LEGACIES OF FOREST MANAGEMENT AND FIRE IN MIXED-PINE FOREST ECOSYSTEMS OF THE SENEY NATIONAL WILDLIFE REFUGE, EASTERN UPPER MICHIGAN

A Thesis

Presented in Partial Fulfillment of the Requirements for the Degree Master of Science

in the Graduate School of The Ohio State University

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2008

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ABSTRACT

Red pine (*Pinus resinosa* Ait.) and eastern white pine (*Pinus strobus* L.) are major components of mixed-pine forest ecosystems of eastern Upper Michigan. Following European settlement, the distribution of these forests were greatly reduced due to past timber harvesting, agricultural conversion, and fire-suppression practices. Consequently, these forest ecosystems are of great conservation priority and in need of restoration. Before we can develop restoration strategies for these ecosystems, more detailed information on their successional dynamics is needed, including a better understanding of how past timber harvesting has influenced forest ecosystem development. In particular, an understanding of how forest ecosystems respond to a frequent surface fire-return interval is needed. We examined age structure and radial growth patterns, and related these patterns to known fires in old-growth mixed-pine stands in the Seney Wilderness Area, an area with old-growth mixed-pine forests. These results suggest that natural fire appears to effect radial growth of surviving trees negatively for several years following the fire, but also allows for some individuals to show increased growth as well as promoting the establishment of pine seedlings.

ACKNOWLEDGMENTS

I would like to thank my co-advisors, Dr. Charles Goebel and Dr. David Hix, for their support and encouragement. I also appreciate the helpful comments from my third graduate committee member, Dr. Dawn Ferris. Thank you to Dr. Greg Corace for providing support and assistance during data collection at Seney. Thank you to the many people involved in the inventory process including: James Downs, Seney National Wildlife Refuge staff and Dr. Igor Drobyshev. Finally, I would like to thank the administration and faculty of the School of Environment and Natural Resources for their support and opportunity to be a Graduate Teaching Associate.

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CHAPTER 1

INTRODUCTION

Prior to European settlement, mixed-pine forest ecosystems, dominated primarily by eastern white pine (*Pinus strobus* L.), red pine (*Pinus resinosa* Ait.) and jack pine (*Pinus banksiana* Lamb.) comprised an estimated 39% of eastern Upper Michigan (Zhang et al. 2000). Throughout the northern Lake States where mixed-pine forest ecosystems occurred, these pine stands were likely maintained by stand-replacing crown fires (Heinselman 1973, Bergeron and Brisson 1990). However, in eastern Upper Michigan these forests were maintained by low- to moderate-intensity surface fires occurring on average every 28 years (Drobyshev et al. 2008).

Past anthropogenic practices have resulted in a shift in forest composition and structure. Following European settlement in the mid-1800s, the large-scale logging of mixed-pine forests resulted in the harvesting of many eastern white pine and red pine from 1885-1900 (Graham 1941). Following these timber harvesting activities, the slash left behind resulted in high fuel loads which contributed to catastrophic wildfires in the region (Schulte et al. 2007). The extent of the mixed-pine forests diminished as many mature red pine and eastern white pine seed trees were harvested and the repeated slash wildfires caused high mortality of red pine and eastern white pine seedlings (Whitney 1987). In addition to catastrophic slash wildfires, many areas of the Lake States were converted to agriculture (cropland and pasture) once the forest was removed (Bielecki et al. 2006). However, the climate of this region was not conducive to farming after much of the organic soil layers were either consumed in the fires or were eroded away by the wind after they dried (Losey 2003). Also affecting the shift in forest composition and structure, active fire suppression since the early 20th century has changed the natural frequency of fire in Lake States pine ecosystems (Heinselman 1973, Baker 1992), and without frequent fires, the forest fuel loads have increased and shade-tolerant, fire-sensitive plants have become more prevalent in the understory.

In order to better understand the ecology of mixed-pine forest ecosystems of eastern Upper Michigan, we examined both managed and old-growth stands growing at the Seney National Wildlife Refuge. Specifically, our objectives were to: 1) determine how the timber harvesting patterns and volumes have changed as refuge goals have been modified over the last 72 years; 2) examine how biological legacies have affected current species compositions; 3) determine how radial growth responses of red pine and eastern white pine are affected by fire in the old-growth mixed-pine forests of the Seney Wilderness Area; and 4) determine how differences in fire frequency and size affect the development of old-growth mixed-pine forests. In Chapter 2, we focus on timber harvesting cycles at the refuge since its establishment in 1935 and how the volumes of species harvested have changed over the past 72 years, and we discuss current forest management goals for the refuge. In Chapter 3 we focus on old-growth mixed-pine stands and how natural fire affects the rate of suppression and radial growth patterns in suppressed and non-suppressed pines. We also discuss recommendations for future mixed-pine ecosystem restoration projects.

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CHAPTER 2

LEGACIES OF FOREST MANAGEMENT IN MIXED-PINE FOREST ECOSYSTEMS OF THE SENEY NATIONAL WILDLIFE REFUGE

Abstract

Red pine (*Pinus resinosa* Ait.), eastern white pine (*Pinus strobus* L.) and jack pine (*Pinus banksiana* Lamb.) are major components of mixed-pine forest ecosystems in eastern Upper Michigan. Prior to European settlement (late 1800s), these ecosystems comprised approximately 39% of the region; however, the distribution and extent of these forests have been greatly reduced due to past timber harvesting, agricultural conversion and fire suppression practices during the 20th century. These ecosystems were replaced by early successional species such as jack pine and aspen (*Populus* spp. L.). Consequently, these forest ecosystems are of great conservation priority and in need of restoration. Before we can develop restoration strategies for these ecosystems, a better understanding of the extent and impacts of past timber harvesting is needed. Using historical timber harvesting records dating from 1935 that are included in the annual narratives of Seney National Wildlife Refuge, we identified the species, timber volumes, and locations of past timber harvests. Past harvesting locations were focused primarily on addressing SNWR wildlife management

objectives and refuge developments, e.g., pool construction. Jack pine and aspen were the primary species harvested, mostly removed as pulpwood. Currently, several different silvicultural treatments (e.g., group selection, shelterwood) are being utilized at SNWR to regenerate different stands and restore stand structures. Future research will include comparing how these managed stands compare both structurally and compositionally with naturally regenerated red pine and eastern white pine stands that experience frequent surface fires.

Introduction

Prior to European settlement, mixed-pine forests dominated a large proportion of the northern Lakes States, particularly in eastern Upper Michigan where they comprised approximately 39% of the total land area (Zhang et al. 2000). These forest ecosystems were found on many of the glacial landforms characterized by sandy soils, and were characterized by red pine (*Pinus resinosa* Ait.), eastern white pine (*Pinus strobus* L.), jack pine (*Pinus banksiana* Lamb.), and associated paper birch (*Betula papyrifera* Marsh.), red maple (*Acer rubrum* L.), and trembling aspen (*Populus tremuloides* Michx.) (Palik and Zasada 2003, Benzie 1977). These relatively open-canopy forests were maintained by a frequent fire regime; however, they also experienced other natural disturbances including wind-throw and insect outbreaks. Natural fires helped support dense shrub layers of blueberry (*Vaccinum* spp. L.) and other species, which were important for many wildlife species and Native American communities (Loope and Anderton 1998). The frequent fires may have influenced seed production of these pines, which are important food sources for seedconsuming mammals. For example, deer mice (*Peromyscus maniculatus* Wagner), are known to preferentially consume jack pine seeds following fire (Krefting and Ahlgren 1974).

From approximately 1860-1910, many of these mixed-pine forests in the northern Lake States, also known as “pineries,” were harvested by numerous lumber companies (Crowe 2002). These timber harvesting practices (high-grading) significantly altered the composition and structure of the mixed-pine forest ecosystems (Karamanski 1989). For example, following the peak harvesting from 1890-1910, most mature eastern white pine and red pine had been removed across the northern Lake States (Stearns 1997). After extracting the usable timber, considerable slash was left behind, which quickly dried and became extremely flammable. This scenario increased the likelihood of catastrophic wildfires throughout the region (Schulte et. al. 2007). In addition to catastrophic fires, many areas of the northern Lake States were converted to agriculture (cropland and pasture) once the trees were removed (Bielecki et al. 2006). However, the climate was not conducive to farming, and much of the organic matter in the soil was either consumed in the fires that followed harvesting or eroded away by the wind (Losey 2003). After the failure of agriculture, many of these lands were abandoned and early successional species re-colonized these areas. As a result of these trends, the longer-lived red pine and eastern white pine that dominated the original mixed-pine forest ecosystems of the region were often replaced by the shorter-lived jack pine and trembling aspen. Compounding this shift in composition and structure, active fire suppression since early 20th century has modified the natural frequency of fire in Lake States’ forest ecosystems (Heinselman 1973, Baker 1992), and without fire the forest fuel loads have increased and shade-tolerant, fire-sensitive plants have become more prevalent.

Currently, there is interest in restoring mixed-pine forest ecosystems of the northern Lake States. This is especially true for eastern Upper Michigan where the USDA Forest Service, USDI Fish and Wildlife Service, and Michigan Department of Natural Resources are actively working to develop forest management and restoration techniques that will help restore the structure and function of these important forest ecosystem types which increase the biodiversity of the region. Many of the restoration treatments being considered focus on fuel-reduction and are compatible with ecological restoration, defined here as the guided recovery of natural ecosystem composition, structure, and function (Society of Ecological Restoration 2004). In fact, there are silvicultural practices that may be utilized in mixed-pine management that attempt to emulate natural disturbance processes such as fire. As a result, not only do we need to develop a better understanding of the natural processes operating in relatively undisturbed mixed-pine forest ecosystems (see Chapter 3), we also need to understand how the legacies of past forest management have influenced current forest compositions and structures.

In this paper, we examine the past timber harvesting activities since the 1935 establishment of Seney National Wildlife Refuge (SNWR), located in eastern Upper Michigan. Our objectives of the study were: 1) to determine how the timber harvesting patterns and volumes have changed during the past 72 years; and 2) to determine the periods of intensive harvesting and explore potential reasons for these harvesting events.

Study Area

The 38,541-ha Seney National Wildlife Refuge (46º16'59.988"N 85º57'00.0"W) is located within the Seney Sand Lake Plain Ecoregion (Albert 1995). This landscape was heavily influenced by the last glacier (Wisconsinan glacier) during the Pleistocene epoch (Sinclair 1959). Much of SNWR is a lake plain, with raised sand ridges interspersed among extensive patterned bog areas (also referred to as "string bogs") in the western portion of SNWR (Heinselman 1965) and outwash channels located along streams and rivers in the eastern portion. SNWR is divided into two main areas: a federally designated wilderness area, and a managed area that includes a created pool system designed to provide habitat for migratory waterfowl.

Climate is influenced by both Lake Superior from the north and Lake Michigan from the south. The average frost-free period during the summer is 73 days (Anderson 1982). The closest meteorological station is located at SNWR headquarters and has been recording weather data since 1950 (Michigan State Climatologist's Office 2008). The long-term average (1950-2000) temperature is 5.7 ˚C; the average annual precipitation is 80.65 cm, and including an average of 302 cm of snowfall per year.

Prior to European settlement, SNWR was dominated by both extensive wetland ecosystems and upland mixed-pine and northern hardwood forest ecosystems (Fig. 2.1). Low- to moderate-intensity surface fires burned in the mixed-pine forest ecosystems at a frequent fire interval, often allowing the surviving trees to attain large size (Fig. 2.2). Prior to SNWR establishment in 1935, much of the area was harvested following European settlement in the late 1800s. By the 1930s, the majority of SNWR, along with most of eastern Upper Michigan, was dominated by second-growth forests of jack pine and trembling aspen.

Timber harvesting has been a part of the forest management of SNWR since 1935. The main management objective for SNWR is to provide habitat for migratory birds. Following the establishment of SNWR in 1935, the trees were harvested in the areas that were to be flooded to create pools for the waterfowl. After the pools were created, SNWR also began to manage the forests for wildlife. For example, jack pine and aspen (includes trembling aspen and bigtooth aspen (*Populus grandidentata* Michx.)) stands were harvested to create younger stands to promote wildlife species that utilize early successional habitat (Fig. 2.3), such as sharp-tailed grouse (*Tympanuchus phasianellus* L.), ruffed grouse (*Bonasa umbellus* L.) and sandhill crane (*Grus canadensis* L.).

Methods

The annual narratives (documents compiled by SNWR staff describing refuge activities on a yearly basis) and timber harvesting receipts of SNWR have been kept on file since its establishment in 1935. The sales of the timber harvesting was contracted out and performed by government programs (Civilian Conservation Corps and Works Progress Administration) and numerous local timber harvesting operations. We reviewed these records and determined the following for each harvesting activity: location, species, volume, and year. General notes were also reviewed and recorded. Some records did not include detailed information on the species harvested, therefore, we combined the data into the eleven following general groups: jack pine, aspen (includes trembling aspen and bigtooth aspen), balsam fir (*Abies balsamea* L.), spruce (includes black spruce (*Picea mariana* Mill.) and white spruce (*Picea glauca* Moench)), red pine, white pine, birch (includes yellow birch (*Betula alleghaniensis* Britton) and paper birch), beech (*Fagus grandifolia* Ehrh.), hard maple (sugar maple (*Acer saccharum* Marsh.)), soft maple (red maple) and other (includes eastern hemlock (*Tsuga canadensis* L.), northern white-cedar (*Thuja occidentalis* L.), tamarack (*Larix laricina* Du Roi), American basswood (*Tilia americana* L.), American elm (*Ulmus americana* L.), mixed-fuelwood, mixed hardwood and mixed conifer). We summarized the total volume of timber removed by group in terms of pulpwood (cords) and sawtimber (board feet).

Pulpwood was the utilized the most following refuge establishment allowing for trends to be recognized. For this reason pulpwood volume fluctuations were examined more than sawtimber. To examine changes in pulpwood volume removed over the 72-year period from 1935-2007, we utilized Non-Metric Multidimensional Scaling (NMDS) using PC-ORD version 5.0 (McCune and Mefford 1999). NMDS uses rank order to find differences that occur in the data matrix and is a preferred analysis for examining trends with non-normal data (McCune and Mefford 1999). We conducted a medium-intensity NMDS running the permutation tests 50 times. In order to help with interpretation, we divided the 72-year period into seven approximately ten-year periods beginning with the SNWR establishment date (1935) and ending with the summer of 2007. In each of these sub-periods, the twelve townships within SNWR were used to specify where the timber was removed.

Results

Total Volume Removed

The total volumes of hardwood and softwood pulpwood and sawtimber removed from SNWR from 1935-2007 were 101,490 cords and 6,437,620 board feet, respectively. There were two main periods of intensive harvesting, the first in the late 1940s and the second in the 1970s (Fig. 2.4). There were three periods with minimal or no harvesting activity, including the early 1960s, late 1980s and early 2000s (Fig. 2.4). Typically, harvesting activities at SNWR follow a cyclical pattern where an intense period of harvesting was followed by decreased harvesting activity.

Volume removed by species

Overall, jack pine was the most common species harvested (Fig. 2.5). The aspen group was the second most harvested pulpwood species, but was only about 1/6 of the volume harvested of jack pine (11,262 cords vs. 57,075 cords). Over the past 72 years, timber harvesting practices at SNWR experienced cycles that favored certain groups of species, especially jack pine and aspen (Fig. 2.8 and Fig. 2.9, respectively). Jack pine, harvested primarily in the 1940s and 1970s, accounted for nearly 60% of all pulpwood sales. Aspen was only sporadically harvested prior to the 1970s, when harvesting intensity increased dramatically. The aspen species have not been heavily removed over the past fifteen years.

