

DYNAMICS OF OLD-GROWTH FORESTS OF MINNESOTA

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Dedication

To my dear friend and mentor
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Abstract

Disturbances are an essential part of almost every ecosystem. I studied disturbances in three different old growth forests in Minnesota. These old-growth remnants include the white and red pine forest of the Lost 40 in northern Minnesota, the balsam fir and white spruce forest at Itasca State Park in northern Minnesota, and the hardwood forest of the Big Woods in south-central Minnesota. In the Lost 40, white and red pine are not regenerating and shade-tolerant trees are abundant in the understory and canopy. This lack of regeneration is probably due to the lack of a disturbance like fire. If a management plan were to be implemented, the advancement of the shade-tolerant species into the canopy and the shifting climate space of white and red pine need to be taken into consideration. The white and red pines in Itasca State Park are actively managed, but not the fir–spruce forest. Now, mature fir–spruce forest is dying because of a recent spruce budworm outbreak. Spruce budworm, a defoliating insect that prefers balsam fir and spruce, has been in the park before the most recent outbreak. Before the two outbreaks that were reconstructed, the climate was wet, whereas other studies found dry conditions before an outbreak of the spruce budworm.

In reconstructing canopy disturbances of eight remnants, I tested several methods for evaluating canopy disturbance in closed canopy forests. The sequential t-test (regime shift) method had best results when reconstructing canopy disturbances of these forests. I then used the sequential t-test method to reconstruct the canopy-disturbance history. Although a drought-disturbance relationship was detected by other authors, I did not find a consistent relationship in my data.

I studied three different old-growth forests in Minnesota. In these stands, disturbances are an integral part. Methods of disturbance-history reconstructions were tested and one (sequential t-test) subsequently used. I made contributions to reconstructing canopy disturbances using release and suppression periods in tree rings of forest types that previously had not been studied this way. The information that I gathered could now be used to inform a management plan, to apply a possibly more precise method to reconstruct a canopy-disturbance history, and to inform the public.

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CHAPTER 1

Introduction

Minnesota is one of the few states that has three distinct biomes—the prairie, deciduous forest, and coniferous forest—because of a latitudinal gradient (i.e. a north-south gradient in temperature) and a longitudinal gradient (east-west) in moisture and is, therefore, diverse in forest types and tree species. European settlement began relatively late, and land clearing started around 1880 (Frelich 2002). Logging removed numerous old-growth forests in the Lake States leaving few hectares (14,000 to 150,000 ha) of old growth (Frelich 2002).

The term old-growth forest is difficult to define. Hunter (1989, 33) notes that the simple definition of “a climax forest that has never been disturbed by humans” is too restrictive for two reasons: first, climax forests are hardly ever reached because of disturbances, and second, disturbances by humans may also include air pollution on a global scale, setting of fire by early humans, or transporting invasive species, which would affect almost every forest on earth and no old-growth forest according to that restrictive definition would exist anymore. Hunter (1989) concludes that a universal definition of old-growth forest might not be possible. He proposes that a definition should be prepared for each forest type. At its core, a definition might be: “old-growth forests are relatively old and relatively undisturbed by humans” (Hunter 1989, 33), but

ultimately different age and disturbance criteria should be considered to create a precise definition of old-growth in a certain locale.

A concept that was first put forward by Oliver (1980) is that of four basic stages of forest growth—stand initiation, stem exclusion, understory reinitiation, and old growth—after a disturbance. Therefore, Oliver’s (1980) definition of old growth would be when the forest is in the last stage of stand development. This definition does not include a specific age but rather focuses on growth stages. Although Oliver (1980) discusses the old-growth stage as the last stage, he does not argue that the old-growth stage needs to be the climax community. Frelich (2002) took Oliver’s (1980) concept and modified it slightly. Frelich (2002) argued that “old growth” is a term that should be replaced in Oliver’s (1980) model by “multi aged”, because Oliver’s (1980) model of the four stages can also occur after clearcutting a plot and the “multi-aged” stage would not be considered old growth anymore.

Frelich (2002, 144) provided a rather general definition: “Any forest at or beyond a politically established threshold stand age, threshold diameter for canopy trees, or threshold vegetation growth stage.” In Minnesota, the commonly accepted threshold stand age is 120 years (Frelich 2002). However, Frelich (2002) states that even though trees might not be old, as long as the canopy species replace themselves, the forest would still be called old-growth. As an example he uses balsam fir. In Minnesota, where the species reaches its southern range limits, balsam fir is stressed and dies at 40–60 years (Frelich 2002, Rauchfuss et al. 2009). Yet, it replaces itself and could, therefore, be considered old-growth. For the purpose of this dissertation, I adopted Frelich’s (2002) definition of old-growth forests.

Old-growth forests are invaluable because they provide information about presettlement forest dynamics, structure, and composition (Foster et al. 1996). Old-growth forests such as maple–basswood, oak, fir–spruce–cedar, Jack–red–white pine, and aspen–birch forests were once an important part of the Minnesota landscape (Frelich 2002). Today, due to land use practices, the importance of most of these forest types has decreased and with the overall acreage of forested land reduced as well (Frelich 2002). Old-growth forests are also important because fallen trunks of trees, standing snags, and large branches provide unique habitat for different forest species (Jonsson 2000). The few remnant forests that were protected from logging also provide a wide variety of genetic material for the different species (Frelich and Reich 2003). To maintain those few old-growth forests that are left after the logging era, knowledge is needed of their spatio-temporal variations and attributes (Frelich 2002, Frelich and Reich 2003). After acquiring that knowledge, hypotheses and eventually theories of old-growth dynamics can be formulated and these in turn can inform management strategies.

Recognizing from scientific research that old-growth forests play an important role, people may be more willing to protect the few remnants left. A more informed public is a more engaged public (Steel et al. 2005). Before the public can be informed, knowledge needs to be gathered. What is the disturbance history of the forest? Are there regional disturbances that are fairly rare? Or is the forest disturbed by fairly frequent and more local disturbances? What types of disturbances perturbed the forest? Wind? Fire? Insects? These and other questions were answered in this dissertation for three old-growth forests in Minnesota.

In this dissertation, I considered three different types of old-growth forest: the white and red pine forest in the Lost 40 in northern Minnesota, the fir–spruce forest of Itasca State Park in northern Minnesota, and the Big Woods of south-central Minnesota, which is a maple–basswood–oak forest (Figure 1). All three are considered old-growth forests using Frelich’s (2002) definition. The trees in the white and red pine forest in the Lost 40 are big; they are not, however, replacing themselves because the disturbance regime changed from one dominated by fire to one that experiences no fires. The fir–spruce forest in Itasca is replacing itself. For the Big Woods, the species in the overstory are the same as in the understory (mainly maple).

Conservation of old-growth forests is important because they provide several important roles for flora, fauna, and humans. Although some old-growth forests have been protected for over a century from loggers in Minnesota (like Itasca State Park), it is still not clear how to manage them effectively. Management plans based on scientific studies and local knowledge are valuable (Failing et al. 2007). A management plan for the Lost 40 did not exist, but was desired by the Department of Natural Resources (DNR) in Minnesota. We, Susy Ziegler and I, set out to study the Lost 40 to recommend actions to be taken.

The Lost 40 is another remnant forest that apparently was never cut because of a surveying error. People visit the Lost 40, because they want to see those towering white and red pines. However, those pines are not regenerating and the understory consists of maples and balsam firs. The Minnesota Department of Natural Resources wondered about the future of tall pines at the Lost 40 and wanted to have science-based recommendations for a management plan (Bob Djupstrom, personal communication). In

addition, little was known about the disturbance history in this forest. We tried to get a range of the differences in this forest (in composition) while staying in the part of the Lost 40 where pines exist.

From what we know about how succession proceeds in white and red pine stands, the loss of regeneration of the pines might not be so unusual. What comprises the understory today at the Lost 40 is part of the native plant community. The species in the understory (maple, balsam fir, and spruce) are very shade tolerant. White and red pine, on the other hand, are (moderately) shade intolerant (Logan 1966). Therefore, white and red pine naturally need disturbances (that remove part of the over- and understory) to regenerate. They also have certain soil requirements, which means that they need to have certain disturbances like (surface) fire preparing the soil for establishment (Van Wagner and Methven 1978, Wright and Bailey 1982); red pine especially is very dependent on hot surface fires to prepare the seedbed (exposed mineral soil) (Van Wagner 1970). With no disturbance, the shade-tolerant species will become established. Therefore, forest composition and structure we see today might just be in between two disturbances. To find out, we (1) analyzed stand structure and species composition, (2) determined frequency and intensity of canopy disturbances, and (3) characterized recruitment patterns at the Lost 40.

The Lost 40 is known for its white/red pine forest and so is the Itasca State Park. Itasca is already actively managed, not for the old-growth fir–spruce forest but for the white and red pine forest. Now that the spruce budworm, a defoliating insect that had not been observed by park rangers at Itasca State Park before the most recent outbreak, is in

the park, questions regarding its management need to be asked. For example, is it necessary to manage the old-growth fir–spruce forest actively?

The spruce budworm is a native insect that has evolved with the forest (in parts where it has been for centuries and maybe millennia) to rejuvenate it. However, at Itasca State Park, the insect has never been spotted before this most recent outbreak and it is not clear what this potential lack of budworm history would mean for the trees in this community. Will they equally be able to adapt to this insect or will they die out locally? Along five belt transects, we studied the insect's effect on the trees (on the ring width) to see whether we could detect previous outbreaks. In addition, we studied the relationship between climate and outbreaks to gain knowledge about how the climate affects the spruce budworm at the southwestern range limits to understand under which climatic conditions outbreak-levels rise.

The Lost 40 is only about 110 km northeast of Itasca State Park. Both forests have similar species composition. Now that the spruce budworm is at Itasca State Park and seemingly has expanded its range from the Minnesotan arrowhead to the park, how probable is it that the Lost 40 will also be affected by the spruce budworm soon?

On a local scale, factors like disturbances, competition, and diseases might mask climate responses; however, climate can certainly drive vegetation dynamics (e.g. distribution of biomes). Iverson et al. (1999, 2008) predicted that under doubled CO₂ concentration, by 2100 species would not be able to thrive where they used to thrive. If this potential shift in the climate space becomes reality, spruce budworm might not be an issue in Minnesota anymore because balsam fir would not thrive in Minnesota after this doubling of CO₂ concentration (Iverson 1999). Similarly, how will white and red pine

react to increasing CO₂ concentration and subsequent shifts in temperature and precipitation?

The Big Woods of Minnesota, formerly nearly 9000 km² (Department of Natural Resources Minnesota 2009), has been logged or otherwise cleared for urban development or agriculture over the last 150 years (Frelich 2002). A few remnant old-growth forests are left and they are protected mostly by the Minnesota DNR or The Nature Conservancy (TNC). To the best of my knowledge, most of these remnants are not actively managed, nor do these organizations seem to have a management plan. The Big Woods have been studied using lake sediments (Grimm 1983, 1984, Umbanhowar 2004, Shuman et al. forthcoming). However, reconstructing canopy disturbances from tree rings in the Big Woods had not been determined before my research with Susy Ziegler. Based on analysis of fossil pollen, macroscopic charcoal, and lake-level reconstruction, the Big Woods apparently established within the last 650 years (Umbanhowar 2004, Shuman et al. forthcoming) which is very recent compared to the 11,000 years of post glacial history. Grimm (1983) conjectured that the Big Woods established during reduced fire frequency because of moister conditions. However, Umbanhowar (2004) and Shuman et al. (forthcoming) argued that the reduced fire frequency occurred because of drier conditions, which reduced fuel and, therefore, the likelihood for fire. Nonetheless, lake-sediment analysis is often not as precise (unless varved sediments are present) or spatially as detailed as tree-ring dating, which often has annual resolution. Therefore, dendrochronology is a useful tool to analyze the above contrasting statements and to reconstruct canopy disturbances for the Big Woods. With a canopy-disturbance history, the hypothesis of a steady state and shifting mosaic in northern hardwood forests as

proposed by Bormann and Likens (1979), which has been tested repeatedly in different ecosystems, can then be tested again in the three forest types that I studied.

Many methods that reconstruct canopy disturbances from suppression and release periods in tree rings have been proposed. Some of these methods have been compared by Rubino and McCarthy (2004); however, new methods have been published since 2004 and those methods need to be tested for their precision in identifying release events. I used data from the Big Woods to study the usefulness of four methods and compared those to the visual inspection method.

Collectively, this dissertation examines the dynamics of old growth forest in three prominent Minnesota forest communities. An understanding of the historic role of disturbances is necessary because that knowledge could then be used to inform science-based management plans and the public of the value of old-growth forest. My research explores which method of calculating decadal disturbance histories from tree rings is most precise. I will use the most precise method to calculate the disturbance history and explore a disturbance agent, spruce budworm.

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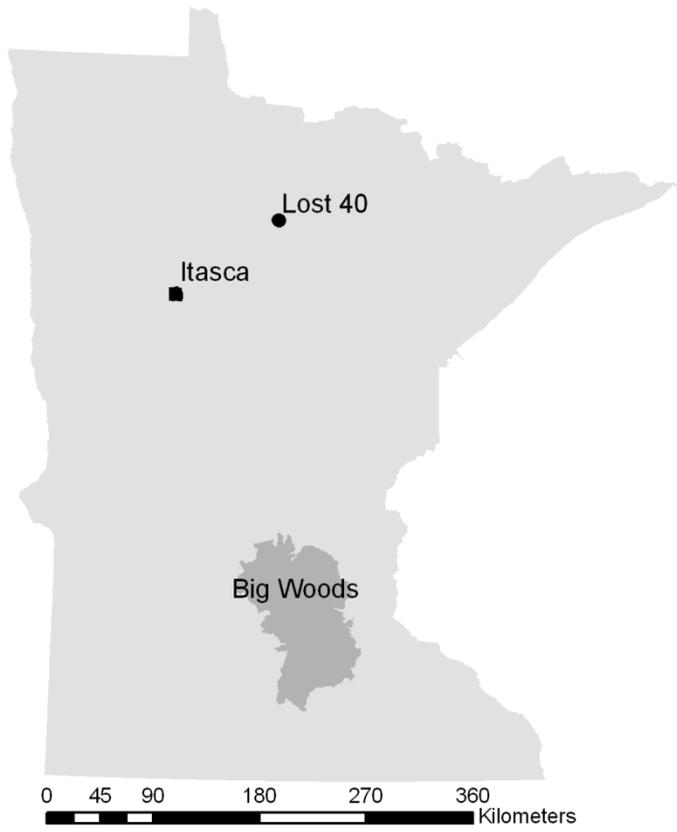


Figure 1. The old-growth forests studied in this dissertation.

CHAPTER 2

Canopy-Disturbance History and Recruitment Patterns at the Lost 40 in the Chippewa National Forest, Northern Minnesota

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Emergent white pine (*Pinus strobus*) and red pine (*Pinus resinosa*) of the 46-ha Lost 40 Scientific and Natural Area dominate one of the few remaining old-growth pine forests in Minnesota outside the Boundary Waters Canoe Area Wilderness. The Lost 40 had no detailed management plan, in part because land stewards desired a science-based strategy for regenerating white and red pines and little was known about the disturbance history at the site. Our objectives were to: (1) analyze stand structure and species composition at the Lost 40, (2) determine the frequency and intensity of canopy disturbances, (3) compare the canopy-disturbance history (1880–1999) of the Lost 40 to the average rate per decade of canopy disturbance in similar forests, and (4) characterize recruitment patterns. On three 0.1-ha plots we determined size and age classes of tree species, calculated their importance values and analyzed tree rings to reconstruct canopy disturbances. The trees represented a wide range of sizes, ages and shade tolerance. The dominant species varied across the three plots, and the canopy-disturbance history of the stands differed despite their proximity. The average percentage area of the canopy disturbed per decade from 1880–1999 ranged from 2.6% to 8.2% for the three plots and was 5.9% for the total area sampled. This amount of canopy disturbance is similar to decadal rates in other temperate forests of the northeastern United States. No white or red pine saplings grew in any of the plots, and only one plot had two small pine trees in the understory. The establishment of a new generation of pines at the Lost 40 will require intense management because the species composition, age structure, disturbance regime, high stand density, disease occurrence, and potential climatic conditions do not promote natural recruitment of white and red pine. *Key Words: disturbance history, fire suppression, Pinus strobus, Pinus resinosa, regeneration*

Introduction

Euro-American settlers cut, burned, or otherwise disturbed more than 99% of the white pine (*Pinus strobus* (L.)) and red pine (*Pinus resinosa* (Aiton)) primary forest of Minnesota, Wisconsin and Michigan (Frelich 1995). Old-growth white and red pine forests are protected on ca. 5–10,000 ha in northern Minnesota (Frelich 1995; Rusterholz 1996). Even though these stands are protected, the loss of forests containing white and red pine continues (McRae, Lynham, and Frech 1994). In some forests, pines might not be regenerating enough to replace the magnificent canopy trees.

Ecologists have examined the factors that limit pine regeneration in Minnesota (*e.g.*, Tester, Starfield, and Frelich 1997; Smidt and Puettmann 1998; Saunders and Puettmann 1999a,b; Ostry 2000; Dovčiak, Reich, and Frelich 2003), and the role that fire plays in perpetuating the pines is well known (McRae, Lynham, and Frech 1994). In general, competition by overstory and understory plants affect white pine establishment (Smidt and Puettmann 1998). Smidt and Puettmann (1998) found that medium light levels are best for white pine establishment: low shade levels result in moisture stress in the soil and high shade levels hinder establishment of white pine because of lack in sunlight. Understory brush needs to be decreased to increase white pine regeneration (Saunders and Puettmann 1999b). High deer levels are also problematic and deer population should be reduced (or terminal buds protected) for successful white pine establishment (Tester, Starfield, and Frelich 1997; Saunders and Puettmann 1999b; Ostry 2000). Other factors influencing white pine establishment are soil type and depth (Tester, Starfield, and Frelich 1997; Dovčiak, Reich, and Frelich 2003) and diseases like white pine blister rust (*Cronartium ribicola* J.C. Fisch.) or white pine weevil (*Pissodes strobi* (Peck)) (Ostry

2000). Two diseases that affect red pine regeneration negatively are Diplodia blight (*Diplodia pinea* (Desm.) Kickx) (Peterson 1981; Albers 2008) and Sirococcus shoot blight (*Sirococcus strobilinus* Preuss) (Nicholls and Robbins 1984). Both diseases affect both understory or mature trees and saplings. The diseases might be dormant and the seedlings, saplings, and trees might not show any signs of the diseases until a drought might stress the trees and the infestation of the trees with the disease becomes apparent.

Most of the unlogged pine stands in Minnesota are in the Boundary Waters Canoe Area Wilderness (BWCAW), at Itasca State Park and on small parcels such as the Lost 40 Scientific and Natural Area (SNA). White and red pine forests are an important component of the Laurentian Mixed Forest ecosystem in Minnesota (Department of Natural Resources Minnesota 2009) and they are an icon of the Northwoods—a popular destination for tourists and recreationists.

The 1883 Government Land Office survey of Minnesota's Township 150N, Range 27W, Section 34 showed a large lake where the land cover was actually a dense pine forest between two smaller lakes (LMIC 2006). This parcel of omitted land, which was resurveyed in 1962, is now known as the Lost 40 SNA. Today, the forest has towering white and red pines because it was protected from the logging of the late 1800s and early 1900s, but land stewards are concerned that pine seedlings and saplings are not abundant in the understory. Preserve managers from the Minnesota Department of Natural Resources (MNDNR) and the United States Forest Service (USFS) recently sought information that would help them develop a scientifically informed management plan for the 21st Century.

Because a management plan has not been developed for the Lost 40 and few scholars have investigated the history of canopy disturbances recorded in tree rings in remnant white and red pine stands, our objectives were to: (1) analyze stand structure and species composition at the Lost 40, (2) determine the frequency and intensity of canopy disturbances, (3) compare the canopy-disturbance history (1880–1999) of the Lost 40 to the average rate per decade of canopy disturbance in similar forests and (4) characterize recruitment patterns to provide land managers with ecological information that could help them predict future species composition and decide how to manage the forest. To meet these goals, we studied the size and age class distribution, calculated the importance values of tree species and analyzed tree rings to reconstruct the decadal disturbance regime following Lorimer and Frelich (1989).

White and Red Pine Ecology

White pine is a disturbance-dependent species because it is intermediate in shade-tolerance and reproduces under medium light levels beneath the canopy (Logan 1966). Before Euro-American settlement, fire and windthrow were the major disturbance agents in the white pine forests of eastern North America (Frissell 1973; Abrams 2001). It was widely believed that, in the absence of major forest disturbances, white pine cannot replace itself when light levels are low on the forest floor (Frissell 1973; Cahayla-Wynne and Glenn-Lewin 1978) and the species is succeeded by shade-tolerant hardwoods such as maple (*Acer* spp.), or conifers like spruce (*Picea* spp.) or firs (*Abies* spp.) (Heinselman 1973). Successful white pine regeneration at specific sites in eastern North America, however, has suggested that the species does not require widespread fire to establish new

seedlings. White pine regenerated in the absence of catastrophic fires in Temagami, Canada, for instance, but the site had local disturbances such as small surface fires and the death of individual trees (Quinby 1991). McRae, Lynham, and Frech (1994) noted that the Temagami sites were rocky and sandy, where competition by hardwoods and softwoods was less than on deep, fertile soils. Carleton et al. (1996) attributed a high density of white and red pine seedlings in Great Lakes forests in Canada to an absence of competition in the forest understory. Logging, deer browsing and livestock grazing might compensate for the lack of fire in some pine stands on sandstone outcrops in Wisconsin (Ziegler 1995, 1997). Elsewhere in the Upper Midwest, though, high densities of white-tailed deer (*Odocoileus virginianus* (Zimmermann)) have hindered establishment of white pine (e.g., Saunders and Puettmann 1999a, 1999b; Rooney and Waller 2003).

Microsite conditions and seed rain must also be favorable for pine establishment (e.g., Sharik, Ford, and Davis 1989; Tester, Starfield, and Frelich 1997; Smidt and Puettmann 1998; Dovčiak, Reich, and Frelich 2003; Dovčiak, Frelich, and Reich 2005; Frelich, Machado, and Reich 2003; Parker, Noland, and Morneau 2004). Whereas white pine can germinate with a few centimeters of duff (i.e., the upper organic layer of the soil) covering the mineral ground (Van Wagner and Methven 1978), red pine germinates and establishes best on bare mineral sandy soil (Wright and Bailey 1982). Red pine, therefore, depends more on fire than white pine does to prepare the seed bed for successful establishment (Van Wagner 1970); fire must burn hot enough to remove the duff. White pine, however, cannot withstand intense fires and the species is more adapted to occasional low-intensity fires (Frelich and Reich 1996).

Red pine is a moderately shade intolerant species (less tolerant of shade than white pine) that relies on high light levels to germinate and become established (Logan 1966; Van Wagner 1970; Wright and Bailey 1982; McRae, Lynham, and Frech 1994). Heinselman (1973, 1981) suggested that 150- to 300-year-old white and red pine forests need intense surface fires that kill some of the mature trees but leave seed trees to regenerate. Light-to-moderate surface fires might also be necessary to clear the litter, shrubs and invading shade-tolerant trees (Heinselman 1981).

Ahlgren and Ahlgren (1984, 106) stated that 25- to 80-year-old white pines were less common on logged land in northern Minnesota than red pines of that age even though white pine's regeneration requirements are not as stringent as red pine's. Ahlgren and Ahlgren (1984) attributed the lack of young white pines to *Cronartium ribicola* (J. C. Fisch.) (a fungus that causes white pine blister rust), which was introduced inadvertently in the late 1800s to the United States. White pine blister rust harms white pines by girdling saplings and trees. In 1999, the white pine blister rust had a high hazard rating in northeastern and north-central Minnesota (Brown, White, and Host 1999) and it continues to hinder successful establishment of white pine.

