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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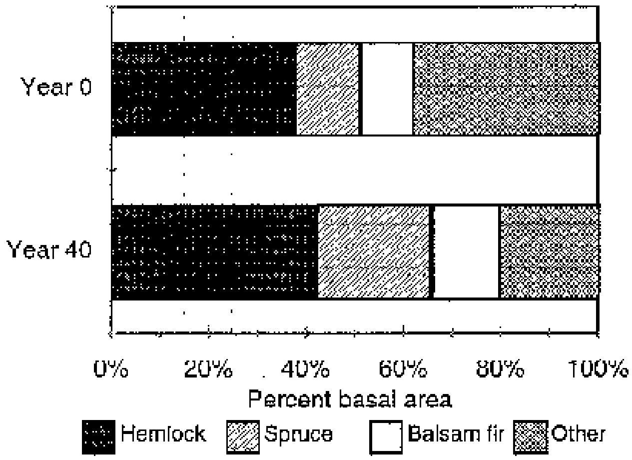

Figure 1.—40-year change in species composition. Vertical dashed lines indicate upper and lower limits of eastern hemlock species composition goal (15-25%).

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

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.

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.

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.

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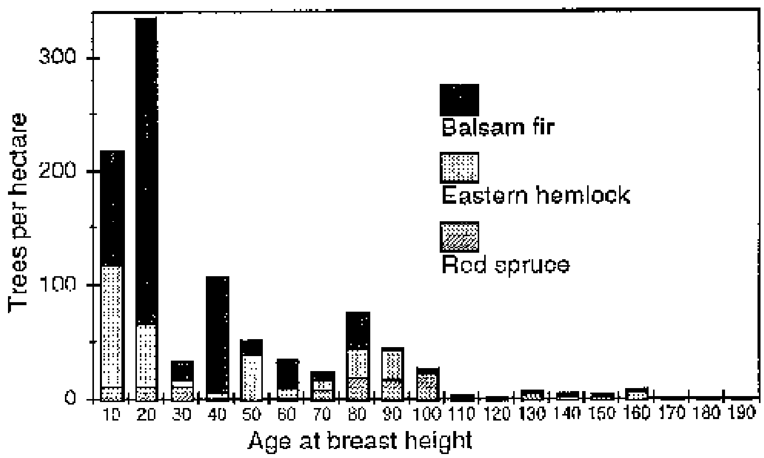

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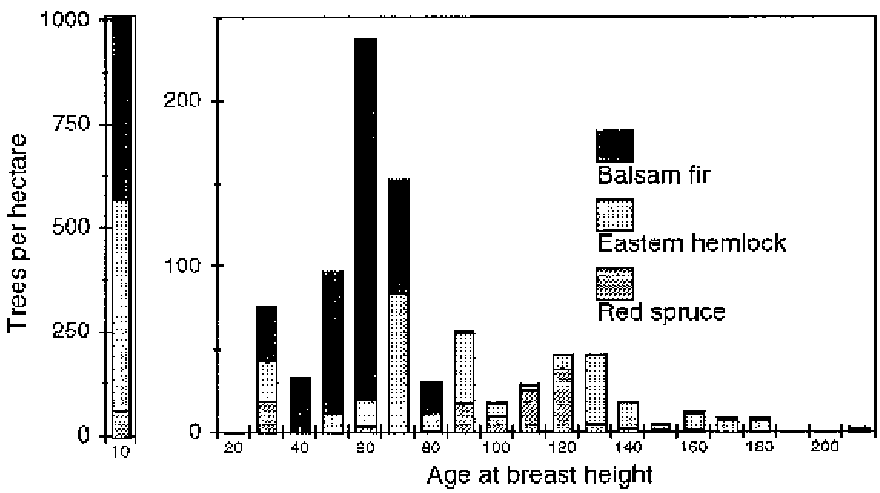

Figure 2.—Age structures for the three dominant species in the Penobscot Experimental Forest 5-year selection stands.

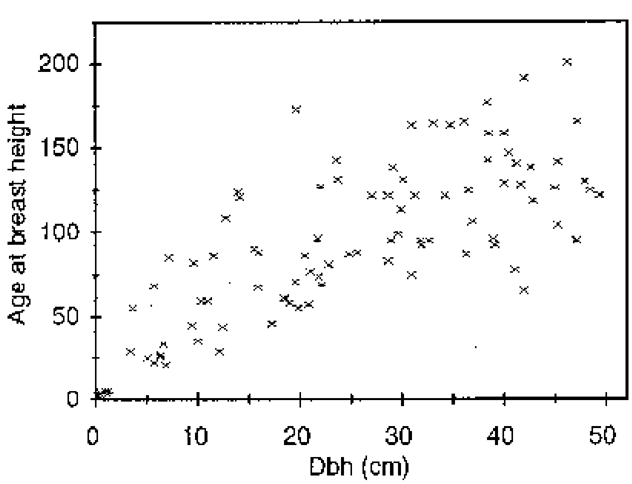

Figure 3.—Eastern hemlock age-size relationship.

