STAND DYNAMICS OF MIXED-SPECIES
CONIFER FORESTS IN MAINE

by
Mary Ann Fajvan
B.S. Cook College, Rutgers University, 1981
M.F.S. Yale School of Forestry and Environmental Studies, 1983

A DISSERTATION
Submitted in Partial Fulfillment of the
Requirements for the Degree of
Doctor of Philosophy
(in Forest Resources)

The Graduate School
University of Maine
August, 1991

Advisory Committee:

Robert S. Seymour, Curtis Hutchins Associate Professor of Forest
Resources, Committee Chairman
Russell D. Briggs, Assistant Research Professor of Forest Resources
Michael S. Coffman, Champion International Corporation, Adjunct
Professor of Forest Resources
George L. Jacobson Jr., Professor of Botany and Quaternary Studies
Alan S. White, Associate Professor of Forest Resources and H.W.
Saunders Professor of Hardwood Silviculture
STAND DYNAMICS OF MIXED-SPECIES CONIFER FORESTS IN MAINE

by Mary Ann Fajvan


Forest stands of red spruce (Picea rubens Sarg.), eastern hemlock (Tsuga canadensis (L.) Carr.), and white pine (Pinus strobus L.) were found to have a multicohort structure. Partial disturbances from insect outbreaks and harvesting affected stand development by initiating a new cohort of trees and causing a growth response in surviving trees. The shade-tolerant red spruce and eastern hemlock comprised more cohorts than the shade intolerant white pine. Stands displayed a vertically stratified canopy with pine usually being the tallest followed by spruce and hemlock. There was more canopy growing space potentially available beneath a dominant pine crown than beneath a dominant spruce or hemlock crown. Total stemwood volumes of sample plots were more affected by variability in age structure than by the presence or absence of pine. Plots with a representation of two or three cohorts were more productive than plots with a single cohort. Management of pine-hemlock-spruce mixtures should focus on 1) maintaining a dominant pine component 2) establishing pine regeneration and 3) maintaining a multicohort structure through implementation of the irregular shelterwood method.

In stands of shade tolerant balsam fir (Abies balsamea L. Mill.) and red spruce, dominant and codominant red spruce trees showing a history of periods of radial growth suppression produced lower site indices than spruce
that had always grown freely. Methods that adjusted or eliminated periods of suppressed growth increased estimates of site index and equated them with the site indices of the freely growing trees. Trees that had experienced competition-induced periods of reduction in diameter growth may also have experienced reductions in subsequent height growth.
ACKNOWLEDGEMENTS

I would like to acknowledge the friends and colleagues whose support and encouragement were invaluable to me during my tenure at the University of Maine. A special thanks to Bob Seymour, my major advisor, for sharing his wisdom in silviculture and guiding me through the development and completion of my research. I also thank the rest of my committee, Russell Briggs, Michael Coffman, George Jacobson and Alan White, for their patience in dealing with my questions and in review of this manuscript. In addition, I thank Champion International Corporation Inc., for their financial support and for providing the study areas used in my research.

Many others were involved in this research and I express my gratitude to them. A special thanks to Ron Lemin for refreshing my memory of SAS; to Ingrid Bartsch and Kitty Elliott for much needed moral support; and to my parents Mary Ann and George Fajvan for always standing behind me with their love and encouragement.

The most special "thank you" is to my husband Rob Lynn, who kept me going through the good and bad times and whose love, patience and encouragement were most crucial to this work.

This work is dedicated to the memory of Gím Gumkin
# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acknowledgements</td>
<td>i</td>
</tr>
<tr>
<td>Table of Contents</td>
<td>ii</td>
</tr>
<tr>
<td>List of Tables</td>
<td>iv</td>
</tr>
<tr>
<td>List of Figures</td>
<td>v</td>
</tr>
<tr>
<td>Dissertation Format</td>
<td>vi</td>
</tr>
<tr>
<td>Chapter One: The influence of growth history and soil type on estimation of site index for red spruce.</td>
<td></td>
</tr>
<tr>
<td>Abstract</td>
<td>1</td>
</tr>
<tr>
<td>Introduction</td>
<td>2</td>
</tr>
<tr>
<td>Methods</td>
<td>3</td>
</tr>
<tr>
<td>Results and Discussion</td>
<td>9</td>
</tr>
<tr>
<td>Conclusion</td>
<td>13</td>
</tr>
<tr>
<td>Literature Cited</td>
<td>15</td>
</tr>
<tr>
<td>Figure Captions</td>
<td>23</td>
</tr>
<tr>
<td>Appendix A</td>
<td>29</td>
</tr>
<tr>
<td>Chapter Two: Structure and development of multicohort stands of white pine, hemlock and red spruce in eastern Maine.</td>
<td></td>
</tr>
<tr>
<td>Abstract</td>
<td>31</td>
</tr>
<tr>
<td>Introduction</td>
<td>32</td>
</tr>
<tr>
<td>Methods</td>
<td>35</td>
</tr>
<tr>
<td>Results</td>
<td>41</td>
</tr>
<tr>
<td>Discussion</td>
<td>51</td>
</tr>
<tr>
<td>Literature Cited</td>
<td>55</td>
</tr>
</tbody>
</table>
Chapter Three: Effect of stand composition and structure on volume production of mixed-species conifer stands in Maine.

Abstract 98
Introduction 99
Methods 102
Results 107
Discussion 109
Conclusion 115
Literature Cited 116
Figure Captions 128
Appendix C 145
Biography 148
LIST OF TABLES

Table 1.1 Climatic description of study area 8
Table 1.2 Patterns of development in increment cores 9
Table 1.3 Mean site indices of free-growing and suppressed trees 20
Table 1.4 Site indices of stem-analyzed trees by suppression history 21
Table 1.5 Soil quality affects on site index 22
Table A.1 Criteria for classification of soil profiles 30
Table 2.1 Documented outbreaks of insects and disease 58
Table 2.2 Species composition and density by stand 59
Table 2.3 Evidence of timber harvests 60
Table 2.4 Combined age classes used in chi-square analyses 61
Table B.1 Percentage growth increases by decade 96
Table B.2 Percentage growth decreases by decade 97
Table 3.1 Ranking of plot basal areas 119
Table 3.2 Total volumes of pine and no-pine plots 120
Table 3.3 Sawlog volume of pine and no-pine plots 121
Table 3.4 Total volumes of pine and no-pine plots by species 122
Table 3.5 Mean age of dominants for pine versus no-pine plots 123
Table 3.6 Mean height of dominants for pine versus no-pine plots 124
Table 3.7 Growing space efficiency of subject trees 125
Table 3.8 Percentage crown area overlap of subject trees 126
Table 3.9 Mean volume by cohort of pine and no-pine plots 127
Table C.1 Characteristics of site trees on pine plots 146
Table C.2 Characteristics of site trees on no-pine plots 147
LIST OF FIGURES

Figure 1.1 Location of study area 24
Figure 1.2 Procedure to establish free-growth period (1936-75) 25
Figure 1.3 Five radial increment patterns of development history 26
Figure 1.4 Mean annual height growth versus total height in 1936 27
Figure 1.5 Relationship of mean annual height and radial growth 28
Figure 2.1 Location of study area 64
Figure 2.2a-e Height distribution by stand 65-69
Figure 2.3a-e Crown class distribution by stand 70-74
Figure 2.4 Age-class distributions 75
Figure 2.5 Age-class distribution of pine 76
Figure 2.6a-e Stand diameter-class distributions 77-81
Figure 2.7a-c Age versus diameter by species and stand 82-84
Figure 2.8a-c Growth decreases occurring each decade 85-87
Figure 2.9a-e Growth increases by decade and cohort structure 88-92
Figure 2.10 Radial growth patterns for spruce and hemlock 93
Figure 2.11 Radial growth pattern for pine 94
Figure 3.1 Determination of crown-area overlap 130
Figure 3.2 Mean basal area of pine and no-pine plots by stand 131
Figure 3.3a-e Mean height of diameter classes by stand 132-136
Figure 3.4 Growth strategy 1: White pine 137
Figure 3.5 Growth strategy 2: White pine 138
Figure 3.6 Growth strategy 1: Spruce and hemlock 139
Figure 3.7 Growth strategy 2: Spruce and hemlock 141
Figure 3.8 Growth strategy 3: Spruce and hemlock 143
This dissertation consists of three chapters. Chapter 1 discusses a particular research project and Chapters 2 and 3 examine a second project. Tables, figures, literature citations and appendices appear at the end of the chapter in which they are referenced.
Chapter 1. The Influence of Growth History and Soil Type on Estimation of Site Index for Red Spruce

ABSTRACT

Shade tolerant species from stands with a history of partial disturbances are not usually considered suitable for site-index determination because the effects of growth history on height growth may mask site influences. This concept was examined in stands of shade-tolerant conifer species that are capable of enduring prolonged periods of growth suppression and still attain dominance. Dominant and codominant red spruce (*Picea rubens* Sarg.) trees with various histories of growth suppression showed lower unadjusted site indices than trees that had always been growing freely. Two methods were tested to remove or adjust for periods of growth suppression: 1) Suppressed periods of radial increment, examined in increment cores taken at 1.37 m, were adjusted or eliminated to represent growth rates when a tree was growing freely. 2) Height/age pairs from stem-analyzed trees were used to identify a known 40-year period without disturbance; site index, and height and diameter growth rates were calculated for this period only. Results showed that a dominant tree with a past history of suppression can be used to predict site index if suppressed periods are appropriately adjusted. A positive linear relationship between height and diameter growth suggested that trees that have experienced competition-induced periods of reductions in diameter growth may also experience reductions in subsequent height growth. This is a deviation from the assumption that height growth is independent of stand density, which is a major determinant of the site-index concept.
INTRODUCTION

The concept of using tree height to predict the potential of forest land to produce wood volume is based on the assumption that height growth is influenced more by site quality than by stand density. The use of site index, the average height of dominant and codominant trees at a specified index age, in predicting the productive capacity of forest land assumes that 1) a given forest stand is even-aged and 2) the dominant or codominant trees have always had a dominant crown position (Spurr and Barnes 1980). Both assumptions can be violated in forest stands that have experienced partial disturbances and contain shade-tolerant species.

Mixed stands of the shade-tolerant conifers red spruce (Picea rubens Sarg.) and balsam fir (Abies balsamea (L.) Mill.) occupy 46 percent of the forested area of the state of Maine. These species provide the major source of pulpwood to a large paper industry (Seymour 1991). Concern for future wood supplies prompts forest managers to focus regeneration efforts on land with the highest yield potential. Under current assumptions, site index is probably not a reliable measure of potential site productivity in spruce-fir forests. Partial disturbances such as harvesting and insect outbreaks have created stands with more than one age class. In addition, the ability of spruce and fir to endure prolonged periods of growth suppression as advance seedlings and saplings (Frank 1990; Blum 1990) makes it difficult to find trees that have always been dominant.

Many attempts have been made to derive satisfactory measures of site index for spruce-fir forests in Maine. Some researchers devised methods for determining site index for stands that had been partially disturbed using trees with periods of growth suppression (Young 1954; McLintock and Bickford 1957;
Safford 1968). These methods have not been widely applied. The data used in more recent studies were from carefully selected, even-aged stands that were relatively undisturbed (e.g. no recent harvesting) (Curtis 1964; Brewitt 1971; Johnson 1976; Allen 1978; Schlitz 1978; Vicary 1982). These and other studies (Davis 1989) suggest that red spruce achieves dominant crown status through a variety of development patterns.

The specific objectives of this study are: 1) to evaluate the utility and assumptions of site index in all stand conditions where red spruce occurs, including stands that are not even-aged; and 2) compare red spruce site indices among a variety of soil classes.

**METHODS**

*Study Area*

The study areas were located on Champion International Corporation Inc., land in Hancock, Washington, and south-eastern Aroostook Counties, Maine (Fig. 1.1). Temperature and precipitation data, summarized from National Oceanic and Atmospheric Administration weather stations, are shown in Table 1.1. Sample locations were randomly selected throughout these areas from Champion’s Permanent Growth Sample (PGS) plot data base. Red spruce is widely adapted to a variety of stand and site conditions, which vary according to soil drainage and topography (Seymour 1991). The study plots represented a range of site conditions.

*Plot Selection*

Permanent growth sample (PGS) plots were established by Champion at 100 m intervals along randomly located cruise lines of five plots each. The
Sample plots for the current study were selected following examination of this data base. Cruise lines with at least two of five plots with red spruce or balsam fir as the main species components were chosen for further examination. Selected cruise lines were then prioritized according to the number of plots per line containing red spruce and balsam fir. Plots that were known to have been harvested during the last five years were excluded.

Plot data were collected during the summers of 1987 and 1988. A total of 360 plots (168 in Washington Co., 117 in Hancock Co. and 75 in Aroostook Co.) were visited.

**Site Tree Selection**

Trees were considered suitable as site trees if they were a dominant or codominant (Smith 1986) red spruce or balsam fir and had been growing freely since attaining breast height (as determined by a lack of suppressed radial growth in an increment core). Dominant trees with a history of suppression were sampled only if a free-growing tree was not available. Site trees were selected from individuals surrounding the PGS plots that were in the same stand and on the same soil type as the PGS plot trees. Other visual considerations for tree selection were healthy crowns and unforked tops. Generally, three trees per plot were sampled for site index. If at least two suitable trees were not available, the plot was rejected. Total height, diameter at breast height (1.37 m), and an increment core taken at breast height, were collected for each site tree. Repeated cores were taken, if necessary, in an attempt to include the pith. A total of 698 red spruce and 160 balsam fir were measured; discussion of the balsam fir data is not included in this paper.

The stems of 98 trees, including 34 of the cored site trees, were also analyzed by stem dissection. An attempt was made to select stem-analyzed
trees in pairs -- one tree growing freely and the other with pith suppression at breast height followed by release. Before a tree designated for stem analysis was felled, a point on the stem 1.37 m from the ground was measured and marked. The tree was then felled and diameter outside bark was measured at .15 m, 1.37 m, 3 m, and every 1.5 m up the stem. Stem cross-sections were then removed at these points. For the initially suppressed trees, the height of release from suppression was determined by noting the approximate height where radial suppression ceased in additional cross sections. Cross sections were air dried, sanded, and annual radial increments measured to the nearest .01 mm along the average radius of each section using a Measuchron®.

Soil Classification

A soil pit, as deep as the bottom of the rooting zone, was excavated near the center of each plot. The total depth and the depths of the major soil horizons were measured, and the texture of the B-horizon was determined. Profiles were classified according to the criteria used by Champion International Corporation Inc., (Table A.1, Appendix A).

Increment Core Analyses

Increment cores were sanded and annual growth rings counted with the aid of a microscope. Suppressed periods were identified as abrupt reductions in the width of radial growth rings, which were visually obvious as groups of very narrow (usually < 1mm) growth rings. The dates of these suppressed periods were also identified. A "breast-height age" was determined for all site trees based on the actual number of growth rings counted on a core plus an estimated number of additional missing rings if the core did not contain the pith (Applequist 1958). Even though an attempt had been made to select free-
growing trees in the field, 42 percent of the cores taken from dominant site trees showed either short (5-15 year) periods of suppressed growth interspersed with free growth, or a 10-30 year period of suppression at the pith followed by free growth, or a combination of these.

If a core showed a period of suppression at the pith and then release, a "release age" was calculated by subtracting the suppressed period from the total age. An "adjusted age" was also calculated for trees showing suppression starting at the pith and followed by release, or any other abrupt reduction in growth, followed by release. Calculation of "adjusted age" entailed measuring the length of the suppressed period and then replacing the number of narrow growth rings found in the suppressed period with the number of wider rings found in the adjacent free growth period of equal length. For suppressed trees, the "adjusted age" was always less than the "breast height age" and slightly greater than the "release age".

Data Analyses

Site Trees.: The age data obtained from the increment cores and their corresponding measures of tree height were used in site-index equations derived by Scott and Voorhis (1986) from Meyer's (1929) yield tables for red spruce (Equation 1). Equation (1) predicts site index based on total age, but because the inputs are from breast height increment cores, the program iteratively computes both site index, time to reach breast height, and total age. Site index was also calculated substituting "release age" and/or "adjusted age" for "breast-height age" in equation (1). Subsequently, Carmean et al. (1989) published a similar equation using age at breast height to calculate site index directly. Equation 2 was used to calculate site indices for the stem-analyzed
trees. Because both the equations are derived from Meyer's yield tables they are assumed to be equivalent.

\[
SI = \frac{[H (1 - e^{-b_3A}) - b_4S_i^{b_5} - b_1]}{B_2}
\]  

where:
- \(SI\) = site index
- \(H\) = total tree height
- \(A\) = total age, and
- \(b_i\) = regression coefficients designated by species

\[
S = BH + c_1HC_2 (1-e^{c_3A})c_4HC_5
\]  

where:
- \(S\) = site index
- \(BH\) = 1.37 m (if age at breast height used) or 0 (if total age is used)
- \(H\) = height
- \(A\) = breast height or total age
- \(c_i\) = regression parameters

In order to determine the difference in site index between suppressed and free-growing trees, the mean site index for all trees showing one or more types of suppression was compared with that for free-growing trees. All site-index comparisons were stratified by soil class.

Stem-Analyzed Trees: The height-age data from the cross sections of the stem-analyzed trees were used to determine the actual height of each tree at age 50. The number of growth rings on each section were counted and the
height of that disk recorded, creating a series of height-age pairs for each tree. Of the 98 trees, 67 were at least 50 years old at breast height permitting site index to be determined directly. Ages at breast height were used so that results would be comparable to those derived from the increment cores.

Mean site indices based on stem-analyzed trees were calculated for free-growing and suppressed trees. Suppressed trees were classified into two groups: 1) trees that showed suppression on the stump disk and then release by the time they reached breast height (e.g., no pith suppression on the breast height disk), and 2) trees showing suppression at breast height followed by release.

An attempt to eliminate the potential effects of growth suppression on site index was made using free-growth in height instead of free-growth in diameter. A free-growth period for each tree was established based on the height and age of the two stem sections that represented the height of the tree in 1936 or later, and the stem section that represented the height of the tree in 1975 or earlier. These two height-age pairs spanned the growth period when the spruce budworm was virtually absent from this region of Maine. Based on the "two-point" principle of growth curve construction (Zeide 1978), a FORTRAN program was used iteratively to determine the exact site-index curve (Equation 2) that included both height-age pairs (Figure 1.2).

Height and diameter growth relationships: The two stem sections previously described for eliminating the effects of growth suppression on site index were also used in calculating mean annual height growth. The data were further screened to remove potential long-term growth reductions resulting from delayed recovery from the 1910-20 spruce budworm defoliation or the effects of competition. The mean annual radial growth (determined from the stem section taken at 1.37 m) was calculated for 10-year periods. Those trees with an
average radial growth rate of greater than 1 mm/year (Lorimer 1980) during each decade of the entire "budworm free" time period 1936-1975 were considered sufficiently recovered from defoliation to use in calculating height-growth rates. This procedure eliminated 14 trees from height calculations. The difference in height between the two stem sections was determined, and the mean annual height growth for the free-growth period was calculated. Regression with dummy variables (Cunia 1973) was used to determine if the relationship between mean annual height growth and mean annual diameter growth (determined from the stem section at 1.37 m) for each of the three soil classes would be described by a single equation.