Sawtimber was harvested mainly in the early refuge years from 1935-1955 (Fig. 2.6). The main group harvested was the other category (150,000 board feet of hardwood harvested in 1944) followed by red pine and eastern white pine (Fig. 2.7). The next group to be harvested was northern hardwood species, hard maple and beech. Very little jack pine and no aspen were utilized for sawtimber. Smaller amounts of sawtimber was harvested from 1955-1990 and then in the 1990s there were several harvests that moved 1,385,000 board feet (20% of all sawtimber harvested since 1935).

NMDS illustrates the patterns in pulpwood removals from SNWR (Fig. 2.10). During the 1940s and 1960s, jack pine, spruce, hard maple and beech were the main groups of species harvested. However, during other periods, including the period from 1975-1986, a wider variety of species were harvested. Finally, there were several time periods where harvesting activities were more random (Fig. 2.10). For example, from 1956-1965, little pulpwood was harvested, corresponding to a decline in the stumpage price for pulp. Additionally, from 1985-2007, timber removals were low, but consistent in the volume of timber removed (Fig. 2.10).

In addition to illustrating the groups of species harvested by decade, the spatial pattern of removals is also evident (Fig. 2.10). The eastern portion of SNWR has many man-made pools, while the western part is the Seney Wilderness Area. During the first 20-year period (1935-1955) the main groups of species harvested were jack pine and spruce, while aspen removal dominated the next ten-year period. During the period from 1966-1985, the groups of species most harvested shifted from early successional species to late-successional species, e.g., beech, hard maple, and soft maple.

Discussion

Harvesting trends: General

Timber harvesting has been part of the forest management of Seney National Wildlife Refuge since its establishment in 1935. The main objective for establishing the refuge was to provide habitat for migratory birds. Most of the trees harvested in the first decades following establishment of the refuge were from areas that were flooded to create pools for the waterfowl, specifically trumpeter swans (*Cygnus buccinator* Richardson), sandhill cranes, and Canada geese (*Branta canadensis* L.). During this time period, the timber was either sold for profit or used to build structures at SNWR.

As early as 1945, the forest ecosystems of SNWR were managed for wildlife species; SNWR was one of the first refuges to start these practices. Initially, jack pine and aspen stands were harvested to create new stands to favor wildlife species that utilize early successional stands. However, according to the annual narratives, by the 1950s pulp markets were low, which caused a reduction in harvesting activities at SNWR during this period. Jack pine prices were so low in 1954 a stand of jack pine was bulldozed by SNWR staff, rather than harvested, prior to dike construction. Also, during this time period, there were several short-term refuge managers of SNWR whom did not offer any new timber harvests for sale.

By the end of the 1960s, the forests of SNWR had been re-inventoried, pulp markets had rebounded, and once again aspen and jack pine were harvested at SNWR. Additionally, salvaging of jack pine occurred after several jack pine sawfly

(*Neodiprion pratti banksianae* Rohwer) outbreaks in the 1970s led to additional harvesting. Beginning in the 1980s, SNWR began managing their forest units for single wildlife species, e.g., sharp-tailed grouse, woodcock (*Scolopax minor* L.), ruffed grouse, and sandhill cranes; management plans that included active harvesting and thinning were developed to help meet these management objectives. Currently, the objectives for timber harvesting at SNWR involve implementing harvests to restore mixed-pine forests and lower heavy fuel loadings. Early successional species are being harvested, while red pine and eastern white pine are left standing as seed trees, when present.

Harvesting trends: Pulpwood

The harvesting of pulpwood fluctuated with the timber markets, as the stands matured to merchantable size following the turn-of-the-century logging activities and associated slash fires that tended to favor jack pine establishment. Years with low pulp prices for jack pine caused harvesting to decline and by the 1950s most of the waterfowl habitat (e.g., large pools) had been created so there was less timber available for sale from SNWR. Timber harvesting began again at SNWR in the mid-1960s and lasted until the late 1970s. After this time period, harvesting was limited to the promotion of certain forest wildlife species through the manipulation of stand structure (e.g., small openings for sharp-tailed grouse).

Harvesting trends: Sawtimber

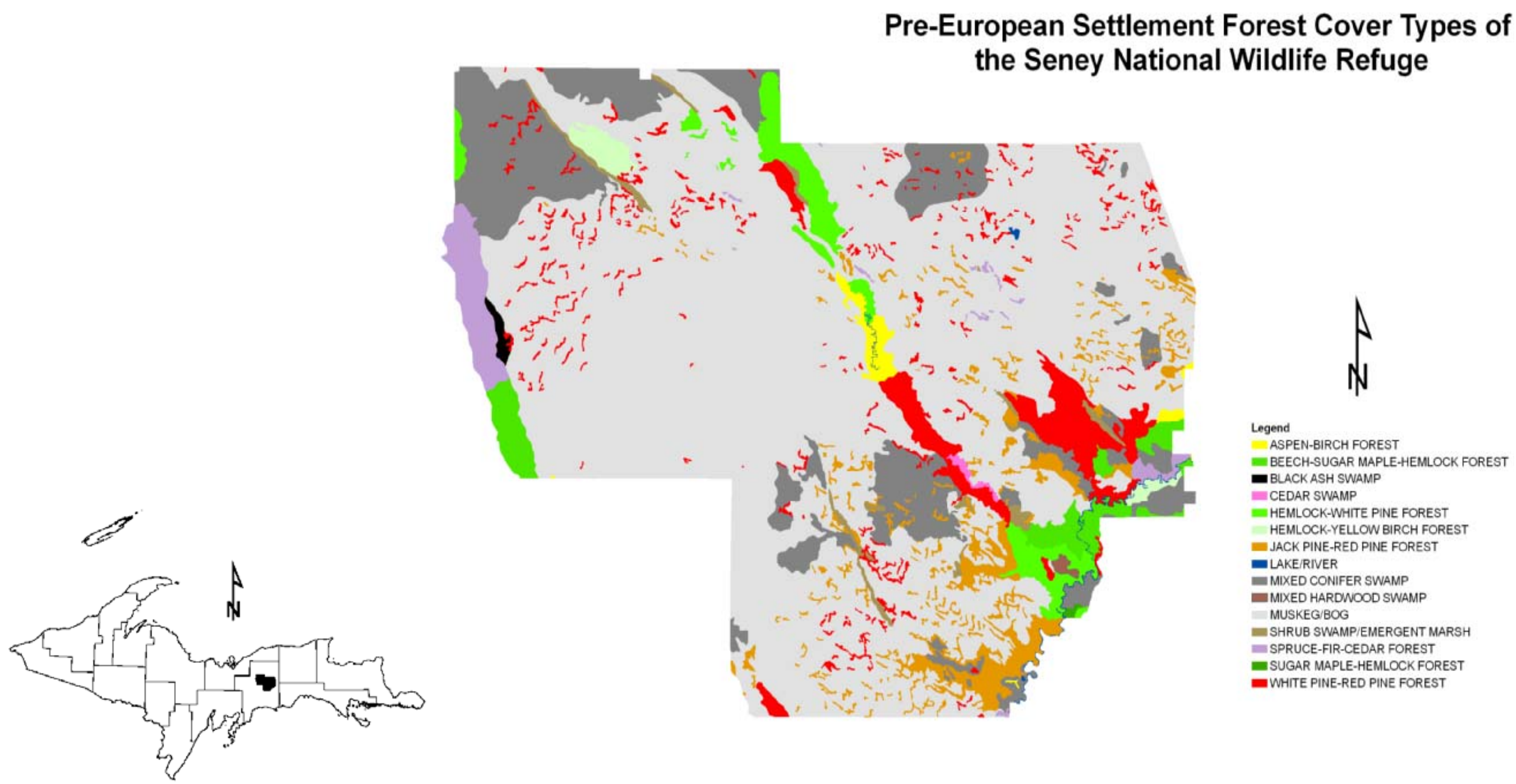
Sawtimber was mainly harvested during the first twenty years following SNWR's establishment. This was when many of the pool bottoms were being cleared and the refuge road system was being created. After the last pool was created in the late 1950 only minimal sawtimber was harvested over the next 35 years. This was due to the demand for pulp and not sawtimber. Also, less sawtimber was available following the "Great Cutover" in the late 1800s and the cutting of northern hardwood species in the early 1900s. As a wildlife refuge the staff focused of creating early successional forests for wildlife, this involved harvesting the jack pine and aspen stands so they would regenerate and create habitat, nesting and foraging locations for the animals. In the 1990s, there were three harvests removing a large volume of sawtimber. This could be due to the forest having a century to grow since the initial harvesting and trees in some locations were reaching merchantable size.

Biological legacies

Past anthropogenic disturbances affect the future development of the ecosystem. Prior to European settlement, mixed-pine forests were maintained by a frequent fire regime. After European settlement, the original forests were clear-cut, or in some cases, high-graded for their highest quality trees. Then, catastrophic wildfires burned through the slash left behind after the harvesting. The removal of the mature trees during timber harvesting and the repeated slash fires killed many of the remaining pine seed trees and pine regeneration (Graham 1941, Whitney 1987). Early successional species adapted to fire (jack pine and aspen) reforested the lands that were once dominated by uneven-aged mixed-pine forest ecosystems. By the 1940s, the pulp markets increased and the jack pine and aspen that established approximately in the 1890s were harvested. These harvesting activities maintained these sites in early successional species, i.e., allowed jack pine and aspen to remain the dominant tree species. Managers also started fire suppression policies in the early 20th century, which has lead to increased fuel loadings and has favored shade-tolerant, fire-sensitive species. These anthropogenic disturbances over the past 150 years have greatly altered forest composition and structure at SNWR.

Future management

The past timber harvesting trends at the SNWR have maintained many areas, including those once dominated by mixed-pine forest ecosystems, as early successional forests. These younger stands usually have both higher fuel loadings and species diversity, but less structural diversity than the original mixed-pine forest ecosystems (Drobyshev et al. 2008b). Based upon these legacies, the future management and restoration of these forests will require various combinations of silvicultural practices. For example, dispersed mature red pine and eastern white pine trees could be retained to provide seed sources, when present in stands being regenerated, in an effort to help size, age, and compositional complexity to these altered stands. Additionally, jack pine and aspen can be removed while red pine and eastern white pine are released and remain as the seed source to restock the area. In contrast with some other studies, our data suggests that these older red pine and eastern white pine will respond to release (see Chapter 3). Prescribed burning (low- to moderate-intensity fires) might also be incorporated using a frequent fire regime (Fig. 2.11) as the natural fire-return interval for SNWR ranges from 11.5 to 32.7 years (Drobyshev et al. 2008a). When fire cannot be used, mechanical thinning can be implemented to maintain fuel loadings at low levels; however, the density of the current stand will dictate the intensity of the thinning. The denser the stand is, the more trees that will need to be removed. It is also important for managers to restore mixed-pine ecosystems to increase the complexity of the forests. Increased complexity in structure and species composition allows the forest to be more resilient when natural and anthropogenic disturbances occur. The combinations of these silvicultural practices should allow forest managers to better emulate natural disturbances and help restore mixed-pine ecosystems that have been altered as a result of past forest management.



A **B**

Figure 2.1: (A) Location of the Seney National Wildlife Refuge, eastern Upper Michigan. (B) and pre-European settlement forest cover types. Based on Comer et al. (1997).

Figure 2.2: Pre-European settlement mixed-pine forest of Upper Michigan. These forests were harvested in the late 1800s and the slash left behind often resulted in large stand-replacing fires. After these fires, jack pine tended to dominate these forests. Source: Library of Congress.

Figure 2.3: Typical timber harvesting operation of a jack pine stand in Upper Michigan in the 1930s that likely originated following the first cutover of mixed-pine forests in the late 1800s. Source: Northern Michigan University and Central Upper Peninsula Archives

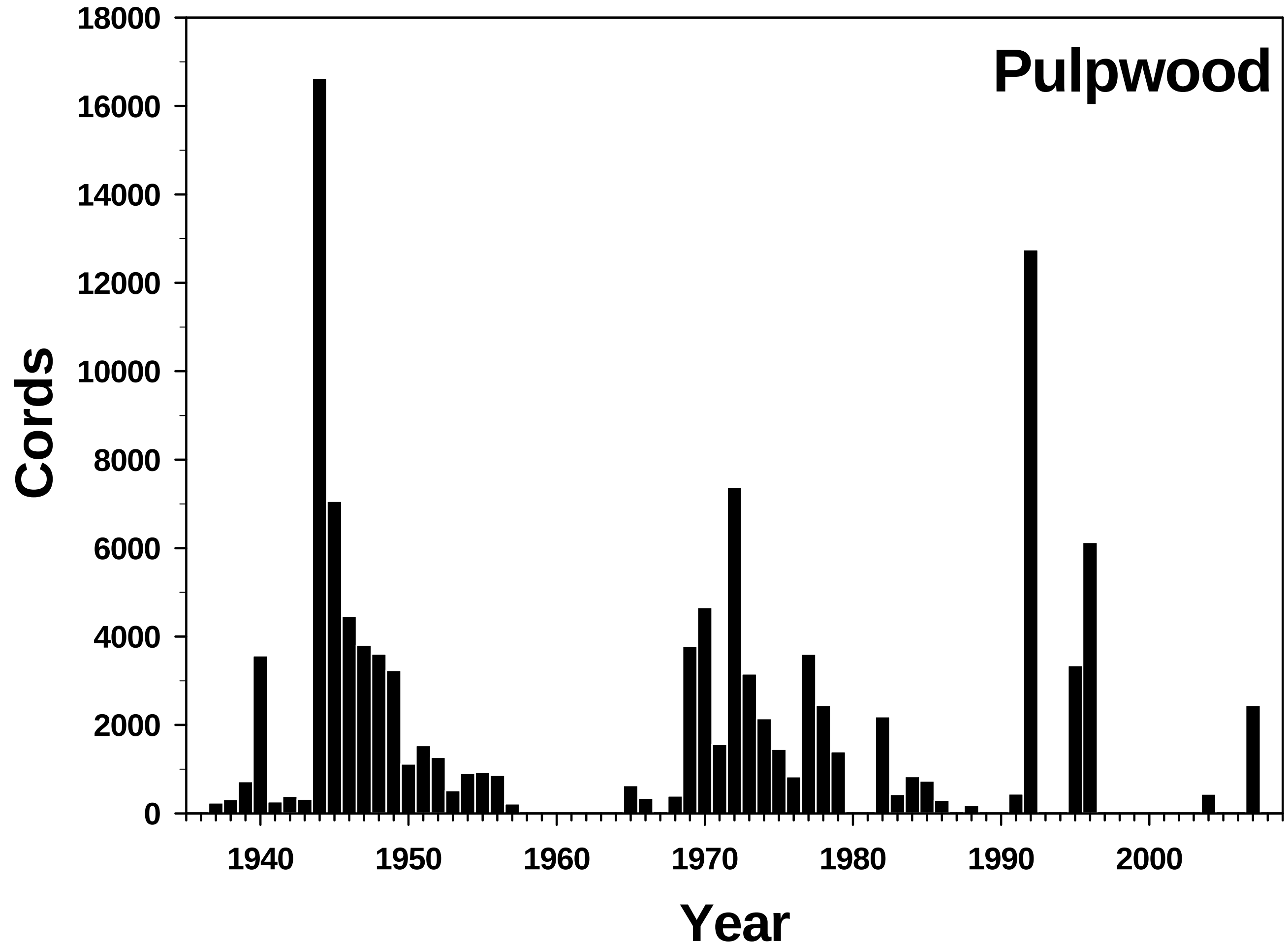


Figure 2.4: Pulpwood for all species harvested from 1935 to 2007 from the Seney National Wildlife Refuge, eastern Upper Michigan.

