Structure, development, and spatial patterns in *Pinus resinosa* forests of northern
Minnesota, U.S.A.

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Emily Jane Silver

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Anthony W. D'Amato
Shawn Fraver

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Abstract

The developmental dynamics and structure of old-growth forests often serve as important baselines for forest management. Nonetheless, long-term information on natural patterns of development and mortality is rare for many commercially and ecologically important forest types. This study uses a long-term dataset from a large (2 hectare), stem-mapped plot within an old-growth *Pinus resinosa* (red pine) forest in Itasca State Park to quantify patterns of forest structural development and mortality events over an 87-year period. These patterns were compared with those found in other old-growth red pine -dominated forests in northern Minnesota, as well as with unmanaged second-growth and extended rotation red pine forests to quantify the range of variation in structural conditions and to evaluate the effectiveness of extended rotation forestry at promoting the development of late-successional structural conditions.

Old-growth forests were more structurally complex than unmanaged second-growth and extended rotation red pine systems, due in large part to the significantly higher volumes of coarse woody debris, higher snag densities, and spatially random patterns of mortality found in old growth. Nonetheless, extended rotation thinning treatments, by accelerating advancement to larger tree diameter classes, generated diameter distributions closely approximating those found in old growth. These results suggest that extended rotation treatments may accelerate the development of old-growth structural characteristics, provided that random patterns of mortality are emulated and coarse woody debris and snags are deliberately retained and created on site. These and other developmental characteristics of old-growth systems can inform red pine

management when management objectives include the restoration of late-successional

forest conditions.

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Chapter One: Introduction

This thesis examines natural mortality – including rates, agents, and spatial patterning – of red pine (*Pinus resinosa*) stands in northern Minnesota (Chapter 2), as well as the development and structure of old-growth, extended rotation, and unmanaged second-growth stands of this same forest type (Chapter 3). The thesis relies heavily on a long-term, repeatedly-measured study plot (the Allison plot, after John H. Allison, University of Minnesota, who established the plot in 1923) in an old-growth red pine stand in Itasca State Park, Minnesota. A further aim of this work was to evaluate the efficacy of extended rotation management at restoring old-growth structural characteristics in managed red pine forests. To accomplish this aim, four studies were utilized: two long-term examinations of red pine stand development, a broad sampling of old-growth red pine forests in northern Minnesota, and a long-term red pine chronosequence study. Using this unique combination of datasets, we were able to quantify multiple aspects of stand structural development including horizontal spatial patterning of mortality, tree size distributions, and coarse woody debris attributes.

Old-growth forests are widely recognized as invaluable resources for guiding the development of forest conservation and management strategies (Foster et al. 1996), but they are relatively rare in the Great Lakes region. Red pine has an extensive natural range in north-central and northeastern North America and is an important tree species occupying a large proportion of both natural areas (e.g., Day and Carter 1990) and managed forests. Red pine is typically managed with even-aged silvicultural methods such as clearcutting followed by planting (Johnson 1995). In contrast, the age structures of old-growth red pine range from single to multi-cohort (Fraver and Palik 2012), and

tree spatial distributions are rather complex, reflecting long-term mortality processes (Aakala et al. 2012). Further, old-growth red pine remnants currently occupy a small fraction of the area estimated at the time of European settlement due in large part to past land use, including logging and associated fires at the turn of the 20th century (Frelich 1995, Schulte et al. 2007). Due to the scarcity of old-growth red pine, it is increasingly important to use the remaining remnants as benchmarks for structural characteristics and natural processes in managed systems.

One method to offset the reduction in old-growth red pine is to restore structural attributes in currently managed forests with the goal of maintaining biodiversity, creating habitat, and providing other ecosystem services. Extended rotation forestry (ERF) has been suggested as one option to manage forests for late-successional structural characteristics. However, little is currently known about the efficacy of this management approach. As of this writing, the state Department of Natural Resources (DNR) is reviewing and revising their policy on extended rotation forestry. Given this scrutiny, evaluating the efficacy of ERF for restoring old-growth structure is timely and critical. Comparing the structure and development of old-growth and extended rotation red pine stands can help achieve this objective and inform future red pine management when restoration of old-growth characteristics is a goal.

The second chapter of this thesis examines long-term spatial patterns of mortality, one important aspect of structural development, in one old-growth red pine stand, namely the Allison plot. Mortality agents, rates, the initial spatial distribution of live trees, the final spatial distribution of dead trees, and the pattern of mortality events were examined. Results indicated that mortality rates were consistent with other studies of shade-

intolerant conifers, with the exception of high rates for jack pine (*Pinus banksiana*), which experienced complete mortality during the 87-year study period of the Allison plot (1923-2010). Mortality events were random during the study period, but the current distribution of dead trees showed small-scale clustering, emphasizing the importance in measuring mortality events separately from the current pattern of dead trees. Mortality agents include windthrow, the root-rot fungus *Armillaria ostoyae*, and insect damage.

The third chapter of this thesis compares stand development of old-growth and extended rotation stands as well as current stand structure of old-growth, extended rotation, and unmanaged second-growth forests. Results indicated that old-growth forests were more structurally complex than extended rotation, and unmanaged second-growth forest, due in large part to the significantly higher volumes of coarse woody debris and higher snag densities. Nonetheless, extended rotation thinning treatments, by accelerating advancement to larger tree diameter classes, generated diameter distributions closely approximating those found in old-growth red pine stands.

The fourth and final chapter of this thesis offers conclusions based on the synthesis of results presented in chapters two and three, with more emphasis on chapter three. Management recommendations are presented based on findings that old-growth stands have spatially random mortality, and are generally more structurally complex then their unmanaged second growth and extended rotation counterparts. Additionally, this chapter presents the future of the long-term studies presented in this thesis and makes recommendations for future research efforts to perpetuate the long-term monitoring plots established in these red pine forests.

Chapter Two: The spatial pattern of mortality in an old-growth *Pinus resinosa* - dominated forest in northern Minnesota, U.S.A.

1. Introduction

Tree mortality is a fundamental process in forest development, effecting changes in resource availability, tree regeneration, stand structure, and stand-level productivity. Tree mortality shifts nutrients into deadwood pools, releases light to understory species through the formation of canopy gaps, and by adding down woody debris, changes local geomorphic processes (Franklin et al. 1987). Mortality can occur as a widespread disturbance, replacing entire forest stands, or more locally, forming large or small canopy gaps. Natural mortality rates and processes provide a benchmark against which current forest conditions can be compared (D'Amato et al. 2008). Establishing these natural benchmarks is becoming increasingly important given the projected increases in mortality rates for forest ecosystems due to global change (van Mantgem 2009, Allen et al. 2010); in fact, tree mortality may be increasing worldwide, from Canada's boreal forest (Peng et al. 2011, Michaelian et al. 2011) to southern Europe (Carnicer et al. 2011) and the tropics (Lewis et al. 2009).

In the absence of stand-replacing disturbance, individual tree mortality occurs episodically, due to various disturbance agents. This temporal variability is evident in low-level background mortality (Franklin et al. 1987, Aakala et al. 2007), as well as in virtually all disturbances that cause partial stand mortality, such as tree-fall gaps (Runkle 1982, Baker et al. 2005), moderate-severity windstorms (Frelich and Lorimer 1991, D'Amato and Orwig 2008, Fraver et al. 2009), mixed severity fires (Niklasson and Granström 2000), insect outbreaks (Swetnam & Lynch 1993), and root rots (Worrall et al.

2005). Non-constant disturbance and mortality can at times be attributable to the interaction of several mortality agents. For example, root rot can weaken structural integrity, making trees prone to fall (McLaughlin et al. 2011), and wood-decay fungi in general exacerbate damage from windstorms in otherwise healthy stands (Hubert 1918, Edman et al. 2007), causing temporal fluctuations in mortality. Worrall et al. (2005) found that spruce beetle outbreaks make trees more susceptible to root rot fungi and windthrow, thus perpetuating episodic disturbance regimes. In these situations, mortality rates and trends are best determined from long-term studies, which provide the temporal extent necessary to properly characterize these non-stationary aspects of tree mortality and forest disturbance (Ryan et al. 1997).

In addition to temporal variability, tree mortality may exhibit strong spatial variability. In general, tree spatial information improves mortality predictions (Das et al. 2008), can guide restoration or management goals based on late-successional forests (Larson and Churchill 2012), provides inferences about past disturbance agents (Worrall et al. 2005, Fraver and Palik 2012), and can illuminate community-level responses to changes in composition and climate (Pacala and Deutschmann 1995). Despite its importance in structuring forest communities, spatial patterning of mortality is rarely studied in natural-origin, late-successional forests (but see Acker et al. 1996, Boyden et al. 2005, Svoboda et al. 2010, Das et al. 2011, Aakala et al. 2012). These studies are rare in part because the repeatedly-sampled, stem-mapped plots ideal for addressing this issue are uncommon in these natural forest systems. Those studies that have examined spatial patterns of mortality in natural forest systems have rarely exceeded 30 years (e.g., Das et al. 2011; Boyden et al. 2005), hampering our ability to predict long-term spatial dynamics

within forest systems. In the absence of such long-term studies, analyses of mortality

patterns are typically limited to comparisons of current live *vs*. dead trees distributions,

which can lead to erroneous conclusions (Goreaud and Pelissier 2003).

