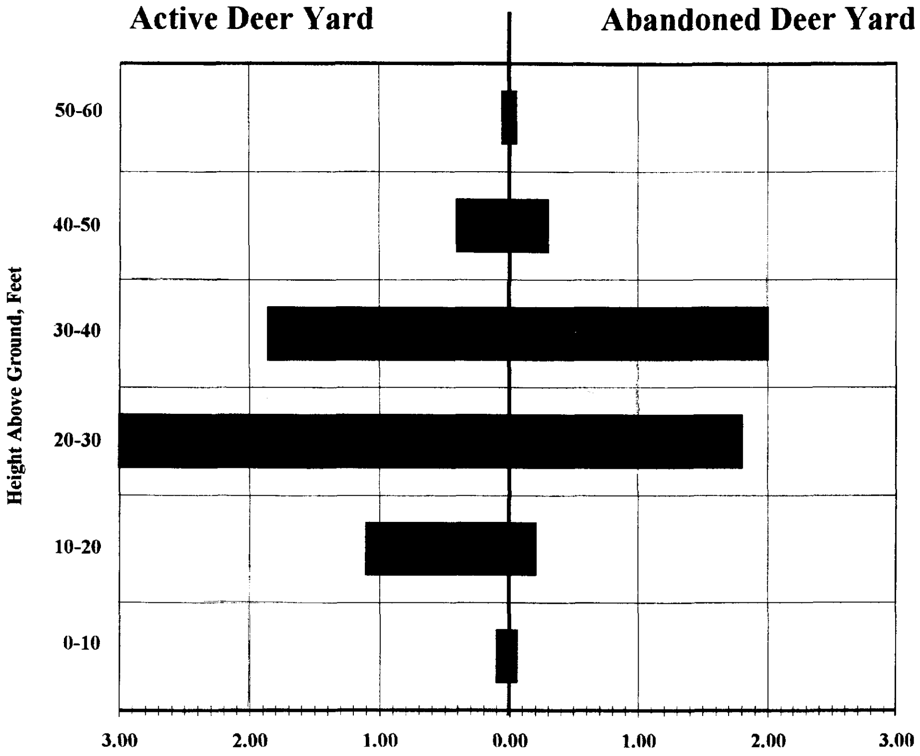

Figure 1.—Volume of space occupied by tree crowns in various height strata. Telfer's figure 1 (1978) converted to English units.

five foot height needed for full establishment may take several decades, especially if destructive browsing occurs. When thinned area recovery proceeds faster than regeneration can be established and brought into the management schedule, the schedule no longer can be applied. This usually means delaying treatments.

One characteristic of hemlock on hemlock sites (a hemlock community), is its tendency to regenerate slowly, one stem at a time, around the perimeter of a predominantly hemlock stand. These stems grow in a supressed condition for many years, and usually do not afford winter shelter. However, if the stems occur in small groups or at a spacing of less than 20 feet they can be released, and the area they occupy can be added to the wintering area. Matt Kelty (1984) found that understory hemlock which appears to be stagnant is frequently vigorous enough to respond to partial release. For management purposes, this understory hemlock can be considered regeneration for purposes of calculating areas of allowable treatment.

Another characteristic of irregular hemlock stands is its tendency to grow as a dominant or lesser component of mixed stands. Common associates are white pine, oaks, beech, maples, and birches, and their incidence is strongly influenced by site quality and land use history. This mixed stand condition is often the deciding factor in implementing wintering area management practices on lands where the owner has a strong timber management objective. Because of its strong shade tolerance, up to 30% of the main canopy of a hemlock wintering area can be in high-value timber species to offset the low value of hemlock (Reay, 1990). In mixed hardwood and hemlock stands, some regeneration attempts may secure hardwood instead of hemlock, and the forest manager should not feel compelled to take extreme measures to eliminate the hardwood. In mixed pine and hemlock stands, the structure can often be described as a hemlock canopy under a white pine superstory. If care is taken to minimize logging damage, the pine stand can be managed indepently of the hemlock. In this instance, stand entries can be made on a pine management schedule, with less attention to the hemlock regeneration imperative.

Two final stand conditions to be considered are those in which there is not enough structural diversity or vigor to allow for recovery of crown closure following a thinning, or stands which are so small that any reduction of winter shelter is unacceptable. The condition of too little structural diversity is usually found in a mature stand with an inactive land use history, or a stagnant stand on poorly drained or extremely shallow soil. These stands will not respond to treatment within a reasonable time frame, and to continue their function as wintering areas, should not be cut. Small stands of hemlock which provide shelter for a few deer during extreme conditions are unlikely to support a commercial entry in only half the area, and there is the significant risk that any cutting will compromise the shelter value of the whole stand. A no-cut prescription is also appropriate in this instance. The longevity of hemlock, up to 900 years, minimizes the risk of such decisions.

Conclusions

Hemlock stands provide excellent winter shelter to whitetail deer in the northern portions of their range. These wintering areas are recognized as valuable resources by natural resource professionals, public agencies, land use regulations, many landowners, and the public at large. Research and experience has shown that wintering areas can be actively managed for wood product yield without unacceptable impacts on the shelter value. Hemlock presents formidable challenges in its difficulty to regenerate, slow juvenile growth rate, and low market value. These difficulties are somewhat offset by the species' ability to regenerate slowly and in low numbers on the periphery of a large stand, its ability to respond to release after long periods of suppression, and its great shade tolerance which allows forest managers to retain a component of higher value species without undue impact on winter shelter.

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The Effects of Moose (*Alces alces* L.) on Hemlock (*Tsuga canadensis* (L.)Carr.) Seedling Establishment in Algonquin Provincial Park, Ontario, Canada

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Abstract

The effects of moose on eastern hemlock (*Tsuga canadensis*) natural seedling establishment in Algonquin Provincial Park, Ontario, were examined. Two thousand seedlings were tagged on 56 sites in 1992 and monitored for six years. Initial data collected included seedling height, browsing history and percent crown closure. At the end of the growing season of the following six years, heights of these seedlings were remeasured; damages on seedlings were assessed according to browsing, physical, logging and unknown factors. After six years, 10.4% of the seedlings had died. Browsing caused 60% of the mortality, followed by unknown factors (18%). Growth rates of healthy, unbrowsed seedlings were significantly affected by initial height, health and percent crown closure. Growth was best at 60% crown closure and least at 80% to 100% crown closure. Healthy, undamaged seedlings grew better than seedlings with browse damage, dieback or both. Mean height losses were 11.1 cm with each browsing incident. Growth rates indicated that seedlings may need to avoid being browsed for up to 30 years to ensure leaders are out of the reach of moose. A negative correlation between moose density and browsing suggested that low moose density in recent years may provide a better opportunity for establishment and canopy recruitment.

Introduction

Eastern hemlock (*Tsuga canadensis* (L.)Carr.) is a shade tolerant conifer common in the Great Lakes - St. Lawrence and Acadian forest regions of Canada. In the United States it is found from Wisconsin east to New England and south in the Appalachians to Tennessee and northern Alabama (Farrar 1995). Common associates include yellow birch (*Betula alleghaniensis* Britt.), beech (*Fagus grandifolia* Ehrh.) and sugar maple (*Acer saccharum* Marsh.) (Fowells 1965).

Hemlock seedling and sapling growth can be slow under heavy shade. In the dense shade of a hemlock-beech forest, growth can be 3 - 5 cm/yr, while under a more open canopy, growth can be 6 - 10 cm/yr (Fowells 1965). Vigorous saplings can grow 20 - 30 cm/yr under light to medium shade, and up to 45 cm/yr with full light and adequate moisture (Anderson *et al.* 1990). Optimal seedling growth under nursery conditions was at 45% light intensity (66 cm in 7 years) (Logan 1973). Most papers describe the slow growth of hemlock saplings under suppression and their rapid growth after release (Marshall 1927, Fowells 1965). Saplings can tolerate shade for up to 400 years (Fowells 1965). Seedling mortality is high, especially in the youngest seedlings. The main causes are desiccation and smothering by hardwood leaf litter (Fowells 1965). Mortality rates of older, established seedlings are unknown.

Browsing by white-tailed deer (*Odocoileus virginianus* Zimmermann) is known to inhibit eastern hemlock growth and establishment (Stoeckler *et al.*1957, Webb 1957, Anderson and Loucks 1979, Euler and Thurston 1980, Frelich and Lorimer 1985, Alverson *et al.* 1988, Anderson and Katz 1993). A recent study in Algonquin Provincial Park, Ontario, identified an age gap in the hemlock population caused by past deer browsing. High deer populations promoted by the creation of suitable habitat from fires and logging resulted in intense browsing pressure on hemlock and other woody species between the 1890's and the 1950's. During this period relatively few hemlock seedlings survived to reach the sapling stage and recruit into the canopy. This created a gap in the age distribution with a distinct lack of hemlock stems between 40 and 100 years of age (Vasiliauskas 1995).

With the final demise of the deer population in Algonquin during the 1970's, moose became the dominant ungulate (Strickland and Rutter 1987). A concern by park staff on the lack of hemlock regeneration led to a study by Vasiliauskas (1995) who determined that current browsing by moose (*Alces alces* L.) on hemlock seedlings was limiting growth and canopy recruitment. Deer were not considered to be a factor in hemlock browsing as they are uncommon and the study by Vasiliauskas (1995) found deer pellets in less than 1% of the plots. Very few studies have examined the effects of moose browsing on hemlock growth and mortality (Vasiliauskas 1995). Browsing may have a major influence on survival as browsed seedlings stand little chance of recruiting into the canopy (Curtis 1959). A better understanding of moose browsing effects on hemlock seedling growth and mortality would empower forest managers in management decision-making, particularly in predicting stand development.

The main objective of this study was to examine the effects of moose browsing on hemlock seedling establishment. Questions addressed include:

- How much does moose browsing attribute to seedling mortality?
- How does height growth respond to moose browsing pressure?
- How does canopy closure affect seedling growth?

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Materials and Methods

Study area - The study area was in the western part of Algonquin Provincial Park, (Algonquin) Ontario, between 78°15' to 78°51' W and 45°19' to 45°40' N. The park is located on the Algonquin Dome (elevation 400 to 550 m a.s.l.), an area 200 to 300 m higher than the surrounding area with a cooler, more humid climate. Soils on the upland areas are primarily sandy loams that originated from glacial tills and till veneers and are usually less than 1 m deep. The area is covered by northern hardwood forest dominated by sugar maple, yellow birch, eastern hemlock and beech. Lakeshores are dominated by hemlock, balsam fir (*Abies balsamea* (L.)Mill.), white pine (*Pinus strobus* L.), white cedar (*Thuja occidentalis* L.) and yellow birch (Strickland 1987).

Seedlings - Fifty-six naturally established seedling populations were randomly selected in the autumn of 1992. Sites we variable in area, but did not have a radius greater than 15 metres for facilitating seedling relocation. At each site, 10 - 40 seedlings were randomly selected from the large number that were available and tagged with numbered aluminum tags for a total of 2000 seedlings. After tagging, height of each seedling was measured. Seedling heights ranged from 10 cm to 3.1 m. Canopy closure above each seedling was measured using a spherical densiometer. Browsing history of tagged seedlings was attributed to moose or hare (*Lepus americanus*), based on the type of damage. Browsing species can be identified by the type of break on the twig. Hares cut cleanly through the twig, while moose or deer leave a ragged end. Because moose and deer browsing is similar, pellet groups in the vicinity of the plot indicated which ungulates were present. The proportion of a seedling damaged by browsing was determined by measuring the distance between the lowermost and uppermost twigs with browse damage, dividing this by seedling height, and expressing it as a percent. Recent germinants were observed on some of the sites and we took the opportunity to determine mortality rates of these seedlings. Twenty-six patches were selected within these sites and all recent germinants were counted. Patch boundaries were outlined with tree-marking paint for relocation. Because snow depth affects the accessibility of seedlings to herbivores, we measured maximum snow depths in March 1993 at five randomly located points in each site. The snow was considered to be at the maximum depth based on observations during the winter.

We defined early September as the end of the growing season and monitored the seedlings from 1993 to 1998. In each year, we recorded seedling height to leader tip, browse damage since the previous year, and cause of mortality if it could be determined. Mortality causes were classified as browsing, unknown, physical damage, and logging damage. Unknown included undamaged seedlings that may have died from any of several different factors, such as disease, desiccation, insect damage or competition. Physical damage included trampling, snow damage, trees falling on the seedlings or being uprooted by falling trees. Seedlings were classified at each survey into several health classes. These classes include healthy (no browse damage ever), browsed once, browsed more than once, leader dieback (not from browsing damage), and dieback with browsing damage. Recent germinants were recounted in 1993 and 1994.

Data analyses - Mortality was summarized by cause and by year for the complete data set, because of the low levels of mortality. Annual seedling growth rates were determined for each seedling by calculating the difference between 1998 and 1992 heights and dividing by six. Percent damaged by browsing and amount of height lost in each browsing incident was determined for each seedling for the complete data set and annual values were calculated from this. Means were calculated by site for crown closure class and annual seedling growth by health class. Analysis of variance was used to determine seedling growth responses to browsing and canopy closure. Linear regression was used to determine individual healthy seedling growth rates as affected by initial height. Statgraphics Version 7.0 (Manugistics 1992) was used in all analyses.

Results

Mortality - Seedling mortality was relatively low (1.7%/yr), with 207 seedlings (10.4%) dying over six years. Over half of the seedlings (60%, Table 1) died from browsing, either from being cut through the stem below the foliage, consumption of all foliage, or declining after heavy browsing. Unknown factors that affected unbrowsed seedlings were the next main cause of death (18.8%). Logging damage, which occurred on five sites, accounted for another 15%. Physical damage from treefalls or trampling accounted for the rest of the seedling mortality (6.2 %).

Mortality was high in the youngest age classes. Forty-nine percent of the 1992 germinants (n=74) and 18.7 % of the 1990 germinants (n=819) died between 1992 and 1994. The difference in mortality between these two cohorts could be attributed to the age difference. Most of the mortality may have occurred for the 1990 germinants by 1992, hence the lower mortality rate. Mortality was due to desiccation, browsing by hares or voles, trampling by moose, or being on a poor microsite. Monitoring of these patches was discontinued after 1994 due to fading of markings around patches.

Table 1.—Number of hemlock seedling dying each year by cause for 2000 tagged seedlings in Algonquin Provincial Park.

Year	Browsed	Unknown	Physical	Logging
1993	6	6		
1994	13	7		18
1995	18	8	2	
1996	29	5	7	13
1997	34	7	3	
1998	24	6	1	
Total	124	39	13	31

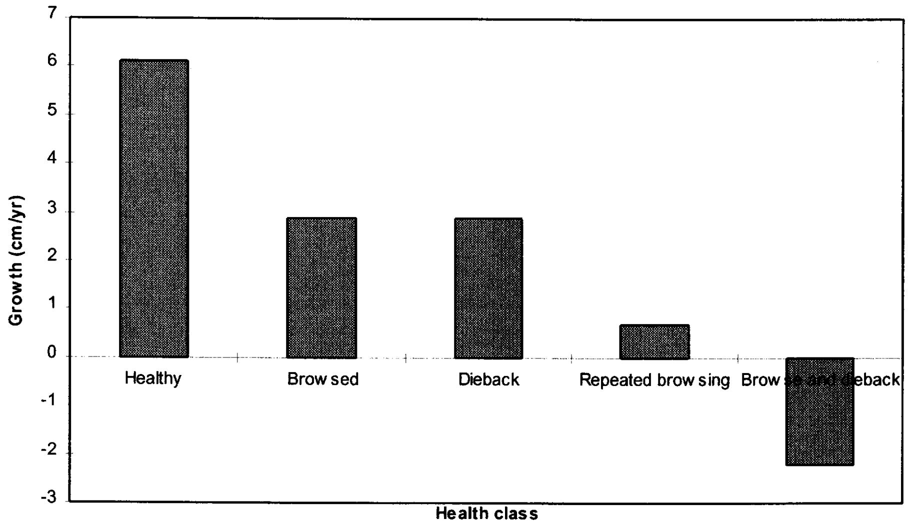

Figure 1.—Mean annual growth rates by health class in 1998 for 2000 tagged seedlings from 56 sites in Algonquin Provincial Park

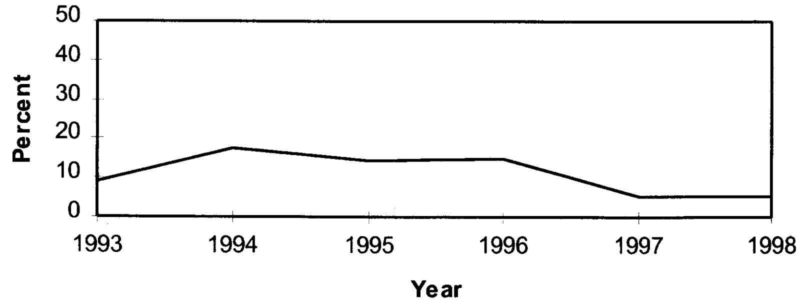

Figure 2.—Percentage of seedlings browsed each year from 2000 tagged seedlings in Algonquin Provincial Park

Browsing - Seedling health class had a significant effect on height growth (Fig. 1, F-ratio = 59.9, $p < 0.001$). Healthy, undamaged seedlings had a mean annual growth rate of 6.6 cm/yr, significantly better than seedling with dieback or browsing damage. Seedlings which had been browsed once, or had leader dieback, had similar growth rates (2.9 cm/yr). Seedlings browsed more than once grew only 0.67 cm/yr. Browsed seedlings that also suffered dieback lost 2.2 cm/yr. Seedlings from these last two classes are most likely to die in the near future.

Browsing rates are probably influenced by moose densities. The higher percentages of seedlings browsed each year during the first half of this study (9.2% to 18%/yr, Fig. 2), coincided with the higher moose densities (0.5 moose km^2, OMNR, unpublished data) at that time. The lower value for 1993 (9.2%) is probably due to moose concentrating their browsing on hemlock tops brought down by a windstorm in November 1992 (pers. obs.). The percentage of seedlings browsed each year has decreased to 5.3 %/yr during the last two years, coincident with a recent drop in moose densities to 0.35 moose /km^2 (January 1998 estimate, OMNR unpublished data). No data is available on snowshoe hare populations during this time, but they are of minor importance compared to moose (Vasiliauskas 1995).

Mean height loss of browsed seedlings after each browsing incident was 11.1 cm (± 0.45 cm), or almost two years of height growth. The mean percentage of a seedling that was damaged from a browsing incident was 34.5 % (± 1.1%).

The other concern during the first part of the trial was the rapid decrease in unbrowsed seedlings, decreasing from 71% in 1992 to 52.3% by 1995 (Fig. 3), a rate of 6.2%/yr. If this trend had continued, there would have been few unbrowsed seedlings by 2003. This decrease abruptly slowed to 0.5%/yr since 1995, and coincided with the decrease in moose densities. It is not known why it started a year before the moose population decreased.

Snow depths in March 1993 ranged from 30 to 70 cm with less snow found under conifer cover. The percentage of seedlings browsed per site that winter was not significantly affected by maximum snow depths (linear regression, F-ratio=2.98, $r^2=0.052$, $p=0.09$). This was not continued in subsequent winters because browsing starts in the fall before there is any snow cover.

Growth Rates - Growth over 6 years of healthy, undamaged seedlings was significantly affected by initial height (linear

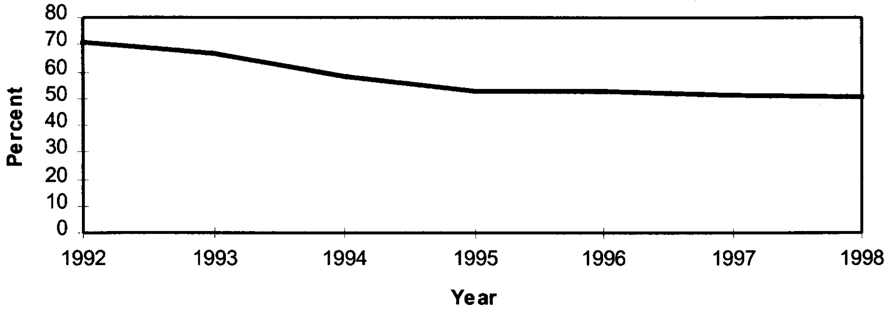

Figure 3.—Percentage of seedlings with no browse damage by year from 2000 tagged seedlings in Algonquin Provincial Park.

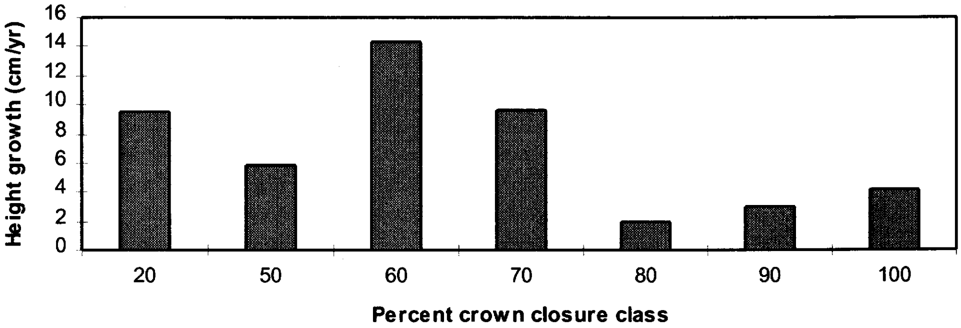

Figure 4.—Annual growth rates by canopy cover class for 828 healthy seedlings from 56 sites in Algonquin Provincial Park.

regression, n=828, F-ratio=654.2, $r^2=0.442$, $p < 0.001$). This is described by the model:

Total annual growth increment (m) = 0.12 m + 0.41 (1992 height)

Current annual height increment was also significantly related to seedling height (linear regression, n=828, F-ratio=406.5, $r^2=0.33$, $p<0.001$), and is described by the model:

Current annual height increment (m) = 0.0065 m + 0.054 (seedling height)

Effect of crown closure on seedling growth - Percent crown closure significantly affected height growth of healthy, undamaged seedlings (Fig. 4, F-ratio = 8.1, $p < 0.001$). The best growth was at 60 % - 70 % crown closure. Competition from other vegetation may be a limiting factor for seedlings growing under higher light conditions (crown closure $\leq$ 50 %). Under deep shade conditions, limited light availability was the primary factor affecting seedling growth.

Discussion

Mortality - Hemlock seedling mortality rates were highest in the youngest seedlings (< 4 yrs old), as would be expected (Fowells 1965). Although seedlings can germinate on unsuitable microsites, they eventually die from desiccation, lack of nutrients, or smothering by hardwood leaves. Unbrowsed, established seedlings appear to have very low mortality rates (0.43%/yr) and die from physical damage or unknown causes such as desiccation, disease or other factors. At this low rate it would take over 200 years for all of the seedlings to die, reflecting the high shade tolerance of hemlock. Browsing is an additive source of mortality, and could cause mortality of most of the seedling population within a few decades, especially if browsing pressure returns to the same high levels as at the start of the study. Browsing intensity tends to be higher at lower seedling densities (Vasiliauskas 1995). Seedlings that could have grown into saplings at these densities have a low probability of doing so due to browsing. At higher seedling densities, browsing may kill some seedlings that would eventually have died from competition effects, but browsing usually affects all larger seedlings in a stand.

The present seedling population originated after the crash in the deer population in Algonquin Park during the late 1950's, based on the age structure from Vasiliauskas (1995). Most seedlings are less than 30 years old, and there is little evidence of earlier high seedling mortality. A dead seedling count by Vasiliauskas (1995) found only 487 dead seedlings out of 20,281, or 2.4% of all seedlings. Dead seedlings are visible for several years (>5) based on observations from this study. Hemlock does not appear to follow the pattern of sugar maple, which is known to have high turnover rates in dense shade (Curtis 1959, Rogers 1978, OMNR 1983). The low turnover rates of hemlock seedings are due to its high shade tolerance and persisting in the understorey for decades before dying from lack of light.

Browsing - Browsing is the main factor influencing seedling growth and survival. Browsed seedlings have little potential to recover lost height and recruit into the future canopy (Curtis 1959) due to leader and foliage loss, resulting in a decrease of hemlock stem density in the long term. Some seedlings are more likely to recover provided that initial browsing was light. Rebrowsed seedlings have little potential to become saplings, because they become bushy and multi-stemmed, and grow at only 10% of the rate for healthy seedlings. In addition, the probability of being rebrowsed doubles if a seedling has been previously browsed (Vasiliauskas 1995). Snowshoe hares play a minor role in hemlock browsing and have the greatest effect on small seedlings that can be nipped off at the base (Vasiliauskas 1995). Snow does not protect seedlings, as browsing starts in the fall before there is any snow cover. The steady decrease in the number of unbrowsed seedlings at the start of the study suggested that few seedlings would escape browsing. The recent decrease in browsing intensity and in the rate of loss of unbrowsed seedlings suggests that there may be a much better chance of seedlings recruiting into the canopy.

If lower browsing levels are maintained, the age gap in the hemlock population started by past deer browsing could end. Hemlock should maintain itself on the landscape at about current levels. However, if browsing intensity increases, the age gap will be extended. This would decrease the area dominated by hemlock and restrict it to areas with little or no browsing pressure. Forest cover will shift to dominance by other species such as sugar maple, as mature hemlock die and are not replaced.

Growth - Seedling growth is similar to other studies (Fowells 1965, Anderson *et al.* 1990). Seedling growth appears to maximize under partial shade (60% canopy closure). Larger seedlings have faster growth rates since they have more photosynthetic surface area, as determined for white spruce (*Picea glauca* Moench.)(Lieffers *et al.* 1996). It is unknown if the lower growth rates under higher light levels was due to increased hardwood competition, or to seedlings producing more side branches and more lateral growth. Monitoring more saplings under open canopy conditions would help to answer this question.

Implications to management

Hemlock is highly sensitive to browsing pressure. Seedlings can lose at least two years of height growth with each browsing incident and recover slowly. Naturally established seedlings can require up to 30 years before the leaders are at least 3 metres above the ground and out of the reach of moose. Ungulate populations need to remain low, or seedlings have to be protected for this length of time to ensure hemlock recruitment. At the stand level, foresters can consider manipulating canopy openings to maximize seedling growth, reducing browsing pressure or protecting seedlings. At the landscape level, foresters can consider managing hemlock in areas with low browsing pressure rather than trying to maintain it in areas with heavy browsing pressure. In areas where hunting is permitted, ungulate populations may be lowered through increased hunting.

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Effects of the Removal of Overstory Hemlock on Redback Salamanders and Other Forest-floor Fauna

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Abstract

Eastern hemlock (*Tsuga canadensis* (L.) Carr.) is the second most abundant conifer species in the northeastern United States. It occurs both in almost pure stands and in stands where it is mixed with hardwoods and white pine (*Pinus strobus* L.). Recently, hemlock in the middle-Atlantic and southern New England states has become infested with the hemlock woolly adelgid (*Adelges tsugae* Annand). This insect pest can result in high levels of mortality, opening up the forest canopy and illuminating the forest floor to full sunlight. The effects of the mortality of overstory hemlock on forest wildlife in hemlock-dominated stands is essentially unknown.

In anticipation of adelgid and hemlock looper (*Lambdina* spp.) infestations, overstory hemlock was harvested from 3 hemlock-hardwood stands on the watershed of the Barkhamsted Reservoir in north-central Connecticut between 1992-1998. Some hemlock remained in the harvested stands due to steep slopes, wet areas, or small diameters. The residual structure of the harvested stands was spatially diverse, with essentially clear-cut patches of pure hemlock mixed with uncut or partially cut patches of hardwoods or mixed species.

To assess the effects of these harvests on forest-floor wildlife, small mammals and terrestrial salamanders were surveyed in the harvested stands and in 3 adjacent and comparable control stands. Vegetation surveys, which included measuring the stumps of harvested trees, showed that the harvested stands were similar to the control stands in both structure and composition prior to the timber harvests. Hemlock seedlings were uncommon in the harvested stands, indicating that it is unlikely that hemlock would predominate in the regenerated stands.

The number of small mammal captures was extremely low in the first year of the study, but increased in the second. In both years, captures were dominated by *Peromyscus* spp. and the number of captured mice were similar in both harvested and control stands. Salamanders, principally the terrestrial, eastern redback salamander (*Plethodon cinereus* Green) occurred in all stands. Salamander numbers were consistently greater in control stands, but they were highly variable among stands within each treatment class. It appears that the terrestrial redback salamander would survive in deciduous and unharvested hemlock refugia in harvested stands, from which they could then repopulate the regenerating stand.

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Milling and Marketing of Eastern Hemlock Lumber

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Abstract

Eastern hemlock lumber is manufactured for use in the construction industry. A brief history from the mid-1970s to the present, production challenges, and marketing issues were presented.

Two high capacity stud mills, St. Regis Paper and Diamond Lumber, were opened in Maine during 1974, each cutting eastern hemlock as a portion of their total production. Approximately 40 million board feet of studs were produced annually for the first 5 years. About 1979, St. Regis Paper changed their strategy for the mill and began cutting spruce, pine, and fir exclusively. This left Diamond International's mill at Passadumkeag, Maine now owned by Champion International Corporation, as the only significant producer of eastern hemlock building studs.

Production Challenges:

- Hemlock comes from scattered mixed species stands.
- Hemlock is difficult to de-bark in winter.
- Hemlock is difficult to mill due to ring shake.
- There are limited outlets for green chips produced in the milling process.
- Grade is poorer and lumber recovery is less than in competing species such as spruce, pine, or fir.
- It is impractical to dry hemlock to the "Kiln Dried" specification; therefore, a "Surfaced Green" grade stamp must be used.
- The heavier weight per ft3 of hemlock is harder on equipment compared to competing softwoods.

Marketing Issues:

- Shipping weight and therefore freight costs are higher than competing species.
- There are few customers for green eastern hemlock studs.
- Eastern hemlock competes directly with green Douglas-fir and western hemlock, but producers of lumber from these species are producing more "Kiln Dried" product because these species are more easily dried and the product more valuable.

Both production and marketing of eastern hemlock lumber are challenging due to a variety of inherent characteristics. The market for green hemlock lumber is a niche or specialty market and needs to be approached with a different strategy from that needed in a larger commodity market such as kiln-dried construction lumber.

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Ring Shake in Eastern Hemlock: Frequency and Relationship to Tree Attributes

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Abstract

Ring shake is a barrier to improved utilization of eastern hemlock, an important component of the total softwood timber resource in the Eastern United States and Canada. Ring shake is the lengthwise separation of wood that occurs between and parallel to growth rings, diminishing lumber yields and values. Evaluating the potential for ring shake is essential to improving estimates of tree and stand volume and value, and identifying forest management practices that could minimize the occurrence of ring shake. To assess the incidence and extent of ring shake in eastern hemlock, we sampled 377 trees containing 1,247 sawlogs from sites in Maine, New York, Pennsylvania, North Carolina, Tennessee, and Georgia. Results include relative frequencies of trees and logs with ring shake detected in dry and green lumber. Relationships between tree attributes and the occurrence of ring shake in dry and green lumber also are presented.

Introduction

Eastern hemlock (*Tsuga canadensis*) is one of the more commonly occurring eastern softwoods. In the 12 northeastern states, hemlock represents 22 percent of the softwood sawtimber inventory. More than half of the softwood sawtimber in Pennsylvania and Connecticut is eastern hemlock (Powell and others 1992). This species also extends west into the Lake States and south along the Appalachians into northern Georgia and Alabama (Burns and Honkala 1990).

The production of hemlock lumber is evenly distributed between the New England States, Middle Atlantic States, and the Lake States (FPL 1987) with lumber being used for building construction and the manufacture of pallets and containers. Properties that favor the use of hemlock lumber for framing and general construction include strength, moderately light weight, and straight grain. Due to the lack of resins, hemlock lumber also stains, paints, and glues well (USFS 1973). Properties damaging hemlock's image in the lumber market include brittleness, density variations, differential swelling, and ring shake (Gardner and Diebel 1995). The occurrence of ring shake, which is the lengthwise separation of wood between and parallel to growth layers, is one of the more serious problems affecting the utilization of hemlock. According to the standard lumber grading rules applied by the Northeastern Lumber Manufacturers Association (NELMA 1998), ring shake is not allowed in the better and more valuable grades of hemlock boards (C, D, Select, or 1 Common grades). The occurrence and extent of ring shake also reduce the grades of dimension lumber produced for structural framing and construction.

Koehler (1933) hypothesized that sudden changes in diameter growth rates that accentuated internal stress attributed to differences in the ratio of circumferential to radial growth could account for the occurrence of ring shake. Based on anatomical studies of ring shake in western softwoods, Meyer and Leney (1968) concluded that "shake is a natural occurring defect in standing trees caused primarily by a separation of contiguous latewood tracheids along the middle lamella," but they could not isolate the factors resulting in ring shake. Wilson (1962) cited several external stress factors such as wind and temperature extremes as possible causes of ring shake, but concluded from a study of hemlock stands in Massachusetts that ring shake was attributable to internal growth stresses. Shigo (1963) found a direct correlation between scars and decay resulting from sapsucker damage and the occurrence of ring shake in eastern hemlock. In a follow-up study, Jorgensen and Lecznar (1964) identified cell structure changes resulting from sapsucker wounds and associated with ring shake, concluding that internal stress contributes to the formation of shake defects.

Whereas these and other studies have attempted to identify the causes of ring shake, assessments of the occurrence and variability of ring shake have not been conducted on a broad geographical scale. Also, information linking site and/or tree attributes to the occurrence of ring shake is needed to improve assessments of wood utilization opportunities.

The objectives of this paper are to present preliminary results of a study conducted to: (1) evaluate the frequency and magnitude of ring shake found in hemlock trees sampled from stands located in six states ranging from Maine to Georgia; and (2) identify tree attributes that could indicate the likelihood of ring shake in hemlock lumber.

Methods

The ring shake related data used in this study were collected as part of a larger study conducted to improve hemlock lumber manufacturing processes through the development of eastern hemlock log and tree grades for estimating lumber grade yields. Because ring shake is one of the more important tree and log attributes affecting lumber yields, detection and evaluation of ring shake was an important aspect of this study. The data were collected from 1968 to 1971 but due to changes in research priorities from softwood to hardwood utilization, data analyses were not completed nor were results published. However, with the recent reductions in softwood harvests from public land in the West, there is renewed interest in utilizing eastern softwoods to meet the growing demands for wood and wood products.

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Table 1.—Sample tree attributes by study site.

State	No. of trees	Dbh		Age		Tree volume[a]	
		Mean	Range	Mean	Range	Mean	Range
		inches		*years*		*board feet*	
PA	126	17.4	9.0 - 30.7	141.2	46 - 244	339.8	40 - 1,079
NY	29	16.2	10.1 - 26.0	131.4	105 - 200	227.9	48 - 593
ME	91	15.6	9.9 - 31.7	98.6	48 - 220	204.3	25 - 850
TN	40	24.9	13.4 - 46.3	217.5	79 - 415	709.4	55 - 2,667
NC	49	25.7	13.2 - 45.6	191.8	92 - 491	880.5	58 - 3,432
GA	42	22.7	13.1 - 44.3	149.5	75 - 309	725.2	86 - 2,970

[a] Lumber tally

Sampling

Data were collected from a total of 377 hemlock trees in three general geographic areas: the Northeast, Pennsylvania, and the southern Appalachians. The northeastern samples were collected at two sites in Maine near Naples and Belgrade and one site in New York on the Pack Demonstration Forest near Warrensburg. The Pennsylvania samples were collected at four sites: Williamsport, Renova, Coudersport, and Emporium. The southern Appalachian samples were collected at one site in each of three states: Tellico Plains, Tennessee; Robinsville, North Carolina; and Clayton, Georgia.

Sampling was conducted on active timber sales located on diverse sites with respect to slope and aspect. Sample trees were selected to include a relatively wide range of tree diameters at breast height (Dbh), ages, and quality classes. Identical sampling procedures were applied at each site. These included measuring and assessing site and stand attributes, measuring tree attributes before and after felling each tree, measuring sawlog attributes after felled stems were bucked into sawlog lengths, and tracking each log through the sawmill to measure and grade all lumber sawn from each sawlog. With the exception of the trees and logs sampled in Maine, lumber was air dried before it was measured and graded. Lumber sampled in Maine was measured and graded green. Because the study did not compare lumber shake in green and dry lumber from the same boards or logs, we could not reliably determine the effects of air drying on the detection or occurrence of ring shake in lumber. As a result, ring shake in green and dry lumber are reported separately.

Lumber grading included evaluation of each board sawn for the presence of ring shake. Following felling and bucking, sawlogs were evaluated for ring shake by examining log ends and recording the length, width, and estimated depth of ring shake, and recording the number of log end quarters showing indications of ring shake. From the large array of tree attributes collected, those relevant to this study include: Dbh, age, number of abrupt changes in growth rates, total lumber volume obtained from all logs in each tree, and the occurrence of occluded or closed bird peck.

Analyses

Data analysis included calculating the total volume of lumber with ring shake sawn from each sample tree, calculating percent shake or volume of lumber with shake as a percentage of total tree lumber tally, and the frequency or percent of all sample trees with at least 1 percent shake. To evaluate the reliability of visible ring shake indicators in log ends as indicators of ring shake in the lumber sawn from those same logs, number of logs with and without shake found in the lumber were calculated for logs with and without shake indicators visible in log ends. To help explain the variation found in the frequency of ring shake found between sample sites and to link tree attributes to the occurrence of ring shake, a probit analysis was conducted (Greene 1997). This analysis was used to estimate the relationship between a binary dependent variable Y coded 1 if 1 percent or more of the lumber volume sawn from the tree contained shake defect, or zero if it did not; and variables that measured tree and site characteristics (X'B), and a random disturbance, e.

$$\mathrm{Prob}(Y=1) = \mathrm{Prob}\,(e<X'B) = F(X'B) \quad [1]$$

Results

Sample Tree Attributes

The largest and oldest trees were sampled on the southern Appalachian sites, where all three sites had trees larger than 40 inches Dbh and older than 300 years (Table 1). Maine sites had the lowest average tree diameters and ages, 15.6 inches Dbh and 98.6 years, respectively. Because of the old age and large Dbh of many sample trees, especially those on the southern Appalachian sites, mean tree volumes ranged from 204.3 to 880.5 board feet lumber tally. Maximum tree volumes ranged from 593 to 3,432 board feet per tree (Table 1).

Shake in Log Ends as an Indicator of Ring Shake in Lumber

Of the 998 hemlock logs with lumber graded dry, 387 logs or 39 percent produced lumber with ring shake (Table 2). Of these 998 logs, 269 or 27 percent showed indicators of ring shake in log ends. However, less than half of the logs producing lumber with ring shake also showed visible indicators of ring shake in log ends. In addition, approximately one-third of logs with shake indicators in the log ends did not produce lumber with ring shake.

Table 2.—Number and percentage (in parentheses) of hemlock sawlogs by shake status of log ends and dry lumber.