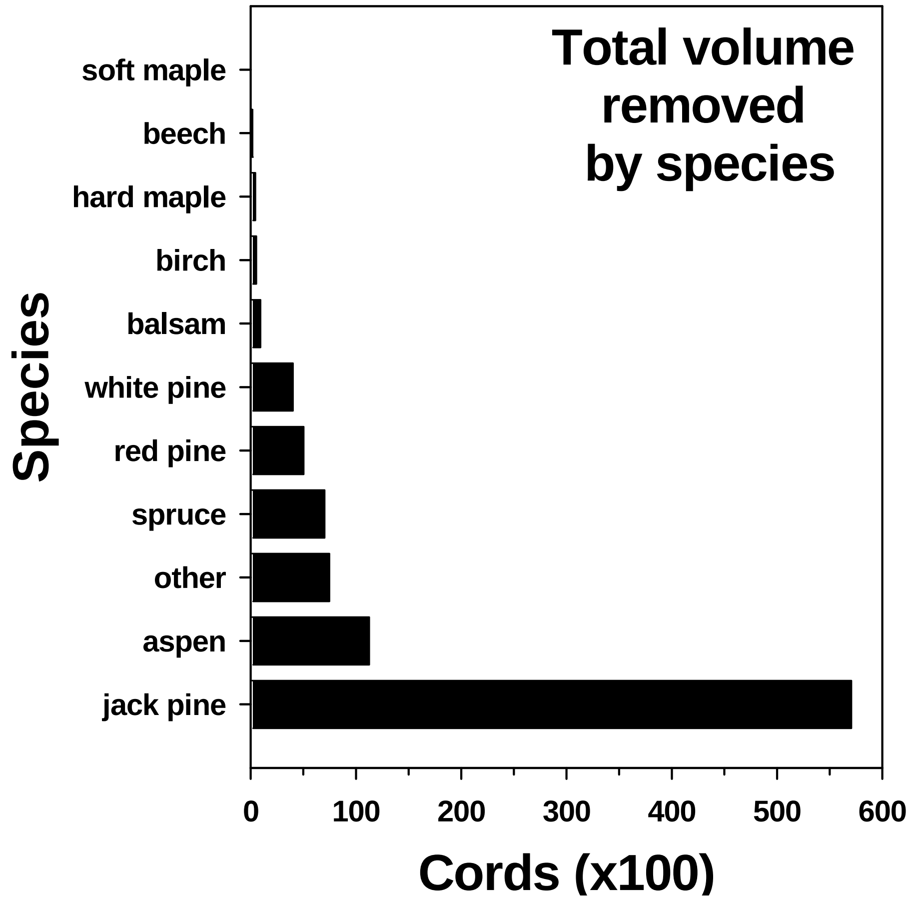


Figure 2.5: Most frequently harvested groups of species based on cords of pulpwood, 1935-2007, from Seney National Wildlife Refuge, eastern Upper Michigan.

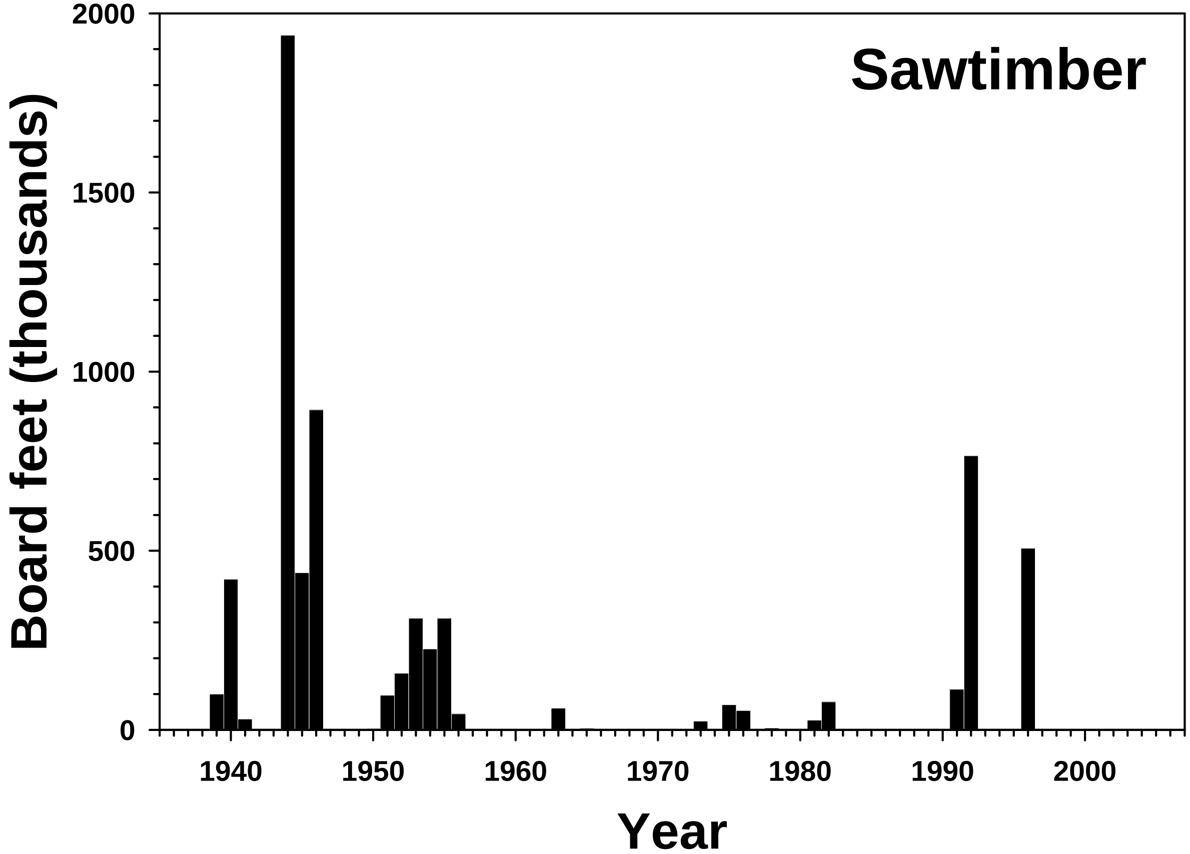


Figure 2.6: Sawtimber (board feet in thousands) for all species harvested from 1935 to 2007 from the Seney National Wildlife Refuge, eastern Upper Michigan

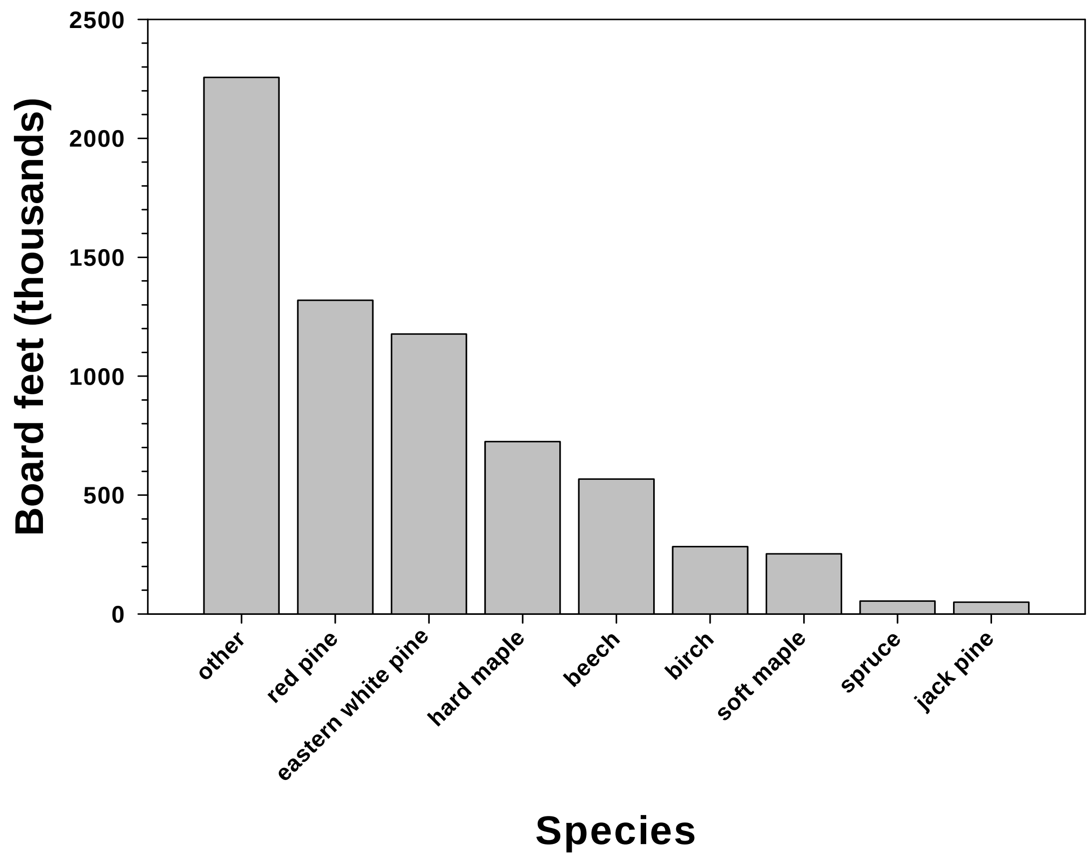


Figure 2.7: Most frequently harvested groups of species based on sawtimber, 1935-2007, from Seney National Wildlife Refuge, eastern Upper Michigan. The category other shows the largest volume harvested due to 150,000 board feet labeled as hardwoods was cut in 1944. No sawtimber was harvested in the balsam and aspen categories.

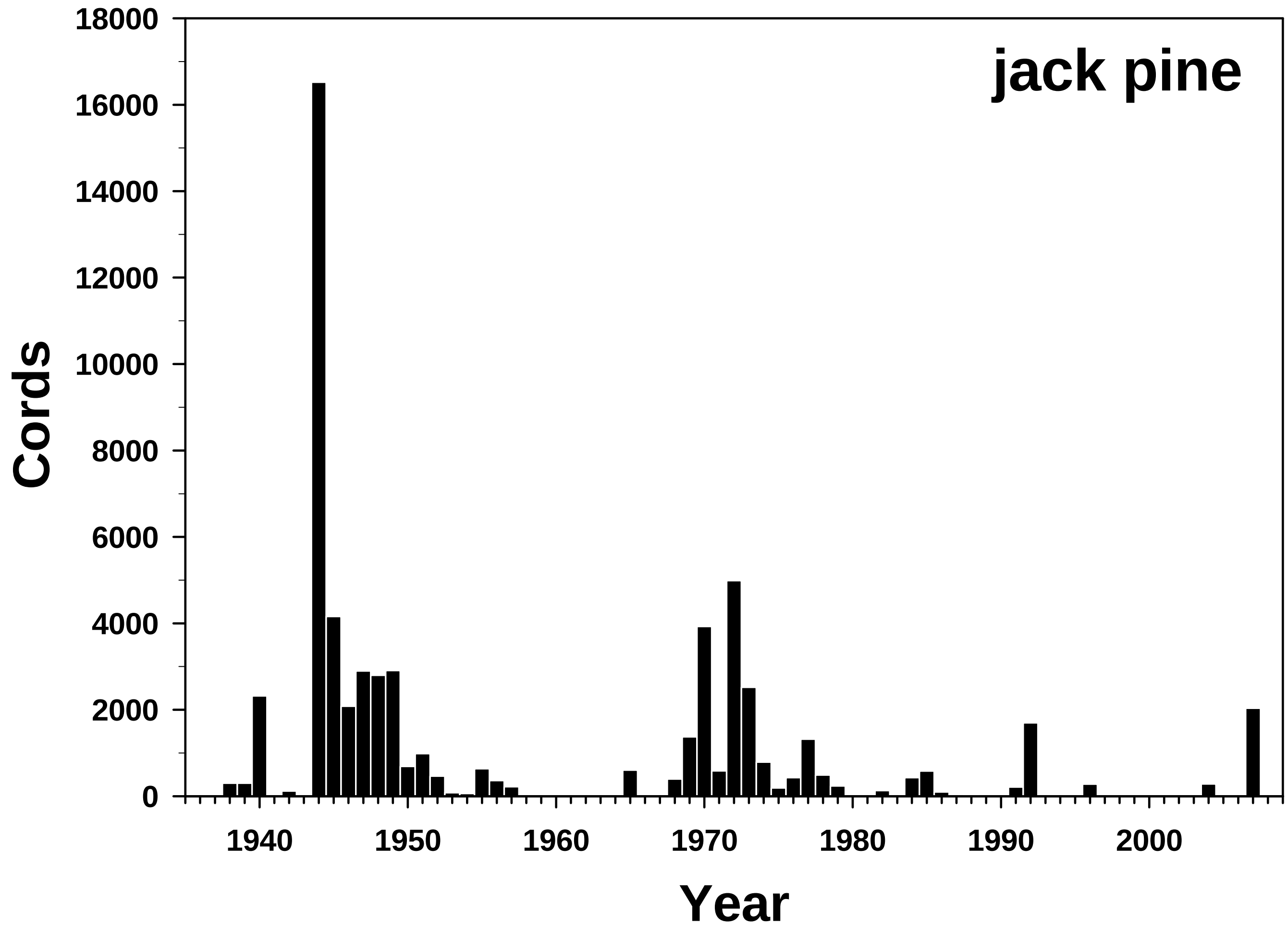


Figure 2.8: Yearly volumes (cords) of jack pine harvested from 1935-2007 from Seney National Wildlife Refuge, eastern Upper Michigan.

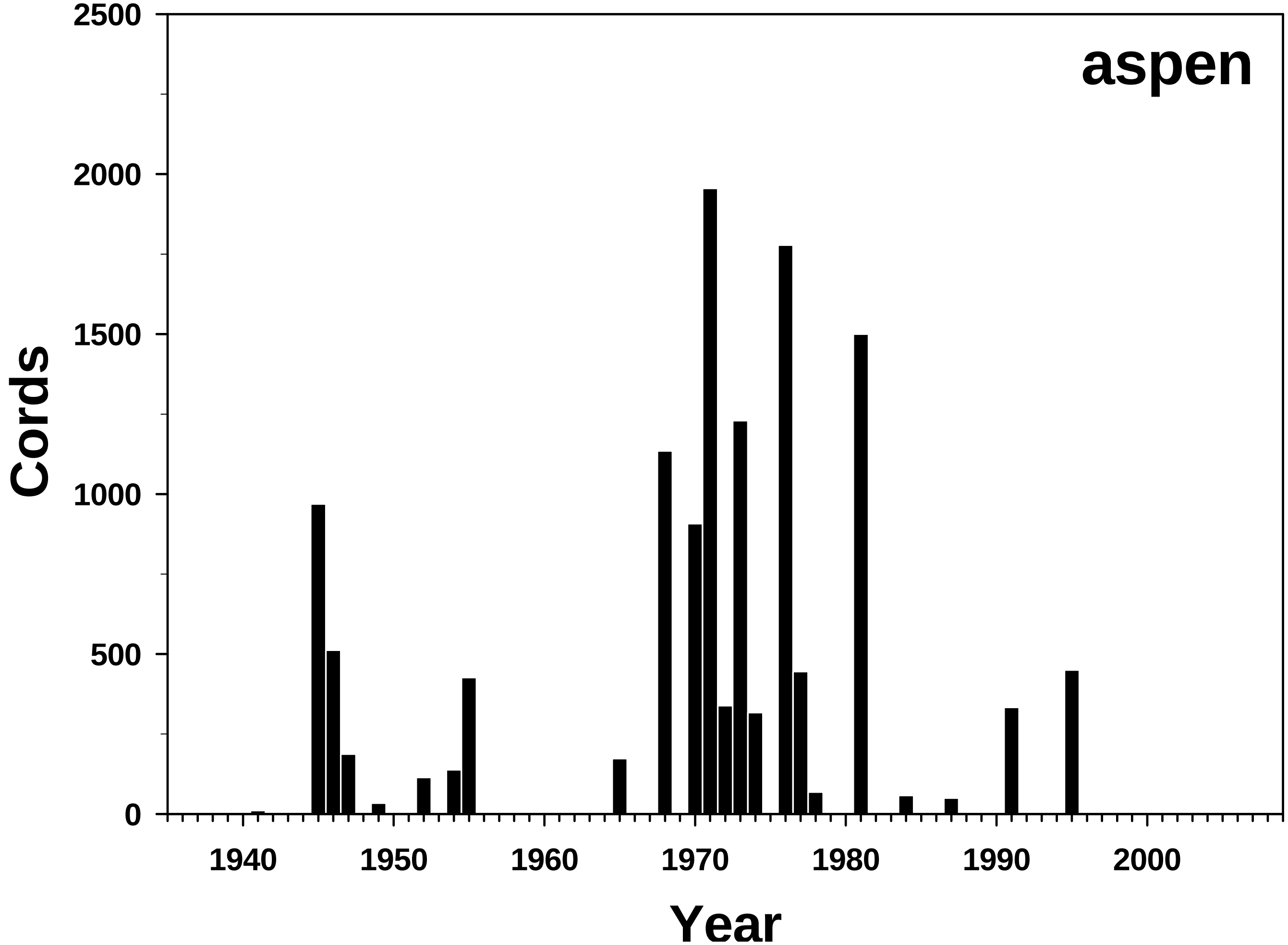


Figure 2.9: Yearly volumes (cords) of aspen harvested from 1935-2007, from Seney National Wildlife Refuge, eastern Upper Michigan.