A recently revived, long-term study, including mapped locations of all trees,

allows us to overcome some of the limitations enumerated above, thereby permitting

detailed analyses of tree mortality rates, and spatial patterns. The study, the longest for

natural origin red pine (*Pinus resinosa*) to our knowledge, was established in 1923 and

includes seven re-inventories through 1963. It consists of a two-ha plot with 1129 trees

(originally) individually tagged, mapped, and measured. At the time of plot

establishment, the forest stand was dominated by *Pinus resinosa* and *Pinus banksiana,*

having regenerated following fire 120 years previous (1803). The stand was never

harvested, which allows us to rule out direct human influence, thereby focusing on

natural mortality processes inherent to late-successional *Pinus resinosa* forests. *Pinus

resinosa* has an extensive natural range in north-central and northeastern North America.

In the northern Great Lakes region, it is an important tree species occupying a large

hectarage of natural areas (e.g., Day and Carter 1990) and managed forests, in which it is

typically grown in plantations (Johnson 1995). Despite its extensive range and

commercial importance, much remains unknown regarding natural dynamics, including

patterns of mortality. Our specific objectives were to (1) determine long-term mortality

rates for natural *Pinus resinosa* systems; (2) quantify spatial patterning of individual tree

mortality events; and (3) assess the relative importance of mortality agents potentially

affecting this system based on the spatial patterns found under Objective 2. This study of

natural tree mortality, including spatial patterning, sheds much light on the ecology and

natural history of this forest type, and provides reference conditions on the historic range of variability in mortality patterns to aid conservation and management efforts related to restoration of old-growth structural conditions (Larson and Churchill 2012).

2. **Methods**

2.1 Study area

The study site is located in a natural (i.e., unharvested), 207-year-old, fire-origin, *Pinus resinosa* stand within the Scientific Wilderness and Natural Area of Itasca State Park, Minnesota, USA (47°13' N, 95°14' W). Stand age was determined by dendrochronological analyses, with tree age estimates refined following methods outlined in Fraver et al. (2011), and corroborated by a documented 1803 fire in Itasca State Park (Frissell 1973). Mean site elevation is ca. 462 meters a.s.l., with undulating slopes of five to ten percent. Soils are well-drained sandy loams and loamy sands derived from glacial outwash. Average annual temperatures range from - 20°C (January) to 25.4°C (July), and average annual precipitation is 653 mm (Minnesota Climatology Working Group 2012). A series of prescribed surface fires were applied in 1998, 2000, and 2003 (pers. comm. Rebecca Marty); however, there was no mortality to the mature pines under study. The stand is currently dominated by *Pinus resinosa* with a lesser component of *Pinus strobus* and *Picea glauca*. Historically, the early-successional *Pinus banksiana* comprised a significant component of the stand, but was no longer present by the time of our 2010 sampling (below). Historic logging activities are well documented for the park, but no history of logging is recorded for this particular stand (Aaseng 1976), although we noted 23 cut trees in scattered locations, but the reason for the cutting is not known.

2.2 Long-term permanent plot sampling

The research plot on which this study is based was established in 1923 by John H. Allison (University of Minnesota) to characterize tree growth and productivity. The plot was laid out such that the southeast corner coincided with a Public Land Survey section corner, and it extended five chains (chain = 66 ft, 20.1 m) to the west and ten chains to the north, that is, roughly 100 m × 200 m. At establishment, all trees (N = 1129) were tagged, and both diameter at breast height (DBH) and height (subset of trees) were measured. The plot was re-inventoried in 1928, 1933, 1938, 1943, 1948, 1952, 1957, and 1963, recording DBH and noting status as "dying" or "dead," in which case DBH was no longer recorded. In 1948, 1952 and 1963, tree locations were approximated on a map within one-chain grid cells (ca. 20 × 20 m, Fig. 1).
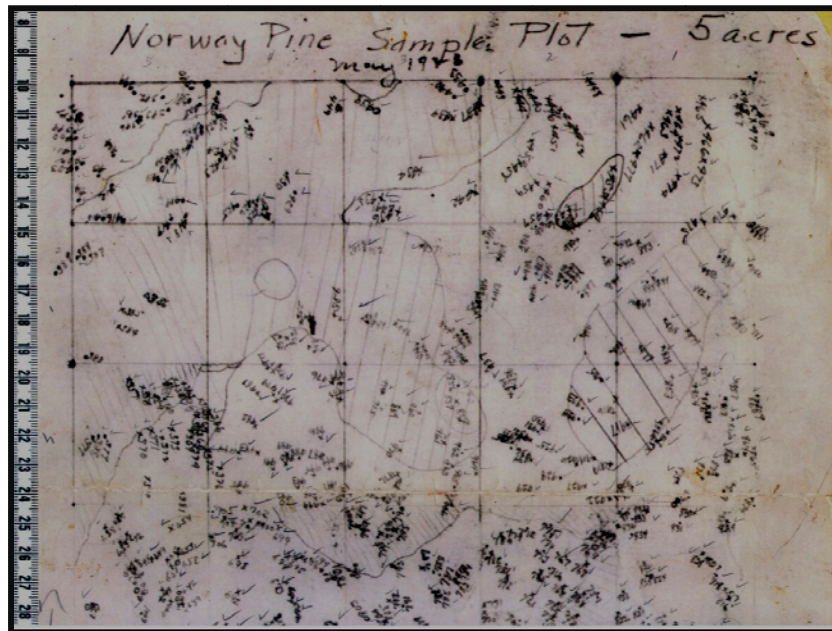
Figure 1. Portion of 1948 hand-drawn plot map showing the location of all trees, as well as minor variations in site conditions.

2.3 Field and laboratory methods

We re-inventoried the plot in 2010, recording DBH and live-vs.-dead status of each tree. During this inventory, we realized that the hand-drawn tree locations from early maps were too imprecise for spatial pattern analyses. We thus re-mapped locations of all living and dead trees. For this purpose, the plot was divided into 20 10 × 100 m transects, and X and Y coordinates were recorded (nearest decimeter), using tapes and electronic measuring devices, within each transect. Most trees still had tags, presumably from intermediate inventories. Tags on fallen trees, many in advanced stages of decay, were located by means of a metal detector, and the former rooted center of each was mapped. Nevertheless, using these methods we were unable to locate and map 32% of the initial trees recorded in 1923, owing to their death and advanced decay. Locations of these trees were taken from the digitized 1952 map, after adjusting for known uncertainty derived from trees that were located (see below). Fall direction and decay class were recorded for trees that had clearly been windthrown.

In an effort to better characterize past mortality agents, we searched historical records and published literature for mention of local windstorms, fire, insect outbreaks, or root rot problems. To investigate the role of wind as a mortality agent, we evaluated windthrow directionality using Rayleigh's test for circular uniformity (Rayleigh 1919). We also collected fungal samples (mycelial fans or fruiting bodies) from six trees with declining vigor apparently from *Armillaria* root rot. Such trees are common within the plot, and considerable mortality presumably from this same agent is visible in locations throughout the larger stand. In the laboratory, samples were isolated first on a selective media for Basidiomycetes (Harrington et al. 1992) and then grown on 1.5% malt extract

agar once a pure isolate was obtained. Representative isolates were identified by DNA

sequencing based on the internal transcribed spacer region of rDNA using previously

described methods (Arenz et al. 2011). Following extraction, a portion of the internal

transcribed spacer region (ITS) of rDNA using *Armillaria*-specific primers AR1 and AR2

was amplified using nested polymerase chain reaction (PCR) (Lochman et al. 2004).

Verification of PCR products and sequencing procedures followed those by Arenz and

Blanchette (2009). Consensus sequences were assembled using ChromasPro software

(Technelysium Ltd., Helensvale, Australia) and were compared to GenBank sequences

using BLAST (Altschul et al. 1990) to determine the best match.

2.4 Data analysis

2.4.1 Mortality rates

Mortality rates were calculated for all species, as well as *Pinus resinosa*

separately, for each sampling interval. We used the equation

[1] $1- [1-(M_1/N_0)]^{1/t}$

where N_0 is the total number of live stems in the previous sampling, M_1 is the total

number of live stems that died during the sampling period, and t is the time between

sampling periods (Sheil & May 1996). Rates were also calculated by diameter class,

using the diameter classes for each individual sampling period, and calculating a final

average over the entire 87-year study period (1923-2010).