Shake indicators in log ends	Shake in lumber Yes	Shake in lumber No	Totals
Yes	181 (67.2)	88 (32.7)	269 (27)
No	206 (28.3)	523 (71.7)	729 (73)
Totals	387 (38.8)	611 (61.2)	998 (100)

Of the 249 hemlock logs with lumber graded green, only 22 logs or 9 percent produced lumber with ring shake (Table 3). Twelve percent of these 249 logs showed indicators of ring shake in log ends. Thirty-one percent of the logs yielding green lumber with shake also showed visible indicators of ring shake in log ends, but approximately 69 percent of logs with shake indicators did not produce green lumber with ring shake. These results imply that the visible indicators of ring shake in the ends of green hemlock logs were not reliable predictors of ring shake in the lumber sawn from these logs.

Table 3.—Number and percentage (in parentheses) of hemlock logs by shake status of log ends and green lumber.

Shake indicators in log ends	Shake in lumber Yes	Shake in lumber No	Totals
Yes	9 (31.0)	20 (69.0)	29 (12)
No	13 (5.9)	207 (94.1)	220 (88)
Totals	22 (8.8)	227 (91.2)	249 (100)

Frequency and Magnitude of Ring Shake in Dry and Green Lumber

The analysis of ring shake frequency and magnitude included only trees with 1 percent or more shake. This level of ring shake in dry lumber occurred in 73.1 percent of trees (Table 4). The frequency of ring shake varied from 52.4 percent of trees sampled in Georgia to 89.6 percent of trees sampled in New York. For the remaining three states where lumber was graded dry, 73.8 to 77.5 percent of trees sampled had shake.

The volume of dry lumber with ring shake averaged 62 board feet per tree (Table 4), ranging from 40.6 to 78.8 board feet per tree. Maximum volumes of lumber with shake varied by site, ranging from 175 to 355 board feet per tree (Table 4). The lumber volume with shake averaged 14.7 percent of the lumber sawn from trees with 1 percent or more shake. For the five states with lumber graded dry, the average proportion of lumber with ring shake ranged from 5.0 percent in Georgia to 34.0 percent in New York (Table 4).

Nineteen percent of the trees sampled in Maine had 1 percent or more shake in green lumber. Ring shake affected an average of 35.4 board feet or 11 percent of the lumber sawn from trees with shake.

Tree Attributes Associated with Ring Shake

The variables included in the probit analysis that link tree attributes with the incidence of ring shake are defined in Table 5. With the exception of the dummy variable indicating the condition of lumber when graded green or dry, the initial choice of explanatory variables was based on tree attributes reported in the literature and thought to be associated with ring shake. It was anticipated that lumber graded green could be different compared to lumber graded dry.

The results of the probit analysis are presented in Table 6. The signs of the coefficients indicate direction of change in probability resulting from an increase in a particular explanatory variable. Positive coefficients were obtained for all variables indicating that shake was more likely: the older the tree, the more times the growth rate changed abruptly, if occluded bird peck was present, and if shake was assessed in dry rather than green lumber. The latter effect is confounded with the location of the sample because only lumber cut from Maine trees was graded green.

The model correctly classified 104 of 151 trees without shake and 198 of 226 trees with shake (Table 7) for an overall accuracy rate of 80 percent.

Discussion

This study is unique in that the results are based on direct evaluations of lumber sawn from trees, permitting analyses of both the frequency of occurrence of ring shake in lumber and the actual lumber volumes affected. Results indicate that ring shake in eastern hemlock can be a serious wood utilization issue because it occurs frequently and often affects a significant portion of the lumber sawn when it does occur. Results also indicate that significant levels of ring shake occurred over a wide range of site conditions and geographic locations that spanned much of eastern hemlock's native range. This widespread occurrence lends support to Wilson's (1962) conclusion that ring shake in eastern hemlock is not strongly linked to site attributes and location.

Although determining the causes of ring shake was not a primary objective of this study, the results of the probit

Table 4.—Percent of trees with shake in dry lumber, and actual and relative volumes of lumber with shake for trees with 1 perecnt or more shake in dry lumber.

		Lumber volume with shake			
	Trees with	Actual		Relative	
State	shake in lumber	mean	range	mean	range
	percent of trees	board feet/tree		percent of lumber	
PA	73.8	56.3	3 - 239	15.4	2 - 45
NY	89.6	62.8	7 - 175	34.0	5 - 100
TN	77.5	78.8	13 - 238	11.7	2 - 32
NC	75.5	78.8	11- 355	8.6	1 - 20
GA	52.4	40.6	8 - 197	5.0	1 - 14
ALL	73.1	62.0	3 - 355	14.7	1 - 100

Table 5.—Summary of variables included in the probit analysis.

Variable	Definition
Age	Age of tree in years from growth ring analysis
Growth	Number of abrupt changes in growth rate over the life of the tree from growth ring analysis
Bird peck	Coded 1 if occluded bird peck was present on the tree bole; 0 otherwise
Dry[a]	Coded 1 if shake degrade was recorded on dry lumber; 0 otherwise

[a] Shake was evaluated for green lumber in Maine and in dry lumber for all other study locations.

Table 6.—Probit analysis results.

Explanatory variable	Coefficient	Standard error	Mean in sample (N=377)
Constant***	-2.1128	0.2448	1
Age***	0.0085374	0.001810	145.76
Growth*	0.10601	0.06124	3.0663
Bird peck**	0.38109	0.1529	0.45623
Dry***	0.92189	0.1994	0.75862

*significant at the 10% level
**significant at the 5% level
***significant at the 1% level

Likelihood ratio statistic = 142.75 (4 d.f)

Table 7.—Frequencies of actual and predicted numbers of trees with and without shake using the probit model.

	Predicted		
Actual	No shake	Shake	Total
No shake	104	47	151
Shake	28	198	226
Total	132	245	377

analysis linking shake occurrence to tree age, numbers of growth rate changes, and presence of occluded bird peck, support the findings and hypothesis reported in the literature. Wilson (1962) found a strong, positive correlation between tree age and ring shake when observing ring shake found in stumps of harvested eastern hemlock. Koehler (1933) theorized that sudden changes in radial growth rates could contribute to stresses causing ring shake, and that the dehydration of parenchyma cells that occurs over time would also contribute to internal stress resulting in ring shake. The relationship between parenchyma cell dehydration and ring shake was observed by Jorgensen and Leczner (1964) in their study of cell structure changes related to bird peck damage. In an earlier study, Shigo (1963) reported finding ring shake associated with bird peck scars in all 25 trees dissected to determine the effects of old yet visible bird peck wounds.

In their evaluation of marketing opportunities, Gardner and Diebel (1995) indicate that the shortage of western softwoods and the declining quality of lumber from alternative eastern softwood species are improving the market potential for eastern hemlock. They also cite utilization practices adopted by the industry to deal with ring shake; including sorting lumber to exclude boards with shake and chipping versus sawing lumber from the first 100 to 200 inches of the tree stem. Because of the confounding effects of sample locations, we could not conclude from the results of our study that lumber drying made ring shake detection easier. However, the results appear to indicate that sorting lumber to exclude ring shake would likely yield better results with dry versus green lumber. Insofar as detecting shake in the felled tree stem or bucked logs to guide utilization decisions such as chipping versus sawing, study results show that indicators in ends of green logs are not reliable predictors of shake in green or dry lumber. However, results of the probit analysis indicate that including tree age, presence of occluded bird peck, and number of growth rate changes to assess the likelihood of ring shake in a log or stem section could improve wood utilization decisions.

Estimated relationships between tree attributes and the occurrence of ring shake also could be applied to assess potential wood quality in specific stands of eastern hemlock based on knowledge of stand history or increment borings to determine age and number of growth rate changes and the observed frequency of occluded bird peck. These results can be implemented in forest management guidelines when wood quality and value are important management objectives. Because of the effects of age and abrupt changes in growth rates on ring shake occurrence, managers should avoid long rotations and frequent and/or heavy thinnings and partial cuts when managing hemlock stands for quality wood production. When forest management objectives dictate long rotations, old growth conditions, or retention of residual hemlock trees in heavily cut stands to enhance aesthetic or wildlife values, managers should be aware of the likely tradeoffs that include reduced wood quality and value due to ring shake.

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Eastern Hemlock: A Market Perspective

Theodore Howard[1], *Paul Sendak*[2], *and Claudia Codrescu*[1]

Abstract

Although it is an important component of the northern forest, eastern hemlock (*Tsuga canadensis* (L.) Carr.) is a secondary species in its regions' markets. In this paper, we examine the markets for hemlock, analyze price trends for stumpage, and suggest implications of market forces for management of forests containing hemlock. The characteristics of hemlock wood limit its use to relatively low-grade products, such as structural lumber, pulpwood, and pallets, although higher value niche markets exist, such as post and beam house frames. Analysis of trends for sawlog and pulpwood stumpage prices from publicly available reports indicates little change in inflation-adjusted prices over long time periods. Such price performance indicates that available supply is more than adequate to meet demand throughout hemlock's natural range. Markets for hemlock have rarely been strong and are not likely to become so. Therefore, forest management plans that require the removal of hemlock may require opportunistic harvesting decisions. Eastern hemlock's nonmarket values must also be incorporated into management plans.

Introduction

Eastern hemlock (*Tsuga canadensis* (L.) Carr.) is an important component of the forests of the southern parts of eastern Canada as well as those of the northern United States stretching from Maine to Minnesota and southward through the Appalachian Mountains into northern Georgia and Alabama. While the species itself is common, its scientific name, *Tsuga canadensis*, has an uncommon origin. All of the other softwoods native to North America, with the exception of *Sequoia* and *Pseudotsuga*, can trace their names to Latin or Greek. *Sequoia* is of Native American origin and *Psuedotsuga* is simply "false hemlock". Hemlock's name comes from the Japanese word for hemlock. The kanji character for *Tsuga siebolii*, southern Japanese hemlock, is a combination of tree and mother.

The objective of this paper is to examine eastern hemlock from a market perspective. We will first outline the wood characteristics that limit hemlock utilization and describe the types of products made from hemlock. Second, we will provide information on the consumption patterns of hemlock sawtimber and pulpwood and analyze price trends for hemlock stumpage. Finally, we suggest how landowners and forest managers can incorporate this market information into their management decisions.

Wood Characteristics

Hemlock has never enjoyed the levels of high demand that many of the other conifers in its range have experienced. Eastern white pine, black, red, and white spruce, as well as balsam fir have had much wider market acceptance. Eastern white pine, for example, was the primary commercial species in the northeast and northcentral United States from the early colonial period to the late 1800s (Howard 1986). Eastern spruce and fir in those same areas and into eastern Canada now account for most of the softwood volumes harvested.

Hemlock has lagged because its wood properties do not compare well to those of other conifers. As Alden (1997) notes, hemlock wood is uneven in texture and tends to have considerable ring shake. It has only moderate strength properties, has low resistance to splitting, is harsh and splintery when worked with tools, and is not decay resistant. Hemlock also is resistant to preservative treatment. The desirable properties of lack of odor and taste once made hemlock an important wood for food containers. One of the earliest commercial uses of eastern hemlock was its bark as a source of tannin for the tanning industry. Hemlock bark is still in demand today, but for landscaping mulch.

Methods

We contacted over a dozen manufacturers throughout the Northeastern United States in an informal survey of the current hemlock end product market situation. We selected our participants from the *Sawlog Bulletin*, generally focusing on those organizations that listed themselves as buying multiple grades of hemlock logs. We felt that the expressed demand for various grades indicated greater market segmentation by the producer and therefore, we would capture a larger view of the variety of hemlock end products.

We collected data from publicly reported sources of hemlock roundwood consumption and stumpage prices. These time series were plotted and rates of annual stumpage price change were estimated for selected series by ordinary least squares regression using the following model:

$$\ln V_t = \ln V_0 + rt \quad [1]$$

where
V_t = future price,
V_0 = initial price,
t = time period for compounding in years,
r = the continuous rate of change, and
ln is the natural logarithm (base e).

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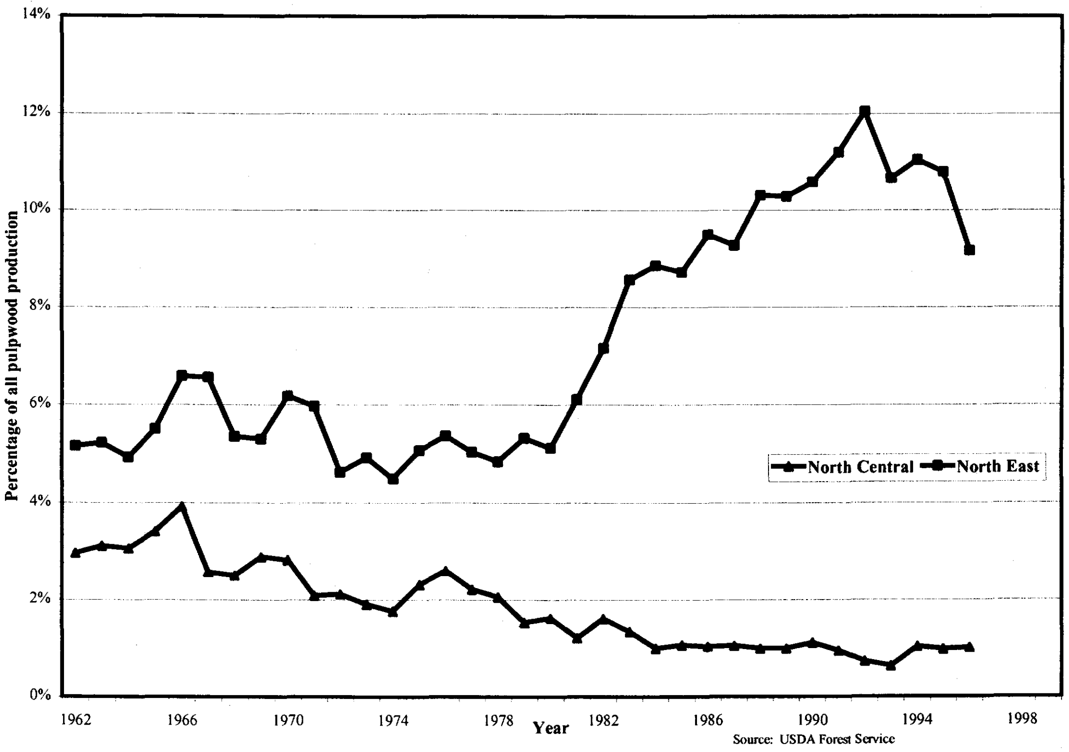


Figure 1.—Hemlock pulpwood production as a percentage of all pulpwood production in North Central and Northeastern United States, 1963-1997.

Results

Perspectives on Utilization

Based on the survey of hemlock roundwood purchasers, the following hemlock products were identified: pulpwood; dimension lumber including studs; boards; timbers for construction, post and beam house frames, and bridges; plywood core veneers; landscape timbers; and bark. Almost all hemlock lumber was sold green and usually not graded, some was air dried. In timber applications, hemlock was not subject to as much twist as eastern spruce and fir although somewhat weaker than those species. Hemlock timbers were used in landscaping despite its poor decay resistance. Hemlock bark for landscaping mulch, pound for pound, may be the most valuable commercial component of the species.

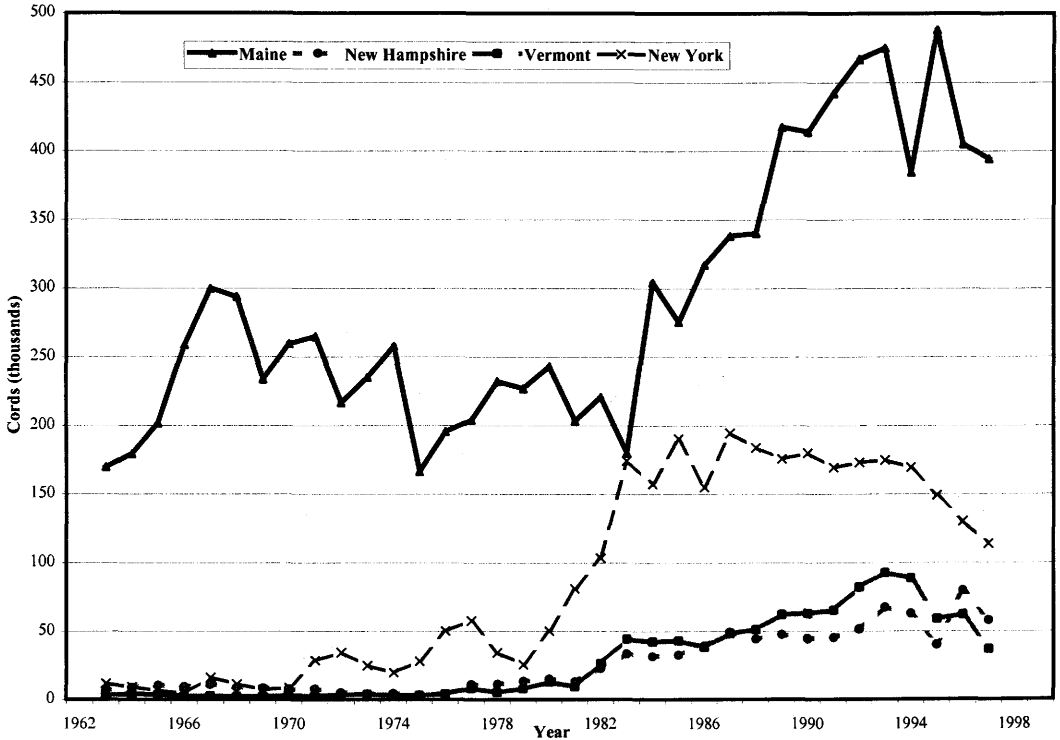
Consumption

The commercial importance of hemlock can be judged partly by examining harvest volumes for pulpwood and sawtimber throughout its range. While the USDA Forest Service publishes pulpwood production data for the North Central and Northeastern states, we focused on only those states whose annual production regularly exceeded 10,000 cords. Because only a few states collect annual sawtimber production data, our analysis of those trends is geographically limited.

Pulpwood production has been moving upward in the Northeast and downward in the North Central region in terms of total volume and as a percentage of all pulpwood produced (Figure 1). In the North Central region, hemlock has practically disappeared from the pulpmill furnish, representing barely 1% of all pulpwood used. Pulpwood production in Wisconsin and Michigan has been highly variable and generally declining. Michigan's production has shown an upward trend during the last few years of the 1990s. Although there has been recent downturn in hemlock's Northeast market share, its representation in that market more than doubled from 1980 to 1991.

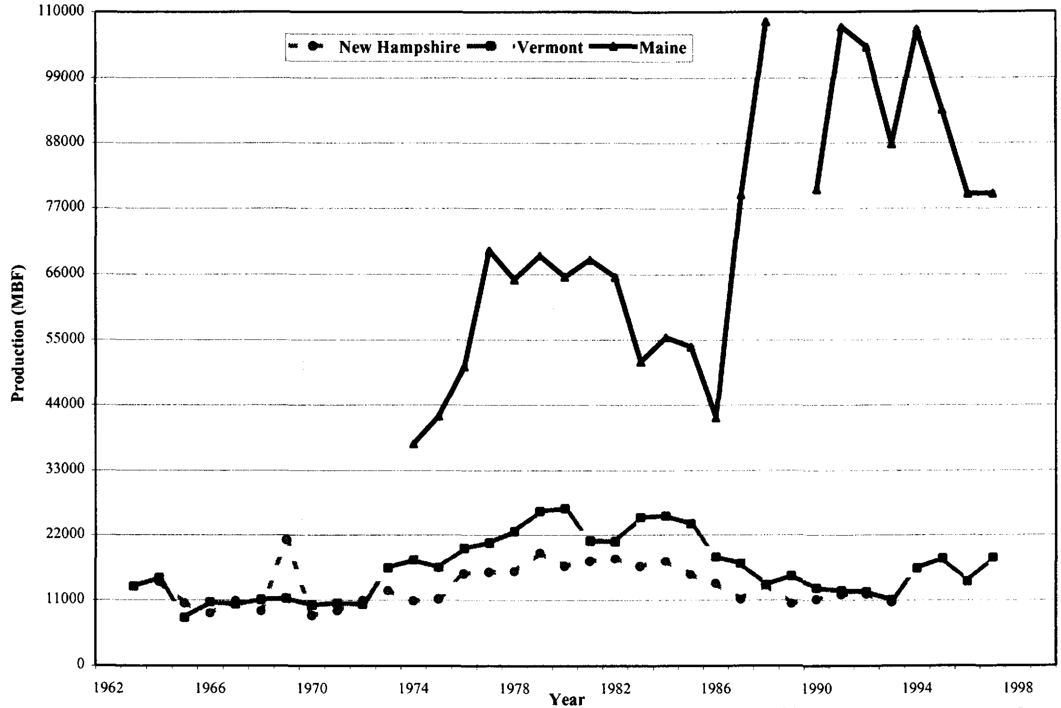
In New Hampshire, Maine, and Vermont, hemlock pulpwood production has been increasing since the early 1980s (Figure 2) while New York experienced a significant jump in production in the mid-1970s. The increase in New England can be partly attributed to changes in supply associated with massive losses of spruce and fir inventory due to the spruce budworm.

Hemlock sawtimber production in New Hampshire and Vermont has been in the range of 10 to 20 million board feet (bf) per year consistently over the last 4 decades (Figure 3). Annual Maine production has been significantly greater compared to New Hampshire and Vermont. Maine had producing in the range of from 40 to 65 million bf of hemlock sawtimber from the mid-1970s to the mid-1980s. But for the last 10 years, Maine hemlock production has been in the range of from 80 to 110 million bf per year (Figure 3). This large increase may, in part, be due to increased utilization of hemlock for stud mills in Maine.



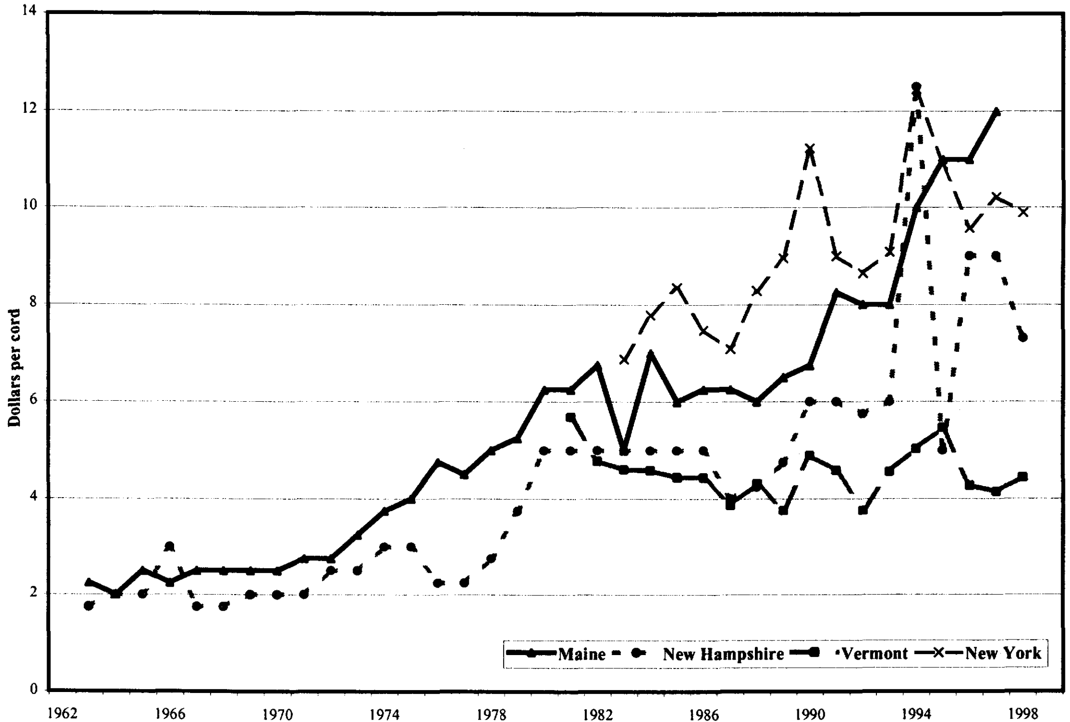
Source: USDA Forest Service

Figure 2.—Significant hemlock pulpwood production by Northeastern states, 1963-1997.



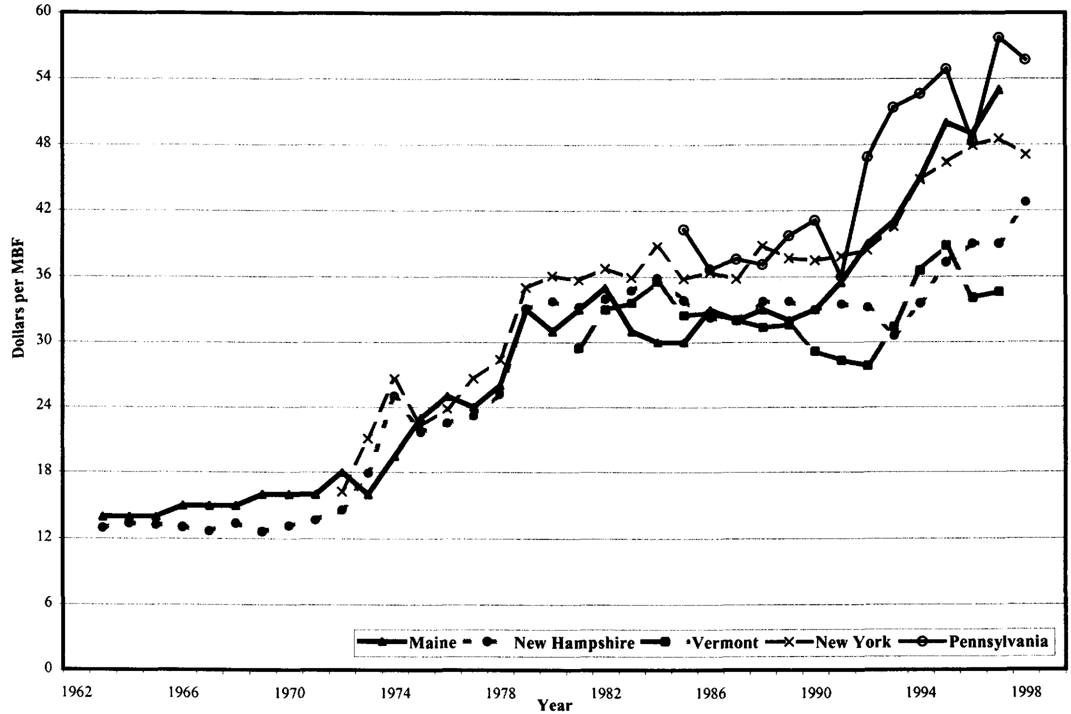
Sources: Maine Forest Service; New Hampshire Division of Forest and Lands; Vermont Dept. Forests, Parks and Recreation

Figure 3.—Hemlock sawtimber production in Maine, New Hampshire, and Vermont, 1963-1997.



Sources: Maine Forest Service; New Hampshire Cooperative Extension Service; New York Division of Lands and Forests; Vermont Extension Forester

Figure 4.—Nominal hemlock pulpwood stumpage prices in Maine, New Hampshire, Vermont, and New York, 1963-1998.



Sources: Maine Forest Service; New Hampshire Cooperative Extension Service; New York Division of Lands and Forests; Vermont Extension Forester; Pennsylvania Cooperative Extension Service

Figure 5.—Nominal sawtimber hemlock stumpage prices in Maine, New Hampshire, Vermont, New York, and Pennsylvania, 1963-1998.

Price Performance

Many states in the range of eastern hemlock maintain stumpage price reporting systems (Lutz, Howard, and Sendak 1992). We selected some of the longer price series for eastern hemlock and analyzed nominal (unadjusted for inflation) price performance and real price performance (adjusted for inflation). We also chose a shorter common time period, 1985 to 1997, to compare price change among all states. The two longest price series in the region were from Maine and New Hampshire. We plotted Maine hemlock pulpwood stumpage prices from 1963 to 1997 and New Hampshire from 1963 to 1998. The general trend for both states has been upward with significantly more volatility in New Hampshire prices in the mid-1990s (Figure 4). Over these periods, the average annual nominal rate of price change was 4.97% in Maine and 4.53% in New Hampshire. Inflation as measured by the Producer Price Index, All Commodity, averaged about 4.6% annually (Table 1). Adjusted for inflation, real prices remained just above to just below constant in Maine and New Hampshire, respectively.

Table 1.—Annual percentage rates of nominal and real hemlock pulpwood stumpage price change in selected states.

State	Period	Rate of change	
		Nominal	Real
Maine	1963-1997	4.97	0.07
	1985-1997	6.24	4.11
New Hampshire	1963-1998	4.53	-0.08
	1985-1997	6.05	3.92
Vermont	1981-1997	-0.39[a]	-2.04
	1985-1997	0.75	-1.28
New York	1983-1998	2.64	-0.88
	1985-1997	2.83	0.77

[a]Not significantly different from zero (p <=0.05), that is, constant.

In the shorter term, 1985 to 1997, nominal hemlock pulpwood stumpage prices were flat in Vermont and trended upward in Maine, New Hampshire, and New York (Figure 4). The average annual rates of price change ranged from 0.75% in Vermont to 6.24% in Maine. Since the rate of inflation averaged 2.05% from 1985 to 1997, there were significant real positive rates of change of about 4% in both Maine and New Hampshire (Table 1). In Vermont, real rate of price change was negative and in New York, less than 1% per year.

Nominal hemlock sawtimber stumpage prices were plotted for Maine, New Hampshire, New York, Pennsylvania, and Vermont. Again, the longest price series were for Maine and New Hampshire (Figure 5). All five series generally trend upward over the period of time that they represent. In Maine (1963 to 1997) and New Hampshire (1963 to 1998), the average annual rates of price change were 3.93% and 3.63%, respectively. Since annual inflation averaged about 4.6%, real rates of price change were negative over the time period (Table 2). This was true for New York from 1972 to 1998 and Vermont from 1981 to 1997. Pennsylvania had the only positive real rate of price change and in general had the highest nominal prices for hemlock sawtimber in the region (Figure 5). Pennsylvania prices average only the two northern reporting regions rather than a state average as for the other states because hemlock and white pine were reported as a species group.

In the shorter term, 1985 to 1997, nominal hemlock pulpwood stumpage prices trended upward in all five states (Figure 5). The average annual rates of price change ranged from 0.97% in Vermont to 4.82% in Maine (Table 2). Since the rate of inflation averaged 2.05% from 1985 to 1997, there were real positive rates of change in Maine (2.71%), Pennsylvania (2.24%), and New York (0.59%). In Vermont and New Hampshire real rate of price change was negative, so that nominal prices were not keeping pace with inflation.

Table 2.—Annual percentage rates of nominal and real hemlock sawtimber stumpage price change in selected states.

State	Period	Rate of change	
		Nominal	Real
Maine	1963-1997	3.93	-0.66
	1985-1997	4.82	2.71
New Hampshire	1963-1998	3.63	-0.94
	1985-1997	1.21	-0.82
Vermont	1981-1997	0.39[a]	-1.35
	1985-1997	0.97	-1.06
New York	1972-1998	3.04	-0.80
	1985-1997	2.65	0.59
Pennsylvania	1985-1998	2.62	0.73
	1985-1997	4.34	2.24

[a]Not significantly different from zero (p <=0.05), that is, constant.

Management Implications

From the perspective of efficient use of forest capital, we can afford timber production as long as the combinations of biological growth rates, per unit price changes associated with higher valued products from larger trees, and the general price growth exceed the landowner's opportunity cost of capital. When timber production cannot pay as well, we can expect poor forest practices and land use changes to occur. The future for eastern hemlock is not very promising for three reasons.

First, the biological growth rate of hemlock is not high. Second, hemlock sawtimber is not particularly valuable so that the price premium for sawlog-size trees relative to that of pulpwood-size trees is not large compared with other species. Finally, the long-term price performance of hemlock sawtimber and pulpwood suggest that hemlock has barely kept pace with inflation and has even lost ground in some markets. Flat or declining real prices for hemlock is a drag on capital returns that cannot be recovered via biology or quality premiums. Landowners simply cannot afford to manage for hemlock for financial returns for strictly timber purposes. The better performance of price appreciation in the shorter term (1985 to 1997), especially for pulpwood stumpage, may be attributed to changes in supply associated with massive losses of spruce and fir inventory due to the spruce budworm. It will be critical to the management and marketing of hemlock if these more recent trends in price can be sustained.

Economics is concerned with more than just the financial returns from timber production. If a standing forest has value in addition to timber value, Hartman (1976) has shown that these other values will have an important influence on "when or whether to harvest." If landowner goals include aesthetics, wildlife habitat, biological diversity, or other nonmarket values, then management of hemlock needs to take that into account. For example, hemlock stands are superior cover for white-tailed deer wintering areas in the northern part of their range (Reay et al. 1990). Practicality suggests that landowners and their forestry advisors should have a clear sense of what they would like to accomplish with their hemlock resource. If timber values are important, they need to harvest when stumpage prices are increasing. When the market strengthens, quick action will yield capital for management purposes. When those windows of opportunity close, hemlock can be safely stored on the stump.

Hemlock rarely grows as pure stands over a large area. So it is most often managed as a major or minor component of a mixed stand that may include other softwoods, hardwoods, or both (Lancaster 1985). Hemlock can be managed as even-aged or uneven-aged stands but the shelterwood system is the best method to regenerate hemlock stands. When hemlock grows in mixtures with other species the other species have to be considered as well as the hemlock in setting management goals. Where hemlock is a minor component it is often harvested along with major species in the stand.

Insect infestations, specifically hemlock woolly adelgid, are the wild card in hemlock markets. To date, the infestations have been in areas that are not overly important to the regional production picture although they are certainly important to the affected landowners. However, large-scale salvage operations in areas where hemlock is more important to the regional production picture could cause a short-term market surplus.

Hemlock has not enjoyed wide acceptance in the market due to "certain inherent undesirable characteristics plus unwarranted prejudice (which) have discouraged the proper use of this valuable resources" (USDA Forest Service 1973, foreword). In the early 1970s, the USDA Forest Service in cooperation with the Vermont Department of Forests and Parks prepared five utilization guides to promote the management of hemlock stands, the processing of hemlock lumber, and its use in construction. Despite this effort, hemlock has remained a secondary species as evidenced by the relatively low consumption across its entire range and the flat to negative real stumpage price performance in nearly every state sawtimber price series.

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Poster Presentations

Relative Contribution of Hemlock Pollen to the Phosphorus Loading of the Clear Lake Ecosystem Near Minden, Ontario

Hugh H. Banks[1] *and James E. Nighswander*[2]

Abstract

The forest stand composition within the terrestrial watershed of a small lake on the southern Precambrian Shield was assessed. Total phosphorus inputs from the terrestrial watersheds were obtained for two sub inflows by measuring flow rates and phosphorus concentrations. Direct aerial phosphorus fallout was estimated from nearby sites sampled by the Ontario Ministry of the Environment. Pollen fallout on the 88 ha lake surface was measured during the growing season with a series of floating pollen traps. Detailed microscopic examination was made of the slides prepared from the trapped pollen samples. Pollen grain volumes, species identification, frequency and percentage composition were obtained. Phosphorus contents of several species of pollen grains were calculated for pollen collected directly from broad leaf tree flowers and coniferous strobili. In the old growth watershed, hemlock (*Tsuga canadensis* (L.) Carr.) contributed the largest component of pollen-source phosphorus to the ecosystem.

Introduction

Phosphorus is one of the most important components of lake ecosystems because, along with nitrogen, it is the nutrient that often limits algal productivity (Vallentyne 1970, Edmonson 1972 and Schindler 1977) and can influence species composition (Levine and Schindler, 1999). Most of the phosphorus input to lakes on the Canadian Shield enters the lakes with runoff or is deposited on the lakes from the atmosphere (Dillon 1974, Schindler *et al.* 1976). Richerson *et al.* (1970), Gomolka (1975), Nichols and Cox (1978) and Scheider et al. (1979) noted that part of the atmospheric influx of phosphorus was due to pollen grains. Richerson *et al.* (1970) estimated that the input of phosphorus in pollen was insignificant when compared with the total phosphorus loading of Lake Tahoe (surface area of approximately 50,000 ha), a lake surrounded by extensive stands of pine and fir. However, the study indicated that under parallel conditions pollen would contribute as much as 5.8% of the total phosphorus budget of Castle Lake, California (surface area = 14.9 ha).

The purpose of this study was to determine the importance of pollen as a source of phosphorus input for Clear Lake, a small lake on the southern Precambrian Shield. Since the amount of phosphorus lost to the terrestrial watershed by the component of pollen influx entering the lake with runoff would be very difficult to estimate, only pollen grains deposited directly onto the lake were considered in this study.

Table 1.—Estimates of Tree Population Percentages for Clear Lake and two Neighbouring Watersheds (trees > 4 in. in diameter)

	Lake		
Tree	Clear	Blackcat	Black Kitten
Hemlock	43	57	62
White Pine	13	5.0	7.1
Red Pine	0.6	0.2	0.4
White Cedar	4.511	20	
Balsam Poplar	1.2	1.3	0.4
Big - Toothed Aspen	1.0	0.2	-
Trembling Aspen	0.1	-	-
White Spruce	0.1	-	-
Black Spruce	-	0.3	-
Sugar Maple	11.3	5.3	0.7
Red Maple	6.3 6.7	5.3	
Striped Maple	0.1	0.5	0.4
White Birch	6.6	3.5	1.1
Yellow Birch	2.6	1.0	0.4
Red Oak	7.3	5.3	1.5
Beech	1.1	1.9	-
Ironwood	1.2	1.1	0.4
Black Ash	0.7	-	-

Clear Lake is in Sherbourne township of Haliburton County, Ontario at 45E 11' N and 78E 43' W. It is completely underlain by very insoluble Precambrian Shield bedrock that lies exposed on steeper slopes. The remainder of the watershed is covered by shallow soils containing scattered pockets of deeper soil with a well defined B horizon (Schindler and Nighswander, 1970).

Clear Lake is a headwater lake with a mean depth of 12.3 m. Its terrestrial watershed is only 146 ha. Two nearby lakes, (Blackcat and Black Kitten) have mean depths of 16.9 m and 6.5 m, respectively, and corresponding watersheds of 44 ha and 3.6 ha. Tree population percentages given in Table 1 were estimated by counting and measuring trees greater than 10 cm in diameter in eight 10 m wide cruise lines extending along the major compass points from a point in the centre of the lake to the perimeter of its watershed.

The small Clear Lake watershed is situated on the Precambrian Shield and, therefore, expected to exhibit relatively low phosphorus loading values. Dillon and Kirchner (1975) found that similar areas export the least phosphorus per unit area. The impermeability of the shield bedrock also limits the influx of phosphorus in groundwater to the extent

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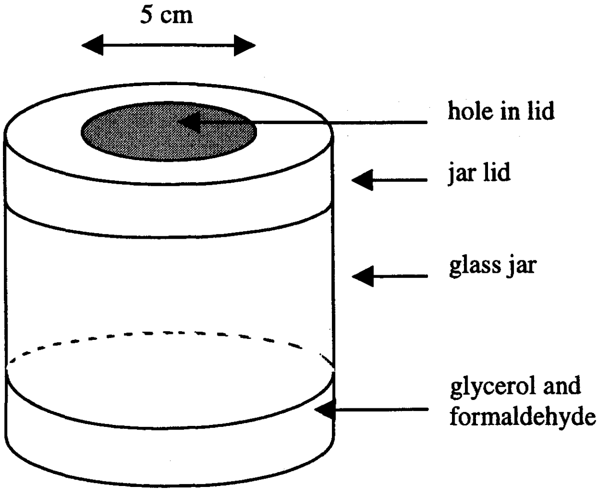

Figure 1.—Pollen trap for airborne pollen.