RESULTS AND DISCUSSION

Growth-Reduction Patterns

Despite careful attempts to select free-growing site trees, 42 percent of the sample showed some degree of growth suppression (Table 1.2). Some trees showed pith suppression in addition to other types of suppression interspersed with periods of free growth. Other types of suppression were identified according to the years of occurrence as: 1) old (1910-20) spruce budworm suppression; 2) recent (1977-83) budworm suppression, or 3) suppression during other decades presumably from competition (Fig. 1.3). The most common type of suppression was from the "old" spruce budworm outbreak.

Adjusted Site Indices

The periods of growth suppression of the site trees had to be addressed to meet the assumptions of the site index concept. The procedure used to
adjust for or eliminate periods of suppressed growth was assessed by comparisons of site indices calculated from free-growing trees with those from suppressed trees (Table 1.3). Soil classes were included in the analyses to stratify potential site effects. The suppressed trees produced significantly lower site indices than the free-growing trees (on fair and poor soil classes) if suppression history was not accounted for. After adjustments to age, both free-growing and suppressed trees produced equivalent site indices in each soil class.

The observed site indices determined from the stem-analyzed trees (Table 1.4) produced a wider range in site index values between suppressed and free-growing trees than did the values calculated from the increment cores. This is because suppressed trees were specifically selected for this analysis but were discriminated against in the site-tree selection. Similar relationships were found for white spruce growing in the Northwest Territory of Canada, where Alemdag (1988) found poor correlations in site index regressions for young (<10 years) and old (>100 years) age classes. He attributed these low values to a lag in time to reach breast height and in high variation in the height/age growth patterns of older trees, also a result of suppression and release periods.

Site indices calculated for the stem-analyzed trees during the budworm-free period also showed that adjusting for or eliminating periods of growth suppression equalized the mean site index of suppressed trees with that determined using only the free-growth periods (Table 1.4). This comparison was not stratified by soil class due to the small sample size.

Both methods used to account for suppression history appear to be successful at adjusting radial growth suppression in increment cores, and decreases in both radial and height growth in stem-analyzed trees. The success of the method for stem-analyzed trees required an awareness of
growth decreases caused by spruce budworm defoliation and the exact timing of the outbreaks. Monserud (1984) used a similar approach to deal with periods of suppression in inland Douglas fir. He noted that if the suppression occurred after the tree reached the index age (50 years) then only observations taken from stem sections before that period should be used to derive site index.

These results imply that a dominant tree with a history of suppression can be used to predict site index if: 1) suppressed periods of radial growth on increment cores are replaced with free-growth periods, 2) or only predetermined periods (without disturbance such as defoliation) of height growth are used to solve the site index equation independent of age. Implicit in both approaches is the assumption that the site indices derived from age at breast height also reliably account for years needed to reach breast height. The shade tolerance of red spruce (Blum 1990) allows it to survive and grow slowly as a seedling or sapling when overtopped causing great variability in the number of years a red spruce can take to reach breast height, even among trees growing in the same stand. Davis (1989) observed red spruce saplings existing in an overtopped, suppressed condition for 90 years before responding to release after a partial disturbance. After 20-40 years of suppression, released trees were found to quickly attain rates of height and diameter growth similar to free-growing trees in the same stand.

Effect of Soil Groups

Because soil properties may influence site index, a comparison was made between the calculated site index of free-growing site trees and calculated site index of the stem-analyzed trees during the free-growth period for trees in the three soil classes. Site index for both groups was determined on a total-age (=50) basis (Table 1.5). This comparison should provide an
unbiased estimate of potential site differences because all site indices have been determined on a "free-growth basis." Data from the site trees showed that the mean site index of the poor soil class was slightly, but significantly, less than that of the good and fair groups. Data from the stem-analyzed trees showed that the mean site index of the good soil class was slightly higher than that of the fair and poor soil classes. The slight differences in the relationships between the two groups could be due to the differences in sample size. However, the high variability in site indices within each soil group, raises questions about the feasibility of inferring a relationship between the soil classification system used, and height growth as embodied in the concept of site index.

Effect of Variable Suppression History and Competition on Height Development

The high variability in site indices prompted an examination of the effect of age on the ability of suppressed spruces to respond to release from competition. Due to the wide range of ages in the sample, height was used to represent age. Mean annual height growth (averaged over a 40-year period) was compared with tree height in 1936 (post-spruce budworm), to test the hypothesis that height-growth response is limited by permanent reductions in vigor resulting from past suppression. The relationship shows a wide range in rate of height growth for a given tree height (Fig. 1.4). Mean annual height growth was found to be significantly but weakly correlated with the height of the tree in 1936 ($r = -0.39$). This negative relationship suggests that the taller (or older) a tree is, the less likely it will achieve or resume a "normal" rate of height growth after an extended period of growth suppression.

The apparent relationship between diameter and height growth ($r = 0.60$; Fig. 1.5) refutes a major assumption in the use of height growth to predict site
index: that height growth is independent of stand density. The physiological mechanisms that influence height growth are different from those that influence diameter growth (Lanner 1985). The variability in the data was not attributable to soil class because there was no significant difference in the slopes of the lines predicted for each soil group, and one regression line \(y = 0.37 + 0.27x; P<0.001\) adequately represented all three soil classes. The relationship implied by these results also supports the correlation found between height growth and height in 1936. In particular, trees that have limited crown growth due to competition, or old age, which are causes of decreases in diameter growth rate, may also experience reductions in height growth rate and should not be used for determining site index. Trees that showed an average annual radial growth rate of < 1.5 mm had a mean annual height growth rate that was below the average for all trees (Fig. 1.5) resulting in lower site indices.

Methods for adjusting height and diameter growth rates in site trees that have been subjected to periods of temporary growth suppression produce site indices equivalent to those for a tree that had grown freely. The concept of site index assumes that each free-growing tree in a particular stand has an equal chance of becoming dominant or codominant. However, potential sources of variability in height growth may exist such as microsite effects and genetic variation between trees. These factors may also affect the estimation of site index.

**CONCLUSION**

Site index can be estimated from trees that have experienced periods of reduced radial growth if growth reductions are appropriately adjusted. Adjusting periods of growth reduction and focusing analyses on periods known
to be without disturbance proved to be viable methods in stem-analyzed trees. Without such adjustment, site index is uniformly underestimated on all soil groups, possibly masking the true relationship between soil and site index. Correlations between competition-induced reductions in diameter growth-rate with reductions in height growth-rate suggest that methodologies for using previously suppressed codominant and dominant trees for site index purposes should also consider potential affects on height growth. Potential sources of variation in height growth from genetic and microsite differences between trees need to be addressed with regard to using height as a predictor of site quality.
LITERATURE CITED


Table 1.1 Climatic description of study area (Source: National Oceanic and Atmospheric Association)

<table>
<thead>
<tr>
<th></th>
<th>Mean Annual Precipitation (cm)</th>
<th>Mean Annual Temperature (°C)</th>
<th>Mean Monthly Minimum Temp.</th>
<th>Mean Monthly Maximum Temp.</th>
<th>Snow Accumulation (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Washington Co.</td>
<td>113</td>
<td>8</td>
<td>-9</td>
<td>26</td>
<td>128</td>
</tr>
<tr>
<td>Hancock Co.</td>
<td>118</td>
<td>10</td>
<td>-7</td>
<td>25</td>
<td>174</td>
</tr>
<tr>
<td>Aroostook Co.</td>
<td>121</td>
<td>8</td>
<td>-10</td>
<td>26</td>
<td>304</td>
</tr>
</tbody>
</table>
Table 1.2. Patterns of development identified in increment cores taken from site index trees.

<table>
<thead>
<tr>
<th>Development History</th>
<th>Number of Trees</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Red Spruce (n=698)</td>
</tr>
<tr>
<td>No suppression; free-growing tree.</td>
<td>408</td>
</tr>
<tr>
<td>Old (1910-20) budworm suppression only.</td>
<td>103</td>
</tr>
<tr>
<td>Initially free growing with suppression during stand development.</td>
<td>69</td>
</tr>
<tr>
<td>Suppression at pith only, followed by release.</td>
<td>35</td>
</tr>
<tr>
<td>Short (&lt;6 yrs.) period of suppression from recent budworm only.</td>
<td>11</td>
</tr>
<tr>
<td>Pith suppression, old budworm suppression, or old budworm suppression,</td>
<td>70</td>
</tr>
<tr>
<td>suppression from competition.</td>
<td></td>
</tr>
<tr>
<td>Pith suppression, old budworm suppression and,</td>
<td>2</td>
</tr>
<tr>
<td>suppression from competition.</td>
<td></td>
</tr>
</tbody>
</table>
Table 1.3. Mean site index (m)* of free-growing trees vs. trees with suppression by soil class. Ages determined from increment cores. Base age=50 (total age).

<table>
<thead>
<tr>
<th>Development History</th>
<th>Soil Class</th>
<th>Site Index</th>
</tr>
</thead>
<tbody>
<tr>
<td>Good</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Free-Growing</td>
<td>12.9 ± 0.36 (35) a</td>
<td>12.4 ± 0.11 (244) a</td>
</tr>
<tr>
<td>Suppressed:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Actual Age</td>
<td>12.4 ± 0.48 (23) a</td>
<td>12.0 ± 0.13 (161) b</td>
</tr>
<tr>
<td>Release Age</td>
<td>12.7 ± 0.51 (23) a</td>
<td>12.3 ± 0.14 (161) a</td>
</tr>
<tr>
<td>Adjusted Age</td>
<td>12.7 ± 0.48 (23) a</td>
<td>12.3 ± 0.14 (161) a</td>
</tr>
<tr>
<td>All Trees (Actual Age)</td>
<td>12.7 ± 0.29 (58)</td>
<td>12.2 ± 0.09 (405)</td>
</tr>
</tbody>
</table>

In pairwise comparisons between free-growing and suppressed trees, means with the same letter are not significantly (alpha = 0.05) different according to Student-Newman-Keuls multiple range tests.

* ± standard error (number of samples)
Table 1.4. Comparison of observed site index\(^a\) of stem-analyzed trees with adjusted site index by development history. Base age=50 (at breast height).

<table>
<thead>
<tr>
<th>Suppression History:</th>
<th>Observed Site Index(^b) (n)</th>
<th>Range</th>
<th>Adjusted Site Index(^c) (n)</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>No Suppression</td>
<td>15.1 ± 0.51 (18) a</td>
<td>10.2 -18.1</td>
<td>15.3 ± 0.34 (27) a</td>
<td>11.3 -18.1</td>
</tr>
<tr>
<td>Stump Suppression</td>
<td>12.6 ± 0.66 (23) b</td>
<td>5.3 -17.2</td>
<td>14.8 ± 0.38 (34) a</td>
<td>9.1 -17.9</td>
</tr>
<tr>
<td>Suppression at 1.4 m</td>
<td>8.5 ± 0.77 (26) c</td>
<td>3.2 -16.3</td>
<td>15.3 ± 0.41 (30) a</td>
<td>11.5 -19.6</td>
</tr>
<tr>
<td>P-value</td>
<td>&lt; 0.01</td>
<td></td>
<td>0.55</td>
<td></td>
</tr>
</tbody>
</table>

Means with the same letter are not significantly different (among suppression histories) according to Student-Newman-Keuls multiple range test.

\(^a\)Mean site index ± standard error (number of samples)

\(^b\)Actual height (m) at age 50 (at breast height)

\(^c\)Predicted height (m) at free-growth age 50 (at breast height), calculated from equation 2.
Table 1.5. Comparison of effects of soil quality on mean site index (m)* of free-grown trees with calculated mean site index of stem-analyzed trees during free-growth period. Base age=50 (total age).

<table>
<thead>
<tr>
<th>Soil Class</th>
<th>Free-Growth Cores</th>
<th>Range</th>
<th>Stem-Analyzed Trees</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Good</td>
<td>12.9 ± 0.36 (35) a</td>
<td>8.8-18.0</td>
<td>12.9 ± 0.40 (13) a</td>
<td>10.0-15.4</td>
</tr>
<tr>
<td>Fair</td>
<td>12.4 ± 0.11 (244) a</td>
<td>6.4-18.9</td>
<td>11.7 ± 0.24 (56) b</td>
<td>7.0-14.8</td>
</tr>
<tr>
<td>Poor</td>
<td>11.8 ± 0.15 (129) b</td>
<td>7.3-16.8</td>
<td>11.6 ± 0.27 (22) b</td>
<td>8.9-13.7</td>
</tr>
<tr>
<td>P - value</td>
<td>&lt;0.01</td>
<td></td>
<td></td>
<td>0.06</td>
</tr>
</tbody>
</table>

Means with the same letter are not significantly different (alpha = 0.05) according to the Student-Newman-Keuls multiple range test.

* ± standard error (number of trees)
FIGURE CAPTIONS

Figure 1.1. Location of study area.

Figure 1.2. Procedure used to establish 1936-75 free-growth period. Two height-age pairs were used to calculate site index.

Figure 1.3. Examples of different radial growth patterns reflecting development history. Y-axis = radial increment (mm).

Figure 1.4. Mean annual height growth (during 1936-75) versus total height in 1936. Symbols indicate soil quality classes.

Figure 1.5. Relationship of mean annual height growth and mean annual radial growth during 1936-75 showing correlation between height growth and stand density.
Calculated heights at age 50 (site index) 1974
1941 1.37 m
Free-growth total age 50
Free-growth bh age 50

- Actual Growth Curve
- Calculated Growth Curve
- Height-age pairs used to solve equation
Figure 1.3

Free-growing tree

Spruce budworm suppression, 1910-20

Initially free-growing followed by suppression, then release

Initially suppressed followed by release

Short period of suppression from 1970's budworm
Figure 1.4

![Graph showing the relationship between mean annual height growth (cm) from 1936-75 and height (m) in 1936. The graph includes data points categorized as Good, Poor, and Fair. The correlation coefficient (r) is 0.39.]
Figure 1.5

The image shows a scatter plot with two axes:
- The x-axis represents Mean Annual Radial Growth (mm).
- The y-axis represents Mean Annual Height Growth (cm) between 1936-75.

Three categories of trees are represented:
- Good
- Fair
- Poor

A dashed line indicates the average for all trees.

The equation of the trend line is given as:

\[ y = 0.37 + 0.27x \]

The correlation coefficient \( r \) is 0.60.
Table A.1. Criteria for classification of soil profiles

**Profile 1- "Good" Soils:**
The soil horizons are thick and well developed. The colors of the soil are red and brown grading gradually into yellowish reds and browns. The lowest part of profile is olive colored. Blotchy combinations of reds, browns, grays (mottling) may be found at depths of 51-69 cm. Rooting depth: > 51 cm.

**Profile 2- "Fair" Soils:**
The soil horizons are thinner and not as well developed as profile 1. Colors of the sub-surface soil are red and brown grading quickly into yellowish tints of these colors. Mottling may be found at depths of 30-69 cm. Below this blotchy color zone the colors are olive brown with rusty stains. Rooting depth: 30-51 cm.

**Profile 3- "Poor" Soils:**
The soil horizons are very thin and may be hard to distinguish. The colors are predominantly dull reds and browns grading very quickly into a heavily mottled zone. Below this zone the subsoil will be bluish gray with rust stains. Rooting depth: 15-30 cm.

* Classification system developed by Tom Saviello, 1987.*

ABSTRACT

Three hypotheses were examined about the development history, structure and cohort distribution of mixed stands of red spruce (*Picea rubens* Sarg.), hemlock (*Tsuga canadensis* (L.) Carr.) and white pine (*Pinus strobus* L.): 1) Partial disturbances initiate a new cohort of trees; 2) Existing trees show an increase in growth rate following a partial disturbance; 3) Spruce and hemlock have similar age-class distributions, but these differ from the age-class distribution of pine. Age-class distributions show that all five stands studied contained trees in at least 13 ten-year age classes. Hemlock and spruce were present in more age classes than pine due to the shade-tolerant characteristics and longevity of these species. Partial disturbances from spruce budworm (*Choristoneura fumiferana* Clemens) outbreaks and harvesting affected stand development by initiating a new cohort of trees, and causing a growth response in surviving trees. All stands were subjected to similar disturbances and the species-specific responses to disturbance were generally the same. However, timing of disturbances relative to species composition, density, size and age of trees in each stand resulted in different development patterns.
INTRODUCTION

Whether forest stands are single- or multiple-cohort depends on the type and frequency of disturbance(s) that have influenced their development. Single-cohort stands typically regenerate after a single stand-replacing disturbance such as a hurricane or fire (Oliver 1981). Multiple-cohort (multicohort) stands result from less severe disturbances, such as insect infestations, which only partially destroy a stand and some of the predisturbance trees survive. The new cohort of trees that regenerates after a partial disturbance competes for site resources with advance regeneration and previously established larger trees (Oliver and Larson 1990).

The temporal and spatial variations of partial disturbances play an important role in the development of many forest types that display a multicohort structure (Lorimer 1977; Oliver and Stephens 1977; Aplet et al. 1988; Betters and Woods 1979; Lorimer 1980; Veblen 1986; Harcombe 1986). A number of possible stand level responses can follow each disturbance: Trees can decline in vigor and possibly die, or mortality can be immediate. Surviving trees often grow faster in response to newly created growing space. A new cohort can germinate or advance regeneration can be released. Alterations in species composition can occur; for example, shade tolerant understory trees can be released and grow into an upper canopy position once held by less shade-tolerant species.

In describing a simplistic model of the development of an idealized multicohort stand, Oliver and Larson (1990) address stand-level responses to the type and extent of disturbances. Their model assumes a single species stand where each disturbance occurs with similar frequency and has the same impact on the stand; the same number of trees are removed each time and the
residual trees are evenly spaced. The same species regenerates immediately after each disturbance and this new cohort occurs uniformly throughout the stand. Existing cohorts increase their growth rate in response to each disturbance and all trees in each cohort maintain similar growth rates.

Mixed-species multicohort stands probably deviate greatly from Oliver and Larson's idealized model. Mixed stands of red spruce (*Picea rubens* Sarg.) and eastern hemlock (*Tsuga canadensis* (L.) Carr.) are well distributed in eastern and central Maine, where the natural ranges of these two species overlap. Eastern white pine (*Pinus strobus* L.) frequently forms a minor association in these stands (Seymour 1991). Preliminary observations suggest that the stands show a vertical stratification of tree crowns with white pine occasionally occupying an emergent canopy position.

The frequent partial disturbances, both natural and anthropogenic, that have occurred in Maine's conifer forests since the late 1800's (Seymour 1991), combined with the species-specific growth characteristics of the spruce-hemlock-pine mixtures, potentially create stands with multicohort characteristics. This study was designed to examine the development history, structure and cohort distribution of mixed stands of red spruce, eastern hemlock and white pine. Several hypotheses were investigated to determine if partial disturbances were the major contributor to current stand structure and have resulted in multicohort stands.

The **first hypothesis** is that a new cohort of trees initiates from new seedlings or advance regeneration after partial disturbance. The **alternative hypothesis** is that a new cohort of trees does not initiate; partial disturbances are not responsible for a new cohort. Analysis of stand structure (e.g., species composition, distribution of tree heights and ages) can provide clues to the number of cohorts present.
The **second hypothesis** is that existing trees have an abrupt and sustained increase in growth rate following a partial disturbance. The **alternative hypothesis** is that growth does not increase following a disturbance or that any increase in growth is too gradual to identify.