2.4.2 Spatial pattern analyses

For 32 % of the initial trees recorded in 1923 where we could not map locations in 2010 (see above), we relied on adjusted locations mapped in 1952. These adjustments were based on discrepancies between mapped (1952) and known tree locations (2010), which showed a bias that increased slightly from south to north within the plot. To account for this non-stationary bias, we made adjustments separately for each 20×20 m grid cell. Adjustments (i.e., shifted coordinates) were based on probability distributions of discrepancies unique to each cell. The 'sn' package in R (Azzalini 2011) was then used to simulate shifted locations for each tree without a 2010 location, based on this distribution of mapping discrepancies.

The resulting coordinates of all living and dead pines allowed for detailed spatial analyses. Currently, the most common global approach to ecological spatial pattern analysis is Ripley's *K* and associated transformations (Ripley 1976, Diggle 2003). However, because the method is based on the cumulative sum of points within ever-increasing radii, it may not accurately detect the distance at which deviations from spatial randomness occur (Perry et al. 2006). A newer method, the pair correlation function (PCF), also known as g (r), is a first-order derivative of the K-function (approximated by a spline function) that overcomes this cumulative distance limitation by measuring the rate of change in the K-function, resulting in a refined assessment of the spatial scale at which patterns occur (Stoyan and Stoyan 1994, Baddeley et al. 2000, Wiegand and Moloney 2004). We analyzed the spatial patterns of mortality using the PCF, which captures the "average pattern" across a given study area (Getis and Franklin 1987, Cressie 1993, Diggle 2003, Fortin and Dale 2005). Our null hypothesis for all spatial

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analyses is complete spatial randomness (CSR) based on the Poisson distribution (Goreaud & Pelissier 2003, Perry et al. 2006). All analyses include isotropic edge corrections (Ripley 1977).

We calculated the PCF statistic for each of four spatial point patterns at 1-m distance classes: 1) univariate pattern of live pines in 1923 (g_{1923}); 2) univariate pattern of dead pines in 2010 (g_{2010}); 3) bivariate pattern of mortality ($g_{1963} - g_{1923}$), 1923-1963; 4) bivariate pattern of mortality ($g_{2010} - g_{1964}$), 1964-2010. For a completely random univariate (Poisson) process, the PCF is equal to one. PCF values greater than one indicate that inter-point differences within radius r are relatively more frequent than would be expected for a random process, thereby suggesting a clustered pattern. PCF values less than one indicate that inter-point differences are more dispersed than would be expected for a random process, thereby suggesting a uniform pattern (Stoyan and Penttinen 2000). Under randomly occurring mortality, the bivariate pattern ($g_{current}$ - $g_{initial}$) is equal to zero. Positive deviations from zero ($g_{initial} > g_{current}$) would indicate more tree mortality events than would occur if mortality were random, suggesting a clustered pattern, whereas negative deviations ($g_{initial} < g_{current}$) would indicate fewer tree mortality events than would be expected if mortality had occurred randomly, suggesting a uniform pattern. The two selected time periods split the complete sampling period roughly in half and were chosen because the number of tree deaths using shorter time periods was too low for robust statistical tests. Similarly, *Pinus banksiana* could not be isolated because of small sample size in the later period.

Finally, the bivariate PCFs (patterns 3 and 4 above) were used to test the null hypotheses of spatially random mortality events using the random-labeling approach

(Diggle 2003, Goreaud and Pelissier 2003), which assesses differences in the initial (live and dead trees) and current (live trees) distributions. Dead trees were randomly assigned locations in the initial distribution, and PCF simulations were used to test if the observed pattern matched those resulting from random assignments. As a consequence, the spatial pattern of mortality events is appropriately constrained by the fixed, initial pattern of all trees. For all analyses we removed in-growth species (non-pines established after the initial pine cohort; the stand had no pine regeneration) from analysis to avoid confounding pine mortality patterns (Aakala et al. 2012). 999 global Monte Carlo simulation envelopes were calculated for all patterns to test for deviations from our null hypothesis using a 95% confidence level. These tests were conducted using all pine species – red, white (*Pinus strobus*), and jack pine- present in the initial inventory. To further explore species influence in spatial patterning, *Pinus resinosa* (being most abundant) was analyzed separately for each of the above distributions, resulting in five additional analyses. Lastly, for each simulation the locations of trees not found in the 2010 inventory (32% of the total, above) were shifted randomly 1000 times within their probability density kernels to determine if the error associated with the uncertain locations would change the results and subsequent interpretation.

Spatial analyses were conducted with the spatstat package in R (Baddeley and Turner 2005, R Development Core Team 2012) using procedures described in Baddeley (2008). For graphing and interpretation, we present the PCF function beginning at four meters because the PCF yields infinitely high values for distance $r = 0$ (the function converges to the y-axis). That is, the critical values are computed as the difference between the highest values and the theoretical mean (1, given complete spatial

randomness), but they are computed over the entire range of r, resulting in arbitrarily high values at small distances. We have thus constrained the results to values at which the PCF function is most reliable.

3. Results

3.1 Mortality rates

During the 87-year sampling period (1923 to 2010), 490 (43%) of the originally mapped trees died. Average annual mortality for *Pinus resinosa* was 0.39% from 1923 to 2010, ranging from 0.03% to 0.93% depending on sampling interval. Average annual mortality for *Pinus banksiana* during this time was 6.1 %, ranging from 2.4% to 11.3%. *Pinus banksiana* had experienced complete mortality by 2010. Annual mortality rates for all species analyzed together was 2.91% ± 0.5 (mean ± SE), but ranged from 0 – 3.8% depending on the sampling interval and diameter class. Mortality rates generally decreased with increasing diameter (Figure 2). Despite persistent mortality, basal area increased (Table 1).

Table 1. Structural characteristics of the Allison Plot, a two hectare old-growth stand in Itasca State Park, dominated by *Pinus resinosa.* Sampling periods represent plot establishment (1923) and the most recent inventory (2010).

	Stand Age	
Structural Characteristic	120	207
Basal area (m^2/*hectare*)	30.4	38
Mean DBH (*cm*)	26	38.3
DBH range (*cm*)	8 – 61	10 – 64
Density (*stems/hectare*)	517	298
Composition (*% basal area*)	*Pinus resinosa:* 69	*Pinus resinosa:* 86
	Pinus banksiana: 23	*Pinus strobus:* 7.5
	Pinus strobus: 6.3	*Picea glauca:* 1.8
	Picea glauca: 1.4	*Betula papyrifera:* 1.4
	Unknown: 0.3	Other: 2.2
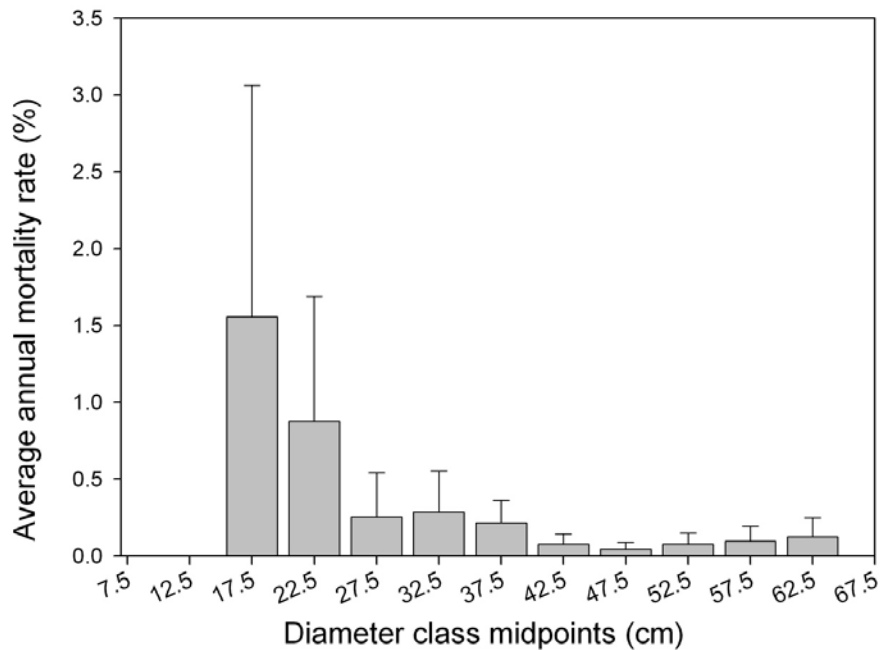
Figure 2. Average annual mortality rates for *Pinus resinosa* in the Allison Plot by diameter class. Rates were calculated using the diameters at the beginning of each sampling interval, then summarized into an annual rate for each size class. Rates represent the average over 87 year period.