Red pine regeneration is hindered by the Diplodia blight and the Sirococcus shoot blight (Peterson 1981; Nicholls and Robbins 1984; Albers 2008). In the 1950s, Diplodia was likely introduced to Minnesota (Albers 2008) whereas the Sirococcus shoot blight was increasingly found in the US by the early 1970s (Nicholls and Robbins 1984). An investigation of the effects of white pine blister rust, Diplodia blight, Sirococcus shoot blight, white-tailed deer and other factors that limit pine regeneration at the Lost 40, however, was not within the scope of our research.

Forest Management

A management plan depends on many things like, for example, the objectives of the study and the desired future conditions, how far advanced along the successional pathway the forest is (forest composition and structure), how close to human settlement the forest is, or what the disturbance history was in the past. Therefore, one management approach is not going to be applicable to every remnant pine forest, and forest stands need to be studied before applying management.

Plans to manage vegetation rely increasingly on a concept called natural variability or range of natural variation. Forest managers should consider that (1) past vegetation assemblages, composition, and structure guide us in managing ecosystems today, and (2) disturbances are a natural part of almost every ecosystem and should be recognized in management plans (Landres, Morgan, and Swanson 1999). The concept of natural variability emphasizes that there are a range of natural conditions in a stand, for example, from early to late successional stages: after a major disturbance the same stand will be different in structure and composition from the forest before a major disturbance.

Falk, Savage, and Swetnam (2008) explained that as patterns of temperature and precipitation change, no-analog climate conditions may develop that flora and fauna have never experienced (at least for whole generations). Spittlehouse and Steward (2003) explained that, “Although forest ecosystems will adapt autonomously [to climate change], their importance to society means that we may wish to influence the direction and timing of this adaptation at some locations.” Even though some vegetation assemblages might be important to us (for example, the tall pines in Minnesota), would

their preservation be reasonable if temperature and precipitation shift to such an extent that no-analog conditions arise? Other factors like disturbances and diseases will also play a role in shaping the range of white and red pine.

These are critical questions with respect to the Lost 40 because the development of a scientific management plan must account for not only returning critical ecosystem processes, but doing so within a system that is perhaps vastly different climatologically than at any point in the recent past. Any management plan must therefore take into account not only vegetation patterns of the past and present but must also include the future.

Methods

Study Area

The Lost 40 SNA is in northwest Itasca County, Minnesota, north of Grand Rapids (47°46'4"N, 94°5'15"W; Fig. 1). The 46-ha SNA, managed by the MNDNR, has 11 ha of pine forest and 7 ha of spruce–fir forest (MNDNR 2007). The white pines in the SNA reportedly are older than 300 years (MNDNR 2007). Old-growth white and red pine also grow on adjacent Chippewa National Forest land administered by the USFS.

The Lost 40 SNA is in the Chippewa Plains subsection of the Ecological Classification System (MNDNR 1999). The dominant trees in this area before Euro-American settlement were white pine, red pine, Jack pine (*Pinus banksiana* (Lamb.)), northern red oak (*Quercus rubra* (L.)), sugar maple (*Acer saccharum* (Marsh.)), American basswood (*Tilia americana* (L.)), black spruce (*Picea mariana* ((Mill.) Britton

et al.)), tamarack (*Larix laricina* ((Du Roi) K. Koch)), northern white cedar (*Thuja occidentalis* (L.)) and black ash (*Fraxinus nigra* (Marsh.)) (MNDNR n.d.). White and red pine grew on moraines, whereas hardwood trees such as northern red oak, American basswood, and sugar maple dominated on sheltered moraines that were close to lakes (MNDNR n.d.).

The Warba series soil at the Lost 40 consists of moderately slowly permeable, deep, well drained sandy and clay loams that formed on glacial moraines and glacial till plains (Nyberg 1987). The mean January temperature is -15.4 C, the mean July temperature is 19.5 C and the mean annual precipitation is 665 mm (Minnesota Division 2 data from 1971–2000; National Climatic Data Center 2005). Peak precipitation in July coincides with the month of highest mean temperature.

Data Collection

We established three 50 m x 20 m (0.1 ha) plots within the Lost 40. Plots SNA and FSE were randomly located in what land managers had designated old growth. Plot SNB was randomly placed in an area that burned at the beginning of the 20th Century, according to an interpretive sign along the trail. Plot SNA and SNB were on MNDNR property and plot FSE was on Chippewa National Forest land 100 m from plot SNA.

With a 5.15-mm increment borer, every tree >10 cm diameter at breast height (dbh) was cored twice at a height of 100 cm to extract a sample of the tree-ring record. Increment cores were stored in paper straws. We measured the diameter and recorded the species of every stem >2 cm dbh to calculate the importance values. To be considered a tree the diameter had to be >5 cm at breast height; saplings were <5 cm dbh, but taller

than 1.5 m. We noted the canopy position of each tree and sapling >2 cm dbh; stems that received direct sunlight were classified as overstory and stems that did not receive direct sunlight comprised the understory. We measured the crown extent (*i.e.*, how many meters the crown spanned in each of the four cardinal directions from the trunk of the tree) on selected trees in and near the plots to estimate the canopy projection area (CPA; sensu Fraver and White 2005a) of each tree so that we could approximate the percentage area of canopy removed in each disturbance event.

Data Preparation

After gluing the air-dried tree cores to pre-fabricated core mounts, we sanded the cores with progressively finer grades of sand paper to produce a surface smooth enough to see individual cells clearly under a microscope. We then crossdated the samples using skeleton plots. We determined the year of formation of each ring by matching marker years, *i.e.*, years with adverse climate conditions that resulted in narrow annual rings of radial growth on multiple trees (Stokes and Smiley 1968). We attempted to obtain a pith date for each tree (*i.e.*, the year that each tree reached coring height), but several large trees with decayed centers were missing too many (*i.e.*, more than five rings) annual rings to determine their ages. Pith dates were estimated by examining the curvature of the innermost rings, averaging the ring width of the 10 rings closest to the center, measuring in millimeters how much curvature to pith was missing, and calculating from those data how many rings were missing to center (Parshall 1995, Ziegler 2002). The ring widths were then measured to the nearest 0.001 mm using a Velmex measuring machine and Measure J2X software (VoorTech Consulting 2004). The visual dating was checked

statistically using COFECHA (Holmes1983, Grissino-Mayer 2001), a standard program in dendrochronology.

Data Analysis

We calculated importance values for the overstory and understory species as the sum of the relative basal area (or dominance) and relative density, which resulted in a maximum value of 200. Relative basal area was calculated as the total cross-sectional area of a species, divided by the total cross-sectional area of all species and multiplied by 100. Relative density was calculated similarly using number of stems.

We reconstructed the disturbance histories for the three plots following the percent-increase method developed by Lorimer and Frelich (1989). We considered using more recently proposed methods (*i.e.*, Black and Abrams 2003, 2004; Fraver and White 2005b) to determine the canopy-disturbance history of our sites, but species-specific thresholds must be established for those approaches. Large data sets are needed to calculate the growth-release thresholds (*e.g.*, 50,000 data points for Black and Abrams' method (Bryan Black, personal communication, Assistant Professor and Senior Research Scientist at the Hatfield Marine Science Center, 22 November 2005, e-mail)), and we did not have enough tree rings to establish the critical values for species at the Lost 40. For the percent-increase method (Lorimer and Frelich 1989), several thresholds have been proposed, but Ziegler (2002) found hardly any differences between the more moderate threshold of 50% and more conservative threshold of 100%. We choose a 75% increase in growth over a 10-year window as our threshold. Values above this 75% increase were recorded as growth releases and we assumed that they resulted from canopy disturbance.

We plotted the annual ring widths of each tree to check for visible sustained growth releases and to confirm the start dates of these periods of increased growth rate.

Rapid early growth greater than 1 mm per year over at least 5 years at the time a tree reached coring height was also labeled a release because the tree most likely established in a canopy gap with abundant resources that enabled relatively wide rings to form. Big-tooth aspen (*Populus grandidentata* (Michx.)) and birch (*Betula* spp.)—early successional species that establish after a canopy disturbance—were also counted as canopy-gap recruited and the dates they reached coring height were added to the list of disturbance events. All of our pines that we had pith dates for fell under the category of rapid early growth.

A tally of growth releases, grouped into decades, represents the number of trees that grew up in or expanded into canopy gaps. A large number of trees with growth releases in a given decade does not necessarily mean that a large canopy gap formed because several small trees could have occupied the disturbed area. The release events, therefore, were weighted by an estimate of the gap size, which assumed that the current tree crowns occupy former gaps (Lorimer and Frelich 1989; Ziegler 2002). We used the canopy projection area (CPA) (Fraver and White 2005a) to weight each disturbance event and approximate the area of canopy removed. After measuring the distance from the trunk of a tree to the edge of the canopy in the four cardinal directions, we calculated the area of the canopy as projected on the ground when looking down on the tree from above. We then calculated the percentage of canopy one tree occupies in comparison to the area of the plot.

Results

White and red pine were the most important species in the overstory in plot SNA and SNB and were second most important in plot FSE (Fig. 2). White and red pine saplings, however, were not growing in the understory when we sampled the plots; only two small red pines were in the understory in SNB (Fig. 2). Shade tolerant species such as balsam fir (*Abies balsamea* ((L.) Miller)) at SNB and sugar maple at SNA and FSE were most important in the understory (Fig. 2).

Plot SNA experienced a moderate disturbance (*i.e.*, 30–60% of the canopy removed (Hanson and Lorimer 2007)) in the 1860s with >50% of the canopy disturbed (Fig. 3). This disturbance was not followed by a recorded pulse of tree regeneration (Fig. 4). The forest in plot SNB was disturbed with moderate severity in the 1920s and 1930s (Fig. 3), followed by a pulse of regeneration of trees that reached coring height in the 1930s and 1940s (Fig. 4). Birch and balsam fir dominated after that disturbance. In 1850, 1930 and 1990, more than 20% of forest was disturbed in plot FSE (Fig. 3). In the 1940s, many maples were recruited to coring height at FSE (Fig. 4).

The average area of canopy disturbed per decade from 1880–1999 was 2.6% at SNA (range: 0–12.9%), 8.2% at SNB (range: 0–31.5%) and 6.8% at FSE (range: 0–23.9%). The average decadal rate of disturbance for the total area sampled was 5.9% over the same 120-year period.

Discussion

Tree Ages

The oldest date at coring height that we obtained for a white pine was 1825, but most white pines had rotten centers so we could not determine their absolute ages. The two oldest red pines we cored with solid centers reached coring height in 1769 and 1776 (and therefore were at least 239 and 232 years old in 2008). Both trees were in plot SNA, which had the highest importance values of white and red pine (Fig. 2). Pith dates could not be estimated confidently for 68 of the 143 trees because many rings in the hollow centers were missing, but we determined from innermost growth rates and the amount of missing wood that it is unlikely that many of the trees are 300 years old at coring height, contrary to what the MNDNR (2007) believed. The results of other studies in northern Minnesota (Heinselman 1973, 1981) would support the hypothesis that today's forest at the Lost 40 grew up after a major fire a few centuries ago, but without a complete record of establishment dates or fire scar records, we do not know whether the stand originated after a single stand-replacing disturbance. From the pith dates that we have, it appears that red pines are older than the white pines. That is not unusual because white pine is more susceptible to scarring and subsequent rotting due to surface fires while red pine bark is more resistant to hot surface fires.

Disturbance Regime

Disturbance in the 1860s in plot SNA removed more than 50% of the canopy. The lack of a visible pulse of regeneration after the disturbance is probably an artifact of missing data or consumption by a later surface fire. From an age-class distribution that

included trees with pith dates and trees with estimated ages at coring height (personal observation), it appeared that birch and pine regenerated after the 1860s disturbance. The Lorimer and Frelich (1989) method of reconstructing canopy disturbances does not show what agent removed the canopy, but we speculate that it might have been drought and/or fire. In 1863–4, northern Minnesota was under drought conditions, with a reconstructed Palmer Drought Severity Index (PDSI) value between -2 and -4 (North American Drought Atlas 2004). In those years, large fires burned in the BWCAW (Heinselman 1973), about 120 km northeast of the Lost 40, and at Itasca State Park, approximately 100 km southwest of the Lost 40 (Frissell 1973; Peter Brown, personal communication, Director of Rocky Mountain Tree-Ring Research, 15 July 2004, conversation). Fire scars were only visible in a few trees near a sign that stated that a small part of the Lost 40 burned around 1900. Most trees did not show visible fire scars in 2005, but bark could have grown over fire injuries in the past 150 years. The trees would have to be cut to determine whether they were scarred by earlier fires. We did not search for charcoal in our plots.

In plot SNB, >30% of the canopy was disturbed in the 1920s and in the 1930s, which resulted in a visible pulse of regeneration of birch and balsam fir in the 1930s and 1940s. The 1920s and 1930s are often referred to as the Dust Bowl in the Midwest. During that time, PDSI values were negative (dry conditions) for a long periods dipping as low as -5 for several month (Minnesota Division 2 data; National Climatic Data Center 2005).

Only two white pines established after 1920/30s disturbance in SNB, perhaps because it was not severe enough for shade-intolerant pines to regenerate or because the site conditions were not conducive to seedling germination or survival (Carleton et al. 1996).

For example, drought and/or wind could have been the disturbance agents. Both agents would more likely kill overstory trees instead of understory trees. Drought conditions are more severe the more foliage and the larger the tree is because more water is transpired; smaller trees in the understory do not transpire as much (because of less foliage) and are also protected from direct sunlight because they are in the understory. Wind also affects larger trees in the overstory more because the large trees cannot bend as much as smaller trees and understory trees are often protected from the wind. Compared to fire, both drought conditions and high winds would not remove the dense understory or remove some of the organic material on top of the soil. Light and soil conditions would not be favorable for pine regeneration.

Three low severity (*i.e.*, <30% of canopy removed) disturbance events removed more than 20% of the canopy in plot FSE in 1850, 1930 and 1990. Big-tooth aspen and white pine regenerated after the 1850s disturbance at FSE, which removed about 20% of the canopy. The fact that aspen and pine regenerated after this disturbance would indicate that an understory-clearing disturbance affected this plot. After the 1930s, a decade in which approximately 25% of the canopy was removed, sugar maple was the dominant species of trees taller than coring height (1m); pines were not recruited to coring height. Even though the percentage disturbed is higher in the 1930s, the type of disturbance is very important. The regeneration of maple would indicate that only the overstory was disturbed in the 1930s but the understory only minimally disturbed, because late successional species that already occupied the understory became the dominant species in the gaps. The magnitude of the most recent disturbances in the 1990s was equal to the

area disturbed in the 1930s, but it is too early to determine what species will dominate in the canopy gaps.

The average percentage of canopy area removed per decade for the three plots (5.9%) over the past 120 years is comparable to the disturbance rate in other temperate forests of the northeastern United States. Runkle (1985) stated that the rate of disturbance was similar for forests of differing species composition and structure in spite of the various types of disturbance. Heinselman (1973) noted in his study of fire in the BWCAW that the presettlement northern forest was disturbed at an average rate of 1% per year (*i.e.*, 10% per decade). Various hemlock (*Tsuga canadensis* (L.))–northern hardwood forests have had 5–6% of the canopy disturbed per decade (*e.g.*, Parshall 1995; Ziegler 2002), similar to the pine-dominated and pine–hardwood stands at the Lost 40. A hardwood forest in south-central Minnesota, the Big Woods, also had a similar disturbance rate per decade (Rauchfuss and Ziegler, in prep.). Before our analysis of tree-ring widths, no study in this region had reported the decadal rates of canopy disturbance in white and red pine stands.

Management Implications for the Lost 40

The Lost 40 forest has variations in tree density and species composition (Table 1) which needs to be considered when implementing a management plan. Red pine is the state tree of Minnesota and pines are often viewed as a symbol of primeval forests. Preserving the few remaining old-growth *Pinus* forests is an important concern to the general public. A new forest type, however, is replacing the pine forest in the Lost 40; the understory species are different from the overstory composition in our plots, with shade-

tolerant species (sugar maple in SNA and FSE and balsam fir in SNB) recruiting instead of pines. While this is part of the succession process, and maple and balsam fir are part of the native plant community, this is succession in the absence of fire. With an intact disturbance regime that includes occasional low severity fires and even less often high severity fires, species like maple and balsam fir would not occupy the canopy layer. White and red pine at the Lost 40 did not regenerate well in the last century—a period with no major disturbance, *i.e.*, >60% of canopy removed (Hanson and Lorimer 2007). It seems that white and red pine would need an altered disturbance regime to regenerate in the near future; however, other factors like deer, disease, and competition will also affect the regeneration of those pines.

Managing the Lost 40 to perpetuate the pine-dominated forest will challenge land stewards. White and red pine have different germination requirements so a variety of seedbed conditions must be provided across the site or at different times to regenerate both species. Development toward a maple forest in some areas and a balsam fir forest elsewhere is advanced at the Lost 40, with those two species already present in the overstory. Prescribing fire to remove unwanted species and undergrowth would be difficult because balsam fir is very flammable and the trees extending up into the canopy could serve as ladder fuel that carries a surface fire up into the crown, potentially killing the pine seed trees.

In the two plots where maple was the most abundant tree species in the understory, a different problem might arise. Forest fires, especially crown fires, do not spread and carry easily through hardwood forests where the trees, in this case maple, are large enough to withstand surface fires (Frelich 2002, 25). At plot SNA, 15 percent of the canopy is

maple, and 20 percent of the canopy is maple at plot FSE. The maple in the overstory might be difficult to kill with surface fire. Select thinning of maple and balsam fir that are already in the overstory followed by prescribed fire might help to prepare the seedbed for pine regeneration in those plots. Future studies could investigate whether ungulate browsing, white pine blister rust, and *Diplodia* are limiting successful pine recruitment at the Lost 40 and if they are then these disturbances must be factored into the management plan.

Vegetation changes naturally over time, so if people have a vision that this wild area should look the same in the future as it did when Euro-Americans arrived, then the forest must be managed heavily—and soon—to help white and red pine regenerate. Iverson et al. (1999) predicted that climate in 2100 under a doubled concentration of atmospheric CO₂ would support white and red pine only in northeastern Minnesota, at least 100 km from the Lost 40. Whether or not pines will still be able to grow under warmer conditions, land stewards should first consider whether the goal of regenerating pine forest is reasonable before they embark on a labor-intensive and expensive restoration project.

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Table 1. Basal area and number of trees per hectare for the three plots and for two size classes

		All Live Trees	All Live Trees and Saplings
		>10 cm dbh	>2 cm dbh
SNA	Basal area (m ²) per ha	71.8	73.7
	Stems per ha	400	730
SNB	Basal area (m ²) per ha	26.8	28.0
	Stems per ha	540	700
FSE	Basal area (m ²) per ha	37.7	39.9
	Stems per ha	490	1040

FIGURE CAPTIONS

Figure 1. Location of the Lost 40 Scientific and Natural Area in the Chippewa National Forest, Minnesota

Figure 2. Relative importance values for the overstory and understory trees of each plot (from all trees >2 cm dbh). N = number of stems, WP = white Pine, RP = red pine

Figure 3. Canopy-Disturbance history of the three plots, which is the percentage area of the canopy removed each decade. Sample depth is the number of canopy trees used in the analyses.

Figure 4. Pith dates at coring height (100 cm) of trees >10 cm dbh for each of the three plots. SNA had two red pine recruitment dates (1769 and 1776). SNB had recruitment dates for three red pines (1876, 1883 and 1883) and two white pines (1938 and 1947). FSE had one white pine recruitment event (1885).

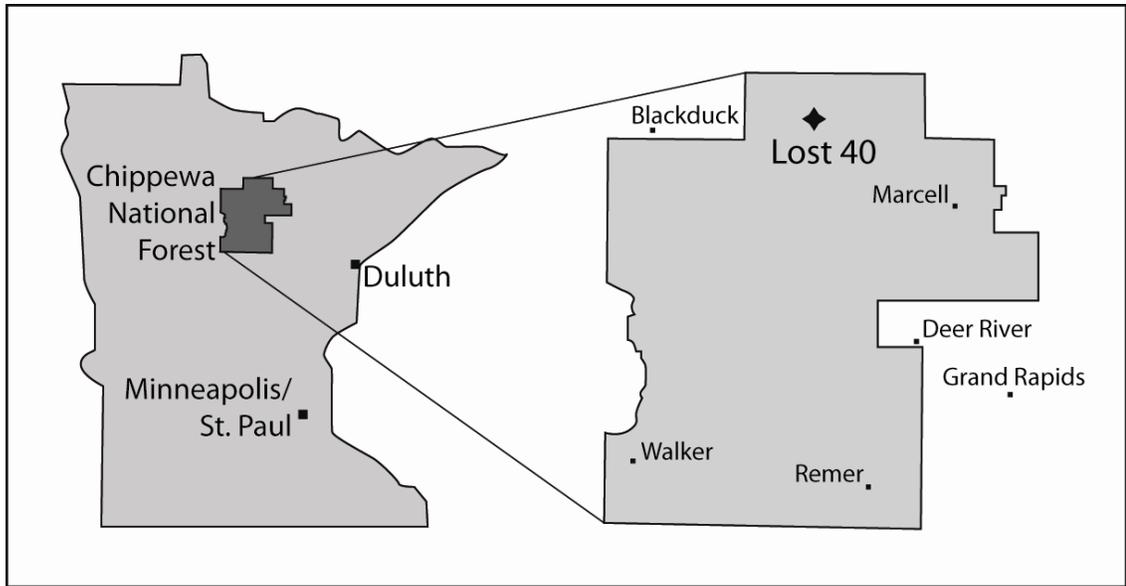


Figure 1.

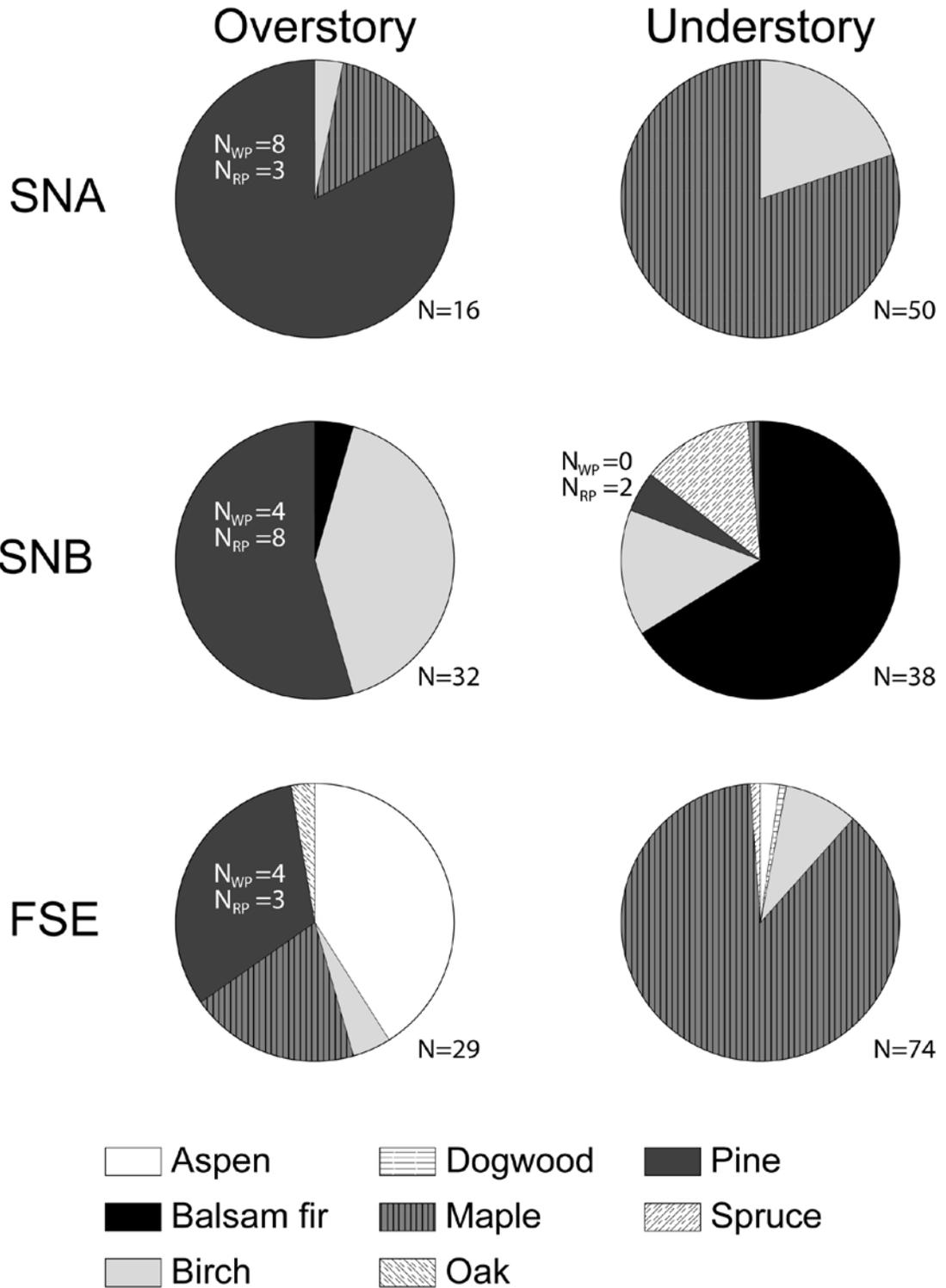


Figure 2.