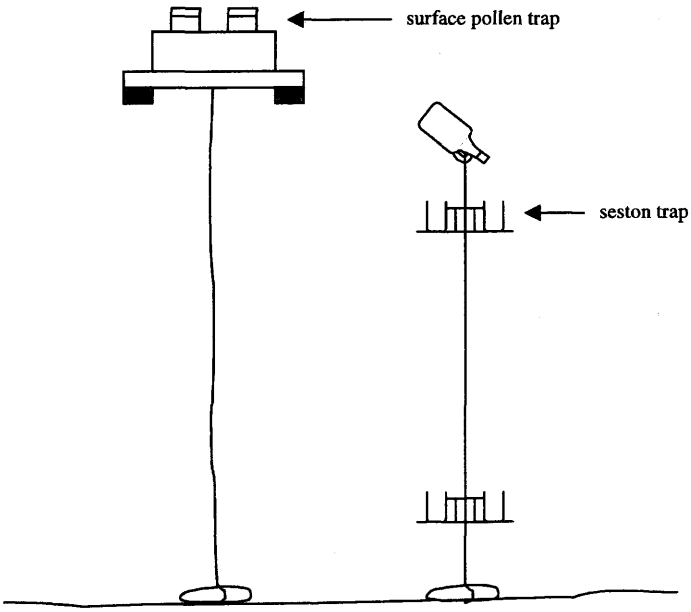

Figure 2.—Deep water sampling site.

that this source of phosphorus loading is often assumed to be negligible (*e.g.* Dillon 1974, Schindler et al. 1976).

There are no permanent dwellings and only a few cottages on the Clear Lake basin. The study area is also a considerable distance from any large urban or industrial centre. Anthropogenic sources of phosphorus loading are, therefore, likely to be comparatively low. More information on Clear Lake and its terrestrial watershed is given in Schindler and Nighswander (1970).

Materials and Methods

The importance of hemlock pollen to the phosphorus budgets of Clear Lake was determined by estimating the phosphorus content of the pollen, the amount of pollen falling on the lake and the phosphorus loading values for the lakes.

Pollen was collected for phosphorus analysis by picking ripe male strobili from the trees and holding them in loosely covered paper boxes for a period of two days to a week until the pollen was released. Strobili were shaken over a 1 mm mesh screen to separate the large flower parts from the pollen. The pollen was separated from small flower pieces by placing the screenings on a slightly tilted piece of paper and gently flicking the underside of the paper with a finger. This process was repeated until all the visible flower parts had been separated from the pollen. Microscopic analysis indicated that essentially pure pollen samples could be collected by this technique.

The pollen samples were oven dried for 48 hr at 90EC. Approximately 0.2 g was subjected to mixed acid digestion (Allen et al. 1974), followed by the molybdic technique of Jackson (1958) for colorimetric analysis to determine the weight of phosphorus in pollen to weight of pollen ratio.

Approximately 50 mg of the sample analysed for phosphorus content was weighed and transferred to a drop of glycerol on a microscope slide. A coverslip was immediately applied and the number of pollen grains counted. This was repeated three times for each species of pollen grain analysed.

Sufficient quantities of *Betula alleghaniensis* Britt., *Betulat papyrifera* Marsh, *Populus tremuloides* Michx., *Pinus strobus* L. and *Pinus resinosa* Ait. pollen were collected to run the minimum three phosphorus analyses necessary to establish 95% confidence limits for phosphorus content. Sufficient *Populus balsamifera* L., *Quercus rubra* L., *Ostrya virgiana* (Mill.) K. Koch, *Tsuga canadensis, Picea glauca* (Moench) Voss and Betula glandulosa Michx. var. *glandulifera* (Regel) Gleason pollen was collected to allow for one phosphorus content analysis. Phosphorus content of pollen grains not available for analysis were established by correlating known pollen phosphorus values to pollen volume values estimated from averages of pollen diameters given by Kapp (1969), Richard (1970) and McAndrews et al. (1973) (see Table 2).

Pollen influx was estimated from pollen counts of samples collected from pairs of surface traps that had been placed on styrofoam floats on the lake. The surface traps were 0.5 litre, wide-mouth specimen jars with a 5 cm hole cut out of the plastic lids. Glycerol, containing a few drops of formalin, was added to the jars to capture the pollen (see Figure 1). Seston traps were placed adjacent to the surface traps to verify the results from the surface traps. For a sketch of a deep water sampling site see Figure 2.

Table 2.—Several Pollen Grain Parameters

				Phosphorus Content per Grain (in g P / grain x 10^{-10})			
				from chemical analysis		from relationship to pollen volume	
Pollen Type	V (μm3)	DW (μg)	95%CI (μg)	PC	95%CI	PC	95%
Tsuga canadensis	113,000	.054	.017	3.73	2.66	.71	
Pinus strobus	66,300	.024	.013	1.37	.88	1.84	.36
P. resinosa	48,800	.022	.004	.957	.33	1.54	.27
Picea glauca	136,000	.037	.031	3.06	.90		
P. mariana	82,900	.053	.015	2.78	2.13	.47	
Abies balsamea	371,000					7.15	2.9
Thuja occidentalis	13,800					.928	.32
Juniperus communis	10,300					.867	.34
Larix larcina	187,000					3.95	1.3
Betula lutea	12,000	.012	.004	1.42	.89	.896	.34
B. papyrifiera	10,500	.012	.005	1.07	.55	.870	.34
B. glandulosa	3,760	.011	.003	.34	.753	.38	
Ostrya virgiana	9,590	.0078	.002	.698	.854	.35	
Populus tremuloides	20,200	.0089	.011	.706	.94	1.04	.29
P. grandidentata	15,600	.0093	.0056	.959	.31		
P. balsamifera	18,100	.0103	.008	1.52		1.00	.33
Quercus rubra	9,140	.014	.006	1.83		.847	.35
Fagus grandifolia	47,100					1.51	.26
Acer rubrum	13,100					.916	.32
A. saccharum	12,800					.910	.33
Alnus rugosa	7,370					.816	.36
Ambrosia(spp.)	3,420					.74	.38
Artemisia(spp.)	8,830					.841	.35
Lycopodiales(spp.)	33,500					1.27	.25
Chenopodinaceae(spp.)	8,180					.830	.35
Gramineae(spp.)	65,400					1.83	.35
Vaccinium(spp.)	33,500					1.27	.25

V = voulme, DW = dried weight, 95%CI = 95% confidence interval and PC = phosphorus content. Confidence intervals for phosphorus content of the pollen grains determined from the relationship between pollen volume and phosphorus content assume that the volume measurements are accurate.

The traps were positioned on two transects roughly traversing the length and width of each lake. Pollen traps were placed on the lakes in May, before locally produced pollen was being released, and emptied four times: at the end of June, the beginning of August, and in the middle of September and November. The traps were removed from the lakes in the winter when it was assumed that a negligible amount of pollen would be released from the frozen, snow - covered watersheds. Traps were placed closer together near the lake shore because most studies on pollen dispersion indicate that pollen rain rapidly decreases as distance from the source increases (Wolfenbarger, 1959, Tauber 1965),

Similarities in size, morphological characteristics and estimated phosphorus content led to the grouping of the following pollen types for counting: *Pinus strobus* with *P. resinosa*; *Betula papyrifera* with *B. alleghaniensis* and *Ostrya virgiana*; *Populus grandidentata* with *P. tremuloides* and *P. balsamifera*; *Picea glauca* with *P. mariana*; *Thuja occidentalis* L.with *Juniperus communis* L.; all *Ambrosia* (spp.); all *Gramineae* (spp.); all periporates - most of which were *Chenopodonaceae* (spp.); all pollen with trilete scars - most of which were *Lycopodiales* (spp.); and all pollen of the general size and shape of *Artemisia* (spp.).

Hemlock pollen fallout at each trap site was calculated by dividing the estimated number of hemlock pollen in the trap by the open area of the trap mouth (0.00196 m²) to give an estimation of the aerial pollen input per square metre. Pollen fallout was then regressed against the distance from shore (linear, log/normal, normal/log and log/log relationships were regressed) to establish the relationship between the two variables. The relationship giving the best correlation coefficient was then used in the "Planimetry and Integration Method" (Banks and Nighswander, 1982) to estimate the total amount of hemlock pollen falling onto the lake.

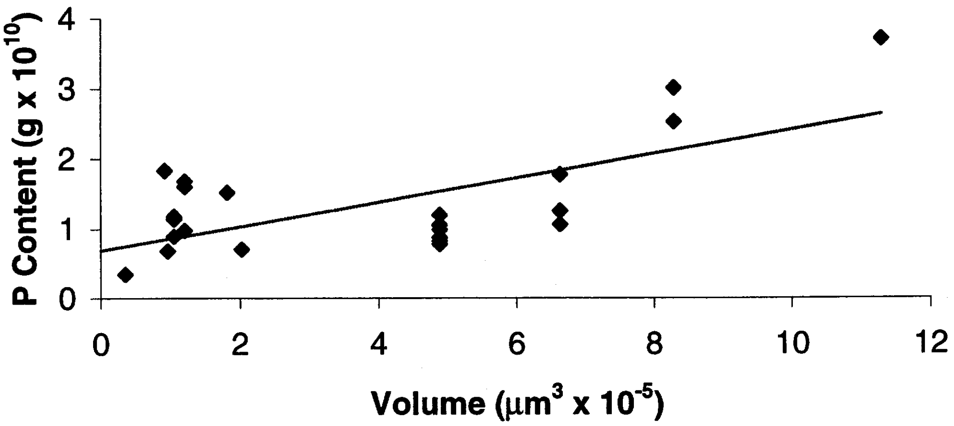

Figure 3.—Relationship between pollen grain volume and phosphorus content.

Phosphorus in hemlock pollen falling onto the lake can then be calculated by multiplying the amount of pollen falling on the lake by the phosphorus content of pollen. A similar method was used to find the total phosphorus in all pollen falling onto the lake.

Table 3.—Components of phosphorus loading (in kg). Values in parentheses give the percentage of the phosphorus loading due to each particular source

Phosphorus Source	Lake		
	Clear	Blackcat	Black Kitten
Loading with Runoff	12.4 (34.8)	3.49 (46.2)	0.31 (48.8)
Direct Deposition (excluding pollen)	20.0 (56.0)	3.33 (44.0)	0.21 (33.1)
Hemlock Pollen	0.55 (1.5)	0.31 (4.1)	0.054 (8.5)
Other Pollen Types	2.74 (7.7)	0.43 (5.7)	0.061 (9.6)

Phosphorus loading with runoff for the three lakes was determined by monitoring the flow rates and phosphorus concentrations of the two Clear Lake inflows and then extrapolating the average phosphorus export value to the entire watershed. Estimates of atmospheric phosphorus inputs were made from the averages of several Ontario Ministry of the Environment 0.25 m^2 bulk precipitation collectors placed on nearby lakes and non-forested areas within a 25 km radius of Clear Lake. Jeffries et al. (1977) shows that accurate chemical precipitation values can be obtained in this manner. All phosphorus analyses of precipitation and stream samples were performed by the Water Quality Branch of the Ontario Ministry of the Environment. As in Dillon (1974) and Schindler *et al.* (1976), phosphorus inputs from groundwater and from resuspension from the sediments were assumed to be negligible.

Results

Table 2 lists the pollen volumes estimated from parameters given in the literature, along with the experimentally determined values for phosphorus content of the several types of pollen grains analysed. The volumes of the pollen grains were regressed against their phosphorus content to generate the relationship given in Figure 3. This relationship was then used to estimate the phosphorus content of the pollen grains not available for phosphorus analysis.

Surface pollen traps caught an average of 3,480 pollen grains / cm^2 / yr. Values ranged from 1,180 to 7,600 grains / cm^2 / yr. Relationships between hemlock pollen deposition and distance from shore are given in Figure 4. Pollen-source phosphorus loading values are presented in Table III. The seston traps analysed for this study held from 1.1 to 6.5 (mean = 3.4) times as many sinking pollen grains per unit area as the surface traps.

Flow rate and phosphorus concentration determinations on the two Clear Lake inflows resulted in export estimates of 8.4 mg / m^2 / yr. and 8.6 mg / m^2 / yr. The mean of these two values was multiplied by the watershed areas to estimate the phosphorus entering the lake with runoff (see Table 3).

Analysis of phosphorus concentrations of samples from Ministry of the Environment bulk precipitation collectors gave an atmospheric phosphorus loading value of 26.3 mg / m^2 for the entire year and 11.2 mg / m^2 in the May-June sampling period. These values were used to determine the atmospheric phosphorus loading values given in Table III.

Percentages of phosphorus deposition attributable to hemlock pollen are listed in Table 3. Hemlock pollen was even more significant in relationship to the phosphorus budgets of the lakes when only the May/June collection

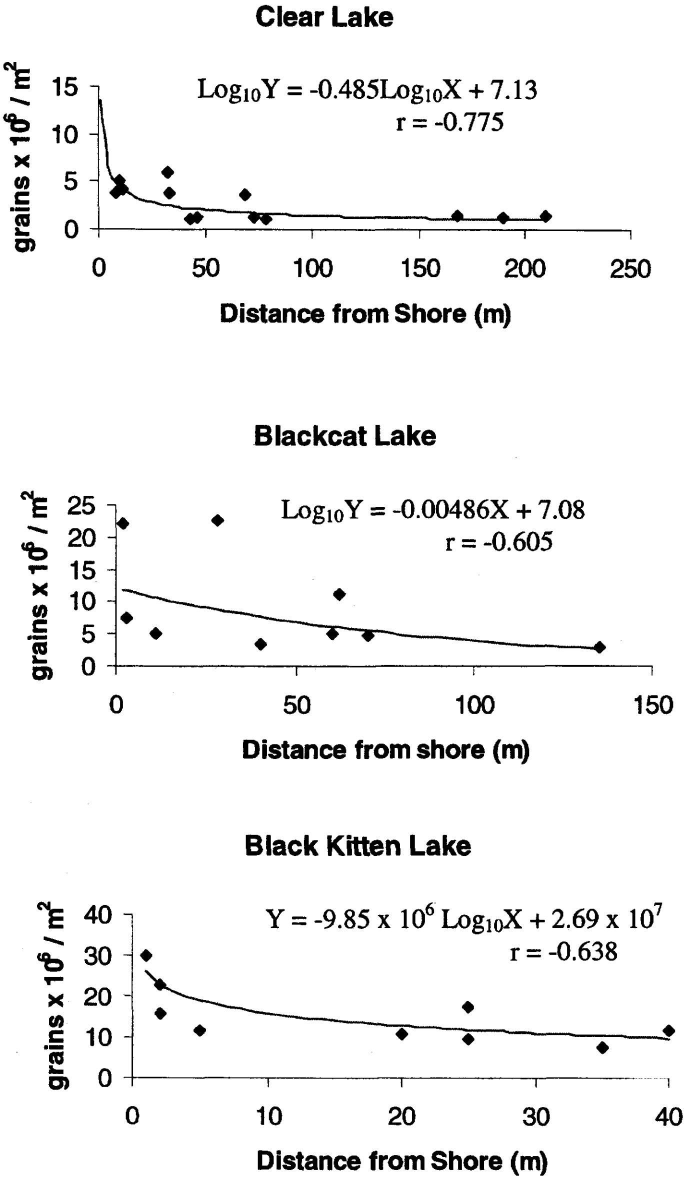

Figure 4.—Relationships between distance from shore and hemlock pollen deposition.

period was considered. At this time of the year, when the hemlock pollen was being released, it accounted for 5.1% of the aerial phosphorus loading and 3.8% of the total phosphorus loading for Clear Lake. Corresponding values increase to 17% and 11% for Blackcat Lake and 35% and 22% for Black Kitten Lake

Discussion

The experimentally determined values listed in the results show reasonable agreement with values from other studies. Experimentally determined phosphorus export values agree well with the 8.8 mg / m^2 / yr. determined by Schindler and Nighswander (1970) for the Clear Lake watershed. The mean phosphorus export value of 8.5 mg / m^2 / yr. is close to the maximum phosphorus export values reported in the literature for forested igneous watersheds (see Dillon and Kirchner 1975); but this could be explained by the small, steeply - sloped watersheds that characteristically exhibit high P export values (see Dugdale and Dugdale 1961 and Mackenthun *et al.* 1964). The atmospheric phosphorus loading value of 26.3 mg / m^2 / yr. is also close to values from areas of similar geology and land use (see Dillon and Kirchner 1975).

Phosphorus concentrations established for pollen grains in this study (per cent phosphorus of the dried weight of pollen) are higher than those reported in the literature for foliage by Son and Gower (1991) and Chapin et al. (1983). Phosphorus concentrations of 0.3% for *B. glandulosa* to 1.5% for *P. balsamifera* pollen (mean value of 0.82% for the eleven types of pollen grains tested in this study) agree reasonably well with values of 0.35% for *Beta vulgaris*, 0.53% for *Alnus* (spp.) (Altman and Dittmer 1964) and 0.4% for a combined sample of *Abies* and *Pinus* pollen (Richerson et al. 1970). Similarly, ranges in pollen influx values of 1,200 grains / cm^2 / yr. to 7,600 grains / cm^2 / yr. from this study are comparable to values from surface traps from other studies (see Davis *et al.* 1973).

Values determined in this study should only be regarded as approximate. There are still problems involving the efficiency of the pollen traps and phosphorus precipitation collectors. Although the pollen loading values expressed here are similar with values from other studies involving surface traps (eg. Ritchie and Liche - Federovich, 1967 and Tauber, 1967), they are roughly an order of magnitude lower than values estimated from sediment studies (see Davis et. al., 1972). Bonny (1978) has shown that Tauber (1974) pollen traps caught approximately half as much pollen as sediment traps under experimental conditions where resuspension of pollen from the sediments and influx from pollen from the watershed could be considered unimportant. Under similar controlled conditions, Reynolds (1979) shows that it is sediment traps that most accurately measure pollen sedimentation rates.

The seston traps analysed for this study held from 1.1 to 6.5 (mean = 3.4) times as many sinking pollen grains as the surface traps per unit area. Some of the pollen caught in the seston traps, however, would probably have been carried into the lake with runoff or resuspended from sediments. Both phosphorus loading values and pollen production values can vary from year to year and this study only represents one year's results.

Atmospheric phosphorus input into the lakes is also likely to be underestimated. The bulk precipitation collectors used by the Ontario Ministry of Natural Resources probably catch less dry atmospheric phosphorus fallout than the water surface for the same reasons that surface pollen traps are less efficient than the water surface at catching pollen. Gomolka (1975) and Jeffries et al. (1977) have shown that atmospheric phosphorus deposition values are higher at on-land station than stations situated on a lake. This suggests an increase in atmospheric phosphorus loading values approaching lakeshores, a factor not considered in this phosphorus loading model.

In spite of methodological limitations, this study does illustrate that hemlock pollen does contribute a significant component of the phosphorus loading of the Clear Lake. Futhermore, pollen-source phosphorus makes up an even a larger proportion of the phosphorus loading during the time of year when the pollen is being released. Finally, the relative importance of pollen-source phosphorus appears to increase as lake area decreases.

Acknowledgements

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Use of Satellite Image Data to Identify Changes in Hemlock Health Over Space and Time

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Abstract

Eastern hemlock (*Tsuga canadensis* (L.) Carrière), is an important component of ecosystems in the northeastern United States and is the primary coniferous species in southern Connecticut. Hemlocks play a unique role in the region by providing spatial and structural habitat diversity that supports many wildlife and fish populations. Widespread damage to this species would have significant impact on water quality, wildlife, and recreational opportunities in the region. Widespread infestations of hemlock woolly adelgid (*Adelges tsugae* Annand) together with occurrences of hemlock looper (*Lambdina fiscellaria* (Guenee) and *L. athasaria* (Walker)), hemlock scale (*Fiorinia externa* Ferris), and shortneedle evergreen scale (*Nuculaspis tsugae* (Marlatt)) have led to a significant decline in hemlock stands in the area. There is a critical need to measure, monitor, and predict the effects that these pests will have on hemlock health. Remote sensing technologies and satellite images can provide a landscape view of the forest. Numerous studies have used satellite-based remotely sensed data to identify and map forests. The purpose of this study was to develop a technique to classify health of eastern hemlock stands using historical satellite images.

The study area included more than 110,000 ha of the lower portion of the Connecticut River watershed, ranging from approximately Middletown, CT, to just north of the river mouth at Long Island Sound. Hemlock covers 2,257 ha (about 2%) of this area. Specific Landsat Thematic Mapper (TM) images of the area were selected based on the least amount of cloud cover present on dates prior to leaf-out of deciduous trees. Images recorded in 1983, 1985, 1988, and 1995 were used in this study. The image dated April 1985 served as a baseline image to locate hemlock stands prior to the time of significant hemlock decline due to hemlock woolly adelgid. Using a Global Information System (GIS), a contiguity analysis was done on the hemlock category to remove all groups of hemlocks less than 1 ha in area, and the hemlock mask file was then used to locate hemlock areas in all TM images. The Modified Soil Adjusted Vegetation Index$_2$ (MSAVI$_2$) transform was then performed on the most current TM image (1995) to provide a hemlock health classification. Techniques described in the U.S. Forest Service Crown Condition Rating Guide were used in Spring, 1996, to evaluate the health of 600 trees in the study area, and a Global Positioning System was used to locate each test site accurately. The overall accuracy of 1996 field data compared to 1995 satellite data was 82.11%. Based on this information, the hemlock mask file and MSAVI$_2$ transform were applied to the images recorded in 1985, 1988, and 1993.

Hemlock decline was monitored by comparing the health classification of each hemlock pixel in images captured at different times. A comparison of the images from the 4 different years showed a general decline in hemlock health over time. Using the baseline image taken in 1985, 60% of hemlock trees in the study area were classified *Average*, 19% *Good*, 17% *Poor*, and 4% *Very Poor*. In 1988, the largest change in the study area was a reduction in the *Average* health class to 45% and an increase in the *Good* and *Very Poor* health classes to 26% and 11%, respectively. There was a substantial decline in hemlock by 1993. The *Good* and *Average* classes fell to their lowest values of the study, 15% and 32%, respectively. Conversely, the *Poor* and *Very Poor* classes reached a peak, 26% and 27%, respectively. By 1995 there was overall improvement in health of hemlock in the study area; *Good* and *Average* classes improved to 64%. The *Poor* and *Very Poor* classes declined to 23% and 13%, respectively.

We conclude that remote sensing and GIS can be used to classify the health of eastern hemlock stands using the MSAVI$_2$ transform and this technique can be used to classify historical images when coexisting field data are not available. This technique may be somewhat subjective, but it does agree favorably with reports of past health conditions in the study area and can serve as an effective tool for future research on forest health.

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Classification and Spatial Analysis of Eastern Hemlock Health Using Remote Sensing and GIS

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Abstract

Over the past decade hemlock stands in southern Connecticut have undergone significant decline coincident with the arrival in 1985 of an exotic insect pest, the hemlock woolly adelgid (*Adelges tsugae* Annand). The objective of this study was to evaluate image enhancement techniques for rating the health of hemlocks at the landscape level using remotely sensed data. We obtained Landsat Thematic Mapper (TM) images of a 110,000 ha area in the lower Connecticut River Basin, an area impacted by the hemlock woolly adelgid. A landcover classification was performed on an April 1985 image to locate the maximum extent of hemlock stands prior to adelgid infestation. Radiance normalization and non-hemlock masking techniques were applied to a May 1995 TM image to locate current stands of hemlock and remove reflectance data for non-hemlock portions of the image. The Normalized Difference Vegetation Index, the Tassel-Cap Transform, and the Modified Soil Adjusted Vegetation Index$_2$ were used to transform the 1995 TM image; each was followed by a cluster analysis to separate hemlocks into 4 levels of tree vigor. We also evaluated 600 eastern hemlock trees at 150 sites within the study area using the techniques described in the U.S. Forest Service Crown Condition Rating Guide. Five indicators of tree vigor were used to measure tree health: live crown ratio, crown density, crown diameter, crown dieback, and foliar transparency. Average indicator values were combined to determine the visual crown rating or health class at each location. The field data were used to measure the accuracy of various health classification techniques. The Modified Soil Adjusted Vegetation Index$_2$ transform provided the best overall accuracy, 82.1%, for classifying hemlock according to tree vigor.

Non-parametric statistics were used to determine if significant variations existed in distribution of hemlock pixels by health class in association with landscape features. Several features were found to be significant; these were aspect of slope, hydrology group (infiltration rate), depth to bedrock, soil order, drainage class (hydraulic conductivity), and surface texture. Based on these data, three hemlock profiles were developed (Table 1). The first profile (most hemlock) describes characteristics of sites in the study area where most hemlocks are located, based on the total number of hectares of hemlock in each subcategory. The second profile (best hemlock) lists characteristics of sites where the best hemlocks are found, based on more hemlock rated in *Good* health than would be expected statistically. The third profile (worst hemlock) lists the characteristics of sites where the worst hemlocks were found, based on more hemlock rated in *Very Poor* health than would be expected statistically.

Initial findings indicate that hemlocks exhibiting the most vigor were located in northwest- and north-facing valleys on deep, medium textured entisols. Hemlocks exhibiting the least vigor were located on southwest- and west-facing slopes and along ridges with shallow, well drained, coarse textured inceptisols.

Table 1.—Characteristics of sites where the most hemlocks, the best hemlocks, and the worst hemlocks were located.

Site Characteristic	Most Hemlock	Best Hemlock	Worst Hemlock
Aspect	SW through NW	NW & N	SW & W
Hydrology Group (Infiltration Rate)	Moderate	High	Very Slow
Depth to Bedrock	60 inches	60 inches	One inch
Soil Order	Inceptisols	Entisols	Inceptisols
Drainage Class	Well Drained	Excessively	Well Drained
Surface Texture	Coarse	Medium/Moderately Coarse	Coarse

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Recovery of Hemlock in Vermont from Defoliation by the Spring Hemlock Looper, *Lambdina athasaria* (Walker)

Barbara S. Burns[1] *and Henry Trial Jr.*[2]

Abstract

Following an outbreak of spring hemlock looper in 1991, ten hemlocks in each of fifteen study plots were monitored annually through 1999. Although some mortality occurred within two years after defoliation, and additional mortality occurred in plots which were subsequently disturbed by logging, most defoliated trees recovered. Twenty-four percent of the trees with 90% defoliation and 43% with 100% defoliation were dead by 1999. Trunk and root collar wounds were more common on dead or unhealthy trees. Overall, tree crown condition improved. In the spring of 1993, only 14% of trees in heavily defoliated plots were in good condition. Six years later, 73% were rated as good. Trees with dead tops usually recovered, maintaining wildlife cover and other values, but the defect may affect timber quality. Three categories of risk are suggested by this study: <50% defoliation (mortality not expected), 50-80% (light risk of mortality), and 90-100% (moderate risk of mortality). Stand assessment two years after defoliation by spring hemlock looper provides an accurate picture of expected mortality, as long as no additional disturbance occurs.

Introduction

In 1991, populations of spring hemlock looper, *Lambdina athasaria* (Walker), increased suddenly in scattered New England locations. Hemlocks were defoliated on about 18,000 acres in five states (Hofacker et al., 1992).

The impact of spring hemlock looper defoliation on hemlocks was not known. Hemlock is vulnerable to exposure (Hepting, 1971) and to defoliation. In Connecticut, 45% of the trees with 90% defoliation by gypsy moth, and 94% with 100% defoliation, subsequently died (Stephens, 1988).

Management recommendations were developed based on the impact of gypsy moth defoliation on hemlock, and early observations of the current fall hemlock looper, *Lambdina fiscellaria* (Guenée), and spring hemlock looper outbreaks (Burns and DeGeus, 1992). Trees were considered likely to die if they had lost all of their older needles and had over 80% defoliation of current-year needles. Trees with no older needles and 50-75% defoliation of current-year needles were also considered at risk.

Plots were established in Maine, New Hampshire, Massachusetts, and Vermont to monitor the impact of spring and fall hemlock looper over a two-year period. In Maine, high levels of hemlock mortality from fall hemlock looper were associated with shallow, ledgy soils (Trial and Devine, 1994). By the end of the regional study, four percent of the trees which had been defoliated by spring hemlock looper were dead (Trial and Devine, 1995). Among surviving, but unhealthy, trees, many were showing signs of recovery. In Vermont, the percent of hemlocks with bare tops decreased from 42% in 1992 to 26% in 1993. Because the fate of defoliated trees was still uncertain, the Vermont plots were monitored annually through spring 1999.

Methods

Monitoring plots were established for this study in fifteen hemlock stands: seven had been heavily defoliated by the spring hemlock looper in 1991, six had been moderately defoliated, and two had received only light or no defoliation. In each stand, ten hemlocks were selected along a transect at thirty foot intervals. All plot trees were evaluated annually, in the spring, between 1992 and 1999.

In 1992 only, each tree was given two defoliation ratings to the nearest 5% class: defoliation of the current year's needles and of previous years' needles. In all years, each tree was rated for transparency using National Forest Health Monitoring standards (Gillespie et al. 1993). Trees were also evaluated as alive or dead and by whether or not a bare top was visible. Bare tops included a range of severities, from trees with little more than a dead leader, to trees with death to the mainstem extending down twenty feet or more from the top. Crown condition, the observers' estimate of the chance that the tree would recover, was rated as good, fair, poor, or very poor. Any wounds present on the trunk or root collar, including damage by hemlock borer, were noted. In 1992 and 1999, diameter at breast height was measured to the nearest 0.1 inch.

Results

In spring 1992, defoliation averaged 77% in heavily defoliated plots, 61% in moderately defoliated plots, and 21% in lightly defoliated plots. Transparency averaged 72%, 47%, and 33%, respectively.

In 1993, 1-1/2 years after defoliation, only 14% of the trees were rated as being in good condition in the heavily defoliated plots and 17% of the trees were rated as good in the moderately defoliated plots (Figure 1).

By 1999, most trees had recovered. At that time 73% were rated as good in both heavily and moderately defoliated plots. Transparency had recovered to 24%, 32%, and 24%, respectively, in the heavily, moderately, and lightly defoliated plots.

Seven of the seventy trees in heavily defoliated plots and five of the sixty in moderately defoliated plots were dead by 1999. Trees that died over the course of the study averaged

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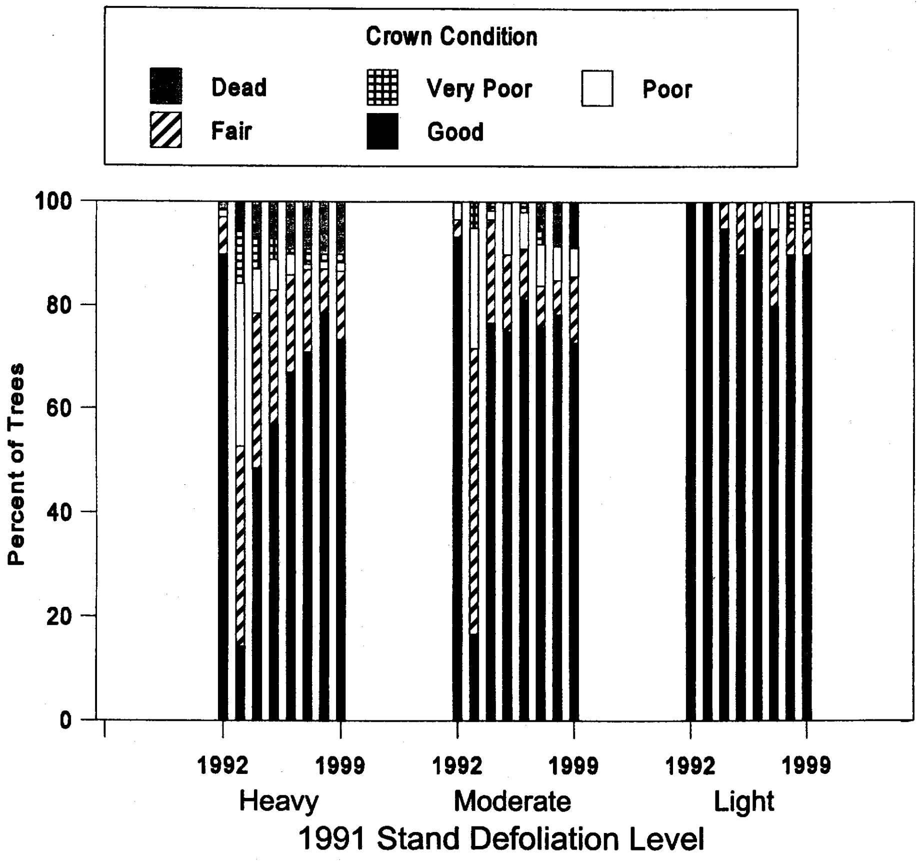

Figure 1.—Annual rating of hemlock condition as percent of trees in each of five crown condition classes, evaluated in spring 1992-1999. Results are grouped by the general severity of the 1991 defoliation by spring hemlock looper defoliation in the stand. Data are from ten trees in each of seven stands which had heavy defoliation, six which had moderate defoliation, and two which had no defoliation.

Table 1.—Percent of hemlocks which were dead eight years after defoliation by spring hemlock looper, by defoliation severity class. Data are from ten trees in each of fifteen plots.

	Severity of 1991 Defoliation[1]									
	10%	20%	30%	40%	50%	60%	70%	80%	90%	100%
Average 1992 % Defoliation	<15	16-25	26-35	36-45	46-55	56-65	66-75	76-85	86-95	>95
Percent Dead[2]	0%	0%	0%	0%	8%	0%	7%	4%	24%	43%
Number of Trees in Class	9	8	9	12	13	17	29	25	21	7

[1] Tree defoliation class based on the average of two estimates of defoliation, defoliation of 1991 needles and defoliation of previous years' needles, as rated in spring 1992.

[2] Cumulative mortality through 1999.

86% defoliation in 1992. Trees which survived averaged 62%. Mortality occurred to 43% of the trees with 96-100% defoliation and 24% of the trees with 86-95% defoliation (Table 1).

Although the mortality rate was similar between heavily and moderately defoliated plots, the progression of mortality was quite different. In the heavily defoliated plots, all of the trees that died were already in very poor condition or dead by 1993. In the moderately defoliated plots, no trees died until 1997, and all trees that had been in very poor condition in 1993 had improved by 1995. However, two of the moderately defoliated plots were logged in 1996. Mortality subsequently occurred in these plots.

Based on the management recommendations made during the outbreak, twenty-one of the plot trees would have been predicted to be "likely to die", because they had complete defoliation of older needles and over 80% defoliation of current needles. Of these, eight had died by 1999, and thirteen were still alive. By contrast, four of the 129 trees which were not considered "likely to die" also died. All four

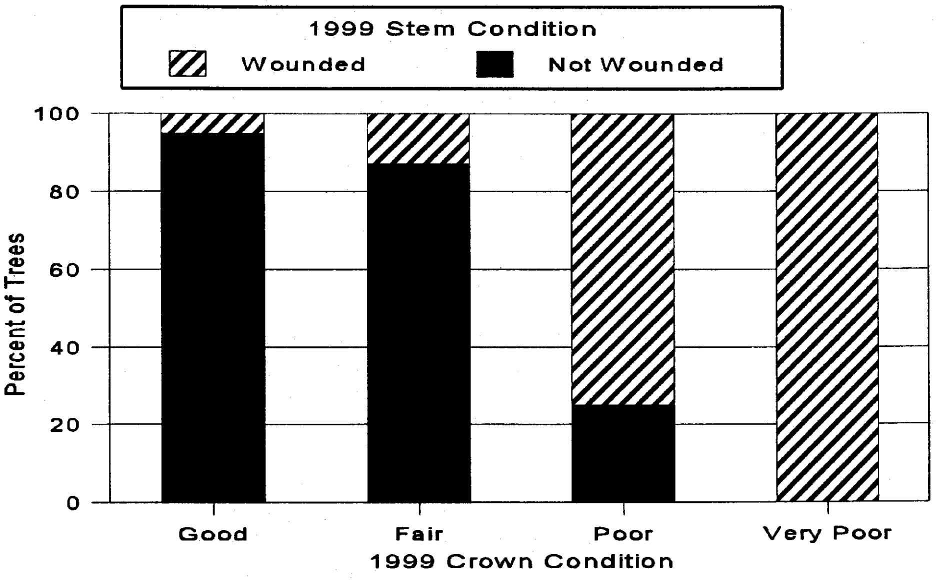

Figure 2.—Percent of hemlocks, in 1999, with and without wounds to the stem or root collar, by crown condition. Data are from fifteen spring hemlock looper impact monitoring plots, with 113 trees in good condition, 18 in fair condition, 5 in poor condition, and 2 in very poor condition.

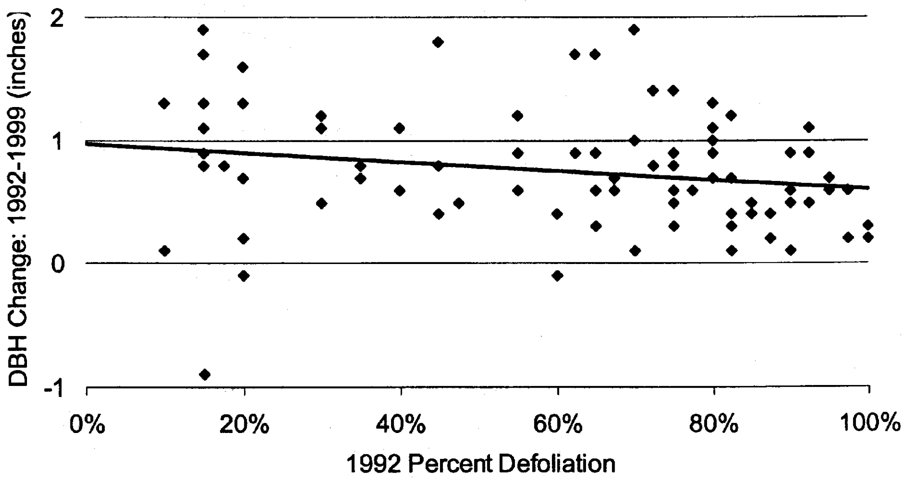

Figure 3.—Change in diameter at breast height between 1992 and 1999, by severity of hemlock looper defoliation in 1991, as measured in spring 1992. Data are from 138 surviving hemlocks in fifteen monitoring plots.

had large root or stem injuries sustained before or during the study.

The presence of stem or basal wounding was related to crown condition in all plots, including those with light defoliation. Only four of the ten trees which had wounds in 1999 were rated in good condition. Four of the five trees rated as poor or very poor had wounds (Figure 2). Exit holes from hemlock borer were not observed on plot trees.

The most severe symptom on surviving trees was a bare top. In 1992, 61% of the trees in heavily defoliated plots and 30% of the trees in moderately defoliated plots had bare tops. Trees with bare tops averaged 80% defoliation, compared to 52% defoliation of trees whose tops were still alive. Of the sixty trees which had bare tops in 1992, nine died over the next seven years. Among the 51 survivors, however, bare tops were no longer visible on 37 (73%) of them by 1999.

Between 1992 and 1999, heavily defoliated trees generally grew less in diameter than lightly defoliated trees (Figure 3), but the relationship was not significant. Diameter growth averaged 0.91" in lightly defoliated plots, 0.75" in moderately defoliated plots, and 0.73" in heavily defoliated plots.