3.2 Spatial patterns of mortality

Univariate spatial tests (all pine species pooled) did not significantly deviate from random, with the exception of the current pattern (stand age 207) of dead stems (Figures 3 and 4). This dead-stem pattern showed a tendency towards clustering at five to ten meters. When *Pinus resinosa* was analyzed separately, univariate tests revealed no significant deviation from random patterning for either the initial or the current dead-tree distributions. The bivariate tests indicate that the pattern of mortality events for the three pine species pooled and for *Pinus resinosa* separately was random during both portions of the sampling period (Figure 5).
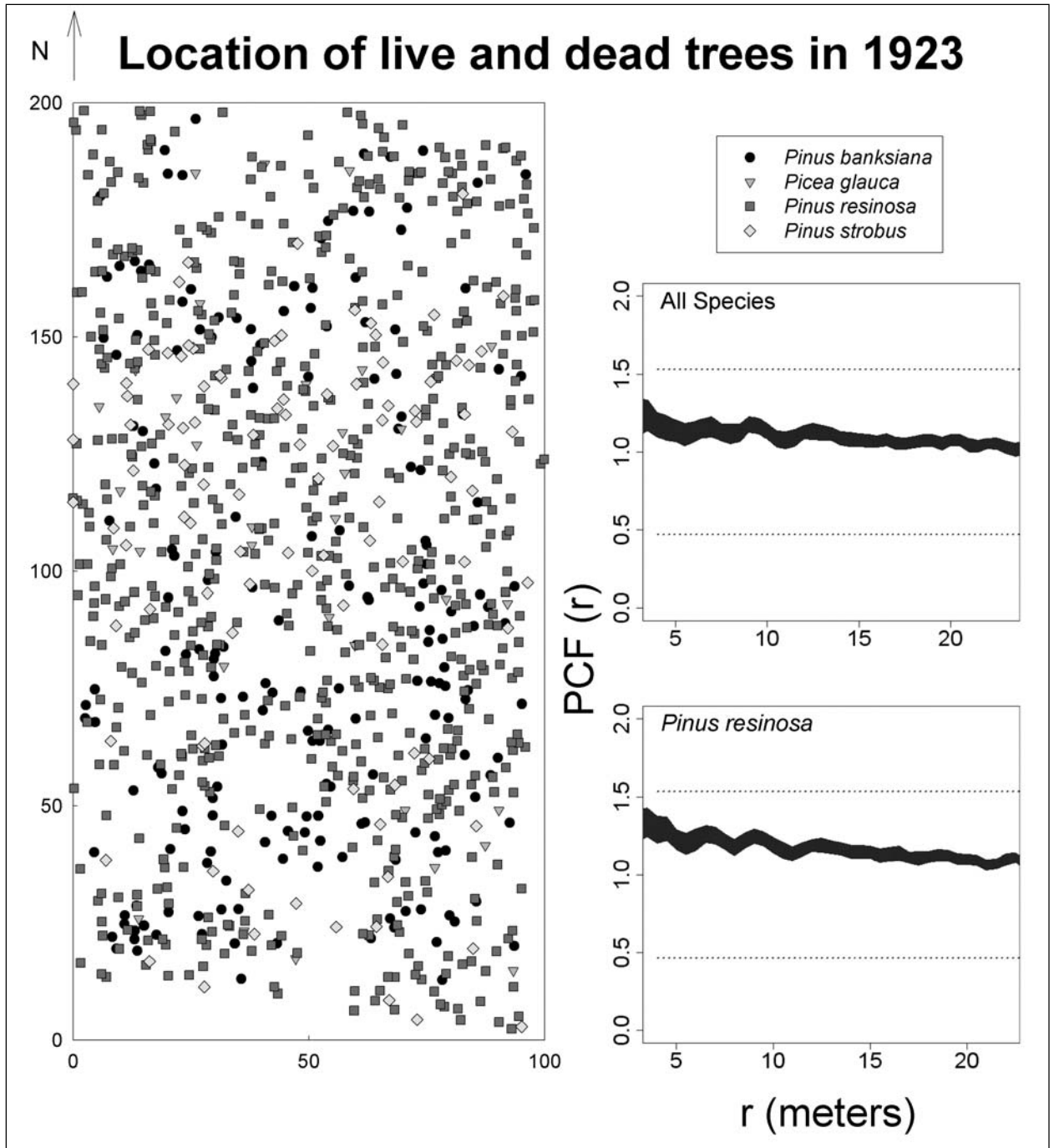
Figure 3. Initial univariate distribution: A stem map of the intial (Live + Dead) distribution by species and the PCF computed for the initial univariate pattern considering all species and *Pinus resinosa* only. No significant clustering or regularity was detected. The dark grey bands are the PCF, which equals 1 under complete spatial randomness. The dotted lines are the confidence intervals as generated from 999 Monte Carlo simulations.
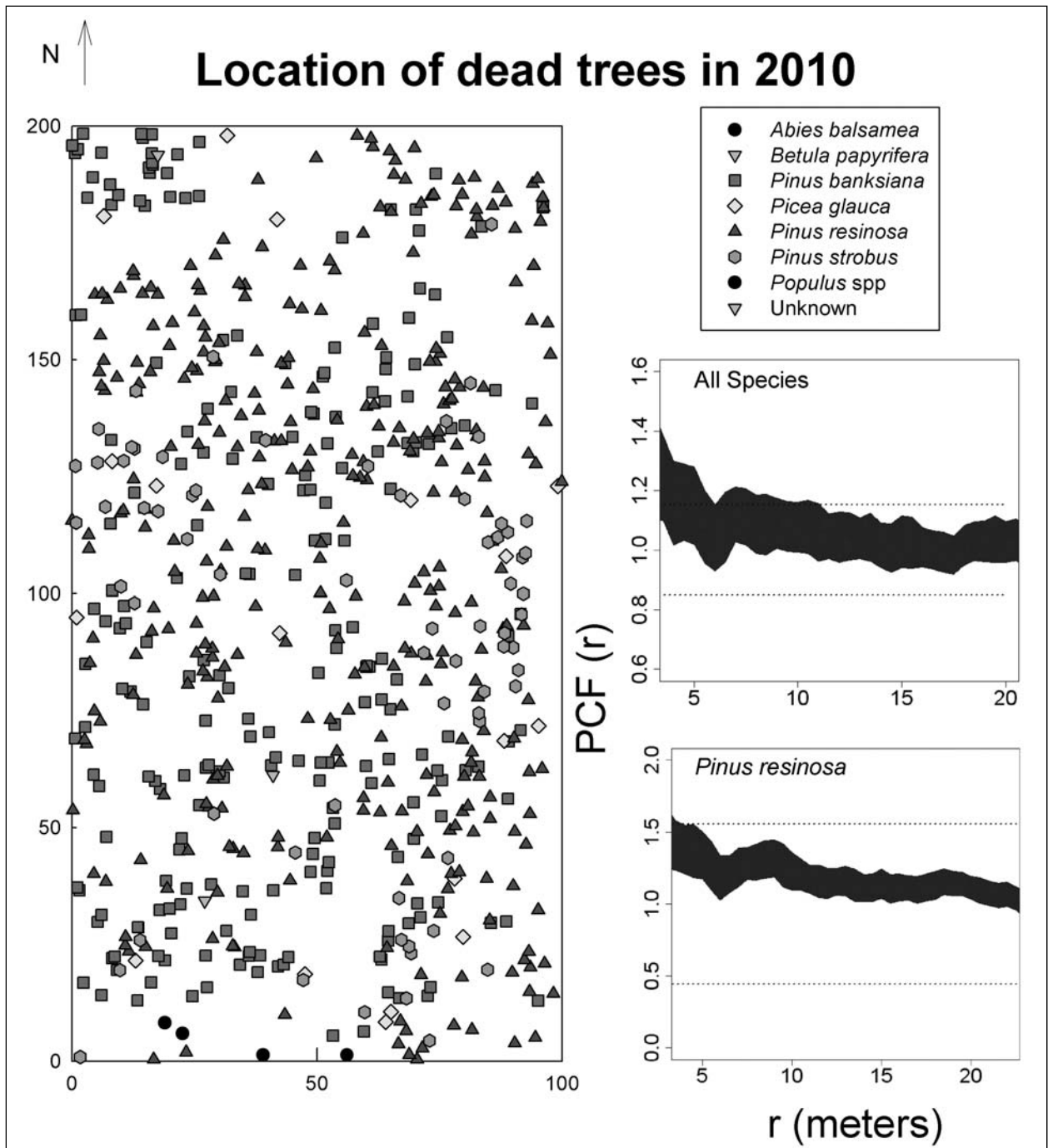
Figure 4. Univariate pattern of deadwood in 2010: A stem map by species and the PCF computed from 5-20 meters for all species and *Pinus resinosa* only. Significant clustering was detected at small spatial scales for all species. The dark grey bands are the PCF which equals 1 under complete spatial randomness. The dotted lines are the confidence interval generated from 999 Monte Carlo simulations.
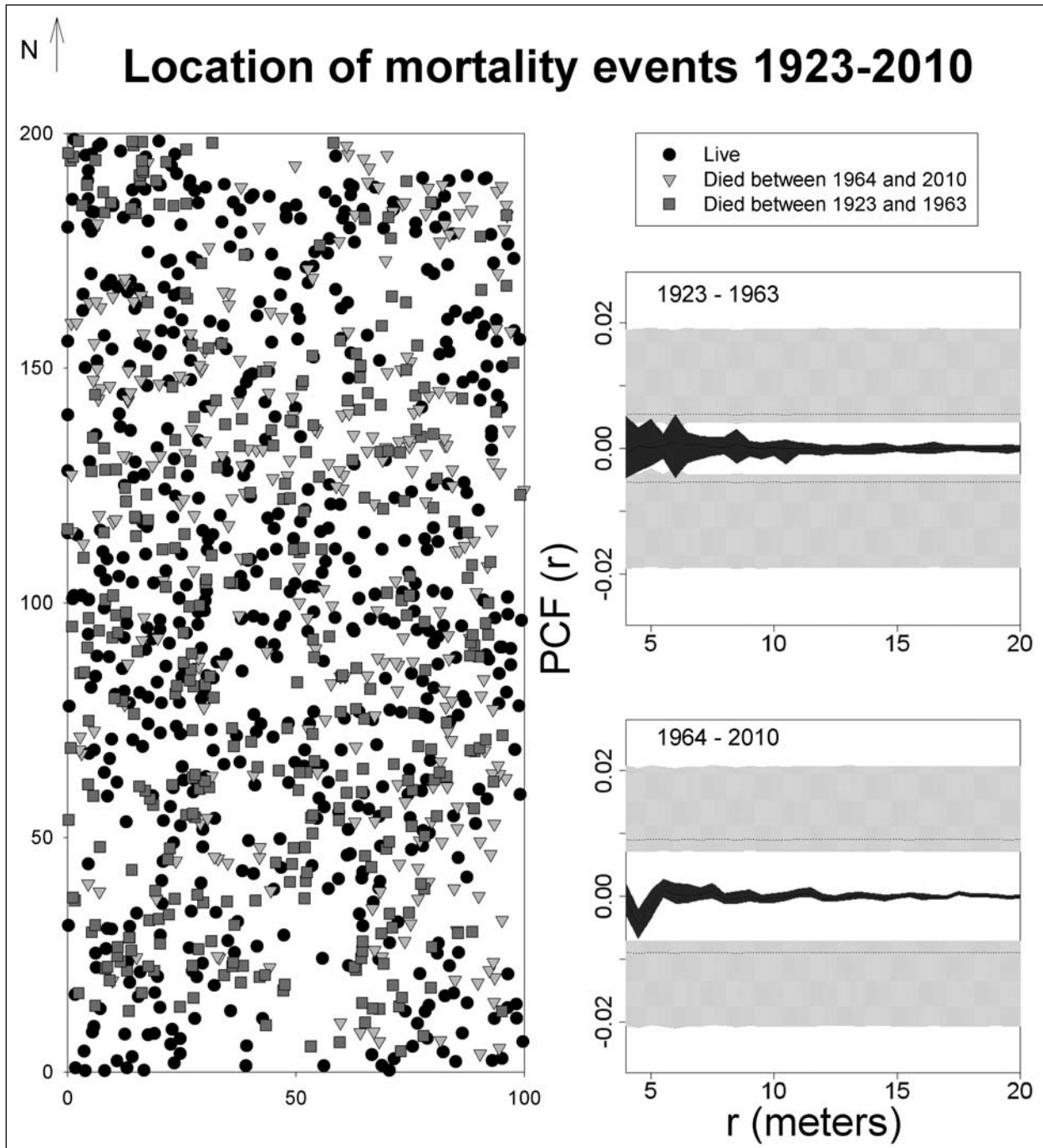
Figure 5. Spatial pattern of mortality: A stem map showing locations of trees dying in each analysis period, and the pattern of mortality events from 1923-2010 split into two halves, 1923-1963 and 1964-2010. No significant clustering or regularity was detected. The dark grey bands represent the PCF function for the mortality events which equals 0 under complete spatial randomness. The light grey bands represent the confidence bands generated from 999 Monte Carlo simulations.