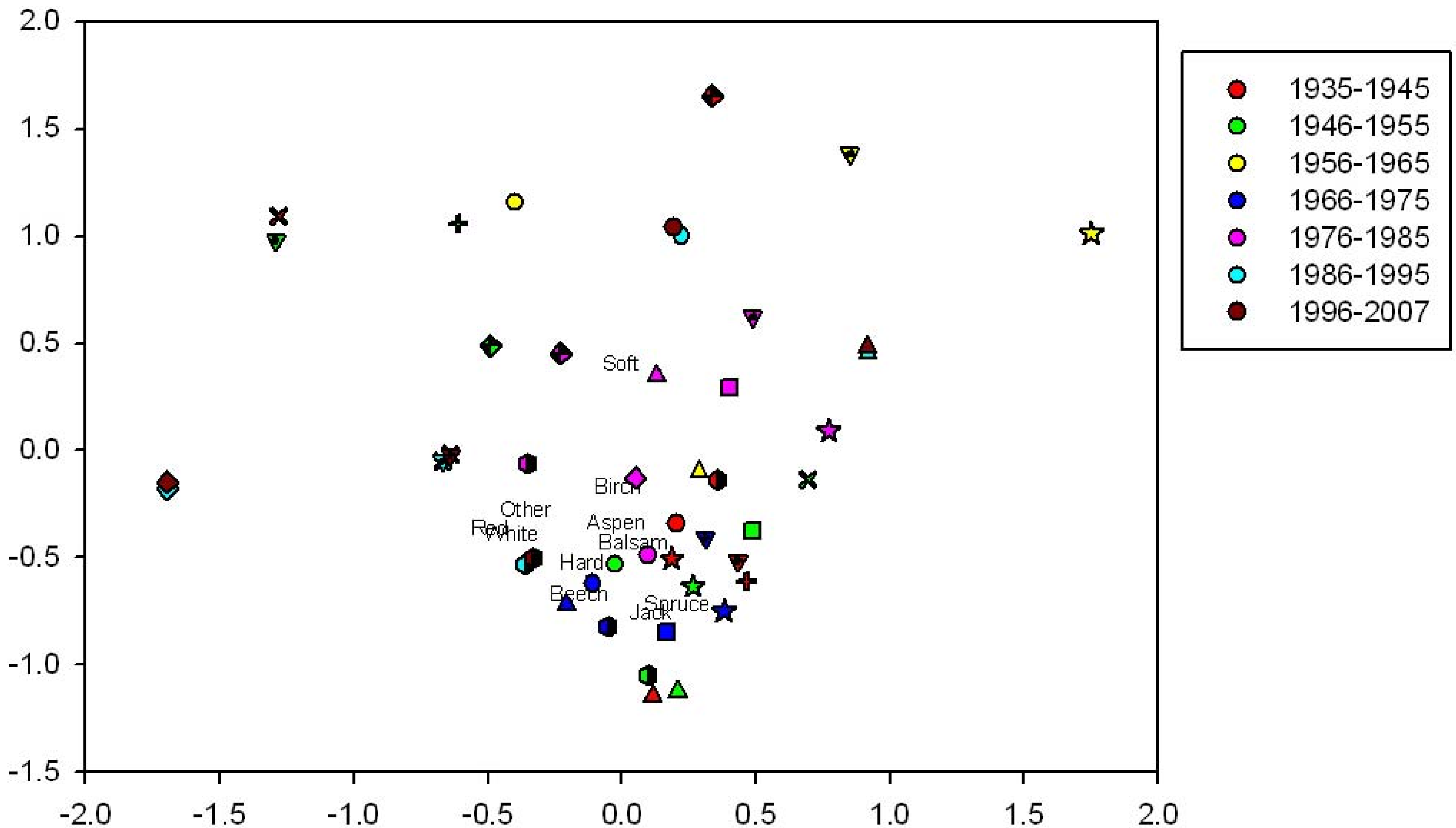


Figure 2.10: Non-metric dimensional scaling ordination of pulpwood removed from individual townships, 1935-2007, at Seney National Wildlife Refuge, eastern Upper Michigan. Symbols represent the different townships and groups of species harvested are labeled using abbreviated names.

Figure 2.11: Mixed-pine stand during a prescribed fire at the Seney National Wildlife Refuge, eastern Upper Michigan. The open understory has few saplings, and the fuel loadings are low in this forest.

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CHAPTER 3

AGE STRUCTURE AND RADIAL GROWTH RESPONSE OF RED AND EASTERN WHITE PINE FOLLOWING NATURAL FIRE IN OLD-GROWTH MIXED-PINE STANDS OF THE SENEY WILDERNESS AREA

Abstract

Fire is an important type of natural disturbance in forest ecosystems dominated by red pine (*Pinus resinosa* Ait.) and eastern white pine (*Pinus strobus* L.) in the northern Lake States. Both species (especially red pine) are adapted to a frequent fire regime characterized by low- to moderate-intensity surface fires occurring every 11.5-32.7 years. These fires prepare the mineral seedbed for regeneration and control competing vegetation. In order to examine the age structure and radial growth patterns, and relate these patterns to all known local fires, we collected a total of 200 samples (160 increment cores and 40 partial cross-sections) from red pine and eastern white pine trees in old-growth mixed-pine stands in the Seney Wilderness Area of eastern Upper Michigan. Based upon these samples, the age structure show pulses of regeneration following known fire events. Additionally, analyses of samples dated from 1652-2006 suggest that the immediate response of the majority of trees to fire in these stands is a decline in radial growth with several trees showing growth increases

that is sustained for five to ten years after a fire. These results suggest that natural fire appears to negatively effect the growth of the surviving pine trees for several years following the fire but also allows for new pine regeneration. Our increased understanding of these patterns will help resource managers design silvicultural systems that emulate natural fire regimes, which will also help restore the structure and function of these once extensive mixed-pine forest ecosystems.

Introduction

Mixed-pine forest ecosystems, dominated primarily by eastern white pine (*Pinus strobus* L.), red pine (*Pinus resinosa* Ait.) and jack pine (*Pinus banksiana* Lamb.), comprised an estimated 39% of eastern Upper Michigan prior to European settlement (Zhang et al. 2000). These widely dispersed forest ecosystems occurred on landforms associated with past glacial activity, including sand ridges interspersed within patterned or string bogs, outwash channels associated with streams and rivers, and broad outwash plains (Heinselman 1965). Unlike other areas across the northern Lake States where mixed-pine forest ecosystems were likely maintained by stand-replacing fires (Heinselman 1973, Bergeron and Brisson 1990), mixed-pine forest ecosystems in eastern Upper Michigan were maintained by low- to moderate-intensity surface fires occurring on average every 28 years (Drobyshev et al. 2008a).

Following European settlement in the mid-1800s, the large-scale logging of mixed-pine forest ecosystems began in earnest, with most eastern white pine and red pine harvesting occurring from 1885-1900 (Graham 1941). Following these activities, the slash left behind resulted in high fuel loading, which contributed to catastrophic wildfires in the region (Schulte et al. 2007). These slash fires negatively influenced the regeneration of both red pine and eastern white pine as many of the mature seed trees were harvested and the repeated slash fires caused high mortality of red pine and eastern white pine seedlings (Whitney 1987). In conjunction with the lack of successful regeneration, many of the sites that once supported mixed-pine forest ecosystems were cleared for agriculture which ultimately failed (Bielecki et al. 2006), and by the early 20th century, fire suppression efforts began significantly reducing both natural- and human-caused forest fires (Drobyshev et al. 2008a). The result has been higher fuel loadings and reduced regeneration of species that are adapted to fire-prone ecosystems, especially red pine (Drobyshev et al. 2008b). Additionally, in the absence of fire, forest composition has shifted to include other hardwood and boreal conifer species (e.g., black spruce (*Picea mariana* Mill.)) that are more shade tolerant, able to persist in the understory, and effectively compete with both red and eastern white pine regeneration (Rudolf 1990; Drobyshev et al. 2008b). In response to these significant shifts in disturbance regimes, particularly the reduction of natural fires, mixed-pine forest ecosystems across eastern Upper Michigan have decreased to only 13% of the current forest area (Zhang et al. 2000), and hardwood-pine forest ecosystems and openlands (non-vegetation, agriculture, herbaceous shrubland and urban areas) have replaced mixed-pine forests ecosystems over the past 150 years as the dominant cover types in eastern Upper Michigan.

Currently, efforts are underway to restore mixed-pine forest ecosystems across the northern Lake States (Goebel et al. 2007, Drobyshev et al. 2008a, Drobyshev et al. 2008b). A variety of silvicultural practices are being utilized in this process, including prescribed burning, mechanical thinning, herbicide application to control competing vegetation, and artificial regeneration. Additionally, overstory retention harvests are being implemented to increase age and compositional complexity in existing red and eastern white pine stands (Palik and Zasada 2003). However, in order to design silvicultural systems that better emulate the stand structures following natural disturbances, more detailed information on the response of natural mixed-pine forest ecosystems to fire is needed. This is particularly true for mixed-pine forest ecosystems located across Michigan, Wisconsin, Minnesota, and portions of southern Quebec where the natural fire regimes were likely quite different from areas on the fringes of this forest ecosystem types distribution (e.g., northern Minnesota, northern Quebec, and New England) (Heinselman 1973, Bergeron and Brisson 1990; Engstrom and Mann 1991; Drobyshev et al. 2008a). It is unclear whether the recruitment and development patterns of mixed-pine forest ecosystems that experience low- to moderate-intensity fires occurring on average once every 28 years are different from mixed-pine forest ecosystems that have developed following more intense stand-replacing fires as observed in northern Minnesota and northern Quebec. Additionally, little is known about how canopy disturbances in these relatively open-canopied forest ecosystems influence establishment and recruitment, and in particular how suppressed and non-suppressed individuals respond to canopy disturbances related to frequent low- to moderate-intensity surface fires. One might anticipate that when fire is absent for extended periods of time, more trees become suppressed, while when multiple fires occur more trees will not be suppressed.

Using perhaps the best remaining relatively undisturbed, old-growth mixed-pine forest ecosystems in the northern Lake States outside of northern Minnesota and Quebec, the primary objectives of this study were to: 1) determine the age structure and patterns of recruitment to 30 cm in eastern Upper Michigan old-growth mixed-pine forest ecosystems and examine these patterns in relation to fire history, and 2) examine radial growth patterns of response to fire and compare the radial growth responses of non-suppressed and suppressed individuals to fire and canopy disturbances. Patterns observed in the old-growth represent reference conditions that can be used to help guide future management and restoration.

Study Area

Our study focused on old-growth mixed-pine forest ecosystems located in eastern Upper Michigan within the Seney Sand Lake Plain Sub-Subsection (Albert 1995). Data was collected at Seney National Wildlife Refuge (SNWR; 46º16’59.988”N 85º57’00.0”W), a 38,541-ha refuge located in Schoolcraft County (Fig. 3.1). The present landscape features of SNWR were influenced by the glaciations of the Pleistocene epoch (Sinclair 1959). During this period the ancient Lake Algonquin covered much of the present area. As a result, the majority of the SNWR landscape is dominated by sandy outwash channels and sand ridges embedded within extensive patterned bog ecosystems.

SNWR comprises two main sections, including a federally designated wilderness area and managed area that includes a created pool system primarily designed to provide habitat for migratory waterfowl. The Seney Wilderness Area, where our sampling occurred, is a 10,178-ha area contains a patterned bog system known as a "Strangmoor." The area exhibits treeless string bogs and embedded within this landscape are raised sand ridges that support mixed-pine ecosystems (Heinselman 1965). The ecotones between the upland sand ridges and patterned bogs contain species more adapted to wet conditions, including black spruce and tamarack (*Larix laricina* Du Roi).

The closest meteorological station is located at SNWR headquarters and has been recording weather since 1950 (Michigan State Climatologist's Office 2008). The long-term average (1950-2000) temperature is 5.7 ˚C. The average annual precipitation is 80.65 cm, and included in this total is an average of 302 cm of snowfall per year. The amount of snowfall is influenced by both Lake Superior and Lake Michigan, however, the snow pack that forms in eastern Upper Michigan does not usually exceed one meter (Verme 1968).

The landscape of SNWR is composed of a variety of ecosystems, including forests, marshes, and created pool systems. The forest ecosystems are dominated by mixed-pines (red pine, eastern white pine, and jack pine) and northern hardwood species including sugar maple (*Acer saccharum* Marsh.), American beech (*Fagus grandifolia* Ehrh.), and yellow birch (*Betula alleghaniensis* Britton). Although many of these forest ecosystems have been heavily influenced by human activities for the past 150 years, the mixed-pine forest ecosystems in the Seney Wilderness Area are believed to be relatively undisturbed and no known logging has occurred in the Seney Wilderness Area. One reason these forest ecosystems escaped the extensive harvesting of the late 19th and early 20th century is that these sand ridges are relatively remote and interspersed within an extensive bog system, which can be periodically flooded. The bog areas contain a variety of species, including bog birch (*Betula pumila* L.), willow (*Salix* spp. L.), leatherleaf (*Chamaedaphne calyculata* L.), bog rosemary (*Andromeda glaucophylla* L.), small cranberry (*Vaccinium oxycoccos* L.), shrubby cinquefoil (*Potentilla fruticosa* L.) and numerous sedges and grasses (Heinselman 1965).

Prior to the establishment of SNWR, large portions of the non-wilderness area experienced the intensive harvesting practices that characterized the northern Lake States in the late 1800s (see Chapter 2). However, in the Seney Wilderness Area there may have been minimal anthropogenic disturbances given the small amounts of merchantable lumber present that would have been hard to access through the bog areas. After logging had cleared parts of the land, some of the bogs were drained for agriculture beginning in the early 1900s. After several decades, much of these lands proved to be non-profitable for agriculture and ownerships often reverted back to the government. In 1935, SNWR was established primarily on these land holdings (Madison and Lockwood 2004). The main objective for SNWR was to provide habitat for waterfowl. This was accomplished by creating a pool system on the eastern part of the refuge. The current management goals continue to be focused on providing high-quality habitat for wildlife, in particular, waterfowl. However, resource managers are also interested in forest ecosystem restoration and management, especially the restoration of the once extensive mixed-pine forest ecosystems that were common on this landscape.

