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# The historical development of bigtooth aspen-dominated forests in northern lower Michigan

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Michigan State University, 1992



# THE HISTORICAL DEVELOPMENT OF BIGTOOTH ASPEN-DOMINATED FORESTS IN NORTHERN LOWER MICHIGAN

By

Brian Josef Palik

# A DISSERTATION

Submitted to Michigan State University in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

Department of Forestry

# ABSTRACT

# THE HISTORICAL DEVELOPMENT OF BIGTOOTH ASPEN-DOMINATED FORESTS IN NORTHERN LOWER MICHIGAN

Ву

# Brian Josef Palik

Presettlement forest composition and post-settlement development were examined within two bigtooth aspendominated landscapes in northern Michigan. Objectives for this study included: i) examining the influence of prevailing disturbance regimes on presettlement and current forest composition; and <u>ii</u>) assessing the applicability of popular even-aged developmental theory in bigtooth aspen forests.

Land survey records were used to reconstruct presettlement forest composition. Vegetation sampling on replicate plots within each landscape was used to determine current composition in forests that established following turn of the century logging. Stem analysis was used to reconstruct age distributions and growth histories of trees in the current forest.

Presettlement forest composition of the two landscapes differed substantially. Landscape 1 was dominated by firesensitive eastern hemlock and American beech, while landscape 2 was dominated by fire-dependent red pine, jack pine and white pine. Compositional differences may have been related to differences in presettlement fire frequency. The current overstories of both landscapes are dominated by bigtooth aspen, red oak, and red maple. Compositional convergence was attributed to similar post-settlement disturbance regimes.

Tree age distributions in the current forests reflected rapid initial cohort establishment, stem exclusion, and understory reinitiation. Within the initial cohorts of both forests, bigtooth aspen, an intolerant species, was typically taller than red oak, a mid-tolerant species, which in turn was taller than red maple, a tolerant species. Within populations of red oak and red maple, stem heights were often highly variable, with some individuals reaching heights equivalent to bigtooth aspen. Age differences had no influence on height patterns. Growth rate differences determined species stratification patterns and height variation within populations. Differences in competitive environment likely contributed to height growth rate variation within red oak and red maple populations.

The duration of stem exclusion was similar on all plots, both within and between the two landscapes. Understory reinitiation often coincided with radial growth overstory stems, releases in suggesting that new establishment occurred in response to an increase in resource availability, possibly following a wave of natural thinning within the overstory.

The results indicate that bigtooth aspen-dominated forests follow a pattern of development characteristic of many forests types that initiate after major disturbance. This dissertation is dedicated to Richard Tracy of Stiles Elementary, John Clark of Ithaca High School, and Professor Richard Bowker of Alma College, for their dedication to teaching and learning.

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v

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# TABLE OF CONTENTS

LIST	OF	TABLES12
LIST	OF	FIGURES14
Chapt	er	

I.	INTRODUCTION

Development of forests following major disturbance1 The development of Great Lakes aspen dominated forests
Radial growth analysis
THE RELATIVE INFLUENCE OF ESTABLISHMENT TIME AND HEIGHT GROWTH RATES ON SPECIES VERTICAL STRATIFICATION DURING SECONDARY FOREST SUCCESSION
Abstract

III.	A COMPARISON OF PRESETTLEMENT AND PRESENT-DAY FORESTS ON TWO BIGTOOTH ASPEN-DOMINATED LANDSCAPES IN NORTHERN LOWER MICHIGAN
	Abstract
	Present-day vegetation sampling
	Presettlement forests
IV.	PATTERNS OF EVEN-AGED FOREST DEVELOPMENT WITHIN TWO BIGTOOTH ASPEN-DOMINATED LANDSCAPES IN NORTHERN LOWER MICHIGAN
	Abstract
v.	THE VERTICAL DEVELOPMENT OF EARLY SUCCESSIONAL FORESTS IN NORTHERN LOWER MICHIGAN
	Abstract

# V. (con'd).

	Stem analysis
	A model for the development of dominance
VI.	THE AGE AND HEIGHT STRUCTURE OF RED MAPLE ( <u>Acer rubrum</u> L.) POPULATIONS IN NORTHERN LOWER MICHIGAN BIGTOOTH ASPEN ( <u>Populus grandidenta</u> Michx.) FORESTS
	Abstract
	Landscape patterns

# LIST OF TABLES

Table 2.1. Forest composition and structure by stratum...30

Table 2.4. Repeated measures analysis of variance for species differences in height-growth rates (m/yr).....48

Table 3.1. Mean climatic variables for the districts containing the UMBS and Huron study areas......67

Table 3.3. Present-day forest composition and structure of the UMBS and Huron study areas......74

Table 4.1. Present-day forest composition and structure of the Huron and UMBS study areas......107

Table 5.1. Regeneration methods of <u>Quercus</u> <u>rubra</u> and <u>Acer</u> <u>rubrum</u> genets in the a) Huron and b) UMBS forests....165

Table 5.2. Repeated measure analysis of variance and species contrasts for mean heights of <u>Populus</u> <u>grandidentata</u>, <u>Quercus rubra</u> and <u>Acer rubrum</u> over time in the Huron and UMBS forests......170

- Table 6.2. Age and site index of bigtooth aspen in five stands within the Huron-Manistee National Forest and analysis of variance for comparisons among stands.....220

- Table 6.7. a) Repeated measure analysis of variance and b) specific contrasts for height increment across time in bigtooth aspen and sprout-origin red maple......245

# LIST OF FIGURES

- Figure 2.3. Vertical stratification patterns among four tree species over a 42 year period in a <u>Populus</u> <u>grandidentata-P</u>. <u>tremuloides</u> forest. Heights are mean values (+/- standard error) of four plots at each age..39
- Figure 2.4. Vertical growth rates (m/yr) for two age groups over four height intervals within two later successional tree species. Old individuals established within 1-21 after stand initiation. YOUNG individuals years established within 22-42 years after stand initiation. Values are back-transformed means of inverse-square root transformed growth rates (m/yr), with 95% confidence intervals. Sample size (number of plots) = 3 for Q. rubra (OLD) and 4 for all other age group-species

- Figure 2.6. Second order polynomial regressions of stem height as a function of stem age for three later successional tree species (A-C) in а Populus grandidentata-P. tremuloides forest. Dashed lines are 95% confidence bands for predicted values. Best-fit lines for all three species are compared in D. Symbols represent number of observation as follows: Quercus rubra, 1-15 years=3-30 observations (per symbol), 16-29 vears=1-15 observations; Fraxinus americana, 1-15 years=8-30 observations, 16-29 years=1-14 observations; Acer rubrum, 1-15 years=2-15 observations, 16-30 years=1-

- Figure 4.3. Five-year height increment curves for the sampled bigtooth aspen in each forest. Values are means <u>+</u> se. Sample size for the Huron forest is 20. Sample size for the UMBS forest is 16 (14 at 5-10 years)....122
- Figure 4.4. Ring-width indices for the Huron plots. Each chronology is the mean for the sample size indicated in the upper right corner of each graph. The doted line at a ring-width index of 1.0 is the standardized mean for the entire chronology (see text for derivation of ringwidth indices). The dashed line in each graph is the establishment distribution cumulative for advanced regeneration (stems > 1.5 m tall). The beginning of each establishment distribution marks the start of understory reinitiation (at least two stems establishing every five year for a minimum of 20 years; this is indicated by an U for plots without advanced regeneration). The C in each qraph marks the start of continuous understory establishment (at least one stem establishing every year, or two every two years, for a minimum 10 years).....124

- Figure 4.5. Ring-width indices for the UMBS plots. Each chronology is the mean for the sample size indicated in the upper right corner of each graph. The doted line at a ring-width index of 1.0 is the standardized mean for the entire chronology (see text for derivation of ringwidth indices). The dashed line in each graph is the cumulative establishment distribution for advanced regeneration (stems  $\geq$  1.5 m tall). The beginning of each establishment distribution marks the start of understory reinitiation (at least two stems establishing every five year for a minimum of 20 years). The <u>C</u> in each graph marks the start of continuous understory establishment (at least one stem establishing every year, or two every two years, for a minimum 10 years)......129

- Figure 5.4. A model for the development of vertical stratification among tree species differing in understory tolerance and relative successional status in an evenaged forest. (a) Immediately following a stand initiating disturbance, initial heights of an intolerant, earlysuccessional species (clear crown) and a relatively moretolerant, later successional species (filled crown) may The intolerant species is numerically be similar. dominant because of superior dispersal ability. (b) With the onset of crown differentiation, some individuals of both species lapse into suppression. A limited number of individuals of the tolerant species may have early height growth rates similar to the intolerant species, probably because of locally reduced competitive pressure from the intolerant species. The initially low number of stems of the tolerant species reduces the probability that many will occur in competitively favorable neighborhoods. (c) In the mature forest, the intolerant species is typically vertically dominant over the more-tolerant species although some stems of the tolerant species have maintained growth rates similar to that of the intolerant species. The population-level height growth rate of the intolerant species will be greater than that of the tolerant species because all suppressed stems of the former have died, leaving only fast-growing stems, while slower growing stems of the tolerant species have
- Figure 6.2. Height growth reconstructions of individual bigtooth aspen and sprout-origin red maple within one randomly selected plot from each of five bigtooth aspen dominated-stands within the Huron-Manistee National Forest. Each line represents an individual stem.....232

- Figure 6.4. The relationship between height increment (meters) over the five-year period immediately prior to sampling and initial height (meters) at the beginning of this period for individual seedling-origin red maple in five bigtooth aspen-dominated stands within the Huron-Manistee National Forest. One randomly selected plot from each of the five stands is shown......238
- Figure 6.5. The relationship between stem age (years) and height growth rate (m/yr) over the first 1.5 m for the fastest growing seedling-origin red maple in five bigtooth aspen-dominated stands within the Huron-Manistee National Forest. For each stand, the fastest growing individuals from consecutive five-year stem-age classes (i.e. 5-10 years old, 10-15 years old, etc.) within each of four plots were pooled for analysis......241
- Figure 6.6. Height increments (m) over consecutive fiveyear stand-age classes, beginning 10 years after stand initiation, for bigtooth aspen and sprout-origin red Values are back-transformed means maple. (+ 95% confidence intervals) of 20, 18 and 19 log-transformed observations for bigtooth aspen, the fastest growing red maple on each plot and the median growing red maple on each plot, respectively. In each graph, the bottom point of the inverted triangle indicates the year after stand initiation (mean of five stands) by which 10% of the seed-origin red maple  $\geq$  1.5 m tall had established. The single open triangle at the right end of each graph is the mean (+ 95% confidence intervals) height increment of the fastest growing seedling-origin red maple over a stand age of 65-70 years.....244

# Chapter 1

# INTRODUCTION

Development of forests following major disturbance

Studies in various forest ecosystems have demonstrated that large-scale, stand-replacing natural disturbances are common features of many forested landscapes (Habeck and Mutch 1973; Heinselman 1973; Kilgore 1973; Rowe and Scotter 1973; Sprugel 1976; Veblen and Ashton 1978; Oliver 1981; Peet 1981; Romme and Knight 1981; Canham and Loucks 1984; Oliver et al. 1985; Whitney 1986). While these works focus on forest development after natural disturbances, there is a clear analogy to large-scale anthropogenic disturbances, such as clearcutting and fire. Indeed, there is an abundant literature on stand development following large-scale anthropogenic disturbance (Cayford 1957; Marguis 1967, 1981; Day 1972; Oliver 1978, 1980; Stubblefield and Oliver 1978; Bormann and Likens 1979; Wierman and Oliver 1979; Christensen and Peet 1981; Oliver 1980, 1981; Carleton 1982; Hibbs 1983; Guldin and Lorimer 1985; Harcombe 1986; Kelty 1986; Larson 1986; Peet and Christensen 1987; Clatterbuck and Hodges 1988; Foster 1988; Scheiner et al. 1988; Hix and Lorimer 1990, 1991; Oliver and Larson 1990; Deal et al 1991; Segura and Snook 1992). Results from many of these studies suggest that certain structural and developmental characteristics are common to а wide range of

forest types originating after major disturbance (Oliver 1980, 1981; Peet 1981; Peet and Christensen 1987):

<u>i</u>) The overstories of forests initiating after major disturbance are often even-aged. An initial cohort of trees establishes within a relatively short period of time, often spanning less than 20% of the pathological rotation age for the dominant tree species in the forest (Smith 1986; Oliver 1981; Oliver and Larson 1990).

<u>ii</u>) In mixed-species forests, the crowns of individuals within initial overstory cohorts are often stratified, following an order paralleling relative understory tolerance and successional status, i.e., intolerant, early successional species are taller than more-tolerant, latter successional species (Oliver 1978; Stubblefield and Oliver 1978; Bormann and Likens 1979; Hibbs 1983; Kelty 1986; Larson 1986; Hix and Lorimer 1990; Oliver and Larson 1990).

<u>iii</u>) After initial cohort establishment, a period ensues during which few or no new individuals of any tree species establish or survive. This period of low establishment and/or high mortality has been termed stem exclusion (Oliver 1981), or the thinning phase of stand development (Peet and Christensen 1987), since it is characterized by intense density-dependent mortality of suppressed overstory individuals within the initial, post-disturbance cohort of trees.

<u>iv</u>) Following stem exclusion, new individuals of tolerant species begin to establish and survive in the forest understory. This event has been termed understory reinitiation (Oliver 1981), or the transition phase of stand development (Peet and Christensen 1987), since the cohorts that begin establishing at this time promote the transition to an uneven-age structure in the forest.

There is little information concerning the generality and repeatability of these developmental features. Most studies that have documented the structural characteristics outlined above have been based on results from one or few replicate plots (Oliver 1978; Oliver et al. 1985; Roberts and Richardson 1985; Kelty 1986; Abrams and Nowacki 1992), or have pooled data from replicate samples into a single forest-level analysis (Bloomberg 1950; Stubblefield and Oliver 1978; Oliver et al. 1985; Harcombe 1986; Sharik et al. 1989; Segura and Snook 1992). These methodologies are inappropriate for assessing the variability and repeatability of developmental patterns within and among landscapes characterized by homogeneous site conditions and disturbance histories. The need for assessing the generality of developmental patterns is demonstrated by the fact that some studies have found no stem exclusion period in forests originating after major disturbance (Peet 1981; Carleton 1982; Roberts and Richardson 1985), while others have found no stratification among species within the initial cohort of

trees (Guldin and Lorimer 1985).

In addition to uncertainty regarding variability of developmental patterns, there is also a lack of consensus concerning the mechanisms that control various structural events. For example, overstory stratification is thought to result from inherent differences in height growth rates among species, i.e., relatively intolerant species grow faster than more-tolerant species (Loach 1970; Drury and Nesbitt 1973; Marks 1975; Bormann and Likens 1979; Canham and Marks 1985; Kozlowski et al. 1991). On the other hand, silvicultural studies have demonstrated that interspecific competitive interactions may be equally important. Relatively intolerant species may possess morphological or physiological characteristics that allow them to outgrow more-tolerant species when in competition. However, in noncompetitive environments, the height growth rates of some tolerant species have been found to equal those of lesstolerant species (Cayford 1957; Stubblefield and Oliver 1978; Wierman and Oliver 1979; Guldin and Lorimer 1985; Smith 1986; Oliver, Clatterbuck and Burkhardt 1990; Oliver and Larson 1990; Deal, Oliver and Bormann 1991; Shainsky and Radosevich 1992).

There is also little consensus regarding the mechanisms that control stem exclusion and understory reinitiation in even-aged forests. Resource-based theories of forest development suggest that stem exclusion occurs as a result of competitive pressure from overstory stems (Oliver 1981;

Christensen and Peet 1981; Peet 1981; Peet and Christensen 1987). Given this assumption, it follows that understory reinitiation should be triggered by an increase in light or soil resource availability during the course of stand development. The cause of this increase has been attributed to a variety of factors including, canopy gap formation by mature overstory individuals (Sprugel 1976; Christensen and Peet 1981; Peet 1981; Peet and Christensen 1987), crown differentiation within the even-aged overstory (Bormann and Likens 1979, Oliver et al. 1985; Oliver and Larson 1990), reductions in rates of root growth (Oliver and Larson 1990), and mortality of suppressed overstory individuals following a concentrated wave of natural thinning (Harcombe 1986; Fried et al 1988; Oliver and Larson 1990). In contrast to resourse-based theories, some studies suggests that understory reinitiation may simply reflect the reproductive maturation а post-disturbance of cohort of later successional trees (Day 1972; Carleton 1982; Roberts and Richardson 1985; Sharik et al 1989; Sakai <u>et</u> <u>al</u>. 1985; Sakai 1990). Prior to this time, seeds are simply not available. This view implies that resource limitation in the forest understory is not so severe enough that it prevents establishment and survival of tolerant species, however growth may be minimal until resource availability does increase.

The development of Great Lakes Aspen-dominated forests

Forest dominated by bigtooth aspen (Populus grandidentata Michx.) and trembling aspen (P. tremuloides Michx.), alone or in combination, occupy over 5 million hectares in the Great Lakes region (Einspahr and Wyckoff 1990). Despite aspen's areal extent, and its importance as wildlife habitat (Brelich <u>et al</u>. 1972; Gullion 1977, 1984) and a source of fiber (Hughes and Brodie 1972; Keays 1972; Blyth and Smith 1988), relatively little is known about patterns of stand development in the covertype.

Aspen's areal extent in the Great Lakes region is directly attributable to post-settlement changes in natural fire regimes. Rapid deforestation and repeated slashedfueled wildfires in the late 19th and early 20th centuries favored aspen on many sites because of the taxon's ability to establish on bare mineral soil and spread readily via clonal growth after fire (Gleason 1923; Benninghoff and Cramer 1963; Whitney 1987). Prior to settlement, various combinations of conifers (Pinus strobus L., P. resinosa Ait., P. banksiana Lam., and Tsuga canadensis (L.) Carr.) are believed to have dominated many of the drier sites currently occupied by aspen (Kilburn 1957; Whitney 1987). No studies have assessed the influence of presettlement forest composition and structure post-settlement or disturbance history on present-day aspen forest structure and development.

even-aged structure among aspen An ramets is а reasonable assumption, given the rapidity with which the taxon occupies soil space following а disturbance (Stoeckeler and Macon 1956; Buell and Buell 1959; Zahner and Crawford 1965; Barnes 1966, 1969; Graham et al. 1963; Kemperman and Barnes 1976; Scheiner et al. 1988). However, little is known about the age structure of associated, later successional species. Limited evidence suggests that many stems of latter successional hardwoods are of vegetativeorigin, having resprouted from root systems surviving wildfires (Graham et al. 1963; Roberts and Richardson 1985). Such forests would be even-aged in a strict sense, however, the generality of this developmental pattern is not known.

Limited studies of overstory canopy structure in these forests suggests that aspen does stratify over latter successional species (Cayford 1957; Graham <u>et al</u>. 1963), however no information on species age structures were given in these particular studies. Results from a study in two contrasting aspen site classes suggest that stem exclusion occurs on productive aspen sites, but not on less-productive sites (Roberts and Richardson 1985). The differences were attributed to the ability of rapidly growing overstory trees to preempt resources on good sites, while on poor sites, tree vigor and density are insufficient to completely preempt resources. There have been no studies designed to assess the generality of these developmental patterns in aspen or any forest-type.

# STUDY OBJECTIVES AND DESIGN

Objectives

The current study was designed to address some of the uncertainties associated with stand development patterns following major disturbance and aspen forest development in particular.

The general objectives of the study were as follows:

<u>i</u>) to assess the influence of original forest composition and post-settlement disturbance history on the origin, development, and potential successional pathways of bigtooth aspen-dominated forests within several landscapes in northern Lower Michigan;

<u>ii</u>) to determine if species age distributions within bigtooth aspen-dominated forests reflect an even-aged pattern of development characterized by rapid initial cohort establishment, stem exclusion, and understory reinitiation;

<u>iii</u>) to determine if height stratification of bigtooth aspen over later successional tree species within the overstory cohort of trees was characteristic of these forests and, if so, to assess the influence of time of establishment and height growth rates on the development of species stratification;

<u>iv</u>) to gain insight into the possible influence of changing resource and seed availability on the induction of stem exclusion and understory reinitiation in even-aged forests;

 $\underline{v}$ ) to quantify spatial variability of forest developmental patterns within and between bigtooth aspendominated landscapes characterized by relatively homogeneous physical site conditions and disturbance histories.

# Study locations

The majority of the research reported on in this study conducted in replicate stands was located within two bigtooth aspen-dominated landscapes in northern Lower Michigan. Site 1 was a 15 km<sup>2</sup> landscape located within the University of Michigan Biological Station in the extreme northwestern portion of Lower Michigan (Cheboygan County). Site 2 was a 18 km<sup>2</sup> landscape located within the Harrisville Ranger District (Oscoda County) of the Huron National Forest in northeastern Lower Michigan. Initial observations indicated that the current overstories of both landscapes were dominated by bigtooth aspen, with lesser amounts of red oak (Quercus rubra L.) and red maple (Acer rubrum L.). Both landscapes were characterized by similar surficial geology, soil type, and postsettlement disturbance histories (see chapter 3 for details).

In addition to the two primary research sites, a pilot study was conducted within a single aspen-dominated stand located in north-central Lower Michigan (Clare County). This pilot project was designed to assess vegetation sampling schemes and to refine destructive sampling and stem analysis techniques, before initiating the primary study.

Vegetation sampling

Arboreal vegetation was sampled in four randomly located circular plots within each stand. Plot size ranged from 250 m<sup>2</sup> to 475 m<sup>2</sup>. In each plot, species and diameter (at 1.37 m) of all overstory individuals (dbh > 10 cm) and saplings (2.5 cm  $\leq$  dbh  $\leq$  10 cm) were tallied. Species and density of tree seedlings (dbh < 2.5 cm) were tallied in 12 1-m<sup>2</sup> frames. Seedling frames were spaced at 3-m intervals along two perpendicular diameters of each plot, beginning at the plot boundary. The regenerative-origin of overstory individuals (sprout or seedling) was assessed when possible.

# Destructive sampling

On each plot, one randomly selected bigtooth aspen, and all individuals  $\geq$  1.5 m tall of other tree species, were destructively sampled to determine total heights, times of establishment, rates of height growth, and rates of radial growth of selected stems. For species other than bigtooth aspen, only the tallest ramets were sampled from multistemmed genets. For bigtooth aspen, one individual from the dominant or codominant crown classes (most ramets were dominant or codominant) was randomly selected (rejecting ramets with internal decay) and destructively sampled on each plot. Sampling intensity for bigtooth aspen was much lower than for other species because little height variation was observed among dominant-codominant ramets within plots and little age variation was expected. On each plot, a

subsample of individuals < 1.5 m tall was sampled by stratifying on species and 0.5 m height classes. Stems < 1.5 m tall were sampled primarily to determine the age range of these stems on each plot, particularly their maximum ages.

Stems were felled at 0.5 m or ground level (depending on size) and total heights were determined. Stem sections were cut at ground level from all larger individuals (generally those greater than 2.5 m in height). An additional section was removed at 1.4 m from all overstory individuals (dbh > 10 cm) for use in radial growth analysis. Additionally, all stems were marked at 0.25-m intervals from the base to 2 m and at 1-m intervals thereafter. Marking continued to the 1-m multiple closest to the end of the dominant leader. Stem sections were cut at each measurement interval up to a 3 cm diameter top. All destructive sampling was completed during summer and fall of 1990.

# Age determination

Small stems of deciduous tree species (generally those < 2.5 m tall) and the terminal leaders of bigtooth aspen were aged by counting the number of terminal bud scale scars preceding each height interval. Small stems of coniferous species (white pine and red pine) were aged by counting branch whorls. Basal stem sections of larger individuals were sanded to a smooth surface and wetted to aid ring examination. Ages of all sections were determined by counting ring number on at least two radii (typically a long

and short axis on oblique-shaped stems) under a dissecting microscope. Terminal bud scale counts, branch whorl counts, and ages of basal stem sections were used to determine time of establishment for all sampled stems and to reconstruct establishment histories of surviving individuals in each plot. The additional section ages were used to reconstruct cumulative height growth curves and periodic height increment curves for each sampled stem.

# Radial growth analysis

Annual ring widths were measured along one randomly selected radii (rejecting decayed or injured areas) on the 1.4 m stem sections of overstory stems (dbh >10 cm). Ring widths were measured to the nearest 0.1 mm using a dissecting microscope and ocular micrometer. Radial growth measurements were used to detect periods of suppression and release possibly indicative of changing resource availability over the course of stand development.

Presettlement forest composition and disturbance regimes

Pre-settlement forests and disturbance regimes of the two primary study areas were reconstructed using General Land Office (GLO) survey records following methods of Lorimer (1977, 1980), and Whitney (1986).

# OVERVIEW OF CHAPTERS

Chapter 2.

THE RELATIVE INFLUENCE OF ESTABLISHMENT TIME AND HEIGHT GROWTH RATES ON SPECIES VERTICAL STRATIFICATION DURING SECONDARY FOREST SUCCESSION

In Chapter 2, the results from the pilot study on aspen forest development are presented and discussed. The research was conducted in a single aspen-dominated stand occurring on a site formerly occupied by a northern hardwood community. Originally, the project was designed to assess and refine the stem analysis methodologies that were to be used in the primary project. The results from this pilot study proved to be interesting in themselves since the developmental pattern for this single stand was found to differ from those previously reported for other stands originating after major disturbance, and from those of the primary study.

Chapter 3.

# A COMPARISON OF PRESETTLEMENT AND PRESENT-DAY FORESTS ON TWO BIGTOOTH ASPEN-DOMINATED LANDSCAPES IN NORTHERN LOWER MICHIGAN

In Chapter 3, presettlement and present-day forest composition of the two primary bigtooth aspen-dominated landscapes are compared. Specific objectives that are addressed in this chapter include: (i) reconstructing and relating presettlement forest composition to the potential natural disturbance regime of each landscape; (ii) comparing presettlement and present-day forest composition of each (iii) landscape; and assessing the influence of postsettlement disturbance history on the development of the current forests and the potential successional pathways of the two landscapes.

Chapter 4.

# PATTERNS OF EVEN-AGED FOREST DEVELOPMENT WITHIN TWO BIGTOOTH ASPEN-DOMINATED LANDSCAPES IN NORTHERN LOWER MICHIGAN

Chapter 4 reports on the generality of establishment patterns within and between the two primary study landscapes provides and insight into the possible mechanisms controlling stem exclusion and understory reinitiation in forests initiating after major disturbance. Specific objectives addressed in this chapter include (i) quantifying the variability of establishment patterns within and between the two study landscapes and (ii) exploring relationships between the timing of understory reinitiation and changes in resource and seed availability during the course of stand development.

## Chapter 5.

# THE VERTICAL DEVELOPMENT OF EARLY SUCCESSIONAL FORESTS IN NORTHERN LOWER MICHIGAN

Chapter 5 examines height structures of tree populations within the post-disturbance cohort trees in the two primary study landscapes. Specific objectives addressed in this chapter include: (<u>i</u>) determining if species height stratification paralleling understory tolerance and relative successional status are characteristic of these forests; (<u>ii</u>) assessing the degree of variability of heights within species populations; (<u>iii</u>) determining if age differences, regenerative-mode (sprout or seedling), or changes in an individuals competitive environment had any influence on population height structures; and (iv) assessing the degree to which height structure in the forests examined deviated that expected under from a model based on inherent differences in height growth rates amonq species of differing understory tolerance and successional status.

# Chapter 6.

# THE AGE AND HEIGHT STRUCTURE OF RED MAPLE (<u>Acer rubrum</u> L.) POPULATIONS IN NORTHERN LOWER MICHIGAN BIGTOOTH ASPEN (<u>Populus grandidenta</u> Michx.) FORESTS

Chapter 6 presents an autecological examination of red maple in the bigtooth aspen forests of the Huron study area. Specific objectives addressed in this chapter include: i) quantifying the compositional importance of red maple in the forests of the study area; ii) characterizing the age and height structures of red maple populations in the study area; iii) examining relationships between time of establishment, height, and height growth rates in overstory and understory red maple populations; and iv) characterizing the degree of variability in age and height structure among red maple populations within a local landscape.

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#### Chapter 2

# THE RELATIVE INFLUENCE OF ESTABLISHMENT TIME AND HEIGHT GROWTH RATES ON SPECIES VERTICAL STRATIFICATION DURING SECONDARY FOREST SUCCESSION

#### ABSTRACT

The vertical growth histories of individual Quercus rubra L., Fraxinus americana L. and Acer rubrum L. growing in a 42-year-old <u>Populus</u> <u>grandidentata</u> Michx.-P. tremuloides Michx.-dominated forest were reconstructed using stem analysis. Species established contemporaneously early in the sere but temporally separated periods of peak individual establishment occurred among species, such that the majority of Q. <u>rubra</u> established prior to the majority of F. americana and A. rubrum. The vertical stratification of species by 42 years paralleled establishment patterns. Vertical growth rates were similar among species and between different-aged individuals within species. This suggests that species vertical stratification of species by 42 years after stand initiation was primarily a function differences in species establishment patterns.