3.3 Mortality agents

We identified several biotic and abiotic mortality agents on the plot. Cultures obtained from dying trees in the plot were used for DNA extraction and sequences showed a best BLAST match of 100% to *Armillaria ostoyae* when comparing the sequences to others in GenBank. Because all the isolates were identified as *Armillaria ostoyae*, one representative sequence was submitted to GenBank with the sequence number JX174637 for documenting the identity of the root rot fungus. *Armillaria ostoyae* was isolated from samples on six poor-vigor *Pinus resinosa*s, although many others were likely infected. Fallen stems with visible tip-up mounds (11% of the originally mapped trees) spanning a range of decay states had significant uniform fall directions, but with a very high standard deviation (mean azimuth 89.9°, Rayleigh's p-value 0.00, n = 127, circular SD = 78.2°), implicating westerly winds as the cause (see Figure A1 in Appendix A).

4. Discussion

Results from this long-term, stem-mapped study suggest that the spatial pattern of tree mortality was not driven solely by competitive processes or initial tree locations; processes that would have led to a more regular or more clustered pattern of trees. As such, the spatial pattern of mortality was more complex than we had expected and underscores the value of examining these patterns over the extended periods of community development as represented in this unique dataset. Importantly, the spatial pattern of mortality events (the arrangement of dead trees within the fixed initial population of live trees) differed from the current spatial pattern of dead trees. This

difference highlights the importance of analyzing the spatial pattern of mortality events in the context of the initial live-tree distribution, rather than simply analyzing the dead-tree distribution as a proxy for mortality patterns. The mortality agents responsible for this spatial pattern were difficult to assign; however, root-rot fungi, windthrow, and self-thinning likely played a significant role during different periods of stand development.

4.1 Mortality rates

Annual mortality rates differed depending on the sampling period analyzed. The average annual mortality rate of 0.39% for *Pinus resinosa* was similar to other studies of shade intolerant pines (Dobbertin et al. 2001, Powers et al. 2010). The average annual mortality rate of 2.91% for all species pooled was higher than the rate found in other studies of old-growth forests, but is reflective of the complete mortality of *Pinus banksiana* during the study period. Given the comparatively short duration of other studies in old-growth systems, mortality patterns related to successional dynamics, such as those observed with the early successional *Pinus banksiana*, are less likely to be captured. Mortality rates also differed among diameter classes. The rates seem to decrease with size class (Figure 2) rather than exhibiting the U-shaped mortality pattern observed by other studies (Lorimer et al. 2001, Fraver et al. 2008). The U-shaped pattern is often explained by smaller trees having higher mortality rate due to competitive exclusion or self-thinning, while the largest trees in the distribution (> 60cm) may have been more susceptible to wind disturbance because of canopy exposure (Goff and West 1975, Westphal et al. 2006, McLaughlin et al. 2011). However, the forest we examined was strongly even-aged relative to the uneven-aged, old-growth populations in which U-

shaped patterns have been documented. In this even-aged system, self-thinning processes may have played a greater role relative to the gap-forming processes more prevalent in systems with canopy trees of more advanced ages, leading to higher mortality rates in smaller size classes.

4.2 Spatial pattern of mortality

Tree mortality events were spatially random during all periods analyzed (species pooled), and for *Pinus resinosa* analyzed separately. Previous studies of mortality patterns show contrasting results based on the mortality agents, temporal variation, and tree size or species. For example, agents such as root-rot fungi can create clustered mortality and gap-forming processes (Dobbertin et al. 2001, Worrall et al. 2005). The developmental stage of a forest is also associated with a particular spatial pattern; younger forests undergoing density-dependent mortality generally develop regular spacing (Ward et al. 1996, Gratzer and Rai 2004, Gray & He 2009, Svoboda et al. 2010); however, these competitive processes may not be as influential in old-growth or late-successional systems (Franklin and Van Pelt 2004, Das et al. 2011). Metsaranta and Lieffers (2008) also found that competitive processes did not strongly influence spatial patterns of mortality in late-successional *Pinus banksiana* stands in Canada, after a peak of mortality when the stand was younger. As described above, spatial patterns of mortality within a developmental stage can also differ by size class and species (Boyden et al. 2005, Hurst et al. 2012) due to niche differentiation, shade tolerance, and differing mortality processes between small and large diameter trees.