Methods

We collected data from fifteen sand ridges within the Seney Wilderness Area at SNWR. At each site, we established one to three 10-by-50-m plots, depending on the sand ridge size. On each plot, all living and dead trees ≥ 10.0 cm dbh (diameter at breast height - 1.37 m) were measured by species. Nomenclature follows the USDA PLANTS Database (2004). To characterize the age structure and radial growth patterns, we collected increment cores from four to nine live trees (with an average of seven trees) that represented the different cohorts greater than 7.5 cm dbh at each site. Increment cores were collected as close to ground level as possible (~ 30 cm) in order to more accurately determine the total age of each sampled tree (Grissino-Mayer et al. 1994). In some instances, one or two additional cores were extracted from each tree if the pith was not visible, and the best core was included in the analyses. Additionally, we utilized zero to seven, with an average of three, partial cross-sections (i.e., wedges) from live fire-scarred trees at each site that were collected to develop a fire history of SNWR (Drobyshev et al. 2008a). In total, we collected 183 samples from red pine and 17 from eastern white pine, which is proportional to the importance of these two species in the mixed-pine ecosystems of Seney Wilderness Area (see Results).

In the laboratory, each sample (increment cores and wedges) was mounted on a wooden board and then sanded with a series of progressively finer sandpapers (e.g., coarse (80 grit) sandpaper to grind the core flat, fine (220 grit) sandpaper to smooth the surface, and extra-fine (400 grit) sandpaper to polish the surface) to allow clear recognition of annual rings under a binocular microscope (using up to 40x magnification). The sanded samples were then scanned at 600 dpi (dots per inch) and analyzed using the tree ring analysis program WinDENDRO (Régent Instruments 2003). Using WinDENDRO, the ring widths of each core were measured to the nearest 0.01 mm. If the pith was missed during coring, a pith estimator was used to determine the approximate position of the pith and the number of rings missing from the sample (Applequist 1958). The number of estimated rings to the pith was added to the number of rings counted in order to estimate the age of the tree.

All samples were cross-dated using a visual approach (following Stokes and Smiley 1968). We developed local chronologies for all sites, and a master chronology for SNWR (also referred to as a pointer-year chronology; Schweingruber et al. 1990), utilizing ring widths, early- and late-wood widths, and late- and early-wood densities (see Drobyshev et al. 2008a for details on developing this master chronology). The resulting master chronology provided a basis for and was used with a visual cross-dating technique (i.e., skeleton plots) to accurately age each sample. The software program COFECHA (Grissino-Mayer 2001) was then used to check for measurement and age determination anomalies of each sample, which were then double-checked for measurement errors. Once all the samples were cross-dated and checked, and adjusted if necessary, final ages were assigned to each sample.

Age structure, establishment and radial growth patterns

A total of 200 increment cores and partial cross-sections were used in our study (Table 3.1). Exact ring-counted and approximate ring-counted samples (n=160) were used to develop the age structure of the Seney Wilderness Area mixed-pine forest. Only one core or partial cross-section was used for each tree; duplicate cores or partial cross-section samples farther from the pith were removed from the analysis. Cores containing the pith and cores within ten years of the pith were used to reconstruct the age structure. The origin dates of the samples were divided into five-year age class intervals to examine patterns of recruitment to 30 cm.

In order to examine the patterns of recruitment to 30 cm and growth, and relate these processes to the fire history, all samples were categorized into the following four classes:

1) Exact ring-counted age with pith present (± 1 year) (n=56): samples taken close to ground level (~30 cm) and containing the entire pith or the edge of the pith.
2) Approximate ring-counted age (± 2-10 years) (n=104): *a*) samples that were estimated to be within ten years of the pith, and *b*) samples that may be missing rings or have an unclear section (suspected false rings) .
3) Cross-dated samples with no pith (n=40): *a*) samples where the pith is estimated to be farther than 10 years, and *b*) samples that have rotten centers. Used only in determining the fire history, was not used in age structure analysis.

All samples that met the first or second criteria above were utilized to determine the recruitment following fires. Following the procedures presented by Lorimer (1980), Glitzenstein et al. (1986), and Bergeron and Brisson (1990), we determined a tree to show a sharp increase in growth if: *a*) ring width is suppressed (ring width less than one mm/yr before year in question), ring width doubles over a three-year time frame and growth ten years after the ring in question doubles the prior ten years growth, or *b*) for tree rings not suppressed (ring width greater than one mm/yr before the year in question), ring width increased by ≥ 50 % over a three-year period and this increase is sustained for ten years as in part (*a*). A sharp decease in growth was determined to occur in non-suppressed trees when a decrease in growth of 50% occurs and for suppressed trees, a decrease in growth of 33%. While the method tends to underestimate the sharp increases and decreases that occur in some tree species (Lorimer 1980, Glitzenstein et al. 1986), and was developed primarily for shade-tolerant species in closed-canopy situations, this method has been shown to be appropriate for open-canopied forest ecosystems (Pederson et al. 2008).

Relating growth patterns to fire history

Drobyshev et al. (2008a) found that the major fire (burning more than 20% of the study area) years at the Seney Wilderness Area were 1791, 1864, 1891, 1910, 1919 and 1976 (Table 3.2). As all these large fires occurred late in the growing season, one can assume that radial growth increases would begin to occur the year following the fire. However, Drobyshev et al. (2008a) also found that numerous, smaller fires also occurred from 1650 to 2006 which were restricted to individual sites within the Seney Wilderness Area. Consequently, we also analyzed the influence of these smaller fires in conjunction with those associated with major fire years on individual-tree radial growth patterns. For both analyses (major fires and all fires), two methods were used to detect the radial growth increases of the sampled trees after known fire events. The first method, a more conservative approach, determined that the increases were associated with a fire event if the increase date is within five years after the fire. A more moderate approach included the increases in radial growth that have occurred within ten years after a fire event were considered to be associated with the fire event. When the increase is outside the five-and the ten-year time frames, the increase was considered to be associated with another type of canopy disturbance, e.g., wind-throw or density-independent mortality. Similarly, we determined if periods of suppression (decreases) were associated with fire events or fire-free periods using both the conservative and moderate approaches above.

Results

Living tree composition

The old-growth mixed-pine forest ecosystems of the Seney Wilderness Area are dominated by red pine, with relative density and relative basal area values of about 80% (Fig. 3.2). Eastern white pine was the second most dominant species (10% relative density and relative basal areas values), while other species including paper birch (*Betula papyrifera* Marsh.), bigtooth aspen (*Populus grandidentata* Michx.), northern red oak (*Quercus rubra* L.), red maple (*Acer rubrum* L.), and trembling aspen (*Populus tremuloides* Michx.), all had low values of relative density and relative basal area (Fig. 3.2). Black spruce, typically found along the ecotone between the sand ridges and patterned bog, had relative density and relative basal area values of less than 1% (Fig. 3.2).

Age structure and recruitment

The age structure of old-growth mixed-pine forests of the Seney Wilderness Area is uneven-aged, with at least three major cohorts and one minor cohort (Fig. 3.3). The oldest age class is from 315-350 years old and is dominated by red pine (Fig. 3.4). Relatively few pines were recruited from 1690-1865, and only three pines in our sample reached coring height in the early 1800s. The majority of the current trees comprise the youngest two age classes, recruited from 1870-1905 and 1930-1965, respectively.

In relation to major fires, the recruitment of red pine during the early 1800s and 1870-1905 occurred within five to ten years following each event. Most of the eastern white pine recruited from 1930-1965; the two oldest stems sampled were in the 80 and 115 year old groups, respectively.

Age – tree diameter relationships

The range of diameters of stems sampled at the Seney Wilderness Area was variable (7.3 – 71 cm dbh) (Fig 3.5). Based upon our sample, tree diameter was not strongly related to age (Fig. 3.6), in part due to the variation in stand conditions, which affected the growth rates of sampled trees. For example, the trees in the oldest age class range from 33 to 71 cm and diameters in the youngest age class (1930-1965) range from 10 to 50 cm; which considerably smaller than the oldest cohort, and is most likely related to the fact that these trees are younger and are more likely to be suppressed by other trees.

Radial growth patterns

From 1650 to 2006, the percentage of trees exhibiting suppressed radial growth was closely related to the frequency of fires (Fig. 3.7). During the first 150 years of this time period (1650-1800), the sampled trees in this age class (n=15 after 1689) generally have a high suppression rate (above 60%). Following the first major fire (1791), there is a decrease in the percentage of trees exhibiting suppression, and this trend continued for 40 years (circa 1800-1840). Before 1860, most of the trees experiencing decreases in growth were suppressed trees and the increases occurring were in suppressed trees that responded positively following canopy disturbances associated with fire (Fig. 3.8). Also, the majority of the trees growing before 1860 show a higher rate of suppression with less frequent fires, but when the fire frequency increased in the early 1900s the rate of suppression decreased (Fig. 3.7). The large interval between major fires (1650-1800) may have caused the surviving trees to have decreased radial growth when younger (Fig. 3.9). Some of the trees from the oldest age class were able to grow under suppression (up to 150 years) until their radial growth increased following a major fire event. Radial growth patterns changed as the fire frequency increased in the late 1800s and early 1900s. From 1891-2006 the frequency of large fires increased and more of the radial growth increases occurred in non-suppressed trees. During this period the percentage of suppressed trees was lower than previous periods, and seemed to fluctuate following fires. Few small fires have occurred since the last major fire (1976), and radial growth decreases have increased in the absence of fires.

Relationships between changes in radial growth and fire

The majority of radial growth increases (62%) occur within ten years of a fire (Fig. 3.10), however, most growth increases followed major fires (59%). For example, using a conservative approach (five years after fire), we found that 80% of growth releases were associated with a major fire, and using a moderate approach (ten years after fire), 95% of radial growth increases are associated with a major fire (Fig. 3.10). Most decreases occur when there is a longer fire-free interval. In both approaches 83% of radial growth decreases following all known fires were due to major fires. The majority of increases and decreases occur following the six major fire events, and not following the thirty-three smaller fires. The conservative approach accounts for the majority of the radial growth responses to fire; few increases and decreases occurred during the five-to-ten-year interval following a fire.

Discussion

Our analysis suggests that the majority of the trees growing in old-growth mixed-pine forests ecosystems of the Seney Wilderness Area were recruited following a major fire event. Based on Drobyshev et al. (2008a) we found the six major fires (1791, 1864, 1891, 1910, 1919, and 1976) had all burned at least 60% of the sand ridges sampled and four of the fires burned more than 80% of the sampled locations . These larger fires likely reduced the overstory density and allowed for more sunlight to reach the forest floor. Additionally, these types of fires prepare the seedbed for pine regeneration, reduce litter and expose bare mineral soil for red pine and eastern white pine seedlings to become established (Alban 1977). Our results also suggest that the three major age classes were recruited to 30 cm within five to ten years following a major fire. This delay may be due to the several years it takes for the ash minerals to leach out of the upper soil before optimal germination occurs (Ahlgren 1976) and for the additional several years it takes for the seedling to reach the sampling height. We found that these regeneration pulses tended to occur for 35 years following the major fires, with the majority of the individuals being recruited in the first fifteen years.

Following these major fires, most red pine and eastern white pine seedlings likely originated from the larger, mature trees that survived the fire. The light-weight, winged pine seeds of these two species are dispersed by the wind about the same distance as the heights of the seed trees (Ahlgren 1976). The typical height of pines in the Seney Wilderness Area was observed as 20-30 meters. The narrow width and relative small size of the sand ridges made it possible for the surviving red pine and eastern white pine to regenerate the sand ridges with a similar species composition.

Frequent fires are needed for red pine to be self-regenerating (Bergeron et al. 1997), and the peaks that occur in regeneration, directly follow within several years of a fire (Bergeron and Brisson 1994). The species is considered a post-fire pioneer species due to its tendency to regenerate after a fire (Drever et al. 2006). When the thick litter layer is reduced by fire, red pine regeneration increases (Millik and Roberts 1994), and the older trees have thick bark which protects them, allowing for higher survival rates following low-intensity fires (Butson et al. 1987, Jackson et al. 1999). Some red pine at the Seney Wilderness Area have survived and grown for over 350 years surviving multiple fires, and the low- to moderate-frequency fire regime has favored a self-sustaining population of this species.

Unlike red pine, eastern white pine has only apparently survived at low densities on these sand ridges. This may be a result of eastern white pine having a lower resistance to fire when young due to thin bark, while older trees have thicker bark has and a moderate resistance to fire (Wendel and Smith 1990). The frequent fires in the late 1800s and early 1900s likely reduced the densities of eastern white pine, especially in the smaller and younger age classes, since the species is not as well adapted to fire as is red pine. After the frequent fires decreased following active fire suppression efforts since the early 20th century, eastern white pine regeneration survival has increased.

Droughts and humans are the main factors related to fire in the Seney Wilderness Area. The 1864 and 1891 fires coincide with two of the three major droughts (1856-1865, 1870-1877, and 1890-1896) on the North American continent during the 19th century (Herweijer et al. 2006). The next two fires (1910 and 1919) were likely caused by embers from distant slash fires or by sparks created by trains traveling on the railroad along the northern boundary of SNWR. In addition, there was a prolonged summer drought during 1910 that cured forest fuels (Heinselman 1973). The last major fire (1976) occurred during a period of lowered precipitation. These large fires occurred mostly during the late season, after the latewood had developed (Drobyshev et al. 2008a). Fires are more common during drought periods and later in the season because the vegetation is drier due to less moisture (Rouse 1988). Late-season fires are also able to travel farther due to the increased fuel loads.

The fires are extinguished by the snowfall and once a snow pack forms the available fuels become covered, removing the likelihood of a fire (Rouse 1988).

The diameters of the trees growing in the wilderness are variable in size when compared with age. This may be partially due to the location of where a tree was growing on the sand ridge. The majority of the smaller-diameter trees were growing on a higher part of the sand ridge which is the driest spot and has the least amount of nutrients. The larger diameter trees have the tendency to grow on the middle and lower part of the sand ridge, were more moisture and nutrients are most likely available. The diameters of some pines are not closely correlated with age. This is demonstrated by the two age classes 1650-1685 and 1870-1905, which have diameters ranging from 33 to 71 cm and 25 to 60 cm, respectively. The two classes have an age difference of approximately 185 years, however the diameters are similar, suggesting the diameters are more closely related to site and stand conditions than to age.

Suppression

Despite growing in relatively open canopies, both red pine and eastern white pine can become suppressed (defined here following Lorimer (1980) as annual radial growth less than one mm). When mixed-pine stands become dense and overstocked, the trees compete for nutrients and light leading to higher rates of decreased growth (Gilmore and Palik 2005). In the old-growth forests of the Seney Wilderness Area, the first 150-year period of growth (1650-1800) of the sampled trees exhibit a high rate (above 60%) of suppression. This is also the time period when smaller fires dominated the landscape, which are believed to have only burned a single sand ridge (Drobyshev et al. 2008a). Following the first major fire (1791), however, many trees showed a decrease in suppression, and a subsequent increase in the number of suppressed trees as the fire-free interval increased. These major fires opened the canopy and released nutrients into the soil. After several decades, the canopy gaps filled and the trees began to compete for resources, increasing the likelihood of an individual tree experiencing suppression. When the fire frequency increased, many trees showed a lower rate of suppression. The last major fire (1976) lowered the percentage of suppressed trees for fifteen years. The 1976 fire burned in a patchy manner with varying degrees of intensity (Anderson 1982). The shorter time of less suppressed trees could be due to the varied intensity of the wildfire. When mortality after a fire is low, the canopy gaps are filled more quickly by the surviving trees. The majority of the sampled trees are currently showing an increase in suppression.