Discussion

Most trees survived spring hemlock looper defoliation. Even trees with severe defoliation were more likely to survive than trees with a similar level of defoliation by gypsy moth. Spring hemlock looper may cause less mortality because its damage occurs late in the growing season, when most carbohydrate production has already taken place. Gypsy moth defoliation peaks in early summer.

Mortality generally occurred within two years of defoliation. Because mortality occurs rapidly, stand assessment two years after defoliation can provide an accurate picture of expected mortality, as long as no additional disturbance occurs. However, partial cutting to salvage dead and dying trees at this time may result in further mortality. Stress from defoliation, hemlock's vulnerability to post-logging decadence, and, possibly, shoestring root rot, may each contribute to these additional losses.

In most of the plots, any role of "secondary" organisms appears to be, in fact, secondary. If shoestring root rot had played an important role, mortality would be expected to build up over several years as the fungus increased within infection centers. This may yet happen in plots which were subsequently logged. Hemlock borer activity was not observed. However, in stands where this insect is active, higher rates of mortality would be expected.

Wounds affected recovery. Wounds existing prior to defoliation or wounds created afterwards were more common on unhealthy trees. Unwounded trees were more likely to survive. Since wounding and exposure often happen simultaneously, for instance during logging, the association between wounds and health may be caused by the wound itself or by the impact of exposure.

The importance of site factors were not specifically evaluated. Nonetheless, these results reinforce previous observations that hemlocks on shallow, drought-prone sites are at greater risk. The shallow roots on these sites would be more vulnerable to wounding and to disturbance, both of which were linked to mortality.

The risk rating system used in 1992 overestimated mortality, but the categories of risk were consistent with observations from this study. Over 60% of the trees considered "likely to die" survived. However, mortality among trees in this category was more common than mortality among other trees. All of the trees which died had at least 50% defoliation, and so were considered "at risk" according to the 1992 system. Three categories of risk are suggested by these results: <50% defoliation (mortality not expected), 50-80% (light risk of mortality), and 90-100% (moderate risk of mortality).

Many surviving trees had dead tops, although new leaders developed over time. Stands with dead tops had healthy, dense foliage eight years after defoliation occurred. In areas where hemlock retention is the goal, dead tops should have little impact on wildlife cover or other values. Where timber production is important, however, dead tops can lead to ring shake or decay, leading to loss of volume. Plans to salvage trees with dead tops should be tempered by concern for the additional impact of disturbance on residual trees.

Diameter growth of heavily defoliated trees was insignificantly slower than lightly defoliated trees. Even defoliated trees grew in diameter over the seven years of the study. However, there was considerable variability in growth, and many trees were growing slowly. More precise diameter measurements or analysis of wood increment growth may have revealed a more important relationship. As crowns continue to recover, the rate of diameter growth should be expected to recover as well.

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Impacts of Hemlock Woolly Adelgid—The Effects on Tree Health and Mortality Probability

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The hemlock woolly adelgid (*Adelges tsugae* Annand) (HWA) was first found on the eastern hemlock (*Tsuga canadensis* (L.) Carriere) in the early 1950s and has been recognized as a significant pest of eastern hemlock since the mid-1980s. In September 1994, the study *Monitoring the impacts of hemlock woolly adelgid on hemlock*, was initiated by the Northeastern Area, Forest Health Protection in Morgantown. The purpose of the study was to evaluate HWA impacts on trees and stands; identify site and stand characteristics that make hemlock more susceptible to attack or vulnerable to mortality; identify other pests that may be compounding observed impacts; determine rates of tree mortality; and determine if hemlock are able to survive or recover from a HWA infestation. Here, we report the current status and describe the future direction of this study. Data have been collected each year since 1993; the database now contains 6,935 observations from 145 10-tree plots in 29 sites over the 4 study areas. At each plot, the average slope, aspect, soil type (4 categories), moisture regime (3 categories), elevation, stand density (3 categories), and stand composition (one 10-BAF prism plot) have been recorded. Ten trees per plot were permanently tagged for revisiting annually; DBH and crown position was recorded. Five variables were used to decide the health of plot tree crowns each year: diameter (widest and at right angles to widest), ratio, density, dieback, and foliage transparency. Defoliation, tree vigor, and any other damage and causal agent notations also were recorded. The plot system does an excellent job of capturing the variation among these measures across hemlock in the eastern United States. A plot-wide assessment of HWA was made using non-destructive sampling of ten 12-inch branch tips per plot, each from a different tree. Samples consisted of (1) the number of terminals present before new growth, (2) the number of terminals producing new growth, and (3) the proportion of terminals infested with HWA. From a regression of the proportion of terminals infested with adelgid against the proportion of terminals that produce new growth, we found a highly significant and rational relationship, but this relationship only explained 1.64% of the total variation. Very few plots have become infested with HWA. We have established a revised sampling plan using variance estimates derived from our area-site-plot system to optimize our chances to capture the impacts of HWA. Initial results from these revised data collection procedures were presented.

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Relationships of Eastern Hemlock (*Tsuga canadensis*) to the Ecology of Small Streams in Delaware Water Gap National Recreation Area

David P. Lemarie[1], *John A. Young*[1], *Craig D. Snyder*[1], *Robert M. Ross*[2], *David R. Smith*[1], *and Randy M. Bennett*[2]

Abstract

Hemlock ravines in Delaware Water Gap National Recreation Area (DEWA) are highly valued because of their distinctive aesthetic, recreational and ecological qualities. We conducted a comparative study designed to determine the potential long-term consequences to aquatic communities of the suspected transition from hemlock-dominated forests to mixed hardwood forests as a result of hemlock woolly adelgid (HWA; *Adelges tsugae*) induced mortality. A landscape analysis of DEWA using Geographic Information Systems (GIS) was used to select 14 hemlock and hardwood site-pairs that were similar in topography (i.e., slope, terrain shape, aspect, light levels) and stream size (first or second order) but differed in forest composition. This paired watershed approach provided a powerful means to discern the influence of hemlock forests on stream communities. This study was designed to provide an aquatic perspective on potential losses of biological diversity should hemlock forests die.

Streams draining hemlock forests supported more aquatic invertebrate species than streams draining hardwood forests. Fifteen of the 184 invertebrate taxa collected were strongly associated with hemlock, three of which were found only in streams draining hemlock. The trophic composition of aquatic invertebrate communities also was different between forest types, suggesting that ecosystem function also may be disrupted by changes in forest composition. Additionally, streams draining hemlock forests had a higher proportion of predators and lower proportion of grazing invertebrates than corresponding hardwood forests. Similarly, fish trophic structure differed, with streams draining hemlock supporting a significantly larger number of predators. In contrast, fish diversity and abundance were higher in streams draining hardwood forests although brook trout was more common in streams draining hemlock. Habitat data collected concurrently suggests hemlock modifies the stream environment by creating a larger variety of microhabitat types and/or a more stable thermal and hydrologic regime. Based on these results, we predict a significant decline in average within-site and park-wide diversity should widespread hemlock mortality result from the HWA infestation.

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Recognizing All-aged Hemlock Forests

Orie L. Loucks[1] *and James Nighswander*[2]

Abstract

Eastern hemlock (*Tsuga canadensis* (L.) Carr.) occurs in old-growth stands sometimes over 400 years old, throughout its principal range from Nova Scotia to Wisconsin. Studies based on aging as well as diameter distributions indicate a stand structure often dominated by an initial multi-decade post-disturbance pulse of seedling establishment, followed after a century or more by one or more subsequent pulses of seedlings and saplings. Over 400 years these new stems tend to produce a truly all-aged forest. The seedling and sapling layers are eliminated when white-tailed deer populations exceed 3 to 4 per km^2 (12-15/sq. mile), and entire stands are lost periodically to wind storms and accidental fires. Management for this old growth type requires two major components: control of deer populations, and maintenance of a mosaic of developmental age classes so that, if the oldest stand is lost, mid-aged younger stands in the area are poised to replace it.

Introduction

Local conclusions vary widely as to whether differences in the structure of eastern hemlock (*Tsuga canadensis* (L.) Carr.) stands should be attributed to this species interactions with regional patterns of climate and soil. The alternative view is that differences in hemlock old-growth are attributable largely to non-climatic influences such as fire, wind-storms and deer browse. The goal of this paper is to summarize evidence from Nova Scotia, central Ontario and Wisconsin indicating that, across this range at 45° north latitude, great similarities exist in eastern hemlock stands when they are free of the external forcings that affect juvenile age-classes. The results indicate an all-aged structure develops regardless of climatic conditions.

Throughout its range, large stands of hemlock have been established within a few decades after new habitat is created by fire or wind events, as long as a seed source remains. Following such disturbances, seed trees often are local, commonly along a steep slope or water course. On the other hand, our results indicate that juvenile age-class establishment may be eliminated over long periods if white-tailed deer populations exceed 3 to 4 individuals per sq. Km.(12 - 15/sq. mi.). Investigations of hemlock in regions from Nova Scotia to Wisconsin have had to use reference all-aged stands as well as younger, relatively even-aged post disturbance stands to distinguish the various agents that have structured hemlock forests, one way or another in the past. In locations where wildlife browsing influences have not been present, all three regions have developed a fully all-aged stand structure with some trees over 400 years old.

Approach

Comparative information has been obtained on eastern hemlock stand structure by investigators working near its moisture deficient western limit (in Wisconsin), in Central Ontario, and in a per-humid environment in Nova Scotia, all at or close to 45° north latitude. Some of the data have been drawn from a long series of studies by the senior author and his graduate students and colleagues (Anderson and Loucks 1979, Loucks 1962, Goff 1967, and Hett and Loucks 1976), and by a colleague working in Nova Scotia (Drinkwater 1952).

Results

Data from the Flambeau Forest in Central Wisconsin (Anderson and Loucks 1979) show the effects of deer browsing on hemlock stand structure (Figure 1, a). A reference site in Menominee County (b) shows that when year-round hunting by native Americans kept white-tailed deer populations low, the seedling and sapling populations of eastern hemlock (solid circles) are high. Triangles are the numbers of all species in these size classes. In the Flambeau Forest, with abundant deer, no saplings and only a very few seedlings were present. In the 12-year-old Flambeau Forest deer exclosures (c), hemlock seedling numbers were restored fully to the level expected in an all-aged forest, while two of four plots in a large four-year old fenced area (d-g), show preliminary recovery of seedlings and a few saplings. The latter are stems released from almost complete needle browse.

When hemlock seedlings are found in the Flambeau, they show direct effects of intensive deer browsing, sometimes combined with leaf litter and snow depression of young stems. Seedling success is improved on logs or stumps (in the absence of deer browsing), because the potentially smothering leaves are blown off these microhabitats.

Another study (Hett and Loucks 1976) undertook tree-ring counts for all hemlock stems found on plots established in two Wisconsin and two central Ontario old-growth stands, Figure 2. When examined in detail, the distribution of hemlock stem numbers, by age-class, is not different between the Wisconsin sites (Gardner Dam, a, and West Branch, b), and the Central Ontario sites (Northwest Lake, c, and Pot Lake, d), just south of Algonquin Park (From Hett and Loucks 1976). The negative exponential model (log number of stems over age) was applied to the data, aggregated in ten-year age classes, but a modest sine wave was added. The filled circles are the observed averages and the open circles are the points estimated by the negative exponential sine wave equation.

The West Branch stand in Wisconsin (see b in Figures 1 and 2) has trees up to 350 years of age (Hett and Loucks 1976). A single large white pine stump with a discarded log was

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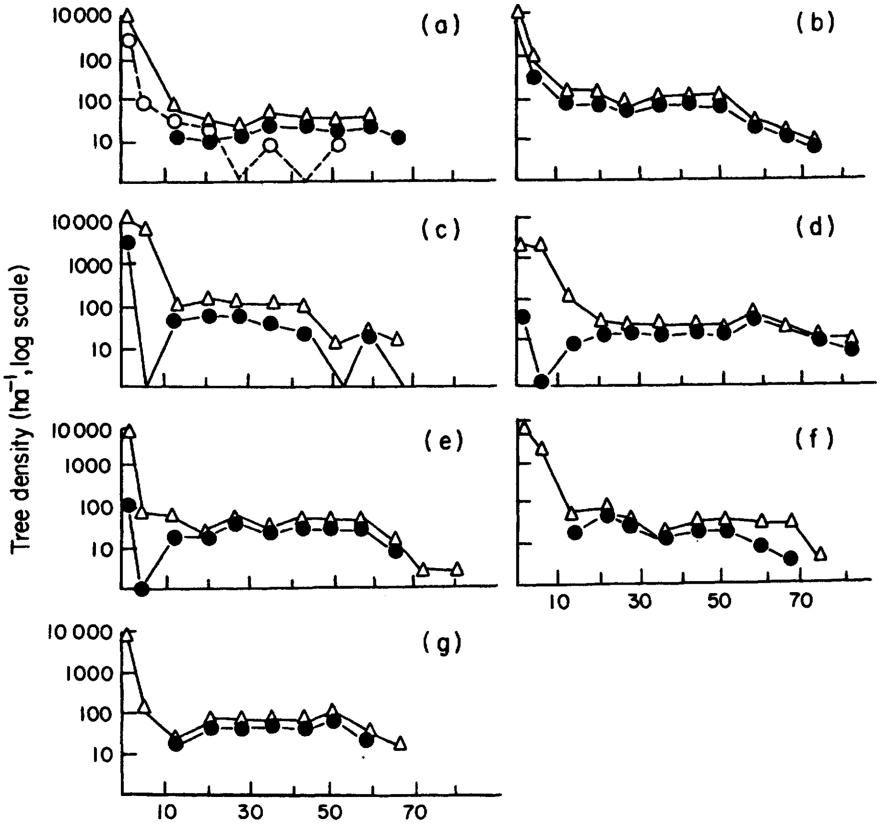

Figure 1.—The relationship between $\log_{10}$ number of stems (ha^{-1}) and stem diameter (cm) for hemlock (closed circle), sugar maple (open circle) and all trees (triangle) for a series of study sites in Wisconsin. Most of the Flambeau Forest (a) has lost the seedling layer, in contrast to a control area in Menominee County (b), areas exclosed in 1961 (c), and exclosed in 1969 (d-g). For clarity, sugar maple is shown for only stand (a), though this relationship is similar to that in other stands in the Flambeau area.

present, and a ring count indicated the stand was of fire origin 475 years prior to the 1967 study. Other younger stands in the area were also of fire origin (Goff 1967), comprised of white pine 300 years old with an understory of hemlock 200 to 280 years old. At the Ontario sites, subsequent studies by the Lamont Doherty Geophysical Laboratory found many individual hemlocks over 400 years old.

The results of an analysis using the residuals (departures as log number of stems) from a power function model for the four hemlock stands show the same sinusoidal patterns (Hett and Loucks 1976). The results in Figures 1 and 2 show that eastern hemlock abundance-age distributions generally conform to the "Type II" distribution expected for plants, that is, a negative exponential decline in numbers, or a gradual straight-line decline in the log of number of stems by age class (Schmelz and Lindsey 1965). Some long-term variation, or pulses, in initial seedling success obviously are present. The sinusoidal variation in input (Figures 2 and 3) has been interpreted by Hett and Loucks (1976) as an auto-induced effect from the intense shading under the early hemlock sapling and pole-sized age classes, followed by opening of the understory as the canopy matures, increasing seedling numbers and sapling success.

For Nova Scotia, data on hemlock stand structure are available from the work of M. H. Drinkwater (1952). He established 30 plots in an old-growth stand on an island in Jordan Lake, Queens County, Nova Scotia. The results showed hemlock to be the dominant species in every size-class from seedlings to the large over-story trees (Table 1). The only significant competitor species is red spruce (*Picea rubens* Sarg.), which Drinkwater concluded could become more important as a future stand develops.

The age of this stand (200 to 300 years) was estimated from tree-ring counts of freshly cut stumps in a nearby clearcut. A majority of the harvested trees were between 200 and 250 years old, indicating that the stand originated after a disturbance (possibly a hurricane) between 250 and 300 years prior to the study. Although few trees were lost in 90 mph winds in 1950, many other hemlock stands were severely decimated in west-central Nova Scotia by hurricane "Edna" in September 1954. Nevertheless, the distribution of stems shown in Table 1 indicates a transition from a relatively long-term pulsed origin of the stand, through a period of limited new stem establishment, into the recent period of a more fully all-aged distribution, similar to the stands in Ontario and Wisconsin.

Discussion

Although many present-day old-growth hemlock stands appear to have originated under pine, birch and aspen following fire (see Loucks 1962 and Goff 1967), devastating windstorms can also have led to the initial several-decade pulse of hemlock seedling establishment. These origins are inferred partly because of the history of devastating storms recorded throughout the range of hemlock (hurricanes in the

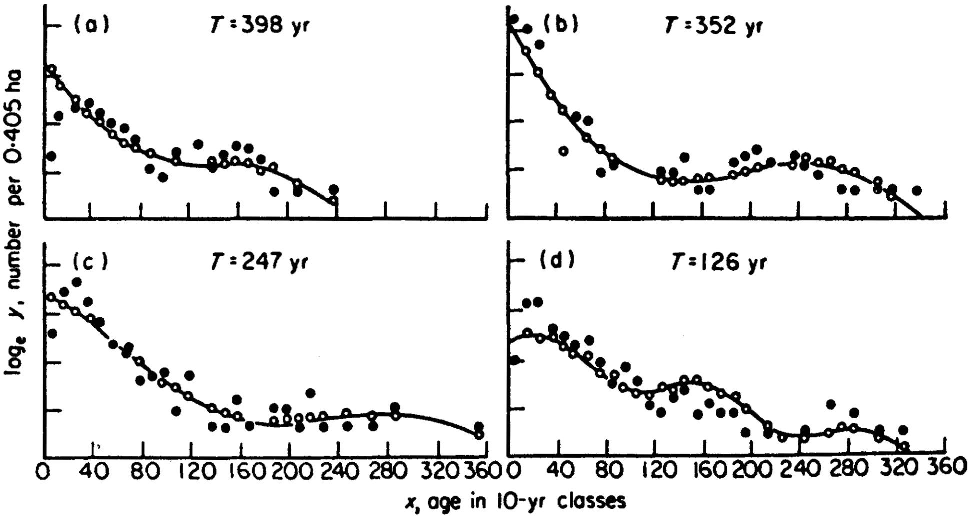

Figure 2.—Application of a negative exponential sine wave analysis using ten-year age classes for four hemlock stands: (a) Gardner Dam stand, (b) Wet Branch stand, (c) Pot Lake stand and (d) Northwest Lake stand. *T* = length of sine wave. The filled circles are the observed averages and the open circles are those points estimated by the sine wave equation.

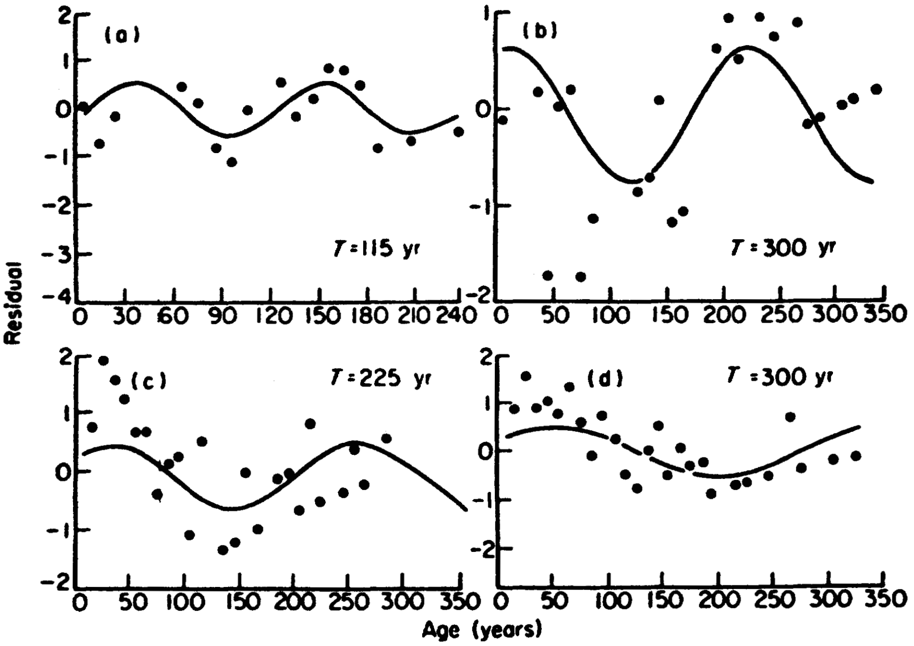

Figure 3.—The results of a sine wave analysis using the residuals from the power function model for the four hemlock stands with a linear age axis: (a) Gardner Dam stand, (b) West Branch stand, (c) Pot Lake stand and (d) Northwest Lake stand. *T* = length of sine wave.

east and thunderstorm downbursts or tornadoes in the central and west), and partly because of the early surveyor records (especially in Wisconsin) showing many miles of blown down forests, some of which now have regenerated to hemlock under intolerant hardwoods. Given the frequency of these naturally occurring events, management for hemlock old growth must ensure that younger stands are maintained in age classes designed to replace the present old growth, should a disaster strike.

For example, the consequences of a downburst storm for old-growth hemlock in Wisconsin is described by Canham and Loucks (1984). This report concerns a storm that struck the 360-acre Flambeau Forest studied by Anderson and Loucks (1979) on July 4, 1977 with winds of over 250 m.p.h., bringing down 100% of the stand in just a few minutes. Remeasurement of the former plots proved impossible because the tangle of trees on top one another was impenetrable and former woods roads and deer fences

Table 1.—Size-class distribution in a 200 to 300-year stand of Eastern Hemlock and Red Spruce, Pitman Point (Jordan Lake) Nova Scotia, 1950 (After Drinkwater 1952).

Size Class	Hemlock	Red Spruce	Other Conifers	Hardwoods
Seedling to 0.5"*	1,533	350	151*	550*
1-3"	21	104		
4-6"	15	16		
7-9"	12	9		
10-12"	17	2		
13-15"	25	2		
16-18"	28			
19-21"	22			
22-24"	9			
25-27"	5			
28" +	2			

* Data available only for the "seedling to 0.5-inch" size class.

could not be relocated even to provide a local landmark. Using the data on extent of blowdown observed by early surveyors, largely from 1840 to 1860, Canham and Loucks were able to calculate the return time for catastrophic windthrow in this region to be 1,210 years, just three times the life span of the trees. As noted above, fires also occur in this region, and for the zonal soils commonly dominated by hemlock, the return time for fire also is believed to be about 1000 years.. The presence of both types of disturbances shortens even further the average natural interval during which truly all-aged hemlock stands could have developed.

The processes described in the previous sections also are influenced by wind-induced single-tree patch openings within mature canopies, allowing some seedling and sapling establishment throughout the 30 to 40 decades of stand development. The data presented by Drinkwater (1952), and by Hett and Loucks (1976) suggest that development of the initial, relatively even-aged young hemlock stand leads to a long period of low reproductive success, followed by quite high success. Both of these responses in stand structure can be seen as part of the shadow cast by the initiating stand onto stand structure up to 3 or 4 centuries later. Although the pulse pattern being seen at the present time is interesting, it may be temporary, i.e., in later years, in the absence of a relatively even-aged overstory, there may no longer be any long-term period of low seeding or sapling establishment. The more important finding, however, is that hemlock stands are all-aged across a broad geographic area, in the absence of wildlife impacts.

These results also indicate that the most important steps in "managing" old-growth hemlock stands are of two kinds: (1) removal of the risks to regeneration that can be controlled, particularly the high levels of deer browsing that are found in some regions; and (2) provision of an area-wide pattern of age-class states so that mid-aged hemlock stands under pine or intolerant hardwoods can develop into old growth if catastrophic events destroy present day stands.

Conclusions

Given the differences in climate east to west along a gradient at 45° N. latitude from Nova Scotia through Central Ontario to Wisconsin, mature eastern hemlock stands have surprisingly similar stand structure in the absence of intensive deer browsing. Successional dynamics following fire or wind storms also is similar across this range (see Loucks 1962, Zedler and Goff 1973, and Canham and Loucks 1984).

The principal differences along the gradient are in the composition of the competing tree species. These include red spruce, balsam fir and occasionally beech in Nova Scotia, mainly sugar maple, yellow birch and some beech in central Ontario; and sugar maple with yellow birch and no beech in central Wisconsin. Young hemlock stands often establish under pine or intolerant hardwoods following fire, but hemlock is not a fire-tolerant species (Loucks 1962). The autecological and competitive adaptations of hemlock appear to be similar across its east to west range, consistent with its relatively homogeneous genetic makeup. Therefore, management for old-growth hemlock should be framed at a landscape level in which multiple, mid-aged stands are allowed to develop toward the old growth structure, recognizing that catastrophe loss of old growth can happen.

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Comparative Biology of Three *Scymnus* Lady Beetles (Coleoptera: Coccinellidae): Predators of *Adelges tsugae* (Homoptera: Adelgidae)

Wenhua Lu[1] *and Michael E. Montgomery*[2]

Abstract

Scymnus (Neopullus) sinuanodulus Yu et Yao, *S. (N.) camptodromus* Yu et Liu, and *Scymnus (Neopullus)* n. sp. (in press[3]) were collected in the People's Republic of China from hemlocks infested with the hemlock woolly adelgid, *Adelges tsugae* Annand. To date, 3 of the 14 provinces in China where hemlock occurs naturally have been surveyed; *S. sinuanodulus* was found in Yunnan, *Scymnus* n. sp. was found in Shaanxi, and *S. camptodromus* was found in Yunnan and Sichuan. The three lady beetles were imported from 1996 to 1998 to the USDA Forest Service Quarantine Laboratory in Ansonia, Connecticut, for evaluation as biological controls of *A. tsugae*. This report discusses the development, oviposition, and feeding behavior of the three species.

Development of immature stages of all three species was compared at 20°C. Eggs of *S. sinuanodulus* and *Scymnus* n. sp. hatched 8 to 10 days after being laid. Eggs of *S. camptodromus* hatched only after they had been held for two or more months at room temperature, followed by a month or more at cold temperature, and then returned to room temperature. Larval development of *S. sinuanodulus* and *S. camptodromus* was completed in 20 days. Larval development of *Scymnus* n. sp. was 4 days faster. All three species spent 8 to 10 days in the pupal stage. Both larvae and adults fed on all stages of *A. tsugae*, but all three species grew best if the egg stage was available. Mortality of first instars was very high unless they had adelgid eggs or first instar crawlers as food.

Adults became quiescent at cool temperatures (5°C). We saw no evidence of a true diapause in adults regardless of temperature or photoperiod. Adults became active within a few hours after removal from overwintering conditions; all of *S. sinuanodulus* and *Scymnus* n. sp. fed within 24 hours and laid eggs within 48 hours. It took several days for all of *S. camptodromus* to begin feeding, and egg laying and oviposition did not occur during the first 2 weeks. The oviposition rate of *S. sinuanodulus* and *Scymnus* n. sp. was much higher during the first 4 weeks if adelgid eggs rather than only nymphs were the food source. Oviposition by *S. sinuanodulus* and *Scymnus* n. sp. was similar, lasting for 12-22 weeks, with peaks around 4 and 14 weeks. Oviposition of *S. camptodromus* started later and continued at a lower weekly rate to the end of summer.

All species have been reared through at least one complete generation in the laboratory and *S. sinuanodulus* has been reared for 3 generations. Adults of *S. sinuanodulus* have lived for 3 years in the laboratory.

Scymnus sinuanodulus occurs in a more northern area of China with lower winter and higher summer temperatures. The climate in the native habitat of *S. sinuanodulus* is more like the southern Appalachians, while the climate of *Scymnus* n. sp. is more like southern New England. Although they differ in oviposition behavior and egg development, the eggs of all 3 species likely hatch when hemlock woolly adelgid eggs are at peak abundance.

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[3] Described as *Scymnus (Neopullus) ningshanensis* Yu et Yao new species in: Yu, G.; Montgomery, M. E.; Yao, D. (in press). **Lady beetles (Coleoptera: Coccinellidae) from Chinese hemlocks infested with the hemlock woolly adelgid, *Adelges tsugae* Annand (Homoptera: Adelgidae).** Coleopterists Bulletin.

Use of Multi-date Landsat TM Imagery to Map Eastern Hemlock (*Tsuga canadensis*) Decline Due to Hemlock Woolly Adelgid (*Adelges tsugae*) in Shenandoah National Park

David D. Morton, John A. Young, and Nissa M. Thomsen[1]

Hemlock woolly adelgid (HWA) was first observed in Shenandoah National Park (SNP) in the mid-1980s. Since then, this exotic insect has expanded its range throughout the park. Most stands were heavily defoliated within several years of infestation. However, several hemlock stands appear to be not affected or only moderately affected to the present date. To investigate this discrepancy in hemlock stand condition, we are analyzing satellite imagery from 1984, 1988-9, 1991-2, 1994, and 1997.

The first step is to map the initial extent of hemlock stands, using the earliest available imagery (1984). This map is crucial because it will act as a "mask", defining the extent for future analyses. We are combining topographic factors, such as relative phenology, slope, northness (aspect), and landform index, with spectral reflectance from Landsat Thematic Mapper (TM) imagery to delineate hemlock from other coniferous forests.

Next, a vegetation index, calculated from TM data, will be used to display hemlock health for each time period. Differences in health from year to year will be quantified. The rate and intensity of defoliation will be analyzed spatially.

The final analysis will result in a hemlock vulnerability model based on the relationship of the intensity and rates of defoliation to landscape and stand factors. It is hoped that this model will aid managers in predicting the area and intensity of future HWA caused hemlock damage.

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Long-term Scientific Benefits from Preserving Old-growth Hemlock Stands at Clear Lake Near Minden, Ontario, Canada

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Abstract

Clear Lake is located in the centre of the 1300 ha Clear Lake Conservation Reserve in Haliburton County, Ontario, Canada. In 1988, the reserve was designated as a protected area representing undisturbed, old-growth ecosystems. The reserve includes several headwater lakes and their associated catchments which support old-growth hemlock stands that are estimated to be up to 400 years old. In addition to scientific studies, the reserve is a popular, year-round recreation area. The reserve is visited by organized field trips involving local naturalist groups, outdoor education programs, and the general public interested in ecotourism. Scientifically, Clear Lake has been studied as a relatively unimpacted reference ecosystem since 1967. We present time-trend data for water chemistry since 1980, historical fish-stocking records, and post-1987 data on littoral-zone benthic macroinvertebrates and crayfish. Because of recent observations that lakes in south-central Ontario are affected by long-term regional weather patterns, the long-term trends in water chemistry, the benthic macroinvertebrate community, and crayfish relative abundances are also compared to a summary El Nino - Southern Oscillation (ENSO) index. Our data reveal several different patterns of long-term change in water chemistry, benthos and crayfish relative abundances. Gradual changes in some water-chemistry parameters are attributed to recovery from the long-range transport and deposition of airborne acids. Strong relationships with the ENSO index were rare, but data from the last few years may be affected by unauthorized, fish-species introductions in 1994. The reserve, and specifically Clear Lake, represents a good example of how scientific studies, government agencies, and the public can work together to preserve and monitor undisturbed ecosystems for future generations. Unfortunately, gradual changes in reference ecosystems are inevitable given the broad geographic scale of anthropogenic activities.

Introduction

In 1988 the provincial government recognised the Clear Lake Conservation Reserve as a protected area supporting old-growth hemlock stands in Haliburton County, in south-central Ontario, Canada. The 1300 ha reserve includes a series of small headwater lakes, their catchments, and unique stands of hemlock that are estimated to be up to 400 years old. The reserve has been protected to ensure that this type of ecosystem is available for public education and recreational use, and scientific study. Traditional activities such as fishing, hunting, and fur trapping are permitted, but logging, mining, hydro-electric development, and other industrial uses are not allowed.

Clear Lake, the largest lake near the center of the reserve, is a 88.4 ha lake with a catchment of approximately 125 ha. This lake has been the focus of scientific studies since 1967 (Schindler and Nighswander 1970). Originally this small, softwater lake was selected as a relatively unimpacted reference lake for monitoring eutrophication impacts that often follow shoreline development associated with building recreational cottages (e.g., see Dillon and Rigler 1975, Dillon et al. 1986, 1994). Despite a modest increase in the number of cottages on Clear Lake, gradual changes in the water chemistry have been observed. Some of these historical changes can be attributed to the long-range transport of airborne acids originating far beyond the reserve boundaries (e.g., LaZerte and Dillon 1984). Recently, climate change has been implicated as a factor contributing to changes in the water chemistry of inland lakes (Dillon et al. 1997, Schindler 1998).

In addition to the scientific studies, Clear Lake is used throughout the year by organized field trips involving naturalist groups, outdoor education programs, and members of the general public interested in ecotourism. The old-growth hemlock stands and the relatively undisturbed lakes and wetlands provide a unique recreational experience. However, there are growing concerns that the ecosystem embodied by the Clear Lake Conservation Reserve is gradually changing. This paper examines: (1) time-trend data on the water chemistry of Clear Lake; and (2), bioassessment data using nearshore benthic macroinvertebrates and crayfish, to search for evidence of long-term changes in this reference ecosystem. Our analyses suggest that broad-scale, regional stressors such as acid deposition and climate change, as well as local stressors associated with the unplanned introduction of predatory fish are contributing to the observed changes in Clear Lake.

Methods

Clear Lake is a small headwater lake located in Sherborne Township, in the County of Haliburton (latitude 45° 11' N, longitude 78° 43' W), roughly 250 km northeast of Toronto, Ontario (Figure 1). The lake is on the Precambrian Shield which is characterized by noncalcareous bedrock, thin soils, numerous lakes and wetlands (Jeffries and Snyder 1983). The annual precipitation averages 900 mm/yr with snow representing approximately 200 mm of this total (Schindler and Nighswander 1970). The July mean temperature is 18 C, whereas the January mean temperature is -10 C.

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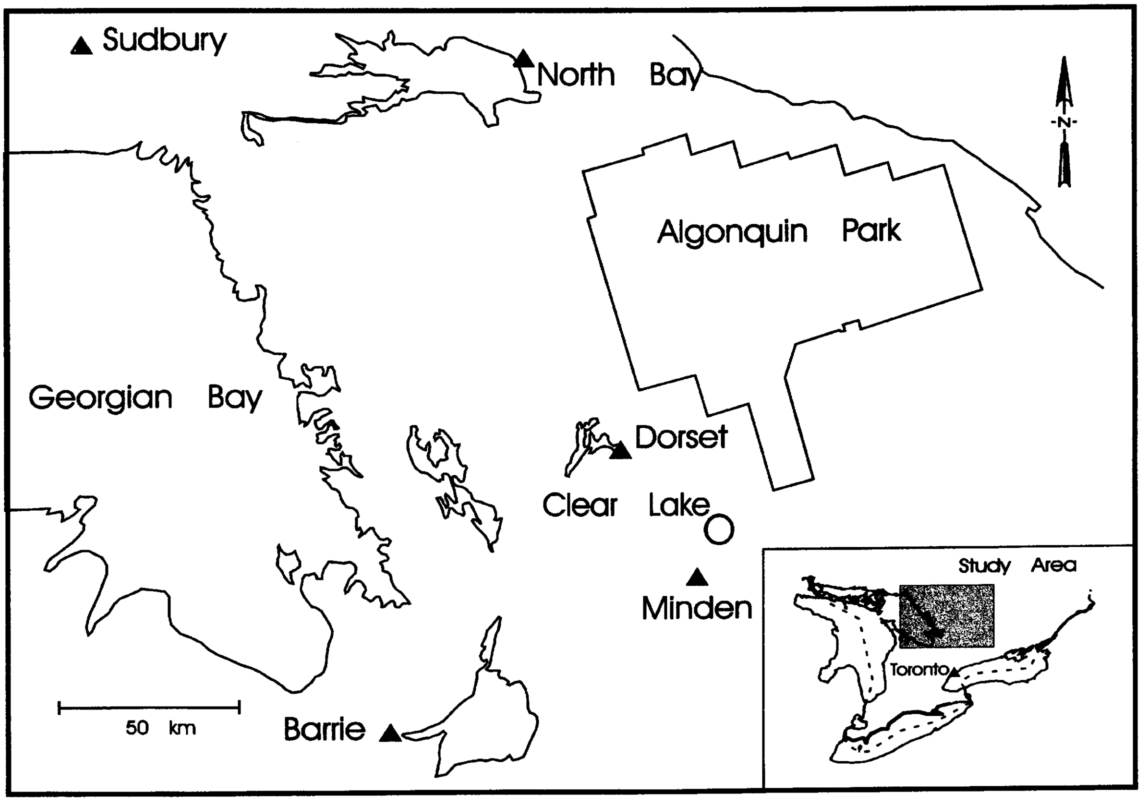

Figure 1.—Location of the Clear Lake Conservation Reserve in south-central Ontario.

Clear Lake is 88.4 ha in surface area, with a maximum depth of 33 m and a mean depth of 12.4 m (Girard and Reid 1990). The lake lies at an elevation of 369 m ASL. Gunn et al. (1988) found the following fish species in the lake during a mid-1980s inventory: lake trout (*Salvelinus namaycush*), white sucker (*Catostomus commersoni*), northern redbelly dace (*Phoxinus eos*), lake chub (*Couesius plumbeus*), common shiner (*Notropis cornutus*), bluntnose minnow (*Pimephales notatus*), fathead minnow (*P. promelas*), blacknose dace (*Rhinichthys atratulus*), creek chub (*Semotilus atromaculatus*), pearl dace (*S. margarita*), pumpkinseed sunfish (*Lepomis gibbosus*), and yellow perch (*Perca flavescens*). The fish community represented by this set of species is characteristic of softwater lakes in this part of south-central Ontario (Gunn et al. 1988, Jackson 1988). The large number of minnow species suggests minimal human disturbance and an absence of introduced predators that is consistent with the results of a regional-scale survey of lakes in the northeastern United States (Whittier et al. 1997).

Water Chemistry - Interest in the water chemistry of Clear Lake began in 1967 (Schindler and Nighswander 1970). The data reported in this study were collected using a standard sampling protocol from 1980 through 1998 (Girard and Reid 1990). However, no samples were collected in 1995, 1996 or 1997. The frequency of sampling over the ice-free period varied over the years, but water samples were always collected at a station located over the deepest spot in the lake. Once the water samples were collected they were kept in a cooler in the field, and then they were refrigerated at the analytical lab. Nineteen water-chemistry parameters were determined using standard analytical methods (Anonymous 1983) in a chemistry laboratory. These parameters included: total inflection-point alkalinity (ALK), pH, dissolved inorganic carbon (DIC), dissolved organic carbon (DOC), conductivity (COND), calcium, sodium, potassium, magnesium, chloride, sulphate, ammonium, nitrate, total Kjeldahl nitrogen (TKN), total phosphorus (TP), aluminum, iron, manganese, and silica. Nine of these parameters were measured in mg/L. pH was measured in standard units and COND was measured in µS/cm at 25° C. The remaining parameters were measured in µg/L.