Although clustered patterns of mortality have generally been found as the prevalent pattern of mortality in older forest systems; spatially random mortality has also been reported from previous studies. Working in this same ecosystem and region Aakala et al. (2012) also found random mortality, suggesting wider consistency in mortality agents and processes. Similarly, Getzin et al. (2006) and Das et al. (2011) documented spatially random mortality of canopy trees in western U.S. conifer forests; a pattern also documented in a wide review of mortality patterns and processes in fire-dependent forests in western North America (Larson and Churchill 2012). Such patterns have also been described for a mixed-deciduous forest in Denmark using long-term data (Wolf 2005).

The initial pattern of trees was spatially random, suggesting that although mortality events occurred randomly within a randomly dispersed population, starting conditions may have influenced this patterning. Simulation studies have shown that random patterns remain random over time when mortality is not dependent on neighboring trees (Kent and Dress 1979), which is opposite the hypothesis that clustered or random patterns become more regular over time due to competition among neighboring trees (Leps and Kindlmann 1987, Kenkel 1988). This finding suggests that mortality events in our stand were not strongly dependent on competition or influence from neighboring stems, but may have been more influenced by successional processes (i.e., *Pinus banksiana* mortality) and stochastic events, such as windstorms.

Despite the fact that mortality events were shown to be random, the spatial distribution of dead trees tended toward a clustered pattern, suggesting that individual trees susceptible to *Armillaria*, windthrow, or surface fires were spatially clustered. Previous studies have reported the spatial pattern of dead trees to be either random or

clustered (e.g. Acker et al. 1996, Dobbertin et al. 2001, Aakala et al. 2007). It is important here to note the difference between spatial patterns of mortality events and the spatial pattern of dead trees. The former characterizes the arrangement of dead trees within the fixed initial arrangement of live trees (in 1923), while the latter simply characterized the locations of current dead trees based on univariate tests. This distinction is critical because spatially random mortality occurring in a population of initially clustered trees may still show some degree of clustering. This finding makes a compelling argument for quantifying both patterns before interpreting the agents and processes responsible for tree mortality.

4.3 Mortality agents

The presence of *Armillaria* root-rot and documented windstorms (below) during this study period did not appear to result in clustered mortality events, which suggests trees within this system respond individually to local stressors and exogenous mortality events. Paine et al. (1998) argued that disturbance interactions yield unpredictable outcomes in multiple ecosystems. This stand underwent several prescribed fires in 1998, 2000, and 2003 that, in combination with the presence of *Armillaria*, insect outbreaks, and windthrow, may have led to the pattern of random mortality events documented here. In fact, Santoro et al. (2001) found increased mortality from bark beetles (*Ips* spp.) after prescribed burns on *Pinus resinosa* sites in Itasca State Park, suggesting an interaction between these disturbances. Other major fires that may have affected the plot occurred in 1811 and 1865 (Spurr 1954, Frissell 1973), and major wind storms occurred in 1941, 1983, and 1995 (Buckman 1953, Webb 1988), the evidence of which was seen as

uniform fall directions of windthrown trees. Fire has been shown to result in patchy mortality at multiple scales in pine forests of the western US (White 1985, Mast and Veblen 1999); a finding supported by the spatial clustering of dead trees in this stand. Worrall et al. (2005) identified proximate and ultimate causes of tree mortality, and Mclaughlin et al. (2011) studied abiotic and biotic mortality factors in a *Pinus resinosa* community; however, causal agents of mortality are typically difficult to identify. In this stand, multiple disturbance agents likely interacted to drive mortality and spatial patterns.

4.4 Conservation and management implications

   Pinus resinosa in the Great Lakes states is often managed in plantations where the spatial pattern tends towards regularity (Gilmore and Palik 2006, D'Amato et al. 2009) for operational efficiency. However, managers worldwide are increasingly interested in restoring late-successional or old-growth characteristics to forest systems as well as to manage forests for better adaption to global change (Franklin et al. 2007, Bauhus et al. 2009, D'Amato et al. 2011). Incorporating old-growth spatial pattern characteristics is important in realizing structural restoration goals (Larson and Churchill 2012), but little information exists on spatial patterns of reference or natural stands of this forest type. If old-growth structure is a restoration goal, these spatial patterns suggest a natural-disturbance based silvicultural approach that mimics mortality patterns in the absence of stand-replacing disturbance. The spatially random initial condition in this stand suggests that variable density thinning might benefit these systems early in stand development. O'Hara et al. (2010) found that variable density thinning treatments accelerated tree growth and increased stand-level variability, which both contributed to enhancing old-growth structure. In contrast, Dodson et al. (2012) found that while variable density

thinning did create greater spatial variability, it did not encourage growth of large trees or maintain CWD and snag volumes. Variable density thinning later in stand development has also been suggested to promote biodiversity in managed systems when old-growth restoration is a goal (Carey and Curtis 1996). The spatially random mortality events we found suggest that the application of thinning treatments should be distributed randomly among existing trees. The thinning method applied (e.g. thinning from above or below) could also vary at each tree removal location to emulate the patterns of mortality across different size classes found in this study. Finally, information on the spatial pattern of mortality is also necessary to parameterize many growth models (e.g. FORET, SORTIE); point process models can provide starting configurations for these growth models (Stoyan and Penttinen 2000).

Itasca State Park managers are also very interested in maintaining the *Pinus resinosa* component of the forest (Dobie 1955, Zenner and Peck 2009b) given the 1891 mandate from the legislation of the state of Minnesota to 'preserve intact the primeval forest now growing.' Due to fire suppression and recent ineffectiveness of surface fires at regenerating *Pinus resinosa*, park management has considered mechanical preparation and planting to maintain or restore this pine legacy. The spatial pattern of current stands may inform this effort. In concert with other studies of old-growth *Pinus resinosa* structure and spatial pattern (Aakala et al. 2012, Fraver and Palik 2012), this study will help managers incorporate natural mortality processes into thinning, establishment, and protection efforts.

4.5 Conclusions

Long-term demographic data from old-growth systems are invaluable resources for documenting natural processes and population dynamics and developing benchmarks for conservation and management. Our study made use of long-term data from the oldest known *Pinus resinosa* study to quantify spatial patterns of mortality over an 87-year period. Counter to the findings of other works, live tree and mortality events were spatially random over this period, suggesting that these late-successional forests experience random canopy disturbance without stand-replacement. These small-scale disturbances result from interacting mortality agents such as windthrow, root rot fungi, insect damage, and surface fire. The long-term nature of this study allowed us to assess the temporal variability in these disturbance agents and their effect on the spatial pattern of individual mortality events. We found evidence of windthrow, root rot fungi, and surface fires, although it is likely there may have been other mortality agents within the stand. Additionally, the long-term nature of this study allowed us to compare the aggregation of dead trees with the initial distribution and determine that actual mortality events occurred randomly despite dead-tree aggregation. Finally, the mortality rates reported in this study also capture the temporal variability of disturbances enumerated above and are consistent with rates for other coniferous forest types. These findings have important implications for efforts aimed at restoring the natural range of variability in horizontal spatial structure to managed forests. In the absence of a stand-replacing disturbance, these managed systems may require silvicultural efforts that emulate random mortality. Moreover, future monitoring of the rates and spatial patterns of mortality from

this unique study site will serve as a critical benchmark for assessing the influence of

global change on mortality processes within natural forest systems.

Chapter Three: Structure and stand-development of old-growth, unmanaged second-growth, and extended rotation *Pinus resinosa* forests in northern Minnesota, U.S.A.

1. Introduction

Old-growth forests are widely recognized as invaluable resources for guiding the development of forest conservation and management strategies (Foster et al. 1996). In particular, a great deal of research has focused on quantifying the natural range of variability in ecosystem structures and processes characterizing these systems, to develop reference conditions to which managed systems are compared (Foster et al. 1996, Hunter and White 1997). Recent concerns over declines in biodiversity in managed forest systems have also led to the expansion of management strategies to promote development of old-growth conditions. Such approaches typically use information on natural disturbances to guide harvest planning and implementation (Curtis 1997, Palik et al. 2002, Keeton 2006, Bauhus et al. 2009). Despite widespread endorsement and application of these approaches, few studies have explicitly evaluated their efficacy in restoring the range of conditions found within old-growth systems.