Radial growth

Trees surviving a fire have their radial growth pattern affected in three ways: an increase may occur, a decrease may occur, or it may remain unchanged. The radial growth responses of the sampled trees from the Seney Wilderness Area over the last 350 years illustrate a strong and direct relationship between fire and radial growth patterns. Since 1650, six major fires (defined as more than 20% of the sampled area showing fire scars during a given year) have occurred as well as 33 smaller fires (i.e., less than 20% of the sampled area show fire scars during a given year). The major fires affected a larger portion of the wilderness area, and more often resulted in the radial growth increases and decreases.

The largest decreases in radial growth occurred within five years of the major fires. The reduction in radial growth is due to the trees recovering from needle loss from crown scorch and having parts of the cambium killed by the heat of the fire (Johansen and Wade 1987). When a fire heats a portion of the cambium layer to greater than 60.6 ˚C, the living tissue will die creating a fire scar (Wade and Johansen 1986). The higher rates of decreased radial growth occurred when fire was less prevalent. When fires do not occur on a frequent cycle, fewer openings in the canopy are present, which causes the trees to slow their growth as there is more competition for nutrients and sunlight with neighboring trees. During 1650-1800, only one major fire and thirteen smaller fires occurred in the Seney Wilderness Area. During this time period the trees were competing with their neighbors for nutrients and sunlight, which caused the decreases in radial growth. During the next 205 years (1801-2006), there were five major fires and twenty smaller fires in the wilderness area. The increase in fire frequency and intensity opened the canopy and returned nutrients into the soil, and lowered the rate of decreases in radial tree growth in suppressed trees.

The decreases in radial growth can be divided into two categories. The first category shows a decrease where a 33% decline in growth occurs in suppressed growth rings (less than one mm of annual radial growth) (Lorimer 1980, Glitzenstein et al. 1986). The second category is a decrease where a 50% decline in growth occurs in non-suppressed growth rings (more than one mm of annual radial growth) (Lorimer 1980, Glitzenstein et al. 1986). These two types of decreases tend to be associated with fire intensity and frequency in the sampled trees. When fires were less frequent, growth decreases associated with suppressed trees tended to be higher, due to slower growth caused by the competing trees. After the fire frequency increased, there were a higher number of trees showing decrease in non-suppressed trees.

Similarly the radial growth increases were divided into two categories. An increase occurs when radial growth doubles within three years and ten years following this growth rate is double the growth rate of the previous ten years (Lorimer 1980, Glitzenstein et al. 1986). This criterion was used with both suppressed and non-suppressed individuals. A large number of increases occurred following known fire events, primarily after large fires but also after some small fires. When the fire frequency was lower, the suppressed trees were mostly showed increases in radial growth following fires. This was due to the surviving trees having less competition and more available nutrients. As the fire frequency increased during the late 1800s and early 1900s, radial growth increases occurred in more non-suppressed trees. The frequent fires allowed faster growing trees to increase their growth after the reduction in competition and the increase in nutrients. The fire suppression policies of the past century have lead to higher suppression, but this is not fully evident in the data due to the major wildfire that occurred in 1976.

While the Seney Wilderness Area is characterized by a frequent fire regime of low- to moderate-intensity surface fires, mixed-pine forest ecosystems in other portions of the northern Lake States and Canada have a frequent fire regime that includes stand-replacing fires occurring during the typical life cycle of these pine species. In the northern Lower Michigan, low-intensity fires occurred on a 26-69 year interval and stand-replacing fires occurred on a 50-170 year cycle (Cleland et al. 2004). The Seney Wilderness Area has not experienced stand-replacing fires on a regular basis, as indicated by fifteen trees recorded from 315 to 350 years of age. The fire regime is most likely influenced by the spatial pattern of mixed-pine stands growing on the isolated sand ridges. The sand ridges are scattered throughout the wilderness area with lowland bog areas in between them. This landscape pattern is not conducive for stand-replacing fires to travel from sand ridge to sand ridge. When lightning starts a fire on one sand ridge during typical years, it has a tendency to remain contained due to the bogs acting as natural fire breaks (Bergeron 1990). During drought years, however, the bog areas dry out and the vegetation becomes cured, allowing a fire to spread to multiple sand ridges. This appears to be the case for at least four major fires (1864, 1891, 1910 and 1976).

Radial growth responses to fire

Two approaches were used to relate the radial growth increases and decreases to all known fire events. The first method is a conservative approach which includes all radial growth responses for five years directly following a fire. The second method is a moderate approach which includes all radial growth responses for ten years directly following a fire. Both approaches show similar tendencies. When a tree shows an increase or decrease outside the ten-year range after a fire, it was assumed that the tree was affected by other natural disturbances (e.g., wind, natural mortality of a neighboring tree). The conservative and moderate approaches resulted in determining that a large portion of the increases occurred after a fire, 46% and

62%, respectively.   Fire plays a major role in increasing trees radial growth. These trees exhibit increased radial growth due to the increased available nutrients and reduced canopy cover. The decreases follow a different trend. The conservative and moderate approaches showed a smaller portion of decreases were due to fire, 32% and 40%, respectively. More decreases occur directly after the fire due to crown scorch and injured cambium, however, after that short period the radial growth patterns of a tree is less affected. Decreases in growth are more likely to occur when fire is less frequent because the trees are competing for resources. The majority (greater than 80%) of the radial growth responses of all known fires were due to major fires.

Future considerations

Managers of mixed-pine forest ecosystems of eastern Upper Michigan that are being considered for restoration can use this information to plan prescribed fire frequency intervals. Fire is an important component of mixed-pine forest ecosystems. Prescribed burning is more controllable in intensity and season of burn than wild fires. Prescribed burning is the primary silvicultural method that returns nutrients back to the soil for plant use (Stark and Steele 1977). The practice of prescribed burning also alters the structure of the forest by creating openings and allowing more sunlight to reach the forest floor (Coleman and Rieske 2006), frequently clearing the understory by removing the less fire-adapted species and weaker individuals. The created openings in the forest canopy allowed for the surviving trees to increase their growth rates, since there is an increased nutrients and sunlight (Guyette and Dey

1995). Where fire cannot be used, mechanical thinning may be implemented to possibly emulate some of the effects of fire. Current forest stands in eastern Upper Michigan can be managed to restore the mixed-pine ecosystems utilizing our results. An important observation of this study showed that red pine has the ability to increase its radial growth following a major fire. Red pine was able to grow in a suppressed state (less than one mm of growth per year) for decades and in some cases up to 150 years. Then following a disturbance, such as a major fire event, the trees showed an increase in radial growth. Forest managers can use this to their advantage in older, overstocked red pine stands with trees exhibiting suppressed radial growth, where harvests can be used to reduce density to allow the remaining trees to increase their radial growth. Retaining red pine and eastern white pine provides seed sources and increases age and structural complexity of these pine ecosystems.

Projects in the future focusing on mixed-pine forest ecosystems can expand on this study in a several ways. The first would be to study the effects of fire on other mixed-pine ecosystems in different locations of the range. It would be best to focus on stands that have had the least human disturbances in the past, but it would also be important to document the species composition and structure of these stands. More studies will need to be conducted on how radial growth changes are affected by fire in eastern white pine since there were fewer trees of this species sampled in the current study. Also, the effects on radial growth patterns following other natural disturbances (e.g., wind) and climate effects in the eastern Upper Michigan need be explored in detail.

Location	Species		Number of samples				
Fire site #	red pine	eastern white pine	Increment cores	Partial cross-section	Pith	Estimated within 10 years to pith	Fire history only
36	20	1	14	7	11	9	1
38	17	3	17	3	1	13	6
39	14	3	15	2	2	11	4
43	7	0	7	0	2	4	1
44	6	0	5	1	3	2	1
45	18	0	16	2	6	8	4
49	20	1	20	1	5	11	5
56	14	4	13	5	3	10	5
58	12	1	11	2	4	7	2
60	22	3	21	4	11	13	1
65	7	0	5	2	3	3	1
66	11	1	7	5	3	5	4
67	5	0	1	4	1	2	2
68	9	0	6	3	0	6	3
95	1	0	0	1	1	0	0
Total	183	17	158	42	56	104	40

Table 3.1: Division of samples according to the fifteen fire site numbers, in the Seney Wilderness Area, eastern Upper Michigan. Total number of samples is 200.

Year							Site								
	36	38	39	43	44	45	49	56	58	60	65	66	67	68	95
1595									X						
1600															
1605															
1610															
1615															
1620															
1625															
1630									X						
1635															
1640															
1645															
1650															
1655															
1660															
1665									X						
1670															
1675															
1680															
1685															
1690					X							X			
1695															
1700															
1705															
1710							X			X					
1715									X					X	
1720															
1725					X										
1730	X														
1735			X												
1740															
1745												X			
1750	X						X			X					
1755															
1760										X					
1765								X					X	X	
1770							X								
1775															
1780															
1785															
1790	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
1795							X								

Table 3.2: Known fire events occurring on individual sand ridges in five-year intervals (e.g. 1595-1599, 1600-1604), Seney Wilderness Area, eastern Upper Michigan. X denotes a sample with a fire scar during interval.

Continued

Table 3.2 continued

1800															
1805															
1810															
1815															
1820						X			X						
1825													X		
1830															
1835									X						
1840										X			X		
1845									X		X				
1850															
1855					X										
1860	X	X	X	X		X	X	X	X	X	X	X		X	X
1865				X		X	X		X	X					
1870															
1875			X						X						
1880							X		X				X		
1885												X	X		X
1890	X	X		X		X	X		X	X	X	X			
1895									X					X	
1900															
1905															
1910	X	X	X	X	X	X	X	X	X	X		X			
1915	X		X		X	X	X	X	X	X	X	X		X	X
1920												X		X	
1925	X	X	X					X							X
1930	X														
1935	X	X					X	X							
1940							X	X							
1945					X		X								
1950		X									X				
1955					X										
1960															
1965															
1970															
1975	X	X	X	X	X	X	X	X		X	X	X	X	X	X
1980															
1985		X													
1990															
1995															
2000															
2005															

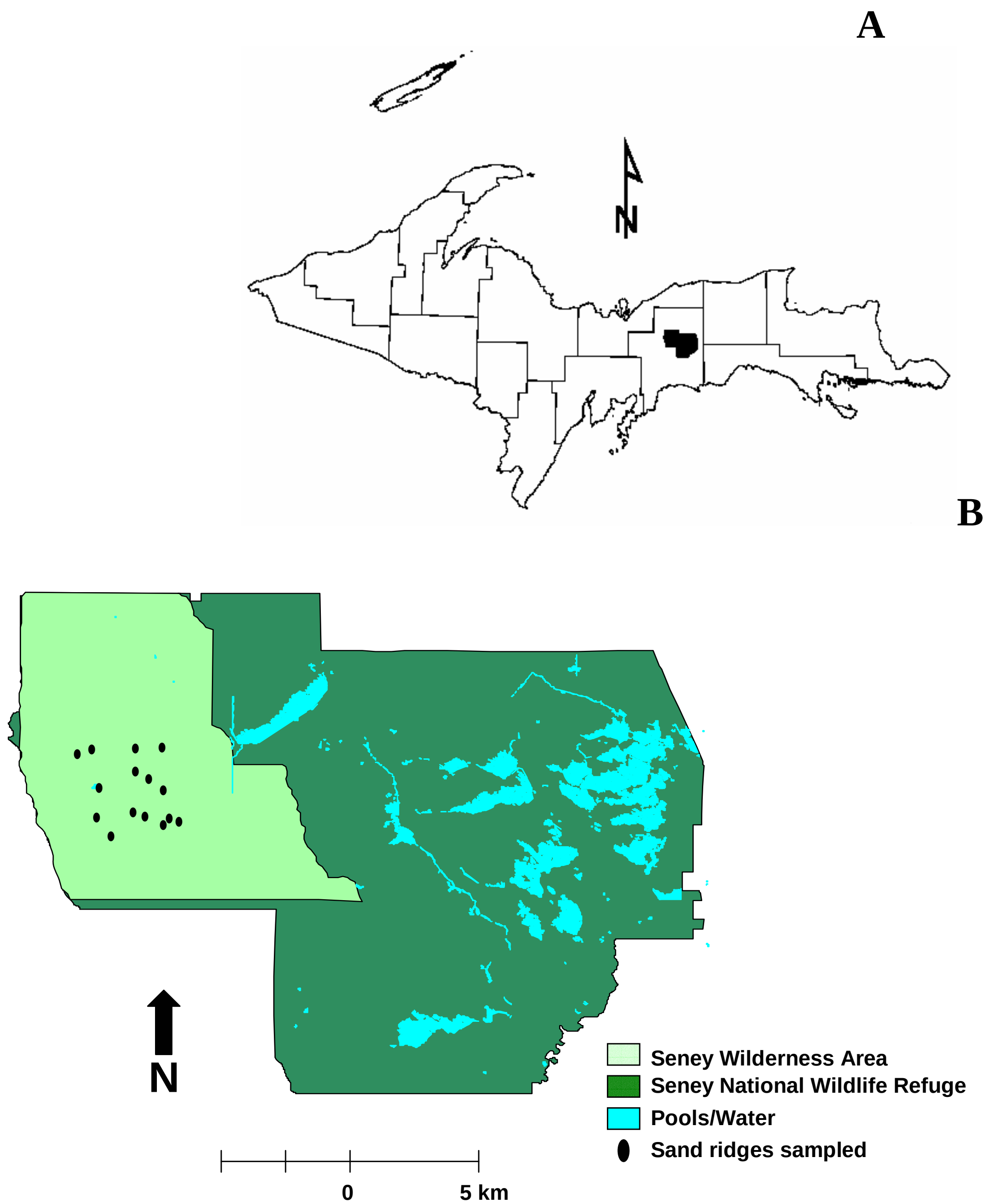


Figure 3.1: Location of Seney National Wildlife Refuge (A) and Seney Wilderness Area with location of study sites (B).