#### INTRODUCTION

species establishment during secondary forest Tree succession has often been characterized by an initial floristic model in which the majority of individuals for all overstory tree species that will occur in the sere are assumed to be present at the time of, or soon after, stand initiation (Egler 1954; Drury and Nisbet 1973; Oliver 1978; Oliver and Larson 1990; Hibbs 1983; Abrams and Dickmann 1984; Sakai et al. 1985). Under this model. seral relationships among species, as manifest in vertical stratification, must result primarily from interspecific differences in height growth rates (Hibbs 1983). Species replacement during secondary succession is assumed to be a function of differential growth and mortality of component species, such that dominance shifts from relatively fast growing, short-lived species to relatively slow growing, longer-lived species (Drury and Nisbet 1973; Peet and Christensen 1980; Hibbs 1983; Tilman 1988).

This scenario becomes less straightforward if there has been temporal separation in establishment of individuals, within a species level initial floristics framework, such that the majority of individuals within each species established at different times. This is not true relay floristics (sensu Egler 1954) since all species were initially present. Delayed individual establishment may translate into differential resource acquisition such that early-establishing individuals achieve and maintain size superiority (Harper 1977, pp. 247-248; Huston and Smith This has been demonstrated by several workers in 1987). herbaceous monocultures (Black and Wilkinson 1963; Ross and Harper 1972; Adul-Faith and Bazzaz 1979; Naylor 1980; Howell 1981) and within naturally established populations of trees in early successional forests (Sakai and Sulak 1985; Larson 1986). Within tree populations, early establishing individuals may gain size superiority by virtue of enhanced resource capture and either increased vertical growth rates, relative to rates given contemporaneous establishment of individuals, suppression later or of establishing individuals (Oliver and Larson 1990). Alternatively, vertical dominance may be a function of increased residence time, i.e. early establishing individuals have simply had a longer time to grow.

Given temporal separation in establishment of individuals, species level relationships in the vertical profile will be dependent on when the majority of individuals within each species established, as well as rates of vertical growth. Thus, an initial floristics model would not sufficiently account for observed patterns of vertical stratification. An examination of individual success, as reflected in vertical growth pattern, and as influenced by establishment time, would further our understanding of the mechanisms driving secondary forest succession.

Stem analysis was used to reconstruct the vertical growth histories of individuals from three later successional tree species in a pioneer Populus grandidentata Michx.-P. tremuloides Michx. forest. Study objectives were to: 1) describe species establishment patterns; 2) compare vertical growth rates between different aged individuals within species and among species; and 3) compare and contrast the influence of time of establishment and vertical growth rates on individual and species position in the vertical profile.

#### METHODS

Stand Description and Vegetation Sampling

This study was conducted in a one hectare <u>Populus</u> <u>grandidentata- P. tremuloides</u> forest located in northcentral Lower Michigan, U.S.A. (SW 1/4, SEC 3, T19N, R3W, Clare County). Soil of the study area is classified as an Alfic Haplorthod and has developed on a morainal landform. The 42 year old aspen stand was initiated in 1947 (as determined from basal ages of several overstory <u>Populus</u> spp.) on a formerly grazed old field subsequent to fire. Remnant old trees and fire charred stumps suggest the original forest contained both <u>Pinus strobus</u> L. and northern hardwood species, in particular <u>Acer saccharum</u> Marsh.

Arboreal vegetation was sampled in four 250  $m^2$  circular plots distributed randomly within the stand. In each plot, species and diameter (at 1.37 m) of all overstory

(> 10 cm dbh) and sapling (2.5 cm  $\geq$  dbh  $\leq$  10 cm) individuals were determined. Tree seedlings (< 2.5 cm dbh) were sampled in 12 one m<sup>2</sup> frequency frames spaced at 3 m intervals along four opposing radii of each plot.

Stem Sampling

Stratified random sampling was used to select individual Quercus rubra L., Fraxinus americana L. and Acer rubrum L. for reconstruction of vertical growth histories using stem analysis. Sampled individuals were all from single-stemmed genets which appeared to be of seed rather than sprout origin. Selection was stratified by height class as follows. In each plot, one to five individuals within each species were randomly selected from the 0.5-1.0 m height class and from each 1 m height class thereafter. Some height classes did not contain any individuals. Selection proceeded to the height of the tallest individual of each species in each plot. A total of 33 Q. rubra, 58 F. americana and 26 A. rubrum were sampled. Additionally, one overstory Populus grandidentata from each plot was sampled to determine stand age and the growth pattern of the dominants. All stems were felled at 10 cm above mineral soil. Stems were marked at .25 m intervals from the base (10 cm) to 2 m and at 1 m intervals thereafter. Marking continued to the 1 m multiple closest to the end of the dominant leader. Stem sections were removed from large individuals (usually > 2 m in height) at each measurement interval.

Stem Analysis

Small individuals (usually  $\leq 2$  m in height), and terminal leaders of larger individuals, were aged by counting the number of terminal bud scale scars preceding each height interval. Stem sections from larger individuals were sanded to a smooth surface and wetted to aid ring examination. Ring number was counted on two radii of each section under a dissecting microscope. Section ages were used to reconstruct the vertical growth history (time of establishment and years to reach a given height) of each sampled individual. Vertical growth trajectories of all individuals were plotted together by plot. Section ages were also used to determine vertical growth rates (m/yr) for each one meter height interval (e.g. growth rate over 0-1 m, 1-2 m, etc.) of all sampled trees.

#### Data Analysis

Mean times of establishment (number of years after stand initiation) were compared among Q. rubra, F. americana and <u>A</u>. rubrum using one-way ANOVA. All establishment time data sets met assumptions of normality of residuals and homogeneity of variances. Tukey's test was used to separate individual species means. Mean species heights, at a stand age of 42 years, were compared using a Kruskal-Wallis test (data failed to meet assumptions of normality of residuals and homogeneity of variances even with transformation). Under the main test, mean species heights differed at the P =.1 level. Mann-Whitney U-tests were used to locate

differences between individual species means. Plots were used as replicates for comparisons of establishment times and heights among species.

Vertical growth rates were compared between early establishing individuals (22-42-year-old stems) and later establishing individuals (1-21-year-old stems) within each species. Vertical growth rates were compared among all species by pooling individuals across the two age groups. Comparisons were made using the growth rates determined for each one meter height interval as described in the Stem Analysis section. For intraspecific comparisons, the number of height intervals used in each analysis depended on the maximum height shared by both age groups on at least three plots (0-1 m for A. rubrum, 0-1 m through 3-4 m for Q. rubra and F. americana). For the interspecific comparison, growth rates for the first eight height intervals (0-1 m through 7-8 m) were used.

A t-test was used to compare mean growth rates, over the 0-1 m height interval, of early and later establishing <u>A</u>. <u>rubrum</u>. Growth rates were compared between age groups within <u>Q</u>. <u>rubra</u> and <u>F</u>. <u>americana</u>, and among all species, using split-plot repeated measures ANOVA, where height interval was the repeated measure. The sphericity assumption was accepted for both intraspecific comparisons (P > .25; Gurevitch and Chester 1986) but was rejected for the interspecific comparison (P < .001). For the latter analysis adjusted F values were used to test hypotheses regarding

height interval and height interval by species effects on growth rates (Moser <u>et al</u>. 1990). Orthogonal polynomial contrasts were used to separate trends in growth rates across height intervals. Plots were used as replicates for all growth rate analyses. Data were inverse-square root transformed to meet assumptions of normality of residuals and homogeneity of variances.

The relationships between stem age and stem height were examined by fitting least-squares regression lines to individual age-height curves, pooled across plots, within each species. Regression lines were fit to untransformed data so that the natural relationship between stem age and stem height, often sigmoid or hyperbolic (depending on age and vigor of the tree; Husch <u>et al</u>. 1972) would not be obscured.

#### RESULTS

#### Forest Composition and Structure

The forest overstory was dominated by <u>Populus</u> <u>grandidentata</u> and <u>P. tremuloides</u>, while regeneration was characterized by species typical of the northern mesic hardwood association in the upper Lake States (Braun 1950; Curtis 1959; Table 2.1). <u>Quercus rubra</u>, <u>Fraxinus americana</u> and <u>Acer rubrum</u> were the only later successional species in the overstory. Additionally these species had the highest

	Overstory	Sapling	Seedling		
	Density; Basal Area (stems/ha); (m²/ha)	Density (stems/ha)	Density stems/ha		
Species	19 19 19 19				
Populus grandidentata	390 <sup>a</sup> (173); 10.4 (4.5)	80 (32)	400 (361)		
P. tremuloides	310 (234); 7.3 (5.1)	30 (19)	60 (39)		
<u>Duercus rubra</u>	90(45); 1.2(0.7)	260 (90)	552 (199)		
Acer rubrum	30(19); 0.5(0.4)	210 (145)	9900 (4343) 8260 (1118)		
Prunus serotina	30 (19) , 0.5 (0.2)	470 (330)	2230 (1118)		
Pilia americana		60 (39)	6000 (2868)		
Ostrva virginiana		30 (10)	150 (100)		
Fagus grandifolia		20 (20)	130 (105)		
Acer <u>saccharum</u>		10 (10)	1650 (425)		
<u>Carya</u> <u>cordiformis</u>			10 (10)		
Total	850 (150); 19.7 (3.7)	1490 (555)	29.391 (4516)		

# Table 2.1. Forest composition and structure by stratum.

<sup>a</sup>Values are means (+/- standard error) of four replicates. Overstory dbh  $\geq$  10cm;

sapling, 2.5 cm  $\leq$  dbh < 10 cm; seedling, dbh < 2.5 cm.

understory density among later successional species, with the exception of <u>Prunus serotina</u> Ehrh. Individuals of the latter species were found primarily in one plot, hence its importance was not considered representative of the stand in general and for simplicity sake it was not included in the vertical growth reconstruction.

# Patterns of Establishment and Vertical Stratification

Individual age-height reconstructions by plot are illustrated in Figure 2.1. The four Populus grandidentata that were sampled achieved vertical dominance both by virtue of early establishment and rapid early growth rates. The establishment patterns for Q. <u>rubra</u>, <u>F</u>. <u>americana</u> and <u>A</u>. rubrum were characterized by temporally separated periods of peak individual establishment. Differences in establishment patterns among species are better illustrated by examining frequency distributions of individual establishment as a function of stand age (Figure 2.2). While all three species were present early in stand history, the majority of surviving Q. rubra established prior to the majority of F. americana and A. surviving rubrum. Mean time of establishment (number of years after stand initiation) for Q. <u>rubra</u> was significantly earlier than for <u>F</u>. <u>americana</u> and (P < .05;Table 2.2). The establishment Α. rubrum distributions of the latter two species were very similar Further, mean time of establishment of was (Figure 2.2). not significantly different for these species (P > .05;

Figure 2.1. Vertical growth reconstructions of individual <u>Populus grandidentata</u>, <u>Quercus rubra</u>, <u>Fraxinus</u> <u>americana</u> and <u>Acer rubrum</u> over a 42 year period in four plots. Each line represents an individual stem.



Figure 2.2. The number of new individuals establishing as a function of stand age for three later successional species in a <u>Populus</u> <u>grandidentata-P</u>. <u>tremuloides</u> forest.



Table 2.2.	Mean tim	e of es	tablish	ment	(number
of years	after sta	nd init	iation)	for	three
later suc	cessional	tree s	pecies	and a	analysis
of variar	nce for sp	ecies d	lifferen	ces :	in –
establish	nment time	•			

Species		Years	S.E.	n <sup>a</sup>
<u>Quercus</u> rub <u>Fraxinus</u> ar <u>Acer</u> rubrur	ora nericana n	19.2a 25.2b 25.9b	(0.8) (1.3) (1.8)	4 4 4
	Analys	sis of Varia	nce	
Source of Variation	df	SS	P > F	
Species Error	2 9	104.803 66.030	0.010	n, <sub></sub>

<sup>a</sup>Sample size (number of plots). Note: within the years column, means followed by the same letter were not significantly different at P=.05. SS, Sums of Squares.

•

Table 2.2). The right skewed establishment profiles for  $\underline{F}$ . <u>americana</u> and <u>A</u>. <u>rubrum</u> (Figure 2.2) could be the result of recruitment from seed produced by a limited number of early establishing individuals that reached reproductive maturity by 20-35 years (see Figure 2.1), thus providing a local seed source for additional establishment.

By year 42, vertical stratification of Q. rubra, F. americana and A. rubrum approximated the stratification in establishment times. pattern seen Most Q. rubra individuals were taller than most F. americana and A. rubrum individuals (Figure 2.1). The heights for individuals of the latter two species show considerably more overlap. Occasional individuals of F. americana (see Figure 2.1, plots 2-4) and <u>A. rubrum</u> (see Figure 2.1, plots 1,3 and 4) established earlier than was typically observed. These and individuals maintained achieved taller vertical positions in the profile than the "average" species level positions.

Mean species-level changes in vertical stratification over the 42 year stand history are illustrated in Figure 2.3. <u>Populus grandidentata</u> was taller than all other species throughout the period of examination. <u>Quercus rubra</u> was taller than both <u>F. americana</u> and <u>A. rubrum</u> by year 32 and remained so through year 42. The greater height of <u>Q</u>. <u>rubra</u> over the other two species at year 42 was only marginally significant ( $U_s$ =16, n=4 and 4, P <.1 and  $U_s$ = 14, n= 4 and 4, .1< P <.2, for comparison with <u>F. americana</u> and

Figure 2.3. Vertical stratification patterns among four tree species over a 42 year period in a <u>Populus</u> <u>grandidentata-P</u>. <u>tremuloides</u> forest. Heights are mean values (+/- standard error) of four plots at each age.



Figure 2.3

<u>A.</u> <u>rubrum</u> respectively). Mean heights of the latter two species were not significantly different ( $U_s$ = 11, n= 4 and 4, P >.2). The height profile for <u>A</u>. <u>rubrum</u> reflects the influence of newly established individuals in the sere between 27 and 32 years after stand initiation. These individuals reduced the mean height of the species at 32 years, relative to 27 years.

#### Intraspecific Height Growth Rates

Within each species, vertical growth rates of individuals establishing within 1-21 years after stand initiation and those establishing within 22-42 years after stand initiation were similar. For A. rubrum, growth rates (means followed by 95% confidence intervals for 0-1 m) of the older and younger age groups were 0.10 (0.07-0.15) m/yr and 0.12 (0.08-0.17) m/yr, respectively. The difference was not significant (t= -1.030, df= 3, 4, P > .3). Growth rates for Q. rubra and F. americana, across the four height intervals examined, are illustrated in Figure 2.4. Within each species, overall growth rates of the two age groups were not significantly different (P > .5; Table 2.3). For both species, there was a significant linear increase in growth rates from lower to upper height intervals (P < .005 and .001 for Q. rubra and F. americana respectively; Table 2.3, Figure 2.4). The quadratic term within the height interval effect was significant for F. americana only (P <.005; Table 2.3). This is a reflection of the non-linear Figure 2.4. Vertical growth rates (m/yr) for two age groups over four height intervals within two later successional tree species. <u>Old</u> individuals established within 1-21 years after stand initiation. <u>YOUNG</u> individuals established within 22-42 years after stand initiation. Values are back-transformed means of inverse-square root transformed growth rates (m/yr), with 95% confidence intervals. Sample size (number of plots) = 3 for Q. <u>rubra (OLD)</u> and 4 for all other age group-species combinations.

Figure 2.4



Table 2.3. Repeated measures analysis of variance for age group differences in height-growth rates (m/yr) within two later successional tree species.

Species							
<u>Quercus</u> <u>rubra</u>				<u>Fraxinus</u>			
df	SS		P > F	df	SS		P > F
1 5	0.003 0.165		0.779	1 6	0.056 0.542		0.460
3 1 1	3.386 2.566 0.536	< >	0.012 0.005 0.100	3 1 1	9.021 8.481 0.481	< <	0.001 0.001 0.005
3 15	0.012 3.259		0.997	3 18	0.083 0.793		0.608
	df 1 5 3 1 1 3 15	Quercus       df     SS       1     0.003       5     0.165       3     3.386       1     2.566       1     0.536       3     0.012       15     3.259	Quercus     r       df     SS       1     0.003       5     0.165       3     3.386       1     2.566       1     0.536       3     0.012       15     3.259	Quercus     rubra       df     SS     P > F       1     0.003     0.779       5     0.165       3     3.386     0.012       1     2.566     < 0.005	Quercus   rubra     df   SS   P > F   df     1   0.003   0.779   1     5   0.165   6     3   3.386   0.012   3     1   2.566   < 0.005	Quercus     rubra     Fraxinu       df     SS     P > F     df     SS       1     0.003     0.779     1     0.056       5     0.165     6     0.542       3     3.386     0.012     3     9.021       1     2.566      0.005     1     8.481       1     0.536     >     0.100     1     0.481       3     0.012     0.997     3     0.083       15     3.259     18     0.793	SpeciesQuercus rubraFraxinusdfSS $P > F$ dfSS10.0030.77910.05650.16560.54233.3860.01239.02112.566< 0.005

SS, Sums of Squares.

increase in growth rate between 2-3 m and 3-4 m seen within the older age group of this species (Figure 2.4b). Overall, the interaction between height interval and age group was not significant for either species (P > .5; Table 2.3).

### Interspecific Height Growth Rates

Height growth rates of early and late establishing individuals within each species were similar over shared height intervals. This suggests that species vertical stratification at 42 years was not a result of significant changes in growth rates between early and late establishing individuals within a species, thus, different aged individuals within species were pooled for a comparison of growth rates among species.

The pattern of vertical stratification seen among species at 42 years (Figures 2.1 and 2.3) was necessarily a function of establishment time interacting with interspecific vertical growth rates. The separation in time of peak establishment among species found in this study could be coupled with: i) similar interspecific vertical growth rates; ii) higher vertical growth rates for Q. rubra relative to F. americana and A. rubrum; or iii) increased vertical growth rates in the latter two species. While all three scenarios could result in the observed species vertical stratification profile, the influence of the second possibility would tend to accentuate the pattern, while the third would tend to ameliorate it.

Growth rates for Q. rubra, F. americana and A. rubrum, across the eight height intervals examined, are shown in Figure 2.5. Overall growth rates were not significantly different among species (P > .05; Table 2.4). There was a significant linear increase in growth rate from lower to upper height intervals (P < .001; Table 2.4, Figure 2.5). The quadratic term was also significant (P < .01; Table 2.4). This is a reflection of the decrease in growth rates over 6-8 m seen in both Q. rubra and A. rubrum (Figure 2.5). This decrease did not occur in F. americana, which accounts for the marginally significant height interval by species interaction term (Padj. < .04 to .10; Table 2.4). The cubic term was also significant (P < .01;Table 2.4) but interpretation of this is difficult given the high amount of variability in growth rates across mid- to upper height intervals within all species (Figure 2.5).

The similarity of vertical growth rates among the three species can be seen by examining regression lines fit to stem age-stem height data. For this analyses, age-height curves for all individuals were pooled across plots because too few individuals were sampled within each plot to fit separate regressions. Regressions were restricted to a maximum age, within each species, with at least four height observations.

For all three species a second order polynomial function provided the best interpretable fit to the data  $(r^2 = .659, .822 \text{ and } .910 \text{ for } Q. \underline{rubra}, \underline{F}. \underline{americana} \text{ and } \underline{A}.$ 

Figure 2.5. Vertical growth rates (m/yr) for three later successional tree species over eight height intervals, pooled across age groups. Values are back-transformed means of inverse-square root transformed growth rates (m/yr), with 95% confidence intervals. Sample size (number of plots) = 3 for <u>A</u>. <u>rubrum</u> and 4 for <u>Q</u>. <u>rubra</u> and <u>F</u>. <u>americana</u>.





		· · · · · · · · · · · · · · · · · · ·			
Source of				<u>Adj.</u>	$P > F^{a}$
variation	df	SS	P > F	G-G	H-F
Species	2	0.382	0.092		
Plot	8	0.468			
Height interval	7	17.257	0.001	0.001	0.001
Linear	1	9.072	< 0.001		
Quadratic	1	6.281	< 0.010		
Cubic	1	0.699	< 0.010		
Height interval x Species	14	1.748	0.041	0.104	0.041
Error	56	3.601			

Table 2.4. Repeated measures analysis of variance for species differences in height-growth rates (m/yr).

<sup>a</sup>Adj. P > F are probabilities associated with the Greenhouse-Geisser (G-G) and Huynh-Feldt (H-F) adjusted F-tests. SS, Sums of Squares. <u>rubrum</u> respectively, P <.01; summary statistics in Table 2.5). Individual age-height plots and regression lines for the three species are shown in Figure 2.6. A visual comparison of the lines (Figure 2.6d) indicates that the age-height relationships among the three species were very similar. A 10-15 year period of relatively slow growth was followed by increased growth over the remainder of the 42 year period. The greater mean height of Q. <u>rubra</u> at a stand age of 42 years, compared to <u>F. americana</u> and <u>A. rubrum</u> (Figure 2.3), was achieved despite lower predictability of the age-height relationship, relative to the other species (Figure 2.6a-c, Table 2.5) and lower growth rates over 6-8 m (Figure 2.5).

#### DISCUSSION

The influence of life history traits, including establishment requirements, shade tolerance and growth rates, on promoting species replacement during succession has been incorporated into several successional models (Noble and Slatyer 1980; Huston and Smith 1987; Tilman 1988). Under these models, combinations of attributes that convey competitive success change over a sere. For example, Populus grandidentata, by virtue of a mineral seed bed requirement (or prolific resprouting), shade intolerance, and a high vertical growth rate, achieves early successional soon after a stand-initiating disturbance. importance Conversely, for a species such as Acer saccharum, an organic seed bed requirement, shade tolerance and a relatively

Table 2.5. Summary information for second order polynomial regressions of stem height as a function of stem age for three later successional tree species in a <u>Populus</u> grandidentata-P. tremuloides forest.

		20	21 1.02	-2			
Species	Coefi	ficients	s (SEE)	r <sup>2</sup>			SEE
<u>Quercus</u> <u>rubra</u>	B <sub>0</sub> : B <sub>1</sub> : B <sub>2</sub> :	.4038 .0341 .0095	(.2609) (.0443) (.0016)	.659	(P<	.001)	1.465
<u>Fraxinus</u> <u>americana</u>	B <sub>0</sub> : B <sub>1</sub> : B <sub>2</sub> :	.4513 0238 .0127	(.1276) (.0231) (.0008)	.822	(₽<	.001)	0.895
<u>Acer rubrum</u>	B <sub>0</sub> : B <sub>1</sub> : B <sub>2</sub> :	0390 .0287 .0109	(.2034) (.0321) (.0010)	.910	( P<	.001)	0.768

Model: HEIGHT =  $B_0 + B_1 * AGE + B_2 * AGE^2$ 

Figure 2.6. Second order polynomial regressions of stem height as a function of stem age for three later successional tree species (A-C) in a <u>Populus</u> <u>grandidentata-P</u>. <u>tremuloides</u> forest. Dashed lines are 95% confidence bands for predicted values. Bestfit lines for all three species are compared in D. Symbols represent number of observation as follows: <u>Quercus rubra</u>, 1-15 years=3-30 observations (per symbol), 16-29 years=1-15 observations; <u>Fraxinus</u> <u>americana</u>, 1-15 years=8-30 observations, 16-29 years=1-14 observations; <u>Acer rubrum</u>, 1-15 years=2-15 observations, 16-30 years=1-5 observation.








slower vertical growth rate leads to later successional importance.

The underlying reasons for changes in relative importance among species over time is not so easily resolved when considering species with a similar suite of life history characteristics. The three later successional species examined in this study, <u>Quercus</u> rubra, Fraxinus americana and Acer rubrum, are similar in terms of successional status (climax adaptation numbers= 6.0, 8.0, and 6.0 respectively; Curtis 1959) and understory tolerance (Spurr and Barnes 1980). Differences in species importance, both in terms of traditional horizontal measures (basal area and density) and in the vertical profile, may depend on subtle differences in life history characteristics. For example, Hibbs (1983) and Oliver (1978) found that changes in vertical relationships among species in central New England hardwood forests resulted primarily from small differences in height growth rates. Interspecific differences in height growth rates would account for differences in relative species positions in a vertical profile given contemporaneous establishment of species.

Alternatively, relative importance may be less influenced by species characteristics and more dependent on differences in establishment time. In the present study interspecific height growth rates of <u>Quercus rubra</u>, <u>Fraxinus</u> <u>americana</u> and <u>Acer rubrum</u> were very similar through much of the 42 year period examined (Figure 2.5). While species establishment was contemporaneous, temporally separated periods of peak individual establishment among species occurred (Figure 2.2). The majority of <u>Quercus rubra</u> individuals established prior to the majority of individuals from the other two species. Species relationships within the vertical profile by 42 years (Figure 2.3) were largely influenced by differences in establishment times. <u>Quercus</u> <u>rubra</u> achieved a vertically dominant position in the forest, relative to <u>F</u>. <u>americana</u> and <u>A</u>. <u>rubrum</u>, primarily because most individuals of the species had been there longer and hence had a longer period to grow, rather than as a result of higher height growth rates.

The ability of early establishment to convey vertical importance to an individual was shared among the three species examined in this study. This is evident from the greater heights of the several F. americana and A. rubrum individuals that established prior to the bulk of individuals for each species (Figure 2.1). Ross and Harper (1972) found that early establishing herbaceous individuals gained a size advantage beyond that conveyed by additional growth time alone. They concluded that competitive superiority, through enhanced resource acquisition, led to suppression later establishing individuals, of thus enhancing the advantage gained through additional growth time. In the present study, the similar vertical growth rates over shared height intervals among species suggests that early emergence has not yet led to a competitive

advantage through enhanced resource acquisition. Rather, relative species success in the vertical profile was primarily a function of length of time available for growth. Of course all three later successional species have been, and will continue to be, influenced by the competitive effects of the early establishing <u>Populus</u>.

It is clear from the results that the rate of height growth accelerated as individuals of all three species grew McConnaughay and Bazzaz (1991) have shown, through time. that for some annual species, increasing the volume of soil available to an individual can have a positive influence on growth rate. They suggest that changes in root morphology, in response to differences in available space, may alter the ability of an individual to acquire resources. Results from the current study suggest that tree height growth may also be directly related to occupation of physical space in competitive understory environments. Whether this results from increased acquisition of below-ground or above-ground resources, or both, in response to changes in morphology is not known.

Early establishment may yet convey a competitive advantage both within and among species. As the stand matures and the overstory continues to develop, the resource environment experienced by smaller, younger individuals will be very different from that currently experienced by larger, older individuals. Resource limitation will result in reduced growth rates in many of the smaller individuals

(Oliver and Stephens 1977; Hibbs 1983; Sakai and Sulak 1985) and high rates of mortality within these populations (Oliver and Larson 1990).

#### SUMMARY AND CONCLUSIONS

Rates of height growth for <u>Quercus rubra</u>, <u>Fraxinus</u> <u>americana</u> and <u>Acer rubrum</u> in the secondary sere examined were very similar. For all species, growth rates increased as trees became larger. The increase with size was not influenced by time of establishment. The vertical stratification apparent 42 years after stand initiation was primarily a result of differences in time of establishment among individuals and species.

The results of this study may prove to be applicable to secondary forest successions on other highly disturbed or xeric sites in the Lake States. In these situations, either resource limitation, relative to more productive sites, or reduced propagule availability can lead to initially low levels of overstory stocking. For example, basal area of the study site was low (19.7 m<sup>2</sup>/ha) relative to Populus grandidentata dominated stands on relatively less disturbed, more productive sites in northern Lower Michigan (33-47  $m^2$ /ha at 65-70 years; Chapter 3). Reduced overstory stocking may in turn favor an extended period of stem establishment. This has been observed for xeric and highly disturbed forests in western North America (Franklin and Waring 1979; Oliver et al. 1985) but is less widely recognized in forests of eastern North America where

individuals in similar aged stands have been found to establish within shorter periods of time than documented in the present study (Oliver 1978; Hibbs 1983).

The generality of patterns and mechanisms of secondary forest succession could be resolved to some degree by expanding the examination of the interaction between individual establishment and growth, and its influence on succession, to the landscape scale. Of course, this is more than a trivial task when using the stem analysis technique.

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#### Chapter 3

# A COMPARISON OF PRESETTLEMENT AND PRESENT-DAY FORESTS ON TWO BIGTOOTH ASPEN-DOMINATED LANDSCAPES IN NORTHERN LOWER MICHIGAN

#### ABSTRACT

composition within Forest а local landscape is influenced by physical site characteristics and prevailing disturbance regimes. In many areas of eastern North America, natural the disturbance that regimes influenced presettlement forest composition have been altered by human activities associated with settlement. These alterations have led to substantial changes in composition and the development of successional pathways markedly different from the presettlement conditions. In this study, presettlement and present-day forest composition of two bigtooth aspendominated landscapes in northern Lower Michigan were examined. Objectives were to: (i) reconstruct and relate presettlement forest composition to the potential natural disturbance regime of each landscape; (ii) compare presettlement and present-day forest composition of each landscape; and (iii) assess the influence of postsettlement disturbance history on the development of the current forests and the potential successional pathways of the two landscapes.