A primary focus for studies on old-growth forests is quantifying the range of forest structural conditions that characterize these systems. The emphasis on structure highlights its key role in regulating ecosystem processes and controlling patterns of biodiversity (Spies 1998, McElhinny et al. 2005). Forest structure may be quantified by a suite of attributes, including coarse woody debris (CWD) volumes, snag densities, vertical foliage distribution, canopy structure, horizontal spatial distribution, tree basal area, and live-tree size classes. The variation in forest structural attributes often reflects disturbance history and rates, and differences in functional traits among constituent tree

species in a community (Harmon 1986, Tritton and Siccama 1990, Vanderwel et al. 2006, D'Amato et al. 2008). Comparisons of structural conditions between old-growth and second-growth systems have emphasized the profound influence that anthropogenic disturbance can have on forest structural conditions, including reducing the abundance and complexity of structural attributes (McLachlan et al. 2000, Liira et al. 2007, D'Amato et al. 2008). These differences often stem from the comparatively young age of most second-growth systems and the deliberate extraction of larger trees that otherwise would contribute to live tree complexity and forest deadwood pools in unmanaged systems.

One management approach that has been proposed to restore old-growth forest structure to systems managed for wood products is to extend the final harvest age beyond that traditionally used for maximizing economic returns or productivity (Curtis 1997, Lindenmayer and Franklin 2002). Generally referred to as extended rotation forestry (ERF), this approach assumes that extending the period of stand development allows accrual of structural attributes (e.g., more age classes, variety of tree sizes, large trees) characterizing old-growth forests (Curtis and Carey 1996). However, the efficacy of ERF to restore these critical structural elements in managed forests remains unknown (Hale et al. 1999).

To evaluate the efficacy of ERF at restoring old-growth structure, we compared the structure and development of old-growth, extended rotation, and unmanaged second-growth red pine (*Pinus resinosa*) stands in the upper Great Lakes region, U.S.A. *P. resinosa* has an extensive natural range in north-central and northeastern North America and is an important tree species occupying a large proportion of natural areas (e.g., Day

and Carter 1990) and managed forests. *P. resinosa* is typically managed with even-aged silvicutural methods such as clearcutting followed by planting (Johnson 1995). In contrast, the age structures of old-growth *P. resinosa* range from single to multi-cohort (Palik and Zasada 2003, Fraver and Palik 2012), and tree spatial distributions have a high degree of complexity reflecting long-term mortality processes (Aakala et al. 2012). Further, old-growth *P. resinosa* remnants currently occupy a small fraction of the area estimated at the time of European settlement due in large part to past land use, including logging and associated fires at the turn of the 20th century (Frelich 1995, Schulte et al. 2007). These changes to historic *P. resinosa* forests highlight the need for a better understanding of forest structure and developmental pathways in these systems.

Our objectives were to: 1) characterize and compare the range of variation in a set of structural attributes among old-growth, extended rotation, and unmanaged second-growth *P. resinosa* forests; and 2) evaluate the long-term temporal changes in structural attributes for each of these forest types. We designed these objectives to determine if ERF accelerated the development of structural characteristics towards those found in old-growth forests, using a unique approach with two long-term studies. By comparing extended rotation and old-growth *P. resinosa* at different stages of stand development, we hope to determine the efficacy of management for old-growth structure in a system that is similar to many other fire-dependent forest ecosystems in the northern temperate region.

2. Methods

2.1 Study sites

We utilized existing studies on old-growth, extended rotation, and unmanaged second-growth forests to address the study objectives above. Sites are located in northern Minnesota, specifically Itasca and Scenic State Parks and the Chippewa and Superior National Forests (Figure 1). Sites occurred on a range of substrates, but all were fire-origin stands dominated by *P. resinosa* on well-drained, low-fertility, sandy soils (Table 1).

The old-growth stands used in this study included the 2-ha Allison plot located in Itasca State Park in north-central Minnesota (Spurr and Allison 1956), plus seven sites scattered throughout northern Minnesota that were established as part of a detailed study on old-growth *P. resinosa* age-cohort structure (0.5-ha plot at each site; Fraver and Palik 2012). A more detailed history of these areas is found in Chapter 1 and in Fraver and Palik (2012). Old-growth stands were defined as forests of natural-origin with minimal anthropogenic disturbance and canopy trees > 50% of the maximum age for the species, a definition specific to this ecosystem type (McGee et al. 1999, Mosseler et al. 2003). The Allison plot was comprised of a single age cohort; stand age at the time of our 2010 sampling was 207 years. The seven remaining old-growth stands represent a variety of cohort structures, the oldest living trees having been established 201 to 317 years prior to sampling, depending on site.

The extended rotation stands were part of the Red Pine Growing-Stock-Levels study, a long-term study on the Chippewa National Forest (see D'Amato et al. 2010). This study was established as a randomized complete-block design initiated in 1949 with

five basal-area treatment levels (13.8, 18.4, 23.0, 27.5, 32.1 m^2/ha) that were maintained with repeated thinning every 5-10 years from 1954 to 2003. The stand was comprised of a single age cohort; stand age at the time of final sampling was 143 years. Each basal area treatment was repeated in three blocks in which three 0.08-ha plots were permanently installed, resulting in 45 total plots.

Finally, the unmanaged second-growth stands represent a portion of a *P. resinosa* chronosequence study on the Chippewa National Forest (see Bradford and Kastendick 2010). These six single-cohort stands ranged in age from 137-165 years at time of sampling in 2009, and each included three 0.02-ha plots. These stand ages are comparable to those of the extended rotation stands (143 years), which allows examination of the effects of repeated thinning treatments on forest structure relative to second-growth systems with no management history.

The existence of repeatedly-measured, long-term datasets for both the Allison plot and the extended rotation stands provided a unique opportunity to track the structural development of natural and actively managed forests over time. The Allison plot provides this information from stand age 120 through age 207, whereas the extended rotation study provides this information from stand age 85 through age 143.
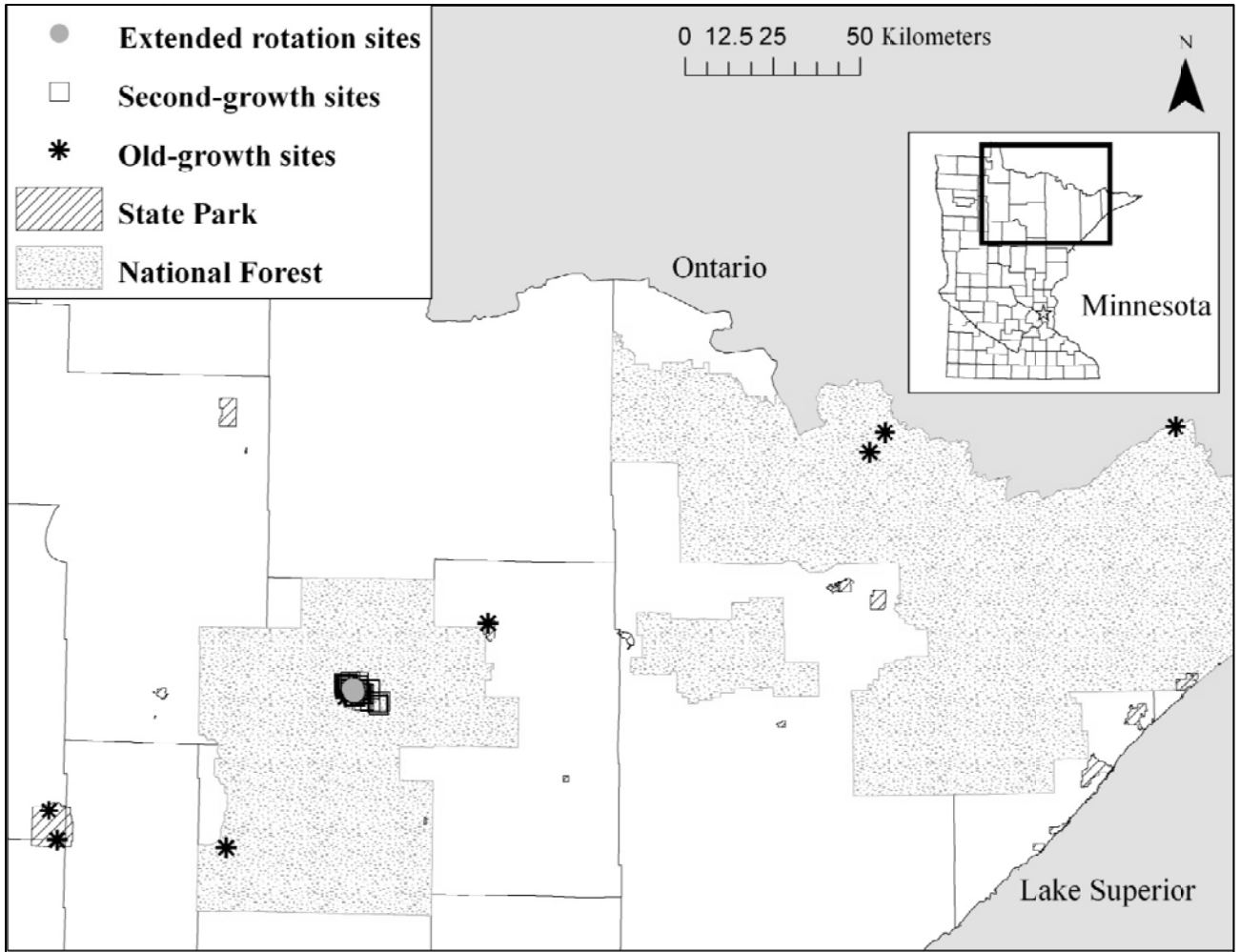
Figure 1: Location of *Pinus resinosa* old-growth, extended rotation, unmanaged second-growth stands in northern Minnesota. See Table 1 for site descriptions.