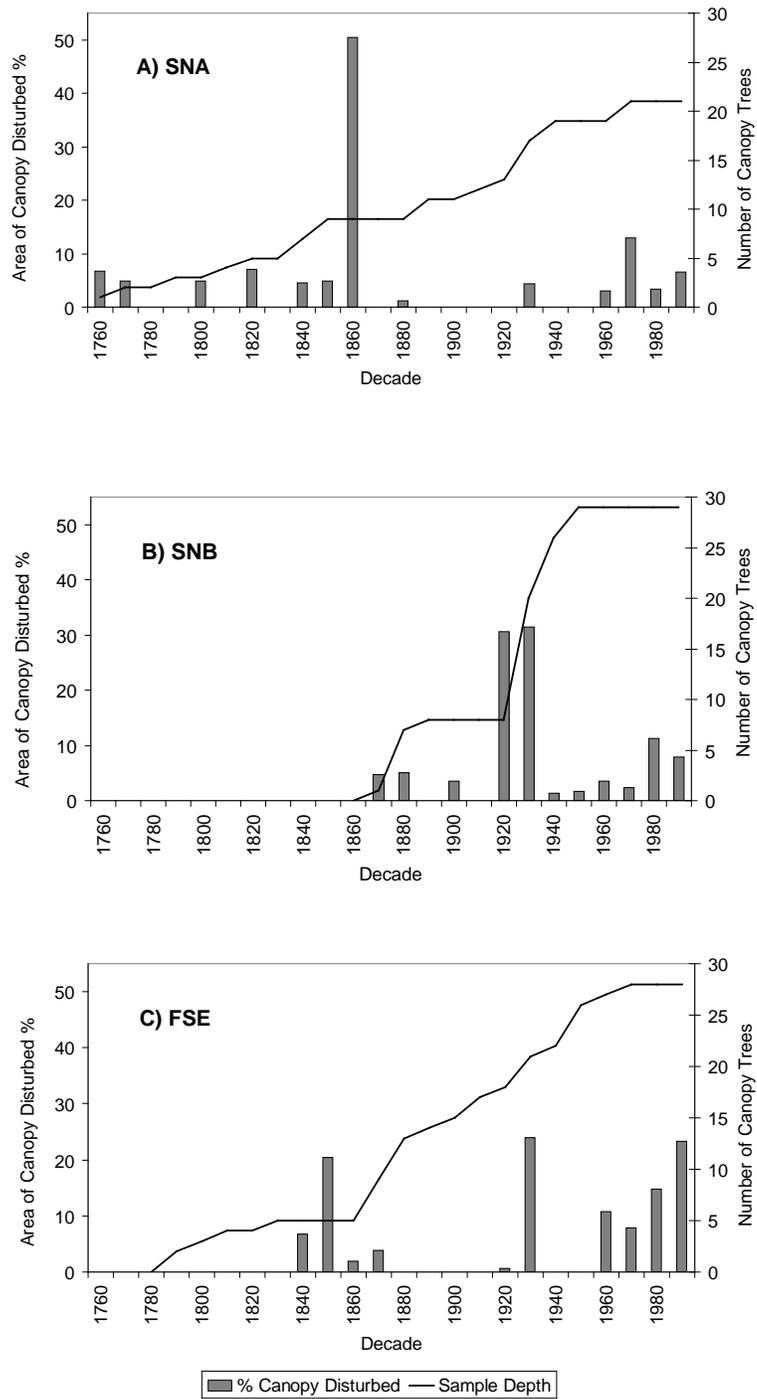


Figure 3.

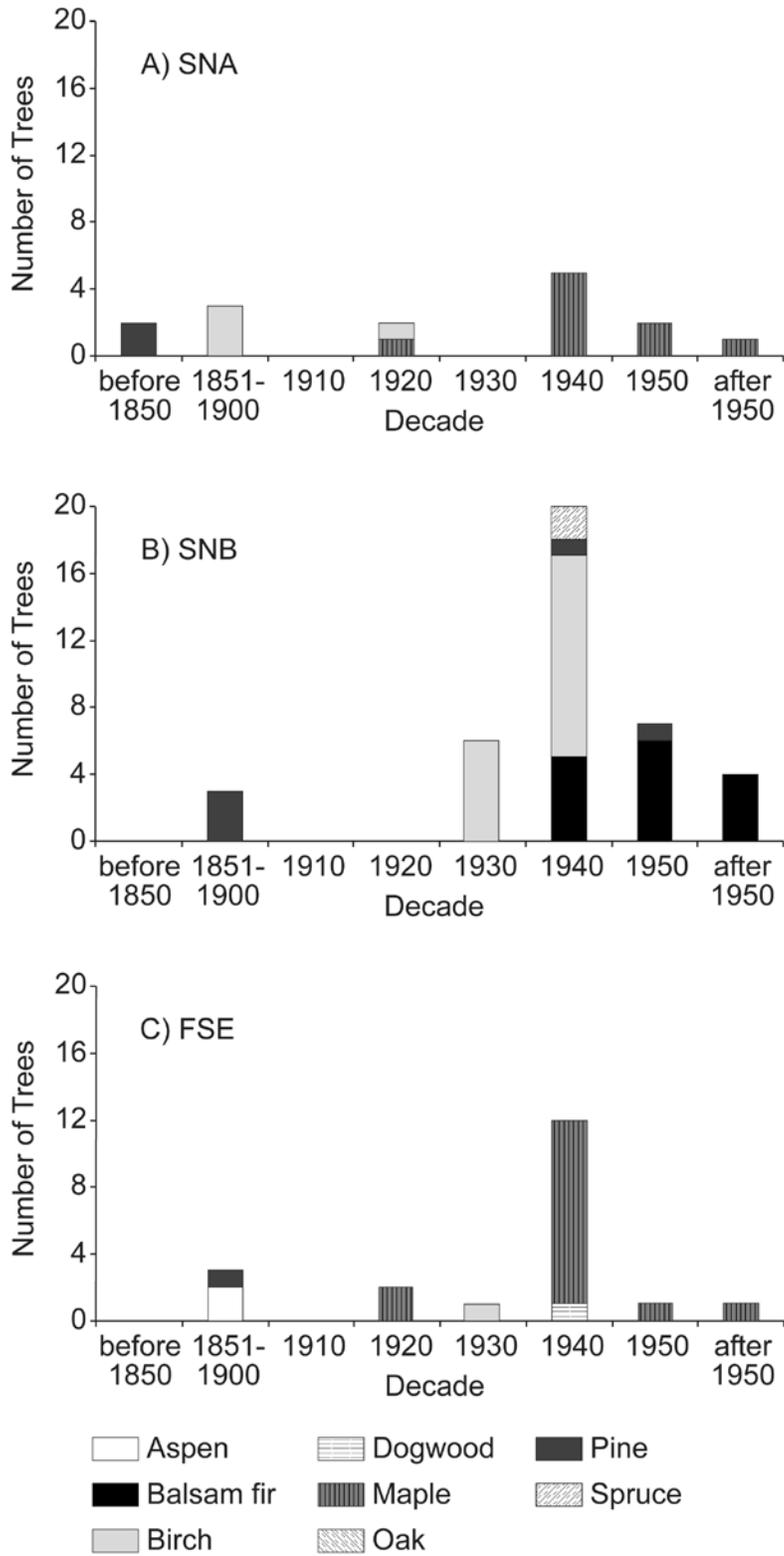


Figure 4.

CHAPTER 3

**DENDROECOLOGICAL ANALYSIS OF SPRUCE BUDWORM OUTBREAKS AND
THEIR RELATION TO CLIMATE NEAR THE PRAIRIE–FOREST BORDER IN
NORTHWESTERN MINNESOTA**

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We investigated the effects of spruce budworm (*Choristoneura fumiferana*) on balsam fir (*Abies balsamea*) and white spruce (*Picea glauca*) at Itasca State Park in northwestern Minnesota. We studied the species composition, age structure, and radial growth patterns in tree rings along five belt transects at sites infested with spruce budworm. Our objectives were to (1) discover when the latest spruce budworm outbreak started; (2) determine whether tree growth was similarly reduced in earlier decades suggesting earlier spruce budworm outbreaks; and (3) test whether radial tree growth and the start of the outbreak(s) were correlated with climate. We used the computer program OUTBREAK to determine that the current spruce budworm infestation began to reduce tree growth in the 1990s, before it was detected by park officials in 2001. The tree-ring record indicated that growth of the host-species trees was periodically reduced at all sites prior to the 1990s. We found no consistent relationship between temperature/ precipitation and the initiation of spruce budworm outbreaks, as reconstructed by the OUTBREAK program, at the southwestern edge of the distribution of balsam fir. Palmer Drought Severity Index, however, was positive (i.e., wetter-than-normal conditions) before increased spruce budworm activity at all sites. Outbreaks are related to climatic conditions, but they also depend on other factors such as the availability of sufficient food for the spruce budworm. [Key words: *Abies balsamea*, balsam fir, *Choristoneura fumiferana*, spruce budworm, outbreak, prairie–forest border, Minnesota, *Picea rubens*, white spruce.]

INTRODUCTION

Spruce budworm (*Choristoneura fumiferana* Clemens) is one of the most injurious insect pests of fir and spruce forests in the eastern U.S. and Canada. Populations of this native defoliator increase when buds, flowers and needles are abundant in forests with a high density of mature host trees (Blais, 1954; Graham and Knight, 1965; Magnussen *et al.*, 2004). Annual growth increments from live trees in eastern Quebec indicate that spruce budworm has defoliated trees periodically at least over the last 300 years (e.g., Blais, 1985). Tree rings of timbers from old buildings in Quebec record evidence of spruce budworm outbreaks with a mean return interval of about 30–50 years since the mid-1500s (Krause, 1997; Boulanger and Arseneault, 2004). While many studies describe spruce budworm dynamics in New England, New York, and eastern Canada, the insect's influence on radial tree growth in the Upper Midwest at the southwestern edge of its distribution has not been examined.

Despite the insect's name, balsam fir (*Abies balsamea* (L.) Miller) is the species most affected by repeated spruce budworm defoliation in eastern North America. Outbreaks may last five to twenty-five or more years (Boulanger and Arseneault, 2004). Balsam fir mortality following an outbreak may be as high as 90–100 percent in mature stands (MacLean, 1980; Solomon *et al.*, 2003). White spruce (*Picea glauca* (Moench) Voss), black spruce (*P. mariana* (Mill.) Britton *et al.*) and red spruce (*P. rubens* Sarg.) are other host trees that are susceptible to spruce budworm infestation but are not as vulnerable to defoliation-induced mortality as balsam fir because of differences in the timing of springtime bud break and growth in the host trees (Nealis and Régnière, 2004). In eastern North America, the broad distribution of spruce budworm corresponds closely

with the range of balsam fir (Volney, 1985; U.S. Department of Agriculture Forest Service, 2002). Spruce budworm also defoliates white spruce throughout the host species' range, extending north of the Arctic Circle in Alaska and the Northwest Territories (Alfaro *et al.*, 2000; Volney and Fleming, 2000; Burleigh *et al.*, 2002; Natural Resources Canada, 2004).

Carroll *et al.* (1985) cited reports of spruce budworm outbreaks in Minnesota from 1825 onward. A decade-long outbreak of spruce budworm began in Minnesota (in Koochiching County moving eastward) in 1912 (Graham and Orr 1940). Since the early 1950s spruce budworm has been in a broad-scale outbreak in the conifer forest of northeastern Minnesota (Erickson and Hastings, 1978; Miles *et al.*, 2003; U.S. Department of Agriculture Forest Service, 1997–2004). In the 1990s, spruce budworm outbreaks began in fir–spruce forests at the southwestern edge of balsam fir's range near the prairie–forest border, and were observed south of the natural southern limit of fir and spruce in tree plantations (Forest Insect & Disease Newsletter, 1997–2004; U.S. Department of Agriculture Forest Service, n.d.).

Various factors are often associated with the onset of a spruce budworm outbreak and typically affect mortality rates of host trees (e.g., Lynch and Witter, 1985; Hix *et al.*, 1987; Régnière and Lysyk, 1995; MacLean and MacKinnon, 1997; Magnussen *et al.*, 2004). Pilon and Blais (1961) observed in Quebec that the presence of mature balsam fir, moth dispersal and certain climatic conditions (early summer drought) were needed for an outbreak to commence. Royama (1984, 1992), however, challenged hypotheses that egg-carrying adult spruce budworm moths trigger outbreaks and that dry, warm summers precede spruce budworm outbreaks. Wellington *et al.* (1950) examined biological and

meteorological records for one site in northeastern Canada and determined that three or four years of early summer drought often preceded the beginning of spruce budworm outbreaks. Several other studies of spruce budworm and western spruce budworm noted that outbreaks occurred during years of low precipitation and/or warmer temperature when trees presumably were moisture stressed (cf Royama, 1992). Candau and Fleming (2005) associated high defoliation frequencies in Ontario with dry Junes and cool springs. Swetnam and Lynch (1993), in contrast, documented regional outbreaks of western spruce budworm in the twentieth century that often coincided with above-average spring precipitation. Ryerson et al. (2003) also found that outbreaks of the western spruce budworm often coincided with wet periods.

We investigated the effects of spruce budworm on tree growth at five areas within Itasca State Park in northwestern Minnesota near the southwestern margin of the range of balsam fir (Fig. 1). Our first objective was to determine when the latest spruce budworm outbreak began. Park officials first noticed spruce budworm at Itasca State Park in 2001 (Becky Marty, Resource Manager, Minnesota Department of Natural Resources, pers. comm., July 6, 2004), although the severity of defoliation and a cryptic reference in 2002 to “the fourth year of defoliation on this site [with no particular site clearly specified]” (Forest Insect & Disease Newsletter, 2002) suggested that the effects of increasing populations of spruce budworm were observed earlier, more than five years before we collected data in 2006. The second objective of our study was to determine whether previous outbreaks of spruce budworm had occurred, even though we found no written records of prior budworm influence on forest health at Itasca State Park. Our third objective was to examine whether radial tree growth and the start of such spruce

budworm outbreak(s) could be correlated with climate variables. To meet these objectives, we analyzed tree rings in an attempt to detect decreased annual growth rates that could be associated with the stress caused by spruce budworm defoliation (Swetnam *et al.*, 1985).

METHODS

Study Area

Itasca State Park encompasses nearly 12,950 ha within Becker, Clearwater, and Hubbard Counties in northwestern Minnesota (47°13'N, 95°12'W; Fig. 1). At Itasca State Park, the mean January temperature is -14.8°C, the mean July temperature is 19.7°C, and the mean annual precipitation is 686 mm (National Climatic Data Center, 2008). *Abies* (fir) has been a widespread but not regionally abundant taxon over the past 12,000 years (McAndrews, 1966; Wright *et al.*, 2004). Lake sediments revealed that from 11,600 years ago to A.D. 1890 the vegetation at Itasca State Park changed from late-glacial spruce forest, to mixed conifers and hardwoods, to pine forest, to oak savanna and prairie, to mixed hardwoods, then back to pine forest (Whitlock *et al.*, 1993). Currently, the temperate broadleaf deciduous forest and the northern needleleaf evergreen (coniferous) forest overlap at Itasca State Park (Westman, 1968), and the treeless prairie and agricultural land lie just 50 km to the west.

The park was established in 1891 to protect old-growth pine. Some tracts of forest in Itasca State Park were logged between 1901 and 1919 (Aaseng, 1976), but many stands with (presumably) 300-year-old red pine (*Pinus resinosa* Aiton) and eastern white pine

(*Pinus strobus* L.) trees were preserved. Today, the park contains more than 2200 ha of uncut pine forest—the largest contiguous area of old-growth pine in Minnesota (Becky Marty, Resource Manager, Minnesota Department of Natural Resources, pers. comm., February 25, 2005).

In July 2004, we observed that fir trees along the southern stretch of Wilderness Drive were heavily defoliated by spruce budworm. We sampled five budworm-infested areas in 2006 totaling 248 trees. Stands near Schoolcraft Trail (STA), Nicollet Trail (NTA), the University of Minnesota Biological Station (BSA), and Wilderness Drive (WDA) have red pines close to the transects, whereas the site near the DeSoto Trail (DSA) has paper birch (*Betula papyrifera* Marshall) intermixed with the balsam fir and white spruce. We developed a park-wide red pine chronology to use as the nonhost (i.e., not defoliated by spruce budworm) chronology for each site including DeSoto Trail.

Few if any of our study sites were affected by logging operations in the 1900s (Aaseng, 1976). The DeSoto Trail site is very close to one logging site and it is not clear whether trees were removed between the years 1901–1919. The Wilderness Drive site is also near a part of the park that was logged, but harvest maps indicated that no timber was removed from the area we sampled (Aaseng, 1976). There are other disturbances in Itasca like wind and surface fires. High winds would most likely kill the red pine before killing the balsam fir because the red pines are taller and, therefore, more susceptible to high winds. Surface fires would most likely kill the balsam fir before killing mature red pine, because balsam fir's branches reach down to the ground and the trunk has thinner bark.

Field Methods

First, we identified five fir and spruce stands on a vegetation map of Itasca State Park (Huberty 1989). At each randomly selected site within each stand, we cored every tree >10 cm diameter at breast height (dbh) with a 5.15-mm increment borer along a 10×50-m transect. From each tree we extracted at least two increment cores at coring height (100 cm). For each tree, we recorded the species, the dbh, the canopy position, and whether the tree was dead or alive. Where it was possible to receive a signal under the tree canopy, we took GPS (Global Positioning System) coordinates along the transects at 0, 25, and 50 m. We collected cores from additional trees (mostly red pine [n=22], but also one white spruce) outside of the transect area in three stands (Biological Station, Nicollet Trail and Schoolcraft Trail) to add depth to the sample (Table 1).

Laboratory Methods

Laboratory methods of preparation and crossdating followed standard dendrochronological techniques (Stokes and Smiley, 1968). Increment cores were dried, glued to core mounts and sanded with progressively finer grits to expose the annual tree-rings. We crossdated the cores, matching marker years (i.e., narrow rings caused by adverse growing conditions) to determine the precise year of formation of each ring (Stokes and Smiley, 1968). Crossdating assures the detection of false or missing rings, which can form when the trees are stressed by drought or insect defoliation. We also measured the ring widths using a Velmex bench and Measure J2X software (VoorTech Consulting, 2004). From the ring curvature on trees for which we had missed the pith, we estimated how many millimeters the innermost ring was from the growth center of the

tree. We multiplied that distance by the average width of the 10 innermost rings to approximate how many rings we were missing. We counted back that number of rings from the date of the last ring visible to estimate the date that the tree reached coring height.

Data Analysis

We checked the visual crossdating using COFECHA, a common statistical tool used in dendrochronology (Grissino-Mayer, 2001). Balsam fir is very shade tolerant (Frank, 1990) and can be 50 years old when only 40–50 cm tall (Parent *et al.*, 2003). The date a tree reached coring height (100 cm) is more recent than the date of seed germination but we chose not to add a correction factor to account for the missing rings. Rates of early growth (as determined from innermost ring widths) at all of our sites were relatively high (i.e., average ring width >1 mm), so the tree-ring record might not have many missing years at the inner end of each core. Growth rate was important for determining the timing of outbreaks with narrow rings in the host chronology but not in the nonhost chronology indicating a spruce budworm outbreak, and establishment dates provided additional information about stand development.

Before standardizing the data with the ARSTAN program (Cook and Holmes, 1997) to remove age-related growth trends from ring-width measurements, we averaged the two cores per tree to create one series for further analyses. We used ARSTAN to apply a smoothing spline to each ring-width series and compute index values by dividing the ring-width value by the value of the fitted curve. The standardized ring-widths reflect the

growth response of trees to the environment because the natural decrease in ring width with increasing cross-sectional area is removed.

For standardizing, we used 40-year, 50% frequency response cubic smoothing splines to standardize the ring widths. Such a spline captures variance of >90% (with a wavelength of ≤ 20 years) in the original ring-width series, which means that almost all changes in the ring-width series over a period of less than two decades are retained. This procedure removed not only age-related growth trends but also growth patterns related to competition by neighboring trees and the effects of stand disturbances in a closed-canopy forest while preserving the relatively short-term effects of the insect outbreak (Cook and Peters, 1981; Speer *et al.*, 2001). According to Boulanger and Arseneault (2004), outbreaks can last 5-25 years; however, the outbreaks they reconstructed lasted on average 13.6 years with only two of 11 exceeding 20 years. Ryerson (1999) recommended a smoothing spline of at least 100 years; however, his chronologies were >300 years in length and some of our cores were only 40 years long. We compared the two spline lengths (40 years vs. 100 years) among the shorter chronologies and visually detected few differences (data not shown).

To determine whether host and nonhost species respond to the same climatic variables, we compared climate data from the University of Minnesota Biological Station at Itasca State Park archived by the Historical Climatology Network (HCN, 2008) to the standardized index chronologies from all balsam fir (years 1917-2005) and from all red pine (1912-2005). We then repeated the analysis with chronologies from all white spruce (1912-2005) and from all red pine (1912-2005). We used 17 variables (monthly averages from the previous May to current year September) for mean daily temperature and total

monthly precipitation in a correlation and response function analysis using the program DendroClim2002 (Biondi and Waikul, 2004). The HCN does not have station-level Palmer Drought Severity Index (PDSI) data available for our study area so we did not calculate response functions with PDSI.

The DendroClim2002 (Biondi and Waikul, 2004) output (correlation coefficients) for balsam fir, red pine, and white spruce were then tested for significant differences between the species. The correlation coefficients of balsam fir correlated with previous May temperature and of red pine correlated with previous May temperature were compared by using VassarStats (2009) which uses the Fisher's z transformation (Fisher, 1915) to transform the correlation coefficient to Fisher's z to then test for significant differences between the two correlation coefficients.

To determine the timing of spruce budworm infestation, we visually inspected the cores and skeleton plots for a sudden decrease in ring width (Weber and Schweingruber, 1995) and we analyzed growth rates with the computer program OUTBREAK (Holmes and Swetnam, 1996; Speer *et al.*, 2001). OUTBREAK compares standardized ring-width chronologies of trees that presumably responded similarly to climate and allows us to identify differences in tree rings that are attributed to some factor other than climate, such as a decrease in growth rate resulting from defoliation by insects. When trees are defoliated, photosynthesis and transpiration decrease because of needle loss, less wood is produced, and growth rings are narrower.