All species growing in the upper canopy can take advantage of a disturbance by expanding their crowns into the new growing space. In sub-canopy positions, suppressed spruce and hemlock have the ability to respond and grow into the upper canopy after a disturbance creates additional growing space in a stand (Marshall 1927; Henry and Swan 1974; Oliver and Stephens 1977; Lorimer et. al. 1988; Davis 1989).

The **third hypothesis** is that spruce and hemlock have similar cohort age-distributions that differ from the cohort age-distribution of pine. The **alternative hypothesis** is that all three species belong to the same cohort and stand structure can be defined according to the developmental stages of Oliver (1981).

White pine is intermediate in shade tolerance; it requires full sunlight to germinate, and must maintain an upper canopy crown position in order to survive (Wendel and Smith 1990). Hemlock and spruce, on the other hand, are very shade tolerant and are capable of enduring many years of suppression in sub-canopy positions (Blum 1990; Goodman and Lancaster 1990). The similarity of the growth strategies of spruce and hemlock should produce equivalent regeneration responses to disturbance.
METHODS

Study Area

Stands were located on Champion International Corporation Inc., land in Townships 36 (1 stand) and 42 (4 stands) of Washington County, Maine (Fig. 2.1). The mean monthly temperature for the area is 9° C, and the mean annual precipitation is 113 cm. The mean annual snow accumulation is 128 cm (National Oceanic and Atmospheric Administration weather station).

Five stands with principal species components of red spruce, hemlock and white pine were selected from Champion's forest-type maps for investigation of potential disturbance and developmental phenomena. All five stands were mature (mean age >50 years old) and had been harvested by strip clearcutting during the past five years, but there was no other evidence of harvesting during the past several decades. Stands 24, 46, and 50 were each approximately six ha in size, stand 23 was four ha, and stand 36 (in Township 36) was 10 ha. The stands in Township 42 were located within 2-8 km of each other, and the stand in Township 36 was approximately 20 km from the other sites.

Field and Laboratory Procedures

The size of the uncut strips varied within each stand; the width ranged from 18-30 m and the length ranged from 100-250 m. Transect lines were run down the center of each strip and .02 ha circular plots were established every 20 m. A total of 425 plots were established in this manner. Since white pine was the least abundant of the three species, the stem diameter (at 1.37 m or breast height) and crown class of each white pine that was encountered on any of the 425 plots were recorded.
A subsample of 10 plots per stand was then randomly selected for more intensive measurements according to the criteria that five of the plots contain at least one dominant or codominant pine and five of the plots contain at least one dominant or codominant red spruce and hemlock. The purpose of this division was to compare potential impacts of species composition on stand structure and development. One dominant or codominant tree of pine, spruce and hemlock on each plot were labeled "subject" trees. All plot trees that were \( \geq 11.4 \) cm diameter at breast height (dbh) were measured. Trees that were less than 11.4 cm dbh and \( \geq 1.37 \) m tall were sampled on a .008 ha circular plot established within each larger plot. For each tree that met these criteria, species, dbh and crown class were recorded. Within the main canopy, trees were classified as dominant, codominant, intermediate or overtopped (Smith 1986). Any tree with a crown protruding well above the level of the dominant and codominant crown classes was classified as "emergent."

Increment cores were taken at breast height from all subject trees and all trees beneath and surrounding the subject trees. Trees were cored repeatedly until an acceptable core (one containing the pith) was extracted. It was not possible to obtain cores from some of the larger trees due to heart rot. Surrounding trees were identified as those trees that had any portion of their crown touching the subject tree. If the trees surrounding the subject tree were not on the plot, then species, diameter and crown class information was also collected for these trees. In order to identify when regeneration events took place, additional increment cores were taken at stump height (.3 m) from trees selected to represent each species-crown class group on each plot. Total height was measured using a clinometer on all subject trees, surrounding trees, and trees growing beneath subject trees.
No records of past harvests were available for any of the stands, but evidence of old harvests (e.g., rotted stumps) were encountered throughout all stands. The cut stumps were distinguished from stumps resulting from natural tree falls based on an absence of stem segments from the lower bole (i.e., harvested sawlogs) on the forest floor. In order to date these apparent harvests, increment cores were taken at stump height from those trees surrounding old cut stumps. Data were collected from trees surrounding 3-6 stumps per stand resulting in a total of 109 cores. It was anticipated that the age and radial growth patterns of these cores would provide information to date the years of past harvesting activities. For example, the year a tree regenerated and/or showed an abrupt growth increase would suggest a harvest event. Wood samples were collected from the stumps in order to identify species types.

Condition of stumps relative to each other was classified into two categories: 1) Stumps with flat upper surfaces containing sound, easily identifiable wood fragments or, 2) Stumps with irregular upper surfaces, extensive wood decay, and some identifiable wood fragments.

A soil pit was excavated on each of the 50 plots to assess the uniformity of soil conditions. The pits were excavated to the depth of the bottom of the rooting zone. Soils were classified according to a system used by Champion International Corporation Inc., on their permanent growth plots (Appendix A, Table A.1). All soils were classified as "Profile II" with thin, moderately developed soil horizons. Colors of the sub-surface soil were red and brown grading quickly into yellowish tints of these colors. Mottling was sometimes found at depths of 31-69 cm.

In the laboratory, increment cores were sanded and growths rings were measured (to the nearest 0.01 mm) under 4X magnification, using a binocular microscope and a Measuchron®. Slides were prepared of the stump wood
samples, and cell structures were examined with a microscope. Species identification was not possible in all cases due to extensive decay.

Because the increment cores did not necessarily represent the average radius of each tree, an adjustment was made to the radial increment measurements. The sum of the radial increments for each core (excluding bark) was proportionally adjusted using the average radius of the tree based on its inside bark diameter (radius=dib/2). Inside bark diameters were estimated by subtracting an estimated bark thickness from the measured diameter outside bark using tables developed by Nims (n.d.) for softwoods in New York (Forestry Handbook 1984).

In order to determine if the age data collected from the subject trees and all trees beneath and surrounding them (subject tree and associates="age trees") would adequately represent the range of tree sizes present in each stand, age trees were categorized according to diameter and crown class. When age-tree data were compared with the diameter and crown class information averaged over all plot trees in each stand, an imbalanced representation of ages was evident. In order to increase the sample size of tree ages representing the dbh/crown-class categories, a stratified random sample was used to select trees for additional age sampling across the range of diameter and crown classes in each stand. This procedure is similar to one implemented by Aplet et al. (1988). If a class only had 1-5 trees, then all trees were aged. If a class had 6-10 trees then five trees were sampled. A class with 11-20 trees required that a minimum of 50 percent of the number in that category were age trees. A minimum of ten trees were cored if a category had more than 20 trees. Including cores obtained from the subject trees and their associates, and additional cores obtained to fill size-category gaps, a total of 524 ages (at breast height) were measured.
Ages were allocated proportionally according to the number of plot trees in each dbh/crown-class category and an age-class distribution was derived for each stand in the following manner. The number of trees per hectare in each dbh/crown class category was calculated for each stand from the plot data. The number of trees per hectare was then divided by the number of increment cores (age trees) in each size category producing an estimate of the number of trees represented by each age tree. For example, if a size category had 50 trees/ha in it, and there were 5 age trees with ages 50, 53, 65, 68, 69 representing that size category, then there would be assumed to be ten 50-year old trees/ha, ten 53-year old trees/ha . . . etc. in that stand. A similar procedure was used to estimate the number of trees/ha in each height class.

In order to identify possible growth responses to partial disturbance events, classification criteria were used to examine any changes in the rate of radial increment growth for each tree. Radial increments were averaged over ten-year periods, starting with 1979-88, and compared with the previous ten-year period, 1969-78. The comparison groups were then shifted by one year so that average growth rates would be compared for years 1978-87 and 1968-77 and so on, until the pith was reached. A percentage increase or decrease was computed based on the ratio of "most recent ten-year growth rate" to the "previous 10-year growth rate." The percentage increase (or decrease) was then compared to a minimum threshold to determine whether the period qualified as a growth increase (or decrease). If several consecutive comparisons exceeded a particular threshold (indicating a prolonged response or reduction), then the event was dated according to the year when the difference was largest.

The average rate for the more recent ten-year period had to be at least 100 percent greater than (double) the previous period to be considered an
important increase (Lorimer 1980, 1985) and at least 25 percent less than the previous period to be a decrease. The procedure causes increasingly larger sample sizes as the more recent decades are analyzed.

A more stringent classification of growth responses to disturbance was also conducted. Percentage increases were classified according to whether the increase was 150, 250, 500 or 1000 percent greater than the previous 10-year average (Table B.1, Appendix B). A similar procedure was used to determine percentage decreases in growth rates from 25-99 percent (Table B.2, Appendix B).

In addition to examining evidence of disturbance from individual trees, such as abrupt growth decreases and abrupt and sustained growth increases in radial increment cores, an attempt was made to use physical and historical evidence to identify past disturbances. The design of this study was not appropriate to accurately document the frequency and intensity of natural disturbances, especially as there was evidence of human disturbance (e.g. cut stumps) in all stands (Lorimer 1985). Several natural disturbances are well documented as having affected eastern Maine’s forests during the life of the current stands (Table 2.1), and these events were used as an aid in establishing a disturbance history for each stand. No records of severe fires or windstorms exist for the area, and physical evidence of these events was neither systematically examined nor obvious.

Analyses

In order to test the null hypothesis that the age-class distributions of spruce and hemlock are the same, a chi-square test for independence was performed on the age-class distributions of spruce and hemlock. Tests were performed between trees growing on pine and no-pine plots and for all plots...
combined in each stand. The 10-year age class distributions for each species were set up in a 2 (rows) x C (columns) contingency table. Due to missing or low representation of some age classes, certain classes were combined into larger groups.

**RESULTS**

*Stand Structure*

Of the 425 total plots, 33 percent contained one or more pine trees. The low density of white pine was similar among stands, ranging from 24-35 trees/ha. The densities of hemlock and spruce were similar within each stand but varied widely among stands (Table 2.2). Red spruce density ranged from 373-1158 trees/ha and hemlock ranged from 326-1324 trees/ha.

Height (Figs. 2.2a-e) and crown-class (Figs. 2.3a-e) distributions showed that the stands are vertically stratified by species. Hemlock predominates in the overtopped crown class, with at least 50 percent representation, and it also makes up the majority of the height distribution up to about 10 m. The representation of spruce was higher (35-64 percent) than hemlock in the intermediate crown class; spruce also comprised the majority of the codominant crown class as well as the 10-20 m height classes. These results agree with Rogers (1978), who found hemlock to be more successful than red spruce in distributing its stems among two or more sub-canopy layers, probably due to hemlock's greater ability to regenerate and grow in shade compared to spruce (Goodman and Lancaster 1990).

There was some degree of overlap in the representation of spruce and pine in the dominant crown class, but white pine was the only species present
as emergent trees, with heights up to 35 m. Stands 46 and 50 showed the most
distinct separation of pine heights from those of other species. The dominant
and emergent pines in stand 46 were also taller than the pine in any other
stand.

There was also a relationship between crown class and age that differed
by species. The mean age of hemlock differed by 20-100 years between
dominant and overtopped trees (Figs. 2.3a-e). Spruce followed a similar
pattern but the range in mean ages between crown classes was not as broad
and, in stands 24 and 36 the mean ages of the overtopped and intermediate
classes were virtually the same. Generally, the mean age of pine was similar
regardless of crown class with two exceptions: In stand 23 and 24 emergent
pines were older than the rest, and overtopped pines were slightly younger than
the rest in the four stands where they occurred.

The relationship between crown class and age in spruce and hemlock
but not in pine reflects the different growth habits of the species. An obvious
pattern resulting from growth habits typical of shade tolerant species is
prevalent in all stands. Hemlock and spruce can take longer to achieve a
dominant position in the main canopy because they can endure being
overtopped without necessarily succumbing to mortality, as would pine.
Overtopped pine were rare in all stands; there was an average of only two
overtopped and six intermediate pine trees per hectare. Pine must maintain a
rapid height growth in order to achieve a dominant position or it will not survive.
Once a pine crown is firmly established in the main canopy it has unlimited
above-ground growing space and can eventually emerge above the main
canopy of spruce and hemlock.

Age-class distributions (Fig. 2.4) showed an extraordinary diversity in
age structures despite some obvious peaks and gaps. Some trees reached
breast height during at least 13 of the 17 decades examined in each stand. Three patterns of tree establishment were obvious based on an increase in the number of trees reaching breast height in each decade. In stands 23, 24 and 36, there were three periods of major establishment. In stand 50 only one major period of establishment is obvious. Stand 46 had no obvious peaks but equal representation of trees occurred in 15 age classes. The number of pine age classes present in each stand ranged from 5 to 10 but there were only one or two periods of major tree establishment (Fig. 2.5). The distribution of pine age classes was unique to each stand.

Diameter-class distributions (Figs. 2.6a-e), although variable, showed the negative exponential patterns typical of multicohort stands (Oliver and Stephens 1977) or of single-cohort, multi-species, stratified stands (Oliver 1978; Wierman and Oliver 1979; Hibbs 1983; Kelty 1986; Clatterbuck and Hodges 1988). However, pine did not display the same negative exponential pattern as the spruce and hemlock. The pine distributions approximated a normal (bell-shaped) curve typical of the diameter distribution of a single-cohort stand of shade intolerant species (Smith 1986). Lorimer (1980) and Leak (1975) found similar differences in patterns of diameter distribution between shade tolerant and shade intolerant species in mixed stands.

Scatter plots of age (at breast height) versus diameter from the age trees indicated a great deal of variability in the age-size relationships between species and between stands (Figs. 2.7a-e). Pine showed a wide range in diameter distribution but had the least variation in age compared to spruce and hemlock. The age-size relationships for spruce and hemlock showed that the larger trees were usually older than the smaller trees.

The majority of stands had age-size correlations ($r$) $< .77$. Only hemlock in stands 36 and 23 showed a strong relationship ($r = .88$), which is similar to the
diameter-age relationships ($r=.87$) for the hemlock component of a virgin deciduous forest in the southern United States (Lorimer 1980). However, none of the correlations for red spruce were comparable to the relationships between age and diameter found for red spruce growing in a virgin red spruce-balsam fir stand in New Hampshire (Leak 1985). In that study, age and size were fairly well correlated ($r=.94$).

**Identification of Partial Disturbances**

*Growth reductions:* The percentage growth reductions determined from the increment cores were arranged by decade and summarized by species (Fig. 2.8a-c) in order to examine potential impacts from regional disturbances such as insect outbreaks, which may have been masked by competition effects if growth decreases were examined at the stand level. An arithmetic mean of the percentage growth reductions in each decade was calculated for each species to serve as a reference point for comparisons between decades. Decades showing reductions in at least 20 percent more trees than the average for a species were considered significant enough to examine potential causes. Decades where growth decreases were less than the mean were attributable to inter-tree competition during natural stand development.

Red spruce and hemlock showed significant growth reductions (20-60 percent above average) during the periods beginning 1911-20 and 1971-79. The significant decreases in radial growth suppression during these periods can be attributed to two outbreaks of the spruce budworm (*Choristoneura fumiferana* Clemens) that occurred in Maine during 1910-20 and in the mid-1970's, and caused extensive defoliation and mortality of balsam fir, and to a lesser degree spruce and hemlock (Seymour 1985).
White pine showed significant growth reductions (at least 24 percent above average) during 1951-60 in all stands. This period coincides with a documented insect outbreak that affected white pine in Maine (Lowe 1965). The pine leaf adelgid (*Pineus pinifolila* Fitch) has an eastern U.S. range that coincides with red spruce, one of its primary hosts (USDA Handbook). Above average growth reductions during 1971-79 were also observed for white pine. Because pine is not a host of the spruce budworm, the reduction cannot be attributed to a budworm outbreak. Above-average growth reductions were noted in three stands during 1881-90 and in stand 46 for both pine and spruce during 1830-60. It is possible that there were undocumented insect outbreaks during these periods but growth reductions attributable to natural stand-developmental processes are more plausible.

*Growth increases:* The percentage growth increases were arranged by decade and summarized by stand for each species (Figs. 2.9a-e) in order to identify stand-specific disturbances (e.g., harvesting) that may have increased growing space. An arithmetic mean of the percentage growth increases in each decade was calculated for each stand. There were some release patterns common to all stands. During the period beginning 1921-30, there were 22-42 percent more trees of all three species showing growth increases that were greater than the average for each stand. Since 1921-30 was the decade immediately following the first spruce budworm outbreak, the "release" period following the defoliation-induced suppression of radial increment growth showed that many trees recovered during the next 10-years and took advantage of growing space newly created by tree mortality. Similar historical variations in radial growth increment related to spruce budworm defoliation have been found for red spruce in northern Maine (Reams and Huso 1989).
In all stands white pine accounted for the majority of growth increases that occurred during the period beginning 1961-70 even though the number of releases during this period was slightly below the average for each stand. This growth increase in pine probably marks the recovery from the pine leaf adelgid outbreak of the previous decade.

Other decades where significant numbers of all species showed growth increases were not uniform between stands and probably represented stand specific disturbances. There were only two other decades where all three species showed a significant number of releases: 1861-70 in stand 24 and 1891-1900 in stand 46. These decades corresponded with the apparent harvest histories of these two stands (Table 2.3). Growth responses in stand 36 of spruce and hemlock only, also reflected a harvest event in 1891-1900.

Age structure: Because it was obvious from the age class distributions that pine had fewer cohorts, fewer number of trees in each cohort, and a different distribution of cohorts than spruce and hemlock, comparisons of age-class distributions were tested only between spruce and hemlock in each stand.

All the chi-square tests on the age data were highly significant (P < .001). Results were so similar between the pine and no-pine groups in each stand that the influence of species composition on age structure was assumed to be non-significant. The pine and no-pine groups were combined (Table 2.4) and the same chi-square analysis was again performed. Chi-square tests of the combined groups were also highly significant and it was concluded that the age-class distributions of hemlock and spruce were different.

One obvious difference in the age-class distributions of spruce and hemlock was during the decades following the 1910-20 spruce budworm outbreak. Between 1920 and 1960 both species responded similarly in numbers of trees reaching breast height. However, more spruce generally
reached breast height before hemlock; the hemlock response took 2-3 decades longer.

*Recognition of cohorts:* The group of trees that develops after a single disturbance can be referred to as a cohort. The range in ages that can exist within a cohort can span up to several decades depending on how long trees continue to invade after a disturbance (Oliver and Larson 1990). The lack of recorded harvest events for these stands means that cohort delineation is tentative and subjective because it is based on stand reconstruction.

Because the trees were aged at breast height, the age-class gaps do not necessarily indicate a break between disturbance events; the age classes represent the trees when they were 1.37 m tall, not the year they regenerated or were released. However, the ability of spruce and hemlock to germinate in shade means that the germination dates may not be correlated with disturbance events in any case. Aging shade-tolerant species at breast height instead of at the root collar can indicate a time of stem release instead of a time of germination (Oliver and Stephens 1977). Recording age at 1.37 m can also eliminate much of the variability in the number of years spruce and hemlock require to grow to breast height.