Presettlement forest composition, reconstructed using General Land Office survey records, differed substantially between the two landscapes. Landscape 1 was dominated by

fire-sensitive eastern hemlock and American beech. while landscape 2 was dominated by fire-dependent red pine, white pine and jack pine. Compositional differences may have been related to differences in presettlement fire frequency, or to differences in physical site characteristics or regional climates. The present-day overstories of both landscapes are dominated by bigtooth aspen, red oak and red maple; species that were of minor importance in the presettlement forests of the study areas. Compositional convergence was attributed to the similar influence of postsettlement disturbance history on each landscape. Logging and wildfires eliminated advanced regeneration and many remnant seed hemlock, beech and pines sources of and favored the development of forests dominated by bigtooth aspen, red oak Individuals of the latter species survived and red maple. the disturbance and proliferated vegetatively in the postsettlement landscape. Differences in seed source availability in the present-day forests have led to marked differences in species recruitment in the understories of the two landscapes. Changes in seed rain and fire exclusion in the two landscapes are apparently leading to the development of forest types markedly different from the presettlement conditions. The results illustrate how human induced changes in disturbance regimes can have important, long-lasting effects on forest composition.

### INTRODUCTION

Forest composition and tree species abundance are influenced by edaphic and physiographic variation across a local landscape (Romme and Knight, 1981; Pregitzer <u>et al.</u>, 1983; Grimm, 1984; Whitney, 1986; Host <u>et al.</u>, 1987; Roberts and Christensen, 1988). In addition to physical site characteristics, vegetation composition is influenced by natural disturbance regimes (Heinselman, 1973; Sprugel, 1976; Veblen and Ashton, 1978; Runkle, 1982; Grimm, 1984; Whitney, 1986). These relationships are interrelated since natural disturbance regimes are often influenced by physical site characteristics and vegetation composition and pattern (Van Wagner, 1970; Heinselman, 1973; Sprugel, 1976; Foster, 1983; Grimm, 1984; Whitney, 1986).

In eastern North America, the disturbance regimes that defined presettlement forest composition and successional pathways have been altered by human activities. For instance, fire proliferation after deforestation in the upper Great Lakes region eliminated advanced regeneration and remnant seed sources of dominant coniferous species. This favored the development of extensive oak (Quercus spp.) and aspen (Populus spp.)-dominated forests where few existed in the presettlement landscapes (Kilburn, 1957, 1960b; Heinselman, 1973; Whitney, 1987; Crow, 1988; Nowacki et al., 1990). Conversely, fire exclusion in natural oak forests of the eastern and midwestern United States has allowed invasion by mesic, shade-tolerant hardwood species (Dix,

1957; Monk, 1961; Buell <u>et al</u>., 1966; Anderson and Adams, 1978; Lorimer, 1984; McCune and Cottam, 1985; Fralish <u>et</u> <u>al</u>., 1991).

Successional predictability at a scale that emphasizes the influences of local physical site characteristics and natural disturbance regimes is arguably a tenable concept. However, when natural disturbance regimes have been altered by activities associated with settlement, an ensuing change in community composition and successional development will occur. The magnitude of this change, and the potential for a disturbed, postsettlement forested landscape to recover a level of community composition resembling its presettlement condition, may be highly dependent on the degree to which successional potential has been influenced by human activity (for examples see Glitzenstein <u>et al.</u>, 1990; Fralish <u>et al.</u>, 1991).

In this study the presettlement and present-day composition of two forested landscapes in northern Lower Michigan were examined. Initial observations indicated that the current forests of both landscapes are dominated by bigtooth aspen (Populus grandidentata Michx.), with lesser amounts of red oak (Quercus rubra L.) and red maple (Acer rubrum L.). Both landscapes were characterized by similar surficial geology, soil type and postsettlement disturbance histories. The study locations were located within different climatic and physiographic settings. Study objectives were to: (i) reconstruct and relate presettlement forest

compositions to the potential natural disturbance regimes of the two landscapes; (<u>ii</u>) compare presettlement forest composition to the present-day forest of each landscape; and (<u>iii</u>) assess the influence of postsettlement disturbance history on the development of the current forests and the potential successional pathways of the two landscapes.

## METHODS

Study locations

Study area 1 was a 15  $\text{km}^2$  landscape located within the University of Michigan Biological Station (UMBS) in the extreme northwestern portion of Lower Michigan (latitude 45° 40 N, longitude 84° 40' W). Study area 2 was a 18  $\text{km}^2$ landscape located within the Harrisville Ranger District of the Huron-Manistee National Forest (Huron) in northeastern Lower Michigan (latitude 44° 15' to 45° 00' N, longitude 83° 15' to 84° 45' W). The distance between centers of the two study areas was approximately 110 km.

Surficial geology of both study areas consisted of deep outwash sands overlaying till deposits (Cooper, 1981; Padley, 1989). Soils throughout the majority of both study areas were classified as Entic Haplorthods (Cooper, 1981; Lapin, 1990; USDA SCS Cheboygan County soil survey, 1991; Michigan State University, Forestry Department data file).

The study areas were located within different climatic districts of a regional landscape ecosystem classification of Michigan (UMBS= Presque Isle district; Huron= Highplains;

Albert et al., 1986). These districts differ somewhat in several climatic variables, most notably, heat sums, potential evapotranspiration and average temperatures (Table 3.1). The two districts have identical total annual precipitation, May-September precipitation, and July-August precipitation to potential evapotranspiration ratios (Table 3.1). In general, climate does not differ greatly between the two study areas.

The physiographic settings of the landscapes were substantially different. The UMBS study area was located on a 3 km wide strip of land bordered on the north and south by two large kettle lakes. The study area was bordered on the west by a massive north-south oriented morainal ridge (Lapin 1990), with soils generally finer textured than those found in the study area proper (USDA SCS, Cheboygan County soil survey). The eastern portion of the study area was bordered predominantly by farmland. Prior to settlement, lowland conifer-hardwood forests occupied much of this area 1957). The (Kilburn, Huron study area was located immediately east of a 90 km<sup>2</sup> outwash system (Mack Lake outwash plain) dominated by jack pine (Pinus banksiana Lamb.; Simard and Blank, 1982). The northern, southern and eastern portions of the study area graded into a morainal landform characterized by sandy-clay soils (Padley, 1989). Northern hardwood forests currently occupy much of the mesic 1989; portions moraine (Padley, of the personal observations). Both study areas were internally homogeneous

Variable	District					
	Presque Isle (UMBS)	Highplains (Huron)				
Growing season length (days)	120	115				
April-October heat sum ( <sup>O</sup> C-days, base 7.2 <sup>O</sup> C)	2020	2140				
Heat sum prior to last spring freeze ( <sup>O</sup> C-days)	240	300				
Ratio of night heat sum to total heat sum (%)	24	23				
May-September potential evapotranspiration (mm)	470	490				
July-August precipitation to potential evapotranspiration ratio (%)	70	69				
Total annual precipitation (mm)	770	770				
May-September precipitation (mm)	400	400				
Annual average temperature (°C)	6.2	6.7				
May-September average temperature ( <sup>O</sup> C)	15.9	16.9				
Annual extreme minimum temperature ( <sup>o</sup> C)	-29	-28				

Table 3.1. Mean climatic variables for the districts containing the UMBS and Huron study areas.

Data taken from Table 2 of Albert et al. 1986.

with respect to physiographic, edaphic and compositional (bigtooth aspen-dominated) characteristics (Lapin, 1990; Michigan State University, Forestry Department data file).

The regions containing the study locations were deforested in the late nineteenth to early twentieth centuries (Gleason, 1923; Kilburn, 1957, 1960a; Benninghoff and Cramer, 1963; Whitney, 1987). Frequent slash-fueled wildfires swept over these landscapes in the years following logging. Fires eliminated advanced regeneration and most remnant overstory individuals of the dominant presettlement species (Kilburn, 1957, 1960a; Whitney, 1987).

Presettlement forest composition and disturbance regimes

Pre-settlement forests of the two study areas were reconstructed using General Land Office (GLO) survey records. The use of GLO surveys for reconstructing presettlement forests, as well as criticisms of the technique, are discussed in detail by Bourdo (1954, 1956) and Whitney (1986, 1987). During these surveys, the species and diameter of bearing trees (trees used to mark section corners and quarter section points) and line trees (trees used to mark section lines between corners and quarter points) were recorded. Within each study area, a relative measure of importance was derived for each species by dividing the number of times a species was used as a bearing or line tree (citation frequency) by the total number of bearing and line trees examined. A total of 79 and 111

bearing and line trees, from 11 and 19 section lines (one line = 1.6 km), were examined for the UMBS and Huron landscapes, respectively. Only section lines traversing upland forests were examined. The lines examined at UMBS included all or portions of sections 26 and 31-34 of Township 37N, Range 3W. Huron lines included all or portions of sections 2-4 and 9-11 of T25N, R4E and sections 33-35 of T26N, R4E. The physiographic settings of the two study areas precluded larger sample sizes.

Presettlement disturbance regimes of each study area were reconstructed using GLO survey records following the methods of Lorimer (1977, 1980a), and Whitney (1986). Surveyors often recorded any evidence indicative of past disturbance, such as major windfalls or burnt land, in their line descriptions. Typically, the surveyors also recorded the length of a section line affected by the disturbance. This information was used to determine the total length of section lines and percentage of each study area affected by windfall or fire. The percentage of each study area that was annually affected by disturbance was estimated, following Whitney (1986), by dividing each total percentage by 30 and 15. These values represent high and low estimates for the number of years that evidence of a past disturbance would remain visible to а surveyor. Finally, the disturbance recurrence interval (Lorimer, 1977) was estimated by dividing 100 by the percentage of area annually disturbed by a particular type of disturbance. Additionally,

township plat maps (constructed by the surveyors) of the two study areas were examined for any evidence of disturbance.

## Present-day vegetation sampling

Four and five stands were randomly selected from larger data pools (Lapin, 1990; Michigan State University, Forestry Department data file) for the UMBS and Huron study areas, respectively. All stands, within each study area, belonged to similar ecological land classification units (following Barnes <u>et al</u>., 1982), based on surficial geology, soil characteristics and ground flora composition (Lapin, 1990; Michigan State University, Forestry Department data file). Selected stands met the following additional criteria: (1) minimum size of 1 ha; (2) free from obvious disturbance since initiation; and (3) 0-5% slopes. The distance between stands within each study area ranged from 1-4.5 km.

Arboreal vegetation was sampled in four circular plots randomly located within each stand. Plot size was 475 m<sup>2</sup> at UMBS and 272 m<sup>2</sup> at Huron. A larger plot size at UMBS was required to meet an objective of a related study. In each plot, species and diameter (at 1.37 m) of all overstory individuals (dbh > 10 cm) and saplings (2.5 cm  $\leq$  dbh  $\leq$  10 cm) were tallied. Species and density of tree seedlings (dbh < 2.5 cm) were tallied in 12 1-m<sup>2</sup> frames. Seedling frames were spaced at 3-m intervals along two perpendicular diameters of each plot, beginning at the plot boundary. The origin of overstory individuals (sprout or seedling) was assessed when possible.

#### RESULTS

Presettlement forest composition

Presettlement forest composition of the two study areas is summarized in Table 3.2. The UMBS forest was dominated, in decreasing order of bearing and line tree citation frequency, by eastern hemlock (Tsuga canadensis (L.) Carr.), American beech (Fagus grandifolia Ehrh.), white pine (Pinus strobus L.) and red pine (Pinus resinosa Ait.). These species accounted for 87% of all bearing and line trees. The Huron study area was pine-dominated; red pine, jack pine and white pine accounted for 78% of all bearing and line trees. Aspen, red maple and red oak were the only minor overstory species occurring at both study areas. Ά similarity index that proportional integrated species richness and importance (proportional similarity= the sum of the lowest relative measure of importance between two samples over all species; Brower and Zar, 1977) was used to compare presettlement overstory composition of the two landscapes. Proportional similarity (based on relative bearing and line tree citation) was 33%.

## Presettlement disturbance regimes

The line descriptions and the township plat map for the UMBS study area contained no evidence of past fire. Two line descriptions referred to large windfalls ("timber much

	UMBS	Huron		
Species	Percentage of bear	ing and line trees		
Acer rubrum	3.8 (3) <u>a</u>	5.4 (6)		
Acer saccharum	1.3 (1)			
Betula papyrifera	3.8 (3)			
Faqus grandifolia	21.5 (17)	3.6 (4)		
Pinus banksiana		17.1 (19)		
Pinus resinosa	3.8 (3)	45.1 (50)		
Pinus strobus	11.4 (9)	15.3 (17)		
Pinus sp. <sup>b</sup>	6.3 (5)			
Populus sp. <u>C</u>	1.3 (1)	7.2 (8)		
Ouercus alba		3.6 (4)		
Ouercus rubrad	2.5 (2)	2.7(3)		
<u>Tsuga</u> canadensis	44.3 (35)			

Table 3.2. Presettlement forest composition of the UMBS and Huron study areas.

 $\frac{a}{b}$ Values in parentheses are numbers of individuals.  $\frac{b}{b}$ The lack of <u>P</u>. <u>banksiana</u> citations at UMBS suggests that these individuals were <u>P</u>. <u>strobus</u> and <u>P</u>. <u>resinosa</u>. <sup>C</sup>Site characteristics suggest these were mostly <u>Populus</u> <u>grandidentata</u>. dMay include some <u>Quercus velutina</u> (Lam.) and <u>Quercus</u> <u>ellipsoidialis</u> (E. J. Hill).

fallen") but the extent of the disturbance was not recorded. Thus, no estimate of disturbance recurrence interval could be calculated.

The line descriptions for the Huron study area did not indicate recent burns. They contained, however, some evidence possibly indicating older burns. Approximately 13.3% of the section lines fell within "aspen and pine thicket" or "oak thicket". Some references to these areas indicated that they included many, small individuals. The township plat maps corroborated the locations and extent of these areas. Assuming these areas were recovering burns within the older pine matrix, which they may not have been, the presettlement fire recurrence interval for the Huron study area was 114-227 years. There were no references to large windfalls within the Huron line descriptions.

# Present-day overstory composition

Both the UMBS and Huron overstories were dominated by bigtooth aspen (Table 3.3). Relative basal area for this species was 74% at UMBS and 73% at Huron. Later successional species of minor importance occurring at both locations included red maple and red oak. Proportional similarity of present-day overstories for the two locations (based on species relative basal areas) was 90%. Mean basal area ( $m^2$ /ha) and density (stems/ha) were both substantially higher in the Huron forest, than at UMBS (Table 3.3).

Species	UMBS							
	Canopy <sup>a</sup>			Sapling <sup>b</sup>		Seedling <sup>C</sup>		
	m <sup>2</sup>	/ha	ster	ns/ha	ste	ems/ha	sten	ıs/ha
Populus grandidentata	21.3	$(1,2)^{d}$	560	(41)	4	(4)	573	(225)
Ouercus rubra	2.5	(0,6)	67	(20)	82	(23)	4740	(635)
Acer rubrum	2.4	(0.4)	93	(23)	335	(69)	64687	(8805)
Betula papyrifera	0.9	(0.3)	46	(12)	54	(13)		
Pinus resinosa	0.9	(0.4)	18	(10)	44	(20)		
Pinus strobus	0.6	(0.2)	45	(15)	642	(127)	1562	(569)
Fagus grandifolia	0.02	(0.02)	3	(3)	17	(7)	104	(71)
<u>Abies balsamea</u>					3	(3)		
Totals	28.6	(1.5)	890	(44)	1180	(112)	71666	(8777)

Table 3.3. Present-day forest composition and structure of the UMBS and Huron study areas.

Table 3.3	(cont'd)	).
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Species	Huron							
	Canopy <sup>a</sup> m <sup>2</sup> /ha stem			ms/ha	Sapling <u>b</u> stems/ha		Seedling <sup>C</sup> stems/ha	
Denulus anadidenteto		(2 1)d		(40)				
Populus grandidentata	30.3	$(2.1)^{-}$	030	(48)			2025	
Quercus rubra	5.5	(1.0)	100	(29)	13	(6)	3625	(669)
<u>Acer rubrum</u>	4.9	(0.6)	282	(28)	644	(89)	64833	(6522)
<u>Quercus velutina</u>	0.5	(0.2)	14	(7)				
Quercus alba	0.3	(0.2)	10	(5)			458	(260)
Fraxinus americana	0.06	(0.06)	4	(4)	4	(4)	167	(97)
Betula papyrifera	0.05	(0.05)	2	(2)			42	(42)
Prunus serotina	0.01	(0.01)	2	(2)	26	(9)	14583	(3813)
Totals	41.6	(2.0)	1117	(48)	686	(96)	83708	(8205)

 $\frac{a}{Dbh} > 10 \text{ cm}; \frac{b}{2.5} \text{ cm} \le dbh \le 10 \text{ cm}; \frac{c}{d}dbh < 2.5 \text{ cm}.$  $\frac{d}{Values}$  are the means (<u>+</u> SE) of 16 observations at UMBS and 20 observations at Huron.

Most red oak and red maple were apparently of sproutorigin. Individual ramets were often part of multi-stemmed genets that had branched at or below the soil surface. Additionally, many ramets were growing in a circular arrangement or had crescent shaped stem bases, both of which are indicative of development around remnant stumps.

# Regeneration

White pine dominated the sapling layer at UMBS (Table 3.3). Red maple was moderately abundant in the sapling layer and dominated the seedling layer (Table 3.3). Minor components included red oak, American beech, paper birch (<u>Betula papyrifera Marsh.</u>) and red pine. The vast majority of Huron saplings and seedlings were red maple (Table 3.3). Black cherry (<u>Prunus serotina Ehrh.</u>) and red oak were minor understory components. The sapling and seedling layers of the two locations had proportional similarity indices (based on mean relative densities) of 30% and 84%, respectively. Mean total sapling density was substantially higher in the UMBS forest.

### DISCUSSION

# Presettlement forests

The compositions of the UMBS and Huron presettlement forests were markedly different, despite similarities in soil type and surficial geology. The occurrence of a mixedpine community on the Huron landscape is not surprising. The study area occurred on sites that were edaphically and physiographically similar to the sandy uplands described by Whitney (1986). The forests of these sites were also mixedpine communities. Pine dominance is believed to have been maintained by periodic fires that eliminated competing hardwood vegetation, thinned the overstory, and provided a mineral seedbed for new pine establishment (Van Wagner 1970; Heinselman 1973; Whitney 1986).

The Huron landscape was located in a physiographic setting conducive to fire. The Mack Lake outwash plain, located adjacent to the study area on the east, had a presettlement large-fire (4,000+ ha) interval of 35 years (Simard and Blank, 1982). Fires spreading up from the plain, with the prevailing westerly winds, may have predisposed the study area itself to fire, but at a lower frequency than the plain proper. This interpretation is supported by the estimate of the fire recurrence interval for the Huron landscape (114-227 years), which was similar to Whitney's (1986) estimate (129-258 years) for the mixed-pine forests he examined. The Huron fire recurrence interval should, however, be interpreted with caution since it was based on the occurrence of particular vegetation types (aspen, oak, and pine "thickets") that may be indicative of past fire (Heinselman, 1973; Whitney, 1987, 1990; Nowacki et al., 1990), rather than the presence of obvious burns themselves.

A presettlement hemlock-beech-pine forest at UMBS is consistent with Kilburn's (1957; 1960b) reconstruction of hemlock-pine and hemlock-beech forests for the same area. The importance of hemlock and beech, both fire-sensitive

species (Barnes and Wagner, 1981), suggests that the presettlement fire frequency at UMBS may have been low, despite edaphic and physiographic characteristics that have been associated with fire elsewhere in northern Michigan (Whitney, 1986). An interpretation of low fire frequency is supported by the lack of evidence for fire in the presettlement line descriptions.

The UMBS study area was located within a physiographic have reduced likelihood setting that mav the of presettlement fire. The lakes to the north and south of the study area would have acted as barriers to the spread of fires from these directions, protecting hemlock and beech from fire originating outside of the study area proper. Heinselman (1973) and Grimm (1984) found that fire-sensitive vegetation was often associated with the leeward sides of water bodies within landscapes prone to fire. The moraine to the west of the study area would have acted as an additional barrier to fires moving east, with the prevailing westerly winds. Much of the moraine, prior to settlement, was covered by a sugar maple (Acer saccharum Marsh.)dominated northern hardwood forest (Kilburn, 1957). Mesic hardwood forests are believed to be quite resistant to fire (Vogl, 1967; Canham and Loucks 1984; Grimm 1984; Whitney 1987) and thereby act as natural fire barriers. Interestingly, the township plat map at UMBS did show a large burnt area abutting the northwest terminus of the moraine outside of the study area. Finally, fires

originating in the lowland conifer-hardwood forest to the east of the study area were probably rare. Whitney (1986) estimated that the fire recurrence interval for this forest type was 3000-6000 years; the longest of any northern Michigan forest type he examined.

The presettlement compositional differences between study areas may have been related to differing natural fire regimes, however, there alternative, are possibly interacting, explanations. Compositional distinctions may have been related to differences in physical site characteristics less apparent than landform and soil type (for example, sand particle size distribution, depth to till, or the frequency of finer-textured soil bands). Climate may also have been influential. Modern climatic statistics (Table 3.1) suggest that the UMBS study area was somewhat cooler and wetter than the Huron study area. Eastern hemlock in particular, and American beech to some extent, are often associated with a cool, humid climate (Godman and Lancaster, 1990; Tubbs and Houston, 1990). In addition to influencing composition directly, a cooler, wetter climate at UMBS could also have contributed to lower fire frequency.

# Present-day forests

Early successional, postsettlement forest composition of the two study areas was similar, despite marked differences in presettlement forest composition. This

convergence was a function of both species elimination and it occurred because of similarities proliferation; in postsettlement disturbance regimes (logging followed by These disturbances eliminated most recurrent wildfire). pines, hemlock and beech. The species that did proliferate in these early successional landscapes (bigtooth aspen, red oak and red maple) were those best able to exploit the availability of abundant mineral seedbeds (bigtooth aspen; Graham et al., 1963) or propagate vegetatively from roots or stumps able to survive frequent fire (bigtooth aspen, red oak and red maple; Gates, 1930; Hutnick and Yawney, 1961; Sander, 1990). The resulting forest type was unrepresented, or rare, in the presettlement landscapes of the region (Kilburn, 1957, 1960b; Whitney, 1986, 1987).

There were differences in composition of tree regeneration between the two landscapes; primarily a lack of pine in the sapling layer of the Huron stands. At least one or two large remnant overstory white pines were observed in all UMBS stands (although not in any plots), but none were found in the Huron stands (formerly pine-dominated). This graphically illustrates the importance of a remnant seed source to species recovery following major disturbance. Seed source elimination may also be responsible for the failure of hemlock to recover at UMBS. Additionally, hemlock recovery may be inhibited because of preferential browsing by white-tail deer (Odocoileus virginianus Zimmerman; Curtis, 1959; Anderson and Loucks, 1979; Frelich and

Lorimer, 1985) or a lack of coarse, moist woody germination substrates (Oosting and Hess, 1956; Olson <u>et al</u>., 1959; Coffman, 1978; Hix and Barnes, 1984).

The present-day forests of the two landscapes were structurally different. The possible reasons for this are purely speculative. Lower overstory density and basal area at UMBS may be related to the intensity of past disturbance or to site differences. Lower overstory stocking in the UMBS forest, relative to the Huron forest, may have led, in turn, to increased understory establishment and greater recruitment to sapling size classes.

The loss of bigtooth aspen from the overstories of both study areas is imminent, since most ramets are approaching the limit of the species pathological rotation age in the Great Lakes region (70-80 years; Graham <u>et al.</u>, 1963). New overstory recruitment of bigtooth aspen, a shade-intolerant species (Laidly, 1990), is dependent on complete overstory removal through either silvicultural manipulation or natural stand-replacing fire (Graham <u>et al.</u>, 1963). The latter is now uncharacteristic of the region because of fire suppression (Whitney, 1987). In contrast, red oak will remain an overstory component of both forests after loss of bigtooth aspen simply because it is a long-lived species (300+ years; Barnes and Wagner, 1981).

Bigtooth aspen mortality will result in the formation of numerous canopy gaps. Shade-tolerant red maple (Hutnick and Yawney, 1961) and mid-tolerant white pine (Wendel and

Smith, 1990) both have the potential for release and recruitment in canopy gaps (Gerrard, 1969; Lorimer, 1980b; Hibbs, 1982). Increased overstory recruitment for both species could occur, given a natural disturbance regime now characterized by small to moderate sized canopy gaps. The potential successional trends toward increasing red maple importance, alone, or in combination with white pine, may signal the development of forest types unrepresented in the presettlement landscapes of the upper Lake States. Similar trends have been suggested for oak-dominated forests in several areas of the eastern United States (Lorimer, 1984; Host, <u>et al</u>. 1987; Abrams and Nowacki, 1992).

The cultural histories of the UMBS and Huron landscapes may have long-lasting effects on their respective forest communities. Continued fire exclusion and the lack of pine seed sources on the Huron study area assures that forest composition will remain markedly different the from presettlement condition. A reduced fire frequency at UMBS may reflect the presettlement condition. However, postsettlement forest composition has been heavily influenced by the availability of seed sources and the differential ability of various presettlement species to recover following fire.

The results of this study illustrate the importance of the link between disturbance and composition in plant communities; a relationship that is now widely recognized by ecologist. The results also illustrate how historical circumstances can influence composition and successional pathways. Ecologists have recognized for some time that historical factors may influence composition (Gleason, 1926; Cain, 1947; Whittaker, 1953; Egler, 1954; Curtis, 1959; Auclair and Cottam, 1971; Oliver, 1981; Heinselman, 1981). Recently, the importance of historical influences has been reemphasized and critically examined (for example see Pickett, 1989). The current study, and others comparing forests of pre- and postsettlement landscapes, illustrate how human-associated historical circumstances can have important, long-lasting effects on forest composition.

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### Chapter 4

# PATTERNS OF EVEN-AGED FOREST DEVELOPMENT WITHIN TWO BIGTOOTH ASPEN (<u>Populus grandidentata Michx.</u>)-DOMINATED LANDSCAPES IN NORTHERN LOWER MICHIGAN, USA

### ABSTRACT

development following major disturbance Forest is purported to follow a fairly repeatable temporal pattern. An initial cohort of trees establishes relatively rapidly (stand initiation), new establishment is precluded for an extended period of time (stem exclusion), finally, new individuals again begin to establish, creating new age classes in the forest understory (understory reinitiation). The current study was designed to assess the generality of this developmental pattern at the landscape-level and gain insight into the possible mechanisms controlling stem exclusion and understory reinitiation in even-aged forests. Research was conducted within two bigtooth aspen-dominated landscapes (Huron and UMBS) having similar physical site characteristics, overstory compositions, and disturbance histories. The objectives for the study included i) describing forest development patterns within each landscape and assessing the repeatability of development patterns within and between the two landscapes, and <u>ii</u>) exploring relationships between the timing of understory reinitiation overstory growth characteristics and and seed-source availability. Stem analysis was used to reconstruct

establishment and growth histories of sampled stems on replicate plots within each landscape.

The age distributions of surviving individuals in both forests reflected a developmental pattern characterized by rapid initial cohort establishment, stem exclusion, and understory reinitiation. The duration of development stages was similar both within and between the two landscapes. There were, however, a small number of plots in the UMBS forest with substantially reduced stem exclusion lengths, relative to the remaining plots in this forest. Variation in the timing of understory reinitiation in the UMBS forest was related to characteristics of remnant seed trees. The stem exclusion period was shorter, or nearly non-existent, on plots in close proximity to several large seed trees. Substantial increases in establishment frequency on all UMBS plots, as well as all new understory establishment within the Huron forest, were associated with moderate to large radial growth releases in overstory stems. These results suggest that the timing of understory reinitiation in the forests examined was influenced by an interaction between seed availability and changing resource levels in the forest understory. A limited amount of new establishment occurred relatively early in forest development on plots that experienced abundant early seed rain, yet the bulk of new establishment occurred after an increase in radial growth of overstory stems. The radial growth releases presumably reflected an increase in resource availability in the forest

understory, possibly occurring in response to natural thinning within the bigtooth aspen-dominated overstory. The general patterns of forest development described in this study were strikingly similar both within and between Similar descriptive studies are needed to landscapes. address the repeatability of development patterns at the landscape-level within additional forest-types. Additionally, experimental studies are needed to unequivocally identify the mechanisms controlling stem exclusion and understory reinitiation in even-aged forests. Particular attention should be given to the combined influence of seed-source and resource availability on understory establishment patterns.