We used OUTBREAK to compare host (balsam fir and white spruce) and nonhost (red pine) chronologies. When the non-host tree-ring chronology is subtracted from the host chronology, a remaining period of suppressed growth in a series may indicate the timing

and duration of an insect infestation or other prolonged effect of disturbance (Swetnam *et al.*, 1985; Fritts and Swetnam, 1989; Veblen *et al.*, 1991; Hadley and Veblen, 1993; Speer *et al.*, 2001). In our study, we assumed that multiple balsam fir and white spruce trees with the same date of suppressed growth indicated an outbreak of spruce budworm. Red pine, as a nonhost species, would not show this suppressed growth for the same date.

We used the following default parameters in OUTBREAK, which were also used by Ryerson *et al.* (2003), to identify spruce budworm defoliation: (1) ring-width indices ≥ 1.28 standard deviations below the mean ring-width index, and (2) reduced growth of this amount for at least eight years. We chose a more conservative eight years, because with a less conservative five years, the whole chronology seemed to be in a constant outbreak. The OUTBREAK program determined how many balsam fir trees exhibited outbreak characteristics (i.e., how many of the balsam fir trees' ring-width series differed from the nonhost chronology).

To compare between climate variables and the outbreaks as detected by OUTBREAK, we used long-term temperature and precipitation data from Itasca State Park (HCN, 2008) and divisional climate data for Palmer Drought Severity Index (PDSI) (National Climatic Data Center, 2008). Itasca State Park is located close to the boundary between Minnesota climate Divisions 1 and 2, and we correlated ring width indices with PDSI values using Division 2 data because the vegetation of Itasca State Park is more similar to the forest cover of Division 2 than to the open prairie and agricultural fields in much of Division 1. We supplemented the correlation analysis with response function analysis. We plotted the temperature and precipitation data (HCN, 2008) against the outbreak chronology (i.e., the chronology that showed how many trees have outbreak

characteristics) to look for a consistent relationship. In addition, we plotted the PDSI data from the divisional data (National Climatic Data Center, 2008) against the outbreak chronology and visually inspected the graphs for consistency in the climate before an outbreak.

Not every part of the climate-year is important to the development of the spruce budworm. For example, the moths emerge from the pupae in late June or early July. A couple of weeks later, the first instar larvae emerges, spins a hibernaculum, and overwinters. At that time, the larva does not feed. After an extended warm period the next spring, the larvae emerges from its hibernaculum in late-April to mid-May and begins feeding on last year's needles, buds or flowers and later on the current year's growth as buds break and shoots begin to grow (Coulson and Witter, 1984). Therefore, the most critical time in the development of the spruce budworm larvae is from March through June. Additionally, Swetnam and Lynch (1993) suggested that the March through June (MAMJ) climate has the most influence on regional-scale western spruce budworm (*Choristoneura occidentalis* Freeman) outbreaks. We used the MAMJ temperature, precipitation, and PDSI to compare the data to the dendrochronologically inferred outbreaks. Superposed epoch analysis (SEA) may be used to test statistical relationships between climatic conditions and the timing of growth-rate patterns, but we did not use SEA for two reasons. First, the calculated statistics would not have been very strong because we identified only two outbreaks (events) in our record. Second, it is difficult to use SEA effectively with chronic diseases where an arbitrary threshold must be established of when an outbreak began, e.g., a single year that the insect population was high enough to be called an outbreak.

RESULTS

Site Comparison

Stem density varied considerably among the five plots (Table 1). The Nicollet Trail site had only 280 stems >10 cm dbh per hectare whereas the Schoolcraft Trail site had 1560 stems >10 cm dbh per hectare. Because we targeted fir–spruce stands, balsam fir was the most abundant tree in all transects (Fig. 2). The hardwood component differed among the transects: the DeSoto Trail site had the highest percentage of hardwood stems >10 cm dbh (34.5%) and the Itasca Biological Station site had no hardwoods at all (Fig. 2).

Few of the sampled trees of any species grew to 1-m height during the 1910s, 1920s, 1930s, or 1940s (except for one tree in the 1910s and two trees in the 1940s; Fig. 3). We were able to crossdate or estimate pith for 79% of the 247 cores from all sites (BSA = 72%, DSA = 92%, NTA = 32%, STA = 87%, WDA = 78%). Most undated cores were from trees with rotten centers. Many balsam fir grew to 1-m height in the 1960s and the 1970s (58% and 29% of all balsam fir trees, respectively; n = 136 total balsam fir trees) which is true for almost all sites except for NTA.

Spruce Budworm Disturbance

The correlation coefficient and response function analysis showed that April and July precipitation of the current year have a significant influence on the growth of balsam fir (Fig. 4). For white spruce, previous year July temperature and current year July precipitation are most important (Fig. 4). For red pine, April temperature and July precipitation of the current year have the greatest effect on their growth (Fig. 4). July and

April, therefore, are months in which climate influences tree growth the most at our study sites. Comparing the correlation coefficients of one species (red pine, balsam fir, or white spruce) correlated to the climate variables with the correlation coefficient of another species (red pine, balsam fir, or white spruce) correlated with the different climate variables showed that there was only one significant difference between red pine compared to balsam fir in the current year August precipitation ($z = 1.99$, $n_1 = 89$, $n_2 = 94$, $p = 0.047$ two-tailed) (Table 2). Therefore, red pine and balsam fir, red pine and white spruce, and balsam fir and white spruce respond similarly to climate.

The overall patterns detected by OUTBREAK between the host species balsam fir and white spruce are similar (Fig. 5). Spruce budworm defoliation peaked in the 1970s with approximately 50% of balsam fir and white spruce showing reduced growth compared to red pine (Fig. 5). Levels of spruce budworm activity rose again in the early 1990s for all of the plots combined, and peaked in the year before sampling (2005) with 93% of all balsam fir and spruce showing reduced growth compared to red pine.

Outbreak–Climate Relationships

The relationship between MAMJ temperature/precipitation and the onset of increased spruce budworm activity is not consistent (data not shown). The relationship between PDSI (average values of the March through June time period) and the outbreak chronology, however, indicates that conditions had been wetter (i.e., sustained positive PDSI values) immediately before the outbreaks (Fig. 5).

DISCUSSION

Site Comparison

Three scenarios could explain the lack of recruitment to 1-m height in the 1910s through 1940s. First, spruce budworm could have killed the trees that germinated during that window and the pulse in recruitment in the following decades could be because seedlings and saplings in the understory were released from suppression following canopy disturbance. Second, balsam fir and white spruce from that age cohort might have been logged, in spite of the detailed records of Aaseng (1976) that claimed otherwise, but if loggers had removed trees from the forest in the early twentieth century, they probably would have harvested pines rather than species with low commercial value. Third, trees might have grown to coring height during those decades but later senesced and died before we conducted this study. We suspect that the third explanation is most plausible. The average temperature and precipitation at Itasca are not ideal for balsam fir. The mean July temperature of nearly 20°C is above balsam fir's optimum range of 16–18°C, and the annual precipitation of 69 cm is lower than the ideal range of 76–110 cm (Frank 1990). We hypothesize that trees might be stressed at the range margins and might not have as long of a life span as they do in the middle of the species' geographic distribution. Maximum age of balsam fir is 200 years (Frank 1990), but on average they get to be 100-200 years old (Bakuzis and Hansen, 1965).

Spruce Budworm Disturbance

The results of the response function analysis and the test for differences between the correlation coefficients indicated that red pine and balsam fir, red pine and white spruce,

and balsam fir and white spruce respond similarly to climate at Itasca State Park. Red pine, therefore, appears to be suitable for the nonhost chronology in the analyses of spruce budworm outbreaks in this region, because red pine, balsam fir, and white spruce have similar climate responses.

Even though OUTBREAK identifies a year in which an outbreak began according to selected criteria, the actual year in which spruce budworm arrived in the region is difficult to pinpoint because the timing and rate of increased spruce budworm defoliation differs from site to site (data not shown). OUTBREAK can document when the trees started to decrease growth as a result of the outbreak, but that date can differ from the onset of the outbreak because the first year of significant decrease in ring width in the lower part of the stem (i.e., the height at which we cored) of mature balsam fir might occur one to three years after the first year of severe defoliation by spruce budworm (Swaine *et al.*, 1924; Graham and Orr, 1940; Krause *et al.*, 2003; cf Speer and Holmes, 2004). Park officials first noticed spruce budworm activity in 2001 along Nicollet Trail. Our data suggest that the current spruce budworm outbreak began as early as the 1990s. This corroborates the observation made by Blais (1985) that it may take several years for an endemic population of spruce budworm to build to a size that causes noticeable defoliation and suppressions in ring width. Our data provide at least a bounding date of the outbreak, and the outbreak started at or a few years before the first documented suppression.

Counterintuitively, spruce budworm may disturb the forest enough to help maintain a fir-dominated forest (see Filion *et al.*, 1998). Shade-tolerant balsam fir can grow in the understory until neighboring trees die and fir trees are released into the canopy. Balsam

fir seedlings and saplings already in the understory at the time of the outbreak (i.e., advance regeneration) may replace the defoliated and dead balsam fir in the overstory and in turn provide more host resource for future budworm outbreaks (Graham and Orr, 1940; MacLean, 1984).

Outbreak–Climate Relationships

Temperature and precipitation affect dispersal rates, feeding, fecundity and survival of spruce budworm, and the phenology and growth of the host species (balsam fir and spruce) (Gray, 2008). The parasites that feed on spruce budworm are also affected by temperature and precipitation (Gray, 2008). We focused, however, on the relationship between climate (i.e., temperature, precipitation, and PDSI as a proxy for moisture availability) and the increased outbreak levels of spruce budworm at Itasca State Park.

In our study, we did not detect a consistent relationship between temperature/precipitation and the dendrochronologically inferred spruce budworm outbreak. However, the relationship between the averaged PDSI values for March through June and increased spruce budworm activity shows sustained positive PDSI values (i.e., wetter conditions) before the outbreak (Fig. 5). The availability of food (needles on balsam fir and spruce) for spruce budworm affects the timing of spruce budworm outbreaks (Gray, 2008). Because balsam fir trees are stressed at the range limit and on average do not receive the optimum amount of precipitation, wetter conditions may have enabled the trees to produce more buds and flowers when springtime precipitation was above average, providing additional food for budworm larvae that in turn facilitated the beginning of the spruce budworm outbreak. This hypothesis merits

further testing, especially because spruce budworm activity did not follow every case of positive PDSI values. The lack of consistent correlation between climate and outbreaks might also be because undermature stands potentially provide less food than do forests of mature trees. Even though the climate might be ideal for an outbreak to commence, the forest species composition and age structure might not support high insect populations (Gray, 2008).

Balsam fir in this region is already under temperature and moisture stress. Increased stress on the trees from projected higher temperature and lower precipitation may make them more susceptible to widespread defoliation in the future because drought has been found to precede spruce budworm outbreaks (Wellington *et al.*, 1950, Candau and Fleming, 2005). However, specific triggers will be site and scale dependent, affected by a complex mix of increased food availability and a decrease in predators and disease for the spruce budworm (Gray, 2008).

CONCLUSION

We documented outbreaks of spruce budworm near the southwestern edge of the range of balsam fir along the prairie–forest border. Regional patterns are not always the same as local patterns (Swetnam and Lynch, 1993) and it would be beneficial to expand this study to additional fir–spruce stands at the species’ range margin to learn how other forests have responded to spruce budworm defoliation. Another future project could compare tree response to spruce budworm at the prairie–forest border with the forest–

insect dynamics farther from the edge of the species' distribution, such as in northeastern Minnesota.

Because environmental alterations, including climate change, will affect the frequency and intensity of insect outbreaks, especially at the margins of host ranges (Fleming, 1996; Volney and Fleming, 2000), it is important to ask what the long-term implications for spruce budworm near its southwestern range limit are. Warmer temperatures might support more insects in the short term, but their host resource could eventually decrease in abundance with global warming as balsam fir and white spruce migrate northward. The current average temperature and precipitation at Itasca State Park already are not ideal for balsam fir, and the climate in Minnesota under a doubled concentration of atmospheric CO₂ is predicted to be unsuitable for balsam fir (Iverson *et al.*, 1999, 2008). Further studies will help test predictions of the effects of global change on forest–insect interactions.

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Table 1. Number of Stems^a >10 cm cored at Each Site^b

	DSA	NTA	BSA	STA	WDA
	Southern sites		Northern sites		
Host species:					
ABBA	28	7	28	69	20
PIGL	4	3	19	3	2
Non-host species:					
PIRE	2	3	1	2	1
Other (softwood)	--	--	1	--	--
BEPA	13	--	--	3	5
Other (hardwood)	5	1	--	1	4
Total # of trees per 0.05 ha	52	14	49	78	32
Total # of trees per 1 ha	1040	280	980	1560	640
PIRE (outside of transect)	--	7	8	7	--
PIGL (outside of transect)	--	1	--	--	--

^a ABBA = balsam fir, PIGL = white spruce, PIRE = red pine, BEPA = paper birch.

^b DSA = DeSoto Trail, NTA = Nicollet Trail, BSA = Biological Station, STA = Schoolcraft Trail, WDA = Wilderness Drive.

Table 2: Correlation coefficients between PIRE/ABBA/PIGL and 34 climate variables (in the columns labeled PIRE, ABBA, and PIGL). In the last three columns, we tested for significant differences between the correlation coefficients. Only once was the difference significant at the 95% confidence level (two-tailed). PIRE – red pine, ABBA – balsam fir, PIGL – white spruce, MAY – previous year, May – current year, T – temperature, P – precipitation.

		PIRE	ABBA	PIGL	PIRE vs. ABBA	PIRE vs. PIGL	ABBA vs. PIGL	
Temperature	MAY T	0.08	0.02	0.05				
	JUN T	-0.07	-0.12	-0.24				
	JUL T	-0.25	-0.24	-0.37				
	AUG T	-0.15	-0.12	-0.23				
	SEP T	-0.18	-0.20	-0.22				
	OCT T	0.16	0.16	0.07				
	NOV T	0.06	0.03	0.11				
	DEC T	0.14	0.01	0.12				
	Jan T	0.04	0.14	0.00				
	Feb T	0.13	0.19	0.07				
	Mar T	0.24	0.11	0.25				
	Apr T	0.24	0.00	0.02				
	May T	-0.03	-0.16	-0.20				
	Jun T	0.01	-0.15	-0.15				
	Jul T	-0.06	-0.12	-0.10				
	Aug T	0.08	0.07	0.07				
	Sep T	-0.10	-0.14	-0.13				
	Precipitation	MAY P	0.17	-0.02	0.14			
		JUN P	0.01	0.05	0.02			
JUL P		0.12	0.08	0.19				
AUG P		0.11	-0.04	0.09				
SEP P		0.18	0.06	0.03				
OCT P		0.08	0.16	0.11				
NOV P		-0.02	-0.04	-0.05				
DEC P		-0.01	0.01	-0.08				
Jan P		0.00	0.06	0.01				
Feb P		-0.21	-0.07	-0.10				
Mar P		0.17	0.11	0.04				
Apr P		0.13	0.28	0.15				
May P		0.16	0.19	0.07				
Jun P		0.15	0.23	0.13				
Jul P	0.39	0.26	0.31					
Aug P	0.29	0.00	0.07	z=1.99, p=0.0466				
Sep P	0.09	0.05	-0.06					

Fig. 1. Land cover and study sites at Itasca State Park, Minnesota.

Fig. 2. Species composition of all transects based on the total number of trees (n) and the proportion of each species in the plot (ABBA = balsam fir, PIGL = white spruce, PIRE = red pine, BEPA = paper birch, soft = unidentified softwood, hard = unidentified hardwood).

Fig. 3. Recruitment dates of trees on all sites (including trees outside of transect; ABBA = balsam fir, PIGL = white spruce, PIRE = red pine, BEPA = paper birch). The numbers 79 and 40 refer to the numbers of trees recruited to 1 m height in decades 1960 and 1970, respectively.

Fig. 4. Climate responses of red pine, balsam fir, and white spruce; PMAY = previous year May, May = current year May, solid line = Correlation coefficients, lighter-colored squares = significant correlation coefficients (at 95% confidence level), darker-colored circles = significant correlation coefficient AND significant response function coefficient.

Fig. 5. Comparison between dendroecologically inferred spruce budworm activity (gray columns) and PDSI patterns (average of March through June PDSI values; line graph with triangle points) for all plots combined for balsam fir (ABBA) and white spruce (PIGL). The line with the diamond-shaped points represents the sample depth of tree-ring data.

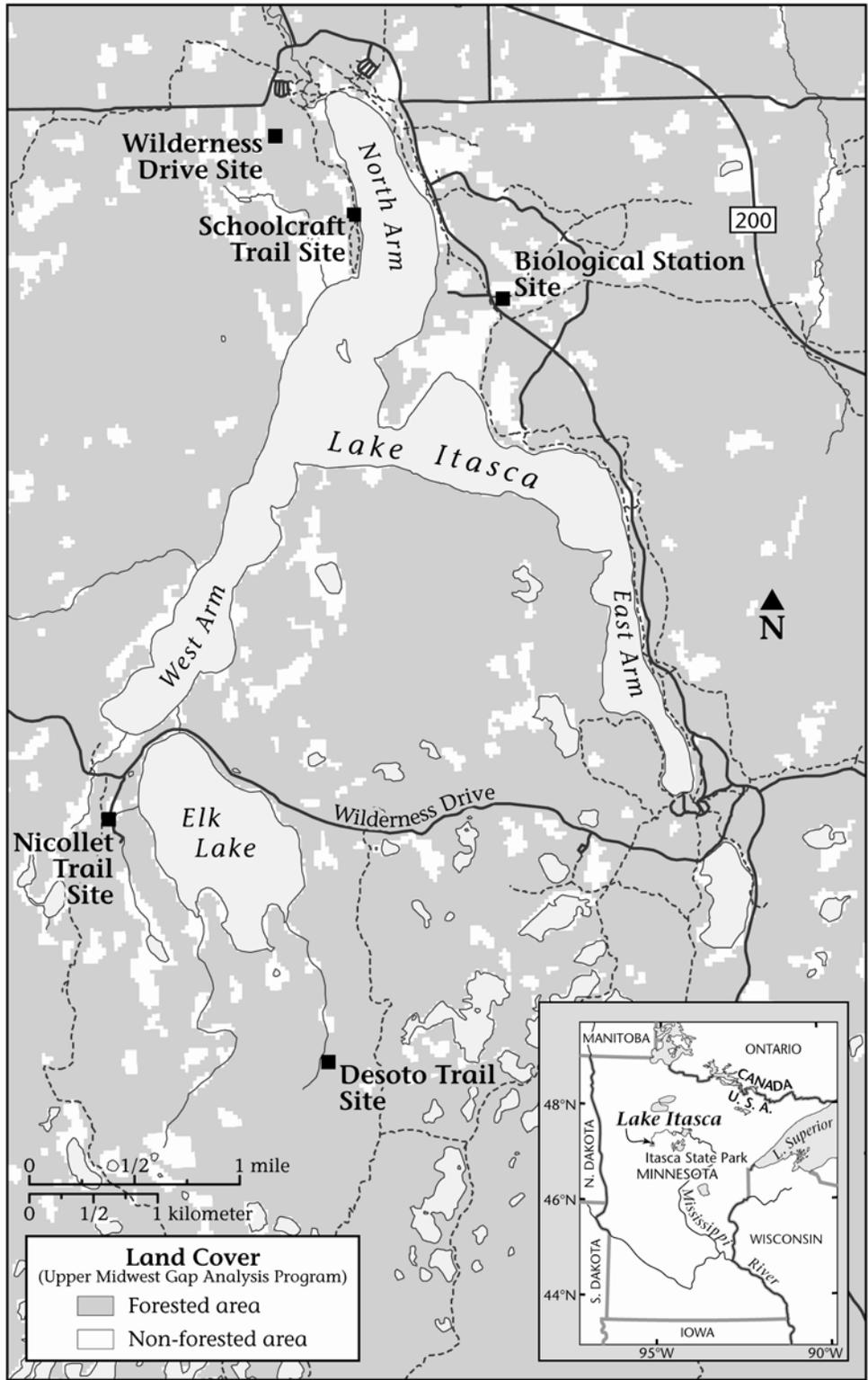


Fig. 1.

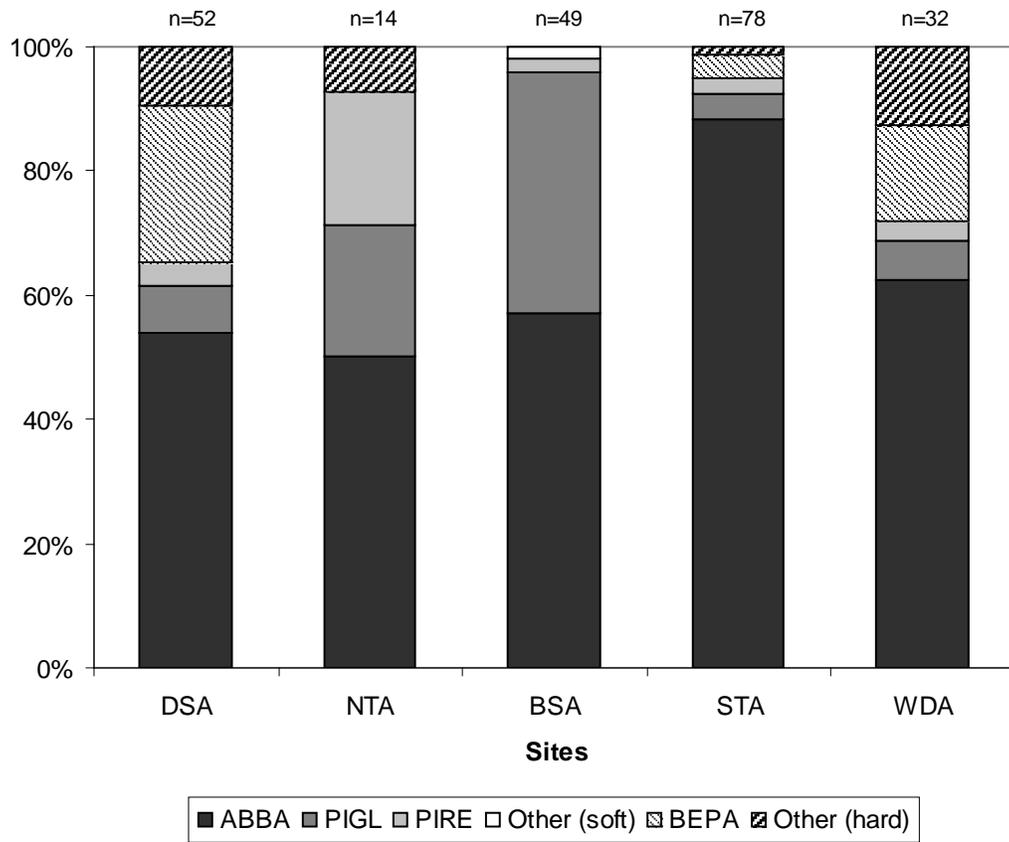


Fig. 2.