Alternatively, aging trees at breast height should be a reliable method for designating pine cohorts because white pine is intermediate in shade tolerance and will not survive early crown suppression for very long; the time it takes to reach breast height is thus fairly short and consistent. Comparisons between stump cores and cores taken at breast height indicated an average of six (range 4-15) years to reach breast height. Since pine requires full sunlight for germination and growth, the creation of a pine cohort implies an increase in the availability of sunlight caused by a partial disturbance.
Cohorts were identified in each stand based on peaks in the age-class distributions (Figs. 9a-e). The number of cohorts identified in each stand ranged from 1 (stand 50) to 4 (stand 46). Except for stand 50, all stands had a cohort that originated between 1910 and 1930. This cohort spanned 4 or 5 decades because large numbers of hemlock (and some spruce) continued to reach breast height for up to 3 decades after pine.

**Stand-Specific Developmental Patterns**

**Stand 50:** The age-class distribution of this stand (Fig. 2.4) most closely resembled a single-cohort stand. There is a minor representation of survivors of an older cohort ranging in age from 150-200 years but most of the stand originated in a stand-replacing event that was coincident with a harvest about 120 years ago. This stand contained the largest component of shade intolerant species such as bigtooth aspen and red pine; it also had the highest density of paper birch compared to the other stands (Table 2.2). Radial growth patterns (from stump cores) of hemlock, spruce, red maple and white birch trees surrounding two old pine stumps (Table 2.3) showed the rapid (>1 mm) early growth typical of seedlings in an open-grown condition. These trees regenerated around 1870. Increment cores obtained from miscellaneous paper birches showed an influx of a cohort of this shade-intolerant species also occurred about 1870. The 1870 harvest may also have regenerated or released balsam fir, which was later killed by the 1910-20 spruce budworm outbreak. The elimination of most fir, and probably some older spruce and hemlock, by the spruce budworm created only enough growing space in the stand to release existing trees, as evidenced by a growth increase in 60 percent of the existing trees (Fig. 2.9e). As a result, no cohort originated during the 1920's, unlike the other stands discussed in the following sections.
Stands 23 and 24: Since stands 23 and 24 were located within 1 km of each other and showed similar disturbance histories and developmental patterns, they will be discussed together. The oldest cohort in these stands became established between 1810 and 1870 and is now composed of remnants that were not removed or died in more recent disturbances. Growth increases in over 50 percent of the existing trees occurred between 1850-1870 but there was no other evidence that could be used to define a disturbance or suggest the establishment of a cohort.

According to peaks in the age-class distributions, the two other cohorts in these stands originated during 1871-80 and 1921-30 (Figs. 2.9a,b). Evidence of a harvest event triggering the establishment of the older cohort is not definitive. Examination of increment cores from pine, spruce and hemlock trees surrounding 11 old stumps showed different years of origin but a growth increase during the 1920's was common to all of them (Table 2.3). This growth response can be attributed to the spruce budworm and/or to a harvest event. The stumps also appeared to be of two different vintages. Four of the stumps were in a much more advanced state of decay than the others and the cut surface was very jagged compared to the flat surface of the "younger" stumps, probably reflecting at least two different harvest events. The trees surrounding the more decayed stumps also showed growth responses during either 1870 or 1900; a 1934 origin hemlock and a 1926 origin paper birch were growing on top of two of these stumps, strongly suggesting a harvest several decades before 1920.

The most prominent cohort originated after the 1910-20 budworm outbreak as evidenced by a high percentage of growth increases in 1921-30. A harvest event may also have occurred during the budworm outbreak because for seven of the trees surrounding the "younger" cut stumps the 1920's growth increase
was the only growth release noted. The fact that a new cohort originated during the 1920's lends supporting evidence for a harvest in the early 1920's, and the greater decay of some of the stumps and the origin of an 1870-1900 cohort supports the notion of an earlier harvest(s).

Stand 36: Stand 36 had the highest density of hemlock and spruce compared to the other four stands (Table 2.2). It also contained some of the oldest hemlocks, which comprised the majority of the oldest cohort in the stand ranging in age from 150-300 years, as well as the youngest cohort of pine. The initiation of a pine cohort and above-average percentages of hemlock and spruce showing growth increases during 1900-1910 (Fig. 2.9c) support a disturbance occurring around the turn of the century. Since there was evidence of pre-1920's harvesting in stands 23, 24 and 50 it is likely that the disturbance was a harvest. There was also a peak in the age-class distribution during 1870-80 however, there was no other evidence of an 1870-1890 harvest. That the youngest cohort is a result of spruce budworm affects and a harvest is documented by definitive 1920's growth responses of trees surrounding five cut stumps identified as spruce and hemlock.

Stand 46: Of the five stands sampled, stand 46 contained the greatest density of an older cohort (150-190 years old) even though trees older than 190 years were found in other stands. All but three of the pine age trees originated before 1850 so this stand contained the oldest cohort of pine.

From examination of the 10-year age-class distribution there appeared to be four cohorts present in this stand (Fig. 2.9d). It is hypothesized that the stand originated after a heavy disturbance around 1800. Pine was harvested from the stand 70-90 years later. Radial growth information collected from trees surrounding cut pine stumps showed that three stumps represent trees harvested around 1890 and one stump provided evidence of an earlier harvest.
around 1870. Growth increases in existing pine, spruce and hemlock trees also support the occurrence of harvesting during these decades. The initiation of two cohorts, probably as a result of these harvests, is supported by slight peaks in the age-class distribution between 1850-70 and 1890-1900. There is no evidence of a 1920’s harvest, but spruce budworm defoliation caused growth increases in over 60 percent of existing trees and the initiation of the fourth cohort.

Although the disturbance history of this stand since 1870 appears to be very similar to that of stand 50, structural differences give the current stands very different appearances. The 1870’s harvest prompted abundant regeneration in stand 50 but it is possible that a higher density of the residual older/larger trees in stand 46 prevented the regeneration of as large a cohort. The 1920’s spruce budworm outbreak appeared to cause higher mortality in stand 46 because a new cohort was initiated. Stand 50 did not have a cohort originating in the 1920’s because it may not have been as affected by the outbreak. The majority of the trees in stand 50 probably did not succumb to mortality from the defoliation because they were younger and more vigorous than those of stand 46.

Discussion

Hypothesis I: Cohorts initiated in each stand as a result of disturbance events, which ranged in intensity from light to practically stand replacing. However, each disturbance event that affected a stand did not necessarily initiate a new cohort. Cohorts initiated after all documented harvests. In addition, in four of the five stands (23,24,26,46) cohort initiation coincided with the 1910-20 spruce budworm outbreak; three of these stands (23, 24, 36) also
were harvested simultaneously. There was no new cohort initiated as a result of spruce budworm defoliation in stand 50.

The severity of a disturbance determines species-specific patterns of cohort initiation. In order for regeneration to occur from new seedlings of shade-intolerant species, the disturbance had to alter stand structure in a way that created new growing space in the overstory as well as in the sub-canopy. Regeneration of pine and intolerant hardwoods requires more sunlight (more severe disturbance) than regeneration of hemlock and spruce.

Lesser disturbances can establish a cohort of shade-tolerant species. If the newly created sub-canopy growing space created by a partial disturbance was not sufficient for new regeneration (e.g., not enough light reaching forest floor), or if there was already an abundance of advance seedlings of spruce, fir and hemlock, then the new cohort would contain existing shade-tolerant seedlings and saplings that were released.

**Hypothesis II:** In addition to establishing new cohorts, all harvests caused a growth increase in the surviving cohort. The suppression and release patterns of the five stands in this study showed that all species responded to both stand level (e.g., harvesting) and regional disturbances (e.g., spruce budworm) (Figs. 2.8a-c; 2.9a-e). The effects of competition for growing space and climatic variations also influenced growth fluctuations. Regional disturbances such as the spruce budworm and pine adelgid caused growth reductions followed by growth increases in canopy trees. Budworm defoliation also had a releasing effect on trees occupying sub-canopy crown positions, and inflicted some mortality, especially of balsam fir. Documented harvest events always caused a growth increase in residual trees near cut stumps.

Shade tolerant species are physiologically adapted to survive in stands where partial disturbances periodically influence stand development. Shade
tolerant species have the ability to endure crown competition for several
decades without inhibiting their later growth capacity (Fajvan, Chapter 1;
Assman 1970). As a result, they can increase or decrease their growth rate in
response to available resources. The existence of shade-tolerant species in all
crown positions can be explained by the fluctuations in growth of suppressed
sub-canopy individuals and their variability in ages. The radial growth rates of
the spruce and hemlock in this study fluctuated in response to the availability of
site resources, particularly sunlight (Fig. 2.10).

Shade tolerant individuals alternate periods of slow steady height growth
during suppressed periods with periods of moderate to rapid height growth
(Assman 1970) following partial disturbances and eventually attain status in the
main canopy. The current lack of hemlock and red spruce in dominant crown
positions can be partially attributed to past harvesting of the largest individuals.
In addition, spruce and hemlock usually take longer to achieve a dominant
crown position than pine. White pine employs a different growth strategy; it can
survive short periods of growth reduction from insect attacks (e.g., pine adelgid)
(Fig. 2.11) but otherwise it cannot endure prolonged periods of crown
competition and must maintain a constant or accelerating growth rate to
maintain a dominant status.

Hypothesis III: Spruce and hemlock have cohort distributions that differ
from pine and from each other. Hemlock and spruce generally responded
equally in numbers of trees reaching breast height following disturbance but the
hemlock response took several decades longer. Even though hemlock and
spruce have been found to be equal competitors for understory growing space
(Rogers 1978), hemlock has more rigorous germination (temperature and
moisture) (Godman and Lancaster 1990) requirements than spruce.
Age-class distributions generally showed that spruce appeared to react more quickly in number of trees reaching breast height after a disturbance than hemlock. Hemlock's response can equal spruce's, but it is more prolonged. Hemlock is slightly more shade tolerant than spruce and it also is more proficient at regenerating in shade.
LITERATURE CITED


<table>
<thead>
<tr>
<th>Pest or pathogen</th>
<th>Date(s)</th>
<th>Impact on Host</th>
<th>Evidence in Current Study</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spruce Budworm</td>
<td>1910-20</td>
<td><em>Abies balsamea</em> principal host. Defoliation of <em>Picea</em> and <em>Abies</em>. Growth reduction and/or death.</td>
<td>Dead standing fir present. Reductions in radial growth of <em>Picea</em> and <em>Tsuga</em>.</td>
<td>Seymour, 1985</td>
</tr>
<tr>
<td>(Choristoneura fumiferana)</td>
<td>1975-86</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Beech Bark Disease</td>
<td>1930-40</td>
<td>Beech scale causes bark cankers in <em>Fagus grandifolia</em>. Infection by <em>Nectria</em> fungus causes death.</td>
<td>Very few beech present; all are small and infected.</td>
<td>Houston and Valentine, 1987</td>
</tr>
<tr>
<td>(Cryptococcus fagisuga)</td>
<td>(Nectria coccinea var. faginata)</td>
<td>(Nectria galligena)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Birch Dieback</td>
<td>1945-55</td>
<td>Crown and root deterioration in <em>Betula papyrifera</em>. Growth reduction and/or death.</td>
<td>Large, dead <em>B. papyrifera</em> stems scattered throughout study area.</td>
<td>Clark, 1961</td>
</tr>
<tr>
<td>(Environmentally induced)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(Pineus pinifoliae)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 2.2. Species composition and density by stand.

<table>
<thead>
<tr>
<th>Species</th>
<th>23</th>
<th>24</th>
<th>36</th>
<th>46</th>
<th>50</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tsuga canadensis</td>
<td>675 (12.3)</td>
<td>995 (10.7)</td>
<td>1324 (12.8)</td>
<td>471 (13.8)</td>
<td>326 (9.2)</td>
</tr>
<tr>
<td>Picea rubens</td>
<td>541 (20.1)</td>
<td>754 (18.1)</td>
<td>1158 (29.4)</td>
<td>373 (13.4)</td>
<td>544 (12.2)</td>
</tr>
<tr>
<td>Pinus strobus</td>
<td>28 (2.8)</td>
<td>35 (4.4)</td>
<td>24 (2.0)</td>
<td>25 (5.6)</td>
<td>31 (4.6)</td>
</tr>
<tr>
<td>Abies balsamea</td>
<td>121 (2.7)</td>
<td>115 (1.3)</td>
<td>62 (0.9)</td>
<td>92 (0.9)</td>
<td>17 (0.2)</td>
</tr>
<tr>
<td>Thuja occidentalis</td>
<td>0</td>
<td>10 (0.3)</td>
<td>4 (0.1)</td>
<td>30 (0.8)</td>
<td>5 (0.1)</td>
</tr>
<tr>
<td>Pinus resinosa</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>54 (5.2)</td>
</tr>
<tr>
<td>Fagus grandifolia</td>
<td>5 (0.2)</td>
<td>15 (0.4)</td>
<td>0</td>
<td>27 (1.2)</td>
<td>5 (0.1)</td>
</tr>
<tr>
<td>Betula papyrifera</td>
<td>5 (0.6)</td>
<td>59 (0.8)</td>
<td>44 (0.2)</td>
<td>20 (1.1)</td>
<td>126 (3.9)</td>
</tr>
<tr>
<td>Acer rubrum</td>
<td>15 (2.1)</td>
<td>87 (1.3)</td>
<td>141 (1.2)</td>
<td>35 (2.8)</td>
<td>55 (2.0)</td>
</tr>
<tr>
<td>Populus tremuloides</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>10 (0.3)</td>
</tr>
<tr>
<td><strong>All Species</strong></td>
<td><strong>1390 (40.8)</strong></td>
<td><strong>2070 (37.3)</strong></td>
<td><strong>2757 (46.6)</strong></td>
<td><strong>1073 (39.6)</strong></td>
<td><strong>1173 (37.8)</strong></td>
</tr>
</tbody>
</table>
Table 2.3. Timber harvests documented by evidence of: 1) Radial growth response 2) Degree of stump decay 3) Intolerant species initiation 4) Age of tree growing on stump.

<table>
<thead>
<tr>
<th>Stand</th>
<th>23</th>
<th>24</th>
<th>36</th>
<th>46</th>
<th>50</th>
</tr>
</thead>
<tbody>
<tr>
<td>Estimated Decade of Harvest:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1860-70</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Species of Stump (Evidence Type)</td>
<td>Pine (1)</td>
<td>Pine (1,3)</td>
<td>Pine (1,3)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1871-80</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1881-90</td>
<td>Pine (1,2)</td>
<td>No ID (1,2,4)</td>
<td>Pine (1)</td>
<td>Pine (1)</td>
<td>Pine (1)</td>
</tr>
<tr>
<td>Hemlock (2)</td>
<td>No ID (1,2,4)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1891-00</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>?Inconclusive</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1900-10</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1911-20</td>
<td>Spruce (1,2)</td>
<td>Pine (1,2)</td>
<td>Pine (1)</td>
<td>Pine (1)</td>
<td>Pine (1)</td>
</tr>
<tr>
<td>Pine (1,2)</td>
<td>Hemlock (1,3)</td>
<td>Hemlock (1,3)</td>
<td>Hemlock (1,3)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pine (1,2)</td>
<td>Hemlock (1,3)</td>
<td>Hemlock (1,3)</td>
<td>Hemlock (1,3)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spruce (1,2)</td>
<td>Hemlock (1,3)</td>
<td>Hemlock (1,3)</td>
<td>Hemlock (1,3)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spruce (1,2)</td>
<td>Hemlock (1)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 2.4. Combined ten-year age class distributions used in chi-square test for independence.

**Stand 23**

<table>
<thead>
<tr>
<th>Species</th>
<th>1964-1940</th>
<th>1939-1930</th>
<th>1929-1920</th>
<th>1919-1900</th>
<th>1890-1849</th>
<th>1848-1790</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hemlock</td>
<td>194</td>
<td>229*</td>
<td>181</td>
<td>10</td>
<td>15</td>
<td>33</td>
</tr>
<tr>
<td>Red Spruce</td>
<td>60</td>
<td>74</td>
<td>179</td>
<td>46</td>
<td>162</td>
<td>15</td>
</tr>
</tbody>
</table>

**Stand 24**

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Hemlock</td>
<td>395</td>
<td>100</td>
<td>288</td>
<td>49</td>
<td>85</td>
<td>35</td>
<td>45</td>
</tr>
<tr>
<td>Red Spruce</td>
<td>72</td>
<td>359*</td>
<td>175</td>
<td>38</td>
<td>78</td>
<td>11</td>
<td>16</td>
</tr>
</tbody>
</table>

**Stand 36**

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Hemlock</td>
<td>468</td>
<td>465</td>
<td>157</td>
<td>85</td>
<td>68</td>
<td>11</td>
<td>52</td>
</tr>
<tr>
<td>Red Spruce</td>
<td>44</td>
<td>411</td>
<td>313</td>
<td>45</td>
<td>134</td>
<td>114</td>
<td>47</td>
</tr>
</tbody>
</table>

**Stand 46**

<table>
<thead>
<tr>
<th>Species</th>
<th>1964-1940</th>
<th>1939-1930</th>
<th>1929-1920</th>
<th>1919-1900</th>
<th>1890-1859</th>
<th>1858-1819</th>
<th>1818-1790</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hemlock</td>
<td>153</td>
<td>44</td>
<td>16</td>
<td>12</td>
<td>93</td>
<td>126</td>
<td>25</td>
</tr>
<tr>
<td>Red Spruce</td>
<td>47</td>
<td>31</td>
<td>105</td>
<td>24</td>
<td>67</td>
<td>94</td>
<td>5</td>
</tr>
</tbody>
</table>

**Stand 50**

<table>
<thead>
<tr>
<th>Species</th>
<th>1964-1930</th>
<th>1919-1900</th>
<th>1889-1879</th>
<th>1878-1790+</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hemlock</td>
<td>0</td>
<td>108</td>
<td>171</td>
<td>49</td>
</tr>
<tr>
<td>Red Spruce</td>
<td>51</td>
<td>53</td>
<td>420</td>
<td>24</td>
</tr>
</tbody>
</table>
FIGURE CAPTIONS

Figure 2.1 Study area in east central Maine.

Figure 2.2 Height distribution, shown as percent trees/ha, for each species by stand.

Figure 2.3 Crown-class distributions, shown as percent trees per hectare, of each stand by species. Numbers above bars are mean age (± standard error).

Figure 2.4. Ten-year age-class distributions for all trees (red spruce, white pine and hemlock) by stand.

Figure 2.5. Ten-year age-class distribution of pine for each stand.

Figure 2.6 a-e. Diameter-class distributions by stand.

Figure 2.7 a-c. Plots of age (at 1.37 m) versus diameter by species and stand.

Figure 2.8 a-c. Percentage growth decreases > 25 % occurring in each decade.

Figure 2.9 a-e. Ten-year age-class distributions by stand for each species compared with the percentage growth increases (> 100%) occurring in each decade. Arrows identify initiation of cohorts.