Benthic Macroinvertebrates - Regional surveys of benthic macroinvertebrate communities in lakes in Ontario have revealed that differences in the benthic communities are correlated with differences in lake water chemistry (Harvey and McArdle 1986, Stephenson et al. 1994). Many of the small lakes in south-central Ontario have been historically impacted by acid deposition (LaZerte and Dillon 1984, Dillon et al. 1997). The littoral areas of these lakes often experience lower pH values relative to mid-lake regions in the early spring (Gunn and Keller 1985). Because water-quality data alone do not adequately characterize the health of aquatic ecosystems (Karr 1993), we initiated a monitoring program to collect littoral-zone benthic macroinvertebrates from a series of acid-sensitive, headwater lakes in 1988 (Reid et al. 1997). Clear Lake was one of these lakes.

Samples of shallow-water sediments (<1 m) were collected at 5 sites around the lake in late September, October, or early November (see Reid et al. [1997] for a complete description of the field and laboratory protocols). The 5 sites were randomly selected in a stratified design based on the predominant nearshore substrates (Reid et al. 1995). If 60% of the nearshore substrates were sandy with macrophytes, then 3 of the 5 sites were randomly selected from areas with predominantly sandy sediments and macrophytes.

Each of the 5 sites was sampled for a period of 10 minutes. An individual with a D-frame, 250 µm-mesh, long-handled net walked out to a depth of approximtely 1 m, turned towards shore and slowly walked towards the shore, kicking the bottom to dislodge the sediments and associated invertebrates. While the sediments were in the water column, the net was swept back and forth in order to collect the disturbed material. Periodically the sediments in the net were shaken into a large pail to prevent the net from clogging with debris. After 10 minutes the pail was sealed and labelled. Once all 5 samples were collected, the pails were returned to the laboratory and refrigerated. Within 36 hours of the field collection, all samples were rinsed over a 1000 µm sieve, sorted and the macroinvertebrates were removed.

Over the 5 years from 1988 to 1992, each sample was sorted in its entirety and the resultant animals were identified to the lowest practical taxonomic level (e.g., some immature insects cannot be identified to the species level unless the adult form is available; Reid et al. 1997). Benthic macroinvertebrates in Clear Lake were not sampled in 1993 or 1994. However, Clear Lake was re-sampled in 1995 and again in 1998. In these last two years, the same field sampling protocol was used and the same 5 sites were sampled, but a rapid bioassessment protocol was used to sort and enumerate the samples (David et al. 1998). Instead of picking all of the animals from a given sample, each sample was randomly subsampled and only 100 animals were removed (Somers et al. 1998). These animals were identified to a relatively coarse taxonomic level such as order or family.

To provide comparable data over the period of this study, the total counts of the various taxa at the 5 sites were summarized into a single, whole-lake total for a given year using the following 14 taxonomic groups: Amphipoda, Coleoptera, Diptera - Ceratopogonidae, Diptera - Chironomidae, Ephemeroptera, Gastropoda, Hirudinea, Lepidoptera, Megaloptera, Odonata - Anisoptera, Odonata - Zygoptera, Oligochaeta, Pelecypoda, and Trichoptera. The individual totals for a given taxonomic group were converted to simple proportions of the total count for a given year. Four additional taxonomic groups were included in the lake total, but were excluded from subsequent data analysis because they were only found in three-or-fewer years (i.e., Decapoda, Hemiptera, Hydracarina, and Plecoptera).

Crayfish - In addition to the monitoring program for littoral benthic macroinvertebrates, we also initiated a program in 1988 to monitor crayfish populations in a series of south-central Ontario lakes under the assumption that changes in crayfish relative abundances would reflect anticipated improvements in water quality (David et al. 1994). A related study using the same sampling protocols collected crayfish from 100 lakes in south-central Ontario between 1989 and 1994 (David et al. 1997). That study concluded that an unusually large proportion of the lakes in the vicinity of Dorset (i.e., within 15 km of Clear Lake, see Figure 1) did not support crayfish populations. Although there are no historical data on crayfish populations in most of these lakes, France and Collins (1993) present data from Plastic Lake (which is less than 8 km directly west of Clear Lake) documenting the disappearance of crayfish during a period in the 1980s when Plastic Lake gradually acidified (Dillon et al. 1987). Although the water chemistry of many of the Dorset-area lakes has improved (Dillon et al. 1997), recovery of the crayfish populations has not been observed (David et al. 1994).

Crayfish were captured with baited, wire-mesh, minnow traps with the funnel entrances enlarged to 3.5 cm to accommodate large crayfish (Collins et al. 1983). Three sites representing (1) rocky or cobble areas, (2) silt and sand with macrophytes, and (3) detritus-covered sediments with woody debris were selected to span the range of habitats commonly used by the different crayfish species in Ontario (Crocker and Barr 1968). At each site a series of traplines consisting of six traps were set perpendicular to shore. The traps were at least three m apart along a given trapline, and the traplines were set at least three m apart within a site. Traps were only set for a single night in July or August of a given year. In 1988, the first year of the study, 180 traps were set. This number was reduced to 60 in 1989, and to 18 in 1990. Thereafter, a total of 54 traps was used each year. Because of this variation in trapping effort over the first three years, all crayfish catches are expressed as the total number of crayfish caught per trap per night (i.e., as catch per unit effort, or CPUE).

Each trap was baited with fish-flavoured, canned cat food that was placed in a perforated plastic film (35 mm) canister. A single canister was placed in each trap. Similar baits were used each year because different baits attract different species and different sizes of crayfish (Somers and Stechey 1986). Traps were set at depths ranging from <1 m to > 6m and left in place from the afternoon of one day to the morning of the next. Crayfish were sampled during their midsummer intermoult period which is the best time of the year to estimate crayfish relative abundance (Capelli and Magnuson 1983). Trap catches exhibit minimal seasonal variation at this time of the year (Somers and Green 1993).

Statistical Analysis - The 3 sampling programs produced single numbers for a given parameter in a given year. Time trends in the water-chemistry data were assessed with simple, least-squares regressions between a given concentration and the year of collection. Those variables with significant, non-zero slopes were flagged as an indication that the Clear Lake ecosystem was changing over time ($P<0.05$). Time trends in the 12 benthic invertebrate indices and the crayfish CPUEs were evaluated in a similar

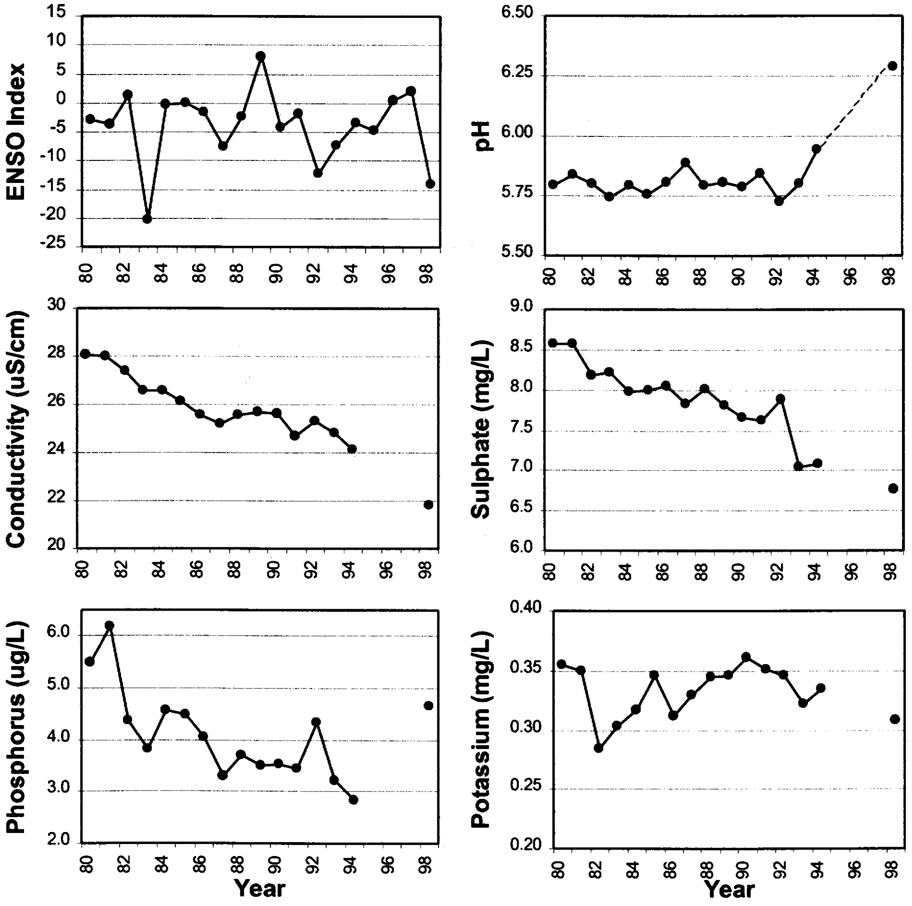

Figure 2.—Temporal trends in the ENSO index and 5 water-chemistry parameters from 1980 through 1998.

manner for the period 1988-98. Simple Pearson product-moment correlations between the benthos and crayfish data, and the water chemistry were assessed for those years where matching data were available. Significant correlations between biological and chemical parameters may reveal interactions that are not linearly related to the year of sampling. Because of the relatively small number of data points, nonparametric Spearman rank correlations (r_s) were also calculated and assessed for significance. In addition, Pearson and Spearman coefficients were compared to determine if outliers (i.e., $r > r_s$) or curvilinear relationships (i.e., $r < r_s$) affected the Pearson correlations.

Because of growing interest in the impacts of climate change on inland lakes (Dillon et al. 1997, Schindler 1998), we also correlated the various water chemistry and biological parameters with an El Nino - Southern Oscillation (ENSO) index which presumably reflects yearly changes in global weather patterns. This index was proposed by Rusak et al. (1999) as the sum of the standardized monthly sea-level air pressure differences between Darwin, Australia and Tahiti spanning the six-month period from October to March. Because a climate-change signal may require some period of time to cascade through the various trophic levels of a lake, we also evaluated correlations between the ENSO index and the various chemical and biological parameters with lags of one and two years. To obtain the lag-one correlation, the observed ENSO index for a given year was paired with the Clear Lake data for the following year. The lag-two correlation was calculated by shifting the Clear Lake data by two years.

Results and Discussion

Water Chemistry - Time trends in midlake water chemistry varied considerably (Figure 2), although only the gradual increase in pH produced a positive Pearson correlation that was statistically significant ($r=0.584$, $P<0.05$). By contrast, 7 of the 19 chemical parameters produced strong negative time-trend correlations that were significant (i.e., COND, Ca, SO_4, TP, Fe, Mn, and Si). Our comparison of Pearson and Spearman correlations indicated that both coefficients generally provided similar results. Only pH and ALK produced Pearson correlations that were noticeably different (larger) than the Spearman correlations suggesting that the data for 1998 might represent an influential outlier (see Figure 2). The remaining chemical parameters varied over time (e.g., see K in Figure 2), but no long-term trends were evident. The ENSO index revealed a similar degree of variation over time.

Of the Pearson correlations between all-possible pairs of the 19 water-chemistry parameters, 22.8% were statistically significant ($P<0.05$). Almost 80% of these significant

Table 1. —Pearson correlations between the benthic taxa and sampling year, the ENSO index, and ENSO lags of 1 and 2 years.

Taxonomic group	Sampling year	ENSO index	ENSO lag 1	ENSO lag 2
Amphipoda	-0.082	0.306	0.397	-0.907
Coleoptera	0.087	-0.527	-0.156	-0.093
Diptera - Ceratopogonidae	-0.186	-0.035	-0.561	0.721
Diptera - Chironomidae	-0.654	0.306	-0.199	0.571
Ephemeroptera	-0.045	0.262	-0.481	0.453
Gastropoda	-0.051	-0.069	0.849	0.364
Hirudinea	0.344	-0.120	-0.225	-0.447
Lepidoptera	-0.338	0.801	-0.409	-0.617
Megaloptera	-0.389	0.160	-0.652	-0.379
Odonata - Anisoptera	0.800	-0.305	-0.042	-0.275
Odonata - Zygoptera	0.482	-0.488	0.226	0.152
Oligochaeta	0.255	-0.549	-0.354	0.038
Pelecypoda	0.487	-0.823	0.556	0.176
Trichoptera	0.813	-0.275	0.089	-0.310
Cambarus bartoni	-0.353	0.438	0.438	-0.239
Orconectes propinquus	-0.674	0.258	-0.081	0.357

correlations were positive indicating strong temporal coherence (or synchrony, see Rusak et al. 1999) among many of the parameters. In all cases, the significant negative correlations involved pH, ALK or NH_4 indicating that the positive temporal trends in these 3 parameters differed markedly from the long-term declines in the other parameters. In several instances, significant positive correlations were obtained between parameters that showed no long-term temporal trends. These parameters included K, Na, Cl, NO_3, TKN, and Al.

The Spearman rank correlation analysis confirmed our findings, with 19% of all-possible rank correlations being significant ($P<0.05$). Apparently one-or-more outliers may have undue influence on the Pearson correlations because we found fewer significant rank correlations compared to the Pearson analyses. From the time-trend plots (Figure 2), the data for 1998 are suspect, but additional data are required because water-chemistry samples were not collected between 1995-7. Almost 91% of the significant Spearman correlations were positive, emphasizing strong concordance among many of the parameters. The significant negative rank correlations involved pH or NH_4, but not ALK, suggesting that the rank-order trend for ALK was weaker than the trend observed in the raw data.

Only one of the Pearson correlations between the 19 water-chemistry parameters and the ENSO index was significant (Mg, $r=0.576$, $P<0.05$), and none of the rank correlations was significant. When the water chemistry was shifted by lags of one and two years, none of the Pearson or Spearman correlations with the ENSO index was significant. These results suggest that annual weather-related events embodied by the ENSO index did not significantly influence the observed variation in Clear Lake water chemistry.

Benthic Macroinvertebrates - Because the biological data were collected over a shorter time frame than the water-chemistry data, we required larger correlations for statistical significance (i.e., 7 versus 16 years). Of the 12 benthic macroinvertebrate indices, only two revealed significant changes over time (Table 1). Both dragonflies (Odonata, Anisoptera) and caddisflies (Trichoptera) increased in relative abundance between 1988 and 1998 (Figure 3). Clams (Pelecypoda), damselflies (Odonata, Zygoptera), and leeches (Hirudinea) also increased in relative abundance, whereas chironomids (Diptera, Chironomidae) declined over the same time period (Figure 3), but not significantly. The corresponding Spearman rank correlations were generally lower than the Pearson correlations (and not significant) suggesting that one-or-more outliers affected the Pearson results. From the time-trend plots, the data for 1995 and 1998 are potential outliers underscoring the possibility of recent changes in the littoral benthic community.

Only 5 Pearson correlations between all-possible pairs of the 12 benthic indices were significant ($P<0.05$). Negative correlations between the chironomids versus the dragonflies

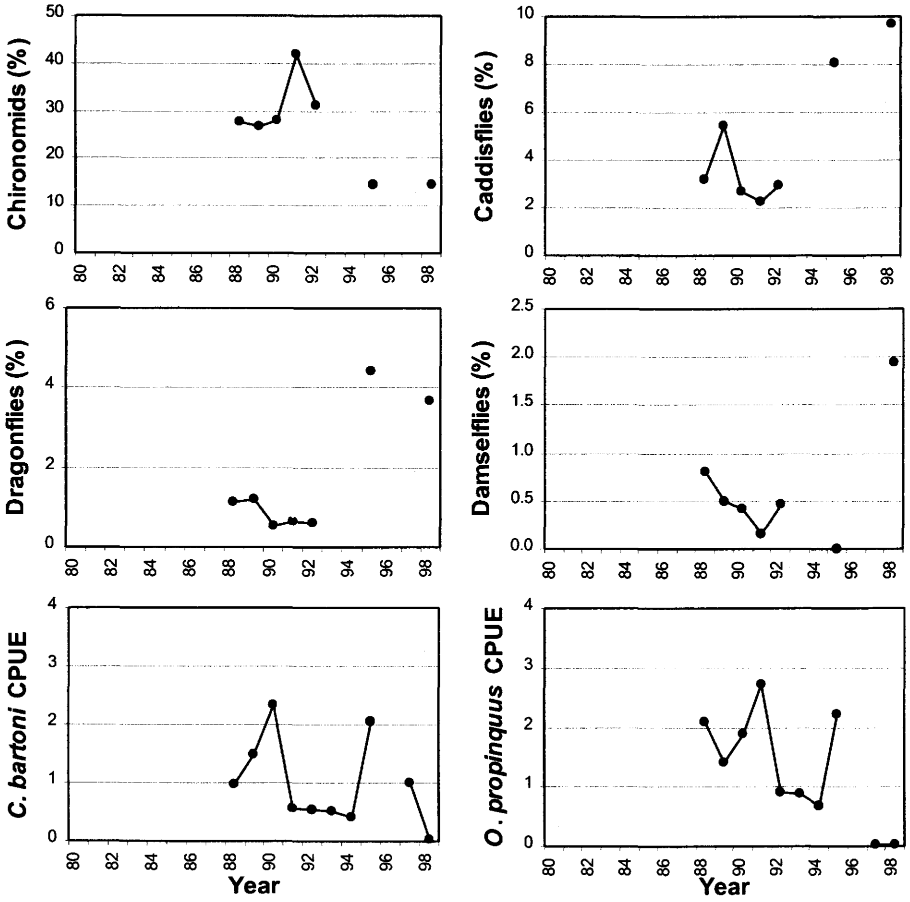

Figure 3.—Temporal trends in 4 benthic macroinvertebrate groups and the trap catches of two crayfish species from 1988 to 1998. Marked changes are apparent after the unauthorized introduction of bass predators (*Micropterus* spp.) in 1994.

and caddisflies, and a positive correlation between the dragonflies and caddisflies simply reflected the significant time trends in these 3 taxonomic groups (Figure 3). Significant negative correlations between the relative abundances of beetles and amphipods (Coleoptera versus Amphipoda), and clams (Pelecypoda) and aquatic Lepidopterans may simply be chance relationships, given the large number of correlations that were calculated. These same relationships were also statistically significant when Spearman rank correlations were used, suggesting that outlying values did not have undue influence on these estimates. By contrast, a significant negative rank correlation between the relative abundances of snails (Gastropoda) and alderflies (Megaloptera) revealed a curvilinear relationship because the Pearson correlation was not significant (i.e., $r_s > r$).

Lepidopteran relative abundance exhibited a significant positive correlation with the ENSO index ($r=0.801$, Table 1), whereas clam relative abundance was negatively correlated with the index ($r=-0.823$, $P<0.05$). These opposing trends undoubtedly contributed to the significant negative correlation observed between these two taxa ($r=-0.789$), and suggests that this significant correlation may not simply be an artifact of examining a large number of correlations. The corresponding rank correlations with the ENSO index were both weaker ($r_s=0.744$ and -0.639, respectively) and not significant indicating that the Pearson correlations were influenced by one-or-more unusual years (i.e., 1995, and to a lesser degree 1998). Only the relative abundance of snails ($r=0.849$) was significantly correlated with the lag-one ENSO index (Table 1), whereas the amphipods were significantly correlated with the lag-two index ($r=-0.907$). The rank lag-one correlation for the snails was not significant ($r_s=0.598$), but the rank correlation for the lag-two index and amphipod relative abundance was significant ($r_s=-0.805$).

Most of the correlations between the 12 benthic macroinvertebrate groups and the 19 water-chemistry variables were not significant (Table 2). Only the dragonflies, damselflies and caddisflies produced more significant correlations with the water-chemistry parameters than might be expected by chance. Surprisingly, most of the significant correlations were negative, suggesting that the increases in the relative abundances of these 3 taxa over time (Figure 3) coincided with decreases in the concentrations of parameters like SO_4 or COND (Figure 2). The significant positive correlations involved ALK and pH, but some of the highest negative correlations involved K, Cl (but not Na), and Mn despite the fact that K and Cl were not correlated with sampling year or the ENSO index and its lags.

Crayfish - The trapping data spanned 1988 through 1998 with the exception of 1996 when crayfish were not sampled.

Table 2. —Summary of the Pearson correlations between the benthic taxa and the 19 water-chemistry parameters.

Taxonomic group	Positive Values (P<0.05)		Negative Values (P<0.05)	
	Number	%	Number	%
Amphipoda	0	0.00	0	0.00
Coleoptera	1	0.05	0	0.00
Diptera - Ceratopogonidae	0	0.00	0	0.00
Diptera - Chironomidae	0	0.00	0	0.00
Ephemeroptera	0	0.00	0	0.00
Gastropoda	1	0.05	0	0.00
Hirudinea	1	0.05	0	0.00
Lepidoptera	1	0.05	0	0.00
Megaloptera	0	0.00	1	0.05
Odonata - Anisoptera	2	0.11	5	0.26
Odonata - Zygoptera	2	0.11	4	0.21
Oligochaeta	0	0.00	0	0.00
Pelecypoda	1	0.05	2	0.11
Trichoptera	2	0.11	6	0.32
Cambarus bartoni	4	0.21	0	0.00
Orconectes propinquus	3	0.16	0	0.00

Two crayfish species were captured in the traps, *Cambarus bartoni* and *Orconectes propinquus*. Both of these species are common in lakes in south-central Ontario (David et al. 1997), although *C. bartoni* was reported to have disappeared from nearby Plastic Lake in the 1980s (France and Collins 1993).

Trap catches of both crayfish species declined over the 11 years (Figure 3). The Pearson correlation between *C. bartoni* CPUE and sampling year was not significant (Table 1). The Spearman correlation provided a similar value (r_s=-0.402) suggesting that outliers or curvilinear trends were not present. By contrast, the CPUE of *O. propinquus* was significantly correlated with sampling year (Table 1). As with *C. bartoni*, outliers or a curvilinear trend were not indicated by the Spearman correlation (r_s=-0.671, r=-0.675). Despite similar downward trends (Figure 3), the catches of the two species were not significantly correlated. Closer examination of the time-trend plots indicates that the catch of *C. bartoni* increased over the first 3 years, then precipitously dropped in 1991, and gradually declined through 1994. The catch of *O. propinquus* dropped from 1988 to 1989 and then increased through 1991, only to drop suddenly in 1992, a year after the drop in *C. bartoni* CPUE. After the gradual decline in the CPUE of both species through 1994, the catches were unusually high in 1995, only to drop to their lowest values in 1998. Although there was a weak correlation between *C. bartoni* CPUE and the ENSO index (r=0.438, r_s=0.433), all of the correlations between crayfish CPUEs and the ENSO or ENSO lag values were not significant (Table 1).

The *C. bartoni* CPUE was not significantly correlated with any of the 12 benthic macroinvertebrate indices (P>0.05). By contrast, the catch of *O. propinquus* was significantly negatively correlated with both damselfly (r=-0.811) and clam (r=-0.781) relative abundances. The Spearman rank correlations for these two relationships were somewhat lower than the Pearson correlations (both were r_s=-0.748) and they were not significant suggesting that an outlier contributed to the significant Pearson correlations. Surprisingly the rank correlation between *C. bartoni* CPUE and aquatic beetle (Coleoptera) relative abundance was significant (r_s=-0.788), but this is probably just a chance result given the large number of correlations that were calculated.

Crayfish catches were significantly correlated with several of the 19 water-chemistry parameters (Table 2). The CPUE of *C. bartoni* was positively correlated with DIC (r=0.772), Na (r=0.940), K (r=0.754), and TKN (r=0.712), whereas the CPUE of *O. propinquus* was correlated with K (r=0.785), Fe (r=0.718), and Mn (r=0.747). The rank correlations between the catch of *C. bartoni* and DIC and TKN were not significant, suggesting that outliers contributed to the significant Pearson correlations. However, rank correlations with COND (r_s=0.894) and Mn (r_s=0.757) were significant suggesting a curvilinear relationship between these parameters and *C. bartoni* CPUE. Only the rank correlation of the catch of *O. propinquus* and K (r_s=0.797) was significant, indicating that outliers probably affected the other significant Pearson correlations.

The significant correlations between crayfish CPUE and K are interesting. In a study of crayfish populations in 14 lakes, including Clear Lake, David et al. (1994) observed a decline in crayfish CPUEs between 1988 and 1992 that coincided with a gradual increase in Al concentrations in many of those lakes. However, we found no such correlation with our longer time series (r=-0.122 and -0.091 for *C. bartoni* and *O. propinquus*, respectively). Our results suggest that changes in crayfish relative abundances in Clear Lake are not correlated with Al, but the strong correlations with K suggest that processes within the catchment may be affecting the crayfish. Perhaps the changes in water chemistry require some time to influence crayfish relative abundances. Thus, lag correlations like those used for the ENSO index may provide interesting insights into the role of water chemistry in crayfish population dynamics.

Fish Stocking - Historically, Clear Lake has been stocked with salmonids in order to supplement the sport fishery. From 1932 through 1962, brook trout (*Salvelinus fontinalis*) were stocked in the lake although natural recruitment was never documented. From 1964 to 1970, rainbow trout (*Oncorhynchus mykiss*) were stocked, but again no natural recruitment was observed. As a result, the native population of lake trout was supplemented with stocked fish from 1974 through 1979, although stocking has not continued during the period of this study. However, smallmouth bass (*Micropterus dolomieui*) and largemouth bass (*M. salmoides*) have been found in the lake in the last several years. Apparently these two species were introduced by anglers in approximately 1994 in an attempt to supplement the fishery. Both of these species are predators that impact crayfish populations (Stein 1977, Collins et al. 1983, Somers and Green 1993), as well as minnow assemblages (Whittier et al. 1997). As a result, the pronounced changes in several benthic macroinvertebrate groups and the crayfish populations after 1994 (Figure 3) may simply reflect the introduction and establishment of these two bass species. A follow-up survey of the fish community in Clear Lake would probably reveal changes from the mid-1980s survey, especially among the minnow assemblage. This introduction may also impact lake water chemistry given the well established top-down, cascading effects of predators on food webs and lake productivity (Carpenter et al. 1985).

Summary

Although Clear Lake has been protected as a conservation reserve, time-trend data on water chemistry, benthic macroinvertebrates, and crayfish populations revealed gradual changes in a number of parameters. Some of these changes may be attributed to reductions in acid deposition, and subsequent recovery from the historical effects of acidification (Yan et al. 1996). Climate change, as indicated by an ENSO index, did not correlate with these long-term trends, although climate-change impacts are expected (Dillon et al. 1997, Schindler 1998). The recent introduction of two predatory fish species coincided with marked changes in the benthos and crayfish over the last few years of this study. In combination, the relatively short data record and the recent predator introduction limit our ability to unequivocally distinguish long-term recovery from acidification, from signals associated with climate change.

Despite Clear Lake being a protected reference ecosystem, long-term changes are inevitable (Underwood 1992, Hughes 1995). Continued study will document these changes and provide a better understanding of the consequences of seemingly simple actions like the introduction of sportfish by anglers. Data from long-term monitoring studies of multiple reference ecosystems are required to disentangle the impacts of multiple stressors from natural variation in relatively undisturbed ecosystems (Underwood 1991, White and Walker 1997).

Acknowledgements

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Evaluation of Aestival Diapause in Hemlock Woolly Adelgid

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Abstract

Hemlock woolly adelgid, *Adelges tsugae* Annand (Homoptera: Adelgidae), has two generations/year that feed and reproduce on hemlock, *Tsugae* spp. The spring generation, present from March to June, is called progrediens. The next generation, present from June until the following March, is called sistens (McClure 1987, Gray and Salom 1996). In June, after sistens eggs hatch, they settle at the base of needles and immediately go into an aestival diapause that lasts until October, a duration of 4 months. The occurrence of aestival diapause in HWA sistens is a barrier when trying to continuously rear its predators. *Pseudoscymnus tsugae* Sasaji and McClure (Coleoptera: Coccinellidae), a biological control agent brought in from Japan (Cheah and McClure 1998), do not produce eggs when feeding on diapausing sistens (Bob Chianese, N.J. Dept. of Agric., personal communication). Year-round production of *P. tsugae* could be achieved if we could prevent HWA from going into diapause. The goals of our research were to: 1. determine if diapause in HWA is obligative or facultative and 2. if facultative, determine what conditions are optimal for continuously rearing HWA.

An experiment conducted in 1997 was the first demonstration that aestival diapause in HWA sistens is facultative, with up to 50% of sistens developing without delay at 12°C and a 12L:12D photoperiod. It also provided the first evidence that response by progrediens to environmental cues is necessary for the induction of diapause.

In 1998 experiments at 12°C, molting and development of sistens was delayed under photoperiods shorter than 12L:12D. Molting was not delayed under longer photoperiods, at both 12 and 14.5°C. Therefore, a 12L:12D photoperiod was determined to be a standard for rearing HWA. The necessity of pre-conditioning progrediens was confirmed when "wild sistens" went into diapause for two months. However, the lower temperature of 14.5°C may have shortened the duration of diapause, as it lasted ca. 5 weeks longer at 17°C in the 1997 experiment.

In a 1999 experiment, we showed that by removing 2nd instar progrediens from pre-conditioning conditions of 14.5°C, that diapause can be avoided. This suggests that the lifestages sensitive to diapause inducing cues range from progredien eggs to 2nd instar. We also were able to shorten development time by placing these nymphs at higher temperatures, making the rearing process for HWA more efficient.

Further experiments are planned to try to identify the precise lifestages sensitive to diapause inducing cues. This could help us shorten pre-conditioning period even further.

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The Role of Site Conditions in Survival of Hemlocks Infested with the Hemlock Woolly Adelgid: Amelioration through the Use of Organic Biostimulants

Saroj Sivaramakrishnan and Graeme P. Berlyn[1]

Abstract

Both greenhouse and field studies have shown that it is the combined stress of drought and infestation by the hemlock woolly adelgid that causes death in eastern hemlocks,. In three separate greenhouse studies it was found that the presence of adelgids alone did not cause the death of the plants over a period of 1, 2 or 5 years respectively, if they were well watered and received sufficient nutrients. Another greenhouse study found that drought hastened the death of infested hemlock seedlings. This was reflected in the rapid fall in the rate of chlorophyll fluorescence. In this study the effect of the adelgids alone was not sufficient to cause the death of the seedlings, however the added stress of drought did result in the death of the seedlings, within a period of a few weeks.

In the field, ring widths were reduced in infested trees growing on a ridge-top site, as opposed to a well-watered moist site. The results of the seedling studies are consistent with field observations that suggest hemlocks growing outside their optimal range are more susceptible to death when infested with adelgids. Also trees on ridge top sites especially with SouthWest exposures are more susceptible than trees in riparian zones.

Organic biostimulants have been shown to ameliorate the effects of adelgid feeding on eastern hemlock seedlings. These compounds are essentially, a stress vitamin-mix for plants and work particularly well on plants under water stress. Cell wall thickness, needle and cuticle thickness and ring widths in infested seedlings treated with organic biostimulants were significantly higher than infested controls.

Introduction

Seedling studies were conducted on eastern hemlock in the Greeley Greenhouse at Yale University, in order to study the following:

1. Feeding effects of hemlock woolly adelgid on seedling growth, health and vigor.
2. The combined effect of water stress and adelgid feeding on seedling physiology.
3. Bio-remedial and bio-pesticidal uses of organic biostimulants

The hypothetical bases of this study are:

a) feeding by the hemlock woolly adelgid increases probability of seedling death.
b) the addition of water stress further increases the chances of tree death.
c) regular supply of water and nutrients helps maintain health and vigor of seedlings and reduces the impact of adelgid feeding.
d) the use of organic biostimulants reduces the negative impacts of the adelgids and drought stress, by reducing insect densities and at the same time increasing tolerance to stress.

Background Information

The hemlock woolly adelgid, *Adelges tsugae* Annand (Homoptera: Adelgidae), is a well-known pest of eastern hemlock *Tsuga canadensis* (L.) (Carr.), in the hemlock-hardwood forests. This adelgid is not native to North America (McClure et al 1996) and effective controls against the spread of this pest have not been achieved. Eastern hemlock is an important component of the northern hardwood forest, and the loss of this species will have a serious impact on the flora and fauna associated with it. Hemlock is a slow growing, shade tolerant species that occupies a niche that few other evergreen species compete for. In a study done by Kelty (1989), on mixed hardwood-hemlock stands to measure productivity, it was found that hemlocks formed a dense understory beneath the hardwood overstory. In hardwood stands not containing hemlock no comparable dense understories of any species was found. The mixed stands were found to have higher yields than the pure hardwood stands, due to the additive effect of the hemlocks Kelty (1989). Although it can grow under a variety of site conditions, in regions where the hemlock grows outside its preferred habitat of relatively moist sites, death is brought about more quickly after infestation by the adelgid.

Organic biostimulants are a product of this laboratory, and are environmentally friendly, non-polluting, growth promoters for plants. These are biologically active compounds consisting of a mix of humic acids, marine algae extracts, B vitamins and two anti-oxidants vitamins C and E (Russo and Berlyn, 1990). Marine algae is a commonly used organic supplement for increasing plant growth and stress resistance (Russo and Berlyn, 1990). The addition of ascorbic acid increases the various growth responses elicited by the organic biostimulant and has resulted in a four-fold increase in leaf chlorophyll content in some cases (Berlyn et al. 1992). This may be due to an increase in cell wall and membrane permeability. The antioxidant vitamin E (alpha-tocopherol) was tested as an anti-herbivory agent in soybean plants against cabbage looper larvae, and was found to decrease herbivory (Neupane and Norris, 1991). Organic biostimulants improve root and shoot growth, increase resistance to stress, and reduce the need for high levels of nitrogen fertilization through increased efficiency of nutrient and water uptake (Russo and Berlyn, 1990). These compounds increase plant growth and vigor. Plant growth stimulants increase resistance to stresses such as low water

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potential and residual levels of certain herbicides and fungicides in soil (Berlyn et al 1993, 1993b).

Chlorophyll Fluorescence: measures the photosynthetic efficiency of photo-system II and can be used as an index of plant stress. As photons strike photo-system II, they elevate electrons in the chlorophyll molecule to a higher orbital. These electrons may return to their ground state via an electron transport system, that transfers energy between photo-systems I and II. However if any of the system components is impaired due to nutrient deficiency, water deprivation or tissue damage, it cannot transfer electrons needed to reduce CO_2 to carbohydrate in the dark reactions of photosynthesis (Kraus and Weis 1991). The un-transferred electrons return to their ground state by emitting fluorescent light. The amount of light harvested by photo-system II that is re-emitted at fluorescent wavelengths indicates the efficiency of the electron transport system between photo-system I and II. This parameter is expressed by the ratio of F_v/F_m. F_v is variable fluorescence or the difference between (F_o) the initial level of fluorescence and (F_m) the maximum level reached during measurement.

Methods and Materials

Two separate seedling studies of the effect of drought and infestation were conducted. In the first study 20 seedlings, approximately 5 years old, were divided into 4 treatments: Drought-Infested, Drought-Uninfested, Watered-Infested, Watered-Uninfested. Chlorophyll Fluorescence was used to measure plant health. Measurements were taken every week for 5 weeks since the start of the drought to determine the combined effects of adelgid feeding and drought stress on eastern hemlock seedlings.

In the second seedling study on the effect of drought and infestation on eastern hemlock seedlings approximately 200 seedlings were divided into the following treatments: Controls, Roots™, and Nitrogen. Of these 100 were infested. A subset of these seedlings was used in a drought study. The remaining 150 seedlings are still alive.

In the third seedling study 100 seedlings were divided into four treatment groups: Controls, Roots™, Control-Infested and Roots™-Infested. This study was run for 2 years. Regular measurements of height and diameter growth were taken. Destructive sampling was done at the end of the study.

The field study was conducted in Connecticut. Ten adelgid-infested and uninfested trees were selected from a ridge-top site and a similar number from an ever-moist site. Trees were cored and ring-widths measured using a microscope and a computerized ring counting program developed by one of the students here.

Results and Discussion

The results of the seedling studies and field study are given in the following graphs, which have self-explanatory sub-titles.

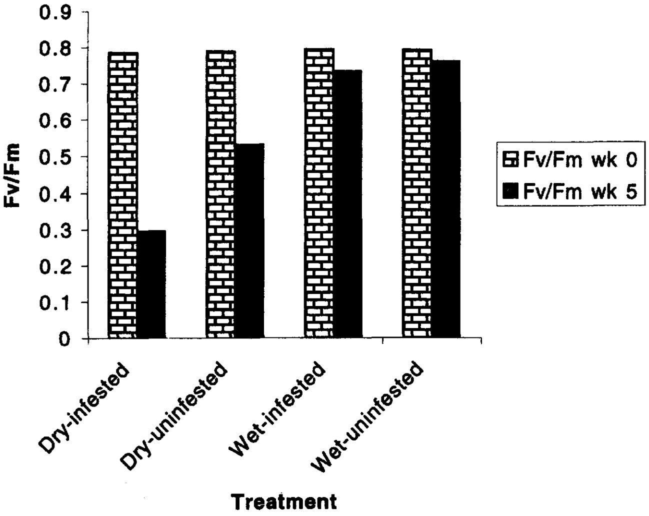

Figure 1.—Comparison of Chlorophyll Fluorescence at start and end of drought experiment.

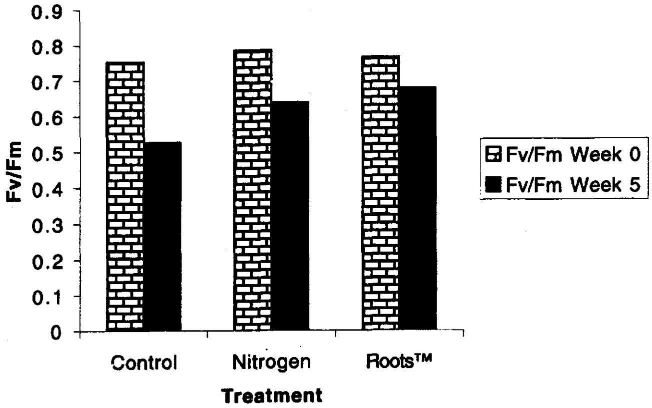

Figure 2.—Effect of Drought and Infestation on Chlorophyll Fluorescence, in seedlings treated with organic biostimulants and Nitrogen.

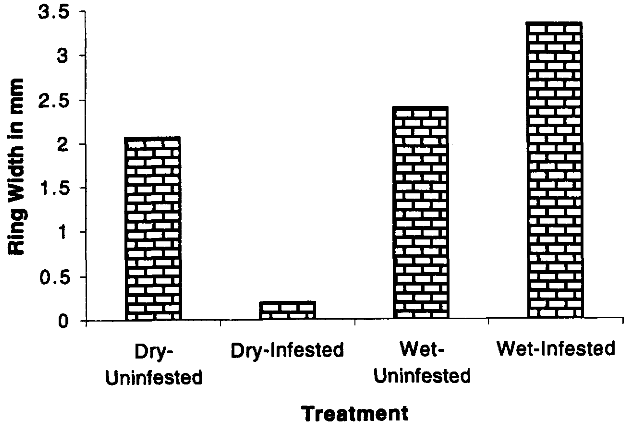

Figure 3.—In field trees, infested hemlocks on dry sites have significantly lower ring widths than uninfested trees on same sites (p<.0001). On wet sites infestation does not reduce ring widths.