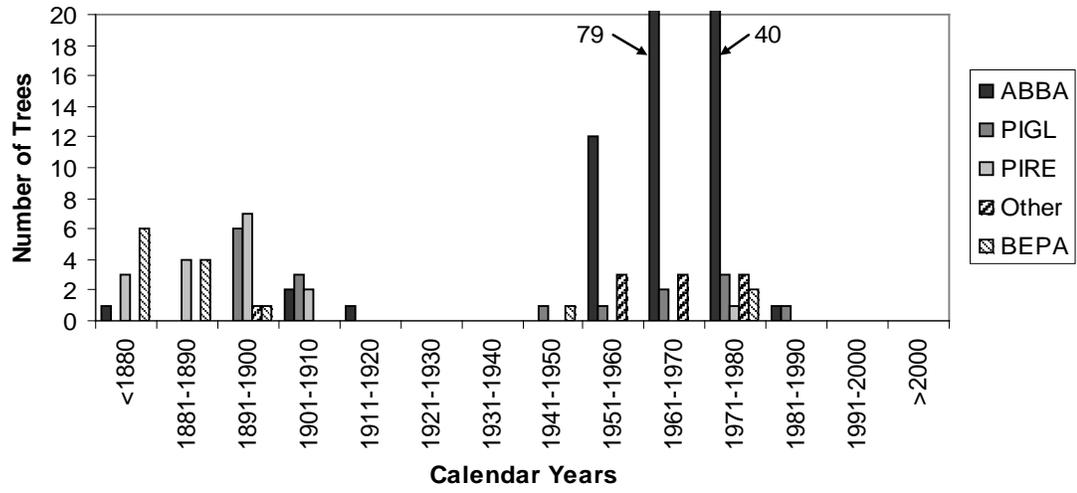


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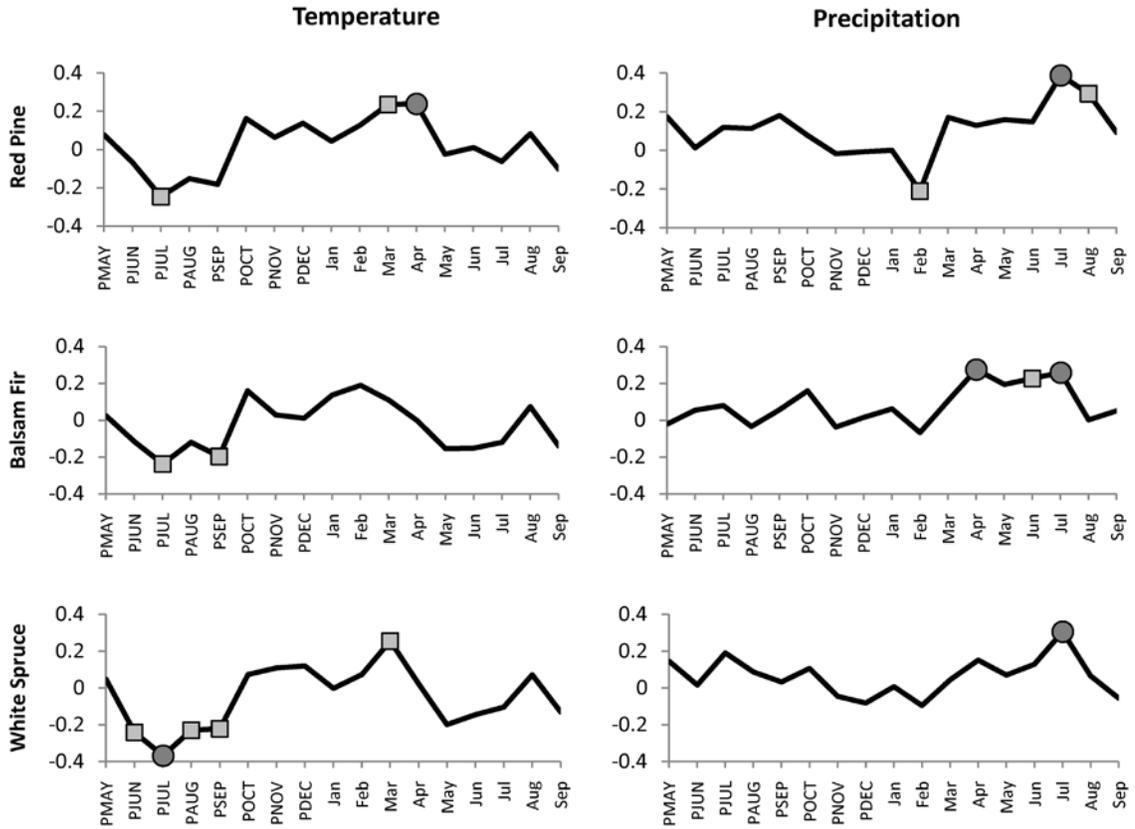


Fig. 4.

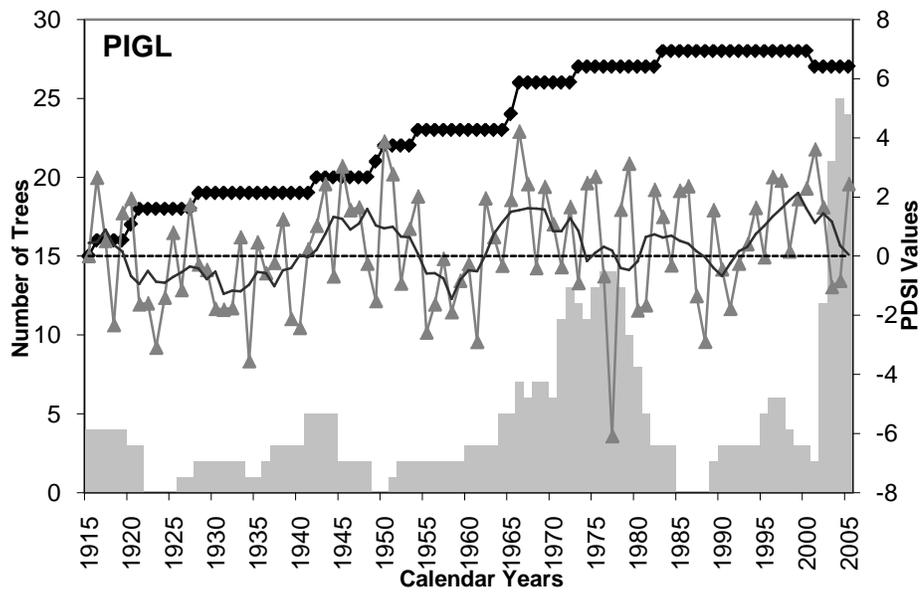
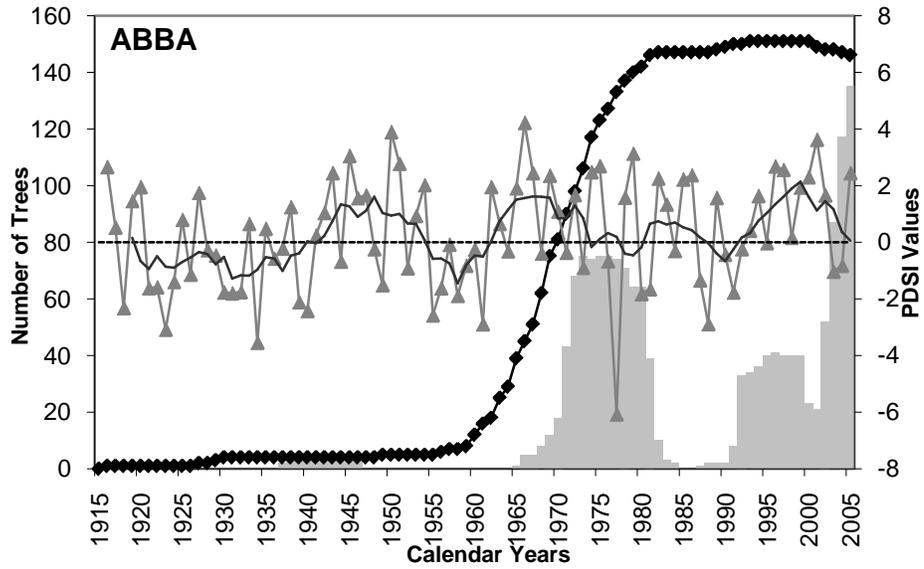


Fig. 5.

CHAPTER 4

Methods for Identifying Disturbance-Induced Growth Releases in Trees

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A comparison of methods—percent-increase, absolute-increase, visual inspection, sequential t-test (regime shift detection) and time-series analysis with intervention detection—for reconstructing disturbance histories from tree rings is presented. To analyze differences and similarity between the methods, Kruskal-Wallis and Friedman's ANOVA were used. The starting date of disturbances as determined by the different methods can vary appreciably with the percent-increase and absolute-increase methods usually underestimating the release date and sequential t-test and time-series method usually overestimating the release date. For three reasons, the sequential t-test showed the best results based on time invested in the analysis and quality-control measures. First, it gives the closest results to the visual inspection method. Second, the method accounts for autocorrelation and the user can choose different methods to remove autocorrelation. Third, a program is freely available to reconstruct regime shifts in the tree-ring series. Therefore, the sequential t-test might be the best method available at this time to analyze the canopy-disturbance history of different forest types. However, visual inspection should always be done in addition to the statistical methods to supplement the analysis.

Introduction

Disturbances such as fire, windstorms, or insect outbreaks are prevalent in most ecosystems. They can be reconstructed in a number of ways including fire scars, death dates, shift in composition, and suppression/release periods in ring-width series. To reconstruct the canopy-disturbance history of forests, many different methods have been proposed in the past 20–30 years. Although disturbance events were reconstructed in the 1970s from radial growth rates recorded in tree rings (Henry and Swan 1974, Oliver and Stephens 1977), Lorimer and Frelich (1989) were the first to objectively quantify disturbance events using tree rings. They detected suppression periods (decrease in tree-ring width over a certain number of years) and release periods (increase in tree-ring width over a certain period), based on growth-rate change of a certain magnitude and duration.

Rubino and McCarthy (2004) compared 30 methods of reconstructing the canopy disturbances from tree rings. They found that disturbance histories for the same data varied depending on the method used. They acknowledged that most methods were developed for specific types of forests, though. Lorimer and Frelich's method (1989) has been developed for northern hardwood forests, but this method, with some modifications, might be applicable to other temperate forest types according to Lorimer and Frelich (1989, 652). Consequently, Lorimer and Frelich's (1989) method has been applied widely in many different forest types and tree species. Lorimer and Frelich (1989) did not use a species-specific threshold to distinguish releases from non-releases as in some newly proposed methods.

Building on Rubino and McCarthy (2004), I will compare methods of reconstructing canopy disturbances that have been proposed after 2004. Among the

methods are the standard percent-increase (Lorimer and Frelich 1989), absolute-increase (Fraver and White 2005*b*), visual inspection, sequential regime shift detection (Rodionov 2004, 2005) and time-series analysis with intervention (Box and Tiao 1975, Druckenbrod 2005).

Nowacki and Abrams (1997) formalized Lorimer and Frelich's (1989) method using the following equation [1]:

$$[1] \quad \text{Percent increase} = \frac{\text{Mean}_{t_2} - \text{Mean}_{t_1}}{\text{Mean}_{t_1}} * 100$$

where Mean_{t_1} is the mean tree-ring width over a time period prior to the event and Mean_{t_2} is the mean tree-ring width over a time window following the event. Choosing a 10-year time window will allow short-term climatic variations to be excluded from the analysis of canopy disturbances (Lorimer and Frelich 1989, Nowacki and Abrams 1997). Although the time window and percentage of the threshold (above/below which growth irregularities are dubbed releases/suppression) vary widely, the most common time window is a 10-year running mean (for Mean_{t_1} and Mean_{t_2}) and the most common threshold is a 100% increase in growth rates (Fraver and White 2005*b*). Bouriaud and Popa (2007) determined statistically that the 10-year window before and after the event captures release years accurately by testing different windows.

As Fraver and White (2005*b*, 1649) noted, “[t]he percent-increase method is known to be overly sensitive (accepting false positive releases) at low growth rates and overly stringent at higher rates (producing false negative releases)” (Figure 1). Therefore, different methods such as the absolute-increase method (Fraver and White 2005*b*), a method based on boundary-line release criteria (Black and Abrams 2003, 2004), and the

time-series analysis with intervention detection (Druckenbrod 2005, based on Box and Tiao 1975) have been proposed to minimize this oversensitivity and over-stringency.

Fraver and White's (2005*b*) and Black and Abrams' (2003, 2004) methods are similar to one another in that a species-specific threshold must be established to separate growth releases from non-releases (i.e., is the increase in tree-ring width over a certain period of time caused by gap dynamics or climatic shifts?). Both methods consider the magnitude of prior growth when calculating the threshold; that is not done in the percent-increase method (Lorimer and Frelich 1989). Using *Tsuga canadensis* (eastern hemlock) and other species, Black and Abrams (2003, p. 1734) showed that "slow growing trees intrinsically release more vigorously than fast growing trees, and the relationship between prior growth and *release response is largely independent of age, diameter, and crown class*" (emphasis added). They verified this relationship between growth and release using 24 chronologies in the case of eastern hemlock. Black and Abrams (2003, 2004) used many datasets from the International Tree-Ring Data Bank (ITRDB) for each of seven species to calculate the species-specific threshold to separate releases from non-releases. This method seems very promising for the seven species for which the boundary line is already calculated; the major drawback is that many data points (i.e., individual measurements of annual growth rings) are needed (50,000 at minimum, Bryan A. Black, personal communication, Nov 22, 2005) to calculate the boundary line. Even with the vast amount of data in the ITRDB, it is not easy to get 50,000 data points for some species.

Fraver and White's (2005*b*) method does not need as much data as Black and Abrams' (2003) approach, although large amounts of data are still necessary. Fraver and

White's (2005*a*, 2005*b*) analysis used 172–1189 cores depending on species, where each core has tens to hundreds of data points depending on the tree's age. Fraver and White's (2005*b*) method is similar to the percent-increase method in that the mean radial growth following the event (Mean_{t_2}) is subtracted from the mean radial growth before the event (Mean_{t_1}). However, this calculated value is not divided by the Mean_{t_1} to calculate the percentage. If the calculated value is greater than a predetermined species-specific value, it indicates a release in the tree (Fraver and White 2005*b*).

Black and Abrams (2003) addressed the differences between age, diameter, and crown class of the tree by verifying their boundary line for eastern hemlock with data from different chronologies (i.e., different sites), and they concluded that the tree characteristics have less effect on the magnitude of growth releases than prior growth has. Fraver and White (2005*b*, p. 1651) reconstructed canopy-disturbance history from only one old-growth forest, but they stated that their thorough sampling scheme suggests that “the growth rates and patterns observed here likely represent the full ranges possible for these species under natural forest conditions.” They did not, however, deal with the variables (age, diameter, crown class) that Black and Abrams (2003) addressed. Neither of these studies, nor other methods of analyzing canopy disturbances, dealt with how site-specific variations (soil, different climatic conditions) affect the species-specific threshold.

In 1970, Box and Jenkins published a textbook on time-series analysis. Box and Tiao (1975) supported the idea that time-series analysis with “intervention detection” could be applied to economics and environmental problems. Intervention analysis is the detection of outliers which in the case of tree rings are growth-release and suppression events. As

Druckenbrod (2005) suggested, only a few papers (McLaughlin et al. 1987, Segura et al. 1995, Mäkinen 1997) since then have applied intervention analysis to dendroecological disturbance studies. The methods developed by Fraver and White and by Black and Abrams use running means of growth rates, whereas the intervention analysis relies on time-series analysis to identify outliers empirically (Druckenbrod 2005). Running means do not account for autocorrelation between ring-width measurements and may emphasize spurious events, i.e. releases that are not really releases (Druckenbrod 2005). For Fraver and White's (2005*b*) and Black and Abrams's (2003) methods, knowledge of the growth patterns of the species in question is necessary (i.e. the detection of releases that are not really releases and real releases that are not identified need to be minimized). However, this knowledge of the growth pattern of a species is not as pertinent for intervention analysis, because outliers are identified empirically (Druckenbrod 2005). Another difference between the two sets of analyses is that for the intervention analysis there is no need to establish a species-specific threshold, because it is an empirical approach based on significance levels (Druckenbrod 2005).

Druckenbrod (2005) apparently was the first researcher to use time-series analysis with intervention detection to reconstruct unknown disturbances in the past, and he linked dendrochronologically inferred disturbances to "likely" disturbance events. He did not compare his method to other existing methods. Fraver and White (2005*b*) suggested using both the percent-increase and the absolute increase methods to double check the validity of disturbances. Advantages of Fraver and White's (2005*b*) and Druckenbrod's (2005) methods include that they were developed for a variety of forest types. In addition,

the calculations of Druckenbrod's (2005) methods could be streamlined by using a program (Autobox, Automatic Forecasting System 2007) that automates the process.

I also used the sequential t-test (regime shift detection) method (Rodionov 2004, 2005) to compare the methods of analyzing the disturbance regime. Although designed to test climate data for possible regime shifts, this method can also be applied to ring-width series; releases and suppression can be viewed as regime shifts in the time series (ring-width series). Rodionov's (2004, 2005) method uses sequential t-tests to analyze the regime shifts in the mean. Tree-ring series are inherently autocorrelated, i.e. climate in year one affects tree growth in year one and subsequent years (Fritts 1976). The latest version of Rodionov's (2004, 2005) program also accounts for autocorrelation or red noise using different models (e.g. ordinary least square) and prewhitening. In addition, a significance level and cutoff length can be selected, and all regime shifts within that level and with at least the cutoff length will be recorded. As for Druckenbrod's (2005) method, a program is available that will automate the process of reconstructing the canopy-disturbance regimes.

I compared these four methods among each other and also visually assessed disturbances chronologies (hereafter referred to as the visual inspection method). The methods of reconstructing canopy disturbances identify the event years (i.e., years during which a release occurred). The visual inspection method is different from the other four in that I adjusted the event year of the canopy disturbances that were detected by the four methods to the most likely event year according to my visual assessment. Often, the starting date of a release as detected by statistical methods needs to be adjusted manually. Although not mentioned in his papers, Fraver suggested that the statistically identified

event dates are not always the actual event dates (Shawn Fraver, personal communication, Jan 25, 2008). The actual release dates are in most cases within 3-4 years of the ones statistically identified and, therefore, often do not change the outcome of the analysis because disturbance events are aggregated into decades. We summed the release events into decades because I did not crossdate between trees (Lorimer and Frelich 1989).

For the percent-increase and absolute-increase method, releases are not well detected at the beginning and end of a time-series, because, for example, 10 years (if a window of 10 years is selected) will be missing on either end of the time series. In addition, the threshold for the absolute-increase methods is based on statistics but still somewhat arbitrarily set. The percent-increase threshold of, for example, 100% is not based on statistics and is more arbitrary than the threshold for the absolute-increase method. Therefore, event years with 99% increase in growth and a 100% threshold would not be counted as a disturbance release event but might, in fact, be a disturbance release.

In this study, I compared methods —percent-increase (Lorimer and Frelich 1989), absolute-increase (Fraver and White 2005*b*), visual inspection, sequential regime shift detection (Rodionov 2004, 2005) and time-series analysis with intervention detection (Box and Tiao 1975, Druckenbrod 2005)—of reconstructing the canopy-disturbance history of eight sites in the Big Woods deciduous forest of Minnesota. Specific questions include: Do these methods result in similar disturbance histories? If they do, which method is most economical in both time and money?

Methods

Site Description

Tree cores were obtained from eight sites in the Big Woods of south-central Minnesota. The Big Woods encompassed approximately 9000 km² in 1850 (Figure 2). Today the landscape is highly fragmented; not many stands of fire-sensitive hardwood species remain. In the 19th century, the most common tree species were elm (*Ulmus* spp.), basswood (*Tilia americana*), sugar maple (*Acer saccharum*), ironwood (*Ostrya virginiana*), ash (*Fraxinus* spp.), and red oak (*Quercus rubra*) (Umbanhowar 1998). Today the most common tree species is sugar maple in the few Big Woods remnant forest remaining (personal observation).

Field Methods

Eight remnant stands in the Big Woods were systematically selected from the “Big Woods Heritage Forest” map (2005) and after contacting Big Woods specialists (Lee Frelich, Charles E. Umbanhowar, Jr., and Cindy Hale). These eight sites include Henry Woods (HEN), Mary Schmidt Crawford Woods (MSC) Scientific and Natural Area (SNA), Nerstrand State Park (NS), Partch Woods SNA (PAW), Townsend Woods SNA (TW), Whitney Island SNA (WH), Wood-Rill SNA (WRO), and Wolsfeld Woods SNA (WW). Within each remnant forest, one 20 m x 50 m plot was randomly placed. Within those plots, every tree larger than 5 cm in diameter at breast height (dbh, diameter measured at height of 1.37 m) receiving direct sunlight (canopy and subcanopy trees) was cored twice at 1 m height with a 5.15 mm increment borer.

Laboratory Methods

Lab analysis methods followed standard dendrochronological techniques (Stokes and Smiley 1968). These procedures included the preparation of the cores (drying, mounting on prefabricated core mounts, and sanding with progressively finer grits to expose the annual tree rings). After counting the rings and matching growth patterns between the two cores from one tree by inserting missing rings, I averaged the two cores into one tree-ring series. Other than crossdating between two cores from one tree, crossdating was not necessary for this project as I was only interested in comparing five methods of release detection in each single series. I measured the ring width using a Velmex bench and Measure J2X software (VoorTech Consulting, 2004).

Data Analysis

I compared five methods—percent-increase (Lorimer and Frelich 1989), absolute-increase (Fraver and White 2005*b*), visual inspection, sequential regime shift detection (Rodionov 2004, 2005) and time-series analysis with intervention detection method (Box and Tiao 1975, Druckenbrod 2005)—that calculate the number of trees that were disturbed in each decade at the different sites. To be able to compare all methods, I used one species, sugar maple, because it was abundant enough to calculate a threshold for the absolute-increase method. Other species like northern red oak (*Quercus rubra*), basswood, ironwood, and American elm (*Ulmus americana*) were not abundant enough to calculate that threshold.

To analyze the canopy-disturbance history with the percent-increase method a value is calculated for every ring-width in a time series (tree rings) according to Figure 3

using equation [1]. Similarly, to analyze the canopy-disturbance history with the absolute-increase method a value is calculated for each year of every time-series (tree core), using equation [2].

$$[2] \quad \textit{Absolute value} = \textit{Mean}_{t_2} - \textit{Mean}_{t_1}$$

where Mean_{t_1} is the average 10-year growth rate before the event and Mean_{t_2} is the average 10-year growth rate following the event (Figure 3). The absolute value cannot be calculated for the first and last 10 years of a core, so the most recent decade of the canopy-disturbance history is the 1990s.

I set the threshold for the percent-increase method to a conservative 100%, because it is the most common threshold used (Fraver and White 2005b) and I wanted to compare this method to other methods. For the absolute-increase method, a species-specific threshold must be established to identify releases from non-releases; thresholds have already been established for several species including sugar maple (Fraver and White 2005b). To calculate that threshold, Fraver and White (2005b) used (1) an empirical approach based on mean sensitivity (i.e., a measure of interannual variability in the tree rings), mean ring width, and range of growth responses and (2) logistic regression (to validate the threshold from the empirical approach). They concluded that the absolute-increase threshold for determining a release event is approximately 1.25 times the standard deviation of the absolute-increase values calculated, or the 90% quantile. However, I found that 1.25 times the standard deviation of the absolute-increase values calculated and the 90% quantile can vary by 0.2 mm when less than 50 cores are used in the analysis. A minimum number of cores needed for the absolute-increase method was not suggested by Fraver and White (2005b). Here I used 101 sugar maple trees (Table 1)

which yielded 9786 ring width measurements and 7867 data points for the absolute increase values. Once the threshold is established, all values calculated with equation [1] and [2] were screened for those that exceeded the threshold. All years that exceeded the threshold were classified as releases and tallied by decade.

Although Box and Tiao (1975) using time-series analysis with intervention detection statistically checked known events when calculating an intervention (i.e., outliers), unknown events (e.g., growth releases in trees) can also be identified with intervention analysis (Druckenbrod 2005). The timing and magnitude of interventions can be determined through statistical analysis. There are two kinds of intervention events: pulse and step intervention (Box et al. 2008). Pulse intervention is the departure of one annual value from the time series (in this case, the ring-width series), and step intervention is a persistent, significant change of ring-width values that could indicate a release (positive-step intervention) or suppression (negative-step intervention).