Figure 2.10. Examples of radial growth patterns for red spruce and hemlock reflecting growth responses to suppression and release.
Figure 2.11. Example of a radial growth pattern for white pine reflecting growth responses to suppression and release.
Figure 2.1
Figure 2.2a

Stand 23

Percent of Trees/Ha

Height-Class Midpoint (m)

- Hemlock
- Spruce
- Pine
Figure 2.2b

Stand 24

- Hemlock
- Spruce
- Pine

Height-Class Midpoint (m)

Percent of Trees/Ha
Figure 2.2c

Stand 36

- Hemlock
- Spruce
- Pine

Percent of Trees/Ha vs. Height-Class Midpoint (m)
Figure 2.2d

Stand 46

Percent of Trees/Ha

Height-Class Midpoint (m)

- Hemlock
- Spruce
- Pine
Figure 2.2e

Stand 50

Percent of Trees/Ha

Height-Class Midpoint (m)
Figure 2.3a

Stand 23

<table>
<thead>
<tr>
<th>Percentage of Trees</th>
<th>Overtopped</th>
<th>Intermediate</th>
<th>Codominant</th>
<th>Dominant</th>
<th>Emergent</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>47 (0.7)</td>
<td>62 (1.2)</td>
<td>86 (1.5)</td>
<td>107 (6.0)</td>
<td>113 (0.0)</td>
</tr>
<tr>
<td></td>
<td>52 (0.8)</td>
<td>69 (1.7)</td>
<td>65 (4.2)</td>
<td>63 (3.2)</td>
<td>64 (0.8)</td>
</tr>
</tbody>
</table>

- Hemlock
- Red Spruce
- White Pine
Figure 2.3b

Stand 24

<table>
<thead>
<tr>
<th>Category</th>
<th>Hemlock</th>
<th>Red Spruce</th>
<th>White Pine</th>
</tr>
</thead>
<tbody>
<tr>
<td>Overtopped</td>
<td>50 (0.7)</td>
<td>53 (0.8)</td>
<td>54 (4.6)</td>
</tr>
<tr>
<td>Intermediate</td>
<td>57 (0.8)</td>
<td>81 (2.5)</td>
<td>61 (3.1)</td>
</tr>
<tr>
<td>Codominant</td>
<td>125 (6.0)</td>
<td>61 (3.1)</td>
<td>60 (1.7)</td>
</tr>
<tr>
<td>Dominant</td>
<td>99 (3.9)</td>
<td></td>
<td>76 (4.7)</td>
</tr>
<tr>
<td>Emergent</td>
<td>142 (25.5)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

- Hemlock
- Red Spruce
- White Pine
Figure 2.3c

Stand 36

<table>
<thead>
<tr>
<th>Category</th>
<th>Hemlock</th>
<th>Red Spruce</th>
<th>White Pine</th>
</tr>
</thead>
<tbody>
<tr>
<td>Overtopped</td>
<td>51 (0.5)</td>
<td>52 (4.4)</td>
<td>66 (1.2)</td>
</tr>
<tr>
<td>Intermediate</td>
<td>67 (0.9)</td>
<td>56 (3.9)</td>
<td>96 (6.4)</td>
</tr>
<tr>
<td>Codominant</td>
<td>80 (1.5)</td>
<td>62 (3.2)</td>
<td>203 (13.3)</td>
</tr>
<tr>
<td>Dominant</td>
<td></td>
<td></td>
<td>105 (7.2)</td>
</tr>
<tr>
<td>Emergent</td>
<td></td>
<td></td>
<td>65 (4.1)</td>
</tr>
</tbody>
</table>

Percentage of Trees
Figure 2.3d

Stand 46

<table>
<thead>
<tr>
<th>Category</th>
<th>Trees</th>
<th>Percentage</th>
</tr>
</thead>
<tbody>
<tr>
<td>Overtopped</td>
<td>77(2.5)</td>
<td>0.775</td>
</tr>
<tr>
<td>Intermediate</td>
<td>94(4.3)</td>
<td>0.94</td>
</tr>
<tr>
<td>Codominant</td>
<td>116(4.9)</td>
<td>1.16</td>
</tr>
<tr>
<td>Dominant</td>
<td>169(5.3)</td>
<td>1.69</td>
</tr>
<tr>
<td>Emergent</td>
<td>152(8.2)</td>
<td>1.52</td>
</tr>
</tbody>
</table>

- **Hemlock**
- **Red Spruce**
- **White Pine**
Figure 2.3e

Stand 50

<table>
<thead>
<tr>
<th>Percentage of Trees</th>
<th>Overtopped</th>
<th>Intermediate</th>
<th>Codominant</th>
<th>Dominant</th>
<th>Emergent</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>93 (.07)</td>
<td>100 (.73)</td>
<td>107 (2.1)</td>
<td>145 (11.5)</td>
<td>105 (3.8)</td>
</tr>
<tr>
<td></td>
<td>93 (.01)</td>
<td>104 (7.3)</td>
<td>108 (2.4)</td>
<td>102 (6.6)</td>
<td></td>
</tr>
<tr>
<td>Hemlock</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Red Spruce</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>White Pine</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 2.4. Ten-year age-class distributions for each stand. Y-Axis = Number of Trees/Ha.
Figure 2.5

White Pine

# Trees/Ha vs. Decade Reaching 1.37m

Stand
- 23
- 46
- 50
- 24
- 36
Figure 2.6a

Stand 23

#Trees/ha (Log Scale)

Diameter Class (cm)

Class has 0 trees = 1

- Hemlock
- Spruce
- Pine
- Sum
Figure 2.6b

Stand 24

#Trees/Ha (Log Scale)

Diameter Class (cm)

Class has 0 trees = 1

- Hemlock
- Spruce
- Pine
- Sum
Figure 2.6c

Stand 36

- Hemlock
- Spruce
- Pine
- Sum

#Trees/Ha (Log Scale)

Class has 0 trees = 1

Diameter Class

5 10 15 20 25 30 35 40 45 50 55 60 65 70 75
Figure 2.7a

Hemlock

<table>
<thead>
<tr>
<th>Stand</th>
<th>r</th>
</tr>
</thead>
<tbody>
<tr>
<td>36</td>
<td>.88</td>
</tr>
<tr>
<td>24</td>
<td>.81</td>
</tr>
<tr>
<td>50</td>
<td>.66</td>
</tr>
<tr>
<td>46</td>
<td>.68</td>
</tr>
<tr>
<td>23</td>
<td>.88</td>
</tr>
</tbody>
</table>
Figure 2.7b

Red Spruce

<table>
<thead>
<tr>
<th>Stand</th>
<th>r</th>
</tr>
</thead>
<tbody>
<tr>
<td>36</td>
<td>.57</td>
</tr>
<tr>
<td>24</td>
<td>.84</td>
</tr>
<tr>
<td>50</td>
<td>.82</td>
</tr>
<tr>
<td>46</td>
<td>.70</td>
</tr>
<tr>
<td>23</td>
<td>.84</td>
</tr>
</tbody>
</table>
Figure 2.7c

White Pine

<table>
<thead>
<tr>
<th>Stand</th>
<th>r</th>
</tr>
</thead>
<tbody>
<tr>
<td>36</td>
<td>.64</td>
</tr>
<tr>
<td>24</td>
<td>.82</td>
</tr>
<tr>
<td>50</td>
<td>.14</td>
</tr>
<tr>
<td>46</td>
<td>.01</td>
</tr>
<tr>
<td>23</td>
<td>.62</td>
</tr>
</tbody>
</table>
Figure 2.8a

Hemlock

Percentage of Trees Showing Growth Decreases $>$ 25% (all stands)

Average for all trees

First Year of Suppression Period

Stand
- □ 50
- □ 46
- ▢ 36
- □ 24
- ▢ 23
Figure 2.8b

Red Spruce

Percentage of Trees Showing Growth Decreases > 25% (all stands)

First Year of Suppression Period

Stand

- 50
- 46
- 36
- 24
- 23

Average for all Trees
Figure 2.8c

White Pine

Percentage of Trees Showing Growth Decreases > 25% (all stands)

First Year of Suppression Period

Stand

- 50
- 46
- 36
- 24
- 23

Average for all trees
Figure 2.9a

Stand 23

Age

# Trees/ha

Harvest

Harvest

Average for all trees

Percentage of Trees with Growth Increases > 100%

100
90
80
70
60
50
40
30
20
10
0

Figure 2.9b

Stand 24

Age

# Trees/ha

Pine
Spruce
Hemlock

Harvest

Average for all trees

Percentage of Trees with Growth Increases > 100%
Figure 2.9c

Stand 36

Age

Harvest

Harvest(s)

1911-70

Pine

Spruce

Hemlock

Average for all trees

Percentage of Trees with Growth Increases > 100%
Percentage of Trees with Growth Increases >100%

# Trees/ha

- 1971-79
- 1961-70
- 1951-60
- 1941-50
- 1931-40
- 1921-30
- 1911-20
- 1901-10
- 1891-00
- 1881-90
- 1871-80
- 1861-70
- 1851-60
- 1841-50
- 1831-40
- 1821-30
- 1810-20

Average for all trees

Harvest

Spruce

Hemlock

Pine

Figure 2.9e

Stand 50

Age

50

100

150

0

50

100

150

200

300

400

500

600

700

800

900

1000
Figure 2.10

Red Spruce

Partial harvest

Overtopped sapling stage

Spruce budworm outbreak

Hemlock

Overtopped sapling stage

Spruce budworm outbreak

YEAR
Figure 2.11

White Pine

Pine leaf adelgid outbreak

YEAR

.Radial increment

White Pine

Pine leaf adelgid outbreak

YEAR
Table B.2. Number of age trees showing growth decreases by decade*

### Red Spruce

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>25-50</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>6</td>
<td>5</td>
<td>7</td>
<td>7</td>
<td>3</td>
<td>13</td>
<td>4</td>
<td>5</td>
<td>4</td>
<td>5</td>
<td>5</td>
<td>11</td>
<td>11</td>
<td>102</td>
<td>229</td>
</tr>
<tr>
<td>51-75</td>
<td>1</td>
<td>1</td>
<td>6</td>
<td>5</td>
<td>7</td>
<td>7</td>
<td>3</td>
<td>13</td>
<td>4</td>
<td>5</td>
<td>4</td>
<td>5</td>
<td>5</td>
<td>11</td>
<td>11</td>
<td>102</td>
<td>229</td>
<td></td>
</tr>
<tr>
<td>76-90</td>
<td>1</td>
<td>6</td>
<td>5</td>
<td>7</td>
<td>7</td>
<td>3</td>
<td>13</td>
<td>4</td>
<td>5</td>
<td>4</td>
<td>5</td>
<td>5</td>
<td>11</td>
<td>11</td>
<td>102</td>
<td>229</td>
<td></td>
<td></td>
</tr>
<tr>
<td>TOTAL DECREASES</td>
<td>2</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>12</td>
</tr>
<tr>
<td>No. Trees Alive</td>
<td>7</td>
<td>14</td>
<td>23</td>
<td>25</td>
<td>30</td>
<td>38</td>
<td>51</td>
<td>71</td>
<td>91</td>
<td>106</td>
<td>110</td>
<td>145</td>
<td>174</td>
<td>187</td>
<td>191</td>
<td>192</td>
<td>192</td>
<td></td>
</tr>
<tr>
<td>Percent</td>
<td>14</td>
<td>29</td>
<td>48</td>
<td>48</td>
<td>48</td>
<td>48</td>
<td>48</td>
<td>48</td>
<td>48</td>
<td>48</td>
<td>48</td>
<td>48</td>
<td>48</td>
<td>48</td>
<td>48</td>
<td>48</td>
<td>48</td>
<td>48</td>
</tr>
</tbody>
</table>

### Hemlock

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>25-50</td>
<td>3</td>
<td>2</td>
<td>1</td>
<td>3</td>
<td>4</td>
<td>5</td>
<td>9</td>
<td>2</td>
<td>13</td>
<td>7</td>
<td>30</td>
<td>5</td>
<td>16</td>
<td>5</td>
<td>25</td>
<td>24</td>
<td>44</td>
<td>200</td>
</tr>
<tr>
<td>51-75</td>
<td>2</td>
<td>6</td>
<td>4</td>
<td>4</td>
<td>8</td>
<td>6</td>
<td>8</td>
<td>11</td>
<td>16</td>
<td>3</td>
<td>18</td>
<td>17</td>
<td>35</td>
<td>18</td>
<td>31</td>
<td>196</td>
<td></td>
<td></td>
</tr>
<tr>
<td>76-90</td>
<td>2</td>
<td>6</td>
<td>4</td>
<td>4</td>
<td>8</td>
<td>6</td>
<td>8</td>
<td>11</td>
<td>16</td>
<td>3</td>
<td>18</td>
<td>17</td>
<td>35</td>
<td>18</td>
<td>31</td>
<td>196</td>
<td></td>
<td></td>
</tr>
<tr>
<td>TOTAL DECREASES</td>
<td>7</td>
<td>10</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>12</td>
</tr>
<tr>
<td>No. Trees Alive</td>
<td>22</td>
<td>26</td>
<td>30</td>
<td>36</td>
<td>36</td>
<td>44</td>
<td>49</td>
<td>56</td>
<td>67</td>
<td>77</td>
<td>88</td>
<td>96</td>
<td>120</td>
<td>151</td>
<td>173</td>
<td>184</td>
<td>188</td>
<td>188</td>
</tr>
<tr>
<td>Percent</td>
<td>31</td>
<td>38</td>
<td>40</td>
<td>36</td>
<td>36</td>
<td>36</td>
<td>36</td>
<td>36</td>
<td>36</td>
<td>36</td>
<td>36</td>
<td>36</td>
<td>36</td>
<td>36</td>
<td>36</td>
<td>36</td>
<td>36</td>
<td>36</td>
</tr>
</tbody>
</table>

### White Pine

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>25-50</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>51-75</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>76-90</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>5</td>
<td>1</td>
<td>2</td>
<td>5</td>
<td>3</td>
<td>5</td>
<td>7</td>
<td>10</td>
<td>14</td>
<td>14</td>
<td>14</td>
<td>14</td>
<td>14</td>
<td>14</td>
<td>14</td>
</tr>
<tr>
<td>TOTAL DECREASES</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>5</td>
<td>1</td>
<td>2</td>
<td>5</td>
<td>3</td>
<td>5</td>
<td>7</td>
<td>10</td>
<td>14</td>
<td>14</td>
<td>14</td>
<td>14</td>
<td>14</td>
<td>14</td>
<td>14</td>
</tr>
<tr>
<td>No. Trees Alive</td>
<td>4</td>
<td>9</td>
<td>10</td>
<td>11</td>
<td>13</td>
<td>12</td>
<td>27</td>
<td>38</td>
<td>38</td>
<td>46</td>
<td>56</td>
<td>64</td>
<td>116</td>
<td>123</td>
<td>123</td>
<td>123</td>
<td>123</td>
<td>123</td>
</tr>
<tr>
<td>Percent</td>
<td>25</td>
<td>11</td>
<td>10</td>
<td>11</td>
<td>13</td>
<td>12</td>
<td>27</td>
<td>38</td>
<td>38</td>
<td>46</td>
<td>56</td>
<td>64</td>
<td>116</td>
<td>123</td>
<td>123</td>
<td>123</td>
<td>123</td>
<td>123</td>
</tr>
</tbody>
</table>

*Growth decreases prior to 1810 not included due to small sample size.
Table B.1. Number of age trees showing growth increases by decade*

<table>
<thead>
<tr>
<th>Tree Species</th>
<th>PERCENT INCREASE</th>
<th>1810-20</th>
<th>1821-30</th>
<th>1831-40</th>
<th>1841-50</th>
<th>1851-60</th>
<th>1861-70</th>
<th>1871-80</th>
<th>1881-90</th>
<th>1891-00</th>
<th>1901-10</th>
<th>1911-20</th>
<th>1921-30</th>
<th>1931-40</th>
<th>1941-50</th>
<th>1951-60</th>
<th>1961-70</th>
<th>1971-79</th>
<th>TOTAL</th>
</tr>
</thead>
<tbody>
<tr>
<td>100-150</td>
<td>No. Trees Alive</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Total Increases</td>
<td>4</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Percent</td>
<td>77</td>
<td>15</td>
<td>33</td>
<td>17</td>
<td>17</td>
<td>10</td>
<td>5</td>
<td>6</td>
<td>8</td>
<td>6</td>
<td>5</td>
<td>5</td>
<td>5</td>
<td>3</td>
<td>3</td>
<td>6</td>
<td>5</td>
<td>3</td>
</tr>
</tbody>
</table>

* Growth increases prior to 1810 not included due to small sample size.
Chapter 3. Effect of Stand Composition and Structure on Volume Production of Mixed-Species Conifer Stands in Maine

ABSTRACT

The effects of stand composition and structure on volume production were compared in conifer mixtures growing with and without white pine (*Pinus strobus* L.). The five stands examined consisted primarily of the shade tolerant species red spruce (*Picea rubens* Sarg.) and eastern hemlock (*Tsuga canadensis* (L.) Carr.). The mean total volume of sample plots containing pine was significantly higher (*P* < 0.02) than those that had none (355.30 ± 25.24 m³/ha vs. 275.06 ± 16.98 m³/ha). There was more canopy growing space potentially available beneath a dominant pine crown than beneath a spruce or hemlock crown. Total plot volumes were more affected by variability in age structure than by the presence or absence of pine. Plots with a representation of two or three cohorts were more productive than plots with a single cohort.

The development of a silvicultural system for these stands should include pine in the regeneration of shade-tolerant conifer species, and maintain a multicohort structure through implementation of the irregular shelterwood method.
INTRODUCTION

The amount of horizontal above-ground growing space available to individual trees in forest stands is finite. The physical space potentially available to each tree is defined by its crown canopy area in relationship to a portion of unoccupied ground surface. Vertical growing space is virtually unlimited, although both vertical and lateral crown growth can be restricted by trees coming in contact with neighbors. Because growth of wood volume is related to crown size, the space afforded each tree in a stand is a critical factor influencing yield.

Maximum efficiency in the use of canopy space occurs when trees stratify their crown positions. Canopy strata can be thought of as horizontal layers of tree crowns separated from higher and lower layers (Oliver 1978). Stratification is impossible in stands consisting of a single shade-intolerant species because each tree has the same requirement for maximum sunlight. Trees that do not attain a position in the upper strata become shaded and eventually die (Kozlowski and Peterson 1962). Stands with several species of different physiological growth requirements typically have irregular canopies, with many layers of foliage due to the vertical stratification of tree heights. Trees that occupy positions in the lower stratum (C-stratum) can survive and grow in less than full sunlight until natural stand development processes or a disturbance creates space for additional crowns to grow into the partial shade of the B-stratum, (upper continuous canopy), or into the full sunlight of the A-stratum (Oliver and Larson 1990).

In 1941, Langsaeter (Smith 1986) evaluated the relationship between total stand volume and stand growth and determined that an optimum age and density of trees should be grown per unit area to maximize growth rate. This
simple relationship differed by species but was consistent for a particular site and age. Stands of shade-tolerant conifer species generally can maintain optimum growth rates at higher densities and for a longer duration than shade-intolerant species (Zedaker et al. 1987).

Because most of the volume growth in a stand is concentrated in the largest trees, stand structure is also an important determinant of yield. A weak relationship was found between basal area (density) and volume growth in stands of Douglas-fir unless stand structure was also considered (Oliver and Murray 1983). In larger diameter or crown classes Douglas-fir grew more volume per hectare per year for a given density than did small trees. In mixed-species stands, most volume growth occurs in dominant trees exposed to full sunlight in the A- and B-strata. Trees in the lower strata achieve major gains in volume only after a partial disturbance increases the amount of growing space available to them (Oliver and Larson 1990).