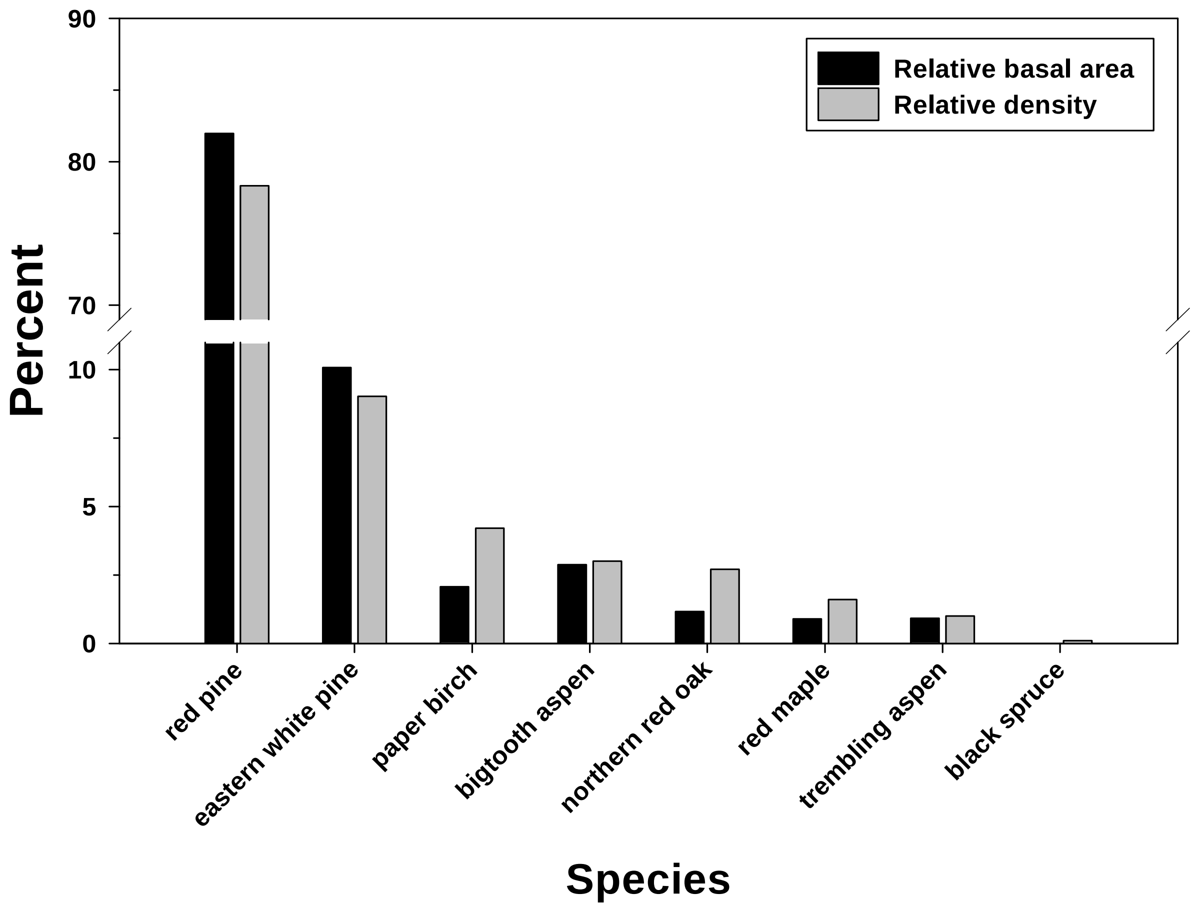


Figure 3.2: Relative basal areas and relative densities of species sampled in the Seney Wilderness Area, eastern Upper Michigan. The data were collected from measurements of all living trees (≥ 10.0 cm dbh) on 27 vegetation plots (each 500 m^2).

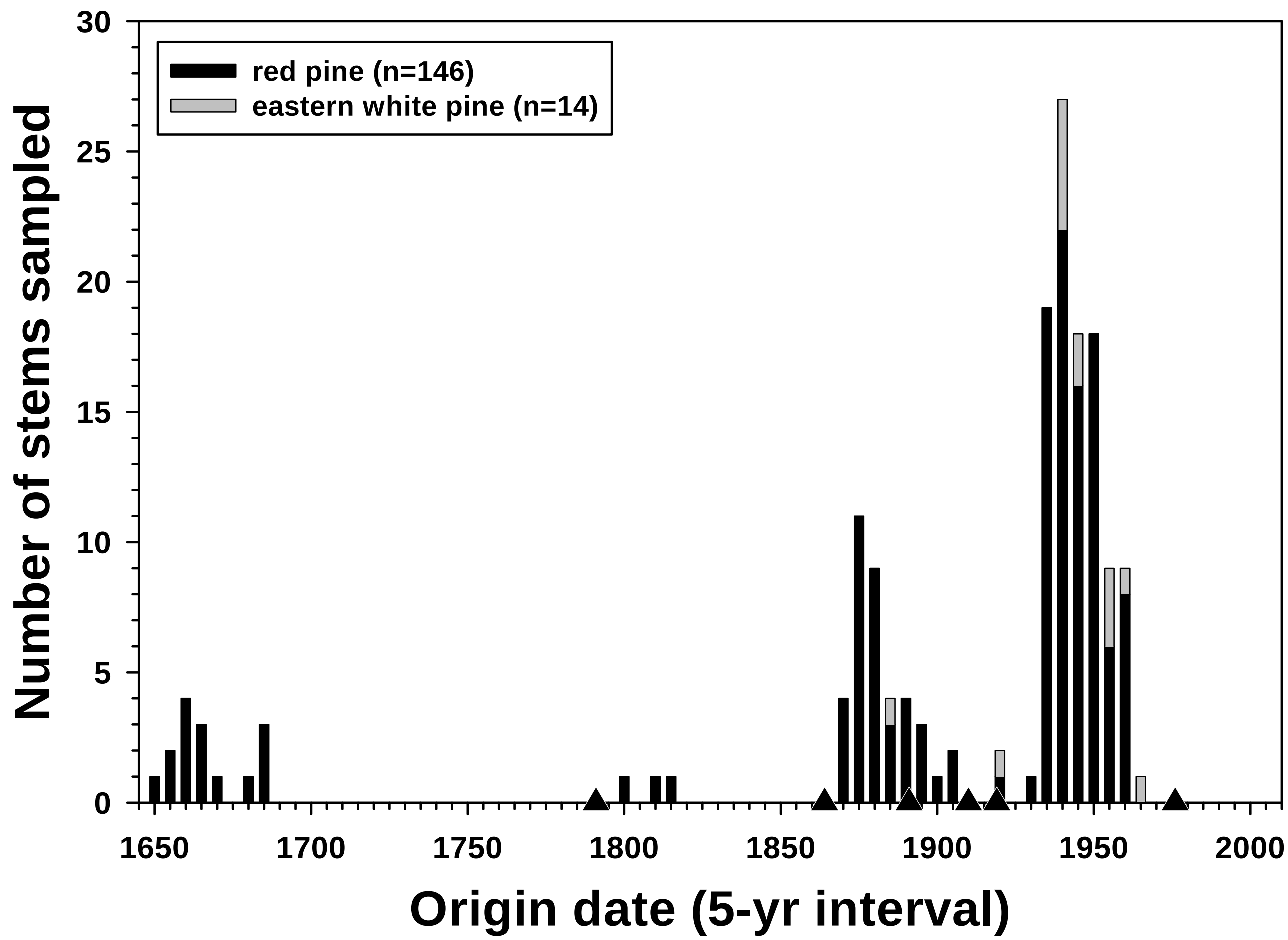


Figure 3.3: Number of stems sampled by origin date and species, in five-year intervals, in the Seney Wilderness Area, eastern Upper Michigan. Triangles on the x-axis denote major fire years.

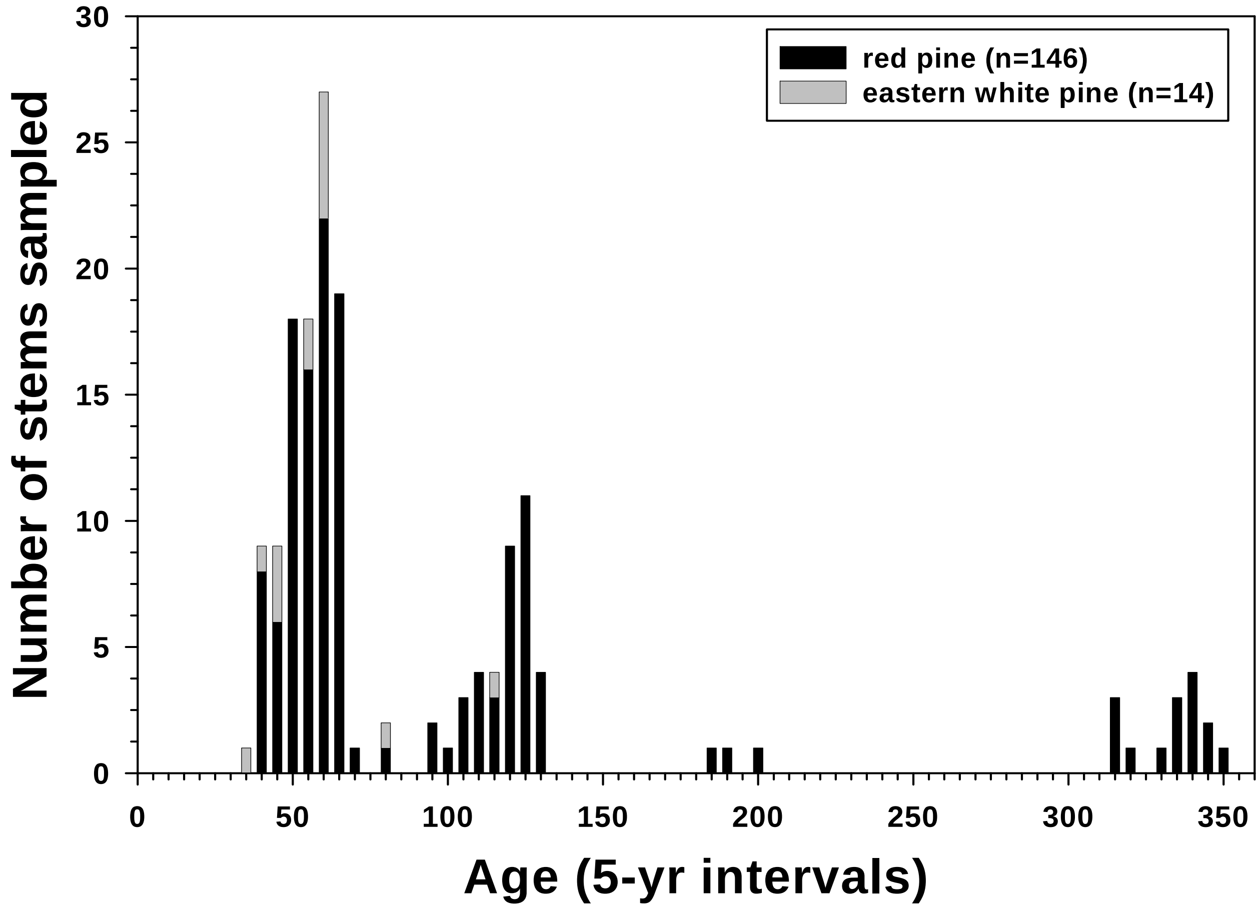


Figure 3.4: Number of samples grouped by five-year intervals according to age, in the Seney Wilderness Area, eastern Upper Michigan.

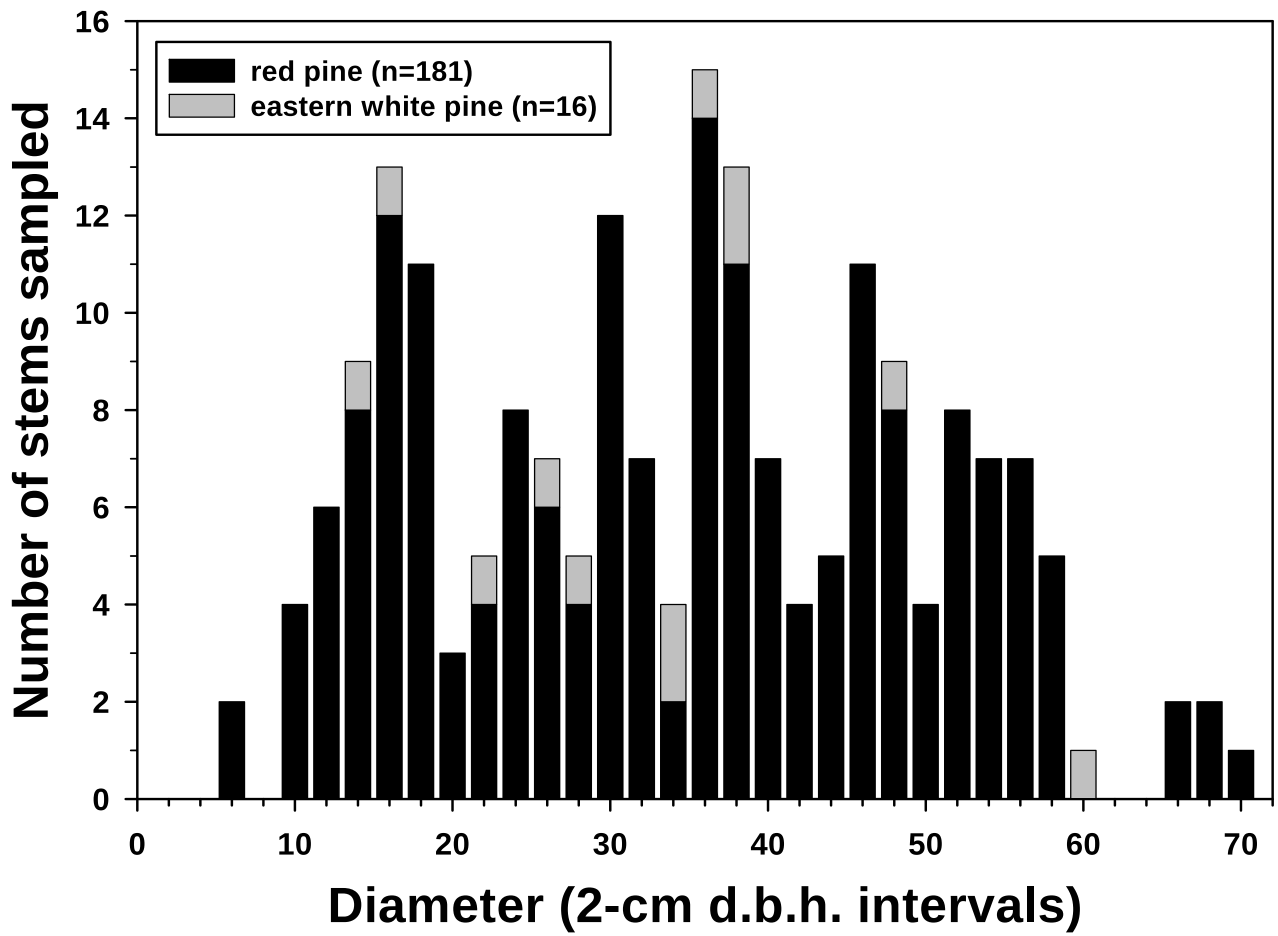


Figure 3.5: Diameter distributions of red pine and eastern white pine stems sampled, in 2-cm intervals, in the Seney Wilderness Area, eastern Upper Michigan. Three samples were not included due to sampling error.