Several procedures are necessary for intervention analysis (McLaughlin et al. 1987). First, every ring-width series for every core was modeled using the autoregressive integrated moving average (ARIMA) method by Box and Jenkins (1970). With ARIMA, significant (to the 5% level) departures (interventions) of the actual series from the modeled series were identified. After detecting one intervention in one tree-ring series, the departure for that particular intervention was not considered again when modeling the tree-ring series again and that same tree-ring series was again screened statistically for another intervention. To analyze the tree-ring data with intervention analysis, I used the program Autobox (Automatic Forecasting Systems 2007). The version of Autobox used

identified a maximum of five interventions in a tree-ring series if they were significant at the 0.05 level.

I also used the sequential t-test method (Rodionov 2004, 2005) to compare the methods of analyzing the disturbance regime. I used a significance level of 0.05 and the regime shifts had to be detected in the mean (the other option is the detection of regime shifts in the variance). The minimum number of years that the shift has to be in a new regime (cutoff length) is 10 to be able to compare it to the other methods where I also used 10 years. Autocorrelation should be removed, because previous 'bad' years for the trees might mask the occurrence of a release event. To account for red noise (i.e. autocorrelation) I used the ordinary least square option with a subsample size of six (the subsample size depends on the cutoff length). Before applying the regime shift detection calculation, the program also used a prewhitening procedure to account for autocorrelation.

Using the visual inspection method, I adjusted the statistically detected release years visually to the more likely release years by individually inspecting the growth release dates and moving them forward or backwards depending on their position in relation to the actual release. I added releases (by searching for abrupt releases in the tree-ring series) that were not detected at the beginning and end of the time series, because the percent-increase and absolute-increase method cut the time-series short at the beginning and end (because of the way it is calculated).

Because the release data were not normally distributed, a nonparametric test (Kruskal-Wallis) was performed to test for similarity between the different methods. First, I determined the number of releases per decade for each plot. I compared that

number among each method. Second, the test was performed on the total number of releases in each plot. Third, I summed all releases over all decades and all plots and performed the test. In addition, a Friedman's ANOVA was performed. This ANOVA is calculated on ranks (and, therefore, for non-parametric data) and was performed on the total number of releases in each plot and method. All significance levels are reported at a 95% confidence interval (unless otherwise noted). All statistical analysis was performed in Minitab (Minitab Inc. 2007)

Results and Discussion

The different methods of analyzing the canopy-disturbance history resulted in differences of starting dates for release periods (Figure 4). However, the Kruskal-Wallis tests resulted in low significance levels between 0.204 (site PAW, $H = 5.94$, $n = 55$, p adjusted for ties) and 0.984 (site WRO, $H = 0.38$, $n = 40$, p adjusted for ties) indicating that the null hypothesis, which was that the different methods are similar, cannot be rejected. I did this test on each individual plot and for all plots combined (with releases ordered per decade). In addition, I calculated the Kruskal-Wallis on the total number of releases in a plot by methods. This additional test was also not significant comparing number of releases with methods ($H = 2.98$, $n = 40$, $p = 0.561$ adjusted for ties); however, the total number of releases compared by plots became significant ($H = 34.34$, $n = 40$, $p=0.000$ adjusted for ties).

Although there are differences in the starting date of a release detected by the different methods (e.g. a range of 9 years in the example in Figure 4), the Kruskal-Wallis

test did not find differences between the different methods. On the one hand, the release dates were summarized as releases per decade. Therefore, the changing of the release date by 9 years might not have an influence on how many trees per decade have a release (although it did in the example for the first release in Figure 4). On the other hand, the Kruskal-Wallis ranks the values (in this case the number of releases) and calculates its statistics on the mean of the ranks. Friedman's ANOVA also ranks the values, but does not compare the means of the ranks but rather the paired ranked values. Therefore, I believe that Friedman's ANOVA is more appropriate compared to the Kruskal-Wallis. Friedman's ANOVA found that the methods are statistically different from each other ($S = 20.05$, $n = 8$, $p = 0.000$ adjusted for ties). This test also found a difference between the number of releases compared to the plots ($S = 33.11$, $n = 40$, $p = 0.000$ adjusted for ties).

Inspecting the data (Table 3), there seem to be major differences between the methods. For example, for all plots combined, the sequential t-test counted 185 releases whereas the absolute-increase method resulted in 121 releases. Exploratory analysis (two-way ANOVA between the visual inspection method and the four other methods) shows that between the plots are always significant differences ($p < 0.001$) meaning the sites differ significantly from each other. Therefore, the null hypothesis can be rejected; this makes sense, because the canopy-disturbance history is different between the plots. Two-way ANOVA on the methods (visual inspection vs. all other methods) yielded significant results except for the sequential t-test method which is not significant ($S = 2.299$, $n = 2$, $p = 1.000$). Therefore, only for the sequential t-test method, the null hypothesis (that the results of the methods are similar) can be accepted, i.e. the sequential t-test method is the only one that does not differ significantly from the visual inspection method.

The release dates that the methods calculated were often not the actual release dates as visually detected. The percent-increase and absolute-increase method seem to predate the actual release by several years; the sequential t-test and time-series method result in a release date that is one to two years after the actual release date (Figure 4).

The advantages and disadvantages of each method are as follows (Table 4): Whereas the percent-increase method and its variations are the most widely used in analyzing the disturbance histories and is easy to calculate, this method has some drawbacks. First, this method uses a running mean and autocorrelation in the tree-ring series is not accounted for. This autocorrelation could result in the detection of releases that are not really releases or in not detecting releases that are really releases. This problem of not accounting for autocorrelation is the same for the absolute-increase method. Second, the releases detected start usually several years earlier than the actual releases. Third, the method cannot be used for the first and last 10 years of the core's range because 10 years are averaged together at either end of the core. This problem is similar in the absolute-increase method. Fourth, no automation of this process (as in a software or add-in) is available. Fifth, as Fraver and White (2005*b*) pointed out, the percent-increase method is very sensitive at lower growth rates and very stringent at high growth rates. Therefore, at the one end of the spectrum (low growth rate), using this method results in releases that are not really releases and, at the other end of the spectrum (high growth rate), it results in not accepting releases that are actually releases.

The absolute-increase method has the same disadvantage as the percent-increase method except for the last (fifth) point in that the absolute-increase method accounts for prior growth. However, another drawback is that a large number of cores or data points of

one species are needed to calculate a threshold for a certain species. Although thought to be usable in different habitats, the threshold for sugar maple was much different in this study in Minnesota compared to the study by Fraver and White (2005a, 2005b) in Maine. The two study sites are approximately 1900 km apart and the forests are different in species composition. Whereas the Minnesota Big Woods has only hardwoods, Fraver and White's (2005a, 2005b) plots had conifers like white-cedar (*Thuja occidentalis*) and red spruce (*Picea rubens*). Another explanation for this discrepancy is the differing mean ring width and mean sensitivity (i.e., the sensitivity of the ring width to changing climatic conditions) (Table 2). I used 101 time series (samples), whereas Fraver and White (2005b) had 288 time series. I calculated the threshold that I use in this study from Fraver and White's (2005b) threshold equations.

The sequential t-test is based on running means. However, in that method the running means are tested with a t-test from one year to the next, i.e. a sliding window. Therefore, the release date as detected by the differences in the mean by the t-test is closer to the release date of the visual inspection method (Figure 4). In addition, Rodionov (2007) provides a program as an add-in for Microsoft Excel where the data can be imported and analyzed with a few simple steps. Another advantage of the sequential t-test method, is the inclusion of the option to remove red noise. The ring widths in tree-ring series are autocorrelated and using a running mean can therefore result in spurious results (releases that are not really releases and false releases are counted as real releases). Rodionov's (2007) program includes the option of removing the autocorrelation using a different method (e.g. the ordinary least square method). In addition, a significance level can be chosen and only releases within that level are valid releases. Rodionov offers the

magnitude of the release and suppression periods (also called regime shifts). I found that releases with less than 0.1 magnitude in the regime shifts index are, in general, not releases after all when looking at the ring-width graphs. In the 101 series used in this analysis, 185 disturbance release events were detected with nine releases having a magnitude below 0.1. This method resulted in a number of disturbance release-events closest to the visual inspection method when compared to all plots combined and to each individual plot (Table 3).

Using tree-ring data in intervention analysis to detect unknown growth releases in tree-ring data was first suggested by Druckenbrod (2005) and later by Bouriaud and Popa (2007). Time-series analysis has the same advantages as the sequential t-test method: (1) it is automated with the program Autobox (Automatic Forecasting System 2007); (2) autocorrelation is removed (with the ARIMA model); (3) a significance level can be chosen which the releases have to pass in order to be counted as releases; and (4) it gives the magnitude of the intervention, i.e., the size of the change in the mean ring width. One disadvantage of the Autobox Pro+ program is that only five interventions can be calculated per series (and, therefore, a sixth intervention if it existed would not be shown). More interventions can be identified by purchasing Autobox Enterprise (Automatic Forecasting System 2007).

The visual inspection method has the advantage of having the most exact growth-release date. Disadvantages are the time investment and the subjectivity in this task. Fraver and White (2005*b*) suggested using two methods of reconstructing canopy disturbances for comparison. Fraver also suggested inspecting the release dates visually and adjusting them according to the growth rates (Shawn Fraver, personal

communication, Jan 25, 2008) as was done in the visual inspection method used in this paper.

Conclusion

Statistical test for measuring similarity (Friedman's ANOVA) between the methods of identifying dates of disturbances did show differences between them. The starting date between the different methods can vary appreciably, with the percent-increase and absolute-increase methods usually underestimating the release date and sequential t-test and time-series method usually overestimating the release date. For three reasons, the sequential t-test showed the best results based on time invested in the analysis and quality-control measures. First, it gives the closest results to the visual inspection method. Second, it accounts for autocorrelation and the user can choose different methods to remove the red noise. Third, it is automated by Rodionov's (2007) program which is freely available. Therefore, the sequential t-test might be the best method available at this time to analyze the canopy-disturbance histories in this forest type. However, visual inspection cannot be substituted for by any statistical method and should always be done to supplement statistical methods.

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Table 1: Number of trees (sugar maple and other species) in the different plots (0.1-ha plots).

	# of Sugar Maple Trees	# of Trees of All Other Species	# of All Trees in Plot
HEN	23	2	25
MSC	9	2	11
NS	14	0	14
PAW	14	16	30
TW	6	19	25
WH	12	12	24
WRO	5	8	13
WW	18	0	18
Total	101	59	160

Table 2: Absolute-increase threshold calculation data.

	Sugar Maple (Fraver and White 2005 <i>b</i>)	Sugar Maple (this study)
Mean sensitivity	0.300	0.372
Mean ring width (mm)	0.98	1.446
1.25 x standard deviation	0.51	1.03
90% quantile	0.52	1.09
Absolute-increase threshold (mm)	0.52	1.06
N (# of cores to determine threshold)	288	101

Table 3: Total number of releases found in each plot and for each method.

	Visual inspection	Percent increase	Absolute increase	Seq t- test	Time- series
HEN	37	38	22	44	26
MSC	18	13	13	17	12
NS	35	28	23	34	25
PAW	25	15	10	21	13
TW	8	6	4	7	7
WH	19	20	16	20	17
WRO	8	6	6	6	7
WW	35	30	26	36	25
All Plots	185	156	121	185	132

Table 4: Comparison of methods to calculate canopy disturbances.

Tests	Visual inspection	Percent-increase	Absolute-increase	Sequential t-test	Intervention analysis
Based on:	Own judgment	Running mean	Running mean	Running mean	Time-series (ARIMA)
What to do:	Visual inspection of undetected tree-ring series (in graph form) for sustained releases after sustained suppressions and rapid early growth	Calculations of a value according to eq. 11] and Fig. 3 for each value in each tree-ring series (except for of 10 years at either end of series) → screening all calculated values for those over chosen threshold (100%) → summarizing the releases in a table	Calculations of a value according to eq. 12] and Fig. 3 for each value in each tree-ring series (except for of 10 years at either end of series) → screening all calculated values for those over chosen threshold (e.g. for sugar maple: 1.06) → summarizing the releases in a table	Making choice as to the options for this test → letting the program run → eliminate all neg. regime shifts and all regime shifts that are < 0.1 → looking at the graphs that were produced and at the summary table/graph	Adjusting parameters (sign. levels and length of intervention) → writing down all releases as they are shown → compiling those releases in a table/graph
Advantages	- Accurate release dates	- Can be used in a variety of forest types - It has been used in many studies → comparison between studies: potentially possible - Easy to calculate	- Accounts for prior growth - Said to work in a variety of forest types (but see disadvantages) - Easy to calculate	- Can potentially be used in a variety of forest types - AC removal option - Closest results to the visual inspection method - Significance level can be chosen - Automation of process possible (Excel plug-in)	- Can potentially be used in a variety of forest types - AC is removed (ARIMA) - Program is available - Magnitude of intervention given - Significance level can be chosen
Dis-advantages	- Time consuming - Subjective	- AC not accounted for - Releases detected are several years before the actual release - 10 years missing at either end of series - No automation of process available - Sensitive at lower and stringent at higher growth rates	- AC not accounted for - Releases detected are several years before the actual release - 10 years missing at either end of series - No automation of process available - Large number of data needed for species-specific threshold - Species-specific threshold for same species different in two different studies: method might not be usable in different forest types	- Regime shifts with Magnitude of <0.1 not real releases → need to be removed manually	- Program is pricey - version used in this study [Autobox Pro+] can identify only 5 interventions

AC = autocorrelation

Figure 1: The percent-increase method is overly sensitive at lower growth rates (a) and more stringent at higher growth rates (b) compared to the absolute-increase method. The x-axis shows mean prior growth rate (mm per year) and the y-axis records the percent increase in growth rate. The area around a and b shows the disagreement between the percent-increase and absolute-increase method (redrawn and modified from Fraver and White 2005b).

Figure 2: The Big Woods in the ecological subsections in Minnesota (Department of Natural Resources Minnesota 2009) and the eight study sites. Site NS and PAW are just outside of what was considered the Big Woods in the ecological classification system by the Department of Natural Resources. Nevertheless, NS is called the Nerstrand Big Woods State Park and both, NS and PAW (site suggested by Lee Frelich), exhibit classic Big Woods tree species composition.

Figure 3: $Mean_{t1}$ is the mean 10 year pre-event growth rate and $Mean_{t2}$ is the mean 10 year post-event growth rate. The ‘event’ year in this example is 1990 (redrawn and modified from Black and Abrams 2004).

Figure 4: The different starting dates for release events in one sample tree as analyzed by the different methods. The different types of arrows correspond to the different methods of analyzing canopy-disturbance history. After each disturbance method, years are mentioned. These years are the years that the method identified as release years. The gray solid line is the ring-width series. The shaded area with the arrows inside represents the range of years over which different methods identified the same release event.

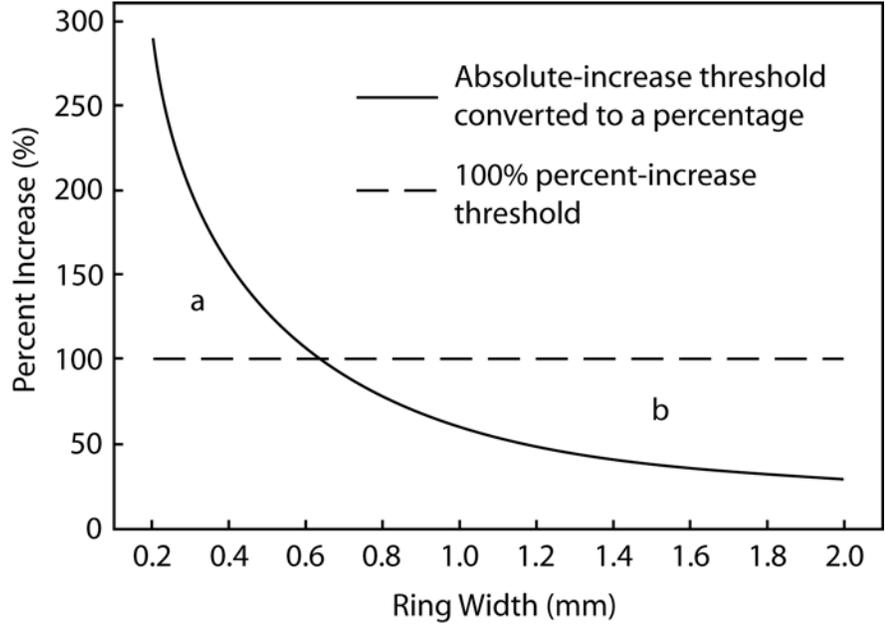


Figure 1

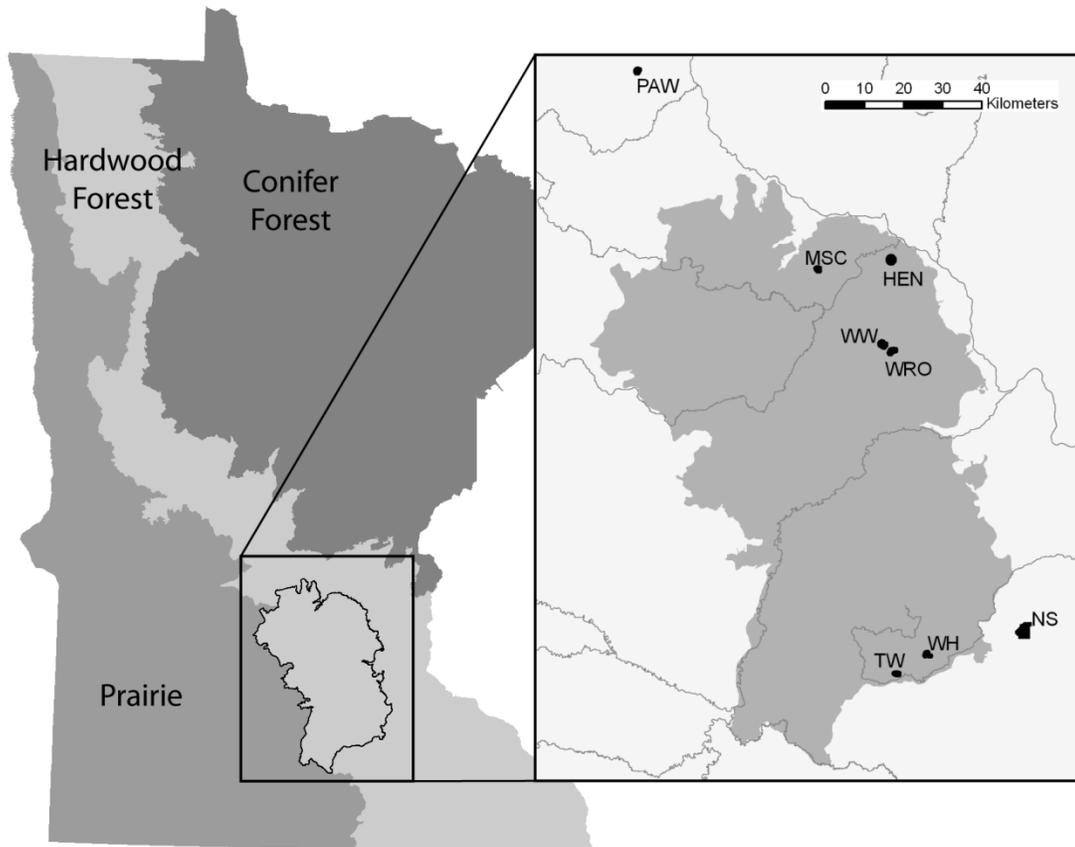


Figure 2

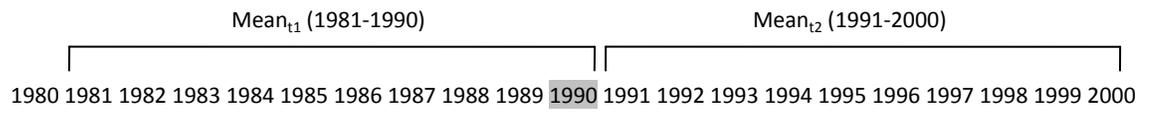


Figure 3

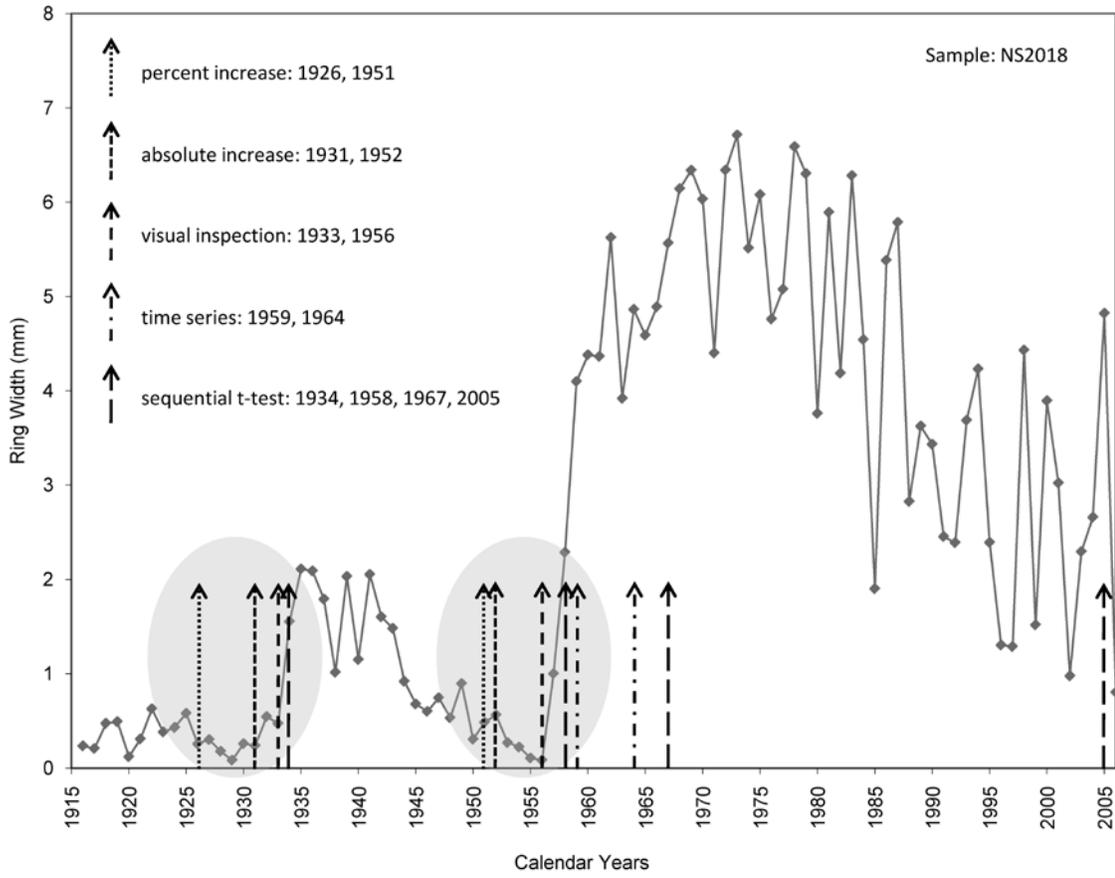


Figure 4

Chapter 5

Canopy-Disturbance history and regeneration patterns of the Big Woods in Minnesota

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Question: At the prairie-forest ecotone in Minnesota, does the canopy-disturbance history of old-growth forest correlate with climatic condition? In other words, did the local hardwood forest disturb during dry or wet periods?

Location: Eight plots in the Big Woods in south-central Minnesota, USA.

Methods: We used the sequential t-test (regime shift) method on ring-width measurements to reconstruct the disturbance histories of several forested sites. We used Kendall's tau-b and Spearman's rho to analyze the climate-disturbance relationship at decadal scales.

Results: The average percent of canopy disturbed in all eight plots is 6.1%. Only three of eight sites showed significant values in Spearman's rho and Kendall tau-b when comparing Palmer Drought Severity Index and the local canopy-disturbance history.