#### INTRODUCTION

Even-aged forest development has received considerable attention over the last several decades (for example, see Bormann and Likens 1979; Oliver 1980, 1981; Peet and Christensen 1987). This interest can be attributed in part to the prevalence of an even-aged structure in managed forest landscapes, but also to the realization that largescale natural disturbances have created single-age class forests in many regions (see examples in Lorimer 1980; Oliver 1981). The development of even-aged forests is thought to follow a fairly repeatable temporal pattern (Oliver 1981; Peet 1981; and others cited in Peet and Christensen 1987). First, an initial post-disturbance cohort of trees becomes established during a relatively short period of time (stand initiation sensu Oliver 1981). A second period follows during which few or no new individuals become established (stem exclusion). Finally, individuals of overstory tree species again begin to establish succesfully, the creating new classes in forest age understory (understory reinitiation).

Many silvicultural studies of even-aged forest development have explored growth patterns within the initial post-disturbance cohort of trees (Cayford 1957; Marquis 1967, 1981; Oliver 1978; Stubblefield and Oliver 1978; Wierman and Oliver 1979; Hibbs 1983; Guldin and Lorimer 1985; Kelty 1986; Larson 1986; Clatterbuck and Hodges 1988; Hix and Lorimer 1990, 1991; Deal et al. 1991). Less attention has been given to characterizing and understanding, from a mechanistic perspective, the stem exclusion and understory reinitiation phases of even-aged forest development. While one or both of these developmental stages have been documented in a wide variety of foresttypes (Bloomberg 1950; Sprugel 1976; Oliver 1978: Christensen and Peet 1981; Peet 1981; Oliver et at. 1985; Roberts and Richardson 1985; Harcombe 1986; Sharik et al. 1989; Abrams and Nowacki 1992; Segura and Snook 1992), few studies have been designed to assess the repeatability of stand development patterns within and among landscapes characterized by similar physical site characteristics. species compositions, and disturbance histories (for a notable exception see Sprugel 1976). The need for assessing the generality of developmental patterns is demonstrated by the fact that some forests initiating after maior disturbance have actually been found to lack a stem exclusion period (Peet 1981; Carleton 1982; Roberts and Richardson 1985; Chapter 1).

There is also a lack of consensus regarding the mechanisms that control stem exclusion and understory reinitiation in even-aged forests. Some studies suggests that stem exclusion may simply reflect an initial lack of local seed-sources early in forest development, while understory reinitiation reflects the reproductive maturation of a post-disturbance cohort of trees (Day 1972; Carleton 1982; Roberts and Richardson 1985; Sharik <u>et al</u> 1989; Sakai

1985; Sakai 1990). In contrast, resource-based et al. theories of forest development (Oliver 1981; Christensen and Peet 1981; Peet 1981; Peet and Christensen 1987) suggest that stem exclusion begins after the initial cohort of trees attains full site occupancy, thereby limiting successful establishment through competition, despite the presence of a local seed-source. Understory reinitiation is thought to begin only when resources become less-limiting. Various mechanisms have been proposed to account for this increase in resource availability, including canopy gap formation following density-independent mortality of mature overstory individuals late in even-aged development (Sprugel 1976; Christensen and Peet 1981; Peet 1981; Peet and Christensen 1987), crown differentiation within the even-aged overstory (Bormann and Likens 1979, Oliver et al. 1985; Oliver and Larson 1990), reductions in rates of root growth (Oliver and Larson 1990), and density-dependent mortality of suppressed individuals following a concentrated wave of natural thinning (Harcombe 1986; Fried et al 1988; Oliver and Larson 1990).

This paper reports on a mensurative study designed to assess the generality of developmental patterns in even-aged landscape-level and gain insight forests at the into mechanisms stem possible controlling exclusion and understory reinitiation. The study was conducted within two bigtooth aspen (Populus grandidentata Michx.)-dominated landscapes in northern Lower Michigan, USA. Both landscapes

are representative of aspen-dominated forests that occupy over 5 million hectares in the Great Lakes region (bigtooth and trembling aspen (P. tremuloides Michx.) combined, Einspahr and Wyckoff 1990). The initial objective was to reconstruct the establishment history of individuals from species these all tree in forests, describe forest development patterns, and assess the repeatability of patterns within and between the two landscapes. A second objective was to explore relationships between the timing of understory reinitiation and overstory growth characteristics and seed availability. A working hypothesis associated with this objective that understory reinitiation is was controlled by an increase in resource availabilitv associated with natural thinning within the bigtooth aspen overstory. Testable corollaries to this hypothesis were that i) understory reinitiation would begin prior to the onset of mortality in mature, overstory dominants, <u>ii</u>) understory reinitiation would be associated with increased radial growth in surviving overstory individuals, suggesting increased resource availability as a factor influencing survivorship in the understory, and iii) the timing of understorv reinitiation be unrelated would to characteristics of remnant seed trees (proximity, number, size) when they were present.

## STUDY LOCATIONS

Research was conducted within the Huron-Manistee National Forest (Huron) in northeastern Lower Michigan (latitude  $44^{\circ}$  15' to  $45^{\circ}$  00' N, longitude  $83^{\circ}$  15' to  $84^{\circ}$  45' W) and the University of Michigan Biological Station (UMBS) in the extreme northwestern portion of Lower Michigan (latitude  $45^{\circ}$  40 N, longitude  $84^{\circ}$  40' W). The two landscapes are separated by approximately 150 km. Surficial geology, soils, and the physiographic and climatic settings of the two study areas have been described previously (Chapter 3).

Prior to settlement, the Huron landscape was dominated by red pine (<u>Pinus resenosa</u> Ait.), jack pine (<u>P. banksiana</u> Lam.) and white pine (<u>P. strobus</u> L.). The UMBS landscape was dominated by eastern hemlock (<u>Tsuga canadensis</u> (L.) Carr.), American beech (<u>Fagus grandifolia</u> Ehrh.), white pine, and red pine. Minor species common to both presettlement forests included bigtooth aspen, red maple (<u>Acer rubrum</u> L.), and red oak (<u>Quercus rubra</u> L.). A more detailed description of the presettlement forests of both areas can be found in Chapter 3.

The regions containing the study areas were deforested in the late nineteenth to early twentieth centuries (Gleason, 1923; Kilburn, 1957, 1960a,b; Benninghoff and Cramer, 1963; Whitney, 1987). Slashed-fueled wildfires swept over these landscapes in the years following logging, eliminating advanced reproduction and most remnant overstory individuals of the dominant presettlement species (Kilburn,

1957, 1960ab; Whitney, 1987). Additionally, the fires promoted vigorous vegetative-regeneration of aspen from rapidly spreading clonal root systems (Graham <u>et al</u>. 1963; Barnes 1966), which led, in turn, to the development of strictly even-aged forests (Graham <u>et al</u>. 1963). The Huron study area did not contain any remnant individuals of the dominant presettlement species. In contrast, remnant white pine and red pine were scattered throughout the UMBS study area (Chapter 3).

#### METHODS

# Plot selection and vegetation sampling

Vegetation was sampled on a series of plots located within five stands in the Huron forest and four stands at Stands within each landscape belonged to similar UMBS. ecological land classification units (following Barnes et al., 1982; Pregitzer and Barnes 1984). Selected stands met the following criteria: i) minimum size of 1 ha; ii) free from obvious disturbance since initiation; and  $\underline{iii}$ ) 0-5% slopes. The distance between stands within each landscape ranged from 1-4.5 km. Four circular plots were randomly located within each stand. Plot size was  $272 \text{ m}^2$  in the Huron forest and 475  $m^2$  at UMBS. A larger plot size was used at UMBS so that a similar number of overstory stems might be sampled as in the higher density Huron forest (see results). Plots were used as replicates in all statistical analyses. The species and diameter at breast height (dbh=1.4 m) of all stems  $\geq$  2.5 cm dbh were recorded on each plot.

Seedling (dbh< 2.5 cm) numbers were recorded in twelve 1  $m^2$  plots, spaced equidistantly at 3 m intervals along four opposing radii of each plot, beginning at the plot boundary. Seedlings were assigned to one of two height classes; < 1.5 m and  $\geq$  1.5 m.

# Destructive sampling

On each plot, one randomly selected bigtooth aspen, and all individuals  $\geq$  1.5 m tall of additional tree species, were destructively sampled to determine total heights, times of establishment, and rates of radial and height growth of selected stems. For species other than bigtooth aspen, only the tallest ramets were sampled from multi-stemmed genets. For bigtooth aspen, one individual from the dominant or codominant crown classes (most ramets were dominant or codominant) was randomly selected (rejecting ramets with internal decay) and destructively sampled on each plot. Sampling intensity for bigtooth aspen was much lower than for other species because little height variation was observed among dominant-codominant ramets within plots and little age variation was expected. The age distribution of sampled bigtooth aspen substantiated the latter expectation (see results).

On each plot, a subsample of individuals < 1.5 m tall was sampled by stratifying on species and 0.5 m height classes. Stems < 1.5 m tall were sampled primarily in an attempt to determine the age range of these stems on each

plot, particularly their maximum ages.

Stems were felled at 0.5 m or ground level (depending on size) and total heights were determined. Stem sections were cut at ground level from all larger individuals (generally those greater than 2.5 m in height). An additional section was removed at 1.4 m from all overstory individuals (dbh > 10 cm) for use in radial growth analysis. Additionally, all bigtooth aspen stems were marked at 0.25-m intervals from the base to 2 m and at 1-m intervals thereafter. Marking continued to the 1-m multiple closest to the end of the dominant leader. Stem sections were cut at each measurement interval up to a 3 cm diameter top. All destructive sampling was completed during summer and fall of 1990.

## Age determination

Small stems of deciduous tree species (generally those < 2.5 m tall) and the terminal leaders of bigtooth aspen were aged by counting the number of terminal bud scale scars preceding each height interval. Small stems of coniferous species (white pine and red pine) were aged by counting branch whorls. The accuracy of bud scale and branch whorl counts was checked by counting rings on basal and 0.25 m stem sections (typically the most difficult portion of the stem to age by these methods) on a subsample of stems under a dissecting microscope. Age determinations for the two methods seldom differed by more than  $\pm 2$  years and then only

on individuals > 2 cm basal diameter.

Basal stem sections of larger individuals were sanded to a smooth surface and wetted to aid ring examination. Ages of all sections were determined by counting ring number on at least two radii (typically a long and short axis on oblique-shaped stems) under a dissecting microscope. The oldest age of each section was recorded if the counts Precision of ring counting was assessed by differed. periodically recounting 20% of the stem sections from lots of 15-25 sections each. Recounts seldom differed by more than 1 year. Faint annual rings made accurate ageing of paper birch (Betula papyriferia Marsh.) impossible. All genets of this species were apparently of vegetative-origin (all multi-stemmed) and were probably of equivalent age as the sampled bigtooth aspen. Further, paper birch was not an important component on any of the sample plots (see results). American beech, white ash (Fraxinus americana L.) and balsam fir (Abies balsamea L.) were also rare in the sample plots (see results) and were excluded from analysis.

Terminal bud scale counts, branch whorl counts, and ages of basal stem sections were used to determine time of establishment for all sampled stems. Time of plot initiation (years before sampling) was based on the mean age of all individuals that established within the first 10 years of plot development. Time of understory reinitiation was defined as the plot age (years after plot initiation) after which at least two new individuals established every 5 years

for at least a 20 year period. For this study, establishment was defined as survival to the time of sampling. Unequivocal inferences cannot be made about the changing rates of natality or mortality that led to observed age distributions.

## Radial and height growth analysis

Annual ring widths were measured along one randomly selected radii (rejecting decayed or injured areas) on the 1.4 m stem sections of overstory stems (dbh >10 cm). Ring widths were measured to the nearest 0.1 mm using a dissecting microscope and ocular micrometer. For each stem, a standardized, dimensionless index of radial growth (ringwidth index) was derived by dividing the mean ring-width for the entire series into the actual ring-width at each year. Ring-width series were not detrended, as is often done in dendroclimatological studies (Fritts 1976), since there was <u>a priori</u> reason to remove age effects no from the chronologies. Mean chronologies were developed by averaging the ring-width indices of several individuals on each plot. The ring-width standardization prevented fast-growing individuals from dominating the mean chronologies (Veblen et al. 1991). Individual tree chronologies were averaged in an attempt to dampen any non-synchronous changes in radial growth patterns, while retaining any synchronous suppressions or releases that might reflect plot-level changes in resource availability during the course of forest

The mean chronologies were developed using development. several red oak and red maple on each plot. Subtle changes in resource availability within the matrix of bigtooth aspen ramets would be reflected best in the radial growth patterns of red oak and red maple, since these species are longlived, relatively more understory-tolerant than bigtooth aspen, and are known to respond to release with increased radial growth (Laidly 1990; Sander 1990; Walters and Yawney 1990). The number of individuals used to form the chronologies varied from 2 to 9 and depended on i) the number of genets of these species on a plot, ii) their age at 1.4 m (the goal was to extend chronologies as far back as possible without dropping individuals from the record), and iii) their total heights (individuals < 15 m in the Huron forest and < 13 m in the UMBS forest were typically suppressed so they were excluded from this analysis). Ringwidth indices from sampled bigtooth aspen were not used in the chronologies. These ramets always grew relatively rapidly, as might be expected for stems of a very intolerant species (Laidly 1990) that were in dominant-codominant crown positions at maturity.

The additional stem sections from the sampled bigtooth aspen were prepared and aged as described previously. The section ages were used to reconstruct 5-year height increment curves for each stem. In some instances interpolation of stem height at a given plot age was necessary since the stem sampling method controlled stem

height but not age. In these cases, the shapes of ageheight plots for the individuals involved were examined to insure accurate determination of heights at the 5-year plotages of interest.

## White pine seed-source characteristics

The distance to and diameter of all remnant white pine seed trees were measured for each UMBS plot. Remnant trees were easily seen after leaf-fall of bigtooth aspen. Potential remnant seed trees were restricted to a 130 m radius around the center of each plot. This was the distance to a sole remnant tree (within a 500 m radius) for a plot that contained a small amount of white pine regeneration. Large white pine could not be aged accurately because most individuals (from a subsample examined with an increment bore) had extensive internal stem rot. Instead, a remnant tree was defined as one > 45 cm dbh. The 45 cm diameter limit was based on two lines of evidence. First, nonpublished age-diameter data for white pine (UMBS data file) indicated that trees < 45 cm at the time of sampling in the current study would have predated bigtooth aspen by no more than 25 years. These individuals would have been too young to have reached reproductive maturity by the time of forest Second, sampling of white pine in the current initiation. indicated that maximum diameter study the of stems establishing at or soon after stand initiation was < 20 cm. Only one stand (four plots) contained any apparent remnant individuals with diameters greater than 20 cm but less than 45 cm.

Multiple regression was used to develop an exploratory model to examine the relationship between white pine seedsource characteristics and time of understory reinitiation for this species. The independent variables used in the model included i) distance to the closest potential seed tree, <u>ii</u>) mean distance to all potential seed trees, iii) total number of potential seed trees, and iv) mean basal area of all potential seed trees. The assumption associated with these variables was that plots in close proximity to several, large seed trees would have had а greater probability of early white pine establishment because of greater seed rain early in forest development. Mean basal area was used not only as а measure of potential reproductive output, i.e. larger trees more seeds, but also as a crude measure of timing of reproductive maturation. Larger diameter trees may not necessarily have been older than smaller diameter trees, however, they probably reached the size necessary for reproduction earlier than smaller trees. Ranked data were used in the regression analyses because of sample sizes and poor structure low of standardized residual plots. For all analyses, adjusted coefficients of multiple determination (Sokal and Rohlf 1981) are reported. There were too few plots with associated remnant red pine to conduct a similar regression analysis.

#### RESULTS

Forest composition and structure

The present-day forest composition and structure of the Huron and UMBS study areas are summarized in Table 4.1. Bigtooth aspen was the dominant overstory species in both forests. Minor overstory species found in both forests included red oak, red maple and paper birch. Red maple was virtually the only species regenerating in the Huron forest. White pine and red maple were both abundant as regeneration in the UMBS forest. Both overstory (dbh > 10 cm) basal area and density of the Huron forest were substantially higher than at UMBS. Sapling  $(2.5 \le dbh \le 10 cm)$  density was higher in the UMBS forest, while seedling densities were similar.

### Population age structures

The age-height distributions for all sampled individuals on the Huron and UMBS plots are shown in Figures 4.1 and 4.2. Recall that only one bigtooth aspen ramet was sampled per plot. Each plot contained an additional 15-35 bigtooth aspen ramets of similar age. In the Huron forest, an initial cohort of trees established within a 10-year period (Figure 4.1), beginning 65-70 years prior to sampling (see plot ages in Table 4.2). All plots were characterized by an obvious period of stem exclusion during which few or no surviving individuals of any species established (Figure

Species	Huron							
	Canopy <sup><u>a</u> m<sup>2</sup>/ha stems/ha</sup>		ns/ha	Sapling <u>b</u> stems/ha		Seedling <u>C</u> stems/ha		
Bigtooth aspen	30.3	$(2,1)^{d}$	638	(48)				•
Red oak	5.5	(1.0)	166	(29)	13	(6)	3625	(669)
Red maple	4.9	(0.6)	282	(28)	644	(89)	64833	(6522)
Black oak	0.5	(0.2)	14	(7)				
White oak	0.3	(0.2)	10	(5)			458	(260)
White ash	0.06	(0.06)	4	(4)	4	(4)	167	(97)
Paper birch	0.05	(0.05)	2	(2)			42	(42)
Black cherry	0.01	(0.01)	2	(2)	26	(9)	14583	(3813)
Totals	41.6	(2.0)	1117	(48)	686	(96)	83708	(8205)

Table 4.1. Present-day forest composition and structure of the Huron and UMBS study areas.

Table 4.1 (cont'd).

Species	UMBS					
	Canop m <sup>2</sup> /ha	y <u>a</u> stems/ha	Sapling <u>b</u> stems/ha	Seedling <sup>C</sup> stems/ha		
	d					
Bigtooth aspen	21.3 (1.2) <del>⊆</del>	560 (41)	4 (4)	573 (225)		
Red oak	2.5 (0.6)	67 (20)	82 (23)	4740 (635)		
Red maple	2.4 (0.4)	93 (23)	335 (69)	64687 (8805)		
Paper birch	0.9 (0.3)	46 (12)	54 (13)			
Red pine	0.9(0.4)	18 (10)	44 (20)			
White pine	0.6(0.2)	45 (15)	642 (127)	1562 (569)		
American beech	0.02(0.02)	3 (3)	17 (7)	104 (71)		
Balsam fir			3 (3)			
Totals	28.6 (1.5)	890 (44)	1180 (112)	71666 (8777)		

 $\frac{a}{Dbh} > 10 \text{ cm}; \frac{b}{2.5} \text{ cm} \le dbh \le 10 \text{ cm}; \frac{c}{dbh} < 2.5 \text{ cm}.$ Values are the means (<u>+</u> SE) of 20 observations in the Huron forest and 16 at UMBS.

Figure 4.1. Age-height distributions for all sampled stems on the 20 Huron plots. Individuals ≥ 1.5 m tall were completely sampled on each plot. Individuals < 1.5 m tall were subsampled. Note that each plot contained an additional 15-35 bigtooth aspen ramets of similar age as the sampled stem. Red oak and black oak are combined in the figure.

Figure 4.1





Figure 4.1 (cont'd).

Figure 4.2. Age-height distributions for all sampled stems on the 16 UMBS plots. Individuals ≥ 1.5 m tall were completely sampled on each plot. Individuals < 1.5 m tall were subsampled. Note that each plot contained an additional 15-35 bigtooth aspen ramets of similar age as the sampled stem. The red oak in the upper right corner of plot U15 was actually a individual from plot U16 that predated the remaining individuals on the plot by approximately 20 years.







		Huron		
Plot #	Overstory <u>1</u> m <sup>2</sup> /ha	Plot Age (yrs) mean <sup>3</sup> (max)	Understo: $\geq$ 1.5 m	ry <sup>2</sup> (stems/ha) ht 0-1.5 m ht
	A			
1	54.3 (83)∸	66 (70)	735	128785
2	44.8 (72)	67 (70)	74	46887
3	32.6 (71)	67 (68)	515	93210
4	40.9 (93)	64 (65)	2720	72941
5	32.1 (53)	66 (69)	478	37941
6	34.7 (59)	67 (69)	37	52537
7	31.1 (81)	67 (70)	1838	56703
8	35.9 (81)	65 (66)	919	42941
9	36.3 (85)	66 (67)	4154	66666
10	36.1 (64)	66 (66)	4411	90833
11	39.3 (72)	66 (70)	3272	46666
12	44.3 (66)	66 (70)	993	129166
13	46.5 (80)	65 (67)	662	107499
14	49.4 (78)	66 (67)	993	111666
15	38.3 (60)	65 (68)	0	175833
16	47.3 (80)	67 (69)	551	67500
17	65.0 (80)	66 (68)	257	66274
18	50.1 (58)	66 (67)	2316	104534
19	35.0 (41)	65 (70)	2757	87107
20	38.9 (88)	64 (66)	2794	48995

Table 4.2. Structural attributes of the Huron and UMBS plots.

Table 4.2 (cont'd).

UMBS					
Plot #	Overstory <u>1</u> m <sup>2</sup> /ha	Plot Age (yrs) mean <sup>3</sup> (max)	Understory <sup>2</sup> $\geq$ 1.5 m ht	(stems/ha) 0-1.5 m ht	
1	21.6 (75)	71 (75)	716	79187	
2	30.3 (88)	69 (72)	1221	40854	
3	26.3 (74)	72 (73)	1010	35833	
4	37.7 (76)	72 (75)	1116	54188	
5	27.0 (63)	71 (74)	1558	44166	
6	28.2 (84)	72 (73)	632	34167	
7	17.7 (87)	71 (73)	1179	100833	
8	20.6 (69)	71 (75)	526	22500	
9	32.7 (62)	76 (79)	1979	68354	
10	29.5 (89)	75 (82)	1179	79166	
11	25.7 (74)	81 (83)	1642	65833	
12	26.5 (68)	78 (81)	1726	159166	
13	30.8 (78)	67 (71)	2231	89187	
14	33.8 (77)	70 (73)	2968	99166	
15	29.4 (65)	71 (74)	1200	112500	
16	39.8 (71)	71 (73)	1326	58333	

 $\frac{1}{2}$ Stems > 10 cm dbh.  $\frac{2}{3}$ Stems establishing subsequent to the start of understory

reinitiation. <u>3</u>Mean age of all stems establishing within 10 years of plot initiation.

 $\frac{4}{2}$  Plot total (relative basal area of bigtooth aspen).

4.1). Mean ( $\pm$ 1 sd) time to understory reinitiation from the time of plot initiation was 34.5 (3.8) years. The near synchronous timing of understory reinitiation on all plots is reflected in the low coefficient of variation for this event (11%). Note that in only one instance was a stem < 1.5 m tall older than the oldest understory stem  $\geq$  1.5 m tall, and then only by 1 year (plot H7, Figure 4.1). Plot-level densities for stems establishing subsequent to understory reinitiation are shown in Table 4.2.

the UMBS forest, most In overstory individuals established within a 10-year period (Figure 4.2), beginning 71-83 years prior to sampling (see plot ages in Table 4.2). Most plots were characterized by an obvious period of stem exclusion, however in several plots (U1, U13-U16) this period was less-obvious or non-existent (Figure 4.2). Mean  $(\pm 1 \text{ sd})$  time to understory reinitiation was 24.9 (12.0) years. Understory reinitiation in the UMBS forest occurred significantly earlier than in the Huron forest (t-test for unequal variances: t=-3.05, df=17, P=0.007), but variability for this event at UMBS was high, as reflected in the high coefficient of variation (48%). Note that in the UMBS forest no stems < 1.5 m tall were older than the oldest understory stem  $\geq$  1.5 m tall.

In some Huron plots, and most UMBS plots, there was an increase in establishment frequency beginning 30-40 years after plot initiation (Figure 4.2). The timing of this increase was used to define a more conservative definition

of understorv reinitiation. Continuous understory establishment was defined as the number of years until at individual established every year, or least one two individuals established every 2 years, for at least a 10year period. Determination of the timing of this event was not biased by incomplete subsampling of stems < 1.5 m tall since the maximum ages of these individuals never exceeded, and, in fact, rarely approached, the age of individuals  $\geq$ 1.5 m tall that typically defined the start of continuous understory establishment (note that this period was defined exclusively by stems < 1.5 m tall on plots H2, H6 and H15 because of a lack of stems  $\geq$  1.5 m tall; Table 4.2).

In the Huron forest, mean time to continuous understory establishment, from plot initiation, was 36.8 (3.5) years (C.V.= 9%). The mean  $(\pm$  se) difference between time to understory reinitiation and continuous establishment of -2.3 (0.5) years was low, but significantly different from zero (one-tailed Wilcoxon's rank difference test:  $T_{\underline{s}}$ = 36, n=20, P< 0.005). Mean (+1 sd) time to continuous establishment in the UMBS forest was 33.8 (7.1) years (cv=21%). The mean (+ se) difference between time to initial understory reinitiation and continuous establishment of -8.8 (2.1) years was significantly different from zero (one-tailed Wilcoxon's rank difference test: T<sub>S</sub>= 1, n=16, P< 0.005). Non-normal residual distribution and heterogeneous variances prevented statistical comparison of time to continuous understory establishment between the Huron and UMBS forests.

Failure to meet these assumptions was attributed to the presence of a single outlier among the UMBS plots (plot In this plot, continuous establishment occurred much U15). earlier than in the remaining 15 UMBS plots (13 years versus a mean  $(\pm 1 \text{ sd})$  of 35.1 (4.6) years). After excluding plot U15 from the analysis, variances were homogeneous (but residuals were still distributed non-normally), and the mean time to continuous understory establishment was not significantly different between the Huron and UMBS forests (Wilcoxon two-sample test:  $U_s = 181$ , n= 20 and 15, P >0.20). Also, variability in the timing of continuous understory establishment in the remaining 15 plots at UMBS was low (C.V.=13%).

Bigtooth aspen heights and height growth during understory reinitiation

In the Huron forest, the mean  $(\pm 1 \text{ sd})$  height of the sampled bigtooth aspen at the time of understory reinitiation was 15.5 (2.1) m, while mean height at the time of continuous understory establishment was 16.5 (1.8) m. These heights were 63 (6)% and 67 (5)% of total heights at the time of sampling, respectively. The analogous heights and percentages in the UMBS forest were 8.4 (3.8) m and 39 (17)% and 10.9 (2.9) m and 50 (13)%, respectively. For the five UMBS plots relatively with early understory reinitiation times (U1, U13-16) mean (±1 sd) heights and percentages at times of initial and continuous understory establishment were 3.6 (1.3) m and 16 (7)% and 8.6 (4) m and 38 (17)%, respectively. The sampled bigtooth aspen in the UMBS forest ranged from 15-35 years old at the time of understory reinitiation. In both forests, the sampled bigtooth aspen were, at most, 35 years old at the time of continuous understory establishment.

Height increment over time for the sampled bigtooth aspen are shown in Figure 4.3. The overall trend in the Huron forest was one of early culmination in height increment, 20-25 years after forest initiation, followed a large decline after this period. Both understory reinitiation and continuous understory establishment occurred subsequent to the decline. The height increment pattern of aspen in the UMBS forest shows an initial early decline followed by a secondary increase, 40-45 years after plot initiation, and a gradual decrease thereafter. The start of continuous understory establishment typically coincided with the secondary peak in height increment. Overall, height growth rates of bigtooth aspen at UMBS were low and only approached those of Huron bigtooth aspen early in forest development.

# Patterns of radial growth and understory reinitiation

Ring-width chronologies for the Huron plots are shown in Figure 4.4. The chronologies are missing for plots H17-H20 because the stems sections from these plots were inadvertently destroyed prior to measuring radial growth. The most obvious and consistent feature of the Huron

Figure 4.3. Five-year height increment curves for the sampled bigtooth aspen in each forest. Values are means  $\pm$  se. Sample size for the Huron forest is 20. Sample size for the UMBS forest is 16 (14 at 5-10 years).

Figure 4.3



Figure 4.4. Ring-width indices for the Huron plots. Each chronology is the mean for the sample size indicated in the upper right corner of each graph. The doted line at a ring-width index of 1.0 is the standardized for the entire chronology (see text mean for derivation of ring-width indices). The dashed line in cumulative each graph is the establishment distribution for advanced regeneration (stems  $\geq$  1.5 m tall). The beginning of establishment each distribution marks the start of understory reinitiation (at least two stems establishing every five year for a minimum of 20 years; this is indicated by an  $\underline{U}$  for plots without advanced regeneration). The graph marks the start of continuous <u>C</u> in each establishment understory (at least one stem establishing every year, or two every two years, for a minimum 10 years).



124

Figure 4.4


Figure 4.4 (cont'd).

chronologies was a marked increase in mean ring-width index that occurred 15-25 years after plot initiation (Figure 4.4). At their peak, these growth rate increases averaged 90% and lasted 5 to 10 years. In most plots, the initial growth rate increase followed a period of reduced radial growth that lasted approximately 5 years. Other lessobvious, but fairly consistent features of the Huron chronologies included increases in mean ring-width indices that occurred 30-35 years after plot initiation and again 45-50 years after plot initiation. At their peak, these increases averaged 60-65%, lasted a short period of time (5-10 years) and typically followed a short period of reduced growth (lasting 5 years or less).