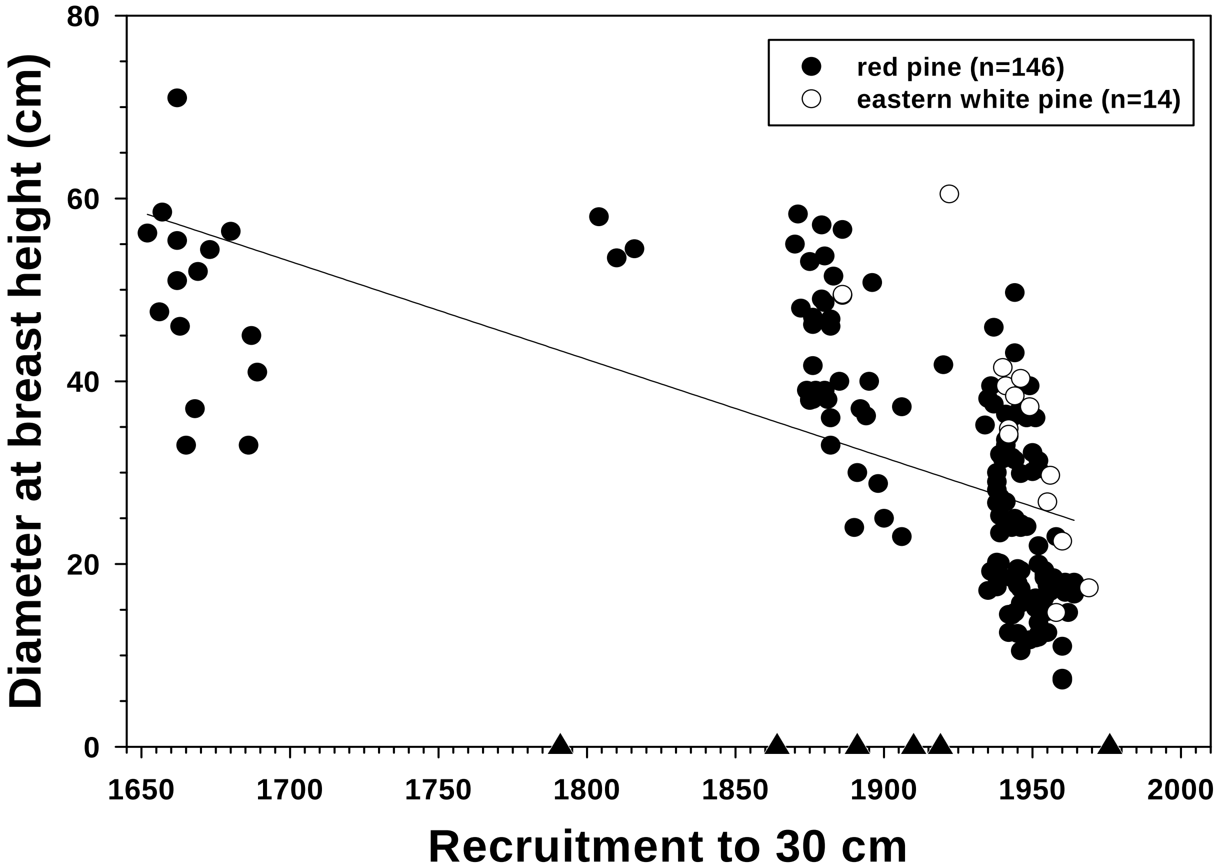


Figure 3.6: Diameter at breast height in relation recruitment to 30 cm in height, in the Seney Wilderness Area, eastern Upper Michigan. Samples included contain the pith or were within ten years of the pith. Triangles on x-axis denote major fire years. Line denotes linear relationship between the recruitment age and diameter.

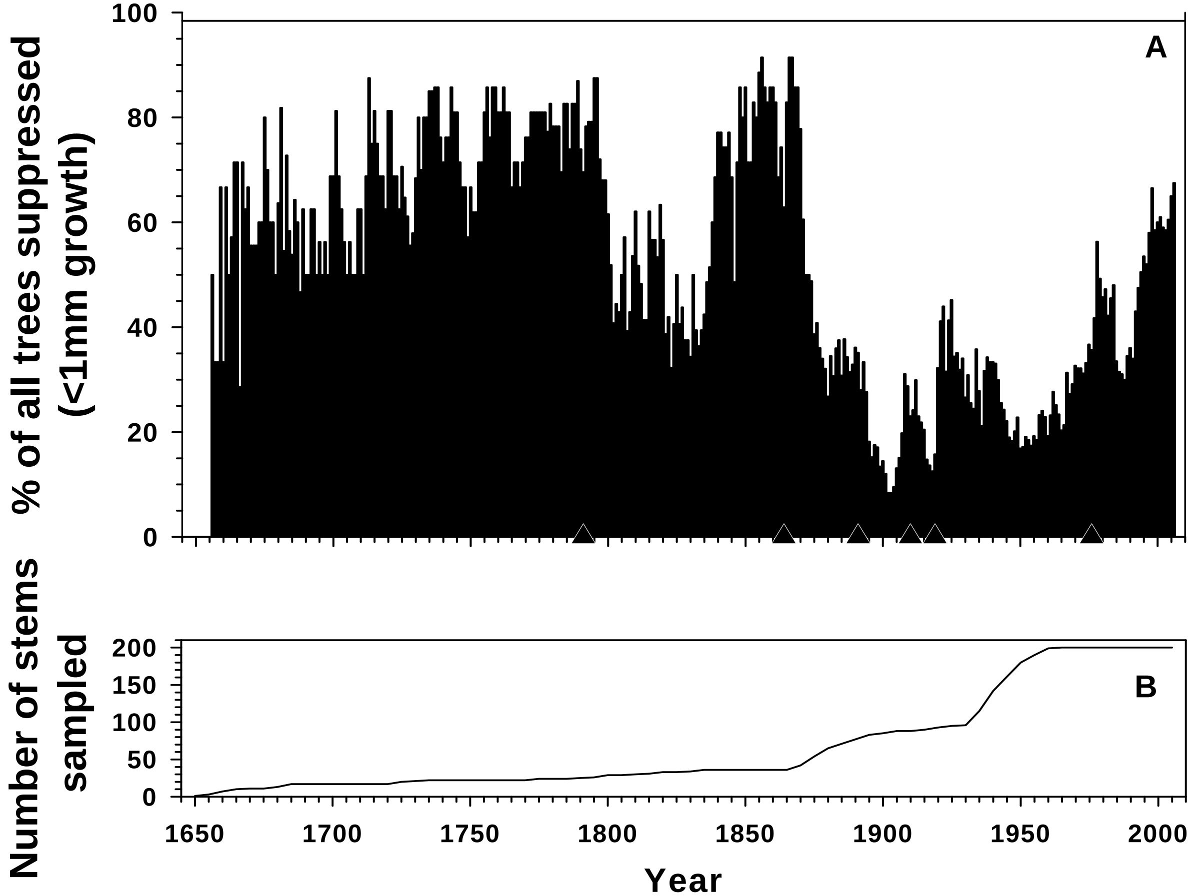


Figure 3.7: (A) Percent of sampled trees exhibiting suppression (less than one mm of radial growth) on a yearly basis, in the Seney Wilderness Area, eastern Upper Michigan. Triangles on the x-axis denote major fire years. (B) Sample size of increment cores and partial cross-sections used to show percent of trees that were suppressed.

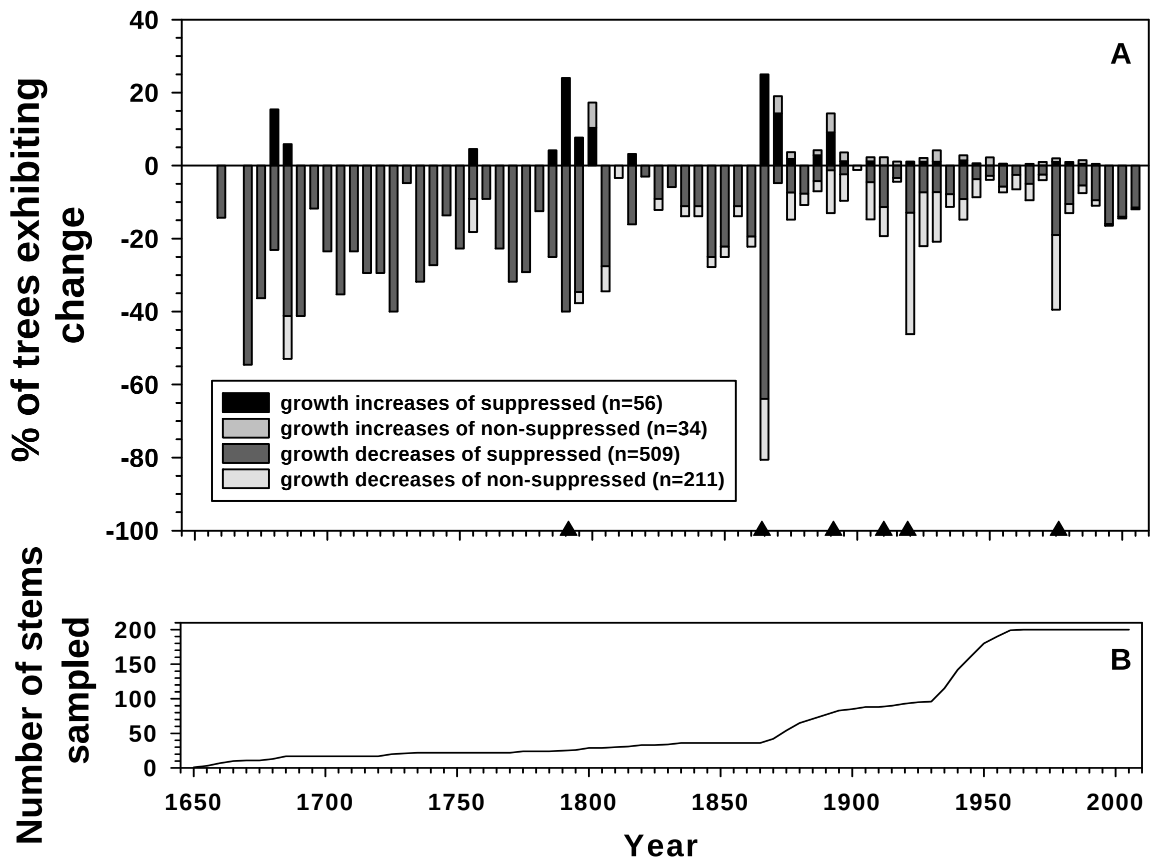
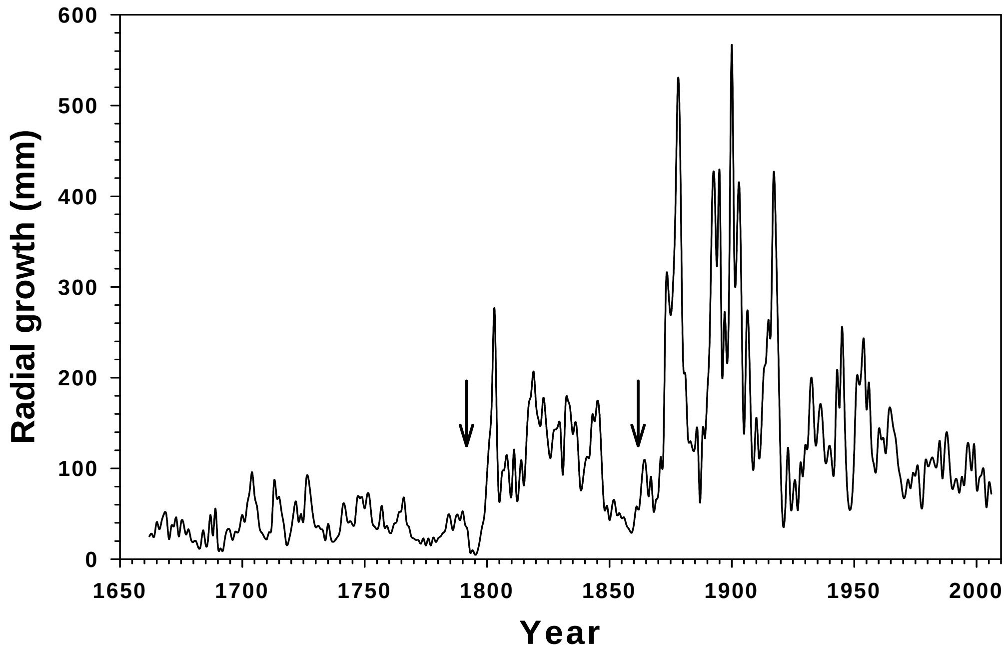


Figure 3.8: (A) Percent of trees exhibiting increases and (or) decreases in radial growth (sensu Lorimer (1980), Glitzenstein et al. (1986) and Bergeron and Brisson (1990)), in the Seney Wilderness Area, eastern Upper Michigan. Triangles on the x-axis denote major fire years. (B) Sample size of increment cores and partial cross-sections used to show percent of trees exhibiting increases and (or) decreases.

A



B

Figure 3.9: (A) Image of partial cross-section 95-1. (B) Radial growth pattern of a representative sample (partial cross-section 95-1) from 1662-2006, in the Seney Wilderness Area, eastern Upper Michigan. Downward facing arrows above the x-axis denote radial growth increases following suppression.

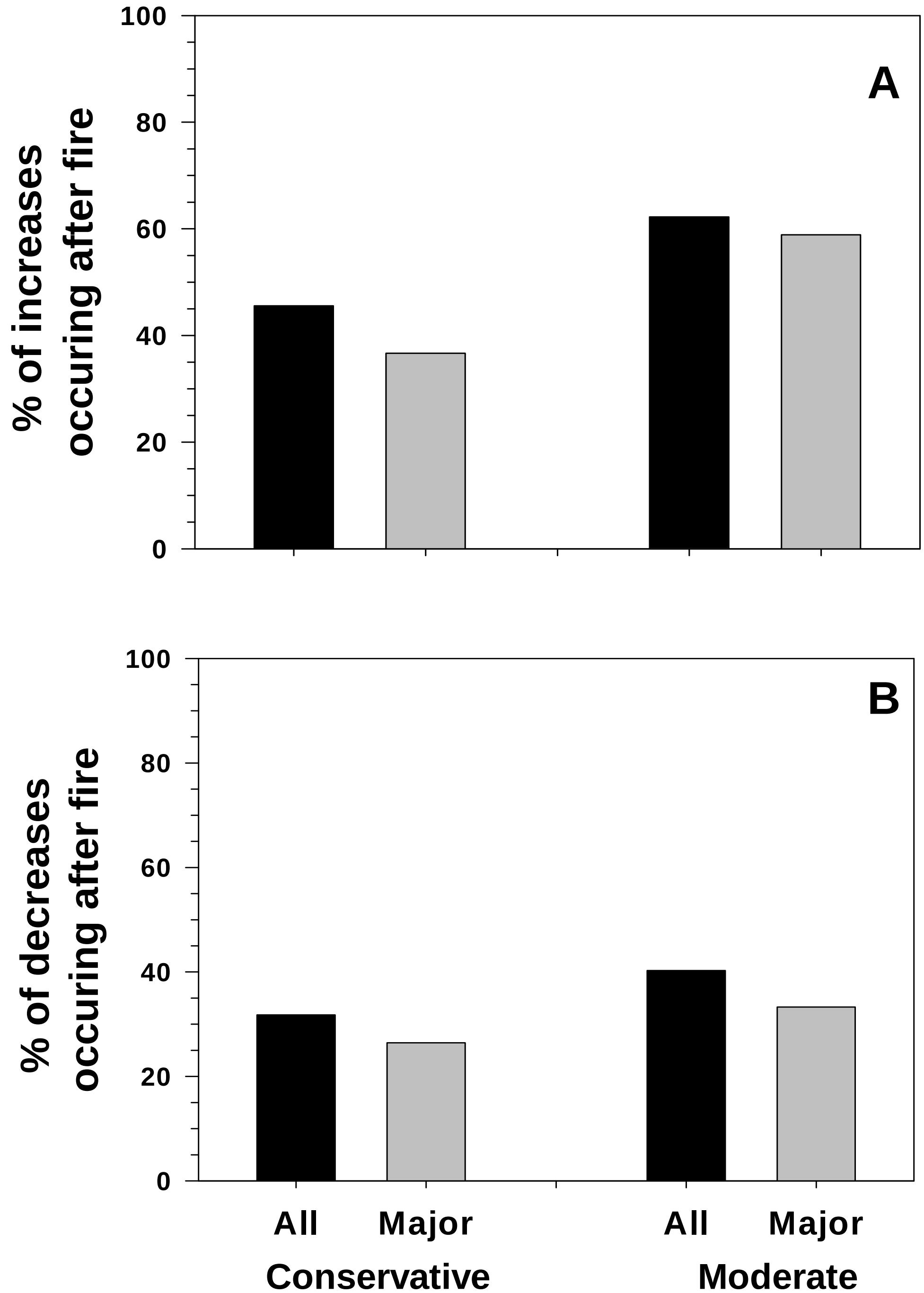


Figure 3.10: (A) Percent of increases occurring after all fires (n=39) and after major fires (n=6), utilizing both a conservative approach (within five years after fire) and a moderate approach (within ten years after fire), in the Seney Wilderness Area, eastern Upper Michigan. (B) Percent of decreases occurring after all fires and after major fires, using the same two approaches.

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