Conclusion: The average percent of the canopy disturbed in the Big Woods remnants is similar to this measure in other studies of similar and different forest types. Although other studies have found a drought–disturbance relationship, in this study drought and disturbance were significantly negatively related at only three out of eight plots.

Keywords: Big Woods, Minnesota, disturbance history, sequential t-test, regime shift,

Nomenclature:

Abbreviations: dbh = diameter at breast height; RSI = regime shift index; CPA = canopy projection area; PDSI = Palmer Drought Severity Index

Introduction

The geography of plants at continental to global scales has long been explained by differences in climate that vary with latitude, altitude, and distance from large bodies of water (e.g., Humboldt 1805, cited in Brown and Lomolino 1998; Clements 1916; Küchler 1966). The distribution of plants at local scales is often explained by historical events, or by the influence of natural and human disturbance (e.g., Cowell and Dyer 2002; Vale 2003; Ziegler et al. 2004; Arabas et al. 2006). Until recently, less attention has focused on how climate and disturbance interact at intermediate scales to influence biogeography (but see, for example, Bergeron and Archambault 1993; Kitzberger et al. 1997; Swetnam and Betancourt 1998; Grissino-Mayer et al. 2004; Brown and Wu 2005; Shuman et al. forthcoming). Dale et al. (2000) called for an increased emphasis on interactions between climate change and forest disturbances such as fire and drought. There is a growing need to understand vegetation history and responses to global change at these crucial intermediate scales in space and time. It is also important to know about the relative roles that natural conditions (e.g., periodic drought) played in determining the location of the grasslands that bordered on the forested region in the Upper Midwest (Sauer 1944, 1975; Borchert 1950; Curtis 1959; Davis 1977; Dyer and Baird 1997). If we knew the extent to which, for example, drought influenced forest/savanna/grassland establishment, it will be possible to predict how those ecosystems will change with global climate change.

In this study, we focus on the prairie–forest ecotone in south-central Minnesota. Future environmental change might be rapid in such borders between ecosystems, because if the climate were to change as projected then ecotones might be most affected (Allen and Breshears 1998). The complex deposits of glacial moraines and outwash

plains in the area previously occupied by the Big Woods—with their variable soils, gently rolling topography, and myriad lakes—influenced the spread of fires and the development of the assemblages that comprise the ecotone (Grimm 1984). When Euro-Americans arrived in the mid 1800s, southeastern Minnesota was a patchwork of deciduous forest (Big Woods), prairie, oak savanna, and wetlands (Marschner 1974; Grimm 1984; Umbanhowar 2004). Daubenmire (1936) observed that the presence and structure of the Big Woods were related to climate, fire, and soils. Almost 50 years later, Grimm (1984) reconstructed the 19th century species composition of the Big Woods from Government Land Office survey records. Grimm (1983) also analyzed the pollen record from lakes within the Big Woods area.

About 4000 years ago, oak woodland expanded westward into the prairie (Camill et al. 2003). The open oak woodland eventually was replaced by dense deciduous forest when ironwood (*Ostrya*), elm (*Ulmus*), basswood (*Tilia*), maple (*Acer*) and ash (*Fraxinus*) increased in abundance. Umbanhowar (2004) determined from a thorough study of lake sediments that the Big Woods formed over the past 650 years, which is surprisingly recent in the 11,000-year post-glacial period. Grimm (1983) speculated that the Big Woods established following a decrease in fire frequency because of moister and cooler conditions during the Little Ice Age (AD 1250–1850).

The long-standing hypothesis that resulted from Grimm's work was that wetter conditions resulted in wetter soils and fuels that would resist burning, and in more lakes that could intercept fires and limit their spread. When fire frequency decreased, trees established in the prairie where previously they had been burned. This prevailing opinion led Sprugel (1991, p. 14) to conjecture that “the Big Woods might have reverted to oak

savanna during the drought of the 1930s (if it had not been converted to farmland and housing developments first).”

Analysis of fossil pollen, macroscopic charcoal, and lake-level reconstructions suggest an alternative hypothesis: The composition of tree species associated with the Big Woods developed during dry, rather than wet periods (Shuman et al. forthcoming).

Umbanhowar (2004) completed a detailed analysis of charcoal and pollen records from lakes throughout the prairie–forest border region. He presented evidence that forests expanded during drier rather than wetter periods, and he concluded that “a better understanding is needed of...the relationship between precipitation and fire in grasslands versus forests...in order to understand past interactions of climate, fire and vegetation and to predict future change along the prairie–forest border and elsewhere”

(Umbanhowar 2004, p. 675). Clark et al. (2002) reported a decrease in fire frequency during droughts in grasslands of the northern Great Plains. Shuman et al. (forthcoming), too, has analyzed pollen, charcoal, and lake-level reconstructions in the Big Woods and concluded that forests expanded during dry periods in the past 800 years, possibly because fire frequency decreased with reduced flammable material in dry prairies.

More research is needed to explain how vegetation at the prairie–forest border responded to past climate variability. Such information is essential for filling a gap in this knowledge base, and the findings of our study will allow improved predictions of vegetation response to global change.

The objectives of our research are to analyze tree-rings to (1) determine whether peaks of tree establishment occurred primarily under wet or dry conditions and (2) reconstruct the canopy-disturbance history of several old-growth Big Woods sites. Our

two specific questions are (1) Were trees recruited (i.e., did trees grow to coring height of 1m) during dry climatic conditions in the Big Woods? and (2) Were the disturbance histories different at different sites within the Big Woods area, which would imply how wide spread patterns of disturbances are and whether decades of peak disturbances are similar in the Big Woods?

Methods

Site Description

Encompassing approximately 9000 km² in 1850 (Figure 1), the Big Woods of south-central Minnesota are highly fragmented today with only a few stands of fire-sensitive hardwood species remaining. When settlers came to this area in the 19th century, the most common tree species were elm (*Ulmus* spp.), basswood (*Tilia americana*), sugar maple (*Acer saccharum*), ironwood (*Ostrya virginiana*), ash (*Fraxinus* spp.), and oak (*Quercus* spp.) (Umbanhowar 1998).

The climate of the Big Woods region is continental, with relatively cold winters and warm summers. The Big Woods has two distinct climatic gradients (Grimm 1984): mean annual temperature increases from north to south by about 2°C, and mean annual precipitation increases by about 10 cm from northwest to southeast. The two dominant soil orders in the Big Woods are Mollisol, which is associated with prairies, and Alfisol, which is associated with forests (Grimm 1984). The area that became the Big Woods was mostly prairie in the mid-Holocene (Grimm 1983); however, woodland invaded and soils slowly changed from Mollisols to Alfisols (Grimm 1984).

Field Methods

Eight remnant stands in the Big Woods were systematically selected from the “Big Woods Heritage Forest” map (2005) with input from ecologists who have studied the Big Woods (Lee Frelich, Charles E. Umbanhowar, Jr., and Cindy Hale). These eight sites are Henry Woods (HEN), Mary Schmidt Crawford Woods (MSC) Scientific and Natural Area (SNA), Nerstrand State Park (NS), Partch Woods SNA (PAW), Townsend Woods SNA (TW), Whitney Island SNA (WH), Wood-Rill SNA (WRO), and Wolsfeld Woods SNA (WW). Within each remnant forest, one 20 m x 50 m plot was randomly placed. Within each plot except for WRO, every tree ≥ 5 cm in diameter at breast height (dbh, diameter measured at height of 1.37 m) was cored twice at 1 m height with a 5.15 mm increment borer to extract the tree-ring record. We cored at 1m height because of rotten centers that we tried to avoid by not coring at the base and because of buttresses on larger trees. At WRO, we cored every tree ≥ 10 cm dbh twice at 1 m height because of permission limitations. For each tree, we recorded data such as tree species, dbh, tree-crown position (canopy, subcanopy, understory), crown extent (how many meters the crown spans in each of the four cardinal directions from the trunk of the tree), and latitude and longitude of the plots.

Laboratory methods

Standard dendrochronological techniques were used to prepare the cores for analysis (Stokes and Smiley 1968). Cores were dried, glued to prefabricated core mounts, and sanded with increasingly finer grits to expose the annual tree-rings. We counted the rings, matched growth patterns between the two cores from one tree by inserting zero to three

missing rings (Lorimer et al. 1999), and averaged the two cores into one tree-ring series. Other than crossdating between two cores from one tree, crossdating between the trees was not performed because the release and regeneration dates were summarized into decades (Lorimer and Frelich 1989, McLachlan et al. 2000). Canopy-disturbance history data (i.e., how much percent of the canopy was disturbed per decade) are summed into decade because we wanted to compare the decadal disturbance rate to other studies which presented the disturbance rate in that way. We measured the annual ring widths using a Velmex bench and Measure J2X software (VoorTech Consulting, 2004). We did not detrend the tree-ring series because of the loss of potential release and suppression period.

Data Analysis

We attempted to obtain a pith date for each tree (i.e., the year that each tree reached coring height), but several large trees with decayed centers were missing too many annual rings to determine their ages ($n = 106 = 31.5\%$ of total number of trees cored). To estimate pith dates we examined the curvature of the innermost tree rings when possible, measured how many millimeter of curvature to pith were missing, averaged the ring width of the earliest 10 rings (closest to the center), and calculated (growth rate in mm/year times mm of core missing) how many rings were missing to center (Parshall 1995, Ziegler 2002).

We reconstructed the canopy-disturbance histories for the eight plots following the sequential t-test method (Rodionov 2004, 2005, 2007). Based on the result of a recent study by Rauchfuss (in prep.), this method is with the visual inspection method the most

reliable and economical approach compared to one classic method (percent-increase by Lorimer and Frelich 1989) and two newly proposed methods (time-series analysis with intervention detection by Druckenbrod 2005 and absolute-increase by Fraver and White 2005b). Rubino and McCarthy (2004) also compared different methods (but not the ones that Rauchfuss (in prep.) compared) and found differences in the canopy-disturbance histories of the same plot depending on which methods they used. Rauchfuss (in prep.) also identified differences between the methods; the sequential t-test method yielded results most similar to what Rauchfuss termed the visual inspection method. Tree cores and graphs of ring-width patterns should be inspected for visible releases (Shawn Fraver, personal communication, Jan 25, 2008). Because statistical analysis is just an approximation used to study natural phenomena, release periods can be identified that clearly are not releases as seen in tree-ring graphs. Some of those mistakes can be removed by inspecting the tree-ring graphs and adjusting the numbers of releases by subtracting or adding releases. This subjectively adding and subtracting of releases was often necessary with the percent-increase method (Lorimer and Frelich 1989) because prior growth was not considered. With newly proposed methods, this step has been reduced, but is still necessary in some cases.

This method uses t-tests to compare the running means of a window before and after a specific year. If the results are significantly different, a regime shift is indicated (which is synonymous to a release or suppression event). The magnitude of those regime shifts or releases are expressed in the regime shift index. This index is based on the significance of the regime shift, the cutoff-length (the window before and after the event year), the method for removing red noise (autocorrelation), and the subsample size (which is based

on the cutoff-length). We used a target significance level of 0.05, a cutoff-length of 10 years, ordinary least squares to remove red noise with prewhitening, and a subsample size of 6 (Rauchfuss, in prep).

All releases detected by Rodionov's program were scanned visually for false releases using the regime shift index (RSI) (Figure 2). In general, each release with an RSI of < 0.1 was not a real release (based on the ring-width graphs that do not show a visible release) (Figure 2). Rapid early growth > 1 mm per year at the time a tree reached coring height was also labeled a release because the tree most likely grew up in a canopy gap with abundant resources that enabled relatively wide rings to form (Lorimer et al. 1988).

A tally of growth releases, grouped into decades, represents the number of trees that released. A large number of trees with growth releases in a given decade does not necessarily mean that a large canopy gap formed because several small trees could have occupied the disturbed area. The release events, therefore, were weighted by an estimate of the gap size, which assumed that the current tree crowns occupy former gaps (Lorimer and Frelich, 1989; Ziegler 2002, p. 2109); we used the Crown Projection Area (CPA) (Fraver and White 2005a) to weight each release event and approximate the area of canopy removed.

The CPA was then approximated by calculating the size of the four quarter ellipses from the crown measurements extending from the trunk to the drip line of the canopy, and then summing the area of the four quarter ellipses (Fraver and White 2005a). We calculated the percentage of canopy disturbed by dividing the CPA for a tree by the total CPA for the whole plot.

Not all growth releases result from new openings in the canopy layer. Trees in the canopy may also increase growth rates when they extend their branches into a gap created by a neighboring tree that fell. Including those crown-extension releases in the canopy-disturbance history will result in an overestimate of the percentage of gaps formed (Frelich 2002). We were careful to identify those crown extension releases by estimating the dbh at which, on average, a tree of a certain species is already a canopy tree (Lorimer and Frelich 1989). The threshold dbh was calculated using an approach similar compared to Lorimer and Frelich (1989). Instead of graphing the dbh versus the percentage of trees in the canopy layer, we calculated the percentage of canopy trees versus understory trees. The dbh at the 5% threshold, as established by Lorimer and Frelich (1989), was the threshold dbh for the canopy versus understory trees. We calculated these thresholds for each species individually. Releases were not counted when the tree was above that threshold dbh at the time of the release. The threshold dbh's for sugar maple, American elm, and basswood were 20.4cm, 26.5cm, and 22.1cm, respectively. We had no oaks in the understory and a threshold dbh could therefore not be established. We set the threshold dbh for oaks at 26.5cm (same as American elm), because, in general, oaks and American elms are intermediate in shade tolerance (Bey 1990, Rogers 1990, Sander 1990). We recorded 14 releases in oaks < 26.5cm dbh at the time of the release. Three releases in oaks occurred when the oaks were between 20cm and 26.5cm dbh at the time of the release. It is, therefore, unlikely that we overestimated the percent canopy disturbed because of not having a threshold calculated for the oaks.

After summing the percentage of canopy disturbed per decade, we plotted the reconstructed Palmer Drought Severity Index (PDSI) from grid point 198 of the

reconstructed PDSI grid (Cook et al. 1999, 2004), which is the closest to the Big Woods, comparing the PDSI with the canopy-disturbance history (Figure 3). At grid point 198, the R value is 0.84 between the reconstructed and actual PDSI data (1900-2003). We chose PDSI and not temperature or precipitation because PDSI is a measure of moisture availability. Just because precipitation record shows a lot of rain or snow it does not mean that it was wet, because it could have been a year with high temperature (and the rain would have been evaporated quickly). Because the data are not normally distributed, we calculated Spearman's rho and Kendall's Tau-b on the PDSI (averaged for the whole decade) versus the decadal canopy-disturbance history. For this analysis we eliminated all disturbance decades before the 1880 decade to avoid issues pertaining to the lack of sample depth and the 2000 decade which is incomplete. We also calculated the average disturbance rate per decade by plot and for the whole Big Woods for 120 years (1880–1999) (Lorimer and Frelich 1989, Parshall 1995).

Results

From the 160 canopy and subcanopy trees that were used in the analysis, 255 releases were detected by the sequential t-test method. After visually inspecting the ring-width graphs (see Figure 2 for an example for a single tree), 15 releases were deemed false releases (their regime shift index was less than 0.1) and were eliminated from the disturbance chronologies. Some of these releases were perhaps due to canopy extension instead of canopy accession. Subtracting the canopy extension releases and inserting 18 releases because of rapid early growth, we have 156 canopy accession releases in the

disturbance chronology. The average percentage area of disturbances per decade from 1880 to 1999 is 6.7%. The average canopy-area disturbed varies by site from 3.2% at MSC to 11.0% at NS (Table 1).

Spearman's rho and Kendall's Tau-b were calculated to analyze the correlation between the canopy-disturbance history and the decadal average of the reconstructed PDSI (Table 2) and the relationship was plotted (Figure 5). WRO and MSC have a significant Kendall's Tau-b (-0.559 and -0.408, respectively) with a relatively high and significant Spearman's rho (-0.660 and -0.543, respectively). HEN was also significant in the Kendall's Tau-b test-statistics (-0.394), but not the Spearman's rho test-statistics (-0.490).

Spearman's rho and Kendall's Tau-b were also calculated to analyze the relationship between pith dates (at 1m height) aggregated into decades and the decadal average of the reconstructed PDSI (data not shown) to see whether recruitment shows a significant relationship to the PDSI. There was no significant relationship between drought and recruitment to 1m height at any of the plots (WRO was not used in this analysis, because the other plots had cores from all trees > 5 cm dbh, but WRO had cores from all trees > 10 cm dbh). Because we cored at 1m height and trees might need a few years to grow to coring height, we also calculated Spearman's rho and Kendall's Tau-b for all decades with the pith dates shifted one decade back to test whether establishment would be related to PDSI. We compared, for example, the PDSI value of the 1910 decade with the number of pith dates in the 1920 decade. Those calculations were not statistically significant.

Discussion

Average decadal disturbance rates (or percentage of canopy disturbed) in this study are comparable to averaged percentages of disturbances per decade in other studies and in other forest types in the eastern United States (e.g. Parshall 1995, Ziegler 2002, Fraver and White 2005a, D'Amato and Orwig 2008, Rauchfuss and Ziegler, in prep.). No single decade shows moderate disturbances (30–60% of the canopy disturbed; Hanson and Lorimer 2007) at all plots. Just four plots (NS, WH, WRO, WW) had a decade with more than 30% of the canopy disturbed (Figure 3). However, the 1950s show a disturbance in four of our eight plots (NS, MSC, PAW, TW). These plots are not geographically close (NS and TW are in the southern part and PAW and MSC are in the northern part of the Big Woods).

The data indicate that no major disturbance (i.e., a disturbance of more than 60% of the canopy area) affected the plots studied in the Big Woods in the past 120 years. The data further suggests that smaller, local disturbances were more important in the Big Woods than stand-replacing disturbances. Noted by other authors (e.g. D'Amato and Orwig 2008 and references therein), this study supports the idea that stand-replacing disturbances are infrequent.

Shuman et al. (forthcoming) found that the Big Woods must have developed under dry climatic conditions. Parshall (1995) found that disturbances seemed to synchronize with drought conditions in a hemlock–hardwood forest in Upper Michigan. A significant drought–disturbance relationship exists in three plots. WRO, a site that Shuman et al. (forthcoming) included in their study, had a strong and significant drought–disturbance relationship (Table 2), and HEN and MSC also had a moderate but significant

relationship, but the other sites showed no significant relationship between drought years and increased canopy disturbance.

One reason why WRO shows such a strong relationship could be because of the high percentage of the canopy disturbed in the 1930s, which was a major drought in the Midwest with 10-year PDSI average of -1.29 (reconstructed PDSI) and actual PDSI values as low as -5.07 (in 1934). During that decade, WRO had a release of > 37% canopy disturbed (Figure 3) whereas the other decades had lower canopy disturbance rates of 5-14%. Shuman et al. (forthcoming) described a peak of *Acer* recruitment during the 1930s drought which coincided with the peak of disturbance that we recorded. If the 1930s decade is removed and Spearman's rho and Kendall's Tau-b are calculated again, the results are still significant (at $\alpha = 0.1$) but both values decline by 0.1 to -0.55 and -0.46, respectively. So, although weaker, the drought-disturbance relationship still holds at WRO.

Parshall (1995, 1472) noted that “[s]usceptibility of trees to disturbances can vary because of site characteristics [...], differences in age and size structure [...], and differences in structural characteristics among species.” Although the drought in the 1930s certainly had dramatic effects on flora and fauna, the 37% of the forest canopy disturbed at the WRO site could simply have coincided with a major drought of the 20th century, but have been caused by site characteristics, stand demographics, and factors other than those driven by drought like a major wind event. Except for at HEN and MSC, the relationship between drought and disturbance events was not significant at any other site. The relationship between drought years and the years trees reached coring height

(pith dates) is not significant (data not shown); however, recruitment to 1m height occurred in the 1930s in some plots (PAW, TW, WW; Figure 3).

Conclusion

The average percent of the canopy disturbed in the Big Woods remnants is similar to this measure in other studies of similar and different forest types. Although other studies have found a drought–disturbance relationship (Parshall 1995) or drought–establishment relationship (Shuman et al. forthcoming), in this study drought and disturbance were significantly negatively related at only three out of eight plots. This lack of consistent relationship does not indicate that there is no relationship between drought and Big Woods establishment; however, it suggests that disturbance chronologies from tree rings might not be the best way to study drought–establishment relationships. In our study, we were only able to look at a narrow window in time because of a lack of old trees extending to the Big Woods formation approximately 650 years ago.

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Table 1: Average percentage of canopy disturbed from 1880-1999 for each plot and for all plots combined.

Plot	Average Percentage of Canopy Disturbed (%)
HEN	5.7
MSC	3.2
NS	11.0
PAW	5.1
TW	5.2
WH	6.6
WRO	8.0
WW	8.5
All Plots	6.7

Table 2: Comparison between decadal (averaged) PDSI and the disturbance chronology with $n = 12$ decades (1880-1999).

Plot	Spearman's	Kendall's
	rho	Tau-b
HEN	-0.490	-0.394*
MSC	-0.543*	-0.408*
NS	-0.406	-0.296
PAW	0.278	0.254
TW	0.327	0.286
WH	0.347	0.293
WRO	-0.660**	-0.559***
WW	-0.312	-0.230

* significant at 0.1 (two-tailed)
** significant at 0.05 (two-tailed)
*** significant at 0.02 (two-tailed)

Figure 1: Former extent of the Big Woods in Minnesota (Department of Natural Resources Minnesota 2009). The enlargement shows the study sites within the Big Woods. Sites NS and PAW are just outside of what was considered the Big Woods in the ecological classification system by the Department of Natural Resources. Nevertheless, NS is called Nerstrand Big Woods State Park, and the forest at both NS and PAW (site suggested by Lee Frelich) have classic Big Woods tree species-composition.

Figure 2: Ring width (gray line) and regime shift detection (black line) for a single tree. The regime shift index (RSI) is very low for the first release (arrow on the left) and that release was not counted in the disturbance chronology, because no release is visible in the ring-width graphs. The second release is valid (right arrow with high RSI) and was included in the disturbance chronology.

Figure 3: 7-year average Palmer Drought Severity Index (PDSI) on the PDSI axis (upper y-axis on the left side; gray solid line) and the actual PDSI values as averaged over each decade (upper y-axis on the left side; black solid line) relative to the canopy-disturbance history (secondary y-axis on the right side; bars) expressed as percent canopy disturbed. The lower y-axis on the left side shows sample depth (dashed black line).

Figure 4: Graphs shows the pith dates (actual pith dates and estimated pith dates) at 1m height (bar graph) and the sample depth (line graph). WRO is not depicted because only trees with a dbh of >10cm were cored were for the other plots trees with a dbh of >5cm were cored.

Figure 5: Scatterplots comparing the decadal (averaged PDSI) and the canopy disturbed per decade (%).