Timing of understory reinitiation on each Huron plot is shown relative to the radial growth patterns in Figure 4.4. The dashed line in each graph is the cumulative establishment distribution for advanced regeneration (stems  $\geq$  1.5 m tall that established subsequent to the beginning of understory reinitiation). The beginning of each cumulative establishment curve marks the year (plot age) that understory reinitiation began. The timing of understory reinitiation on three plots with little or no advanced regeneration (plots H2, H6, and H15; Figure 4.4) is indicated by an  $\underline{U}$  on the graph. Also, the timing of continuous understory establishment, regardless of stem height class, is indicated by a <u>C</u> on each graph. Typically, understory reinitiation and continuous understory

establishment both began within a 5-year period immediately following the moderate radial growth increase that occurred 30-35 years after plot initiation (Figure 4.4). The one exception was plot H6. On this plot understory reinitiation  $(\underline{U})$  began almost 10 years after the 30-35 year growth rate and continuous understory establishment increase, (C) occurred concurrently with a second moderate growth increase beginning 50 years after plot initiation. The shapes of the cumulative establishment distributions for advanced regeneration are worth examining because they represent the establishment patterns of individuals that are presumably most likely to recruit to dominant canopy positions. On most plots, the slopes of the establishment distributions were high initially, or they increased soon after the start of understory reinitiation in concert with increases in the ring-width indices.

A consistent feature of most UMBS chronologies was an increase in mean ring-width index approximately 35-40 years after plot initiation (Figure 4.5). At their maximum, these releases averaged around 83% and persisted for at least 15 years. Radial growth rates prior to release were either low for extended periods of time (plots U1-U2), or were slowly increasing for 15-20 years (plots U5, U7-U8, U14, U16). Some of the chronologies show marked decreases in radial growth 15-20 years after plot initiation (plots U6, U8-U12, U16). The lack of this feature in other chronologies probably reflects actual growth patterns of the sampled Figure 4.5. Ring-width indices for the UMBS plots. Each chronology is the mean for the sample size indicated in the upper right corner of each graph. The doted line at a ring-width index of 1.0 is the standardized mean for the entire chronology (see text for derivation of ring-width indices). The dashed line in each graph is the cumulative establishment distribution for advanced regeneration (stems  $\geq$  1.5 m beginning establishment tall). The of each distribution of marks the start understory reinitiation (at least two stems establishing every five year for a minimum of 20 years). The  $\underline{C}$  in each graph marks the start of continuous understory establishment (at least one stem establishing every year, or two every two years, for a minimum 10 years).



129

Figure 4.

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trees (plots U1, U15), while in others it probably reflects the short lengths of the chronologies (plots U4, U13-U14).

In the UMBS plots, understory reinitiation was not associated consistently with any obvious feature of the ring-width chronologies (Figure 4.5). In contrast, continuous understory establishment on most plots began concurrently with or soon after the radial growth rate increase that occurred 35-40 years after forest initiation (Figure 4.5). A exception to this trend was plot U15. As noted previously, continuous understory establishment on this plot began 13 years after plot initiation, but this did coincide with the start of a 150% ring-width increase that began 10 years after plot initiation and persisted for over years (Figure 4.5). Unfortunately, the ring-width 15 chronology for this plot did not begin early enough to adequately assess growth patterns much before this release. On most plots, large increases in the slopes of the cumulative establishment distributions for advanced regeneration often coincided with the start of continuous understory establishment and the increases in ring-width indices (Figure 4.5).

#### White pine seed-source characteristics

White pine was the dominant tree species regenerating on most of the UMBS plots (Figure 4.2). Notable exceptions included plots U2-U4 and U7 which were dominated by red maple, and plot U14 which had large amounts of both white

pine and red maple. On most plots, white pine was also the first species to begin establishing in the forest understory, including plots U7 and U14. The remnant white pine seed trees provided an opportunity to examine the relationship between seed-source characteristics and the timing of understory reinitiation for this species.

Differences in white pine seed-source characteristics accounted for a large and significant proportion of variation in timing of understory establishment among plots  $(r^2_{adj} = 0.82; see= 1.748; P= 0.0004)$ . This analysis excluded plots U2 and U3 since, by definition, initial understory reinitiation of white pine had not occurred on these plots. Differences in seed-source characteristics accounted for a low and only marginally significant proportion of variation in timing of continuous understory establishment among plots  $(r_{adi}^2 = 0.53; see= 2.468; P= 0.052)$ . Note that this analysis excluded not only plots U2 and U3, but also plots U4 and U7, since continuous understory establishment of white pine, by definition, had not yet occurred on these plots. The model for initial understory reinitiation was reanalyzed after excluding plots U4 and U7, as well as plots U2-U3. The results were marginally improved over the results that included plots U4 and U7  $(r_{adj}^2 = 0.87; see = 1.313; P =$ 0.0008).

The regression results suggest that timing of white pine understory reinitiation, and hence the length of time new stem establishment was prevented for this species, may

have been influenced by remnant seed-source characteristics. Initial establishment occurred earlier on plots in close proximity to several large seed trees, relative to plots with less-favorable seed-source characteristics. In contrast, the influence of remnant seed-source characteristics on the timing of continuous understory establishment of white pine appeared to be much weaker, suggesting additional controls on this event.

# DISCUSSION

Many of the studies that have documented both the stem exclusion and understory reinitiation phases of even-aged forest development have been based either on results from one or few replicate plots (Oliver et al. 1985; Roberts and Richardson 1985; Abrams and Nowacki 1992) or have pooled data from replicate samples into a single forest-level analysis (Bloomberg 1950; Oliver et al. 1985; Harcombe 1986; Sharik et al. 1989; Segura and Snook 1992). These methodologies are inappropriate for assessing the variability and repeatability of developmental patterns within and among landscapes characterized by homogeneous site conditions and disturbance histories. Characterizing the repeatability of developmental patterns may be an important first step in identifying the mechanisms that control stem exclusion and understory reinitiation in various forest-types. For example, Peet and Christensen (1987) argue that understory reinitiation in most even-aged

forests is triggered by an increase in resource availability following density-independent mortality of mature overstory individuals late in even-aged development. In forests dominated by bigtooth aspen, complete overstory deterioration can progress rapidly (< 10 years; Graham <u>et</u> <u>al</u>. 1963; Laidly 1990). If understory reinitiation in these forests is triggered by mortality of senescent canopy dominants then it should begin synchronously across space and it should also occur late in even-aged development.

In the current study, the population age structures of surviving individuals on plots within the Huron landscape reflected synchronous developmental patterns. An initial cohort of trees established within a 10-year period, new establishment was curtailed for approximately 35 years, after which time individuals again began to establish in the forest understory. In contrast, the developmental patterns within the UMBS landscape were more variable. An initial cohort of trees established within a 10-year period, but the length of a stem exclusion period was highly variable (0-35 years). Synchronous development was a characteristic of the UMBS forest only under a more restrictive definition of continuous understory establishment.

In both forests, understory reinitiation and increases in establishment frequency began when the dominant bigtooth aspen were at most 67% of their total heights at maturity (and often much less) and no more than half of their maximum age in the Great Lakes region (Graham <u>et al.</u> 1963). The

mechanism triggering understory reinitiation in these forests was not increased resource availability occurring in response to overstory deterioration late in even-aged development, despite the synchrony of development in the Huron forest. The results do suggest that an increase in resource availability occurring relatively early in forest development may have influenced the timing of understory reinitiation.

Understory reinitiation was hypothesized to be associated with radial growth releases in surviving overstory stems; with both events occurring in response to resource availability increases in following natural thinning within the bigtooth aspen overstory. Indeed, on most plots, the bulk of new understory establishment typically began soon after moderate to large radial growth releases that occurred 30-35 years after forest initiation. The releases may not have occurred in response to natural thinning, however, concentrated waves of density-dependent mortality, subsequent increases in resource availability, and growth releases of surviving stems are believed to be characteristic developmental features of most even-aged forests (Oliver and Larson 1990). For example, Graham et al. (1963. p. 90-94) report that two or three waves of natural thinning occur within the first 40 years of aspen forest development. Short periods of reduced growth and subsequent releases within the aspen overstory were attributed to subtle changes in resource availability occurring im

response to the mortality waves. As in the current study, the releases reported by Graham <u>et al</u>. (1963) were of lesser magnitude and shorter duration than those that typically occur following a major canopy-opening disturbance (for examples of the latter see Lorimer 1980, 1983, 1984).

new understory establishment If the majority of response occurred in increased to light availability following mortality of suppressed stems then, by default, crown growth of the remaining overstory individuals must have been inadequate to maintain complete canopy closure. It has been hypothesized that canopy closure in even-aged forests is reached asymptotically early in the course of stand development, and decreases thereafter (Zeide 1987, 1991), because of the combined influence of natural thinning and a reduced rate of crown expansion in surviving individuals. The height increment patterns for the few sampled bigtooth aspen ramets did suggest that crown expansion rates may have been low at times coincident with understory reinitiation (Figure 4.3). In the Huron forest, height increment dropped substantially just prior to understory reinitiation. At UMBS, bigtooth aspen height increment actually increased slightly at a time coincident with continuous understory establishment, however, overall height growth rates were always low in this forest, except for early in forest development.

Low height growth rates of bigtooth aspen at UMBS, combined with the low overstory basal area of this forest

(Table 4.1), may indicate that light limitation was not the primary factor leading to stem exclusion. Low basal areas are characteristic of aspen-dominated forests on dry-mesic and nutrient-poor sites in the Great Lakes region (Roberts and Richardson 1985; Scheiner et al. 1988; Laidly 1990; Chapter 2). Previous studies have shown that these forests may lack a stem exclusion period, presumably because incomplete canopy closure leads to continuous resource availability in the understory (Roberts and Richardson 1985; Chapter 2). The results of the current study demonstrate that stem exclusion, or substantially reduced frequency of establishment, can be a characteristic feature of these forests, despite low overstory basal areas. In fact, the UMBS plots that had age distributions suggesting definite periods of stem exclusion were also those that had some of the lowest current basal areas in the forest (U7-U8, U11-U12; Table 4.2).

If light is not limiting in the forest understory, changes in the ability of root systems to preempt soil resources during the course of forest development may be a more important factor influencing understory establishment. Changes in rates of root growth may be a particularly important factor influencing understory establishment in aspen-dominated forests given the taxon's ability to saturate soil space rapidly following fire through growth of clonal root systems (Stoeckeler and Macon 1956; Zahner and Crawford 1965; Barnes 1966, 1969; Graham et al. 1963; Kemperman and Barnes 1976; Scheiner <u>et al</u>. 1988). Limited research suggests that a clone's inter-ramet root system deteriorates progressively during forest development, with most ramets having independent root systems by an early age (for example 32 years; Ruark and Bockheim 1987). This gradual deterioration may push soil resource availability above some minimum threshold required for new establishment in the forest understory.

In the current study, the repeatable association between understory reinitiation and releases in radial growth in the overstory suggests that resource limitation was an important factor leading to stem exclusion. However, the patterns of white pine establishment at UMBS suggest that changes in seed availability during the course of forest development may have also influenced the timing of new understory establishment. On some UMBS plots, initial establishment of white pine occurred soon after radial growth releases in the overstory, while on other plots initial establishment began prior to any obvious radial growth release. The variation in timing of initial white pine establishment was significantly related to remnant seed-source characteristics. Initial establishment occurred earlier on plots in close proximity to several large remnant white pine seed trees, sometimes prior to any radial growth This relationship suggests that the timing of release. white pine understory reinitiation may have depended on the maturation or proximity of a local seed-source. A similar

argument has been used to account for differences in initial establishment times of white pine in other bigtooth aspendominated forests at UMBS (Sharik et al. 1989). However, in the current study, there was a correspondence between large increases in the frequency of white pine establishment, subsequent to understory reinitiation, and increases in radial growth rates of overstory red maple and red oak. Additionally, the relationship between timing of continuous white pine establishment and remnant seed-source characteristics was weak. A similar increase in white pine establishment frequency, beginning 46 years after forest initiation, was found in the 73 year-old bigtooth aspendominated forest examined by Sharik et al. (1989; see their Figure 1).

These results suggest that timing of new establishment of white pine may have been influenced by an interaction between changing resource levels in the forest understory and seed availability. Limited early establishment of white pine may have occurred on plots that received substantial seed during input from remnant trees early forest development, however the bulk of new establishment may not have occurred until resource levels in the forest understory survival, possibly following became favorable for а mortality wave within the bigtooth aspen-dominated overstory. Most forests probably contain a limited number of safe establishment sites (sensu Harper 1977) even during the peak of stem exclusion. Saturation of an area with seed

would insure that all of these sites are occupied. An alternative explanation for the establishment patterns of white pine is that increases in resource availability actually hastened the reproductive maturation of seed trees that had either established immediately following disturbance or survived as advanced regeneration from the pre-disturbance forest. A near-synchronous seed-source maturation, acting alone or in combination with improved resource levels in the forest understory, could have led to the large increases in white pine establishment frequency that occurred on most plots.

The establishment patterns on plots with hardwooddominated understories (predominantly red maple) also suggest that an interaction between resource availability and seed-source maturation may have influenced the timing of understory reinitiation. In both forests, the stem exclusion periods for red maple always lasted 30-40 years. This delay in new red maple establishment in aspen-dominated forests has been attributed to low seed availability prior to reproductive maturation of a post-disturbance cohort of sprout-origin trees (Roberts and Richardson 1985; Sakai et Indeed, observations on mature red <u>al</u>. 1985; Sakai 1990). maple (and red oak) in the Huron forest (Chapters 3 and 6) and at UMBS (Roberts and Richardson 1985; Sakai et al. 1985; Scheiner et al. 1988; Chapter 3) do indicate that many overstory individuals were of sprout-origin. Presumably, if a mature red maple seed-source had existed early in the

development of the UMBS forest, some individuals of this relatively understory-tolerant species (Walters and Yawney 1991) would have established at least as early as lesstolerant white pine (Wendel and Smith 1990). While understory reinitiation on plots with red maple-dominated understories may have been dependent on maturation of local seed-sources, new understory establishment of this species typically began following a radial growth release in the overstory; the repeatability of this pattern suggests that it was more than coincidence. As with white pine at UMBS, the correspondence between new understory establishment of red maple and radial growth releases in the overstory suggests that increases in resource availability led to decreased mortality of new stems. Reproductive maturation of red maple seed-sources and the increases in resource availability that led to new establishment may have occurred at similar times simply by chance, or again, it is possible that increases in resource availability actually hastened the maturation of local seed-sources.

## SUMMARY AND CONCLUSIONS

Quantification of variability and repeatability in forest development patterns is an essential first step to developing a comprehensive mechanistic understanding of stem exclusion and understory reinitiation in even-aged forests. The current study provides this first step for a forest-type that has been understudied from a stand development

perspective. The results from the Huron and UMBS landscapes indicate that bigtooth aspen-dominated forests do follow a pattern of development believed to be characteristic of most forests that initiate following major disturbance (Oliver 1981, Peet 1981, Peet and Christensen 1987). Rapid initial cohort establishment, stem exclusion, and understory reinitiation were repeatable features of the age these forests, both within and distributions of among landscapes. While the bulk of regeneration in the forest understory began to establish at near synchronous times within each forest, there was some variation in the timing of early understory reinitiation at UMBS. The sampling scheme used allowed this variation to be detected. For example, if research at UMBS had been restricted to the one stand containing plots U13-U16, there would have been little reason to believe that a true stem exclusion period was a characteristic feature of bigtooth aspen forest development. The results also indicate that understory reinitiation was not triggered by mortality of dominant overstory stems late in even-aged development. The timing of understory reinitiation may have been influenced by an interaction between increased resource availability, possibly in response to natural thinning, and maturation of local seedsources. The factors controlling stem exclusion and understory reinitiation may be even more complex than recent overviews of forest development suggest (Oliver and Larson 1990; Peet and Christensen 1987), since these treatments

have largely ignored the potential influence of seed-source on new establishment. These results suggests that there is still more to be learned about even-aged forest development, particularly with respect to the mechanisms that control stem exclusion and understory reinitiation. The patterns detected in this study will be useful for designing the experimental studies that are needed to correctly identify these mechanisms.

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#### CHAPTER 5

# THE VERTICAL DEVELOPMENT OF EARLY SUCCESSIONAL FORESTS IN NORTHERN LOWER MICHIGAN

#### ABSTRACT

(1) Differences in height growth rates are characteristic of tree species that differ in understory tolerance and relative successional status. Less-tolerant species have greater juvenile height growth rates than more-tolerant species and thus, in a mixed-species forest, the former gain an early competitive advantage after a stand-initiating disturbance. Species-level height stratification is the predicted outcome under this differential growth rate model.

(2) Silvicultural evidence suggests that a species-level differential growth rate model of even-aged forest development is idealistic since height stratification among species differing in understory tolerance and relative successional status is not always consistently expressed within an even-aged forest. In fact, individuals of relatively tolerant species may achieve heights and height equaling those of less-tolerant species. growth rates Stratification may fail to develop if individuals of a relatively tolerant species are competitively uninhibited, released during the course of forest development, establish a few years earlier than less-tolerant species, are present as advanced regeneration, or are of vegetative-origin.

The establishment and height growth histories of three (3) tree species differing in understory tolerance and relative successional status were examined within two forests in northern Lower Michigan, U.S.A. Objectives of the study included: i) determining if species height stratification paralleling understory tolerance was a characteristic of these forests; ii) assessing the degree of height variation within species populations; <u>iii</u>) determining if species age distributions. changes in individual competitive environments, or regenerative origin influenced population height structures; and iv) assessing the degree to which height structure in these forests deviated from that expected under a species-level differential height growth rate model.

In both forests, Populus grandidentata, an intolerant, (4)early successional species was typically taller than Quercus rubra, a mid-tolerant, relatively later successional species, which in turn was taller than <u>Acer</u> rubrum, а later successional species. tolerant, However, within Quercus and Acer populations, heights were often highly variable, with some individuals equaling the heights of Populus. Age differences had no influence on height patterns either among or within species populations. Differential mortality contributed to the development of stratification since many suppressed Populus had died by the time of sampling, where as many slowering growing Quercus and Acer had survived.

(5) Growth rate differences among surviving stems determined species stratification patterns and height variation within populations. Populus typically outgrew both Quercus and Acer, however, some individuals of the latter two species had height growth rates, including juvenile growth rates, equvilent to Populus. Most Quercus and Acer appeared to be of vegetative-origin, as were all Populus ramets. For individuals of the former two species, potential juvenile height growth rates were likely greater than that of true seedlings, thus allowing some individuals to match growth rates of Populus. Stochastic variation in competitive pressure within the matrix of Populus ramets, or variation in competitive ability of individual genets, likelv contributed to height growth rate variation within Quercus and Acer populations.

(6) The root systems of Populus proliferated following the fires that initiated the forests examined, quickly saturating stands with rapidly growing ramets. In contrast, new Quercus and Acer ramets were restricted to the locations of remnant stumps. Populus numerically dominated the forests because a large proportion of growing space was occupied by its root systems and ramets, relative to <u>Quercus</u> and <u>Acer</u>. Vertical domination by Populus was apparently the result of competitive inhibition of most, but not all, <u>Quercus</u> and Acer, not because of inherent, species-specific differences juvenile height growth rates. in This suggests that

numerical dominance by <u>Populus</u> was sufficient in itself to limit height growth rate of most <u>Quercus</u> and <u>Acer</u> sprouts and lead to species-level vertical stratification.

## INTRODUCTION

Physiologically- or morphologically-based differences in height growth rates, particularly juvenile growth rates, are characteristic of tree species that differ in understory tolerance and relative successional status (Loach 1970; Drury & Nesbitt 1973; Marks 1975; Bazzaz 1979; Bormann and Likens 1979, pp.115-128; Canham & Marks 1985; Tilman 1985, 1988, 1990; Kozlowski, Kramer & Pallardy 1991, pp. 100-102). Species-specific growth rate differences are thought to be expressed even in environments with increased resource availability; for example, following a stand-initiating disturbance (Marks 1975; Bormann & Likens 1979, p. 125; Canham & Marks 1985, their Figure 1). Under this view, lesstolerant species should have an initial advantage (sensu Harper 1977) over more-tolerant species early in even-aged forest development because of inherently faster juvenile height growth rates, and would thus achieve competitive (vertical) superiority quickly following a stand initiating disturbance.

Indeed, species height stratification paralleling accepted rankings of understory tolerance and relative successional status is a common characteristic of many evenaged forests (Marquis 1967, 1981; Oliver 1978; Stubblefield & Oliver 1978; Bormann & Likens 1979; Wierman & Oliver 1979; Hibbs 1983; O'Hara 1986; Kelty 1986; Larson 1986; Clatterbuck & Hodges 1988; Foster 1988; Hix & Lorimer 1990; Oliver & Larson 1990). However, silvicultural studies have shown a population-level, differential growth rate model to be idealistic since stratification is often inconsistently expressed within an even-aged stand. In fact, the height range within populations of more-tolerant species can be quite wide, with some individuals attaining heights and height growth rates that equal or exceed those of lesstolerant species (Cayford 1957; Stubblefield & Oliver 1978; Oliver 1980; Guldin & Lorimer 1985; Kelty 1986; Hix & Lorimer 1990).

Stratification may fail to develop when relative spacing between individuals differing in understory tolerance is large (Cayford 1957; Stubblefield & Oliver 1978; Wierman & Oliver 1979; Guldin & Lorimer 1985; Smith 1986; Oliver, Clatterbuck & Burkhardt 1990; Oliver & Larson 1990; Shainsky & Radosevich 1992) or when the competitive environment of an initially suppressed individual of a species during tolerant improves the course stand development (e.g. see Deal, Oliver & Bormann 1991). Facing less resource-limitation, individuals of initially slower growing species may be able to catch up to individuals of species with faster juvenile growth rates. Individuals of tolerant species may maintain early height growth rates comparable to less-tolerant species if relative heights of the former initially exceed that of the latter; for example, when the tolerant species is initially present as advanced regeneration (Marquis 1981; Guldin & Lorimer 1985; Kelty 1986; Foster 1988; Deal, Oliver & Bormann 1991), or when it

establishes several years earlier than a less-tolerant species (Newton, El Hassan & Zavitkovski 1968; Stubblefield & Oliver 1978; Chapter 2). By definition, such forests would still be considered even-aged (Smith 1986). Regenerativeorigin may also influence height relationships since sprouts of hardwood species often have an initial growth advantage over seedlings of the same species (Jensen 1943; Wilson 1968; Oliver 1978; Beck & Hooper 1986). Thus, stratification may be less likely to develop in a forest comprised predominantly of sprout-origin individuals. Given the potential for compensation of differences in speciesspecific in juvenile height growth rates, through the mechanisms outlined above, the expression of stratification within a particular forest may depend on stand structure, regenerative-origin, or population age distributions. Few studies have assessed the influence of these compensating mechanisms on the development of vertical structure in evenaged forests.

This study examined the height and age structures of three tree species differing in understory tolerance and relative successional status in two mature <u>Populus</u> <u>grandidentata</u> Michx. (bigtooth aspen)-dominated forests in northern Lower Michigan. These forests are typically viewed as even-aged, having initiated following region-wide logging and repetitive slashed-fueled wildfires at the turn of twentieth century (Kilburn 1957, 1960; Graham, Harrison & Westell 1963; Roberts & Richardson 1985). The fires promoted

vigorous vegetative-regeneration of <u>Populus</u> from rapidly (Barnes spreading clonal root systems 1966). Initial observations indicated that Quercus rubra L. (red oak) and Acer rubrum L. (red maple) were the only additional tree consistent numerical species of importance in the overstories of the particular forests studied. Limited evidence suggests that many <u>Quercus</u> and <u>Acer</u> in mature Populus-dominated forests may also be of vegetative-origin, having regenerated after fire from stumps remnant from the predisturbance forest (Graham, Harrison & Westell 1963; Roberts & Richardson 1985). The three species differ in understory tolerance and relative successional status; from very intolerant, early successional Populus, to midtolerant, relatively later successional Quercus, to tolerant, later successional Acer (Spurr & Barnes 1980). Objectives for the study included: (<u>i</u>) determining if species height stratification paralleling understory tolerance occurred in these forests; (ii) assessing the degree of variability in heights within species populations; (iii) determining if age differences, regenerative-mode, or changes in an individuals competitive environment had any influence population height structures; on and (iv) assessing the degree to which vertical structure in the forests examined was accounted for by a developmental model emphasizing species-specific differences in juvenile height growth rates.

# STUDY LOCATIONS

Research was conducted within the Huron-Manistee National Forest (Huron) in northeastern Lower Michigan (latitude 44° 15' to 45° 00' N, longitude 83° 15' to 84° 45' W) and the University of Michigan Biological Station (UMBS) in the extreme northwestern portion of Lower Michigan (latitude 45° 40 N, longitude 84° 40' W). The two study areas are separated by approximately 110 km. Surficial geology of both study areas consisted primarily of deep outwash sands overlaying till deposits (Cooper, 1981; Padley, 1989). Soils throughout the majority of both study areas were classified as Entic Haplorthods (Cooper, 1981; Lapin, 1990; Soil Conservation Service, 1991; Michigan State University, Forestry Department data file). Detailed descriptions of the physiographic and climatic settings of the two study areas are found in Chapter 3.

Overstory composition of the two study areas was similar (Chapter 3). Mean relative density of <u>Populus</u> was approximately 60% at both locations. Mean relative densities of <u>Quercus</u> and <u>Acer</u> were 15% and 25%, respectively, in the Huron forest, and 8% and 10%, respectively, at UMBS. Additional overstory species that occurred infrequently in some of the UMBS plots included <u>Pinus resinosa</u> Ait., <u>Pinus strobus</u> L. and <u>Betula papyrifera</u> Marsh. Mean ( $\pm$  SE) total basal area and total density were both substantially higher in the Huron forest ( $41.6\pm2.0$  m<sup>2</sup>/ha and  $1117\pm48$  stems/ha, respectively), than at UMBS ( $28.6\pm1.5$  m<sup>2</sup>/ha and  $890\pm44$  stems/ha, respectively).

#### METHODS

Stand and plot selection

Populus, Quercus, and Acer population structures were examined within five stands at Huron and four stands at UMBS. Stands were selected from larger data pools at both locations (Lapin, 1990; Michigan State University, Forestry Department data file). All stands within a study area belonged to similar ecological land classification units (following Barnes et al., 1982; Pregitzer & Barnes 1984). Selected stands met the following criteria: (i) minimum size of 1 ha: (ii) free from obvious disturbance since initiation; and (iii) 0-5% slopes. The distance between stands within each study area ranged from 1-4.5 km.

Four circular plots were randomly located within each Plot size was 272 m<sup>2</sup> at Huron and 475 m<sup>2</sup> at UMBS. stand. Α larger plot size was used at UMBS so that a similar number of <u>Quercus</u> and <u>Acer</u> stems might be sampled as in the higher density Huron forest. The only criterion for plot selection was that, if possible, at least one overstory (dbh > 10 cm) Quercus and Acer genet occur in each plot. Given this criterion, plots were never rejected because of a lack of Acer. Initial locations for two of the 36 plots were rejected because of a lack of <u>Quercus</u>. The location of one of these plots was retained since an additional randomly selected plot did not contain any Quercus. Plots, rather than stands, were used as replicates in all subsequent

statistical analyses. Replicating on plots was justified since sampling was conducted within forests landscapes characterized by relatively homogeneous composition, physical site characteristics, and disturbance history. Stands were simply subjective units defined by harvesting patterns or road locations within each landscape and not on any obvious criterion which may have influenced overstory development.

## Stem sampling

On each plot, selected <u>Populus</u> and all <u>Quercus</u> and <u>Acer</u> at least 1.5 m tall were destructively sampled as part of a related study of stand development. This paper reports on the development of the initial, post-disturbance cohorts of <u>Populus</u>, <u>Quercus</u> and <u>Acer</u> at each study location. The youngest <u>Quercus</u> and <u>Acer</u> in these cohorts established several decades prior to the next oldest individuals of the species (see Chapter 4).

For <u>Quercus</u> and <u>Acer</u>, only the tallest ramets were sampled from multi-stemmed genets. For <u>Populus</u>, one individual from the dominant crown class (all ramets were dominant or codominant) was randomly selected (rejecting decaying ramets) and destructively sampled on each plot. Sampling intensity for <u>Populus</u> was much lower than for other species because little height variation was observed within a plot and little age variation among ramets was expected. Both total heights of additional <u>Populus</u>, estimated with a clinometer, and ages of the sampled <u>Populus</u>, substantiated these expectations (see Results).

All sampled stems were felled at 0.5 m and total heights were determined. Stumps and stems were marked at 0.25-m intervals from the base to 2 m and at 1 m intervals thereafter. Marking continued to the 1-m multiple closest to the end of the dominant leader. Stem sections were cut at ground level and at each measurement interval up to a 3 cm diameter top. The regenerative-mode of all genets (sprout or seedling) was assessed when possible.