Some studies have focused on productivity comparisons of single-cohort mixed-species, stratified stands with pure stands of the component species. Assman (1970) described the results of several experiments where the productivity of two-species mixtures were compared with those of pure stands of the shade-intolerant component. The mixtures always had greater volume yield. In one example, productivity of the mixtures was compared with a pure stand of the more shade-tolerant component; the mixture was still more productive. Wierman and Oliver (1979) found that canopy-stratified mixed stands of western hemlock (Tsuga heterophylla (Rafn.) Sarg.) and the less shade tolerant Douglas-fir (Pseudotsuga menziesii Franco) had higher per hectare basal areas than naturally established pure stands of either species.

Many natural forest types consist of canopy-stratified mixtures of more than two species representing a range in shade tolerance class (Lorimer 1980;
Kelty 1986; Kittredge 1988; Clatterbuck and Hodges 1988). These mixtures appear to be efficient in the use of canopy space, and presumably would be more productive than a monoculture of any of the components. However, in multi-species stands it is cumbersome to compare the productivity of each species with that of a pure stand. In single-cohort stands that contain three or more species, productivity comparisons have been made among species groups. Kelty (1989) compared two multi-species hardwood stands of similar species composition, age and site except that one stand had an additional dense, sub-canopy strata of eastern hemlock (*Tsuga canadensis* (L) Carr.). The stand containing hemlock had higher per hectare yields in basal area and stemwood volume than the pure hardwood stand.

Multi-species conifer stands occur extensively in eastern and central Maine where they are highly valued by a large paper industry. Here the natural range of red spruce (*Picea rubens* Sarg.) overlaps with that of eastern hemlock. These mixtures also contain a minor component of balsam fir (*Abies balsamea* (L.) Mill.) and a scattering of white pine (*Pinus strobus* L.), a species highly valued for lumber (Seymour 1991). The differences in shade tolerance and cohort distributions between white pine, which is rated as intermediate in tolerance (Wendel and Smith 1990), and the very shade tolerant spruce, fir, and hemlock (Blum 1990; Goodman and Lancaster 1990; Frank 1990) have resulted in stands displaying a vertically stratified canopy with white pine in dominant crown positions (Fajvan, Chapter 2).

The purpose of this study is to test the hypothesis that the presence of white pine increases volume production of stemwood in stands where it occurs with shade-tolerant conifers. Comparisons will be made between the strategies used by hemlock, spruce and pine to achieve status in the main canopy with regards to the most efficient use of canopy growing space and the ability to
produce stemwood volume. The influences of both age and physical stand structure on volume production will also be examined.

METHODS

Study Area

The study area consisted of five stands located on Champion International Corporation Inc., land in east central Maine. Principal species components of the stands were red spruce, hemlock and white pine with hardwood species comprising 2 to 16 percent of stem densities. The density of pine was similar in all five stands and ranged from 24-35 trees/ha. The stand densities of spruce and hemlock were much higher than pine and were similar within each stand but varied widely among stands (Fajvan, Chapter 2). The stands ranged in size from 4-10 ha with the four smallest stands (designated 23, 24, 46, 50) located within a 4 km radius of each other, and the largest stand (stand 36) located 21 km from the rest.

The climate of the area is temperate, with mean annual precipitation of 113 cm. The warmest month is July with a mean temperature of 22° C and the coldest month is January with a mean temperature of -6° C. Elevation of the study area is approximately 150 m with a mean annual snow accumulation of 128 cm (National Oceanic and Atmospheric Administration weather station).

Both crown class and height distributions revealed canopy stratification by species in all stands. With heights up to 35 m, pine is the only species existing as emergents in the A-stratum. Spruce heights are strongly represented in the 10-20 m range, and they overlap with pine in the dominant crown class at the upper end of this range. Hemlock, spruce and pine were all present as codominants, and there were more spruce than hemlock intermediates. Hemlock comprised the majority of the height class up to about
10 m, and hemlock and spruce occupied the majority of the intermediate and overtopped classes (Fajvan, Chapter 2). Ten-year age-class distributions showed a diversity in age structures with trees represented in at least 13 of the 17 decades represented in each stand. The age structures of the stands revealed multicohort distributions promoted by partial disturbances such as insect outbreaks and harvesting (Fajvan, Chapter 2).

*Field and Laboratory Procedures*

Because white pine was generally present as a minor component in all stands, comparisons among stands with and without pine were not feasible. Comparisons within and between stands were based on sample plots that contained pine versus plots that did not. Although pine was the major focus of the study, it also occurred with lowest frequency; an intensive sample of 425 plots was established systematically to examine the distribution of pine. All five stands had been strip clearcut during the past five years and the size of the uncut strips ranged from 18-30 m in width and 100-250 m in length. Transect lines were run down the center of each residual strip and .02 ha circular plots were established every 20 meters. The diameter at breast height (1.37 m) and crown class designation (Smith 1986) of each white pine ≥ 1.37 m tall and located within plot boundaries were recorded.

Fifty plots (10 per stand) were then randomly selected according to the criteria that half the plots contain at least one dominant or codominant pine ("pine" plots) and the other half contain at least one dominant or codominant red spruce and hemlock ("no-pine" plots). These dominant trees ("subject" trees) served as the basis for comparisons of interspecific growth strategies and volume production. On all 50 plots, measurements were taken on all plot trees ≥ 11.4 cm diameter at breast height (dbh). Trees that were less than 11.4 cm
dbh and \( \geq 1.37 \) m tall were sampled on a .008 ha circular plot that was established within each larger plot. Species, dbh and crown class were recorded for all sampled trees. Within the main canopy, trees were classified as dominant, codominant, intermediate and overtopped according to Smith (1986). Any tree with a crown protruding well above the level of the dominant and codominant crown classes was classified as "emergent."

A soil pit was excavated on each of the 50 plots to assess the uniformity of soil conditions. The pits were excavated to the depth of the bottom of the rooting zone. Soils were classified according to a system used by Champion International Corporation Inc., on their permanent growth plots (Table A.1, Appendix A). All soils were classified as "Profile II" with thin, moderately developed soil horizons. Colors of the sub-surface soil were red and brown, grading quickly into yellowish tints of these colors. Mottling was sometimes found at depths of 31-69 cm.

Increment cores were taken at 1.37 m above the ground from all subject trees and all trees beneath and surrounding subject trees. Trees were cored repeatedly until an acceptable core (one containing the pith) was extracted. It was not possible to obtain cores from some of the larger trees due to heart rot. Surrounding trees were those that had a portion of their crown touching the subject tree. Even if the trees surrounding the subject tree were not within plot boundaries, species, dbh and crown class were collected. Total height, and height to the base of the live crown were measured using a clinometer on all subject trees, surrounding trees, and trees growing beneath subject trees. In the laboratory, increment cores were sanded and growth rings were measured (to the nearest 0.01 mm) using a binocular microscope (4X power) and a Measuchron®.
Crown projection maps were constructed for two plots in each stand; one plot randomly selected from the pine group and the other selected from the no-pine group. Crowns of subject trees, trees beneath subject trees, and surrounding trees were measured. Tree stems were located and mapped using a plane table. Crown radii representing the widest point in the crown were measured in four perpendicular directions to the initial radius, which was established in the direction facing the plane table. The intersection of each radius with the line-of-sight from the plane table was mapped. An arc was drawn connecting each radius to represent the approximate area and extent of each crown. In the lab a microcomputer-controlled video digitizer was used to measure the area contained in each crown. The areas contained in zones of crown overlap were also measured.

Data Analyses

Comparisons of basal area, crown area, and total and merchantable volume were made between pine and no-pine plots. Increment cores were used for comparisons of basal-area growth over time between the subject trees and the trees they dominated. Because the radius represented by the core was not necessarily a true average for the tree, basal area could be under- or over- estimated. The radius of the core was doubled and an adjustment was made in proportion to the dbh and bark thickness in the following manner. Values of average bark thickness by diameter class for each species (Nims, nd., as cited in Forestry Handbook 1984) were used in a regression to derive a predictive equation for estimating bark thickness from diameter for each species. The estimated bark thickness for each tree was subtracted from the dbh measurement. The resulting diameter inside bark was compared with the diameter inside bark of the increment core, and radial-growth increments were
adjusted accordingly. Cumulative basal-area growth was calculated from the increment cores for each decade. Mean annual basal-area increment for the last 50 years (based on age of youngest subject trees) was calculated for all subject trees.

The total stemwood volume of individual trees was estimated from dbh and total height using regression equations developed by Honer (1967). Because height was not measured for all trees, calculated volumes were used in a regression of volume (cubic feet) (dependent variable) on diameter (inches) (independent variable) for each species. All resulting equations had an R² of .99.

- **Hemlock**
  \[ \text{Total volume} = 1.16 - (.76 \text{dbh}) + (.19 \text{dbh}^2) \]

- **Spruce**
  \[ \text{Total volume} = 1.41 - (.84 \text{dbh}) + (.22 \text{dbh}^2) \]

- **Pine**
  \[ \text{Total volume} = 6.28 - (2.13 \text{dbh}) + (.30 \text{dbh}^2) \]

The equations were used to estimate total volume (inside bark, including stump and top) for all plot trees. Sawlog volume was estimated from total volume using a ratio of squared diameters: \((\text{merchable top diameter of } 15 \text{ cm})^2 / (\text{breast height diameter})^2\). Sawlog volume was estimated for all trees with a minimum dbh of 23 cm. Total basal area and volume were calculated for all plot trees, and per hectare basal area and volume estimates were derived for each plot. Mean basal area/ha and volume/ha were calculated for pine vs. no-pine plots in each stand. Non-parametric statistical tests (Wilcoxon 2-sample test, Kruskall Wallace test) were used to compare the differences between means.

Crown area data from the 10 plots that were crown mapped were used to calculate the growth efficiency of the site trees on pine and no-pine plots. A ratio of total volume / crown area was determined for each subject tree.

The area of overlap between the crown projection areas of each mapped subject tree and the crown projection areas of all crowns that intersected
subject trees was calculated as a percentage (Figure 3.1). The purpose was to determine how much of the crown projection area of the subject tree was being used twice, once by the subject tree and once by the trees beneath and surrounding it. If the crowns of the non-subject trees also overlapped with each other, the amount of crown area being used three times (once by the subject tree and twice by trees of lower strata) was considered in the calculations of percentage crown overlap.

RESULTS

Volume Comparisons

Basal area comparisons for all species, in pine and no-pine plots, are shown in Figure 3.2. There was no significant difference (at alpha=0.05) in mean basal areas between pine and no-pine plots in each stand. However, when all stands were considered together, the pine plots had significantly higher (Z= -2.42; P>Z=0.01) mean basal areas (46.90 ± 2.31 vs. 39.40 ± 1.72 m²/ha) than the no-pine plots. A closer examination of the basal areas of each of the 50 plots showed that, of the 10 plots with the highest basal areas (50-70 m²/ha), 7 were pine plots. Pine comprised from 12-61 percent of the total basal area/ha in these plots. Alternatively, 7 of the 10 plots with the lowest basal areas were no-pine plots (Table 3.1).

Mean total volume of pine, spruce and hemlock on pine and no-pine plots showed similar trends as the basal area comparisons. There were no significant differences in mean volumes between pine and no-pine plots in each stand but pine plots had significantly higher volumes when all stands were considered together (Table 3.2). In comparisons of sawlog volumes only in stand 46 were pine plots higher than no-pine plots (Table 3.3). Sawlog
volumes were similar when all stands were considered together. The volumes of individual species were also calculated for pine and no-pine plots in each stand (Table 3.4). There is significantly more volume of hemlock and spruce on no-pine plots in stands 23, 46 and 50.

Structural Differences.

The disturbance histories of each stand influenced the spatial distribution of species and resulted in unique age structures (Fajvan, Chapter 2). Patterns of stand development were guided by species-specific responses to disturbance. Therefore, stand structural differences may affect the presence and distribution of pine in each stand.

Dominant/codominant hemlock were older on the no-pine plots in three stands (24, 36 and 46); spruce are older on no-pine plots in two stands (36 and 50) (Table 3.5). Both hemlock and spruce dominants/codominants are significantly taller on the no-pine plots in stands 36 and 50; hemlock is taller in stand 46. Mean heights of hemlock and spruce are higher on the pine plots in stand 23, and the mean height of spruce is greater on the pine plots in stands 24 and 46 (Table 6).

Growth Efficiencies

Growth efficiencies for all subject trees were similar regardless of species or the type of plot (pine or no-pine) they grew on (Table 3.7). The percentage crown projection area occupied by crowns intersecting pine subject trees was generally greater than for crowns intersecting spruce and hemlock subject trees regardless of the type of plot being considered. Four of the five pine subject trees had crown projection area (double overlap) percentages ≥ 70 percent. Only two spruce and one hemlock had values that high. Pine also had the
highest percentages of crown projection area overlap when areas of triple overlap were considered. One pine had 237 percent of its crown projection area occupied by the crowns of intersecting trees (Table 3.8).

**DISCUSSION**

*Effects of Stand Structure on Volume Production*

Because the mean basal areas and volumes of the pine plots were comparable to no-pine plots at the stand level but not over all 50 plots, the influence of stand structure on volume production was more closely examined. The variability in the densities of spruce, hemlock and pine in the 10 plots with the highest basal areas implies that plots with high densities of trees would be more productive regardless of species. However, because 7 of the 10 plots contained pine, a relationship may exist between species density and the conditions that promote pine regeneration.

Height and diameter are the main determinants of volume. Because height and diameter are also assumed to be correlated with age, comparisons are traditionally conducted between height and diameter in estimating volume (Zedaker et al. 1987). Figures 3.3a-e show the mean heights of each species by diameter. An obvious overall pattern that appears to relate shade tolerance to diameter and height growth is present in all stands. Spruce, which is less shade tolerant than hemlock, were always taller than a hemlock of the same diameter. Similarly, pine, which is intermediate in shade tolerance was always taller than hemlock and equal to or taller than spruce in the same diameter classes. However, pine is the only species with individuals greater than 55 cm dbh and these trees are always much taller than the rest of the stand.
The pines in each stand were larger than any other species and there was less variability in relationships of size to age than for spruce and hemlock. General trends in the relationships of size to age for spruce and hemlock showed larger trees to be older than smaller trees (Fajvan, Chapter 2). A comparison of the mean heights of the overstory trees (dominant and codominant crown classes) between pine and no-pine plots showed (Table 3.6) that the mean heights of spruce and/or hemlock were higher on 3 out of 5 no-pine plots than on pine plots. Mean volumes of spruce and hemlock were also higher in two of the same no-pine plots (Table 3.4) suggesting that the absence of pine allowed these trees to grow taller. However, the mean ages of the trees on the no-pine plots were also higher in all three stands (Table 3.5).

The multicohort nature of the stands and the vertically stratified canopy structure result from the growth responses of each species to disturbance. As the pine response to disturbance differs from that of spruce and hemlock, the structure and development of the pine plots may be different from those of no-pine plots, and may help explain some of the variability found in volume comparisons. One possible explanation is that the older spruce and hemlock found on some of the no-pine plots probably existed as advance regeneration in the understory before a disturbance regenerated the "younger" trees of the pine plots. The advance growth trees on the no-pine plots were taller than new seedlings and had a head start.

Without advance seedlings, all three species can potentially regenerate in the new growing space created by a disturbance, and if pine is present it will probably eventually attain dominance. There was no difference in mean heights of hemlock and spruce between pine and no-pine plots in stand 24, even though the hemlocks on the no-pine plots were older. However, pine was taller and similar in age to the spruce and hemlock on the pine plots. In stand
23 the opposite trend was found; hemlock and spruce were taller on pine plots than in no-pine plots but only the hemlock were older on the pine plots.

*Characteristics of Subject Trees*

The affect of stand development on volume production was not conclusive at the stand and plot (pine vs. no-pine) levels. Additional information was sought at the tree level. The growth and yield of pine subject trees versus spruce and hemlock subject trees, and the effects on subcanopy growing space were examined. Generally, there appears to be more potentially available canopy growing space beneath a dominant pine crown than beneath a dominant spruce or hemlock (Table 3.8). Pine subject trees also had the highest values (with one exception) of mean annual basal-area increment for the last 50 years (Tables C.1 and C.2, Appendix C).

The characteristics of pine subject trees suggest that a dominant pine can grow faster, produce more volume in less time, and potentially create more subcanopy growing space than a dominant hemlock or spruce when the species are grown in mixture. The development of each subject tree and its associated dominated trees were examined in order to gain some insight into the growth strategies used to attain dominance. Several patterns became evident in graphs of the cumulative basal area growth rates of these groups; missing cores prevented the use of four subject trees in the comparisons:

1) subject trees belonging to same cohort attain dominance;

2) subject trees belonging to older cohorts have a head start;
3) subject trees belonging to younger cohorts attain
dominance through more vigorous growth.

Pine showed growth strategies 1 and 3. Three of the pine subject trees
and their associates belonged to the same cohort, but the pine surpassed its
associates in height growth and attained dominance (Fig. 3.4). The fourth pine
subject tree belonged to a younger cohort than two hemlocks currently growing
beneath it (Fig. 3.5). The hemlocks reached breast height in the late 1800’s. A
partial disturbance in the 1930’s released the two hemlocks, which had not
grown much during their first 80 years, and regenerated a new cohort of pine
and hemlock. The pine was able to attain dominance over both the new
hemlock seedlings as well as the older saplings.

Because pine cannot survive as an advance seedling in the understory
for very long, they are unable to employ strategy 2 unless they are a residual
overstory member of an older cohort after a partial disturbance. Spruce and
hemlock displayed all three growth strategies (Figs. 3.6-3.8), with strategy 2
being the most common. Due to their high tolerance of shade, spruce and
hemlock are able to remain in a suppressed condition as advance seedlings
and saplings for many years, until a disturbance in the main canopy increases
the amount of sunlight reaching the forest floor and they respond with a growth
increase. Hemlock and spruce can successfully attain status in the main
canopy through several periods of growth flushes interspersed with
suppression in response to periodic partial disturbances (Marshall 1927; Henry
and Swan 1974; Oliver and Stephens 1977; Lorimer et al. 1988; Davis 1989).

The preceding analyses suggested that variability in cohort distribution is
potentially the major cause of differences in volume between pine and no-pine
plots. The number of cohorts in each of the 50 plots was classified as one of
three broad categories timed when breast height was attained: 1) pre-1860 2) 1861-1925 3) post-1925. These categories were derived from examination of Figs. 3.4-3.8. Volumes were then compared between pine and no-pine plots according to the number of cohorts they contained. Results (Table 3.9) showed that the volume of plots with a single cohort was significantly (alpha=0.05) less than the volume of plots with two or three cohorts. In addition, the pine plots in each cohort-category had higher volumes than the no-pine plots, and the difference was most significant in plots containing three cohorts.

Age structure was the only variable that could be used consistently in identification of productivity differences between pine and no-pine plots. The complex disturbance histories of the five stands combined with the species-specific responses to disturbance made it difficult to correlate tree size with age for productivity determination, especially at the stand level. Regardless of the presence or absence of pine, the variability in cohort distributions was most influential in defining volume production. The presence of two or three cohorts appears to be the most productive structure. For example, volume production was highest on plots where pine had established an emergent position in the A-stratum and where the canopy space of the B- and C- strata was occupied by two or more cohorts of spruce and hemlock representing a range in sizes.