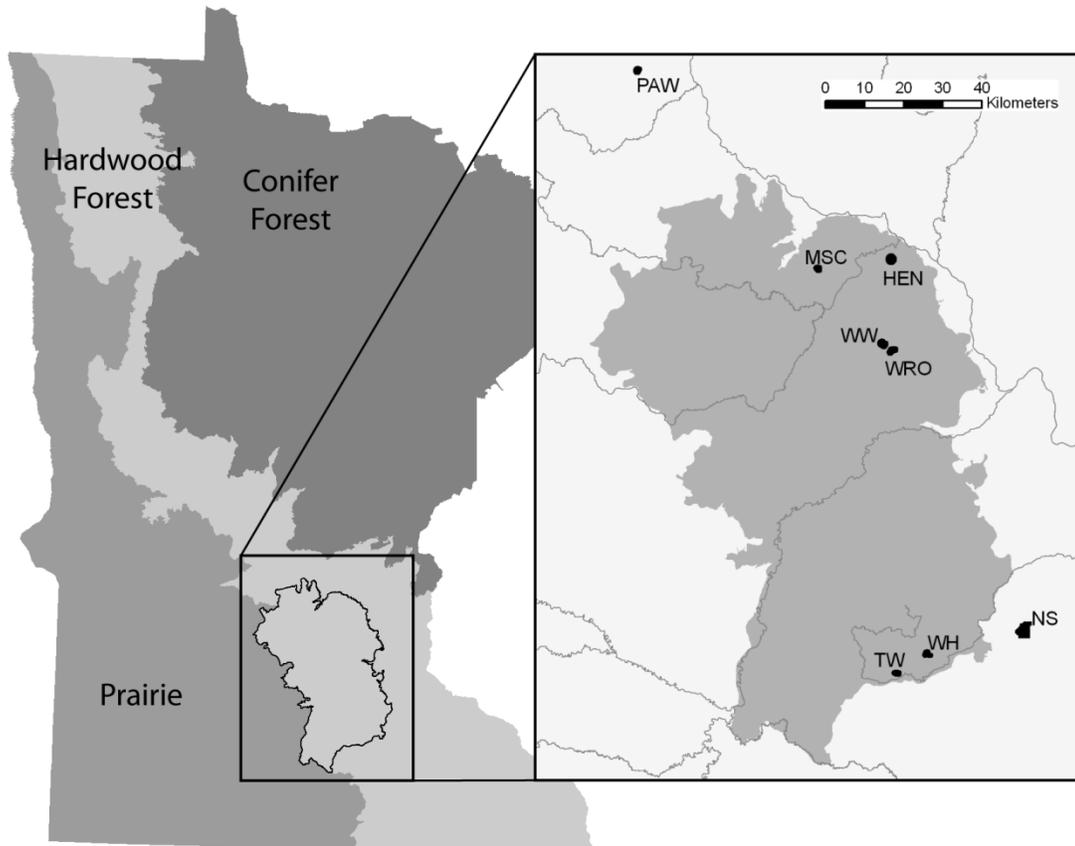


Figure 1

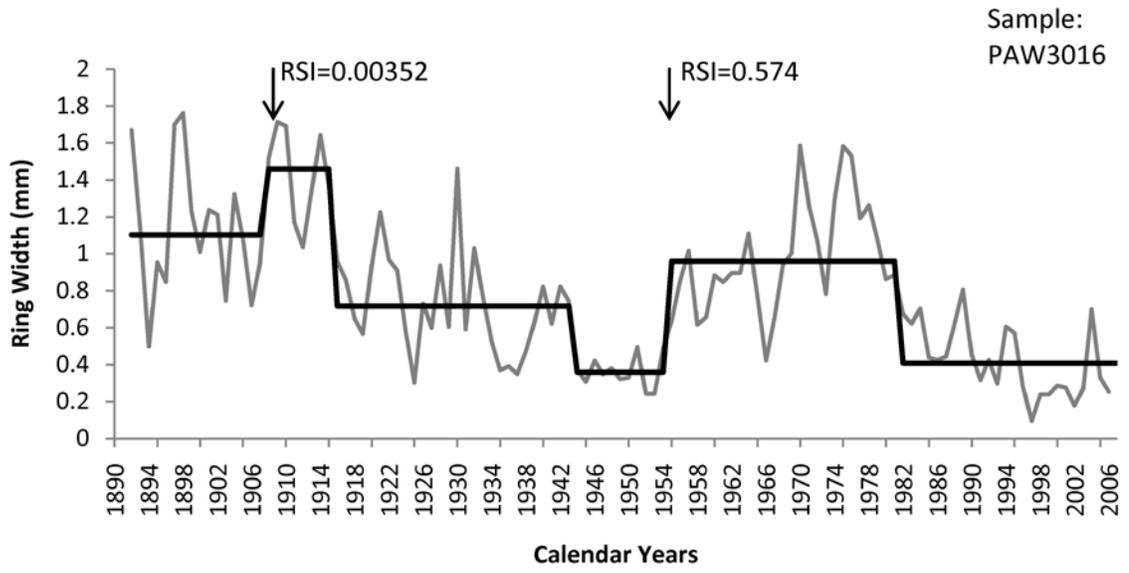


Figure 2

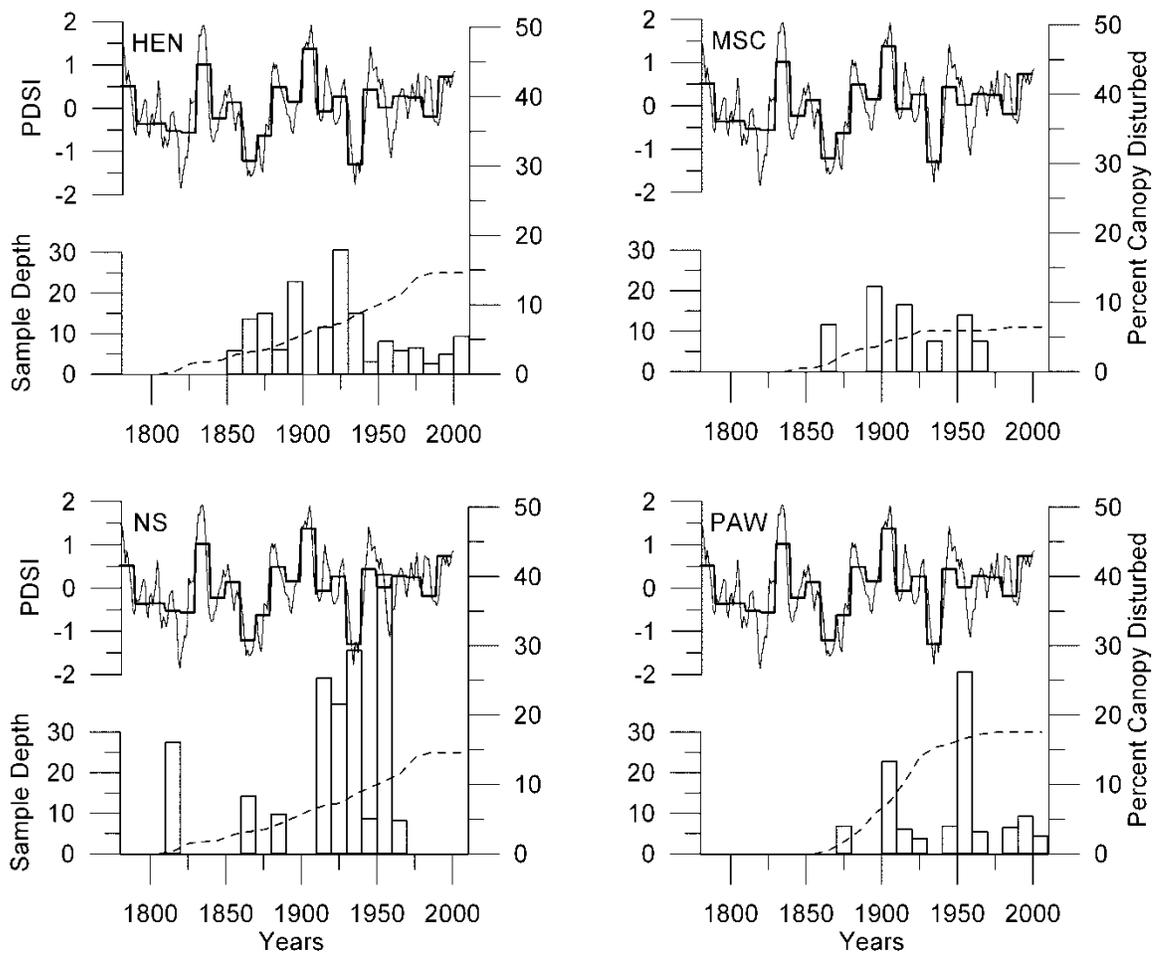


Figure 3

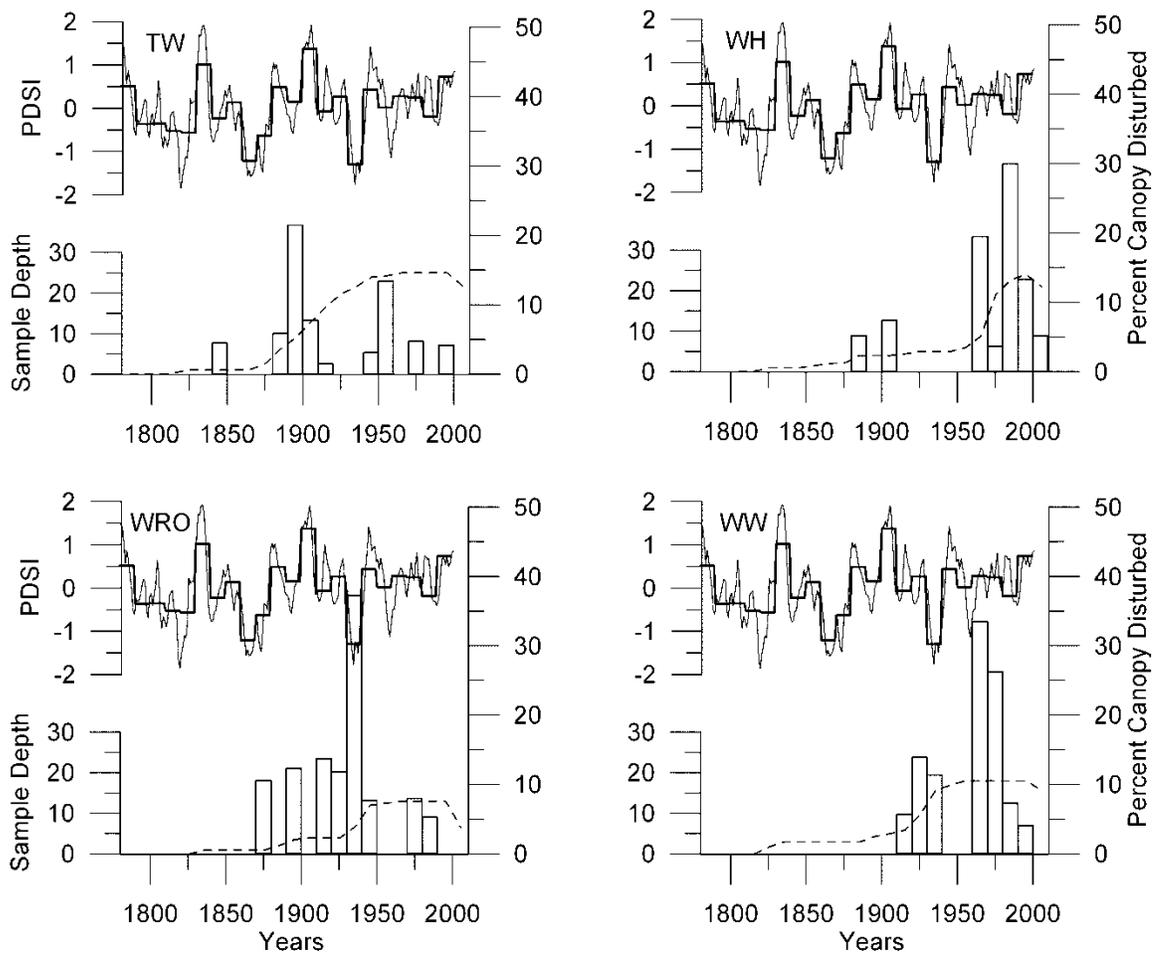


Figure 3 (cont.)

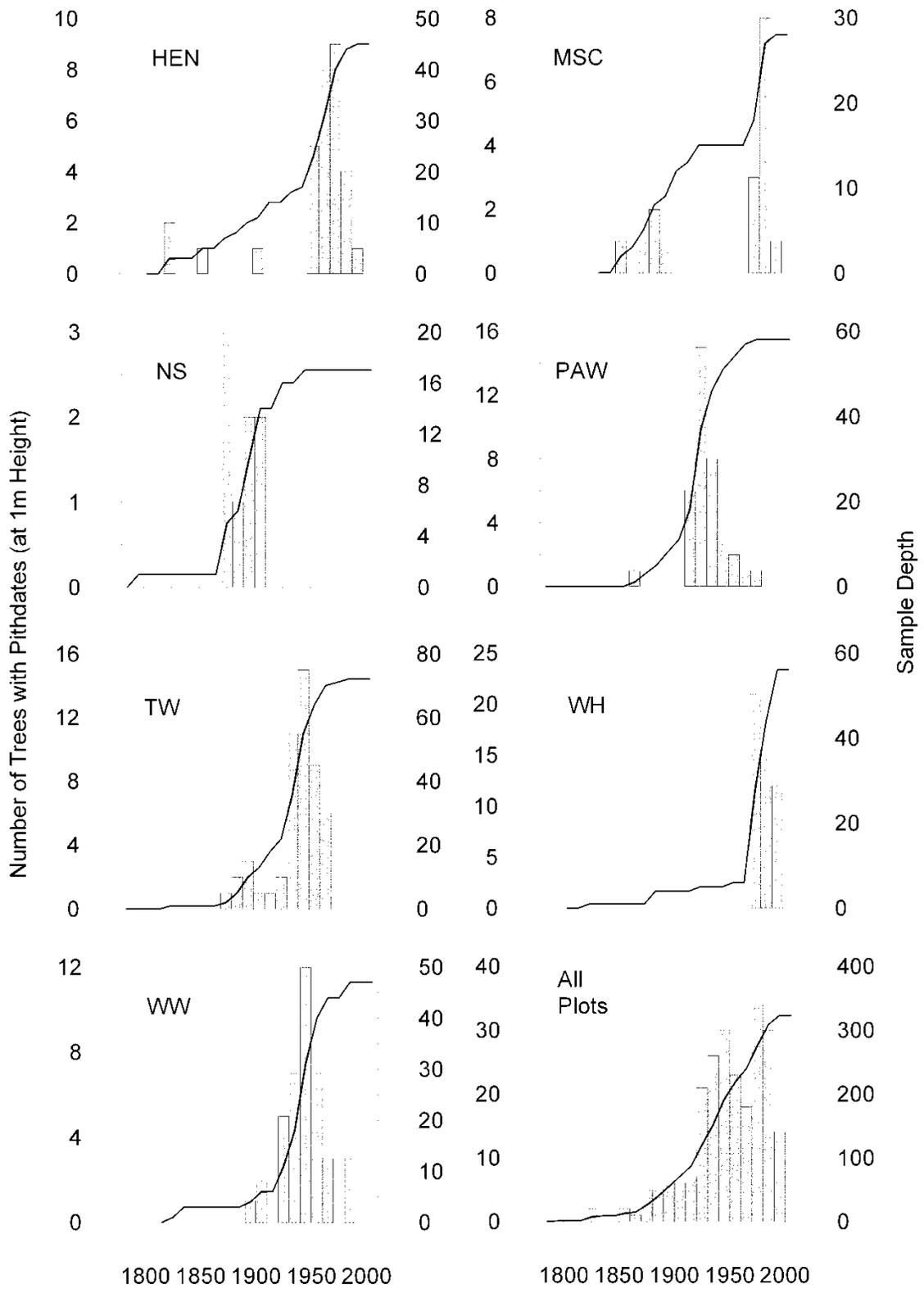


Figure 4

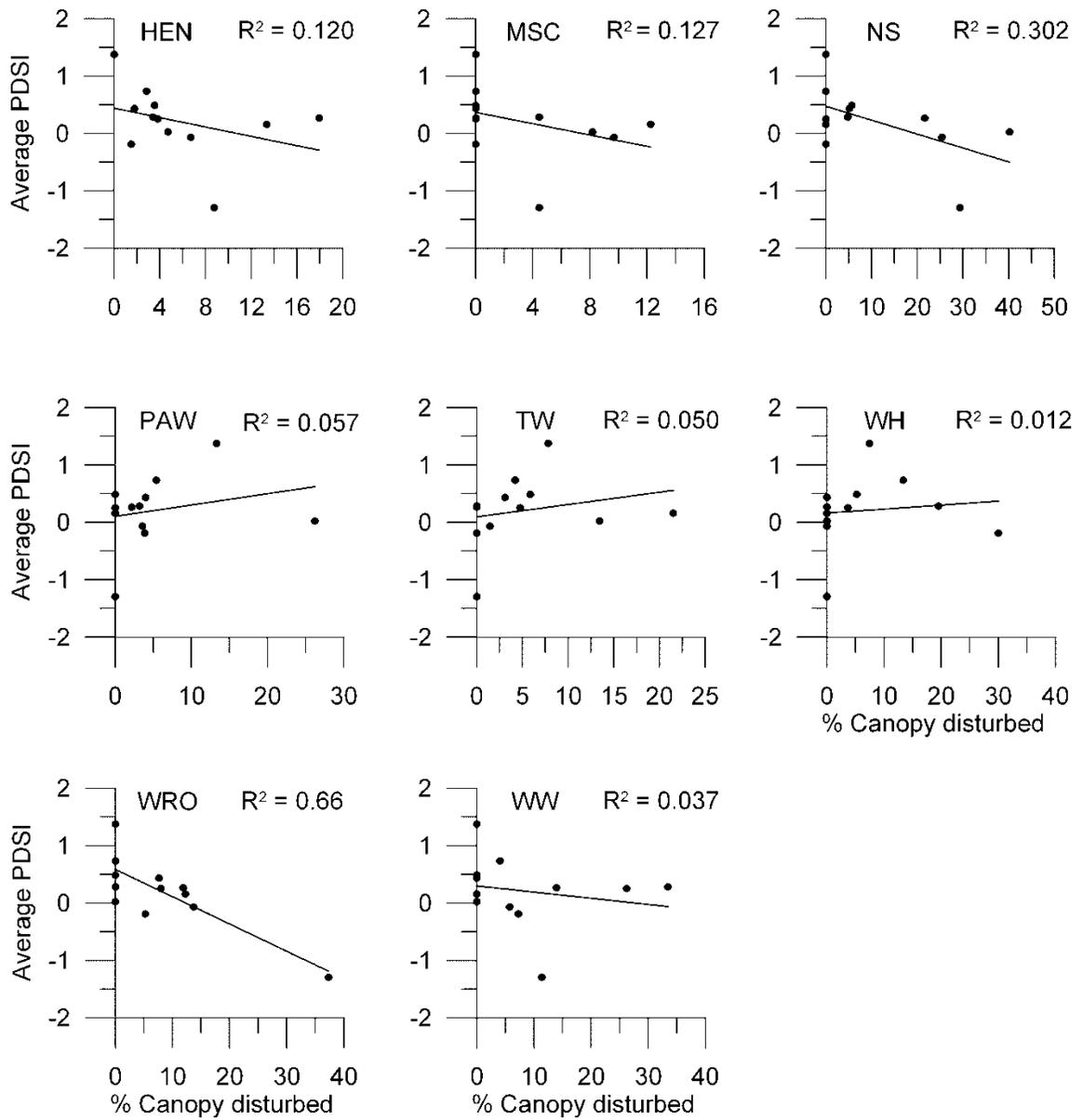


Figure 5

CHAPTER 6

Conclusion

With only a few old-growth forests remaining, people need to protect these from logging and urban sprawl among other things. Not only does old-growth forest provide habitat for unique flora and fauna (Jonsson 2000), the preservation of genetic variation is also very important (Frelich and Reich 2003). The more knowledge people have about the natural ecosystem the more they will protect the natural world. However, scientific knowledge is necessary before we can inform people what needs to be done. Little scientific information was available for our study sites before we set out to study each of the ecosystems for this dissertation.

From what we know about the ecology of white and red pine, fire must have played an important role in the Lost 40 and fire must have been an active disturbance agent in the past. White and red pine depend on fire to clear the understory and prepare the seedbed (Heinselman 1973). Because only few fire scars were present and hardly any white or red pine regenerated over the last 120 years we inferred that fire is not as frequent a disturbance-agent today as it was in the more distant past. The somewhat shade-intolerant white and red pine are not regenerating and shade-tolerant species such as maple and balsam fir are dominating the understory and (some of) the overstory. With some of the pines possibly reaching the end of their typical lifespan and no pine saplings in the understory, the future of white and red pine is contingent on an active management plan. However, with the changing climate and the climate space of the pines (i.e. the

climate in which pines thrive) potentially moving out of Minnesota, does pumping money into this project make sense? In addition, other factors like diseases, deer browsing, and competition will play an additional role to the potential shift in climate.

Even if it is decided that management makes sense, will it happen? Tourists have played a strong role when foresters implemented management strategies in other places (Orams 1995). Does the public desire a cut and burned Lost 40? The Lost 40 is a tourist attraction; the white and red pine an icon of the Northwoods. If with thinning and fire a major disturbance is recreated in this remnant stand, will the public want to see that happen? The forest will look desolate after the disturbance.

Changing environmental conditions, especially at ecotones or range limits, will have dramatic effects on species/individuals living in a given area (Allen and Breshears 1998). In chapter 3, we studied the spruce budworm at its range limits. The long-term implications for the survival of the spruce budworm at Itasca State Park are unknown. Warmer temperatures might support more insects in the short term. However, balsam fir and spruce also have their climate space shifting north (Iverson et al. 1999).

Spruce budworm rejuvenates the fir-spruce forest by killing the “old” trees (in Itasca the firs are about 60 years old when they die or get killed) but not the understory trees. The killing of the overstory trees frees nutrients and sunlight for the understory and the advanced regeneration can grow rapidly. However, if the climate space is shifting, the trees will become more and more stressed. If understory trees do not grow as well anymore and spruce budworm is killing the overstory trees, that might result in faster loss of the fir-spruce forest in Itasca State Park and northern Minnesota in general.

In the Big Woods, localized, frequent disturbances might be the major perturbation of the few remnant forests that are left after the logging era and clearing of the area for agriculture and urban sprawl. In the last 120 years, no major disturbances (> 60 percentage of canopy removed) occurred in the plots studied in the Big Woods. Even though within those 120 years of human presence, I believe that the lack of major disturbances is not an artifact of humans being there. Humans cannot protect the forest from wind disturbances or drought conditions. Also, the fact that no major canopy disturbance occurred in those stands means that people did not create a major disturbance.

Moderate disturbances of 30-40 percent canopy removal perturbed some of the plots in a few decades. However, no single decade had disturbance at all the plots, which points to the fact that no major, widespread disturbance perturbed the forests in my sites. The average percent of canopy disturbed in the Big Woods compares to this measure in other old-growth forests. However, a drought-disturbance relationship as found by Parshall (1995) or a drought-establishment relationship as found by Shuman et al. (forthcoming) was not consistently found in our data set. Parshall (1995) noted that trees are susceptible to disturbances only when site characteristics, age and size structure, and structural characteristics between species are favorable to disturbance. We found in three plots the decadal (averaged) PDSI significantly related to the decadal canopy-disturbance history. More of these forests were disturbed during drought conditions (or drought might have caused the disturbance). In the other five plots, no such relationship was found, which means that more disturbances happened during climatic conditions other than drought.

Disturbances are a vital part of most ecosystems (Pickett and White 1985). Without disturbances, we would not have the ecosystems we currently see and wish to preserve. It is important to know the history of canopy-disturbances in a forest before starting to manage it. Methods to reconstruct the canopy-disturbance history are abundant, but not every method is appropriate for every forest type. Rigorous statistical analysis was necessary to test each method before suggesting the sequential t-test (regime shift) method. The suggested method could now be used in other studies in this particular forest type without additional statistical analysis to test its applicability. A method that represents the canopy-disturbance history correctly is important, because without a correct disturbance history, managing ecosystems for biodiversity will be difficult.

In this dissertation, I studied three different old-growth forests in Minnesota. I made contributions to reconstructing canopy disturbances using release and suppression periods in tree rings of forest types that previously had not been studied this way. While others (e.g. Frissel 1973, Heinselman 1973) have also studied the disturbance history in some of those ecosystems that I studied, they looked at fire scars to reconstruct the disturbance history. The information that I gathered could now be used to inform a management plan (as in the case of the Lost 40), to apply a possibly more precise method to reconstruct a canopy-disturbance history, and to inform the public (of, for example, old-growth remnants in their neighborhood).

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