#### Stem analysis

The terminal leader of each stem was aged in the field by counting the number of terminal bud scale scars preceding each height interval. Stem sections were removed to the lab where they were sanded to a smooth surface and wetted to aid ring examination. Ages were determined by counting ring number on at least two radii (typically a long and short axis on oblique-shaped stems) of each section under a dissecting microscope. The oldest age of each section, if the counts differed, was recorded. Precision of ring counting was assessed by periodically recounting 20% of the stem sections from lots of 15-25 sections each. Recounts seldom differed by more than one year. Section ages were used to determine time of establishment and to reconstruct the height growth trajectories of each sampled individual. Stem heights at 10 year stand age intervals were derived
from the growth trajectories (see Data analysis below). In some instances interpolation of stem height at a given stand age was required since the stem sampling method controlled stem height but not age. When this was required, the shapes of age-height plots for the individuals involved were examined to insure accurate determination of height at the 10-year stand-age of interest.

The age-height trajectories of each Quercus and Acer were examined for evidence of suppression or release that might reflect changes in an individual's competitive These environment ability. episodes were or defined following a procedure similar to one suggested for radial growth analysis (Lorimer 1984). Height trajectories were examined for obvious slope changes that persisted for at least 15 years and resulted in height growth rates that were minimally 50% above or below growth rates for the previous 15 year period. The 15 year minimum was used to filter out short periods of increased or reduced growth that might be related to factors other than a change in competitive status, such as climate change or insect defoliation. The 50% minimum growth rate change was used to filter out slower declines in height increment that occur as a stem matures (Oliver & Larson 1990; Zeide 1991).

### Data analysis

Total heights were compared among species over time using random-order crossover, split-block repeated

measurement analysis of variance. For these analyses, plots were considered blocks, species were considered random-order "mensurational treatments" within blocks, and time was the repeated measure. With this design, the overall effects of species can be analyzed as a randomized block design, since no nuisance trends are associated with a random sequence of "treatments" within a block (Gill 1978).

Variances in height over time were often heterogeneous within a species (F-max test, P< 0.2). Additionally, the correlation structure of most data sets were not homogeneous across time (sphericity assumption rejected at P= 0.25; Gurevitch & Chester 1986). In most cases, variances were homogeneous among species at specific times. For some data sets, log or square-root transformations were used to homogenize variances over time (and within time when In some instances these transformations were required). effective at homogenizing variance over time but resulted in increased heterogeneity among variances within time and lessened the normality of residuals. When this was the case, untransformed data were analyzed using conservative adjustments for heterogeneous variance-covariance structure as described in the next two paragraphs. All of the final data sets used met the assumption of normality of residuals (Shapiro-Wilke test,  $P \ge 0.1$ ).

When variance-covariance structure was heterogeneous over time, F-tests for the overall effects of time and time x species interactions were evaluated using the highly

conservative Greenhouse-Giesser degrees of freedom (Gill 1978). This test reduces the degrees of freedom for time from (b-1), (b-1)(r-1)(t-1) to 1, (r-1)(t-1), where b is the number of time periods, r is the number of blocks, and t is the number of treatments. For time x species interaction, degrees of freedom are reduced from (b-1)(t-1), (b-1)(r-1)(t-1) to (t-1), (r-1)(t-1). Box's adjusted degrees of freedom was used to evaluate overall F-tests for species effect when time x species interaction was not significant, but variances among species were heterogeneous (Gill 1978).

Individual species means at specific time periods were separated using Bonferroni contrasts (two-sided) to test a priori hypotheses regarding height patterns based on understory tolerance differences among species. Test were conducted to determine whether (i) Populus (intolerant) was taller than <u>Quercus</u> (mid-tolerant) at a specific time and (ii) <u>Quercus</u> was taller than <u>Acer</u> (tolerant) at the same time. These contrasts were designed to allow ranking of height patterns in <u>Ouercus</u> and <u>Acer</u>, relative to <u>Populus</u>, not to imply that <u>Quercus</u> may have been consistently influencing the growth of Acer throughout the forests. Variances of contrast means and degrees of freedom were adjusted, according to Gill (1978), when variances were heterogeneous within specific times (some cases) or variance-covariance matrices were not uniform across time (most cases). For all statistical tests, a type-one error probability of 0.05 was considered significant.

#### RESULTS

Regenerative-modes

Regenerative-origin of <u>Quercus</u> and <u>Acer</u> was assessed by assigning genets to one of following categories: (i) vegetative-origin (multi-stemmed genets); (<u>ii</u>) high probability of vegetative-origin (single-stemmed genets with highly convoluted or crescent shaped stem bases, both of which may be indicative of development around remnant stumps); and (iii) seed-origin (single-stemmed genets with uniform, approximately circular stem bases). Ninety percent of the Acer genets in both forests were apparently of vegetative-origin and 90% of these were multi-stemmed (Table 5.1). The apparent seed-origin genets were restricted to the smallest height classes. Apparent sprout-origin genets were found in a wide range of height classes. All of the tallest Acer sampled in this study appeared to be of vegetative-origin, however not all of these were multi-Eighty-four percent of the Quercus genets in the stemmed. Huron forest appeared to be of vegetative origin; two-thirds of these were multi-stemmed (Table 5.1). At UMBS, only 66% of the <u>Quercus</u> genets appeared to be of sprout-origin and only one-third of these were multi-stemmed (Table 5.1). Both apparent sprout-origin and seed-origin Quercus occurred in a range of height classes, including some of the tallest individuals, but apparent sprout-origin genets were not found in the smallest height classes. Most Quercus did have high early radial growth rates, relative to later years,

Table 5.1.	Regenerati	ion methods	s of <u>Qu</u>	ercus	<u>rubra</u>	and	<u>Acer</u>
<u>rubrum</u> ge	nets in the	e a) Huron	and b)	UMBS	forest	s.	

		Vegetative <sup>a</sup>	Regeneration method Likely vegetative <sup>b</sup>	Seedling <sup>C</sup>	n <sup>d</sup>
a)	Huron				
Q. <u>A</u> .	<u>rubra</u> rubrum	0.57 <sup>은</sup> 0.83	0.27 0.06	0.16 0.11	75 92
b)	UMBS				~ <u>~~</u>
Q. <u>A</u> .	<u>rubra</u> <u>rubrum</u>	0.22 0.78	0.44 0.11	0.33 0.11	35 69

<u>a</u>Multi-stemmed genets. <u>b</u>Single-stemmed genets with highly convoluted stem bases. <u>C</u>Single-stemmed genets with uniform, circular stem bases. <u>d</u>Number of genets. <u>e</u>Proportion of total genets sampled.

including those that appeared to be of seed-origin (<u>unpublished data</u>). Rapid early radial growth suggests that even apparent seed-origin <u>Quercus</u> may have been vegetative-sprouts (Sander 1990).

#### Population age and height structures

All sampled stems in the Huron forest established, or resprouted, within a 10 year period following disturbance approximately 70 years prior to sampling. The ages of the 20 sampled Populus differed by no more than four years. In the UMBS forest, stand ages ranged from 74 to 82 years. Within stands, Populus ages differed by 4 to 10 years. Also within stands, the age distributions for all species combined ranged from 4 to 15 years, with the exception of one plot containing a <u>Quercus</u> that was approximately 20 years older than the oldest of its associates. In both study areas, the youngest individuals were always the slowest growing Acer. These individuals may have been several years older than they appeared if they had dropped rings near their stem bases, as suppressed stems sometimes do (Larson 1956; Bormann 1965). Their influence plot on age distributions was likely minimal since mean ages among species (years + SE; all individuals pooled by species on a plot) were similar (Huron, <u>Populus=65.9+0.2</u>, <u>Quercus=</u> 65.4<u>+0.2</u>, <u>Acer</u>=65.8<u>+0.2</u>, n=19; UMBS, <u>Populus</u>=73.3<u>+</u>1.1, Quercus=73.8+1.2, Acer=71.0+1.1, n=16) and not significantly different at either location (Friedman's randomized block

method: Huron, P= 0.368; UMBS, P= 0.051). For both forests, power to detect a mean age difference of <u>+</u>2 years (at alpha=0.05) was high (Huron= 0.99; UMBS= 0.82).

Mean heights of Populus, Quercus and Acer (all individuals pooled by species on a plot), over 10 year stand age intervals, are shown in Figure 5.1. These comparisons were extended to 70 years, the maximum 10 year interval shared by all stands within both study locations. In the Huron forest, species x time interaction was significant (P< 0.0001; Table 5.2), indicating that temporal patterns of cumulative height increase differed among species. Within time periods, heights among species were significantly different at all stand ages (P< 0.05-0.01; Table 5.2) except 10 years (P> 0.05; Table 5.2). The differences followed the predicted order based on shade tolerance; Populus was taller then <u>Quercus</u> which in turn was taller than <u>Acer</u>. At UMBS, species x time interaction was not significant (P= 0.096; Table 5.2), indicating that temporal patterns in height increase were similar among species. The overall species effect was significant (P< 0.0001; Table 5.2). Within time, Populus was taller than Quercus at almost all time periods (Fig. 5.1), however the differences were significant only at stand ages of 60 and 70 years (P< 0.05; Table 5.2). Quercus was significantly taller than <u>Acer</u> at all 10 year intervals (P< 0.01; Table 5.2). The relative height relationships among species remained unchanged at the time of sampling in the older UMBS stands (data not shown).

Figure 5.1. Heights of <u>Populus grandidentata</u>, <u>Quercus</u> <u>rubra</u>, and <u>Acer</u> <u>rubrum</u> at 10 year stand age intervals in the Huron forest (a) and the UMBS forest (b). Huron values are means ( $\pm$ SE) of 19 observations. UMBS values are backtransformed means ( $\pm$ 95% confidence intervals) of 16 square-root transformed observations. <u>Q. rubra</u> and <u>A. rubrum</u> values are the means of all individuals pooled by species on each plot. Figure 5.1



Table 5.2. Repeated measure analysis of variance and species contrasts for mean heights of <u>Populus</u> <u>grandidentata</u>, <u>Quercus</u> <u>rubra<sup>a</sup></u> and <u>Acer</u> <u>rubrum</u><sup>b</sup> over time in the Huron and UMBS forests.

		Huron		UMBS <sup>b</sup>				
Source	df <sup>C</sup>	SS	P > F <sup>⊆</sup>	df	SS	P > F		
Plot	18	641.437		15	8.171			
Species Error (Spp.)	2 36 (27)	1329.998 504.199	0.0001 (0.0001)	2 30 (26)	44.317 13.161	0.0001 (0.0001)		
Time Time x Plot	6 (1) 108	16656.831 203.734	0.0001 (0.0001)	6 (1) 90	297.292 3.985	0.0001 (0.0001)		
Time x Spp. Error (Time)	12 (2) 216 (36)	357.171 207.089	0.0001 (0.0001)	12 (2) 180 (30)	0.924 5.424	0.004 (0.096)		

Table 5.2 (Conc u).	Table	5.2	(cont'd).
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		Huron			UM	1BS		
<u>P. grandidentata</u> vs. <u>Q. rubra</u>		<u>Q. rubra</u> vs. <u>A. rubrum</u>		<u>P. grandidentata</u> vs. <u>Q. rubra</u>		Q. <u>ru</u> <u>A. r</u>	<u>Q. rubra</u> vs. <u>A. rubrum</u>	
Stand age (years)	t <u>b</u> d	df <u>d</u>	t <u>b</u>	df	t <u>b</u>	df	t <u>b</u>	df
10	1.250	36	1.647	36	0.778	27	4.195	30 **
20	3.986	36 **	2.767	36 *	1.596	30	4.788	30 **
30	2.788	36 *	4.660	36 **	1.491	30	4.994	30 **
40	2.711	36 *	4.140	36 **	1.416	30	4.585	30 **
50	3.931	36 **	3.294	36 **	1.960	30	5.797	30 **
60	4.876	36 **	3.231	36 **	2.635	23 *	5.471	30 **
70	5.406	36 **	2.809	36 *	2.424	21 *	5.663	30 **

<u>All</u> individuals pooled by species on each plot.

**<u>b</u>**UMBS analysis done on square-root transformed data.

<sup>C</sup>Degrees of freedom (df) and probabilities in parentheses are associated with Box's (Species) or Greenhouse-Giesser (Time and Time x Species) conservative F-tests. <sup>d</sup>tb-values are for Bonferroni contrasts; df values may vary depending on variance structure within and across time.

Critical value=  $\pm t_{\underline{b}} \alpha/2$ , 2, df; \* significant at P= 0.05, \*\* significant at P= 0.01.

Population height variation

The examination of species mean heights over time (Fig. 5.1) suggests stratification of Populus over both Quercus and Acer in the Huron and UMBS forests. However, within plots, individual heights for the latter two species were often quite variable. This variability can be seen by examining time-height reconstructions for several of the plots (one randomly selected from each stand) in Figure 5.2. In the Huron forest, the mean  $(\pm 1 \text{ SD})$  plot-level height ranges of <u>Quercus</u> and <u>Acer</u> were 8.7 (3.2) m and 7.3 (0.4) m, respectively. At UMBS, the analogous ranges were 5.4 (3.4) m and 5.8 (2.4) m. These height ranges are conservative since some of the shorter ramets came from genets having additional shorter, slower growing but similar aged ramets. Ages (mean years  $\pm$  SE) of individuals at the extremes of the height ranges on a plot were similar for all species-study area combinations (Huron Quercus, tall=65.5+ 0.3 vs. short= 65.6+0.5, n=16; Huron <u>Acer</u>, tall= $66.2\pm0.4$ vs. short= 64.8+0.6, n=19; <u>Acer</u>, tall=72.9<u>+</u>1.6 UMBS vs. short= 70.0<u>+</u>1.2, n= 15; UMBS <u>Quercus</u>, tall=72.5<u>+</u>1.5 vs. short= 72.1+ 3.9, n=8). In all cases, the mean differences were not significantly different from zero (paired t-tests: Huron Quercus, P= 0.837; Huron Acer, P= 0.099; UMBS Acer, P= 0.156; Wilcoxon's test: UMBS Quercus, P> 0.10). Power to detect a mean difference of  $\pm 2$  years (at alpha= 0.05) was high (0.80 or greater) for all comparisons, except Acer at UMBS (0.50).

Figure 5.2. Height growth reconstructions of <u>Populus</u> <u>grandidentata</u>, <u>Quercus rubra</u>, and <u>Acer rubrum</u> within randomly selected plots from the Huron forest (a) and the UMBS forest (b). Each line represents an individual stem.

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There was less variability in the heights of <u>Populus</u> within plots. In the Huron forest, the mean ( $\pm$  SE) height at the time of sampling of the 20 <u>Populus</u> used in stem analysis was 24.5 (0.5) m. The mean height of the additional <u>Populus</u>, estimated with a clinometer, was 25.2 (1.2) m. The mean difference was not significant (paired t-test, P= 0.773). In the UMBS forest, the mean height of the 16 sampled <u>Populus</u> was 21.7 (0.3) m, while the mean height of the additional <u>Populus</u> was also 21.7 (0.5) m. Again, the paired heights were not significantly different (P= 0.970).

Many plots had at least one <u>Quercus</u>, and some had an Acer, that approached the height of Populus at 70 years (for examples see Fig. 5.2). The potential for <u>Ouercus</u> and <u>Acer</u> to attain dominant canopy positions was assessed by tabulating the number of individuals on each plot that were within 2 m of (or exceeded) Populus in height at the time of sampling (Table 5.3). In the Huron forest, 37% of the Quercus ramets had total heights that approached or exceeded the heights of Populus, compared to 13% for Acer. At UMBS, 53% of the <u>Quercus</u> ramets approached or exceeded the heights of the Populus, while only 6% of the Acer ramets were this tall.

Similarity in height growth rates of <u>Populus</u> and dominant <u>Quercus</u> and <u>Acer</u> (the tallest stem from each of the plots that contributed individuals to Table 5.3) was assessed by comparing mean cumulative heights between species pairs at 10 year stand age intervals (Fig. 5.3).

		Q.	rubr	<u>ta</u>	<u>A</u> .	rubru	<u>1m</u>
a)	Huron	n <u>a</u>	#/h	na <u>b</u>	n	#/ł	na
1.	Dominant height class <sup>C</sup> a) equals or exceeds P. grandidentata	28 13	52 24	(10) (9)	12 6	22 12	(6) (5)
	b) 0.5-1 m shorter than P. grandidentata	5	10	(4)	3	6	(3)
	c) 1-2 m shorter than <u>P. grandidentata</u>	10	18	(6)	3	6	(3)
2.	Subdominant height class <sup>d</sup>	47	84	(9)	80	149	(15)
Tot	tal cohort	75	136	(20)	92	171	(21)
b)	UMBS	n	#/r	na	n	#/ł	na
1.	Dominant height class a) equals or exceeds P grandidentata	19 10	25 13	(6) (5)	4 3	5 4	(3) (3)
	b) 0.5-1 m shorter than P. grandidentata	4	5	(2)			
	c) 1-2 m shorter than <u>P. grandidentata</u>	5	7	(3)	1	1	(1)
2.	Subdominant height class	16	25	(6)	65	87	(13)
То	tal cohort	35	50	(9)	69	92	(14)

Table 5.3. Numbers and density of <u>Quercus</u> <u>rubra</u> and <u>Acer</u> <u>rubrum</u> genets by height class in the a) Huron and b) UMBS forests.

 $\underline{a}_{T}$ Total number of genets sampled, pooled across plots.  $\underline{b}_{V}$ Values are means ( $\pm$ SE) of 20 and 16 plots in the Huron and UMBS forests, respectively.

<sup>C</sup>Dominant Q. <u>rubra</u> and <u>A</u>. <u>rubrum</u> were those that exceeded, equaled ( $\pm 0.5$  m) or approached (2.0-0.5 m shorter) the height of <u>P</u>. grandidentata on the same plot.

<sup>d</sup>Subdominant Q. <u>rubra</u> and <u>A</u>. <u>rubrum</u> were more than 2 m shorter than <u>P</u>. <u>grandidentata</u> on the same plot.

Figure 5.3. Heights of <u>Populus grandidentata</u> compared to dominant <u>Quercus rubra</u> or <u>Acer rubrum</u> at 10 year stand age intervals in the Huron forest (a,b) and the UMBS forest (c, d). Huron values are backtransformed means  $(\pm 95\%$  confidence intervals) of 16 log (y+1) transformed observations for <u>Q</u>. <u>rubra</u>, and 10 log (y+1) transformed observations for <u>A</u>. <u>rubrum</u>. UMBS values are means ( $\pm$ SE) of 13 and 3 observations for <u>Q</u>. <u>rubra</u> and <u>A</u>. <u>rubrum</u>, respectively.



There were only three plots with dominant <u>Acer</u> at UMBS, to few to be included in these analyses, however, the mean total height of these individuals at the time of sampling was only 0.5 m less than <u>Populus</u> from the same plots (Fig. 5.3).

Time x species effects were non-significant in both Populus-Quercus comparisons (Huron: P=0.086; UMBS: P=0.935; Table 5.4), and in the Populus-Acer comparison in the Huron forest (P=0.077; Table 5.4), indicating that the shapes of the cumulative height trajectories were similar between species pairs. Overall species effects were non-significant in both <u>Populus-Quercus</u> comparisons (Huron: P=0.302; UMBS: P=0.550; Table 5.4), indicating a similarity in heights at each 10 year plot age interval. Power to detect a 1-m mean height difference (at alpha= 0.05) was high for both comparisons (Huron= 0.87; UMBS= 0.94). Overall species effect was significant for the Acer-Populus comparison in the Huron forest (P=0.006; Table 5.4), although height differences were clearly minor (Fig. 5.3). For example, heights within time-periods were significantly different only at 20 and 30 years after plot initiation (P< 0.05; Table 5.4) However, power to detect a 1 m mean height difference (at alpha= 0.05) was moderately low (0.29)

Mean ages (years<u>+</u> SE) of <u>Populus</u> and the other species in each of the above comparisons were similar (Huron <u>Populus</u>=  $65.9\pm0.2$  vs. <u>Quercus</u>=  $65.4\pm0.3$ , n=16; Huron <u>Populus</u>=  $66.1\pm0.2$  vs. <u>Acer</u>=  $66.5\pm0.5$ , n=10; UMBS <u>Populus</u>=

Table 5.4. Repeated measure analysis of variance and specific contrasts for heights of <u>Populus grandidentata</u> and dominant <u>Quercus rubra</u> and <u>Acer rubrum</u> over time in the Huron and UMBS forests.

			<u>P. grandidentata</u> v	s. <u>Q</u> . <u>rubra</u>	<u>a</u>	
		Huron <sup>a</sup>			UMBS	
Source	df <u>b</u>	SS	P > F <sup>b</sup>	df	SS	P > F
Plot	15	1.794		12	347.430	
Species	1	0.025	0.302	1	0.982	0.550
Error (Spp.)	15	0.332		12	31.303	
Time	6 (1)	116.584	0.0001 (0.0001)	6 (1)	6890.447	0.0001 (0.0001)
Time x Plot	90	0.626		72	102.151	
Time x Spp.	6 (1)	0.143	0.0005 (0.086)	6 (1)	1.287	0.935
Error (Time)	90 (15)	0.481	· ·	72 (12)	51.518	

Table	5.4	(cont'd).
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	<u>P</u> .	grand	<u>identata</u> ve	s. <u>A</u> . <u>rubrum</u>	P. grandident	<u>ata</u> vs.	<u>A. rubrum</u>
			Huron		Huron	(contras	sts)
Source	df		SS	P > F	Stand age (yrs)	t <u>b</u> c	df <sup><u>C</u></sup>
Plot	9	<u>*</u>	0.850		10	1.269	9
Species	1		0.288	0.003 (0.006)	20	3.050	9*
Error (Spp.)	9	(7)	0.164		30	2.950	8 *
Time	6	(1)	70.130	0.0001 (0.0001)	40	1.678	8
Time x Plot	54	• •	0.453		50	1.807	6
Time x Spp.	6	(1)	0.087	0.077	60	0.824	9
Error (Time)	54	(9)	0.387		70	0.829	9

<sup>a</sup>Huron analyses done on natural log (y+1) transformed data.

<sup>b</sup>Degrees of freedom (df) and probabilities in parentheses are associated with Box's (Species) and Greenhouse-Giesser (Time and Time x Species) conservative F-tests. <sup>c</sup>t<sub>b</sub>-values are for Bonferroni contrasts; df values may vary depending on variance structure within and across time. Critical value=  $\pm t_b \alpha/2$ , 2, df; \* significant at P= 0.05, \*\* significant at P= 0.01.

72.0+1.2 vs. Quercus=73.0+0.8, n=13). In all cases, the mean differences were not significantly different from zero (paired t-test: Huron Populus vs. Quercus, P= 0.289; Huron Populus vs. Acer, P= 0.628; Wilcoxon's test: UMBS Populus vs. Quercus, P> 0.10). For all three comparisons, power to detect a  $\pm 2$  year mean age difference (at alpha=0.05) was 0.80 or greater. The age difference between Populus and the small number of dominant Acer at UMBS was also minimal (Populus=73.3+4.5 vs. <u>Acer=71.0+4.5</u>, n=3). The age similarities, combined with the similarity of heights between species at a plot age of 10 years (Fig. 5.3), indicates that juvenile height growth rates were similar between species. In other words, dominant Quercus and Acer were not initially shorter and then simply caught up later in stand development.

# Individual height growth trajectories

Each sampled <u>Populus</u>, <u>Quercus</u>, and <u>Acer</u> ramet was assigned to one of four categories that described their patterns of individual height growth and reflected changes in an individuals competitive environment or ability. The <u>suppressed</u> category included stems that had at least one period of greatly reduced growth. The <u>released</u> category included stems that had at least one period of greatly increased growth. The <u>constant</u> category included stems showing no periods of major suppression or release in height growth (although actual growth rates were not constant over the entire life of the individual). Finally, the <u>combination</u> category included individuals whose cumulative height trajectories indicated at least one major suppression and release. Examples of suppressed and released stems can be seen in Figure 5.2 (for example, Fig. 5.2a, Plot 9, the shortest <u>Quercus</u> and Fig. 5.2b, Plot 12, the third-shortest <u>Acer</u>).

None of the Populus ramets in the Huron forest showed any evidence for a suppression or release (Table 5.5). Three of the 16 Populus ramets (18%) in the UMBS forest did show evidence for a suppression (Table 5.3). The mean  $(\pm 1)$ SD) growth rate reduction for these stems was 73 (9)% and began at stem ages of 15, 16 and 47 years. The growth patterns of these stems were unique, relative to suppressed Quercus and Acer at UMBS (see below), in that the suppressed <u>Populus</u> had been growing exceptionally fast prior to suppression, compared to non-suppressed Populus from the same stands (for example, see Fig. 5.2b, Plot 6). The suppressions were therefore more of an equalization of growth rates than an actual inhibition. Three (18%) Populus in the UMBS forest showed evidence for a release (Table The mean growth rate increase for these stems was 177 5.5). (108)% and occurred between stem ages of 20 and 40 years.

The majority of dominant <u>Quercus</u> and <u>Acer</u> at both locations showed no evidence for either a suppression or release (Table 5.5). The few that were suppressed, all <u>Quercus</u>, had growth rate reductions of approximately 60%

			Height growt	h pattern <sup>a</sup>	
		Constant	Suppressed	Released	Combination
a) Huron	n <sup>b</sup>		Propor	tion <sup>C</sup>	
<u>P. grandidentata</u>	20	1.00			
Q. <u>rubra</u>					
Dominants <u>d</u>	28	0.71	0.21	0.04	0.04
Subdominants <u>d</u>	47	0.28	0.60	0.06	0.06
<u>A. rubrum</u>					
Dominants	12	1.00			
Subdominants	80	0.49	0.35	0.10	0.06

Table 5.5. Height growth patterns of <u>Populus</u> <u>grandidentata</u>, <u>Quercus</u> <u>rubra</u> and <u>Acer</u> <u>rubrum</u> in the a) Huron and b) UMBS forests.

	Table	5.5	(cont'	d).
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b) UMBS					
<u>P. grandidentata</u>	16	0.75	0.06	0.06	0.12
Q. <u>rubra</u>					
Dominants Subdominants	19 16	0.95 0.50	0.05 0.44	0.06	
<u>A. rubrum</u>					
Dominants Subdominants	4 65	0.75 0.61	0.17	0.25 0.11	0.11

<sup>a</sup>The constant category includes ramets with no evidence for major suppression or release; the suppressed category includes ramets with evidence for one major suppression; the released category includes ramets with evidence for one major release; the combination category includes ramets with evidence for one or more major suppressions and releases.

bTotal number in catagory.

 $\frac{C}{2}$  Proportion of total (n).

<sup><u>d</u></sup>Dominant <u>Q</u>. <u>rubra</u> and <u>A</u>. <u>rubrum</u> were those that exceeded, equaled ( $\pm 0.5 \text{ m}$ ) or approached (0.5-2.0 m shorter) the height of <u>P</u>. <u>grandidentata</u> from the same plot; subdominant <u>Q</u>. <u>rubra</u> and <u>A</u>. <u>rubrum</u> were those more than 2 m shorter than <u>P</u>. <u>grandidentata</u> from the same plot.

that began at a stem age of 40 years or later. Only three of the dominant individuals were released (Table 5.5). The increase in growth rates after release averaged about 120% and occurred early, around a stem age of 15 years.

Between 40 and 72% of the subdominant <u>Quercus</u> and <u>Acer</u> showed some evidence for large growth rate changes (Table 5.5). Most of these were suppressions. The growth rate reductions averaged around 70% and occurred between stem ages of 30-50 years. The mean height growth rate increase for the released stems, most of which were <u>Acer</u>, was over 200%, but was highly variable. Most releases occurred around a stem age of 30 years.

The growth rate potential of suppressed and released <u>Quercus</u> and <u>Acer</u> from the subdominant height classes was assessed by comparing growth rates of these stems to that of <u>Populus</u> from the same plot, over the same stem ages prior to suppression or subsequent to release. Growth rates were considered equivalent if they were within  $\pm 0.03$  m/yr (total heights differing by < 2 m at a stem age of 65 years). Approximately 50% (15 stems) of suppressed <u>Quercus</u> in the Huron forest and 30% (2 stems) at UMBS were growing at rates equivalent to <u>Populus</u> prior to suppression (Table 5.6). A small percentage ( $\leq$  16%) of suppressed <u>Acer</u> in both forests (3-4 stems) were growing at rates similar to <u>Populus</u> prior to suppression (Table 5.6). Examples of suppressed <u>Quercus</u> and <u>Acer</u> having initial growth rates equivalent to <u>Populus</u> can be seen in Figure 5.2. All of the relatively few

Table 5.6. Proportion of suppressed or released subdominant<sup>a</sup> <u>Quercus</u> <u>rubra</u> and <u>Acer</u> <u>rubrum</u> in the a) Huron and b) UMBS forests that had height growth rates equal<sup>b</sup> to or exceeding <u>Populus</u> grandidentata prior to a suppression or subsequent to a release.