**Management Implications**

These results support managing Maine's mixed-conifer stands as multicohort structures with an emphasis on maintaining a pine component in the regeneration. Creation of a multicohort structure does not imply that the range in ages found in stands of the current study should be reproduced. Achievement of irregular height structures, to maintain full occupancy of canopy growing space, should be the goal of management.
Implementation of the irregular shelterwood method (Smith 1986) allows a silviculturist to vary the species composition of a desired forest stand by timing the intensity of harvest operations with anticipated seed years. The method is particularly amenable to mixed-species stands because variations in growth rates means that trees will mature at different times.

Depending on the initial structure of a stand (e.g., amount of advance regeneration; age of dominant pines), two or three cuttings should be implemented. In a regime of two removal cuttings, the first cutting should focus on retaining large high quality pines both to increase their value through additional growth and, as seed trees. If there is insufficient advance growth of spruce and hemlock then retaining some seed trees of these species is also important. Due to the ability of spruce and hemlock to increase growth following a disturbance, harvest goals should include retention of some saplings because these trees can be managed as part of the new cohort. If advance growth is lacking, and/or the dominant pines are of an advanced age and cannot be maintained until the end of the first rotation, then the first cutting may have to occur in two phases: establishment cutting followed by removal.

The partial shade provided by the residual trees should reduce the effects of the white pine weevil (*Pissodes strobi* Peck) on new regeneration. The weevil often kills the terminal leader of trees with tops in the sunshine and a lateral branch usually replaces the terminal forming a crook in the stem (Smith 1986).

The second removal cutting should occur approximately 50-60 years after the first. Most if not all of the pine seed trees should be removed and dominant pines in the new cohort should be thinned if necessary. Management goals should again focus on retention of high value trees for another rotation, and the regeneration of a new cohort.
There are some economic benefits to consider in the promotion and management of conifer mixtures with a pine component. Most pines examined in this study were of good to excellent sawlog quality (although no formal grading was performed) even though the current stands originated without management and past harvesting was in the form of "hygrading" for larger stems. If these pines had been weeviled in the past, then they compensated quickly because most stems were straight. In addition, the pines were generally free of lower limbs possibly due to the pruning effect of hemlock or spruce crowns shading the lower branches. The irregular shelterwood method mimics partial disturbances but in a manner that produces more manageable forest stands with more definite age structures. In addition, conifer regeneration that occurs in partial shade is less likely to contain hardwood species and hence there is less use of herbicides.

CONCLUSION

While the diverse stand development histories of current stands are not necessary to promote the presence of pine in conifer mixtures, the complexities of the stands give insight into many potential development pathways. The presence of pine with spruce and hemlock can increase volume production of a stand. The variability in patterns of height and diameter growth, and in multicohort stand-structures result from species-specific responses to partial disturbances. These disturbances were so influential to the development of the stands that their affects had to be considered to understand productivity. Careful scrutiny and classification of the development patterns suggests the integration of the irregular shelterwood method into the silvicultural system used to manage these stands.
LITERATURE CITED


Table 3.1. Ranking of plots with the ten highest and ten lowest basal areas (m²/ha).

<table>
<thead>
<tr>
<th>Stand</th>
<th>Plot</th>
<th>Type</th>
<th>Total Basal Area</th>
<th>Pine Basal Area</th>
<th>Spruce Basal Area</th>
<th>Hemlock Basal Area</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Ten Highest</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>46</td>
<td>22</td>
<td>P</td>
<td>69.75</td>
<td>42.32</td>
<td>16.99</td>
<td>2.24</td>
</tr>
<tr>
<td>24</td>
<td>57</td>
<td>P</td>
<td>65.19</td>
<td>20.62</td>
<td>14.40</td>
<td>26.68</td>
</tr>
<tr>
<td>36</td>
<td>11</td>
<td>P</td>
<td>63.29</td>
<td>12.52</td>
<td>43.37</td>
<td>7.39</td>
</tr>
<tr>
<td>36</td>
<td>63</td>
<td>P</td>
<td>62.45</td>
<td>2.55</td>
<td>33.72</td>
<td>20.56</td>
</tr>
<tr>
<td>23</td>
<td>22</td>
<td>P</td>
<td>55.65</td>
<td>11.64</td>
<td>4.14</td>
<td>26.03</td>
</tr>
<tr>
<td>24</td>
<td>28</td>
<td>P</td>
<td>55.01</td>
<td>12.90</td>
<td>18.40</td>
<td>16.90</td>
</tr>
<tr>
<td>36</td>
<td>51</td>
<td>NP</td>
<td>54.74</td>
<td>0.00</td>
<td>37.05</td>
<td>17.12</td>
</tr>
<tr>
<td>23</td>
<td>23</td>
<td>P</td>
<td>53.93</td>
<td>6.70</td>
<td>8.02</td>
<td>29.61</td>
</tr>
<tr>
<td>46</td>
<td>32</td>
<td>NP</td>
<td>51.03</td>
<td>0.00</td>
<td>14.85</td>
<td>30.16</td>
</tr>
<tr>
<td>23</td>
<td>74</td>
<td>NP</td>
<td>50.37</td>
<td>0.00</td>
<td>47.25</td>
<td>0.57</td>
</tr>
</tbody>
</table>

|       |      |      | Ten Lowest       |                |                  |                   |
| 24    | 46   | NP   | 16.08            | 0.00           | 3.27             | 12.13             |
| 24    | 54   | P    | 22.18            | 2.66           | 16.55            | 1.33              |
| 50    | 77   | NP   | 25.05            | 0.00           | 14.96            | 7.60              |
| 46    | 14   | P    | 27.17            | 14.06          | 4.50             | 7.70              |
| 50    | 511  | NP   | 27.39            | 0.00           | 13.80            | 2.80              |
| 36    | 23   | P    | 31.19            | 7.70           | 22.12            | 1.16              |
| 23    | 63   | NP   | 33.06            | 0.00           | 28.14            | 4.35              |
| 24    | 88   | NP   | 33.87            | 0.00           | 14.17            | 14.56             |
| 50    | 33   | NP   | 35.03            | 0.00           | 12.59            | 22.45             |
| 23    | 72   | NP   | 35.49            | 0.00           | 18.85            | 15.16             |
Table 3.2. Comparison of mean total volume/ha (m$^3$) of pine, spruce and hemlock, in pine and no-pine plots using the Wilcoxon 2-Sample Test.

<table>
<thead>
<tr>
<th>Stand</th>
<th>Pine (n=5)</th>
<th>No-Pine (n=5)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean Volume (Standard Error)</td>
<td></td>
</tr>
<tr>
<td>23</td>
<td>306.18 (17.44)</td>
<td>298.94 (36.92)</td>
</tr>
<tr>
<td></td>
<td>$z$</td>
<td>-0.84</td>
</tr>
<tr>
<td></td>
<td>$P &gt; z$</td>
<td>0.4034</td>
</tr>
<tr>
<td>24</td>
<td>389.95 (73.40)</td>
<td>208.70 (38.32)</td>
</tr>
<tr>
<td></td>
<td>$z$</td>
<td>-1.67</td>
</tr>
<tr>
<td></td>
<td>$P &gt; z$</td>
<td>0.09</td>
</tr>
<tr>
<td>36</td>
<td>378.22 (52.53)</td>
<td>337.73 (16.93)</td>
</tr>
<tr>
<td></td>
<td>$z$</td>
<td>-0.42</td>
</tr>
<tr>
<td></td>
<td>$P &gt; z$</td>
<td>0.68</td>
</tr>
<tr>
<td>46</td>
<td>436.55 (70.86)</td>
<td>295.47 (26.03)</td>
</tr>
<tr>
<td></td>
<td>$z$</td>
<td>-1.88</td>
</tr>
<tr>
<td></td>
<td>$P &gt; z$</td>
<td>0.06</td>
</tr>
<tr>
<td>50</td>
<td>265.59 (30.75)</td>
<td>234.45 (45.94)</td>
</tr>
<tr>
<td></td>
<td>$z$</td>
<td>-0.42</td>
</tr>
<tr>
<td></td>
<td>$P &gt; z$</td>
<td>0.68</td>
</tr>
<tr>
<td>All Stands</td>
<td>n=25</td>
<td>n=25</td>
</tr>
<tr>
<td>Mean Volume (Standard Error)</td>
<td>355.30 (25.24)</td>
<td>275.06 (16.98)</td>
</tr>
<tr>
<td>$z$</td>
<td>-2.42</td>
<td></td>
</tr>
<tr>
<td>$P &gt; z$</td>
<td>0.01$^*$</td>
<td></td>
</tr>
</tbody>
</table>

* Significant at alpha=0.05
Table 3.3. Comparison of mean sawlog volume (m$^3$/ha) of pine, spruce and hemlock, in pine vs. no-pine plots using Wilcoxon 2-Sample Test.

<table>
<thead>
<tr>
<th>Stand</th>
<th>Pine (n=5)</th>
<th>No-Pine (n=5)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean Volume (Standard Error)</td>
<td></td>
</tr>
<tr>
<td>23</td>
<td>119.36 (23.15)</td>
<td>106.39 (31.65)</td>
</tr>
<tr>
<td></td>
<td>$z$</td>
<td>-0.21</td>
</tr>
<tr>
<td></td>
<td>$P &gt; z$</td>
<td>0.83</td>
</tr>
<tr>
<td>24</td>
<td>163.72 (54.83)</td>
<td>64.47 (30.22)</td>
</tr>
<tr>
<td></td>
<td>$z$</td>
<td>-1.46</td>
</tr>
<tr>
<td></td>
<td>$P &gt; z$</td>
<td>0.14</td>
</tr>
<tr>
<td>36</td>
<td>119.64 (33.49)</td>
<td>122.55 (11.35)</td>
</tr>
<tr>
<td></td>
<td>$z$</td>
<td>0.84</td>
</tr>
<tr>
<td></td>
<td>$P &gt; z$</td>
<td>0.40</td>
</tr>
<tr>
<td>46</td>
<td>246.30 (48.78)</td>
<td>131.24 (19.87)</td>
</tr>
<tr>
<td></td>
<td>$z$</td>
<td>-2.09</td>
</tr>
<tr>
<td></td>
<td>$P &gt; z$</td>
<td>0.04*</td>
</tr>
<tr>
<td>50</td>
<td>109.23 (21.18)</td>
<td>106.26 (37.51)</td>
</tr>
<tr>
<td></td>
<td>$z$</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>$P &gt; z$</td>
<td>0.99</td>
</tr>
<tr>
<td>All Stands</td>
<td>n=25</td>
<td>n=25</td>
</tr>
<tr>
<td>Mean Volume (Standard Error)</td>
<td>151.65 (18.92)</td>
<td>106.18 (12.25)</td>
</tr>
<tr>
<td></td>
<td>$z$</td>
<td>-1.49</td>
</tr>
<tr>
<td></td>
<td>$P &gt; z$</td>
<td>0.13</td>
</tr>
</tbody>
</table>

*Significant at alpha=0.05.
Table 3.4. Comparison of total volume (m$^3$/ha) by species between pine (P) and no-pine (NP) plots using Wilcoxon 2-Sample Test.

<table>
<thead>
<tr>
<th>Species</th>
<th>23 (n=5)</th>
<th>24 (n=5)</th>
<th>36 (n=5)</th>
<th>46 (n=5)</th>
<th>50 (n=5)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>P</td>
<td>NP</td>
<td>P</td>
<td>NP</td>
<td>P</td>
</tr>
<tr>
<td>White Pine</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean Vol.</td>
<td>97.36</td>
<td>0.00</td>
<td>166.75</td>
<td>0.00</td>
<td>64.67</td>
</tr>
<tr>
<td>Std. Err.</td>
<td>(14.78)</td>
<td>(50.15)</td>
<td>(21.20)</td>
<td>(40.98)</td>
<td>(66.80)</td>
</tr>
<tr>
<td>Hemlock</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean Vol.</td>
<td>90.80</td>
<td>73.83</td>
<td>69.40</td>
<td>73.83</td>
<td>66.44</td>
</tr>
<tr>
<td>Std. Err.</td>
<td>(43.87)</td>
<td>(26.34)</td>
<td>(39.82)</td>
<td>(14.69)</td>
<td>(20.14)</td>
</tr>
<tr>
<td>Z</td>
<td>0.21</td>
<td>0.63</td>
<td>0.84</td>
<td>-2.33</td>
<td>0.02*</td>
</tr>
<tr>
<td>P &gt; Z</td>
<td>0.83</td>
<td>0.53</td>
<td>0.40</td>
<td>0.00</td>
<td>0.99</td>
</tr>
<tr>
<td>Red Spruce</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean Vol.</td>
<td>118.02</td>
<td>222.14</td>
<td>153.80</td>
<td>134.87</td>
<td>247.11</td>
</tr>
<tr>
<td>Std. Err.</td>
<td>(31.02)</td>
<td>(57.79)</td>
<td>(16.96)</td>
<td>(41.48)</td>
<td>(35.90)</td>
</tr>
<tr>
<td>Z</td>
<td>0.84</td>
<td>-0.63</td>
<td>0.63</td>
<td>0.00</td>
<td>1.67</td>
</tr>
<tr>
<td>P &gt; Z</td>
<td>0.40</td>
<td>0.53</td>
<td>0.53</td>
<td>0.99</td>
<td>0.09</td>
</tr>
<tr>
<td>Spruce and Hemlock</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean Vol.</td>
<td>208.83</td>
<td>298.94</td>
<td>223.20</td>
<td>208.70</td>
<td>313.55</td>
</tr>
<tr>
<td>Std. Err.</td>
<td>(17.31)</td>
<td>(36.98)</td>
<td>(35.40)</td>
<td>(38.32)</td>
<td>(40.63)</td>
</tr>
<tr>
<td>Z</td>
<td>3.94</td>
<td>0.68</td>
<td>0.88</td>
<td>6.62</td>
<td>5.77</td>
</tr>
<tr>
<td>P &gt; Z</td>
<td>0.05*</td>
<td>0.60</td>
<td>0.35</td>
<td>0.01*</td>
<td>0.02*</td>
</tr>
</tbody>
</table>

* Significant at alpha=0.05
Table 3.5. Comparison of mean age of dominant and codominant trees by species between pine (P) and non-pine (NP) plots using the Wilcoxon 2-sample test.

<table>
<thead>
<tr>
<th>Species</th>
<th>23</th>
<th>24</th>
<th>36</th>
<th>46</th>
<th>50</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>P</td>
<td>P</td>
<td>P</td>
<td>P</td>
<td>P</td>
</tr>
<tr>
<td></td>
<td>NP</td>
<td>NP</td>
<td>NP</td>
<td>NP</td>
<td>NP</td>
</tr>
<tr>
<td>White Pine</td>
<td>n=4</td>
<td>n=5</td>
<td>n=7</td>
<td>n=5</td>
<td>n=16</td>
</tr>
<tr>
<td>Mean Age</td>
<td>88 (23.27)</td>
<td>102 (24.54)</td>
<td>65 (4.68)</td>
<td>155 (8.19)</td>
<td>109 (2.22)</td>
</tr>
<tr>
<td>Stnd. Err.</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Z</td>
<td>-4.63</td>
<td>-2.56</td>
<td>2.62</td>
<td>-3.10</td>
<td></td>
</tr>
<tr>
<td>P &gt; Z</td>
<td>&lt;0.001**</td>
<td>0.01*</td>
<td>0.01*</td>
<td>0.002*</td>
<td></td>
</tr>
<tr>
<td>Hemlock</td>
<td>n=14</td>
<td>n=14</td>
<td>n=20</td>
<td>n=21</td>
<td>n=15</td>
</tr>
<tr>
<td>Mean Age</td>
<td>166 (0.14)</td>
<td>74 (3.61)</td>
<td>85 (5.09)</td>
<td>122 (10.23)</td>
<td>186 (19.01)</td>
</tr>
<tr>
<td>Stnd. Err.</td>
<td>0.00</td>
<td>128</td>
<td>0.00</td>
<td>128</td>
<td>0.00</td>
</tr>
<tr>
<td>Z</td>
<td>-4.63</td>
<td>-2.56</td>
<td>2.62</td>
<td>-3.10</td>
<td></td>
</tr>
<tr>
<td>P &gt; Z</td>
<td>&lt;0.001**</td>
<td>0.01*</td>
<td>0.01*</td>
<td>0.002*</td>
<td></td>
</tr>
<tr>
<td>Spruce</td>
<td>n=10</td>
<td>n=70</td>
<td>n=49</td>
<td>n=63</td>
<td>n=19</td>
</tr>
<tr>
<td>Mean Age</td>
<td>91 (6.21)</td>
<td>97 (4.19)</td>
<td>108 (8.56)</td>
<td>96 (4.80)</td>
<td>96 (8.19)</td>
</tr>
<tr>
<td>Stnd. Err.</td>
<td>0.00</td>
<td>128</td>
<td>0.00</td>
<td>128</td>
<td>0.00</td>
</tr>
<tr>
<td>Z</td>
<td>-4.63</td>
<td>-2.56</td>
<td>2.62</td>
<td>-3.10</td>
<td></td>
</tr>
<tr>
<td>P &gt; Z</td>
<td>&lt;0.001**</td>
<td>0.01*</td>
<td>0.01*</td>
<td>0.002*</td>
<td></td>
</tr>
</tbody>
</table>

* Significant at alpha=0.05  ** Significant at alpha=0.001
Table 3.6. Comparison of mean height (m) of dominant and codominant trees by species between pine (P) and no-pine (NP) plots using the Wilcoxon 2-Sample test.

<table>
<thead>
<tr>
<th>Species</th>
<th>Stand</th>
<th>23</th>
<th>24</th>
<th>36</th>
<th>46</th>
<th>50</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>P</td>
<td>NP</td>
<td>P</td>
<td>NP</td>
<td>P</td>
<td>NP</td>
</tr>
<tr>
<td>White Pine</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>n=7</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean HT</td>
<td>22.94</td>
<td>0.00</td>
<td>24.07</td>
<td>0.00</td>
<td>20.19</td>
<td>0.00</td>
</tr>
<tr>
<td>Stnd. Err.</td>
<td>(0.62)</td>
<td></td>
<td>(2.19)</td>
<td></td>
<td>(0.77)</td>
<td></td>
</tr>
<tr>
<td>Hemlock</td>
<td>n=35</td>
<td>n=45</td>
<td>n=25</td>
<td>n=36</td>
<td>n=24</td>
<td>n=18</td>
</tr>
<tr>
<td>Mean HT</td>
<td>18.54</td>
<td>16.44</td>
<td>17.78</td>
<td>17.05</td>
<td>17.69</td>
<td>19.52</td>
</tr>
<tr>
<td>Stnd. Err.</td>
<td>(0.18)</td>
<td>(0.30)</td>
<td>(0.79)</td>
<td>(0.24)</td>
<td>(0.35)</td>
<td>(0.29)</td>
</tr>
<tr>
<td>Z</td>
<td>5.21</td>
<td>-1.32</td>
<td>2.87</td>
<td>-3.32</td>
<td>&lt;0.001**</td>
<td>0.004*</td>
</tr>
<tr>
<td>P &gt; Z</td>
<td>&lt;0.001**</td>
<td>0.19</td>
<td>0.004*</td>
<td>&lt;0.001**</td>
<td>0.005*</td>
<td></td>
</tr>
<tr>
<td>Spruce</td>
<td>n=84</td>
<td>n=220</td>
<td>n=122</td>
<td>n=142</td>
<td>n=39</td>
<td>n=28</td>
</tr>
<tr>
<td>Stnd. Err.</td>
<td>(0.16)</td>
<td>(0.14)</td>
<td>(0.15)</td>
<td>(0.23)</td>
<td>(0.27)</td>
<td>(0.41)</td>
</tr>
<tr>
<td>Z</td>
<td>4.57</td>
<td>1.92</td>
<td>4.28</td>
<td>3.24</td>
<td>-7.01</td>
<td></td>
</tr>
<tr>
<td>P &gt; Z</td>
<td>&lt;0.001**</td>
<td>0.06</td>
<td>&lt;0.001**</td>
<td>0.001**</td>
<td>&lt;0.001**</td>
<td></td>
</tr>
</tbody>
</table>

* Significant at alpha=0.05  ** Significant at alpha=0.001
Table 3.7. Growing space efficiency of subject trees presented as ratio between total volume produced (m³) and total crown area (m²).