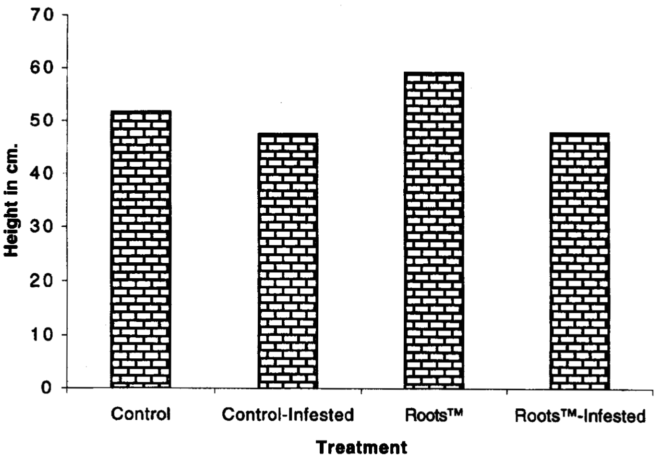

Figure 4a.—Height growth is afffected by adelgid infestation, while organic biostimulants can improve this (p=.01).

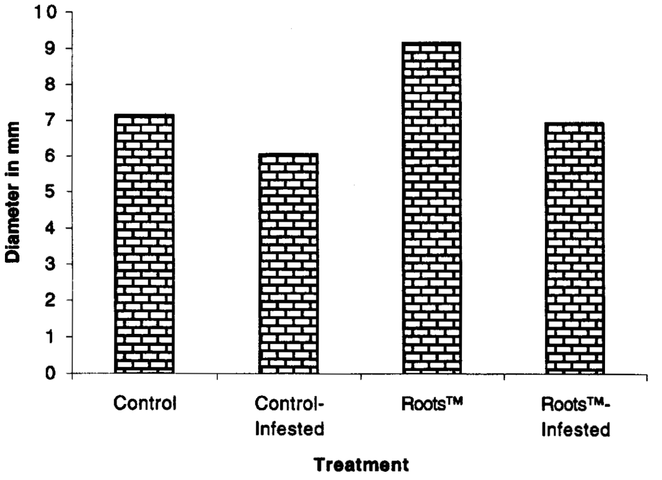

Figure 4 b.—Diameter growth is decreased by adelgid infestation, and increased by using organic biostimulants (p=.0006).

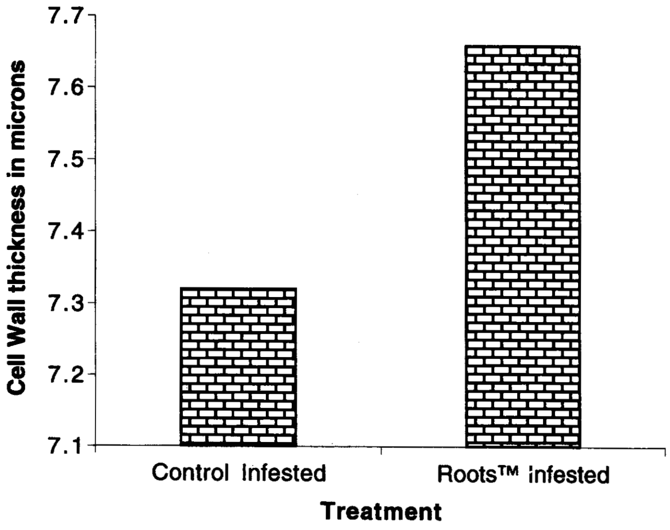

Figure 5.—Treatment with organic biostimulants significantly increases cell wall thickness in infested trees (p<.0001).

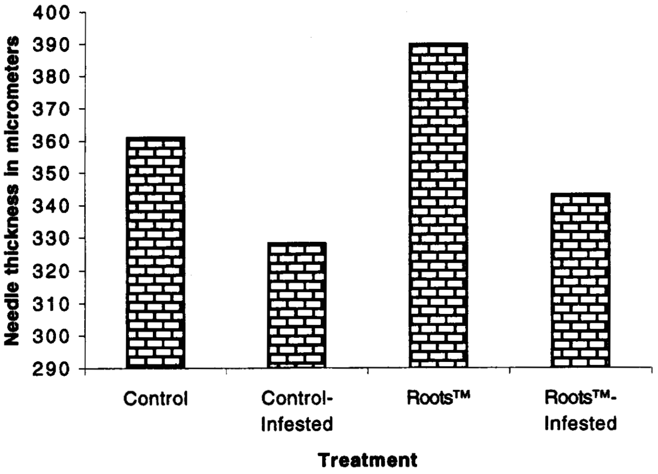

Figure 6.—Needle thickness is significantly reduced by adelgid feeding. Organic biostimulants help to mitigate this (p=.0001).

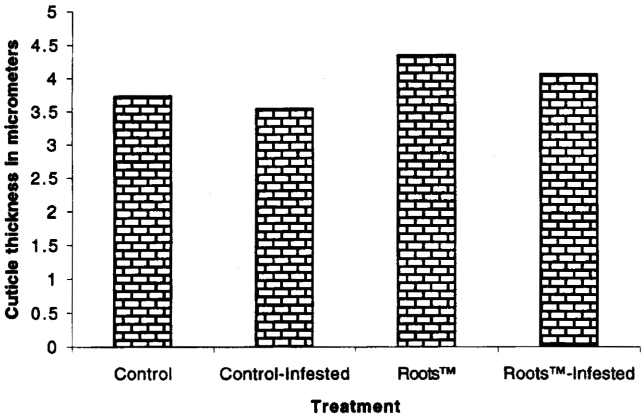

Figure 7.—Adelgid feeding significantly reduces cuticle thickness, but treatment with organic biostimulants alleviates this (p<.0001).

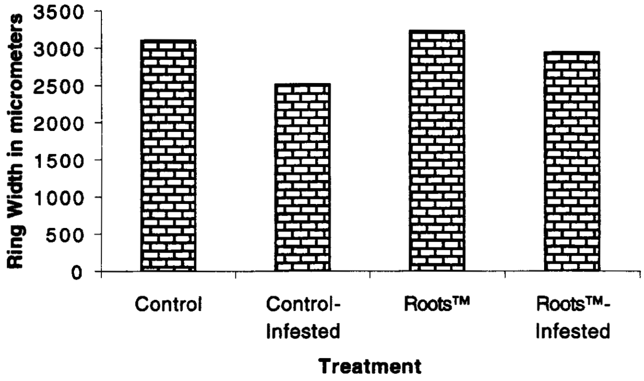

Figure 8.—Adelgid feeding reduces ring widths. Treatment with organic biostimulants reverses this trend (p=.05).

Not shown in the preceding graphs, seedlings that were used in the controlled experimental studies that were not destroyed at the end of the experiments managed to survive into their 5th year, despite heavy infestations. These seedlings are watered regularly and fertilized from time to time. This may be the key to their survival.

Figure 1 refers to the drought study conducted in 1995. Chlorophyll fluorescence is the same for all the plants at the start of the experiment. The graph shows that seedlings subjected to two stresses, water scarcity and adelgid infestation, die by week 5 as witnessed by the rapid fall in chlorophyll fluorescence. The remaining plants subjected to water stress alone, without adelgid infestations, eventually died by week 22 due to lack of water.

Figure 2 refers to the second drought study conducted in 1996, where similar findings were recorded. Death occurred around week 5 in the control-infested group of seedlings. Treatment with mineral nitrogen helped to delay death in infested and droughted seedlings for several weeks. Similarly, it was observed that treatment with the organic biostimulant Roots™ delayed the onset of death in infested seedlings also subjected to drought. The treatment with the organic biostimulant (Roots™) and the Nitrogen appears to have made these plants withstand the dual stress of infestation and drought better.

Figure 3 shows the results of the field study, which confirms the findings of the seedling study that annual growth is not affected significantly by the presence of adelgids alone, on moist sites. The addition of drought to infestation, leads to a significant drop in annual growth. Measurements of ring widths of infested trees are significantly lower in dry sites, in comparison to wet sites (p>.0001).

Figures 4 a and b refer to the seedling study conducted from 1994 to 1996. Height and diameter growth was significantly lowered by the presence of the adelgid. Seedlings treated with the organic biostimulant (Roots™) experienced significantly higher height growth (p =.01) and diameter growth (p=.0006), both in infested and uninfested seedlings.

Other parameters considered when measuring the effect of adelgid feeding were, cell wall, needle and cuticle thicknesses. Figures 5, 6 and 7 refer to these measurements respectively. The results of the study show that all three parameters were significantly lowered by infestation (p<.0001), Treatment with Roots™ caused a significant increase in these parameters, offsetting the negative effects of insect feeding (p<.0001). Figure 8 refers to the effect of ring widths in infested seedlings. Infested controls are the most affected by the adelgids, while Roots™ treated seedlings show the same growth as uninfested seedlings.

Recommendations for management

Eastern hemlocks infested with the Hemlock Woolly Adelgid, growing within their preferred range of ever-moist sites can survive longer than their counterparts on dry sites. Using organic biostimulants will help improve tree health and vigor, leading to increased chances of surviving attack by the hemlock woolly adelgid.

This has implications both for nursery managers and forest health managers. The organic biostimulants improve health and vigor, increase resistance to drought and insects, thereby increasing the chance of survival of seedlings, and improving recovery following insect attack. Use of organic biostimulants reduces fertilizer inputs by upto half, and can reduce pesticide loading in the environment due to the increased resistance observed in biostimulant treated plants.

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Researchers: Bronwen Berlekamp, H. Casey Cordes, Amy McCoy, Claire Thompson and Anne Osborn

Interpretation of Age-structure Gaps in Hemlock (*Tsuga canadensis*) Populations of Algonquin Provincial Park, Ontario, Canada

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Casual observations have suggested that intermediate size and age gaps may exist in the eastern hemlock (*Tsuga canadensis* (L.)Carr.) populations of Algonquin Provincial Park, Ontario. This was confirmed in vegetation surveys reported here. Several hypotheses, involving mortality risks at different points in the life cycle of hemlock, are proposed to explain the age gap. The hypotheses include seed predation (a period of intense seed predation), seedling establishment (a period of environmental or climatic changes limiting seedling establishment), hare browsing (a period of high snowshoe hare populations and intense browsing), ungulate browsing (a period of heavy ungulate browsing limiting hemlock recruitment), stem exclusion (normal stem dynamics), and canopy suppression (long-lived canopy stretching tolerance limits of hemlock seedlings).

Two hundred and sixteen 0.04 ha plots were randomly placed in stands throughout the west side of Algonquin and classified by five factors: three stand types (hemlock dominated, hemlock patch and scattered hemlock sites); two disturbance types (cut and uncut); three aspect types (north, south and knoll); lakeshore versus non-lakeshore (upland) sites; and deeryard versus nondeeryard sites. Within each plot, all stems $\geq$ 5 cm dbh were recorded by species, age, height and diameter; and stumps by species, diameter and year of cut. Data collected on all hemlock seedlings and small saplings < 5 cm dbh included age at ground level, height and percentage of seedling damaged by browsing, and type of browsing (hare or ungulate).

In the main survey, 5,159 stems $\geq$ 5 cm dbh from 25 species and 19,794 hemlock seedlings < 5 cm dbh were measured. A gap was present in the age structure, with a distinct scarcity of hemlock stems between about 40 and 125 years old. The gap was most distinct in deeryard-nonlakeshore plots and least distinct in lakeshore-nondeeryard plots. Past browsing by white-tailed deer (*Odocoileus virginianus* Zimmermann) had limited hemlock recruitment in former deeryard areas while current heavy browsing by moose (*Alces alces* L.) appears to be limiting hemlock recruitment in upland areas and extending the age gap. The latter is suggested by the tagging experiment (17% chance of being browsed if not browsed before, and 34% chance if previously browsed). The browsing hypothesis appears to be the most likely explanation of the hemlock age gap. The age gap also appears to involve older age groups in older stands, suggesting a contributing role of stem exclusion in generating the age gap. There was little support for the canopy suppression hypothesis, as the age gap generally involved ages < 100 years, which is below the limit of shade tolerance for hemlock. There was little evidence in support of the seed predation, hare browsing and seedling establishment hypotheses. Sugar maple (*Acer saccharum* Marsh.) appears to be replacing hemlock, especially in areas with past heavy browsing. A qualitative model is proposed to describe the role of browsing and stem exclusion in the dynamics of hemlock and sugar maple in Algonquin Park.

Implications to management

Managers need to be aware of ungulate population levels in their area and the negative effects they may be having on tree regeneration and recruitment. They also need to be aware of unbalanced age structures in forest stands and how this may affect future wood requirements. If a species such as hemlock has not been recruiting for several decades or more on the landscape level, logging and natural mortality will decrease the abundance of hemlock and change forest composition to dominance by more browse tolerant species, such as sugar maple.

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Winter Water Relations at the Upper Elevational Limits of Hemlock on Mt. Ascutney, Vermont

Chandra B. Vostral and Richard L. Boyce[1]

Abstract

Winter water relations have been monitored in hemlock (*Tsuga canadensis* (L.) Carr.) at their upper elevational limits for three winters, 1997, 1998, and 1999, on Mt. Ascutney, Vermont. Hemlock and white pine trees (*Pinus strobus* L.) reach their elevational limit on Mt. Ascutney at 640 m (2100'), while the summit has an elevation of 960 m (3150'). Relative water contents (RWCs), water potentials, and cuticular conductances were monitored in combination with micrometeorological weather information on both species. These data were incorporated into a winter water relations model which predicts relative water contents based on climate information.

Measured RWCs and water potentials of hemlock fell below those of white pine. Although RWCs were generally above 60%, considered a threshold of desiccation damage for conifers, foliage was damaged in the winter of 1998. Possibly the January ice storm of 1998 damaged and killed a portion of foliage by the end of that winter. Hemlock cuticular conductances were consistently greater than white pine conductivities, most markedly in second year foliage and when damaged. White pine trees did not experience high cuticular conductivities during any winter nor did they lose older foliage from the ice storm. Results from this hemlock study could lend support to the hypothesis that upper elevational limits are determined by winter water relations.

Introduction

Timberline is a prominent vegetation boundary, where woody plants often experience shoot death related to winter desiccation. Drying of conifer needles during winter is considered to be the defining factor for tree distribution at upper elevational limits (Sakai 1970, Wardle 1971, Tranquillini 1979). Excessive water losses occur through the cuticles and bark due to abrasion (Hadley and Smith 1983, Maruta 1996), inadequate cuticle development during short cool summers (Wardle 1971, Hadley and Smith 1986, 1990, 1994), or lack of water availability due to frozen soil or stem tissues (Sakai 1970, 1982). Some timberline species do not experience winter drought (Marchand and Chabot 1978, Cochrane and Slatyer 1988, Grace 1990) and some species experience shoot dieback without winter desiccation (Slatyer 1976, Kincaid and Lyons 1981). Research has often focused on alpine treeline without looking at forces that cause upper elevational limits of trees in general.

Tranquillini (1976) stated that "...probably all evergreen conifers at timberline are subject to marked winter desiccation...the degree of this desiccation increasing with increase in altitude." Challenges to this statement have clearly been made by Cochrane and Slatyer's (1988) work in the Snowy Mountains of Australia, which demonstrated that water potential and RWC did not cause shoot dieback at treeline. Water content and water potential in cembran pine and mountain beech at timberline did not change over the winter, even though mountain beech experienced increased cuticular conductivity (McCracken et al. 1985). Poor cuticular development does not explain treeline in Scotland as Wardle (1971) suggested, rather stomates seem to dysfunction due to mechanical abrasion.

It is important to examine current assumptions of winter damage on low elevational species at their upper elevational limits. Damage caused by factors related to upper elevational limits reduce plant productivity and further limit the geographical range where such species can grow (Sakai, 1970). Knowledge of winter damage and the process of establishing upper elevational limits could lead to the development of new strategies to improve plant drought and freezing tolerances. Discovering the mechanisms that cause damage could be used by forest managers to increase forest productivity and survival when confronted by multiple stresses.

Present understanding of winter drying and subsequent injury in conifers at treeline is derived from empirical studies as well as mathematical models (Sowell et al. 1996, Boyce et al. 1991, Boyce et al. 1992). Empirical studies are intermittently sampled over an entire winter season. Gaps in the season's data can be predicted through modeling. The purpose of this study is to examine desiccation stress of two low elevational conifers at upper elevational limits by utilizing physiological measurements and a winter water relations model (WINWAT). Environmental and plant factors will be identified that affect current assumptions regarding winter water relations at treeline.

Materials and Methods

Study Area

The study site was located at 640-m elevation on the north facing slope of Mt. Ascutney (43°27' N, 72°27'W) in Eastern Vermont. The mountain rises to an elevation of 960 m (3150'). The research site is located along the Brownsville Trail and is accessible only by this hiking trail. The vegetation on the Mt. Ascutney north facing slope changes from predominantly hardwood species at lower elevations to conifers at higher elevations, while the summit is populated by red spruce and balsam fir. White pine extend from 490 to 665 m on Mt. Ascutney while hemlock is found in a wider range of 230 to 650 m elevation (Boyce, 1998). The site's canopy consists of white pine, red pine, red spruce and hemlock trees. The mid-canopy is mostly balsam fir and red spruce trees and the under story is red spruce, balsam fir and hemlock seedlings. Snow cover remained throughout

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the sampling period at depths of 20-40 cm, which dissipated by the end of April.

Microclimate Measurements

A meteorological tower was installed at the site and positioned so instruments measured within the canopy. A 10-m telescoping tower with mounted instruments reaches into the upper half of each mature conifer forest stand. Shielded thermistors (Campbell Scientific) measured air temperature and relative humidity. Cup anemometers (R. M. Young) measured wind speeds greater than 0.2 ms^{-1} and wind direction was measured by a wind vane. Instrumentation also included a soil temperature probe (Campbell Scientific), a pyranometer (Licor) to measure irradiance (%), and leaf wetness sensors (Campbell Scientific). To monitor needle temperature, thermocouples were constructed of 40-gauge (0.0799 mm) copper-constatan loops which were placed on individual needles of well exposed south-facing branches. Four thermocouples were placed on an individual tree, two on first year needles and two on second year needles of white pine and hemlock trees. Hourly measurements were stored on a programmable Campbell Scientific CR-10 data logger as mean, maximum, and minimum values.

Water Relations

From January through April of each winter season over the course of three winters, shoots were removed from four individuals of each species on a weekly basis. Foliage was removed from the same trees throughout the entire study, with the exception of 1 hemlock and 1 white pine tree which were removed from the study in 1999 due to lack of obtainable foliage. Sun exposed shoots were removed using a telescoping pole pruner and kept in sealed plastic bags over ice and in darkness while transported to the laboratory. Measurements were conducted within 6 hours after collection. First and second year shoots were used to determine the relative water content and cuticular conductances of each species. To measure shoot relative water contents, shoots were weighed (w_f) then floated on deionized water for 24 hours at 4 °C in the dark (Koides, 1991). The shoots were blotted dry, reweighed (w_t), and oven dried at 60 °C for three days before weighing again (w_d). Shoot relative water contents were calculated as:

RWC (%) = 100 x $w_f - w_d / w_t - w_d$

Cuticular conductances were determined on a monthly basis for the same shoots that were used to calculate RWC and water potential. Procedures followed those described by (Herrick, 1991) and (Boyce et al. 1991, Boyce et al. 1992). After turgid weights of shoots sampled on those dates had been determined, shoots were placed in a dark chamber at approximately 4 °C and 20% relative humidity. Temperature and relative humidity were monitored and recorded by a temperature and relative humidity probe connected to a CR-10 data logger (Campbell Scientific). The shoots were weighed at approximately 12 hour intervals for 3 days. The shoots were then oven dried and weighed. Foliar surface area was determined from a dry weight-surface area relationship developed for mature trees from this site (R.L. Boyce, unpublished data).

Water potential measurements were made following the procedure developed by Scholander et al. (1965) using a pressure bomb (PMS instruments, Corvallis, Oregon). After stripping off a portion of bark, xylem pressure measurements were made for white pine shoots. It was not necessary to remove bark from the slender hemlock shoots. Measurements were averaged using four water potential measurements per tree and four trees per species.

WINWAT Model

The WINWAT model was used according to procedures developed by Boyce et al. (1992) for red spruce RWCs. Measured meteorological parameters were used to simulate changes in hemlock and white pine first and second year shoot RWCs during the three winters. The single state variable in the model is the water content of an average shoot per unit area. Stomata are assumed to remain closed and shoots are assumed to remain connected to a reservoir of water available in the stem above -4 °C. The rate of loss of water to the atmosphere is driven by: air temperature, needle temperature, relative humidity, and cuticular conductance. Relative water content, recharge, and the vapor density difference between air inside the leaf and outside the boundary layer are auxiliary variables.

Results

Microclimate

Micrometeorological weather information is summarized on Table 1. Usable data were collected in January and February in 1997, December through April in 1998, and December through March in 1999. The warmest winter of the three occurred in 1998 (average temperature of -2.5 °C), probably due to an early spring warming trend which began in March. The coldest temperatures occurred in January of 1999 (-27.6 °C) when the average monthly temperature was -9.7 °C. Soil temperature fluctuated with air temperature within a much smaller range. The warmest soil temperatures were recorded in December of 1999 (1.9 °C). Average monthly soil temperatures were below zero for all other months monitored.

The wind speed and direction sensors were destroyed by the ice storm (1998), and were often frozen during January of 1998. Values from the other three months which data were collected indicate a mean wind speed of 1.1 ms^{-1}, with maximum speeds of 5.3 ms^{-1} (Table 1). The surface of the leaf wetness sensor was often frozen, especially during the ice storm. In this condition, it is not wet, and is a poor indicator of wetness experienced by foliage. However, the relative humidity sensor provided a more reliable indicator of general moisture at the site. The most humid month occurred in January of 1998 (93.8%) which was also the most humid year on average (82.8%). The wettest month of all the winter seasons was January. The least humid month

Table 1.—Summary of micrometeorological infomration collected on Mt. Ascutney. Values are for 24-hour day measurements. Data were collected in January and February in 1997, December through April in 1998, and December through March in 1999.

	White Pine and Hemlock Site				
Parameter	Min.	Max.	Mean	Std. Dev.	n
1997					925
Air T (°C)	-19.0	12.1	-4.5	5.8	
Soil T (°C)	-16.4	4.5	-2.6	2.1	
% Relative humidity	20.7	100	76.1	18.6	
Wind velocity (ms^{-1})	0	5.3	1.2	0.84	
Pyranometer	0	417	10.9	20.3	
1998					2349
Air T (°C)	-22.4	25.2	-2.5	7.1	
Soil T (°C)	-7.1	0.0	-1.0	1.2	
% Relative humidity	19.3	100	82.8	21.0	
Wind velocity (ms^{-1})	0	4.4	0.49	0.06	
Pyranometer	0	579	12.8	24.2	
1999					2782
Air T (°C)	-27.7	17.3	-4.3	7.1	
Soil T (°C)	-2.9	6.5	0.27	1.5	
% Relative humidity	8.74	100	72.2	22.9	
Wind velocity (ms^{-1})	NA				
Pyranometer	0	729	11.7	22.8	

occurred in February of 1999 (64.7%) which also was the most variable of the three winters.

Water Relations

The greatest RWCs were measured in the winter of 1998, when RWCs were often greater than 100% (Figures 1 and 2). The foliage was coated with ice and became supersaturated in transport to the laboratory. The highest RWCs for hemlock (Figure 1) occurred in January of 1998, above 100%, and the lowest average monthly RWC occurred in April of 1998 (81.3%). Over the three winters, foliar RWCs ranged from 30.7% to >100%. Generally, second year foliage have lower RWCs than first year foliage and follow a similar seasonal trend. The winter of 1998 is the most variable year for RWCs in hemlock while 1999 is the least dynamic.

The most variable year for white pine RWCs is 1999 (Figure 2), while both 1997 and 1998 are relatively static. The highest mean monthly RWC occurred in February of 1998 (93.0%) and the lowest in January of 1997 (81.5%). The range of RWCs for foliage during the three winters was 48.2% to >100%. Generally second year foliar RWCs were less than first year foliar RWCs, and were the lowest in 1999.

Hemlock first and second year foliage always had greater conductivity values than white pine foliage (Table 2). The highest conductivity occurred for both species in 1998. Hemlock second year foliar cuticular conductivity averaged 0.20 m/ks in January and in March, while the first year foliage averaged 0.12 m/ks in January and dropped to 0.04 m/ks there after. Hemlock cuticular conductivity increased over the winter of 1999 for first year foliage, while the second year foliage cunductivities generally remained the same (0.08 m/ks). White pine cuticular conductivity for the first year foliage was greatest in March of 1998 (0.04 m/ks). This value is close to the lowest cuticular conductivity experienced by hemlock. During 1999, first and second year white pine foliage have the same monthly mean cuticular conductivity (0.02 m/ks) for all months.

Water potentials of hemlock shoots were more negative and more variable than white pine shoots (Figure 3). Hemlock shoots were the most negative during 1998, when the most negative water potential occurred in April (-5.1 MPa). Water potentials varied the least in 1997, rising from -1.04 to -0.6 MPa over that winter. The average water potential for the entire winter of 1997 and 1999 did not differ (-0.8 MPa) while the yearly average for 1998 was -1.0 MPa. White pine shoots in general varied little over any winter, 1999 being the most variable. Yearly averages during 1998 and 1999 were -0.5 MPa, and -0.7 MPa in 1997. The most negative water potential occurred in February of 1998 (-1.9 MPa) for white pine shoots.

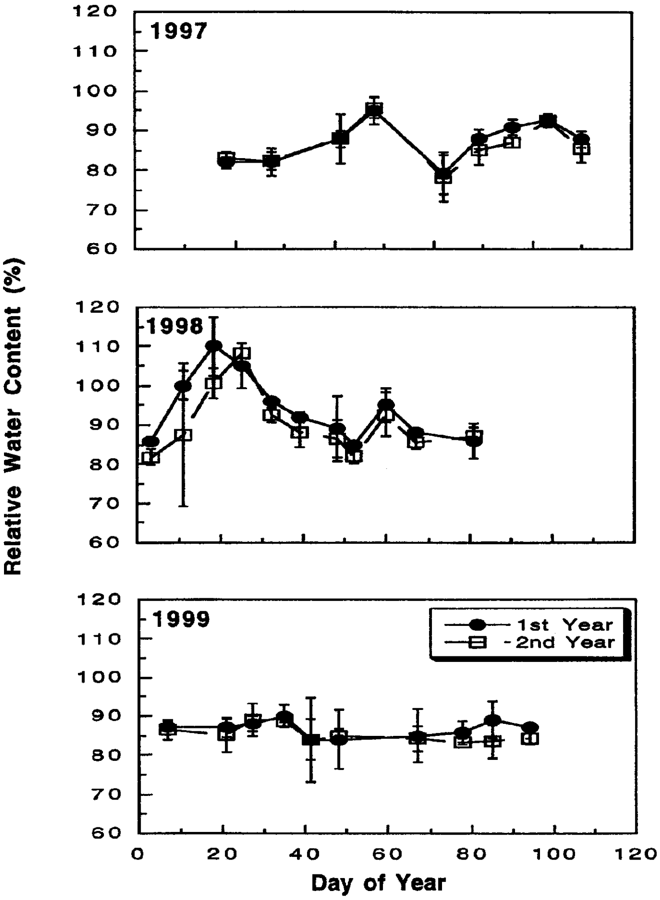

Figure 1.—Relative water contents of hemlock fist and second year foliage during the winters of 1997, 1998, and 1999. Error bars are 1 standard deviation from the mean (n=32).

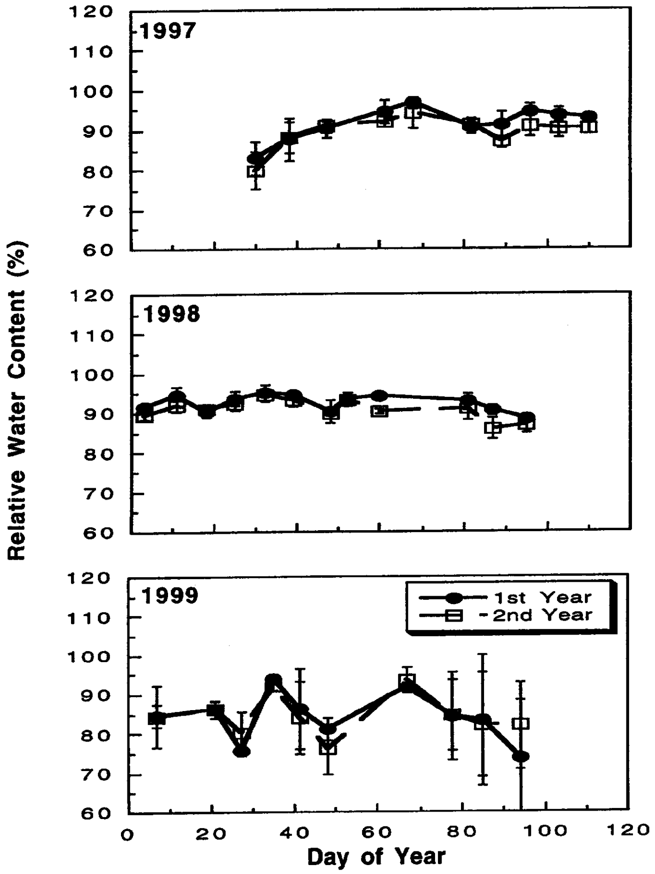

Figure 2.—Relative water contents of white pine fist and second year foliage during the winters of 1997, 1998, and 1999. Error bars are 1 standard deviation from the mean (n=32).

WINWAT Model

The WINWAT model accurately predicted RWCs for the winters with the least variability in measured RWCs (Table 3). RWCs with the most seasonal variablity, in 1998 for hemlock and 1999 for white pine, are poorly predicted. Accuracy was assessed by calculating mean square errors, which is the sum of squares divided by the number of RWCs measured. The sum of squares is the sum of measured minus modeled RWCs squared. WINWAT predicted first year better than second year foliar RWCs, and white pine more accurately than hemlock RWCs (Figures 4 and 5). There are periodic dips and peaksin modeled RWCs which measured RWCs do not show.

Discussion

The purpose of this study is to examine desiccation stress of two low elevational conifers at upper elevational limits by utilizing physiological measurements and a winter water relations model. Hemlock trees from this study experienced lower relative water contents, higher cuticular conductivities, and more negative water potentials than white pine at upper elevational limits. Older foliage was damaged and a portion died by the end of 1998, possibly from the January ice storm. White pine trees did not experience foliage death during any winter. This study quantified microclimatic data of an upper elevational site for hemlock and white pine trees. During the winters of 1997, 1998, and 1999, air temperature, wind speed and direction, relative humidity, solar irradiance, leaf wetness, soil temperature, and needle temperature were monitored on Mt. Ascutney in Eastern Vermont. Relative water content, cuticular conductivity, and water potential in combination with the WINWAT model were used to develop a clear understanding of water relations of two conifers at their upper elevational limits not at treeline.

Controversy surrounds measurements of plant water status used in comparative studies. Many inconsistencies are associated with water relations due to the involvement of additional often opposing factors that may mask or compensate a presumed relationship, and the difficulty of capturing through point samples the dynamic nature of plant responses (Uta Maier-Mairçker, 1998). These difficulties are compounded by the fact that conifers during winter alter solute concentrations, membrane permeability, ice crystal

Table 2.—Monthly average cuticular conductivities of hemlock and white pine first and second year foliage measured in 1998 and 1999.

	Mean Cuticular Conductance (m/ks)				
	First Yr. Foliage	Standard Deviation	Second Yr. Foliage	Standard Deviation	n
Hemlock					
1998					
January	0.12	0.04	0.20	0.03	32
February	0.04	0.01	0.17	0.01	32
March	0.04	0.03	0.20	0.03	32
1999					
January	0.03	0.01	0.08	0.02	24
February	0.04	0.02	0.09	0.02	32
March	0.05	0.03	0.08	0.03	32
White Pine					
1998					
January	0.03	0.004	0.03	0.01	32
February	0.03	0.002	0.02	0.01	32
March	0.04	0.01	0.03	0.01	32
1999					
January	0.02	0.01	0.02	0.002	24
February	0.02	0.003	0.02	0.003	24
March	0.02	0.004	0.02	0.01	24

formation, and the level of drought and freezing tolerances in ways that have not been elucidated. Variation in RWC or water potential individually are unlikely to describe a response to water imbalance (Zobel, 1996). This study draws upon several water relations parameters to confirm similar trends and analogous results. Cuticular conductivity, relative water content, and water potential are used simultaneously to represent the water balance of a plant. If desiccation occurs, the effect should be apparent in all of the parameters used in this study.

Hemlock trees may be considered more susceptible than white pine trees to winter damage, possibly from desiccation. Hemlock experience higher cuticular conductivities, more negative water potentials, and lower relative water contents than white pine trees at 640 m elevation on Mt. Ascutney. The winter of 1998 resulted in the highest cuticular conductivities, indicating the ice storm may have damaged hemlock cuticles. However, cuticular conductivity did not increase over the winter for first year foliage, suggesting that deterioration of the cuticles was not a permanent or continuous condition. Cuticular conductivities remained high throughout that winter for second year foliage (0.2 m/ks). Generally RWCs and water potentials were not lethal during this winter (1998), and it seems unlikely that desiccation alone resulted in shoot death. The WINWAT model did not predict RWCs below 60%, the threshold for desiccation damage in conifers, and measured RWCs seldom fell below 60%. Damage was short-term, over a single winter season and related most to the ice storm. If the effect is damage and needle loss, the specific cause is not revealed by this study.

White pine trees did not experience desiccation at upper elevational limits, with low cuticular conductivities, higher RWCs of both first and second year needles than hemlock, and analogously high water potentials. It has long been noted that white pine trees are susceptible to winter injury less frequently than hemlock trees (Curry and Church, 1952). Winter data from Mt. Ascutney support this observation and do not reveal damage. The WINWAT model predicted RWCs well for white pine, except in 1999. During 1999, RWCs were the most variable and lowest of the three years. Needles appeared chlorotic, but remained viable with low cuticular conductivities and high water potentials. Discolored needles may contribute less to the next season's photosynthesis, and it would be interesting to determine how this would contribute to the following winter's water relations.

The winter climate on Mt. Ascutney at 640 m is characterized by low temperatures and constant snow cover. On average, monthly air temperatures remained below 0 °C in all months except April of 1998 (1.8 °C). Soil temperatures also remained below 0 °C in all months except December of 1999 (1.9 °C). There is little sun exposure at this north facing and heavily shaded site. Needle temperatures seldom

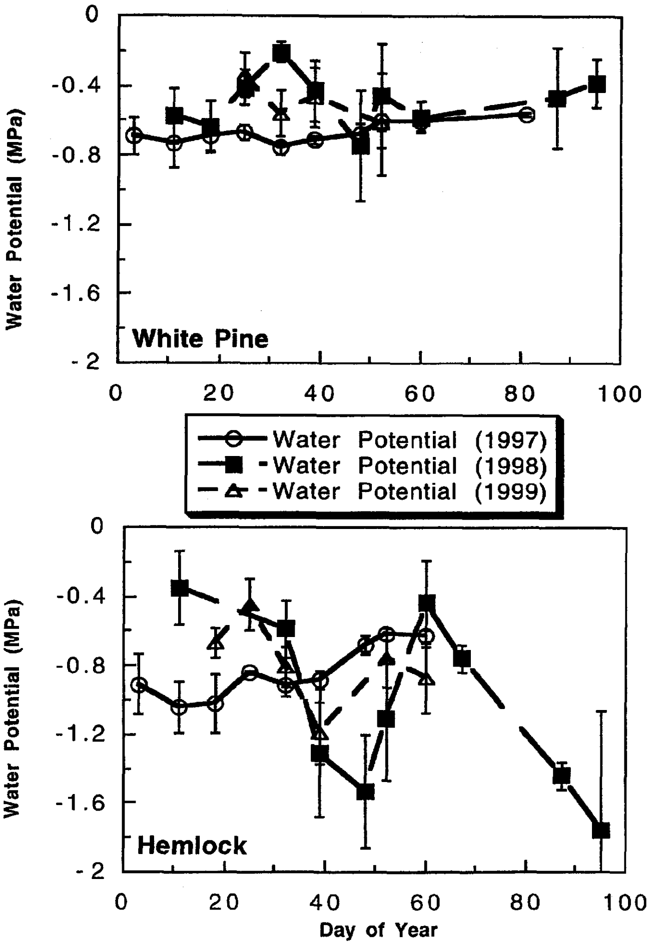

Figure 3.—Water potential (MPa) measured on hemlock and white pine shoots during the winters of 1997, 1998, and 1999.

exceeded air temperatures (data not shown), noted in conifers at other upper elevational limits (Sakai 1970, Hadley and Amundson 1991). On calm and sunny days, needle temperatures can exceed air temperature by 10 and 20 °C, optimizing water loss (Marchand 1987). Drought occurs because soil water, when frozen, is unavailable to the plant yet transpiration proceeds at a finite, minimal rate even in winter. Since needle temperatures did not deviate from air temperatures in this study, and rehydration is possible even when roots are frozen and the ground is covered in snow (Scott and Hansell 1992), it seems unlikely that the relationship between the soil, plant, and air caused desiccation.

The success of regeneration at treeline is vital in an environment which is characterized by limitations. Considering that hemlock trees are shade tolerant, mesic conifers which prefer to establish seeds in moist and decaying logs, it is of little surprise that hemlock would not have developed mechanisms to tolerate drought. White pines grow on rocky cliffs as well as sandy soils, tolerate high levels of irradiance, and are more able to tolerate water shortages. Since mechanisms to tolerate drought are behavioral as well as genetic, it is reasonable that white pines could have developed better mechanisms to deal with desiccation. White pines have been witnessed at other New England summits (personal observation), and hemlock trees seldom if ever reach the upper limit of tree growth.

Hemlock needles may have experienced water and foliage loss during the ice storm through mechanical failure. Ice particles may have impacted the cuticle, disrupted turgor relations of the epidermis and prevented proper stomatal closure. Perhaps as ice formed on the foliage, ice crystals penetrated inside vulnerable needles, resulting in freezing damage and death. Direct mechanical damage has previously been implicated for winter water imbalances (Marchand and Chabot 1978, Hadley and Smith 1983 and 1986, Maruta 1996) and may very well be the cause of damage experienced by hemlock from the ice storm of 1998. The upper elevational limits of hemlock on Mt. Ascutney may establish from severe and sporadic events, such as the 1998 ice storm, rather than symptoms which occur each winter. This study shows that the ice storm damaged hemlock trees, not white pine trees, and was related to elevation since the duration and quantity of ice increased with elevation. This study explored water relations only at upper elevational limits and a study which looks at water relations along an elevational gradient could support these findings.

Stem recharge is assumed to occur at temperatures greater than -4 °C (Sowell 1996, Boyce et al. 1992), and average monthly temperatures remained above -4 °C for half of each winter studied. More information is needed to understand stem recharge during the winter for hemlock and white pine species which may experience stem recharge at a different threshold. Differences in sapwood water storage capacity could have an important influence on winter water relations, and little is known about capabilities of species in this study. Xylem embolism has been noted to result in winter damage in other conifers (Sperry and Tyree 1988,Cochard 1992) but the propensity of hemlock to experience embolism over pine is not known. Differences in rooting architecture have been implicated to take advantage of available soil water (Day et al. 1989) and root distribution may explain elevational distribution of hemlock and white pine trees.