		Species				
		Q. <u>rubra</u>			<u>A. rubrum</u>	
a)	Huron	n <sup>c</sup>	proportion <sup><u>d</u></sup>	n	proportion	
	Suppressed Released	31 6	0.48 1.00	33 15	0.12 0.40	
b)	UMBS	n	proportion	n	proportion	
	Suppressed Released	7 1	0.29 1.00	19 14	0.16 0.43	

 $\underline{a}$ Includes all stems more than 2 m shorter than  $\underline{P}$ . <u>grandidentata</u> from the same plot. <u>b</u>Equivalent growth rate=  $\pm 0.03$  m/yr.

<sup>C</sup>Total number in the catagory (note: total may exceed sums of the suppressed+combination or released+combination catagories from Table 5.5 if a stem in the combination catagory had multiple suppressions or releases.

 $\underline{d}$ Proportion of Q. <u>rubra</u> and <u>A</u>. <u>rubrum</u> in the catagory with growth rates equivalent to or exceeding P. grandidenta over the same stem ages prior to a suppression or subsequent to a release.

released <u>Quercus</u> in both forests (6 and 1 stems at Huron and UMBS, respectively) had height growth rates after release equivalent to <u>Populus</u> (Table 5.6). Approximately 40% of released <u>Acer</u> in both forests (6 stems) had height growth rates equivalent to <u>Populus</u> after release. These results suggest that competitive environments or abilities of many subdominant <u>Quercus</u> and <u>Acer</u> changed over the course of stand development and, in some instances, initial height growth rates prior to suppression, or later growth rate after release, equaled height growth rates of <u>Populus</u>.

#### DISCUSSION

Population height structures

In both of the forests examined in this study, populations of Populus grandidentata, an intolerant, early successional species were, on average, taller than populations of <u>Quercus</u> rubra, a mid-tolerant, relatively later successional species, which in turn were taller than populations of Acer rubrum, a tolerant, later successional species, at least after the first several decades of stand development. Stratification resulted from species-specific differences in height growth rates, with populations age differences having little or no influence on height structures. These results contrast with those from an earlier study of Populus forest development (Chapter 2) that demonstrated the importance of mean age differences among species to the development of height stratification.

Although not quantified in this study, differential mortality species also contributed among to height stratification. Populus ramet density is know to be high immediately following major disturbance (for example, ramets/ha following clearcutting >24,000 and burning; Scheiner et al 1988). Unable to survive even mild suppression (Laidly 1990), most ramets die following the onset of crown differentiation. Thus, in the current study, only dominant-codominant ramets were found in the mature forests. In contrast, many slower growing <u>Quercus</u> and <u>Acer</u> were able to survive varying degrees of suppression, thereby lowering heights and height growth rates for these species relative to Populus.

Within plots, the heights of the surviving Populus ramets were often similar. In contrast, a predictable height was not an attribute of surviving stems within Quercus and Acer populations. Heights often ranged widely and the variation was clearly not related to age. In fact, the ages of individuals differing by up to 15 m in height were Obviously, height growth rates of similar-aged similar. individuals varied widely within <u>Ouercus</u> and Acer populations, so much so that some individuals had height growth rates, including juvenile rates, equivalent to Populus. Individual height growth trajectories indicated that many shorter Acer and Quercus genets in both forests experienced height growth suppression, beyond that which normally develops as a stem ages (Oliver & Larson 1990;

Zeide 1991). Some of these stems also had juvenile grow rates comparable to <u>Populus</u>.

While these results demonstrate that species-specific differences in height growth rates typically led to stratification of surviving Populus over Quercus and Acer, they also imply that lower juvenile height growth rates were not inherent attributes of the latter two species per se. Rather, the typically reduced growth rates of Quercus and Acer may have resulted from competitive inhibition and/or reduced competitive ability of individual genets. Inhibitory influences were spatial and temporally variable, as indicated by the extreme variation in heights within Quercus and Acer populations.

Early inhibition was not a consistent feature of <u>Quercus</u> and <u>Acer</u> populations, probably because of spatial variation in competitive environments. For example, local density variation, by its affect on crown exposure, root crowding, or even direct physical abrasion of soft terminal leaders can result in differential plant growth performance both within and among species populations (Cayford 1957; Ross & Harper 1972; Harper 1977; Oliver 1978; Wierman & Oliver 1979; Weiner 1984; Guldin & Lorimer 1985; Silander & Pacala 1985; Kelty 1986; Goldberg 1987; van der Meijden 1989; Hix & Lorimer 1990; Oliver, Clatterbuck & Burkhardt 1990). In the current study, the tallest <u>Quercus</u> and <u>Acer</u> may have been in relatively uncontested sites throughout stand development. The fact that most dominant <u>Quercus</u> and <u>Acer</u> were not initially suppressed, but rather always grew at rates comparable to <u>Populus</u>, suggests this was the case.

Reduced competitive ability may be a function of mode of regeneration, since within species, sprout-origin characteristically out-grow individuals similar aged seedling-origin individuals (Jensen 1943; Wilson 1968; Oliver 1978; Beck & Hooper 1986). An intermix of seedlingand sprout-origin individuals could lead to height growth rate variation. However, in the current study, most Quercus and Acer genets were apparently of sprout-origin. Although some larger Quercus had stem morphologies suggesting seedling-origin, no obvious remnant individuals were found in any of the stands that might have acted as seed sources (also true for <u>Acer</u>). No cutting has occurred in any of the stands since they initiated, so remnant Quercus and Acer seed trees, if they existed, should have been apparent. It is likely that few seed bearing trees existed for either species at the time the stands initiated, given the frequency and extent of post-logging fires in the region (Kilburn 1957, 1960; Pyne 1982, pp. 199-218). Of course, the potential for long-distance dispersal of acorns cannot be ruled out (Darley-Hill & Johnson 1981).

Even if all <u>Quercus</u> and <u>Acer</u> were of sprout-origin, the age and size of the originating stumps could have influenced early ramet growth rates and therefore competitive ability. For example, in <u>Quercus</u>, sprout height growth rate increases with stump diameter (Sander 1971) and size of advanced

regeneration (Sander 1972). In <u>Acer</u>, younger stumps have higher sprout height growth rates than older stumps (Solomon & Blum 1967). Additionally, ramet number may affect individual growth rates and this in turn may be related to parent stump vigor or size (Solomon & Blum 1967; Johnson 1975; Stroempl 1983). In the current study, <u>Quercus</u> and <u>Acer</u> genets that always grew slower than <u>Populus</u> may have developed from physiologically inferior root systems and were therefore at an initial competitive disadvantage.

The shorter mean height of <u>Populus</u>, <u>Quercus</u> and <u>Acer</u> at UMBS, relative to the Huron forest at comparable stand ages, does undoubtedly reflect the influence of differences in site quality on height growth rate (Hix & Lorimer 1990). However, the low number of dominant <u>Acer</u> at UMBS, relative to the Huron forest, may not. The Huron plots that were most similar to those at UMBS, in terms of total overstory basal area and density, and <u>Populus</u> site index (<u>unpublished</u> <u>data</u>), contained fast-growing, dominant <u>Acer</u>, while some of the apparently more productive Huron plots did not. These results suggests that inherently slower growth rates of <u>Acer</u> populations on the poorer UMBS sites were not solely responsible for the low number of dominants in this forest.

# A model for the development of dominance

Several analyses of secondary forest succession have identified differential growth rates among species as an important factor leading to initial height stratification

and early vertical dominance by a particular species (Drury & Nesbitt 1973; Bormann & Likens 1979; Hibbs 1983; Tilman 1985, 1988, 1990). These treatments present a model of mixed-species stratification based on inherently different juvenile height growth rates, which, in turn, initiate competitive hierarchies. The implication of such a model for stand development is that а successful early successional species must possess life-history traits which allow it to numerically dominate physical space, but it must also have inherently fast juvenile growth if it is to gain an early height advantage over less-abundant species. Such a model appears inconsistent with the developmental patterns found in the current study, namely, the potential for Quercus and Acer to grow in height at rates equivalent to These results suggest an alternative developmental Populus. model in which numerical dominance by Populus is а sufficient mechanism in itself to promote vertical stratification, through the inhibition of Quercus and Acer Under such a model, species differing in height growth. understory tolerance and relative successional status need not have inherently different juvenile height growth rates for stratification to develop.

This model is illustrated stylistically in Figure 5.4. In the forests examined, <u>Populus</u> was able to gain initial numerical dominance because of the its propensity to rapidly saturate soil space with numerous vegetative propagules. Clonal roots of <u>Populus</u> are able to extend greater than 30 m

Figure 5.4. A model for the development of vertical stratification among tree species differing in understory tolerance and relative successional status in an even-aged forest. (a) Immediately following a stand initiating disturbance, initial heights of an intolerant, early-successional species (clear crown) and a relatively more-tolerant, later successional species (filled crown) may be similar. The intolerant species is numerically dominant because of superior dispersal ability. (b) With the onset of crown differentiation, some individuals of both species lapse into suppression. A limited number of individuals of the tolerant species may have early height growth rates similar to the intolerant species, probably because of locally reduced competitive pressure from the intolerant species. The initially low number of stems of the tolerant species reduces the probability that many will occur in competitively favorable neighborhoods. (c) In the mature forest, the intolerant species is typically vertically dominant over the more-tolerant species although some stems of the tolerant species have maintained growth rates similar to that of the intolerant species. The population-level height growth rate of the intolerant species will be greater than that of the tolerant species because all suppressed stems of the former have died, leaving only fast-growing stems, while slower growing stems of the tolerant species have survived.

a)

H. V



c)


from an originating genet (Buell & Buell 1959). Following disturbance, the root system from a single clone can rapidly saturate large areas (up to 1 ha in Michigan) with suckersprouts, resulting in high density stands (Stoeckeler & Macon 1956; Zahner & Crawford 1965; Barnes 1969; Graham, Harrison & Westell 1963; Scheiner et al. 1988). In contrast, Quercus and Acer resprout from stumps or root collars (Fowells 1965), restricting the distribution of vegetative propagules of these species to the locations of the Many of these genets may be remnant originating genets. from the presettlement conifer-dominated forests that originally occupied these sites (Chapter 3). Neither nor abundant in Quercus Acer were these forests. Consequently, the number of vegetatively derived individuals in the current forests may have been a function of Quercus and Acer presettlement abundance.

The large starting capital of <u>Populus</u> ramets insured that this species would continue to dominate most competitive neighborhoods in the mature forest, despite high density-dependent mortality early in forest development. Variation in inherent height growth rates among surviving ramets would have been minimal since most individuals within a given area (for example the plot sizes used) were part of the same clone. The interspecific competitive pressure faced by <u>Quercus</u> and <u>Acer</u> genets within the <u>Populus</u> clonal matrix would have been intense, but spatially variable, probably because of stochastic variation in Populus ramet or root

density within individual competitive neighborhoods. Differences in the physiological state of the parent genets also have influenced height growth potential mav of individual <u>Quercus</u> and <u>Acer</u>. In any case, the low number of remnant Quercus and Acer genets in the early, postdisturbance forests, and the restricted distribution of ramets originating from these genets, insured that few stems of these species would be vertically dominant in the mature forests. Under this model, vertical stratification develops because of species-specific differences in the ability to achieve maximal potential height growth rates in the face of competitive pressure, not because of inherent differences in juvenile growth rates that initiate competitive hierarchies.

This model of forest development may be characteristic only of forests regenerating predominantly through In such forests, inherently lower height vegetative means. growth rates characteristic of seedlings of more-tolerant species (Loach 1970) may sometimes be compensated for by Sprout-origin stems occurring in uncontested sprout-vigor. neighborhoods would then be able to match height growth rates of less-tolerant species. However, as shown in the current study, most individuals of tolerant species, despite being of sprout-origin, experience suppression to some degree, which in turn leads to species-level height stratification.

A remarkable feature of the forests examined in the current study is that the apparent inhibitory ability of Populus has persisted for over 70 years. Not only were the majority of <u>Quercus</u> and <u>Acer</u> in both study areas suppressed to varying degrees but no individuals from younger cohorts for any species (see Chapter 4) have recruited into upper canopy positions. Of course the proposed model needs to be, and can be, examined experimentally in young <u>Populus</u> clearcuts. Should it prove valid, this model would account for a pattern of dominance in a forest type (<u>Populus</u> grandidentata and <u>Populus tremuloides</u> Michx. combined) that covers nearly five million hectares in the northern Great Lakes region of the United States (Jakes 1980; Smith & Hahn 1986; Spencer <u>et al</u>. 1988).

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#### Chapter 6

# THE AGE AND HEIGHT STRUCTURE OF RED MAPLE (<u>Acer rubrum</u> L.) POPULATIONS IN NORTHERN MICHIGAN BIGTOOTH ASPEN (<u>Populus</u> <u>grandidenta</u> Michx.) FORESTS

### ABSTRACT

Red maple (Acer rubrum L.) is often the most abundant later successional tree species recruiting in the understories of aspen and oak-dominated forests on dry-mesic sites in eastern North America. Limited evidence suggests that this species is capable of recruiting to dominant canopy positions on these sites. Given the potential for increasing overstory importance of red maple in these forests, detailed population-level examinations are warranted. This study examined the age and height structures of red maple populations in a bigtooth aspen grandidentata Michx.)-dominated landscape (Populus in northern Lower Michigan, USA. Stem analysis was used to examine relationships between establishment times, heights, and height growth rates for overstory and understory red maple from 20 replicate plots in five stands located within a 18  $\mathrm{km}^2$  area.

Red maple was a minor overstory component in the forests of the study area. The understories of all stands were overwhelmingly dominated by red maple. The populations were composed of two clearly defined age cohorts. The first cohort contained mostly sprout-origin individuals that established concurrently with bigtooth aspen within a 10

year period, beginning 70 years prior to the time of sampling. Mean age of the sprout-origin red maple cohort was not significantly different among stands, nor did it differ from the mean age of bigtooth aspen.

Mean height of the red maple sprout-origin cohort was not significantly different among stands. Within each stand, height growth rates of these individuals were highly variable. The variabliity was not related to differences in stem age. Recent height growth increment of the sproutorigin stems was weakly related to position of an individual in the overstory, suggesting that most red maple were competitively suppressed by taller bigtooth aspen. Some sprout-origin red maple in all stands did approach the dominant bigtooth aspen in height growth rate. These were likely stems that were never competitively suppressed.

The second red maple cohort contained seedling-origin individuals that began establishing 30-35 years after stand initiation, immediately after culmination of height increment in dominant overstory bigtooth aspen and red This suggests that increasing resource availability, maple. as a result of declining overstory vigor and canopy closure, may be a factor triggering understory reinitiation in these In general, heights of seedling-origin even-aged forests. red maple were more dependent on stem age, compared to sprout-origin individuals. However, height growth rates for similar aged individuals within the seedling cohort were still highly variable. The tallest individuals generally had the greatest rates of recent height increment, and thus were at a competitive advantage within the understory environment, but these were not always the oldest stems. There was, in fact, a trend of increasing initial height growth rate over time for the fastest growing seedlingorigin individuals, again suggesting that resource availability in the understory was increasing over the course of stand development.

Red maple's overwhelming understory dominance and ability to reach the dominant canopy positions in the stands examined suggests a potential for increasing overstory importance on dry-mesic sites. Life history attributes, including shade tolerance, vigorous resprouting potential and the ability to respond with increased growth upon release, may foster the development and maintenance of a red maple-dominated cover type in the Great Lakes region.

#### INTRODUCTION

Post-settlement changes in natural fire regimes have led to significant alterations in the composition and structure of many forested landscapes of eastern North America. On dry-mesic sites in the northern Great Lakes region, deforestation and repeated wildfire favored species able to establish on bare mineral soil and resprout readily after fire (Whitney 1987). These historical circumstances led to the development of extensive even-aged oak (Quercus spp.) and aspen (Populus grandidentata Michx. and Ρ. tremuloides Michx.)-dominated forests where pines (Pinus strobus L., P. resinosa Ait. and P. banksiana Lam.) were dominant in the presettlement landscape (Kilburn 1957; Heinselman 1973; Whitney 1987; Crow 1988; Nowacki et al. 1990; Chapter 3).

In many of these second-growth forests, red maple (Acer rubrum L.) is often one the most abundant later successional tree species recruiting in the understory (Brown and Curtis 1952; Benninghoff and Cramer 1963; Graham <u>et al</u>. 1963; Roberts and Richardson 1985; Host <u>et al</u>. 1987; Sharik <u>et al</u>. 1989; Heinen and Sharik 1990; Nowacki <u>et al</u>. 1990). High abundance of red maple has also been noted in the understories of forests historically dominated by oak in the southern Great Lakes region (Gysel and Arend 1953; Larsen 1953; Rudolph and Lemmien 1976; Peet and Loucks 1977; Pastor <u>et al</u>. 1982; Dodge and Harman 1985) and the northeastern United States (Hibbs 1983; Lorimer 1984; Abrams and Nowacki 1992). The development of red maple understories in all of these forests is apparently in response to fire suppression (Lorimer 1984; Dodge and Harman 1985; Abrams and Nowacki 1992). Barring major disturbance capable of redirecting successional pathways, for example extensive cutting, fire, insect or disease outbreaks, red maple may become an increasingly important overstory component in these forests (Lorimer 1984).

Given the potential for increasing overstory importance of red maple in eastern forests on dry-mesic sites, detailed ecological examinations of these populations, following those of Lorimer (1984) and Sakai (1990a,b) are warranted. This is particularly important in aspen-dominated landscapes of the northern Great Lakes region, since in many of these forests the current aspen overstory is approaching the limit of the taxon's pathological rotation (70-80 years old; Graham <u>et al</u>. 1963) and thus its successional replacement is imminent.

This study examined populations of red maple in mature even-aged bigtooth aspen (Populus grandidentata Michx.)dominated forests in northern Lower Michigan, USA. Initial observations indicated that red maple was virtually the only tree species recruiting in the understory of these forests. Specific objectives of the study included: 1) quantifying the compositional importance of red maple in the forests of the study area; 2) characterizing the age and height structures of the red maple populations; 3) examining

relationships between time of establishment, height, and height growth rate in overstory and understory populations; and 4) characterizing the degree of variability in age and height structure among red maple populations within a local landscape.

### STUDY LOCATION AND ORIGINAL FOREST COMPOSITION

Research was conducted within a bigtooth aspendominated landscape on the Harrisville Ranger District of the Huron-Manistee National Forest in northeastern Lower Michigan, USA (latitude 44° 15' to 45° 00' N, longitude 83° 15' to 84° 45' W). The presettlement forests of this area were pine-dominated (Chapter 3). Red pine, jack pine, and white pine accounted for 77.5% of all bearing and line trees in the original General Land Office survey of the area. Aspen, red maple, white oak (<u>Quercus alba</u> L.), American beech (<u>Fagus grandifolia</u> Ehrh.) and red oak (<u>Quercus rubra</u> L.) were minor overstory components (Chapter 3). Red maple accounted for only 5.4% of bearing and line trees in the presettlement forests of the study area.

Virtually all of northern Lower Michigan, including the study area, was deforested in the late nineteenth to early twentieth centuries (Whitney 1987). Frequent slashed-fueled wildfires swept the cut-over landscapes in the years following logging (Pyne 1982). Fires eliminated advanced regeneration and most remnant overstory individuals of the dominant coniferous species (Kilburn 1957, 1960; Whitney

1987) and promoted vigorous vegetative-sprouting of aspen (<u>P. grandidentata</u> and <u>P. tremuloides</u> Michx.) from rapidly spreading clonal root systems (Barnes 1966).

#### METHODS

Stand Selection

Five stands from the same ecological land classification unit, based on surficial geology, soil characteristics and ground flora composition (following Barnes et al. 1982; Pregitzer and Barnes 1984; Host et al. 1987), were selected from a larger data pool (Michigan State University, Forestry Department research file). Stands were restricted to deep outwash sands overlaying till deposits Soils of all stands were classified as (Padley 1989). sandy, mixed, frigid Entic Haplorthods (Rubicon series). Important herbaceous and woody understory species in all stands included: Pteridium aquilinum (L.) Kuhn; Vaccinium angustifolium Ait.; Viburnum acerifolium L.; Maianthemum Desf., canadense <u>Gaultheria</u> procumbens L.; Carex pensylvanica Lam.; Oryzopsis asperifolia Michx. and Amelanchier arborea (Michx. f.) Fern. Nomenclature follows Gleason and Cronquist (1963). The stands selected met the following additional criteria: 1) minimum of 1 ha in size; 2) free from obvious disturbance since initiation; 3) 0-5% slopes; and 4) relative basal area of bigtooth aspen  $\geq$  65%. The distance between stands ranged from 1-4.5 km.

Vegetation Sampling

Arboreal vegetation was sampled in four 272 m<sup>2</sup> circular plots placed by random compass bearing and direction in each stand. Species and diameter (at 1.37 m) of all overstory individuals (dbh > 10 cm) and saplings (2.5 cm  $\leq$  dbh  $\leq$  10 cm) were tallied in each plot. Species and number of tree seedlings (dbh < 2.5 cm) were tallied in twelve 1 m<sup>2</sup> frames spaced at 3 m intervals along four opposing radii of each plot, beginning at the plot boundary. The origin of all red maple individuals (sprout or seedling) was assessed when possible.

## Stem Sampling

In each plot, all red maple  $\geq$  1.5 m in height were destructively sampled to determine year of establishment and subsequent height growth patterns. Only the tallest live ramets were sampled from multi-stemmed genets. In each plot, a subsample of 5-15 individuals < 1.5 m in height were randomly selected from 0.5 m height classes and examined. Additionally, one overstory bigtooth aspen was randomly selected (rejecting decaying individuals) and sampled in each plot. All stems were felled at groung level and total height was recorded. Stems were marked at 0.25 m intervals from the base to 2 m and at 1 m intervals thereafter. Marking continued to the 1 m multiple closest to the end of the dominant leader. Stem sections were cut from large individuals and the basal ends of some small individuals (usually those > 3 m in height) at each measurement

interval.

Stem Analysis

Small individuals (usually those  $\leq$  3 m in height) and terminal leaders of larger individuals were aged by counting the number of terminal bud scale scars preceding each height interval. The accuracy of bud scale counts on small individuals was checked by counting rings on the basal and 0.25 m stem sections (typically the most difficult portion of the stem to age by counting bud scale scars) on a subsample of stems using a dissecting microscope. Aqe determinations for the two methods seldom differed by more than  $\pm$  2 years and then only on individuals > 2 cm basal diameter. Stem sections from larger individuals were sanded to a smooth surface and wetted to aid ring examination. Ring number was counted on two radii (typically a long and short axis on oblique-shaped stems) of each section under a dissecting microscope. The greater of the two ages, if they differed, was recorded.

Section ages were used to reconstruct the height growth history (time of establishment and years to reach a given height) of each sampled individual. Height increment (in meters) for the five year period immediately prior to sampling was determined for each sampled ramet. Height increments over consecutive five-year stand-age intervals, beginning 10 years after stand initiation, were determined for all bigtooth aspen and selected overstory red maple. In

some instances interpolation of stem height at a given stand age was required since the stem sampling method controlled stem height but not age. When this was required, the shape of age-height plots for the individuals involved were examined to insure accurate determination of height at the five-year stand-age of interest.

### Data Analysis

The number of years to understory reinitiation and red maple and bigtooth aspen ages and heights were compared among stands using one-way analysis of variance. All data sets met the assumption of normality of residuals (Shapiro-Wilk test for small sample size, P > 0.1; Gill 1978), but some did not meet the assumption of homogeneous variances ( $F_{max}$  test, P < 0.25). Since the overall F-tests were not significant for any of the data sets with heterogeneous variances no conservative corrections were used. For data sets where the overall F-tests were significant, individual stand means were separated using Tukey's tests.

Paired t-tests were used to compare several attributes of matched red maple and bigtooth aspen on each plot, including ages, heights, growth rates, and height increments. All data sets met the assumption of normality of residual differences (Shapiro-Wilk test, P > 0.1).

Temporal trends in height increment of bigtooth aspen and selected overstory red maple were examined over consecutive five-year stand-age intervals using complete

block repeated measure analysis of variance, where each stem was a block and time period was the repeated measure. Height increments were transformed, as ln(y+1), to the meet assumption of normality of residuals. Because of concern over heterogeneous variance-covariance matrices even after transformation (sphericity assumption rejected for all data sets, P< 0.25) the highly conservative Greenhouse-Giesser degrees of freedom was used to test time period effects. This adjustment reduces degrees of freedom for the F-test from p-1 and (p-1)(r-1) to 1 and r-1, where p is the number of time periods and r is the number of replicates (Gill 1988). Contrasts of mean height increment between specific time periods (or combinations of time periods) were performed using Bonferroni t-tests, modified for heterogeneous variance-covariance structure (Gill 1988).

Correlation analysis was used to examine relationships between stem age, height and height increment. Spearman's rank correlation was used because most data sets failed to meet the assumption of bivariate normality required for parametric correlation analysis. For some of these analyses, stems were pooled across plots in each stand. Pooling was justified since the "mensurational treatments" of age, height or height increment were attributes of individual stems rather than plots. For all statistical analyses, a probability of type-one error 0.05 was considered significant.

#### RESULTS

Forest Composition

The overstories of all stands were dominated by bigtooth aspen (Table 6.1). Individual ramets differed in age by no more than three years both within and among stands (65-68 years). Mean age was not significantly different among stands (P> 0.9, Table 6.2). Site index for bigtooth aspen (50 year base) was not significantly different among stands 1, 3, 4 and 5 (P> 0.05; Table 6.2). The site index for stand 2 was significantly less than all other stands (P< 0.05; Table 6.2).

Later successional species of lesser importance in the overstories of all stands included red maple and red oak (Table 6.1). Additional minor overstory species found in some stands included black oak (<u>Quercus velutina</u> Lam.), white oak, paper birch (<u>Betula papyrifera</u> Marsh.), white ash (<u>Fraxinus americana</u> L.) and black cherry (<u>Prunus serotina</u> Ehrh.; Table 6.1). Red maple contributed 7-18% of total overstory basal area in the five stands.

The majority of saplings and seedlings in all stands were red maple (Table 6.3). Relative densities ranged from 91-100% and 62-90% for the two strata, respectively. Additional species, including red oak, white oak, black oak, black cherry, white ash, and paper birch, were of only minor importance in the understory of some stands (Table 6.3).

St	and:	1	2	3	4	5
Species			Bas	al Area (m <sup>2</sup> /h	a)	
Bigtooth aspen Red maple Red oak Black oak	34.5 5.3 3.2	$(4.7)^{\underline{b}}$ (1.2) (1.1)	23.0 (2.6) 3.3 (0.7) 7.2 (2.5)	27.7 (1.8) 4.8 (1.0) 5.8 (1.7) 0.7 (0.6)	34.1 (3.7) 8.2 (1.1) 2.5 (1.2)	32.4 (7.7) 3.2 (0.7) 8.9 (2.9) 1.6 (0.7)
White oak Paper birch White ash Black cherry	0.2	(0.2) - - -	0.1 (0.1) - - -	- - -	0.2 (0.2) 0.2 (0.3) 0.1 (0.1)	1.1 (0.7) - - -
Total basal area: Total density (#/)	43.2 ha): 1158	(4.6) (88)	33.5 (1.0) 1398 (55)	38.9 (2.0) 996 (58)	45.3 (2.4) 1011 (89)	47.1 (6.7) 1021 (112)

Table 6.1. Overstory composition<sup>a</sup> and structure of five bigtooth aspen-dominated stands within the Huron-Manistee National Forest.

 $\underline{a}_{Dbh} > 10 \text{ cm}$ .  $\underline{b}_{Values}$  are the means (<u>+</u> SE) of four plots.

Table 6.2. Age and site index of bigtooth aspen in five stands within the Huron-Manistee National Forest and analysis of variance for comparisons among stands.

Stand	Age	(years)	Site Index (m at 50 years)
1	66	(0.4) <sup>a</sup>	21.1 (0.3)a <sup>*</sup>
2	66	(0.4)	17.0 (0.5)b
3	66	(0.5)	21.2 (0.6)a
4	66	(0.6)	23.6 (0.9)a
5	66	(0.6)	22.2 (1.0)a

 $\frac{a}{*}$ Values are the means (<u>+</u> SE) of four observations. \*Values followed by the same letter were not significantly different at P=.05.

<u></u>		Age		Site Index	ζ
Source	df <sup>b</sup>	SSC	P > F	SS	P > F
Stands Error	4 15	0.700 16.500	0.96	97.823 28.795	0.0001

 $\underline{b}$ df= degrees of freedom, SS= sum of squares.

			5	apling <sup>a</sup>		
	······			Stand		4
	1		2	3	4	5
Species			<u>s</u>	tems/ha		
Red maple Red oak Black cherry White ash	496 (14 - - -	49) <u></u> 377 28	(118) 12 (18) -	41 (149) 19 (19) 46 (28) 19 (19)	368 (98) 28 (28)	735 (126) 19 (19) 19 (19) -
Sur	n <b>: 496 (</b> 2	149) 405	(106) 13	25 (173)	396 (106)	773 (154)

Table 6.3. Sapling and seedling densities by species in five bigtooth aspen-dominated stands within the Huron-Manistee National Forest.