<table>
<thead>
<tr>
<th>Stand</th>
<th>Pine</th>
<th>Spruce</th>
<th>Hemlock</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>P</td>
<td>NP</td>
<td>P</td>
</tr>
<tr>
<td>23</td>
<td>.03</td>
<td>.04</td>
<td>.04</td>
</tr>
<tr>
<td>24</td>
<td>.10</td>
<td>.06</td>
<td>.04</td>
</tr>
<tr>
<td>36</td>
<td>.04</td>
<td>.04</td>
<td>.03</td>
</tr>
<tr>
<td>46</td>
<td>.06</td>
<td>.05</td>
<td>.12</td>
</tr>
<tr>
<td>50</td>
<td>.05</td>
<td>.02</td>
<td>.07</td>
</tr>
</tbody>
</table>
Table 3.8. Percentage crown area overlap between crown projection areas of subject trees and crown projection areas of all other intersecting crowns.

<table>
<thead>
<tr>
<th>Stand</th>
<th>Pine</th>
<th>Spruce</th>
<th>Hemlock</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>P</td>
<td>NP</td>
<td>P</td>
</tr>
<tr>
<td></td>
<td>% double overlap / % triple overlap</td>
<td></td>
<td></td>
</tr>
<tr>
<td>23</td>
<td>70 / 74</td>
<td>89 / 103</td>
<td>28 / 33</td>
</tr>
<tr>
<td>24</td>
<td>85 / 107</td>
<td>52 / 69</td>
<td>49 / 61</td>
</tr>
<tr>
<td>36</td>
<td>88 / 114</td>
<td>42 / 48</td>
<td>80 / 98</td>
</tr>
<tr>
<td>46</td>
<td>87 / 237</td>
<td>80 / 128</td>
<td>61 / 100</td>
</tr>
<tr>
<td>50</td>
<td>56 / 69</td>
<td>30 / 33</td>
<td>34 / -</td>
</tr>
</tbody>
</table>
Table 3.9. Comparison of mean total volume (m³/ha) among cohort structures using the Kruskall-Wallace test. Comparison of pine and no-pine plot mean volumes uses the Wilcoxon 2-Sample test.

<table>
<thead>
<tr>
<th>No. Cohorts</th>
<th>Pine Plots</th>
<th>No-Pine Plots</th>
<th>All Plots</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean Volume ± Std. Err. (n)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>$279.73 \pm 22.69$ (8)</td>
<td>$204.63 \pm 36.59$ (6)</td>
<td>$247.54 \pm 22.03$ (14)</td>
</tr>
<tr>
<td></td>
<td>$Z$</td>
<td>-1.61</td>
<td></td>
</tr>
<tr>
<td></td>
<td>$P &gt; Z$</td>
<td>0.11</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>$385.83 \pm 45.66$ (11)</td>
<td>$307.91 \pm 23.11$ (10)</td>
<td>$348.72 \pm 27.13$ (21)</td>
</tr>
<tr>
<td></td>
<td>$Z$</td>
<td>-1.30</td>
<td></td>
</tr>
<tr>
<td></td>
<td>$P &gt; Z$</td>
<td>0.20</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>$400.09 \pm 43.26$ (6)</td>
<td>$285.51 \pm 24.48$ (9)</td>
<td>$331.34 \pm 26.40$ (15)</td>
</tr>
<tr>
<td></td>
<td>$Z$</td>
<td>2.18</td>
<td></td>
</tr>
<tr>
<td></td>
<td>$P &gt; Z$</td>
<td>0.03*</td>
<td></td>
</tr>
<tr>
<td>Overall Mean</td>
<td>$355.30 \pm 25.24$ (25)</td>
<td>$275.06 \pm 16.98$ (25)</td>
<td>$315.18 \pm 16.11$ (50)</td>
</tr>
</tbody>
</table>

* Significant at alpha = 0.05.
FIGURE CAPTIONS

Figure 3.1. Procedure used to determine area of horizontal overlap between crown projection areas of subject trees and crown projection areas of all other intersecting crowns.

Figure 3.2. Mean (± standard error) basal area by species comparing pine with no-pine plots in each stand. The Wilcoxon 2-sample test is used for means comparison. Species codes: HE=hemlock; RS=red spruce; WP=white pine; BF=balsam fir; PB=paper birch; RM=red maple.

Figure 3.3a-e. Mean (± standard error) height of each diameter class by stand and species.

Figure 3.4. Pine site trees showing growth strategy 1. A single cohort is identified. Species codes: HE=hemlock; RS=red spruce; WP=white pine; PB=paper birch; RM=red maple.

Figure 3.5. Pine site trees showing growth strategy 2. Initiation of cohorts is identified by arrows. Species codes: HE=hemlock; RS=red spruce; WP=white pine; PB=paper birch; RM=red maple.

Figure 3.6. Hemlock and red spruce site trees showing growth strategy 1. Initiation of cohort is identified by arrows. Species codes: HE=hemlock; RS=red spruce; WP=white pine; PB=paper birch; RM=red maple.
Figure 3.7.  Hemlock and red spruce site trees showing growth strategy 2. Initiation of cohorts is identified by arrows. Species codes: HE=hemlock; RS=red spruce; WP=white pine; PB=paper birch; RM=red maple.

Figure 3.8.  Hemlock and red spruce site trees showing growth strategy 3. Initiation of cohorts is identified by arrows. Species codes: HE=hemlock; RS=red spruce; WP=white pine; PB=paper birch; RM=red maple.
Subject Tree
Crown Projection Area

55 sq.m

10 sq.m overlap
20 sq.m

7 sq.m overlap
14 sq.m

8 sq.m triple overlap
15 sq.m

Area of double overlap (%)
\[
\text{Area of double overlap} = \frac{7 + 10}{55} = 31\%
\]

Area of triple overlap (%)
\[
\text{Area of triple overlap} = \frac{7 + 10 + 8}{55} = 45\%
\]
Figure 3.2

Stand 23

P < 0.53

Stand 24

P < 0.09

Stand 36

P < 0.40

Stand 50

P < 0.21

Stand 46

P < 0.53

Species

Species

Basal Area (sq.m/ha)

Pine

NoPine
Figure 3.3a

Stand 23

Mean Height (m)

Diameter Class (cm)

- Hemlock
- Spruce
- Pine

Hemlock
Spruce
Pine
Figure 3.3c

Stand 36

Mean Height (m)

Diameter Class (cm)

- Hemlock
- Spruce
- Pine

Hemlock
Spruce
Pine
Figure 3.3d

Stand 46

Mean Height (m) vs. Diameter Class (cm)

- Hemlock
- Spruce
- Pine
Figure 3.3e

Stand 50

Mean Height (m)

Diameter Class (cm)

- Hemlock
- Spruce
- Pine
Figure 3.4

Pine (Stand 46, Plot 6-14)

Pine (Stand 50, Plot 5-7)

Pine (Stand 36, Plot 6-2)
Figure 3.5

Pine (Stand 23, Plot 2-2a)

Basal Area (sq. cm)

HE8
HE10
WP11
HE16
HE17

Year

1800 1820 1840 1860 1880 1900 1920 1940 1960 1980

0 400 800 1200 1600 2000 2400 2800 3200 3600
Figure 3.6

Spruce (Stand 24, Plot 5-5 (NP))

Spruce (Stand 24, Plot 5-7 (P))

Spruce (Stand 24, Plot 2-8 (P))
Figure 3.6 (cont'd)

Spruce (Stand 23, Plot 2-2a (P))

Hemlock (Stand 50, Plot 5-7 (P))
Figure 3.7

Spruce (Stand 23, Plot 1-1a (NP))

- HE1B
- HE2
- PE2
- HE3B
- HE4
- RS5
- RS6
- HE7B
- RS9
- RS10
- RS30

Year

Basal Area (sq. cm)

1800 1820 1840 1860 1880 1900 1920 1940 1960 1980

1800 1820 1840 1860 1880 1900 1920 1940 1960 1980

Hemlock & Spruce (Stand 24, Plot 3-3 (NP))

- HE1
- RS3
- HE5
- HE6
- RS2
- HE4
- HE5

Basal Area (sq. cm)

Year

Hemlock (Stand 36, Plot 2-2 (NP))

- HE3
- RS1
- HE2
- RS4
- HE5
- RS7
- HE14
- RS15
- RS16

Basal Area (sq. cm)

Year
Figure 3.7 (cont'd)

Spruce (Stand 36, Plot 3-2 (P))

Hemlock (Stand 36, Plot 6-2 (P))

Hemlock (Stand 46, Plot 6-14 (P))

Year
Figure 3.8

Hemlock (Stand 24, Plot 5-5 (NP))

- RS7
- HE12
- RS13
- RS15
- HE16
- HE17
- HE18
- RS19
- RS20
- RM22
- HE11

Year

Basal Area (sq. cm)

Hemlock (Stand 24, Plot 2-8 (P))

- RS1
- HE2
- HE3
- HE4
- HE5
- HE6
- HE7
- HE8

Year

Basal Area (sq. cm)

Spruce (Stand 36, Plot 6-2 (P))

- RM14
- HE15
- RS16
- RS18
- HE19
- HE20
- HE21
- RS22

Year

Basal Area (sq. cm)
Figure 3.8 (cont'd)

Spruce (Stand 36, Plot 2-2 (NP))

Spruce (Stand 46, Plot 6-14 (P))
APPENDIX C
Table C.1. Characteristics of site trees on pine plots.

<table>
<thead>
<tr>
<th>Stand</th>
<th>Species</th>
<th>DBH (cm)</th>
<th>Basal Area (cm²)</th>
<th>Height (m)</th>
<th>%Live Crown</th>
<th>Crown Area (m²)</th>
<th>MAI * (cm²)</th>
<th>Age</th>
<th>Volume (m³)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Total</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Sawlog</td>
</tr>
<tr>
<td>23</td>
<td>Pine</td>
<td>41.9</td>
<td>1378.8</td>
<td>25.4</td>
<td>42.3</td>
<td>46.1</td>
<td>39.7</td>
<td>67</td>
<td>1.5</td>
</tr>
<tr>
<td></td>
<td>Hemlock</td>
<td>46.0</td>
<td>1605.5</td>
<td>17.6</td>
<td>41.2</td>
<td>30.8</td>
<td>46.7</td>
<td></td>
<td>1.4</td>
</tr>
<tr>
<td></td>
<td>Spruce</td>
<td>24.4</td>
<td>467.0</td>
<td>20.0</td>
<td>29.2</td>
<td>9.4</td>
<td>23.9</td>
<td></td>
<td>0.4</td>
</tr>
<tr>
<td>24</td>
<td>Pine</td>
<td>57.7</td>
<td>2611.0</td>
<td>37.2</td>
<td>41.3</td>
<td>30.9</td>
<td>-----</td>
<td></td>
<td>-----</td>
</tr>
<tr>
<td></td>
<td>Hemlock</td>
<td>20.6</td>
<td>332.5</td>
<td>22.4</td>
<td>31.4</td>
<td>4.8</td>
<td>5.4</td>
<td>65</td>
<td>0.2</td>
</tr>
<tr>
<td></td>
<td>Spruce</td>
<td>18.8</td>
<td>277.5</td>
<td>17.0</td>
<td>25.9</td>
<td>3.4</td>
<td>6.4</td>
<td>62</td>
<td>0.2</td>
</tr>
<tr>
<td>36</td>
<td>Pine</td>
<td>32.0</td>
<td>804.5</td>
<td>20.3</td>
<td>43.8</td>
<td>17.3</td>
<td>16.3</td>
<td>59</td>
<td>0.8</td>
</tr>
<tr>
<td></td>
<td>Hemlock</td>
<td>33.8</td>
<td>896.3</td>
<td>17.6</td>
<td>41.2</td>
<td>30.8</td>
<td>10.3</td>
<td>264</td>
<td>0.7</td>
</tr>
<tr>
<td></td>
<td>Spruce</td>
<td>36.8</td>
<td>1065.4</td>
<td>18.9</td>
<td>47.6</td>
<td>22.2</td>
<td>17.2</td>
<td>63</td>
<td>1.0</td>
</tr>
<tr>
<td>46</td>
<td>Pine</td>
<td>73.9</td>
<td>4289.2</td>
<td>30.5</td>
<td>46.3</td>
<td>95.2</td>
<td>39.8</td>
<td>161</td>
<td>5.7</td>
</tr>
<tr>
<td></td>
<td>Hemlock</td>
<td>42.2</td>
<td>1398.7</td>
<td>20.3</td>
<td>59.4</td>
<td>35.9</td>
<td>19.7</td>
<td>178</td>
<td>1.1</td>
</tr>
<tr>
<td></td>
<td>Spruce</td>
<td>26.2</td>
<td>539.1</td>
<td>17.9</td>
<td>43.3</td>
<td>10.9</td>
<td>24.7**</td>
<td>45</td>
<td>0.5</td>
</tr>
<tr>
<td>50</td>
<td>Pine</td>
<td>55.1</td>
<td>2386.0</td>
<td>28.1</td>
<td>48.2</td>
<td>55.8</td>
<td>24.4</td>
<td>118</td>
<td>2.9</td>
</tr>
<tr>
<td></td>
<td>Hemlock</td>
<td>21.8</td>
<td>374.8</td>
<td>17.1</td>
<td>41.0</td>
<td>16.4</td>
<td>6.7</td>
<td>99</td>
<td>0.3</td>
</tr>
<tr>
<td></td>
<td>Spruce</td>
<td>24.4</td>
<td>457.0</td>
<td>15.3</td>
<td>25.5</td>
<td>21.3</td>
<td>7.3</td>
<td>116</td>
<td>0.4</td>
</tr>
</tbody>
</table>

* Mean Annual (Basal Area) Increment from: 1939-1989.
** MAI calculated over 40 years.
Table C.2. Characteristics of site trees on no-pine plots.

<table>
<thead>
<tr>
<th>Stand</th>
<th>Species</th>
<th>DBH (cm)</th>
<th>Basal Area (cm²)</th>
<th>Height (m)</th>
<th>%Live Crown</th>
<th>Crown Area (m²)</th>
<th>MAI * (cm²)</th>
<th>Age</th>
<th>Volume (m³)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Total</td>
</tr>
<tr>
<td>23</td>
<td>Hemlock</td>
<td>45.0</td>
<td>1587.5</td>
<td>18.4</td>
<td>61.2</td>
<td>34.9</td>
<td>—</td>
<td>196</td>
<td>1.4</td>
</tr>
<tr>
<td></td>
<td>Spruce</td>
<td>38.4</td>
<td>1155.3</td>
<td>20.0</td>
<td>44.1</td>
<td>26.3</td>
<td>12.4</td>
<td></td>
<td>1.1</td>
</tr>
<tr>
<td>24</td>
<td>Hemlock</td>
<td>38.1</td>
<td>1140.1</td>
<td>19.8</td>
<td>61.9</td>
<td>35.1</td>
<td>19.4</td>
<td>137</td>
<td>0.9</td>
</tr>
<tr>
<td></td>
<td>Spruce</td>
<td>38.1</td>
<td>1140.1</td>
<td>21.9</td>
<td>53.5</td>
<td>26.1</td>
<td>16.8</td>
<td>104</td>
<td>1.1</td>
</tr>
<tr>
<td>36</td>
<td>Hemlock</td>
<td>49.5</td>
<td>1926.8</td>
<td>21.2</td>
<td>49.6</td>
<td>33.7</td>
<td>20.6</td>
<td>255</td>
<td>1.7</td>
</tr>
<tr>
<td></td>
<td>Spruce</td>
<td>23.9</td>
<td>447.7</td>
<td>18.0</td>
<td>48.2</td>
<td>13.1</td>
<td>6.1</td>
<td>111</td>
<td>0.4</td>
</tr>
<tr>
<td>46</td>
<td>Hemlock</td>
<td>43.2</td>
<td>1464.4</td>
<td>20.3</td>
<td>52.3</td>
<td>30.9</td>
<td>—</td>
<td>—</td>
<td>1.3</td>
</tr>
<tr>
<td></td>
<td>Spruce</td>
<td>44.2</td>
<td>1534.1</td>
<td>21.4</td>
<td>39.9</td>
<td>12.1</td>
<td>12.8</td>
<td>180</td>
<td>1.5</td>
</tr>
<tr>
<td>50</td>
<td>Hemlock</td>
<td>40.6</td>
<td>1297.2</td>
<td>20.0</td>
<td>62.2</td>
<td>34.7</td>
<td>22.0</td>
<td>99</td>
<td>1.1</td>
</tr>
<tr>
<td></td>
<td>Spruce</td>
<td>52.3</td>
<td>2150.2</td>
<td>26.6</td>
<td>48.3</td>
<td>32.2</td>
<td>23.2</td>
<td>180</td>
<td>2.2</td>
</tr>
</tbody>
</table>

* Mean Annual (Basal Area) Increment from: 1939-1989.
BIOGRAPHY

On March 30, 1959, Mary Ann Fajvan became the first child of Mary Ann R. Fajvan and George Fajvan of Lyndhurst, NJ. During her childhood she was active in community activities through strong involvement with the Girl Scouts of America. With the encouragement and support of her parents, she graduated from Lyndhurst High School with a strong interest in natural resources.

In 1981, Mary Ann received a bachelor's degree in natural resource management, with a concentration in forest management, from Cook College, Rutgers University. During her undergraduate career she spent three summers working as an Interpreter for the National Park Service. She pursued her interest in silviculture by attending the Yale School of Forestry and Environmental studies where she received a Master of Forest Science degree in 1983. From 1984-1987 she was employed by Penn State University as an Instructor in Forest Resources with the Cooperative Extension Service.

In June, 1987, Mary Ann married Robert Lynn and shortly thereafter they moved to Maine where she began work on a doctorate in quantitative silviculture. She served as a research assistant for a project funded by Champion International Corporation Inc. and also was a teaching assistant for a course in silviculture. She is a candidate for the Doctor of Philosophy degree in Forest Resources from the University of Maine, Orono, in August, 1991.