Damage in winter constitutes the greatest limiting factor for growing plants in cold climates and high mountains (Sakai, 1970). Woody plants at their upper elevational limits experience stress from seasonal and sporadic events that can reduce plant productivity and increase susceptibility to injury from other stresses. Researching winter damage and the process of establishing upper elevational limits may elucidate how conifers survive severe conditions.

Table 3.—Calibrated values of recharge parameter A in 1997, 1998, and 1999 for first and second year shoots of hemlock and white pine at their upper elevational limits on Mt. Ascutney.

	Validation of the WINWAT Model								
	1997			1998			1999		
	A	SS^1	MS^2	A	SS	MS	A	SS	MS
Hemlock									
First Year Foliage	90	191.0	23.9	45	274.1	24.3	45	104.3	13.0
Second Year Foliage	140	334.2	42.0	455	1415.8	118.0	95	89.1	11.1
White Pine									
First Year Foliage	105	85.5	10.7	40	188.2	17.1	20	346.6	43.3
Second Year Foliage	70	139.5	17.4	35	215.4	19.6	20	309.5	38.7

SS^1 = Sum of squares = Σ (measured RWC - modeled RWC)^2

MS^2 = Mean square error = SS / (# measured RWC values)

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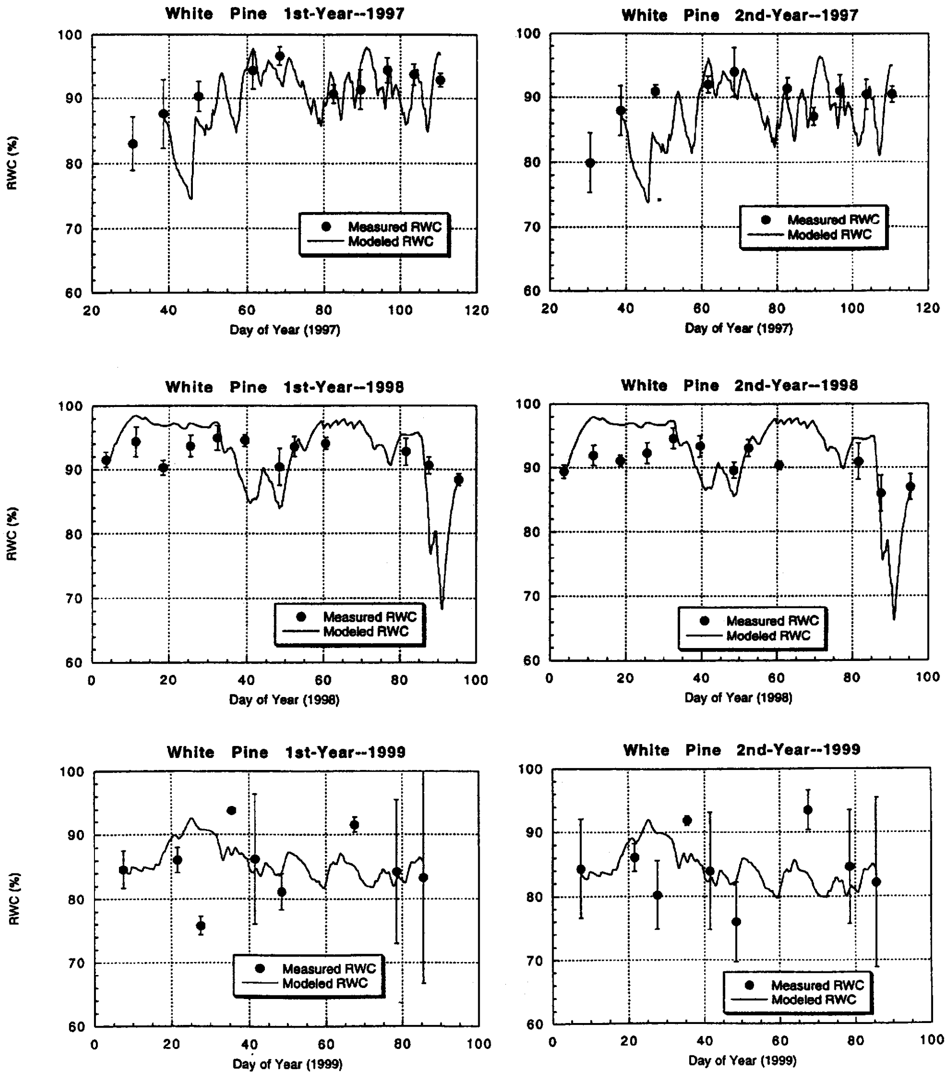

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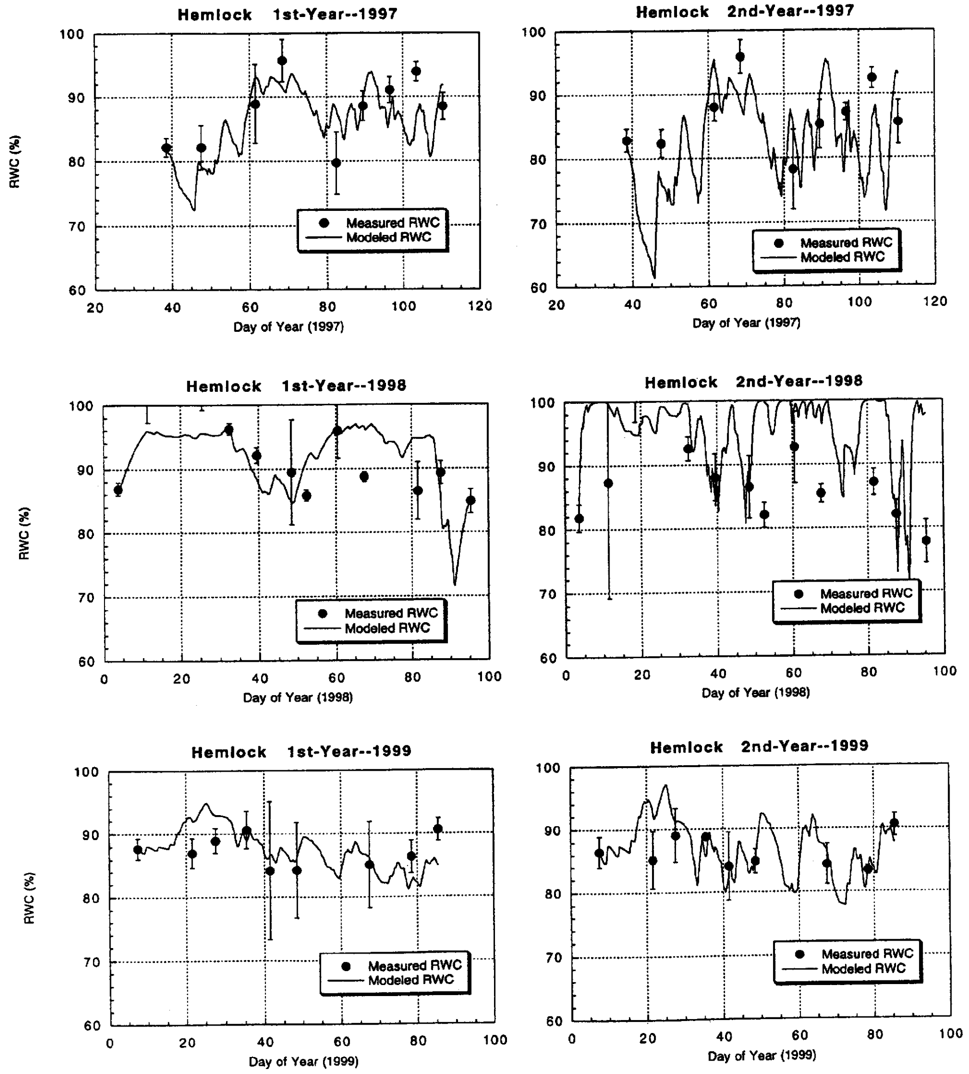

Figure 5.—WINWAT model predictions of Relative Water Contents for Hemlock for 1997, 1998, and 1999.

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Hemlock mortality after hemlock woolly adelgid attack: Role of *Armillaria*

Philip M. Wargo and J. Chris Fagan[1]

Significant mortality of eastern hemlock, *Tsuga canadensis*, associated with the hemlock woolly adelgid, *Adelges tsugae*, (HWA), has occurred in Connecticut forests since a recent introduction of the insect in 1985. Mortality associated with HWA has also occurred recently in the Delaware Water Gap (PA and NJ) and the Shenadoah National Park (NC). Infestation and crown damage usually begins in the lower portions of the crown and moves upward causing decline and eventually resulting in death several years after the initial infestation. Such stress-initiated mortality is consistent with dieback and decline disease etiology which usually involves secondary disease organisms, insects as well as fungi. The most prominent secondary or stress-induced pathogen in decline diseases is the *Armillaria* root disease fungus. A preliminary study was conducted to assess its presence and significance on hemlocks stressed by HWA infestation and defoliation. The status of *Armillaria* on three trees in each of three health categories, older dead, recent dead, and poor crown vitality, was evaluated in five randomly selected plots in Devil's Hopyard State Park in southcentral CT near Millington. Root collars and buttress roots were excavated and evaluated for colonization by *Armillaria*. Trees were also examined for evidence of Hemlock borer attack by peeling a 1/2 m wide band of bark from the main stem at 1 to 1.5 m above ground and estimating the abundance of borer galleries. All older dead trees were extensively decayed and had rhizomorphs of *Armillaria* present on and around them. But their deterioration was such that it could not be determined if *Armillaria* had colonized them prior to death. All recently dead trees (crowns still intact with fine twigs and dead needles) were colonized by the fungus heavily at the root collar and on major buttress roots. Only four of the fifteen trees with poor to very poor crowns (> 75% of crown without needles, some living branches or portions in the upper crown) were colonized by *Armillaria*. Three trees were colonized at the root collar and buttress roots, the fourth only on the buttress roots. Colonization on these trees was not extensive suggesting that it had occurred recently. Additional trees with greater than 50 percent living crown or with full living crowns were excavated in these plots and revealed that no colonization had occurred at the root collar or on the buttress roots excavated to a distance of 1.5-2 m. These results suggest that *Armillaria* is acting as a roguer of weakened trees, colonizing them very late in the decline process after significant crown loss had already occurred, and accelerating the rate of death. It is doubtful that these trees would have recovered to any great extent even in the absence of the fungus, but they probably would have lingered on in the canopy for several more years. The pattern for hemlock borer attack was quite similar to that for *Armillaria*.

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Composition and Structure of Hemlock-Dominated Riparian Forests of the Northern Allegheny Plateau: A Baseline Assessment

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Abstract

We assessed the species composition and structure of three riparian forest stands of differing ages (old-growth, late-successional, mid-successional), dominated by eastern hemlock (*Tsuga canadensis* Carr.), in the Allegheny National Forest of northwestern Pennsylvania. Our objectives were to: 1) quantify structural and compositional attributes of hemlock-dominated riparian forests along a successional chronosequence; 2) describe in-stream coarse woody debris (CWD; logs $\geq$ 10 cm basal diameter and $\geq$ 1 m in length) loadings along this chronosequence; and 3) establish a benchmark series of permanent plots and transects with which future changes in forest composition and structure, and in-stream CWD loadings, could be monitored. Eastern hemlock, yellow birch (*Betula alleghaniensis* Britt.) and American beech (*Fagus grandifolia* Ehrh.) dominated the large (stems $\geq$ 10.0 cm dbh) and small (stems $\geq$ 2.5 cm dbh but < 10.0 cm dbh) tree strata at each site. However, structural data suggested that only American beech was successfully regenerating. Species richness of summer and spring herbs was greater for the mid-successional site than for either the late-successional or old-growth sites, due in large part to the greater habitat heterogeneity provided by small wetland inclusions, and lower canopy cover, at the younger site. In-stream CWD loading varied among sites and increased with riparian forest age. CWD loading at the old-growth site, similar to CWD loading recorded for old-growth hemlock-dominated riparian forest-stream systems in the southern Appalachian Mountains, was more than twice that recorded at the late-successional site and over three times that at the mid-successional site. Remeasurement of permanent vegetation plots and CWD transects at periodic intervals will provide useful information on the dynamics of hemlock-dominated riparian forest-stream systems that can be used in the development of adaptive management plans.

Introduction

Forests dominated by eastern hemlock (*Tsuga canadensis* Carr.) were an important component of presettlement landscapes of the nonglaciated Allegheny Plateau of northwestern Pennsylvania. Most common in mesic coves and stream valleys (Whitney 1990, Abrams and Ruffner 1995), hemlock-dominated forests of the region were heavily exploited for lumber and bark during the late 1800s and early 1900s, greatly diminishing their abundance (Whitney 1990, Abrams and Ruffner 1995). After harvest, many hemlock stands, particularly on upland sites, were converted to stands of early successional Allegheny hardwoods (dominated primarily by black cherry, *Prunus serotina* Ehrh., and red maple, *Acer rubrum* L.) (Whitney 1990). Today, silvicultural practices that perpetuate dominance of valuable hardwoods, and intense browsing by white-tailed deer (*Odocoileus virginianus* Zimmerman), continue to limit the development of late-successional, hemlock-dominated forests in much of the region (Hough 1965, Whitney 1984, 1990, Rooney and Dress 1997).

In contrast to upland sites, eastern hemlock has remained an important overstory species in many headwater riparian forests of the northern Allegheny Plateau. Riparian forests of the region have only recently received focused scientific attention (e.g., Williams and Moriarity 1997) and little is known of the ecological importance of eastern hemlock to the structure and function of stream-riparian systems. In the southern Appalachian Mountains, eastern hemlock is a major source of coarse woody debris to stream systems, especially those that are flanked by old-growth forest (Hedman et al. 1996). By input of persistent wood that accumulates through successional time (Hedman et al. 1996), eastern hemlock may greatly influence aquatic biodiversity (Terrick 1996). In addition, light attenuation by dense hemlock overstory, in conjunction with allelopathy, can regulate the diversity and abundance of ground-layer vegetation in riparian zones (Daubenmire 1930, Ward and McCormick 1982, Williams and Moriarity 1998). Thus, by influencing pattern and process in both aquatic and terrestrial ecosystems, eastern hemlock may be a keystone species (e.g., Mills et al. 1993) in riparian forests and streams.

The goal of this study was to provide baseline ecological information on hemlock-dominated riparian forests of the northern Allegheny Plateau. Our specific objectives were to: 1) quantify structural and compositional attributes of hemlock-dominated riparian forests along a successional chronosequence; 2) describe in-stream coarse woody debris (CWD) loadings along this chronosequence; and 3) establish a benchmark series of permanent plots and transects with which future changes in forest composition and structure, and in-stream CWD loadings, could be monitored. The last objective was of particular interest because of potential invasion of the region by the introduced hemlock woolly adelgid (*Adelges tsugae* Annand) (Homoptera: Adelgidae), and the compositional and structural changes that may occur in riparian forests and streams as a result of extensive adelgid-induced mortality of eastern hemlock (e.g., Orwig and Foster 1998).

Materials and Methods

Study area and sites

This study was conducted in the Allegheny National Forest (ANF) (41° 45' N, 79° 00' W) located in the nonglaciated Allegheny Plateau Physiographic Province of northwestern

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Table 1.—Characteristics of the three study streams in northwestern Pennsylvania and their riparian vegetation. Values in parentheses under basal area and tree density are percentages of each category comprised by *Tsuga canadensis*. Canopy cover and ground cover values are means ± 1 SE. Means bearing the same letter do not differ significantly (one-way ANOVA followed by Tukey test; $P = 0.0001$ for canopy cover; $P = 0.039$ for ground cover).

Site	Seral Stage	Watershed aspect	Stream order	Basal area[1] (m²/ha)	Tree density[1] (stems/ha)	Canopy cover (%)	Ground cover (%)
East Fork Run	Old-growth	NE-SW	3rd	61.1 (79.5)	499.5 (73.3)	91.8 ± 0.5a	13.4 ± 4.0a
Coon Run	Late	N-SE	2nd	50.4 (84.4)	330.0 (69.7)	93.6 ± 0.5a	12.0 ± 3.7a
Waid Run	Mid	W-SE	2nd	43.1 (58.3)	400.0 (67.5)	89.2 ± 0.5b	24.3 ± 2.6b

[1] Stems ≥ 10.0 cm dbh

Pennsylvania. The ANF lies in a transition zone between the hemlock-white pine-northern hardwood forest of Braun (1950) and the more southerly Appalachian oak forest of Kuchler (1964). The landscape is typified by relatively flat to gently rolling plateaus dissected by deep, dendritic, u- or v-shaped stream valleys (Hough and Forbes 1943). Plateau elevations range from 400 to 600 m above sea level; stream valley floors generally range from 300 to 400 m in elevation (Cerutti 1985, Kopas 1985, Whitney 1990). Summers are cool with an average temperature of 18.9°C (Whitney 1990). Precipitation is distributed fairly evenly throughout the year and averages between 100 and 110 cm (Cerutti 1985, Kopas 1985). Sandstones and shales of Pennsylvanian age are the dominant parent material from which soils of the region are derived (Whitney 1990).

Three hemlock-dominated riparian forest stands, each of a different age, were studied (Table 1). East Fork Run, located within the Tionesta Research Natural Area, is an old-growth (overstory age ≥ 300 years) site; Coon Run is a late-successional (overstory age ≥ 150 years) site that may have been selectively logged; and Waid Run is a mid-successional (overstory age = 60-80 years) site. The East Fork Run and Waid Run sites are located on relatively level, undulating floodplains dominated by alluvial soils; the Coon Run site is located near the streamside base of a steep hillslope dominated by colluvial soil (Table 2).

Field sampling

Vegetation was sampled in ten permanently marked 10 X 10 m plots at each site. Plot arrangement differed among sites. At East Fork Run and Waid Run, five generally contiguous plots were placed on opposite sides of the stream; at Coon Run, all ten plots were positioned more or less contiguously on the northeastern side of the stream valley because of the predominance of eastern hemlock at this aspect. All trees ≥ 2.5 cm dbh were identified and measured within each 100 m² plot; each tree tallied was marked by a numbered aluminum tag at its base. Saplings (stems < 2.5 cm dbh but > 1 m tall) were identified and counted in each 100 m² plot. Woody plant seedlings (stems ≤ 1 m tall) were identified and counted, and percent cover by species of herbaceous vascular plants was estimated, in two 1 m² plots located randomly in each 100 m² plot. Woody plant and summer herbaceous layer vegetation data were collected during mid-August 1993 at Coon Run, late-June 1995 at East Fork Run, and mid-July 1996 at Waid Run. At each site, all 100 m² plots were surveyed for vernal herbs (presence/absence) in the spring (late April to mid-May) following respective summer sample years.

Soil and physical site characteristics were recorded within each 100 m² plot. Depth and texture of soil horizons were determined from profiles taken with a soil auger. Plot aspect and slope were measured with compass and clinometer. Plot position on the landform (floodplain, slope), landform shape (concave, convex, linear) and percent rock cover were estimated visually. Plot elevation was determined from topographic maps. The latitude and longitude of each plot was determined with a hand-held global positioning system. A spherical densiometer (Lemmon 1956) was used to estimate percent canopy cover at the center of each plot.

In-stream CWD (logs ≥ 10 cm basal diameter and ≥ 1 m in length) was sampled at each study site by a line-intercept method (Martin 1976) using two contiguous 50 m transects centered within each stream. Each log crossing a transect was identified, and its total length and upper and lower diameter were measured. Logs that could not be readily identified in the field were tallied as unknown. Transect ends were marked with iron rebar to allow subsequent remeasurements.

Data analysis

Density (number of stems/m² or ha), basal area (m²/ha) or cover, frequency (percent occurrence across plots), and importance were used to describe the vegetation of each site (Kent and Coker 1994). Trees were divided into two structural classes for analysis: small (stems ≥ 2.5 cm dbh but < 10 cm dbh) and large (stems ≥ 10.0 cm dbh) trees. The importance value (IV; 0 to 100%) for small and large trees was calculated as relative density + relative basal area + relative frequency/3 (Curtis and McIntosh 1951). The IV for saplings and seedlings was calculated as relative density + relative frequency/2. The IV for herbaceous layer plants (all vascular plants, except for tree seedlings, ≤ 1 m tall) was calculated as relative cover + relative frequency/2. To assess the regeneration status of eastern hemlock and other canopy potential tree species, stem density (number/ha) was summed within sites by structural class (i.e., seedling, sapling, small tree, and large tree). Nomenclature follows Gleason and Cronquist (1991).

Table 2.—Mean (± 1 SE) soil and site characteristics for the three riparian study sites in northwestern Pennsylvania. Means followed by the same letter do not differ significantly (Tukey test, $P \le 0.05$).

Soil/site characteristic	East Fork Run	Coon Run	Waid Run	*P*-value
Elevation (m)	467.6 ± 1.4a	561.5 ± 0.7b	369.0 ± 0.0c	0.0001
Aspect (°N of S)	298.4 ± 14.8a	73.8 ± 7.8b	244.5 ± 6.0c	0.0001
% Slope	10.6 ± 2.8a	72.6 ± 5.8b	3.4 ± 0.6a	0.0001
Plot position	Streamside	Lower slope	Streamside	—
Landform shape	Undulating	Linear/concave	Undulating	—
% Rock cover	20.8 ± 10.5	14.8 ± 3.6	5.2 ± 3.0	0.085
Predominant soil series	Philo-Pope	Buchanan	Ernest	—
Depth of litter layer (cm)	1.7 ± 0.2a	3.7 ± 0.5b	2.3 ± 0.3a	0.011
Depth of humus layer (cm)	3.4 ± 0.3a	1.5 ± 0.2b	2.3 ± 0.3a	0.004
Depth of A horizon (cm)	11.9 ± 2.5a	4.5 ± 0.5b	6.0 ± 1.7a	0.025
Texture of A horizon	Silt loam	Stony silt loam	Silt loam	—
Depth of B horizon (cm)	46.3 ± 7.7a	25.5 ± 3.8b	14.5 ± 2.3c	0.0001
Texture of B horizon	Silt loam	Stony silt loam	Silt loam	—
Total soil depth	63.4 ± 9.4a	34.9 ± 3.6b	20.0 ± 3.4c	0.0001

Table 3.—Importance values (relative frequency + relative density + relative basal area/3) for large (stems ≥ 10.0 cm dbh) and small (stems ≥ 2.5 cm dbh but < 10.0 cm dbh) trees at the three riparian study sites in northwestern Pennsylvania. Nomenclature follows Gleason and Cronquist (1991).

	East Fork Run		Coon Run		Waid Run	
Species	Large Tree	Small tree	Large Tree	Small tree	Large Tree	Small tree
Tsuga canadensis Carr.	86.6	58.1	71.0	—	59.6	62.1
Betula alleghaniensis Britt.	18.5	16.1	4.1	—	18.7	12.5
Fagus grandifolia Ehrh.	7.3	15.0	10.5	81.7	3.1	25.5
Acer saccharum Marsh.	2.9	—	10.5	—	—	—
Acer rubrum L.	—	—	4.1	—	3.8	—
Pinus strobus L.	—	—	—	—	14.8	—
Amelanchier arborea (Michx. f.) Fern.	2.7	5.6	—	—	—	—
Hamamelis virginiana L.	—	5.1	—	10.1	—	—
Acer pensylvanicum L.	—	—	—	8.2	—	—

Log diameter measurements were converted to total volume using the equation for the right frustrum of a parabaloid (Lienkamper and Swanson 1987). Log volume (m^3) by site and species was calculated by summing values obtained from the two 50 m transects and expressing them on a 100 m basis. Log frequency (percent occurrence on transects) and percent log volume were used to construct importance values (IV = % frequency + % volume/2) for each species.

One-way analysis of variance ($P \le 0.05$) was used to examine differences in selected soil, site and vegetation characteristics across community types. When ANOVAs were significant, the Tukey multiple range test was used to separate means. Data were transformed [cos(45 - aspect) + 1 for aspect data; arcsin transformation for percentage data; log(x + 0.5) for other continuous data] prior to analysis to stabilize variances (Beers et al. 1966, Zar 1996) and back-transformed for tabular presentation. Box plots were used to graphically compare variation in in-stream CWD length and basal diameter across sites. Statistical analyses were done using SYSTAT version 7.0 (Wilkinson 1997).

Results

Soil and site characteristics

Eight of 9 quantitative soil and site characteristics varied significantly across study sites (Table 2). Most soil and site factors varied as a result of topography or location in the landscape and not because of differences in stand age (e.g., elevation, aspect, slope). Total soil depth ($F_{2,28} = 14.47$, $P < 0.0001$) and depth of the soil B horizon ($F_{2,28} = 10.84$, $P < 0.0001$) increased significantly with increasing forest age.

Vegetation

Seven species occurred in the large tree stratum across study sites (Table 3). Eastern hemlock was dominant across

Table 4.—Importance values (relative frequency + relative density/2) for woody plant seedlings (stems ≤ 1 m tall) at the three riparian study sites in northwestern Pennsylvania. tr = trace (importance value < 1.0). Nomenclature follows Gleason and Cronquist (1991).

Species	East Fork Run	Coon Run	Waid Run
Tsuga canadensis Carr.	84.1	48.3	—
Betula alleghaniensis Britt.	13.1	16.8	51.1
Fagus grandifolia Ehrh.	tr	6.2	16.3
Acer saccharum L.	—	1.2	17.4
Prunus serotina Ehrh.	tr	3.5	1.5
Acer pensylvanicum L.	tr	11.5	—
Acer rubrum L.	tr	10.0	—
Magnolia acuminata (L.) L.	—	2.2	1.5
Fraxinus americana L.	—	—	12.5
Viburnum alnifolium Marsh.	—	tr	—
Amelanchier arborea (Michx. f.) Fern.	tr	—	—
Hamamelis virginiana L.	tr	—	—

sites with yellow birch (*Betula alleghaniensis* Britt.) and American beech (*Fagus grandifolia* Ehrh.) as important secondary species (Table 3). Large tree density ranged from 330 stems/ha to 499 stems/ha and was greatest at East Fork Run and lowest at Waid Run. Large tree basal area ranged from 43.1 to 61.1 m^2/ha was greatest at East Fork Run and lowest at Waid Run (Table 1). Six species occurred in the small tree stratum across sites with eastern hemlock dominant at East Fork Run and Waid Run; eastern hemlock was absent as a small tree at Coon Run (Table 3). American beech dominated the small tree stratum at Coon Run and, along with yellow birch, was an important secondary small tree species at East Fork Run and Waid Run. Canopy cover differed significantly among sites ($F_{2,28} = 18.26$, $P < 0.0001$) and was lowest at Waid Run and greatest at East Fork Run and Coon Run (Table 1).

Twelve species were recorded from the woody plant seedling stratum across study sites (Table 4). Eastern hemlock was the dominant seedling species at East Fork Run and Coon Run but was absent at Waid Run where yellow birch was dominant. Overall species richness of woody plant seedlings, summed by site, was similar between Coon Run (S = 9) and East Fork Run (S = 8) but was lowest at Waid Run (S = 6). On a per plot basis, species richness of woody plant seedlings differed significantly among sites ($F_{2,58} = 29.81$, $P < 0.0001$); woody plant seedling richness was greatest at Coon Run (mean = 4.9 ± 0.2 SE species/m^2) followed by East Fork Run (mean = 3.7 ± 0.3 SE species/m^2) and Waid Run (mean = 2.2 ± 0.2 SE species/m^2). The sapling layer was the most species-poor vegetational stratum across sites and consisted only of root sprouts of American beech (IV = 100 at each site).

The summer herbaceous layer was generally the most species-rich of all vegetational strata with 28 species recorded across sites (Table 5). Two species, common wood sorrel (*Oxalis acetosella* L.) and wood fern [*Dryopteris intermedia* (Muhl.) A. Gray] strongly dominated the herbaceous layer at East Fork Run and Coon Run; wood fern was dominant, and common wood sorrel absent, at Waid Run. Other moderately important (IV > 5.0) herbaceous species at one or more sites included Canada mayflower (*Maianthemum canadense* Desf.), sweet white violet (*Viola blanda* Willd.), Indian cucumber-root (*Medeola virginiana* L.), New York fern [*Thelypteris noveboracensis* (L.) Nieuwl.], round-leaved violet (*Viola rotundifolia* Michx.), and partridgeberry (*Mitchella repens* L.). Summed by site, Waid Run (S = 24) had the highest overall species richness followed by Coon Run (S = 11) and East Fork Run (S = 5). On a per plot basis, species richness of summer herbs differed significantly among sites ($F_{2,58} = 28.74$, $P < 0.0001$. Summer herb species richness was greatest at Waid Run (mean = 5.1 ± 0.4 SE species/m^2) and lowest at Coon Run (mean = 2.7 ± 0.2 SE species/m^2) and East Fork Run (mean = 2.1 ± 0.2 SE species/m^2). Six species of vernal herbs were tallied across sites with 5 species occurring at Waid Run, 2 species at East Fork Run and 1 species at Coon Run (Table 6). Except for toothwort [*Cardamine diphylla* (Michx.) A. Wood] at Waid Run, vernal herbs were infrequently encountered across sites. Total ground-layer cover (including summer herbs and woody plant seedlings) varied significantly among sites ($F_{2,28} = 4.28$, $P = 0.039$) and was greatest at Waid Run (Table 1).

The distribution of structural data for eastern hemlock and yellow birch was generally bimodal across sites with peaks in the seedling and large tree classes and troughs in the sapling and small tree classes (Table 7). Seedlings of eastern hemlock were not recorded from plots at Waid Run. The structural distribution for American beech approached an inverse-J shaped curve.

In-stream CWD

Three species, eastern hemlock, yellow birch and American beech, were the most important contributors to in-stream CWD across sites (Table 8). Only 14% of logs across sites (n = 7) could not be readily identified to species. Logs of eastern hemlock were generally the most numerically

Table 5.—Importance values (relative frequency + relative cover/2) for summer herbaceous plants at the three riparian study sites in northwestern Pennsylvania. Nomenclature follows Gleason and Cronquist (1991).

Species	East Fork Run	Coon Run	Waid Run
Oxalis acetosella L.	55.9	54.8	—
Dryopteris intermedia (Muhl.) A. Gray	27.8	21.3	41.1
Thelypteris noveboracensis (L.) Nieuwl.	7.0	1.1	—
Medeola virginiana L.	5.4	7.6	—
Maianthemum canadense Desf.	4.0	1.1	9.9
Dennstaedtia punctilobula (Michx.) Moore	—	4.6	1.7
Asplenium montanum Willd.	—	3.6	1.2
Viola blanda Willd.	—	2.4	8.7
Viola rotundifolia Michx.	—	1.2	2.6
Mitchella repens L.	—	—	6.2
Impatiens capensis Meerb.	—	—	5.3
Arisaema triphyllum (L.) Schott.	—	—	3.6
Pilea pumila (L.) A. Gray	—	—	3.4
Galium L. spp.	—	—	2.7
Tiarella cordifolia L.	—	—	2.3
Viola sororia Willd.	—	—	2.3
Hydrocotyle americana L.	—	—	1.8
Trientalis borealis Raf.	—	—	1.8
Adiantum pedatum L.	—	1.7	—
Symplocarpus foetidus (L.) Nutt.	—	—	1.7
Disporum lanuginosum (Michx.) Nichol.	—	1.1	—
Other[1]	—	—	4.2

[1] Includes: *Cardamine diphylla* (Michx.) A. Wood, *Carex* L. sp., *Circaea alpina* L., *Geranium maculatum* L., *Lilium canadense* L., *Prenanthes alba* L., *Streptopus roseus* Michx.

Table 6.—Frequency (%) of spring ephemeral herbs in 100 m² plots (n = 10 plots/site) at the three riparian study sites in northwestern Pennsylvania. Nomenclature follows Gleason and Cronquist (1991).

Species	East Fork Run	Coon Run	Waid Run
Trillium erectum L.	—	30	10
Trillium undulatum Willd.	10	—	10
Cardamine diphylla (Michx.) A. Wood	—	—	60
Panax trifolius L.	—	—	20
Podophyllum peltatum L.	—	—	20
Anemone quinquefolia L.	10	—	—

common of CWD species recorded on stream transects and generally comprised the largest volume. In-stream CWD loadings [log volume (m³)/100 m of stream] varied among sites and increased with riparian forest age. CWD loading at East Fork Run was more than twice that recorded at Coon Run and over three times that recorded at Waid Run (Table 7). Basal diameter (Fig. 1) and length (Fig. 2) of in-stream logs at East Fork Run and Coon Run were strongly skewed toward larger sizes. In contrast, the distributions of basal diameter and length of in-stream-logs at Waid Run showed considerably less variation than logs tallied at East Fork Run and Coon Run, and were generally skewed toward smaller sizes.

Discussion

We observed no major differences in vegetational composition across our riparian study sites that could be clearly attributed to forest age. Composition of arboreal strata (i.e., large trees, small trees, seedlings, saplings) did not differ markedly across sites and was similar to that documented in other studies of regional hemlock forests (Hough 1936, Hough and Forbes 1943). Likewise, summer herbs such as wood fern, common wood sorrel, and Canada mayflower, widespread in hemlock-dominated forests (Rogers 1980), were generally dominant across our study sites, and spring herbs, typically of low importance in hemlock stands (Beatty 1984), were uncommon.

Table 7.—Regeneration of dominant canopy potential tree species across the three riparian study sites. Seedlings = stems $\leq$ 1 m tall; saplings = stems < 2.5 cm dbh but > 1 m tall; small trees = stems $\geq$ 2.5 cm dbh but < 10.0 cm dbh; large trees = stems $\geq$ 10.0 cm dbh.

Site	Species	No. stems/ha Seedlings	Saplings	Small trees	Large trees
East Fork Run	*Tsuga canadensis*	417,200	0	133	337
	Betula alleghaniensis	64,500	0	33	78
	Fagus grandifolia	2,600	555	33	33
Coon Run	*Tsuga canadensis*	1,040,500	0	0	230
	Betula alleghaniensis	190,700	0	0	10
	Fagus grandifolia	15,700	500	120	30
Waid Run	*Tsuga canadensis*	0	0	90	270
	Betula alleghaniensis	50,500	0	10	80
	Fagus grandifolia	9,500	2,170	120	30

Table 8.—Frequency, volume and importance value (IV = % frequency + % volume/2) of logs recorded from the three stream-riparian study sites in northwestern Pennsylvania. Values are per 100 m of stream.

Site	Species	*n*	Frequency (%)	Volume (m^3)	Volume (%)	IV
East Fork Run	*Tsuga canadensis*	11	52.4	22.11	82.1	67.3
	Betula alleghaniensis	4	19.1	2.57	9.6	14.4
	Unknown	4	19.1	0.28	1.0	10.1
	Fagus grandifolia	2	9.5	1.96	7.3	8.4
	Overall	21	—	26.92	—	—
Coon Run	*Fagus grandifolia*	9	52.9	3.33	29.1	41.0
	Tsuga canadensis	4	23.5	4.86	42.4	33.0
	Acer saccharum	1	5.9	1.96	17.1	11.5
	Betula alleghaniensis	1	5.9	1.11	9.7	7.8
	Unknown	2	11.8	0.18	1.6	6.7
	Overall	17	—	11.44	—	—
Waid Run	*Tsuga canadensis*	7	58.3	3.71	46.6	52.5
	Betula alleghaniensis	3	25.0	1.60	20.1	22.6
	Fagus grandifolia	1	8.3	2.53	31.8	20.1
	Unknown	1	8.3	0.12	1.5	4.9
	Overall	12	—	7.96	—	—

Rooney and Dress (1997) found that species richness of tree seedlings and herbs differed significantly between old-growth and second-growth hemlock-hardwood forests in northwestern Pennsylvania. Similarly, we found significantly higher species richness of woody plant seedlings at the 1 m^2 scale at our old-growth and late-successional study sites compared to the mid-successional site. However, species richness of summer herbs did not follow this trend and was significantly greater at Waid Run, the mid-successional site. In fact, overall species richness at Waid Run was over twice that recorded at Coon Run, the late-successional site, and nearly five times that recorded at East Fork Run, the old-growth site. The elevated species richness at Waid Run was probably due in large part to the greater habitat heterogeneity provided by small wetland inclusions, primarily seeps, that occurred at this site, and significantly lower canopy cover due to uprooting of shallow-rooted hemlock and white pine in the comparatively thin soil. Several herbs recorded exclusively at Waid Run are facultative wetland species [e.g., *Impatiens capensis* Meerb. (jewel-weed); *Arisaema triphyllum* (L.) Schott.(jack-in-the-pulpit); *Pilea pumila* (L.) A. Gray (clearweed); *Hydrocotyle americana* L. (marsh-pennywort); *Symplocarpus foetidus* (L.) Nutt. (skunk-cabbage); *Circaea alpina* L. (dwarf enchanter's nightshade)] that are uncommon on sites that lack saturated soils such as the East Fork Run and Coon Run study sites. Also, low canopy cover provides light conditions that allow the coexistence of a wide variety of shade-intolerant and

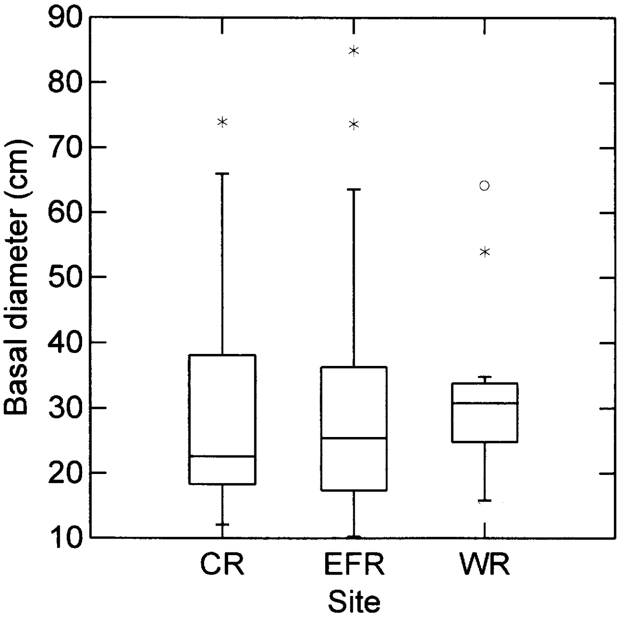

Figure 1.—Box plot diagrams depicting the distribution of basal diameters (cm) for in-stream logs sampled at the three riparian forest-stream study sites in northwestern Pennsylvania. CR = Coon Run; EFR = East Fork Run; WR = Waid Run. The horizontal line through each box depicts the median, the box depicts the central 50th percentile of data, and the vertical lines depict the 95th percentile of data. Asterisks represent outliers, and open circles represent extreme outliers, beyond the 95th percentile range.