Table 6.3 (cont'd)	).
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	,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,			Seedling <sup>C</sup>		
Species		1	2	Stand 3 <u>Stems/m</u> <sup>2</sup>	4	5
Red maple Red oak White oak Black oak Paper birch Black cherry White ash		7.4 (1.3)  0.4 (0.2)  0.2 (0.1)  -  0.7 (0.3)  -  -  -  -  -  -  -  -  -  -	$\begin{array}{cccc} 4.2 & (0.6) \\ 0.5 & (0.2) \\ - \\ - \\ 0.1 & (0.1) \\ - \\ - \\ - \\ - \\ - \\ - \\ - \\ - \\ - \\ -$	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	5.4 (0.8) 0.2 (0.1) - - 1.9 (0.7)
	Sum:	8.8 (1.7)	4.8 (0.4)	9.0 (1.7)	11.8 (2.3)	7.5 (1.2)

 $\frac{a}{2.5}$  cm  $\leq$  dbh  $\leq$  10 cm.  $\frac{b}{2}$ Values are the means (<u>+</u> SE) of four plots.  $\frac{c}{2}$ Dbh < 2.5 cm.

Red Maple Age Structure

The age distributions for red maple  $\geq$  1.5 m tall reflect two clearly defined cohorts (Fig. 6.1). Individuals in the first cohort established within the first ten years of stand development and ranged in age from 60-70 years at the time of sampling. Ninety percent of the genets sampled in the this cohort were apparently of sprout-origin. Most ramets were from multi-stemmed genets that had branched from stumps or root collars. Additionally, many ramets were growing in a circular arrangement or had crescent shaped stem bases, both of which are indicative of development around remnant stumps. The extent of ramification within this cohort (hereafter referred to as the sprout-origin cohort) is reflected in the high ramet to genet ratios for the five stands (2:1-3:1).

Mean age of individuals in the sprout-origin cohort was not significantly different among stands (P> 0.5, Table 6.4). Additionally, there was not a significant difference between the age of the bigtooth aspen and red maple (mean of all individuals in the cohort) on each plot (paired t-test:  $t_s=0.479$ , df=19, P> 0.5; Table 6.5). Of the 20 plots examined, eight had at least one red maple that was three or four years older than the sampled bigtooth aspen on the plot. An additional five plots had at least one red maple that was one or two years older than the sampled bigtooth aspen. Only one plot did not have a red maple at least as old as the sampled bigtooth aspen.

Figure 6.1. The number of new red maple individuals establishing as a function of stand age in five bigtooth aspen-dominated forests within the Huron-Manistee National Forest.

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Table 6.4. Mean age and height of red maple sproutorigin cohorts in five bigtooth aspen-dominated stands within the Huron-Manistee National Forest and analysis of variance for comparisons among stands.

Stand	Age (years)	Height (m) at 70 years after stand initiation
1	67 (0.6) <sup>a</sup>	17.4 (0.6)
2	67 (0.6)	17.3 (1.7)
3	66 (0.1)	18.6 (1.3)
4	66 (0.4)	18.6 (1.0)
5	66 (0.4)	16.3 (0.6)

Age Height

 $\underline{a}$ Values are the means ( $\pm$  SE) of four observations.

df<sup>b</sup> Source SS P > FP > FSS Stands 4 15.292 0.57 2.257 0.64 Error 15 76.233 13.313

 $\underline{b}$ df= degrees of freedom, SS= sum of squares.

Table 6.5. Mean age and height of bigtooth aspen and sprout-origin red maple on 20 plots within the Huron-Manistee National Forest.

			Height (m) at 70
Species	Age	(years)	After Stand Initiation
Bigtooth aspen	66	(0.2) <sup><u>a</u></sup>	24.8 (0.5)
Red maple (all stems pooled by plot)	66	(0.2)	17.6 (0.5)
Red maple (tallest)	66	(0.3)	21.5 (0.8)
Red maple (shortest)	66	(0.5)	14.4 (0.6)

 $\underline{a}$ Values are the means (<u>+</u> SE) of 20 observations.

The second red maple cohort was composed of individuals  $(\geq 1.5 \text{ m tall})$  that began establishing approximately 30-35 years after stand initiation (assuming stand age=70 years; Across all five stands, there were only six Fig. 6.1). surviving individuals that established between 10 and 30-35 years after stand initiation (stands 2, 4 and 5; Fig. 6.1). All individuals in the second cohort were apparently of seedling-origin. The total number of individuals in this portion of the red maple population (hereafter referred to at the seedling cohort) was obviously variable among stands (Fig. 6.1). However, the mean number of years for 10% of the cohort to establish (from the year of bigtooth aspen establishment on each plot) was similar (34.3-38.3 years, all standard errors < 1.7) and not significantly different among stands (F = 2.017, P = 0.17).

The age of individuals within the subsample of stems less than 1.5 m tall ranged from 1 to 30 years. Mean age for these individuals, stratified by 0.5 m height classes, are shown in Table 6.6. It is clear that with inclusion of this segment of the population, the establishment period for the second red maple cohort had continued through the time of sampling. Additionally, since so few surviving individuals exceeding 1.5 m in height established prior to a stand age of 35 years, it is highly unlikely that any unsampled individuals less than 1.5 m tall at the time of sampling, established more than 35 years ago.

Table 6.6. Mean age of red maple seedlings less than 1.5 m tall, stratified by 0.5 m height classes, in five bigtooth aspen-dominated stands within the Huron-Manistee National Forest.

	Height Class (m)				
Stand	0-0.5	0.5-1.0	1.0-1.5		
	Age (years)				
1	11 $(0.1)^{\underline{a}}$	15(1.5)	20 (2.1)		
3	11 (1.3)	16 (4.6)	17(2.1) 17(7.1)		
4	13 (2.5)	19 (3.0)	23 (4.6)		
5	10 (2.6)	17 (2.7)	20 (1.5		

 $\underline{a}$ Values are the means ( $\pm$  SE) of four observations.

Red Maple Height Structure

Mean height of the red maple sprout-origin cohort was not significantly different among stands (P> 0.6, Table 6.4). Within stands and plots, heights were highly variable, as shown by the individual height growth profiles for one randomly selected plot from each stand (Fig. 6.2). There was virtually no difference in age of the tallest and shortest stem from the sprout-origin cohort on each plot  $(t_s=0.894, df=18, P> 0.3;$  Table 6.5), although the mean (+ SE) height range for this comparison was 7.3 (0.1) m. Overall, differences in stem age contributed very little to height variation. Correlations between stem age and total height were low and non-significant ( $r_s$ = 0.09-0.25, P> 0.2) for three of the five stands, while in the other two, the correlations were weak (rs= 0.56, P< 0.02) or of the wrong sign ( $r_s = -0.42$ , P< 0.04), assuming that older stems should have been taller.

On most of the plots examined, the sampled bigtooth aspen equaled and usually exceeded most of the red maple in height throughout the 70 year period examined (for examples, see Fig. 6.2). The mean height difference at 70 years was highly significant (bigtooth aspen versus the mean of the red maple sprout-origin cohort on each plot;  $t_s = 11.08$ , df= 19, P< 0.001; Table 6.5). However, of the 20 plots examined, four had at least one red maple that equaled ( $\pm$  0.3 m) or exceeded (> 0.3 m) the sampled bigtooth aspen in height by 70 years. Eleven plots had at least one red maple that was

Figure 6.2. Height growth reconstructions of individual bigtooth aspen and sprout-origin red maple within one randomly selected plot from each of five bigtooth aspen dominated-stands within the Huron-Manistee National Forest. Each line represents an individual stem.

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Figure 6.2


only 0.3-3 m shorter than the sampled bigtooth aspen on the plot. While heights of the sampled bigtooth aspen and the tallest red maple on each plot were still significantly different ( $t_s$ = 4.99, df= 19, P< 0.001), means for this comparison were much closer, relative to the entire sproutorigin red maple-bigtooth aspen comparison (Table 6.5).

Total heights within the seedling cohort showed a stronger relationship to stem age than was the case for sprout-origin individuals. This can be seen by examining one randomly selected stem age-height plot from each of the (Fig. 6.3). The five stands mean (<u>+</u>sd) plot-level correlation between stem age and total height of seedlings (including the subsample of individuals < 1.5 m in height) All correlations coefficients was 0.63 (0.09). were significant at P $\leq$  0.01. In general, stems from roughly the upper two-thirds of the age distributions were taller than the youngest stems. Within these portions of the age distributions, variability in height among similar aged individuals was a significant feature of the seedling-cohort (Fig. 6.3).

## Red Maple Height Growth Patterns

Obviously, differences in height growth rate about specific stem ages within the both the sprout-origin and seedling cohorts led to the variable height patterns. Height growth rate variability was assessed in greater detail by examining relationships between the competitive Figure 6.3. The relationship between stem age (years) and total height (meters) for individual seed-origin red maple in five bigtooth aspen-dominated stands within the Huron-Manistee National Forest. One randomly selected plot from each of the five stands is shown. In each plot, height classes above the dotted line were completely sampled. Height classes below the dotted line were randomly subsampled.



status of an individual, as reflected by its relative height, and recent patterns of height increment.

Within the sprout-origin cohort, correlations between height increment (in meters) over the five-year period immediately prior to sampling and initial height at the beginning of this period were low ( $r_s$ = -0.08-0.40) and nonsignificant (P= 0.07-0.76) in four of the five stands. This same correlation was higher ( $r_s$ = 0.57) and significant (P= 0.02) in the fifth stand, indicating that some taller overstory red maple were growing faster than shorter conspecifics.

Within the seedling cohort, correlations between initial height and height increment within each plot were moderately high (mean  $(\pm sd)$  $r_{c} = 0.60$  $(\pm 0.24)),$ again indicating that some taller individuals often grew faster than shorter stems (for examples see Fig. 6.4). The three lowest correlation coefficients  $(r_s=0.19-0.37)$ were associated with plots having low maximum initial heights (0.8-1.9 m), relative to the remaining plots (initial heights= 2.2-5.5 m). After excluding these three plots, the mean (+sd) correlation coefficient was 0.68 (0.08). All of the 17 remaining correlations were significant (P< 0.001-0.0001).

Relationships between stem age and height growth rate within the seedling-origin cohort were examined in greater detail by focusing only on the fastest growing stems that were at least 1.5 m in height at the time of sampling. Figure 6.4. The relationship between height increment (meters) over the five-year period immediately prior to sampling and initial height (meters) at the beginning of this period for individual seedlingorigin red maple in five bigtooth aspen-dominated stands within the Huron-Manistee National Forest. One randomly selected plot from each of the five stands is shown.

Figure 6.4



These individuals are those forming the upper bounds of the age-height diagrams (Fig. 6.3). For each stand, the fastest growing individual on a plot was selected from consecutive five-year stem-age classes (for example 0-5 years old, 6-10 years old, etc.) and examined for i) its recent height increment (over the 5-year period prior to sampling), and ii) its growth rate over the first 1.5 m, the height interval shared by all stems. Plots were pooled within stands because of the low number individuals from the fiveyear age classes within each plot. Among stands, the relationship between stem age and recent height increment was inconsistent. Correlation coefficients for two of the stands were weak and negative ( $r_s = -0.59$ , P= 0.01;  $r_s = -$ 0.24, P= 0.42). In the others, the coefficients were either low and non-significant ( $r_s = 0.17$ , P> 0.50) or weak ( $r_s =$ 0.54 and 0.58, P= 0.005). These correlations indicate that the individuals with the fastest rates of recent height growth were not restricted to specific portions of the age distributions. In contrast, there was a strong  $(r_s = -0.69 -$ 0.95) and significant (P< 0.006-0.0001) inverse relationship between stem age and growth rate over the first 1.5 m in all stands (Fig. 6.5), indicating that the individuals with the fastest rates of early height growth were often the youngest stems.

# Temporal Patterns of Overstory Height Increment

The pattern of red maple seedling establishment, beginning 35-38 years after stand initiation (Fig. 6.1), and

Figure 6.5. The relationship between stem age (years) and height growth rate (m/yr) over the first 1.5 m for the fastest growing seedling-origin red maple in five bigtooth aspen-dominated stands within the Huron-Manistee National Forest. For each stand, the fastest growing individuals from consecutive five-year stemage classes (i.e. 5-10 years old, 10-15 years old, etc.) within each of four plots were pooled for analysis.

Figure 6.5



the inverse relationship between stem age and early growth rate (Fig. 6.5), suggests that understory reinitiation might be negatively related to patterns of overstory growth. Specifically, understory reinitiation might occur concurrently with decreasing height growth of overstory individuals, particularly bigtooth aspen. This hypothesis was tested by examining temporal patterns in height increment of bigtooth aspen over consecutive five-year periods. The height growth patterns of the fastest growing and the median growing sprout-origin red maple in each plot were also examined. Analyses of growth increments were begun 10 years after stand initiation, the stand age by which all sampled bigtooth aspen and overstory red maple had established. Contrasts of overstory height increment between stand ages of: 1) 10-35 years and 35-70 years; 2) 25-30 years and 30-35 years; and 3) 30-35 years and 35-40 years were conducted in an attempt to clarify overstory growth patterns relative to patterns of understory development

In general, the trend in height growth of bigtooth aspen and red maple over the sixty-year period was one of increasing growth increment between 10 and 30 years after stand initiation, followed by decreasing increment for the remainder of the period (Fig. 6.6). Time effects were significant in all three cases ( $P \le 0.025$ ; Table 6.7). Mean height increment over a stand age of 10-35 years was significantly greater than height increment over 35-70 years in all cases (P < 0.01-0.001; Table 6.7). Mean height

Figure 6.6. Height increments (m) over consecutive fiveyear stand-age classes, beginning 10 years after stand initiation, for bigtooth aspen and sprout-origin red Values are back-transformed means maple. (± 95% confidence intervals) of 20, 18 and 19 log-transformed observations for bigtooth aspen, the fastest growing red maple on each plot and the median growing red maple on each plot, respectively. In each graph, the bottom point of the inverted triangle indicates the year after stand initiation (mean of five stands) by which 10% of the seed-origin red maple  $\geq$  1.5 m tall had established. The single open triangle at the right end of each graph is the mean (+ 95% confidence intervals) height increment of the fastest growing seedling-origin red maple over a stand age of 65-70 years.



					5	Species					
Source	Bigtooth aspen			Red maple (fast)				Red maple (median)			
	df <u>a</u>	SS	P > F	df		SS	P > F	df		SS	P > F
Plot Time	19 11 (1) <u>b</u>	0.777 9.094	<.0001	17 11	(1)	1.475 5.766	<.0001	18 11	(1)	0.827 3.805	<.0001
Error	209 (19)	8.081	(	187	(17)	10.136	(.01)	198	(18)	10.721	(.023)
		Bigtooth Aspen			Red Maple (fast)			Red Maple (median)			
Stand ages (years)		tj	⊵⊆ ₽>	F		t <u>b</u>	P > F		t <u>b</u>	P >	F
10-35 v 25-30 v 30-35 v	s 35-70 s 30-35 s 35-40	18.3 4.4 -0.0	148 < 0.0 482 < 0.0 011 > 0.5	)01 )01 500		3.584 3.511 -2.245	< 0.01 < 0.01 > 0.10		4.04 0.17 1.41	$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	005 500 250

Table 6.7. Repeated measure analysis of variance and specific contrasts for height increment across time in bigtooth aspen and sprout-origin red maple.

adf= degrees of freedom, SS= sum of squares.

<sup>a</sup>Values in parentheses are adjusted df and probabilities associated with the Greenhouse-Giesser conservative F-test.

 $\underline{C}t_{\underline{b}}$ -values are for Bonferroni contrasts. Critical value=  $\pm t_{\underline{b}}$  alpha/2, 3, df<sub>error</sub>.

increment over 25-30 years was significantly greater than height increment over 30-35 years for the bigtooth aspen and the faster growing red maple (P< 0.01-0.001; Table 6.7), but not for the slower growing red maple (P> 0.50; Table 6.7). Mean height increment over stand ages 30-35 years and 35-40 years were not significantly different for any contrast (P> 0.10-0.50).

Figure 6.6 also shows the mean recent height increment (over a stand age of 65-70 years) for the fastest growing understory red maple relative to bigtooth aspen and overstory red maple. The understory individuals ranged from 5 to 35 years of age at the time of sampling. Height increment of the understory stems was significantly greater than that of both overstory red maple groups over a stand age of 65-70 years (fast:  $t_{\underline{S}}$ = 2.30, df= 17, P< 0.05; median:  $t_{\underline{S}}$ = 2.73, df= 18, P< 0.02), but was not significantly different from that of bigtooth aspen ( $t_{\underline{S}}$ = 0.83, df= 19, P> 0.40).

#### DISCUSSION

Origin of the Red Maple Sprout Cohort

Red maple was historically a minor overstory component of the presettlement pine forests of the northern Great Lakes region. Reconstructions of these forests in Michigan and Wisconsin, using General Land Office survey records, indicate that red maple comprised no greater than seven percent of the bearing and line trees used to locate section lines (Whitney 1986; Nowacki <u>et al</u>. 1990; Chapter 3), but

was more abundant in the understory of these forests (Whitney 1986).

In all of the stands examined, the older red maple cohort was largely composed of sprout-origin individuals. proportions of sprout-origin Hiqh individuals within overstory red maple populations have been reported for mature bigtooth aspen-dominated forests elsewhere in northern Michigan (Roberts and Richardson 1985; Sakai et al. 1985), mixed hardwood forests in the Southern Appalachians (Beck and Hooper 1986), and presumably is true for red maple in oak forests that developed after clearcutting in the northeastern United States (Lorimer 1984).

Red maple genets survive and resprout readily from root collars and stumps following fire or cutting (Fowells 1965). Swan (1970) found no mortality of root systems following surface fires in oak-dominated forests. Scheiner et al. (1988)reported hiqh survival of genets following experimental clearcutting and burning of a 70 year old bigtooth aspen forest. Additionally, they found no new genets establishing over the first four post-fire years the stand was examined, despite a nearby seed source.

Sprout-origin individuals examined in the present study may have developed from root systems remnant from the original presettlement pine forests that occupied these sites, rather than from individuals which established from seed after removal of the pine overstory. This hypothesis is suggested by the data from Swan (1970) and Scheiner <u>et</u> <u>al</u>. (1988) and observations on the spatial pattern of ramets in the current study, which indicated resprouting from large diameter stumps or root collars. Early height growth rates of the sprout-origin individuals in the present study provide some additional evidence for this hypothesis. The height of sprout-origin red maple at three years of age (mean  $\pm$  SE= 0.59  $\pm$  0.04 m) was approximately one-half of values reported for much younger and smaller sprout-origin red maple growing on dry, rocky soils in the northeastern United States (Kays and Canham 1991). It is known that both production and growth rate of red maple vegetative sprouts are negatively related to the age and size of the parent stump or root system (Solomon and Blum 1967; Kays and Canham 1991).

## Red Maple Age Structure

The age distribution of the red maple populations examined in this study (Fig. 6.1) clearly reflect the model of even-aged stand development proposed by Oliver (1981). In all of the stands examined, stand initiation was marked by rapid establishment of the initial overstory red maple within a ten-year period, beginning 70 years prior to sampling. This occurred concurrently with establishment of bigtooth aspen (and all other overstory species; Chapters 4, 5) predominantly via resprouting. Stand initiation was followed by a period of stem exclusion lasting approximately 25 years, after which time red maple, and virtually no other

species, began to establish from seed in the understory. Red maple seedling establishment had continued through the time of sampling (stand age= 70 years). Similar patterns of delayed seedling establishment subsequent to stand initiation have been reported for mesic aspen-dominated forests in northern Michigan (Sakai 1990a; Sakai et al. 1985; Roberts and Richardson 1985), pine-dominated forests in the northeastern and southeastern United States (Tarbox and Reed 1924; Peet and Christensen 1987; Christensen and Peet 1981), and coniferous forests in Alaska and the Pacific Northwest (Alaback 1982a; Oliver et at. 1985; Harcombe 1986; Fried et al. 1988).

## Understory Reinitiation and Overstory Development

Roberts and Richardson (1985) discuss relationships between overstory development and understory reinitiation in aspen-dominated forests of northern Michigan. They suggest that on xeric or highly disturbed sites with low overstory stocking, canopy closure is delayed or incomplete, which in turn allows continuous understory establishment. Indeed, an earlier study found continuous establishment of several later successional species in a understocked bigtooth aspendominated forest that had initiated following cutting, grazing, and fire in a northern hardwood community (Chapter 2). On more favorable sites they suggest that seedlings of tolerant, later successional tree species, including red maple, can establish and increase in height under a closed

canopy. However, recent theoretical and empirical evidence indicates that canopy closure does not remain complete for extended periods of time, even in fully stocked even-aged stands (Zeide 1987, 1991). Rather, maximum canopy closure should be reached asymptotically, early in the course of stand development, followed by a subsequent decrease. The decrease is attributed to a combination of overstory thinning and a decreasing rate of canopy expansion in surviving dominant individuals.

In the present study, the significantly lower height increment in bigtooth aspen, and in overstory red maple, beginning immediately prior to understory reinitiation (Fig. 6.6), suggests a stand-level crown-growth reduction that, coupled with overstory thinning, may result in decreased canopy closure and increased resource availability in the understory. Red maple seedling reinitiation in aspen understories may be dependent on this reduction in canopy This is consistent with the belief that understory closure. development should be negatively correlated with overstory production (Alaback 1982a; Oliver and Larson 1990) and that canopy closure in even-aged stands should begin to decrease immediately after the period of maximum height increment in canopy dominants (Zeide 1987, 1991). A continued increase in understory resource availability, over the time period examined, is suggested by the inverse relationship between age and early height growth rates of the fastest growing red maple seedlings (Fig. 6.5). Changes in seed rain, as sprout-

origin red maple become reproductively mature, may also influence the pattern of seedling establishment.

Increasing light availability during the course of stand development may be a major factor controlling understory reinitiation and development in these and other even-aged forests (Oliver et al. 1985; Alaback 1982a,b; Fried <u>et</u> <u>al</u>. 1988). However, the results of classic trenching experiments (Toumey 1929; Toumey and Kienholz 1931) indicate that understory development can occur even during the peak of stem exclusion, if root competition is reduced. This suggests that increasing soil resource availability during stand development is also an important factor influencing establishment, survival and recruitment of new stems in the understories of even-aged forests. Experimental manipulation of light and soil resource availability will be required to adequately define the mechanism driving understory reinitiation.

#### Red Maple Height Structure

Once established, height growth among individual genets was highly variable in both the sprout and seedling cohorts. For the former, heights at the time of sampling were not particularly dependent on stem age. Height differentiation within the even-aged overstory was more likely a function of differences in microsite-related resource availability, vigor of parent root systems, genetic potential, and the competitive status of individuals (Peet and Christensen

1987; Oliver and Larson 1990). The latter has been shown to particularly important factor leading to be а height differentiation and stratification within and among populations of similar-aged trees (Stubblefield and Oliver 1978; Wierman and Oliver 1979; Guldin and Lorimer 1985: Kelty 1936; Smith 1986; Hix and Lorimer 1990, 1991; Oliver et al. 1990; Oliver and Larson 1990). For example, Hix and Lorimer (1990) found significant, positive relationships between relative height and short-term rates of height growth for several hardwood species. Relative height can be indicative of an individuals ability to compete for light because of the positive relationship between levels of radiation and height in the canopy (Assmann 1970; Hutchison and Matt 1977; Cole and Newton 1986). In the present study, the generally weak relationship between initial height and height increment in sprout-origin red maple suggests that position within the overstory was not an overly important factor influencing growth rate late in stand development, probably because all but the tallest red maple were inhibited competitively by taller bigtooth aspen. Competitive inhibition may have occurred through direct physical abrasion of the terminal leaders of shorter red maple by bigtooth aspen, a mechanism that has been found to limit height growth in both deciduous and coniferous species (Oliver 1978; Wierman & Oliver 1979; Kelty 1986).

Heights of individuals in the seedling cohort were more dependent on stem age. This is not surprising given the

greater age range of the cohort (> 30 years) compared to the sprout-origin individuals (10 year age range). Still, the observed variation in height among similar-aged individuals within the cohort suggests that competitive ability differed greatly among stems. In general, the tallest stems were at an competitive advantage in terms of recent height growth rate, but these were not always the oldest individuals. In fact, among the fastest growing members of the cohort. the individuals with the highest rates of height growth were sometimes the youngest stems. This indicates that position beneath the overstory may be an important factor influencing height growth of understory stems, even prior to the formation of large treefall gaps. It is clear that height variation developed prior to the formation of large treefall gaps, since all the stands examined were characterized by very high basal areas  $(33-47 \text{ m}^2 \text{ at } 66 \text{ years}; \text{ Table 6.2})$  and very few large downed boles were observed. This suggests that availability of resources, at levels required for seedling establishment, survival and early recruitment, may initially be related to factors other than mortality of mature overstory individuals. These additional factors could include the distribution, growth rates and species of dominant overstory individuals, patterns of branch and root mortality in overstory dominants, and competitive interactions with understory herbs and shrubs (Oliver and Larson 1990). Differential browsing pressure may also be important. Similar conclusions were reached by Fried et al.

(1988) to explain height variation within populations of big-leaf maple in even-aged Douglas-fir stands.

It is important to distinguish between the period of stand development during which seedlings of overstory tree species begin to establish and are able to survive and grow slowly in height in the forest understory (understory reinitiation sensu Oliver 1981), and a later developmental period characterized by increased mortality of the original even-aged overstory (old-growth phase sensu Oliver 1981). It is during the latter period that a significant amount of recruitment of more tolerant species to canopy positions from the understories of even-aged stands typically occurs (Alaback 1982a; Oliver 1981; Oliver et al. 1985; Roberts and Richardson 1985; Harcombe 1986; Peet and Christensen 1987). However, as the data show, initial establishment and recruitment to larger seedling or sapling height classes may occur much earlier. This mode of even-aged development is not well addressed by stand development models stressing overstory mortality and the availability of treefall gaps, late in an even-aged sequence, as the trigger for understory reinitiation and early recruitment (see, for example, Bormann and Likens 1979; Peet and Christensen 1987).

## Landscape Patterns

The five stands examined in this research were located within an 18 km<sup>2</sup> bigtooth aspen-dominated landscape. Overstory age data clearly show that all stands were

approximately 66 years old and may have initiated after the same major post-logging wildfire. Although red maple population size was variable among stands, the age and height structures of the populations were very similar. This was true despite some difference in bigtooth aspen site index among stands.

The similarity of red maple population structure among the stands examined may be the result of landscape-wide similarities in the historical circumstances leading to stand initiation. Pickett (1989) has emphasized the important role historical circumstances have on successional While the present study examined only a portion pathways. of the total forest community, the data suggest that the historical circumstances leading to the development of the five stands, including frequency and intensity of cutting, subsequent fire, loss of pine seed sources and advance regeneration, and survival of bigtooth aspen and red maple rootstocks, were apparently very similar. The results of this study compared to earlier work, where continuous recruitment of several tree species beneath bigtooth aspen occurred (Chapter 2), further support the notion that historical circumstances play a major role in how stands develop through time.

# SUMMARY AND CONSLUSIONS

The results of several studies from the eastern United States indicate that red maple is becoming an increasingly

overstory component in forests historically abundant dominated by oak (Lorimer 1984; Heiligmann et al. 1985; Hix and Lorimer 1991b: Abrams and Nowacki 1992). Such a transition should occur much faster in aspen-dominated forests of the Great Lakes region because of the taxon's much shorter life span relative to oak. However. the potential for future overstory dominance by red maple on drv-mesic sites in the Great Lakes region has been Inherently slow growth rate of both seedling questioned. and sprout-origin individuals (Graham et al. 1963) and an inability to survive without the protection of a heatreducing nurse canopy (Aber et al. 1982; Pastor et al. 1982) have been cited as factors that will prevent significant overstory recruitment. While height growth rates of red maple in the present study were variable, and quite low for some individuals, the data clearly show that sprout-origin red maple can reach dominant-codominant canopy positions on the sites examined. Further, rates of height growth for the tallest individuals approached those of bigtooth aspen. Unlike sprout-origin stems, seedling-origin red maple may fail to recruit to dominant canopy positions. While height growth rates for the most vigorous members of the seedling cohort did equal or exceed height growth of both bigtooth aspen and overstory red maple over the same stand ages, these growth rates were still much lower than those of the overstory individuals over comparable stem ages. However, the low growth rates of seedlings in the understory may

simply be the result of resource limitation. Seedling-origin red maple may be successful at attaining dominant canopy positions in gaps produced by the breakup of the current bigtooth aspen overstory. Additional overstory recruitment may also be favored by red maple's ability to respond with increased growth upon release (Gerrard 1969; Oliver and Stephens 1977; Lorimer 1980). Barring future changes in the composition of seed rain, increasing later successional importance and self-replacement of shade-tolerant red maple is suggested by its overwhelming dominance in the understories of the stands examined.

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