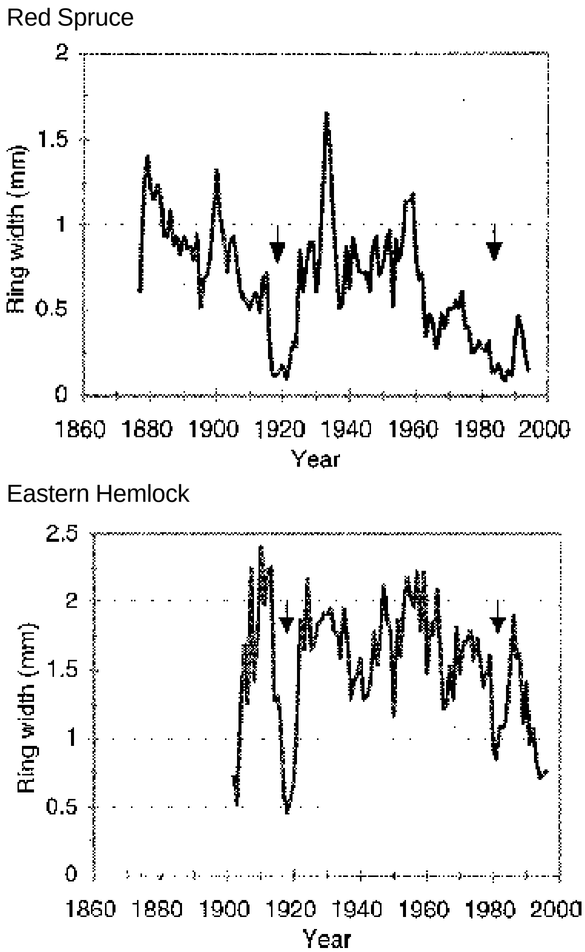

Figure 4.—Examples of individual trees showing budworm suppression.

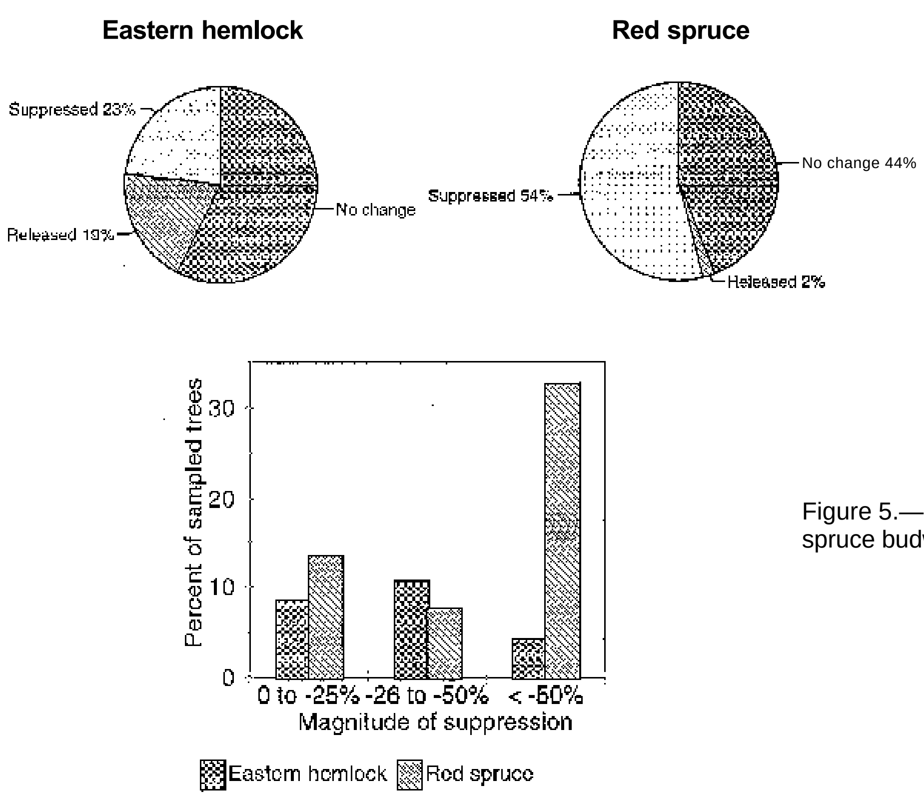

Figure 5.—Radial growth patterns during spruce budworm outbreak ca. 1913-19.

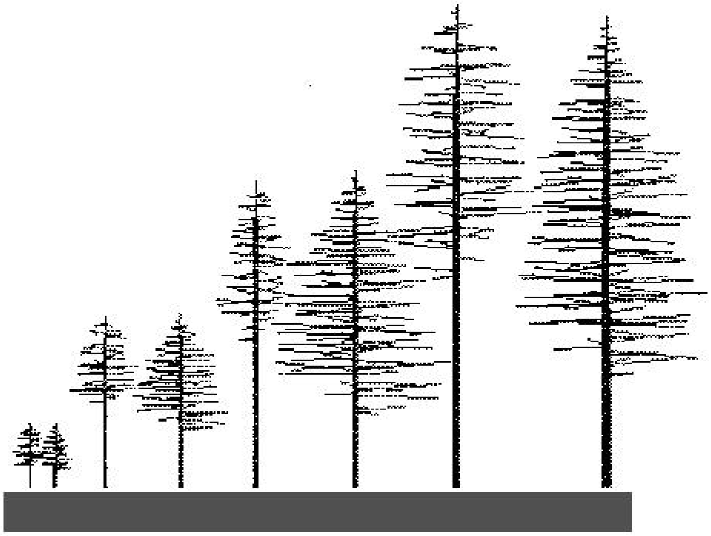

Figure 6.—Crown development of eastern hemlock and red spruce in the Penobscot Experimental Forest 5-year selection stands. Within each stratum, red spruce is shown on the left and eastern hemlock is shown on the right.

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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