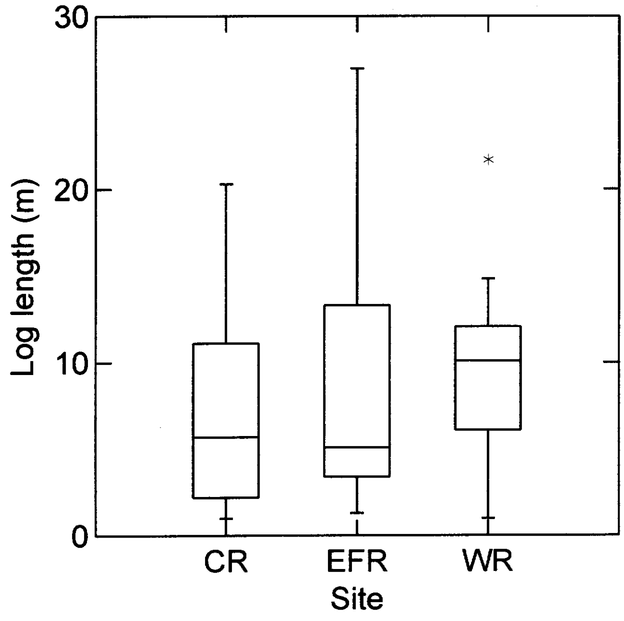

Figure 2.—Box plot diagrams depicting the distribution of lengths (m) for in-stream logs sampled at the three riparian forest-stream study sites in northwestern Pennsylvania. CR = Coon Run; EFR = East Fork Run; WR = Waid Run. The horizontal line through each box depicts the median, the box depicts the central 50th percentile of data, and the vertical lines depict the 95th percentile of data. Asterisks represent outliers beyond the 95th percentile range.

shade-tolerant riparian herb species (Williams et al. 1999). Thus, when comparing plant species richness in a hemlock-dominated riparian forest chronosequence, it may be necessary to first assess the potential confounding influence of within-site habitat heterogeneity on richness measures.

We noted a gap in the sapling and/or small tree structural classes for eastern hemlock and yellow birch across study sites. American beech, in contrast, was well-represented in all structural classes. Hough (1936) and Hough and Forbes (1943) observed very similar patterns in structural classes for these three species in old-growth forests on the northern Allegheny Plateau. They attributed the bimodal distribution of eastern hemlock in particular to episodic recruitment patterned by yearly variation in seed crops and favorable conditions for seed germination and seedling establishment. Since the 1940s, however, white-tailed deer populations have increased dramatically on the Allegheny Plateau and heavy browsing has strongly influenced forest pattern and process (Tilghman 1989). Thus, it is possible that gaps in the smaller size classes of eastern hemlock and yellow birch are due in part to deer browsing in conjunction with seed rain and seed bed conditions. In contrast, seedlings and saplings of American beech are relatively unpalatable to deer; as a result, this species is one of the few to regenerate at high deer densities on the Allegheny Plateau (Whitney 1984). Periodic monitoring of tree regeneration and browse damage, in conjunction with monitoring of deer density and activity, will be necessary to determine the long-term impact of deer browsing on tree and herb populations at our study sites (e.g., Mosbacher 1999, Williams et al. 2000).

Other than large tree basal area and density, in-stream CWD loading was the only structural characteristic that clearly increased with riparian forest age. The in-stream CWD loading that we measured at East Fork Run is similar to values recorded by Hedman et al. (1996) in old-growth hemlock forest-stream systems in the southern Appalachian Mountains. We recorded a total volume of 26.92 m^3/100 of stream at East Fork Run; Hedman et al. (1996) recorded an average volume of 21.9 m^3/100 m of stream in old-growth forest. The in-stream CWD loading that we recorded at Coon Run (11.44 m^3/100 m of stream) also compares favorably with the mean late-successional in-stream loading observed by Hedman et al. (1996) (12.7 m^3/100 m of stream). However, mean in-stream CWD loading for mid-successional sites in the southern Appalachians (13.2 m^3/100 m of stream) is nearly twice that recorded at Waid Run (7.96 m^3/100 m of stream). Hedman et al. (1996) found that carry-over CWD from previous stands contributed significantly to in-stream CWD loading at mid-successional sites in the southern Appalachians. It is unknown how carry-over CWD may influence loadings in streams that drain mid-successional forests of the northern Allegheny Plateau. However, the past practice of using streams to transport logs, aided by large volumes of water released from splash dams in the spring, may have ensured that little CWD remained in streams after their valleys were logged. Instream logs may have been washed downstream when splash dams were opened or they may have been intentionally removed to minimize log jams, diminishing CWD carry-over potential.

Past studies of hemlock-dominated forests of the northern Allegheny Plateau have primarily emphasized descriptions of soil and site factors that affect tree growth and distribution (Hough 1942, 1943, Aguilar and Arnold 1985) or considered potential silvicultural options from stand-level studies (Hough and Forbes 1943). Little direct emphasis was placed on assessment of other forest elements such as downed word or herbaceous plant diversity in hemlock forests of the region (but see Hough 1936, 1965, Rooney and Dress 1997). Our study was designed to provide baseline data on key structural and compositional attributes of hemlock-dominated riparian forest-stream systems with the ultimate goal of monitoring long-term change. Hough's (1965) classic study of compositional shifts in forest understory, induced by heavy deer browsing, clearly illustrates the value of long-term monitoring in detecting subtle ecological change in regional forests. Similarly, we expect that remeasurement of our plots and transects in the coming years will yield information useful for understanding the dynamics of hemlock-dominated riparian forest-stream systems, and to assess their response to both natural and anthropogenic perturbations, such as invasion of the hemlock woolly adelgid. Adaptive management plans for hemlock-dominated riparian forests of the Allegheny Plateau should include a long-term monitoring component, using selected structural and compositional attributes (e.g., Noss 1999), to ensure that current scientific knowledge drives timely, informed management decisions.

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Scott DiLoreto, Eric Mosbacher, Sharon Possessky, Darrin Rubino, Amanda Saul, Jon Settlemyer, Phil Smith, Gary Walters and Bud Wilshire assisted with field sampling. The interlibrary loan staff at Clarion University provided access to key references. This study was supported in part by a participating agreement between the USDA Forest Service, Allegheny National Forest, and Clarion University of Pennsylvania.

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Vascular Plant Propagule Banks of Six Eastern Hemlock Stands and Potential Response to the Hemlock Woolly Adelgid in the Catskill Mountains of New York

Thad E. Yorks, Donald J. Leopold, and Dudley J. Raynal[1]

We examined propagule banks in six eastern hemlock (*Tsuga canadensis* (L.) Carriere) stands in the Catskill Mountains of New York. These stands are at risk of mortality due to the hemlock woolly adelgid (*Adelges tsugae* Annand), but potential effects of mortality on species composition are uncertain. Our objectives were to determine species composition and densities of propagule banks and predict early stand development after hemlock mortality. Aboveground vegetation was characterized using point samples for woody stems and 1-m^2 plots for understory vegetation. Soil samples were collected in June 1997 and kept in a glasshouse for 12 months as germinants were identified, counted, and removed. Hemlock was the dominant tree species in all stands, with minor abundances of red maple (*Acer rubrum* L.), yellow birch (*Betula alleghaniensis* Britton), and/or American beech (*Fagus grandifolia* Ehrh.). Striped maple (*A. pensylvanicum* L.), red maple, yellow birch, evergreen woodfern (*Dryopteris intermedia* (Muhl.) A. Gray), shining clubmoss (*Lycopodium lucidulum* Michx.), and common wood sorrel (*Oxalis acetosella* L.) occurred in understories of most or all stands. Yellow birch seeds, evergreen woodfern spores, and hay-scented fern (*Dennstaedtia punctilobula* (Michx.) Moore) spores germinated in abundance from the propagule banks (means of 722, 2858, and 296 m^{-2}, respectively). Hay-scented fern spores and red-berried elder (*Sambucus pubens* Michx.) seeds were present in propagule banks despite occurring in aboveground vegetation of only one and zero stands, respectively. Seed densities were intermediate and overall propagule species richness was low compared to other studies of eastern US forests. Understory vegetation and propagule banks indicated potential stand replacement by evergreen woodfern and, eventually, yellow birch after mortality (Fig. 1). Hay-scented fern could dominate if woody species are over-browsed by white-tailed deer (*Odocoileus virginianus* Zimmerman).

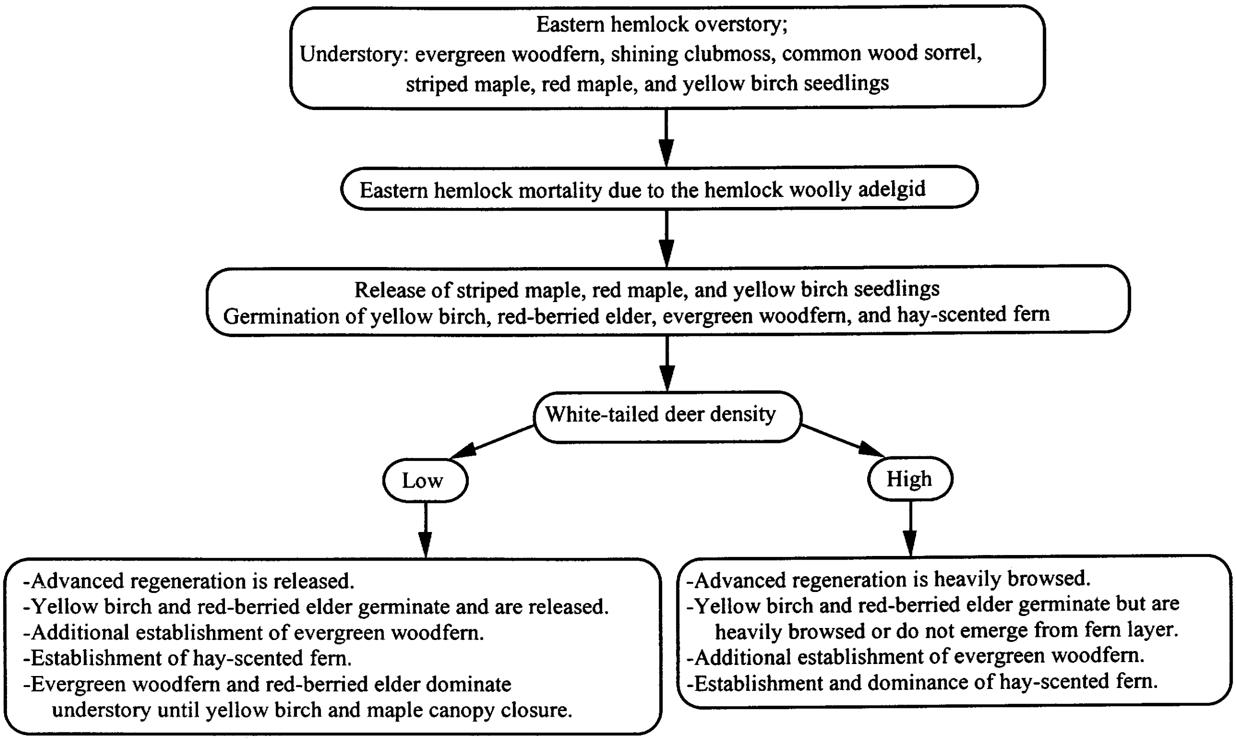

Figure 1.—Potential stand development of six eastern hemlock stands after mortality due to the hemlock woolly adelgid in the Catskill Mountains of New York.

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Management of an Undisturbed Water Ecosystem Containing Old Growth Hemlock, as a Model System of Clear Lake Reserve, Ontario

A.M. Zobel[1], R.A. Reid[2], K. Cybulski[1], K. Glowniak[3], O. Loucks[4] and J.E. Nighswander[1]

Abstract

Since 1969 Trent University researchers have been investigating the chemistry and biotic part of a small undisturbed lake near Minden, Ontario. Clear Lake is surrounded by old growth hemlock stands, some 400 years old. The research was later joined by personnel of the Ontario Ministry of the Environment, and the educational program in the Frost Centre. We are going to discuss changes in pH, phosphorus content and the reaction of two aquatic macrophytes, *Eriocaulon* and *Lobelia dortmana*, to simulated acid rain conditions and increased ultraviolet radiation.

Introduction

Why was it important to establish the Clear Lake Reserve area? The answer would be different depending on whether you are a scientist, tourist or government employee, or a cottager living in the area. For academic scientists the area around Clear Lake has been the oldest site where we and our government colleagues together have done experimental work since the late 1960s, almost from the founding of Trent University. Since then it has become a model system for many investigators working on acidification of that area caused by acid rain. The work started at almost the founding of Trent University, by Schindler and Nighswander, and was published in 1970. The other point of view, of the "users" of the area, will be addressed in the Discussion section.

Clear Lake and several smaller ones are surrounded by forests containing 400-year-old hemlock stands which, in addition to old growth, have all the younger ages of hemlock, thus being an almost unique example of an undisturbed ecosystem, in which we can investigate medicinal plants, and the processes of succession of plants, as well as the inter-reaction between flora and fauna. Nowadays we have realized that plant ecology involves many chemicals, and the influence of the environment on changes in phytochemistry has begun to arouse the interest of plant ecologists (Plant Ecology, 1999). The reactions involve extrusion to the plant surface of phytochemicals (Zobel and Brown, 1988), which are then chemically modified by such environmental factors as oxygen and ultraviolet, and the influence of microbes in the soil. We have investigated the influence of different kinds of radiation on hemlock seedlings growing on the debris of fallen logs of old hemlock trees. We have also chosen to investigate the sponge and the two macrophytes, because they have been influenced to the greatest extent both by changes in ph and by radiation.

Materials and Methods

Hemlock seedlings were collected from the area surrounding Clear Lake (Fig. 1), and water plants from the lake itself, of which the bottom is visible because of the great clarity of the water (Fig. 2). We collected *Meyenia fluriatilis* (freshwater sponge) and two macrophytes, *Eriocaulon septangulare* and *Lobelia dortmanna*, and kept in lake water until the treatment. Plants were irradiated with 366 nm radiation for seven days, or kept in light on a window sill. The seven-day period was chosen because in earlier experiments we had found that this was long enough for plants to produce compounds in amounts sufficient for high performance liquid chromatography (HPLC) analysis. Parallel samples were taken after the plant had been exposed to UV and HCl solutions of pH 5.8, which was the current prevailing value (report of the Ontario Ministry of Natural Resources, 1990). Additionally, the influence of another ion was studied, because cadmium was found in high concentrations in lakes of the Sudbury region some 250 km northwest of this site. Novaspec UV/visible spectrometers were used to measure total absorption of compounds whose peaks approximated 325 nm, and thus was suitable for evaluating coumarins as well as many flavonoids (Harborne, 1967), both groups being well known as phytoalexins — compounds synthesized under stress (Zobel, 1999a; Zobel, 1999).

Results

After exposure to 366 nm radiation these three species investigated reacted differently in the production of phenolic compounds absorbing at 325 nm — most likely coumarins and many flavonoids. *Meyenia* contained more phenolic compounds absorbing at 325 nm than the macrophytes, already while growing in the lake (Fig. 3, field samples), as well as after the seven-day experiment of keeping the sponge under laboratory conditions when the amount still increased by over 30%. After UV irradiation the amounts decreased by 80% when the radiation was the only stress, but the second stress decreased the values less intensely. For instance, acidification plus UV irradiation lowered the phenolics concentration by 60%, and when exposure was to cadmium as well as UV it was lowered only 30%.

Values for *Lobelia* showed a similar trend, although the absolute values were much smaller, not reaching even 20% of the values for the sponge. *Eriocaulon* reacted differently. It showed the smallest concentration of phenolic compounds at the start, while the values for the control, UV alone and UV plus acidification were similar, and only UV plus cadmium caused an increase over threefold.

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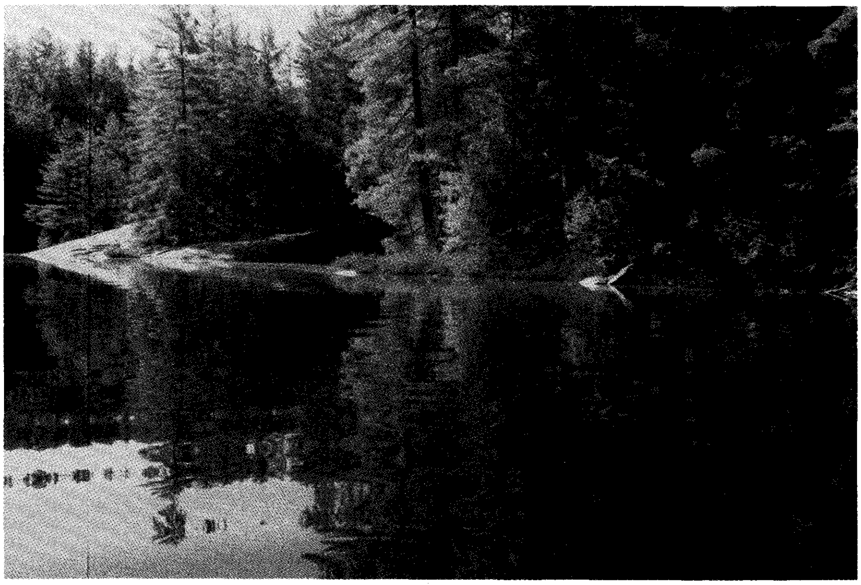

Figure 1.—The bottom of the lake, where the macrophytes grow. Arrow points to the underwater log on whose branches the *Meyenia* grows.

Figure 2.—The great transparency of the water several metres deep at a distance of 50-100 m from the shore. Between the rocks grow macrophytes.

The pH changes in the Clear Lake Reserve (Fig. 4) oscillated around 5.8. The highest measured was in 1994, 5.95, and the lowest in 1992, 5.73. The trend of decline over the 30 years was stable, lowering but not much. Total phosphorus concentration (Fig. 5) seemed to decrease steadily between 1980 and 1994, by half — from 5.5 to 2.8 AU.

Discussion

Meyenia (a symbiotic organism) had the most compounds absorbing UV, the amount being five times that of *Lobelia* and over 20 times that of *Eriocaulon*. This fact is difficult to explain, and we can only speculate that the macrophytes could have evolved additional different protective mechanisms against UV radiation. The inflorescences of these two macrophytes extend above the surface of the water, and are thus exposed to UV, and indeed the whole plant can be exposed to radiation when water levels are low, so they would need protection against UV at least for part of the period of their ontogenesis. It is thus strange that both have low concentrations of phenolic compounds, and there must be some factor other than UV that is responsible for the low phenolics level.

Room temperature and laboratory light conditions, after seven days, caused the concentrations of compounds absorbing at 325 nm to increase in the sponge, but to decrease in both of phenolic concentrations by 50-80%,

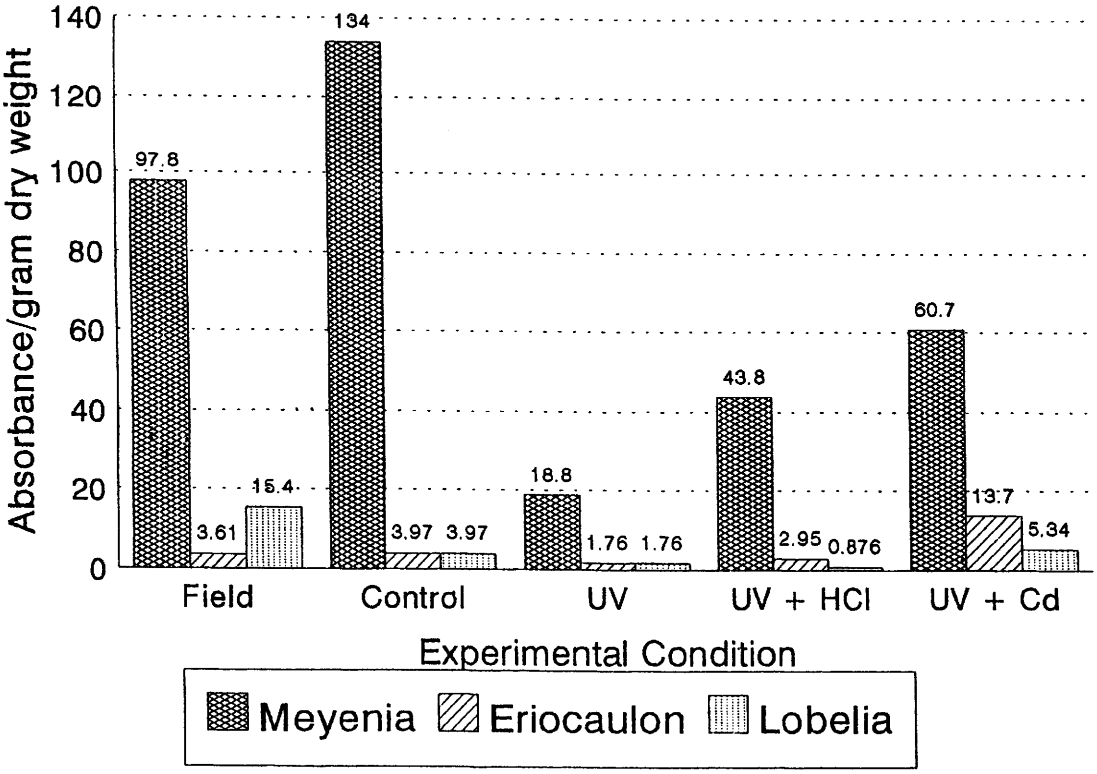

Figure 3.—UV absorbance of *Loeblia dortmanna*, *Eriocaulon septangulare*, and *Meyenia fluviatilis* under various conditions. (UV spec. wavelength of 325nm, experimental wavelength of 366nm).

compared to the control, and by this criterion the stress caused by UV alone (i.e., 80%) was the strongest, showing the lowest concentration of phenolics. However, with acidification, and even more with added cadmium, the lowering of the phenolics concentrations was less pronounced. As stresses in higher plants have been found to increase these concentrations, as in the case of two species of pine (Zobel and Nighswander, 1990, 1991) our present results are unexpected and difficult to explain without further investigation. We suggest that it could be caused by retardation of biochemical pathways or destruction of compounds already produced by the action of UV, as has been found for many photo-inhibited and photo-stimulated drugs (Zobel, 1999b). The fact that UV alone caused the greatest diminution of absorption suggests how important shortwave radiation is.

It is important from the scientific point of view to have a lake as a model system that is relatively undisturbed, on which both academic and government researchers can conduct studies with base comparisons dating from 1967, a period covering much of the progressing acidification. After the papers of Schindler and Nighswander published in 1970, including the analysis of acidification, and zoological and botanical observations, Clear Lake became the model system for ensuing studies (Banks, 1981; MNR report, 1990). Recently macrophytes have been investigated (Sandstrom, 1990; Zobel et al., 1996), and most recently the freshwater sponge was added to the investigation (Cybulski, 1997).

Besides scientists, other groups of people with different interests have been benefiting from formation of this Clear Lake Reserve area. Tourists appreciate the beautiful undisturbed ecosystem, and by learning about the existence of 400-year-old hemlock they appreciate and admire more the beauty of Nature, and the need to preserve it for future generations. Leaving a protected and undestroyed pool of genes of such unique old trees is our responsibility. It is also necessary to protect the surrounding area containing 120-year-old pine forests, as their existence is a necessary precondition for development of the next hemlock old growth. Since a succession of pine and hemlock takes centuries, and since it is important for it to be undisturbed for the next generation, there needs to be very careful planning of future management in that area.

The pH changes in the Clear Lake Reserve were not dramatic over the past 30 years of research, but increased from 1992 until the present. The large changes in pH could be followed by changes in phosphorus availability over that period. The decrease in pH occurred over two periods: 1981-83 and 1990- 94. The pH changes followed the phosphorus concentration except during the 1992-94 period, an unexpected finding, as increased pH lowers phosphorus concentration.

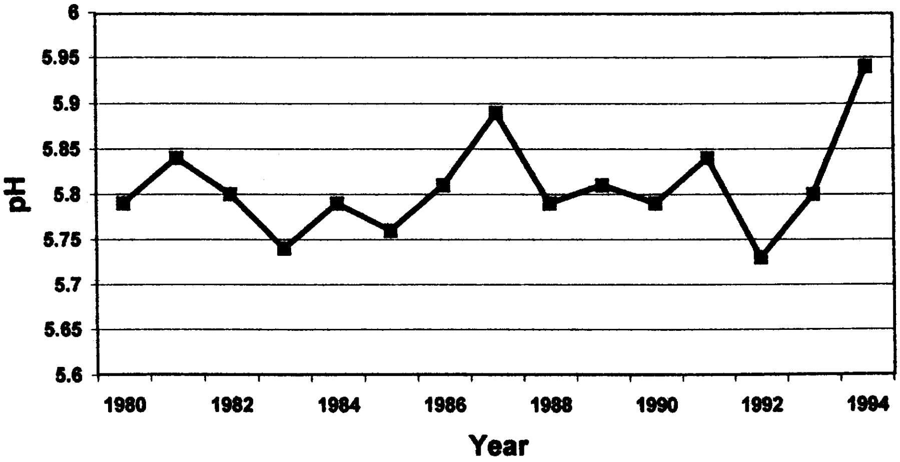

Figure 4.—Clear lake pH 1980 to 1999.

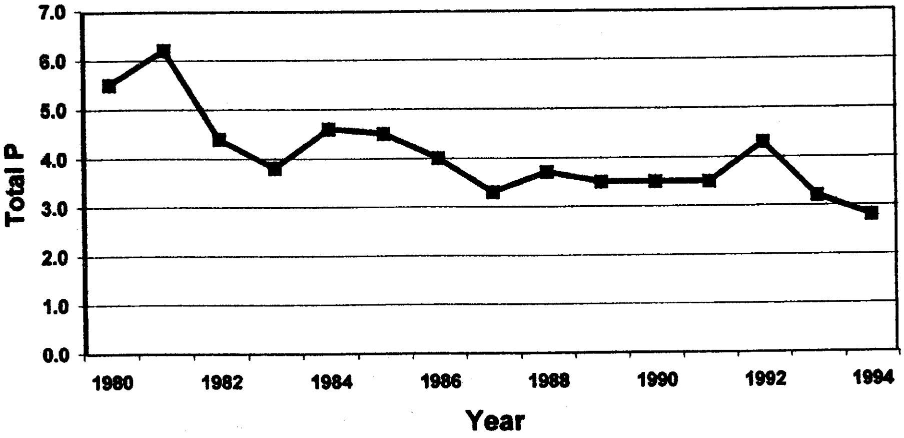

Figure 5.—Clear lake total phosphorus.

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Phytochemistry of Plants Associated with a 400-Year-Old Stand of Hemlock at Clear Lake Reserve, Ontario

A. M. Zobel[1], K. Glowniak[2], J. E.Lynch[3], S. Dudka[4] and A. Alliota[5]

Abstract

Several species of higher plants and mushrooms have been surveyed growing under the canopy of old stands of hemlock surrounding Clear Lake near Minden, Ontario. Some of the hemlock seedlings growing on fallen trunks together with debris in which they were growing were brought to a greenhouse in pots, and some of them were transferred into sandy soil. The conditions of growth involved a gradient of shading. As an analysis of the debris revealed a low pH, the soil in all pots was kept at a pH of 5.5. The best growing seedlings were in the most shaded areas in pots filled with plant debris and the worst growth was in sandy soil in full sunlight. We have measured the concentration of phenolic compounds, which was found to be highest in dying plants in sandy soils in full sunlight, and lowest in shaded areas in pots filled with debris.

Introduction

Phytochemistry deals with the analysis of plant chemicals called natural products, and with changes occurring in such chemicals due to alterations in environmental conditions. Ecology nowadays includes an increased amount of chemistry because communication between a plant and its environment depends to a large extent on secondary metabolites (Zobel and Brown, 1996), of which phenolics make up *ca.* 100,000 different structures (Harborne, 1994). These compounds are involved as well in allelopathy, dealing with the interactions between two plants, which process can change depending upon variations in the phytochemicals produced under particular environmental conditions (Zobel *et al.*, 1999).

Natural conditions in the old growth of hemlock surrounding Clear Lake near Minden have been ideal for investigation of plant-plant interactions and as a source of plants used sometimes as reference samples for the model system because the chemistry of the environment in which they grow has been extensively studied over the past 30 years. Success of preserving 1500 km^2 of the Clear Lake Reserve a few years ago, is an example of how the public, foresters, academics and government can work together. Now we know that our research will continue to be relevant because the preserve is the common denominator for other studies. Since *Tsuga canadensis* has been used as a medicinal plant for at least 500 years (Erichson-Brown, 1979), we chose to investigate it as well as one of the macrophytes, *Eriocaulon.* (Fig. 1).

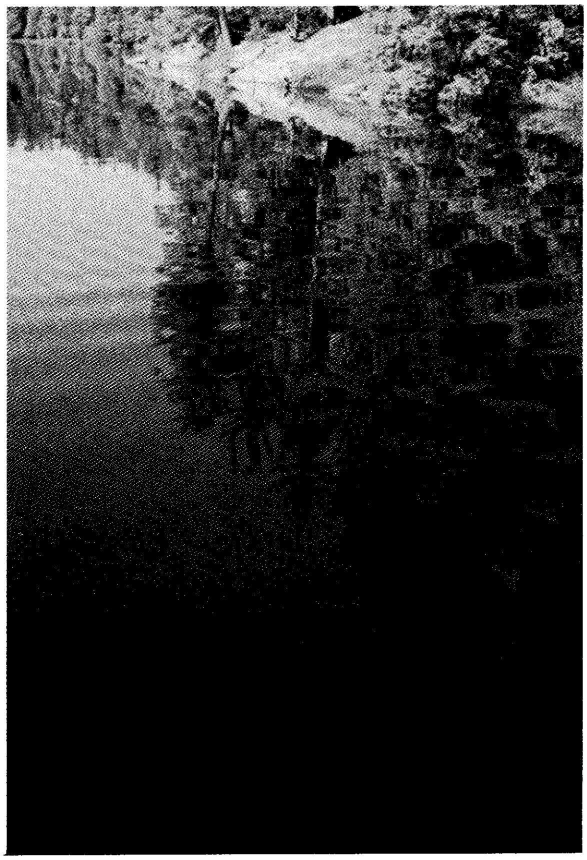

Figure 1.—*Eriocaulon* growing on the bottom of Clear Lake, with stones visible as low as 6 m from the surface, owing to clarity of the water.

Material and Methods

Seedlings of hemlock were removed from fallen, decaying logs of this species (Fig. 2), and transferred into pots containing sandy soil with the pH adjusted to 5.5, or, for comparison, 3.5, as this is almost the lowest pH of acid rain found in this region. Some plants in a Trent University garden were left in the full sun, some were placed in full shade, and the third group in partial shade under a maple tree. The samples were taken after one week, because from our previous experiment we had found that measurable results were obtained after this period (Zobel *et al.*, 1995). The concentration of phenolic compounds was evaluated following the method of Harborne (1964, 1967), using a Nova spectrophotometer at 325 nm, because both flavonoids and coumarins absorb there.

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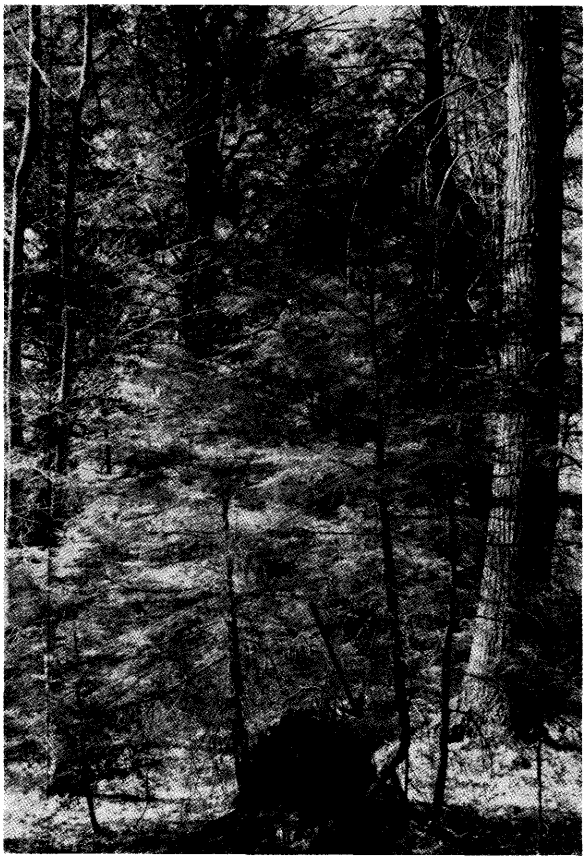

Figure 2.— Decaying stump of old hemlock provides a home to seedlings (arrow) of hemlock. Various age small hemlock trees are visible near the old ones (O).

Warburg apparatus was used for measurement of the oxygen released as an evaluation of catalase activity after *Eriocaulon* from Clear Lake had been exposed to 366nm UV itself or UV and HCl of pH 5.5 or UV and 100 ppm cadmium.

Results and Discussion

The reaction of hemlock seedlings to pH and shading is shown in Table 1. The greatest growth was observed in shaded areas when the pH was 5.5, and the seedlings grew better than under the same light conditions but in more acidic soil. The concentration of phenolics was inversely proportional to depth of shade, and the most phenolics were in dying plants grown in full light and pH 3.5. The worst growing seedlings had almost double the phenolics concentration of the best growing. Increased production of phenolics can be an indication of stress, the response to which is production of the phenolics (Zobel and Nighswander, 1990), but if the plant exceeds a certain threshold some cells inside the leaf would die because of precipitation of their proteins by the phenolics, forming microscopic necroses that, after further reaction, would cause death of the whole leaf. We observed a similar reaction of switching on defense-phenolic compounds both in pine (Zobel and Nighswander, 1991), and in rue shrubs (Zobel *et al*, 1993), when exposed to simulated acid rain or sprays of aluminum or sodium chloride, which would lead to death of the cells. We proposed a very simple test (Zobel, 1986; Zobel and Nighswander, 1991) which could be applied by foresters under field conditions, by performing a reaction for phenolic compounds on hand-cut cross-sections of pine and hemlock needles to locate necrosis and evaluate the stage of suffering of leaves from toxification.

Lakes are included in this 1500 km^2 area. Aquatic plants can be used as indicators of changes in environmental conditions, thus the reaction of our model system, *Eriocaulon*, was used for the evaluation of the plant's ability to scavenge free radicals, by measurement of catalase activity. The results are shown in Figs. 3-4, where we can see that differences were substantial between plants treated with normal light and 366nm UV. The reaction of the extract from the whole plant was different from that of the surrounding water, and roots and shoots, after being separated, showed differences in activity. The reaction of the compounds extruded to the surrounding water, which extensively absorbs UV, can be protective as a shield. This is what we observed under laboratory conditions, but under field conditions the extruded compounds would be quickly diluted. This suggests that there is still another explanation for the high concentration of extruded compounds —possibly the elimination of toxic compounds synthesized in the cells that, if retained within the vacuoles of these cells, might eventually precipitate the proteins, causing cell death. To explain the process, acidification of the lakes in this area should be closely monitored by forest managers, because leachate from forest soils and decaying plants, as well as exudate from living plants, is a substantial source of organic compounds and minerals usable by the fauna and flora in both forest and lake.

It is beneficial to leave behind undisturbed areas of forest larger than merely small clumps, because the smaller ones could be devastated by wind and the larger ones have the possibility of succession of one kind of forest by another, and continuous natural development of the old growth. The role of foresters should be to find such old growth areas, and recommend to governments protection of such areas. If the public is more aware of the process, the pressure on government could be exerted to designate more such areas as the Clear Lake Reserve.

Table 1.—Hemlock Seedling Growth and Phenolic Compound Concentration as Affected by pH and Light Conditions.

pH	Conditions Full light growth phenolics		Semi-shade growth phenolics		Full shade growth phenolics	
		AU		AU		AU
5.5	++	100±18	+++	90±10	+++++	70±15
3.5	±	120±25	+	100±10	++	100±15

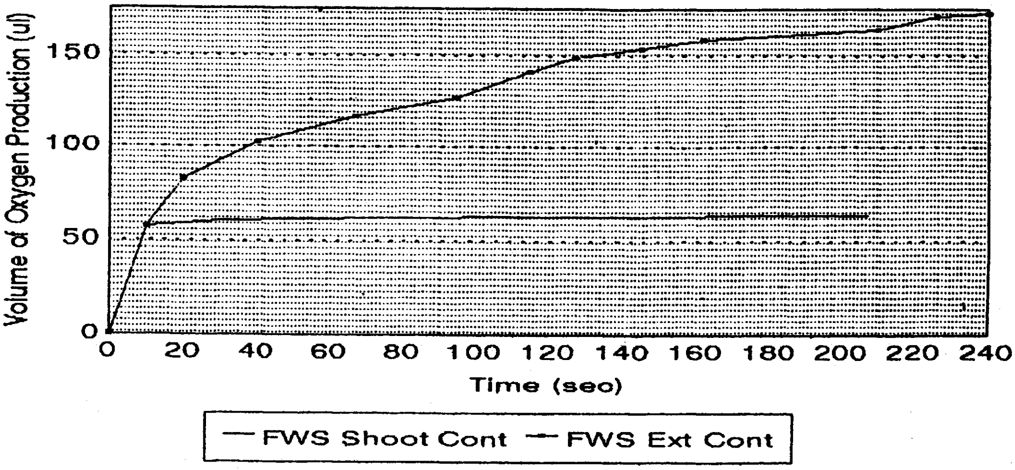

Figure 3.—Catalase-catalysed oxygen production during four hours after visible light treatment of *Eriocaulon*.

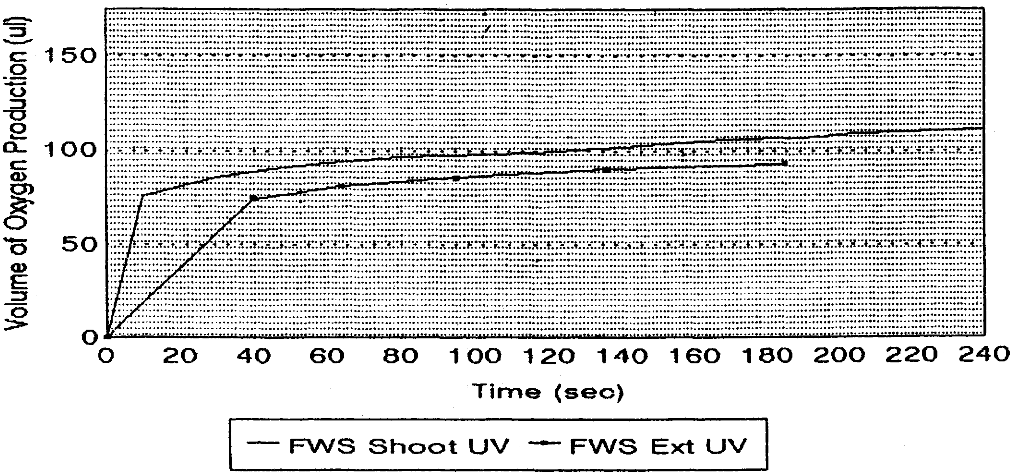

Figure 4.—Catalase-catalysed oxygen production during four hours after UV treatment of *Eriocaulon*.

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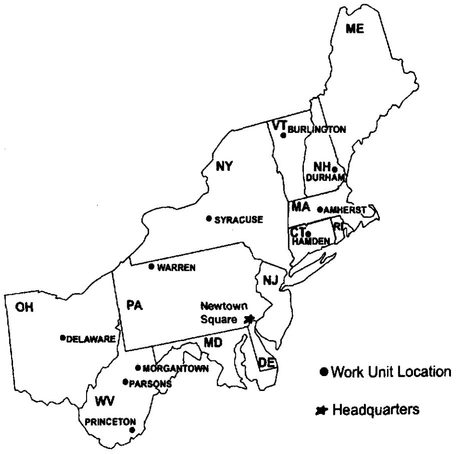

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