Table 1: Environmental characteristics and forest types for the four *Pinus resinosa* studies.

Site	Site type	Soil characteristics	Maximum canopy-tree age (yr)	Sampling design
Allison plot	old growth	well-drained sandy loams and loamy sands derived from glacial outwash	209	1 site, single 2.02-ha plot
Old-growth red pine cohort study	old growth	well-drained sandy, nutrient-poor soils	201 – 331	7 sites, one 0.5-ha plot per site
Red pine chronosequence	unmanaged second growth	Entisols with rapid permeability and low water-capacity	137 – 165	6 sites, three 0.02-ha plots per stand
Growing-Stock-Levels Study	extended rotation	well-drained sands derived from glacial outwash	145	1 site, 5 treatments, 3 replicates per treatment, 3 0.08-ha plots per replicate

2.2 Field methods

Detailed field-sampling protocols for the seven old-growth sites, the extended rotation study, and the unmanaged second-growth study can be found in Fraver and Palik (2012), D'Amato et al. (2010), and Bradford and Kastendick (2010), respectively. We present here a brief overview of those protocols to place the studies in context with one another and to highlight where sampling may have differed between studies. In contrast, we explain the Allison plot protocol in more detail, given that protocols have changed since the original study was established (Spurr and Allison 1956).

For the seven old-growth sites, species and diameter at breast height (DBH, 1.3 m) were recorded for all living and dead trees ≥ 10 cm between 2009 and 2011, depending on site. Downed CWD pieces ≥ 10 cm diameter were inventoried at these sites using the line-intercept method, with eight transects radiating at even intervals from plot center to plot borders, for a total length of *ca.* 342 m per site. For the extended rotation stands, species and DBH were recorded for all living and dead trees > 8.9 cm every 5-10 years from 1949-2007. Downed CWD was measured in these stands in 2010 using the line-intercept method, with three 20-m transects arranged in a 'turkey-foot' configuration (transects radiating from plot center at 0°, 120°, and 240°) at all nine plots per growing-stock treatment. For the unmanaged second-growth stands, species and DBH were recorded for all living and dead trees > 2.5 cm DBH, and downed CWD pieces > 7.6 cm were sampled identically to that of the extended rotation sites.

Upon establishment in 1923, all trees (N=1129, stems > 7.8 cm) on the 100×200 m Allison plot were uniquely tagged and measured for DBH, which allowed the tracking of individuals through time. Sampling occurred roughly every five years through 1963.

We re-sampled the plot in 2010, recording DBH for living trees and snags ≥ 10 cm DBH, including 'ingrowth,' i.e., trees that had become established since the initial inventory. Saplings (tree stems < 10 cm DBH, tree height > 4.5 m) were also tallied by species within fourteen 400 m^2 circular plots systematically located within the larger 2-ha plot. We inventoried CWD using the line-intercept method, with transects arranged in four adjacent (from north to south) 'turkey-foot' configurations (as above), for a total transect length of *ca.* 766 m.

For all studies, increment cores were extracted for age determination where stand or cohort structure was unknown, and CWD was assigned to decay classes using the five-class system after Sollins (1982).

2.3 Statistical analysis

Coarse woody debris volume for each plot was calculated using Van Wagner's (1968) equation, with volumes in decay classes 4 and 5 reduced using decay-class specific collapse (cross-sectional height-to-width) ratios developed from the old-growth *P. resinosa* sites used in this study (Fraver and Palik 2012). For sites with multiple plots, volumes were averaged across plots and expressed on a per-ha basis. On the Allison plot, many snags had lost bark or been burned in a previous surface fire. Thus, the basal area for each snag is only an approximation of the basal area when the tree was still alive. As such, we did not divide snags into size-class distributions. CWD volume, snag density, and snag basal area were each compared between old-growth, extended rotation, and unmanaged second-growth forests using a Kruskal-Wallis test followed by a Wilcoxon

rank-sum test for pairwise comparisons. These non-parametric tests were required

because of failure to meet assumptions of parametric tests.

For all sites and sampling periods, live-tree size-class distributions based on DBH

were constructed using 10 cm diameter classes. Regression equations were fit to the

resulting distributions to determine the overall distribution form using the function PROC

REG within SAS (SAS Institute Inc. 2012). Each curve was assigned a shape description

following the methods of Janowiak et al. (2008), which classifies distributions as

negative exponential, increasing-q, rotated sigmoid, concave, unimodal, or variable

depending on the significance and direction of regression parameter coefficients. The

Gini coefficient (*G*) was used to examine the degree of size inequality within live-tree

distributions between sites and over time. This coefficient ranges from zero (all

individuals are equal) to one (all individuals but one have a value of zero) and is a useful

measure of size class inequality because it can be compared in populations with different

means and in the same population over time (Weiner and Solbrig 1984, Dixon et al.

1987). We used the equation:

[1] $$G = \frac{\sum_{i=1}^{n} \sum_{j=1}^{n} |x_i - x_j|}{2n^2 \bar{x}}$$

where x = DBH and n = total trees, G = the mean difference between each pair of

individual sizes, divided by the total mean size. In addition, *P. resinosa* importance

values (IV; IV = (relative density + relative basal area)/2) were calculated for all sites and

sampling periods.

Nonmetric multidimensional scaling (NMS) ordination was used to examine

patterns in structural variation between sites based on their current conditions as well as

over time for the Allison plot and extended rotation stands (McCune and Grace 2002).

The primary matrix for comparisons among sites based on current conditions contained site-level averages for structural attributes, including volume of CWD, large tree density (trees > 40 cm DBH), degree of size inequality based on Gini coefficients, and other measures of live-tree size distributions (see Table B1 in Appendix B). In contrast, the matrix used to examine patterns in variation over time at the Allison plot and extended rotation stands contained only structural data based on live trees in each sampling period, due to the absence of long-term CWD data from these areas (see Table B1 in Appendix B for full data matrix). For these analyses and comparisons of DBH distributions over time, we used three of the five basal area treatments from the extended rotation stands (13.8, 23.0, and 32.1 m^2/ha) to capture the range of variation in this management type and aid in graphical interpretation of long-term trends. NMS was conducted using PC-ORD version 5.1 (McCune and Mefford 1999) and utilized the *slow-and-thorough* autopilot mode. Optimal dimensionality was determined based on the configuration with the lowest stress. In cases where a three-dimensional solution was chosen, the two-dimensions that explained the majority of the variance were presented for ease of interpretation. Kendall's tau (τ) statistic was used to examine relationships between structural characteristics and NMS axis scores (SAS version 9.2, SAS Institute Inc. 2012). Multi-response permutation procedure (MRPP) was used to test for multivariate differences in structure between old-growth, extended rotation, and unmanaged second-growth systems (McCune and Mefford 1999).

3. Results

3.1 Current forest structure

CWD volumes were higher in the old-growth stand than in the unmanaged second-growth and the extended rotation stands (Table 2, Z = -3.03, P < 0.0001 and Z = -2.85, P = 0.002, respectively). In contrast, CWD volumes did not differ between unmanaged second-growth and extended rotation stands (Z = -1.37, P = 0.178). The old-growth and unmanaged second-growth stands also had a significantly higher snag density than the extended rotation stands (Z = -2.87, P = 0.002, and Z = -2.68, P = 0.004, respectively). Snag basal area was significantly higher in the old-growth stand compared to unmanaged second-growth stands and the extended rotation stands (Z = -2.13, P = 0.029, and Z = -2.85, P = 0.002, respectively).

The overall current structural conditions found within old-growth, extended rotation, and unmanaged second-growth stands, as based on multivariate patterns in live- and dead-tree attributes, were significantly different (MRPP, A = 0.19, P < 0.0001). This result was also illustrated by the grouping of sites in ordination space, based on current structure, which explained 71.1 % of the variation in the data (Figure 2, final stress = 9.8, final instability = 0.0). The greatest variation between these stand types was explained by axis 1 (46.3%), which represented a gradient of stands with high snag basal area and density and high maximum DBH in the negative portion of the axis to stands with low CWD volume, low maximum DBH, but high *P. resinosa* IV and relative basal area in the positive portion of the axis (Figure 2, see Table B2 in Appendix B). Axis 2 (24.8% of the variation) largely represents within-stand-type variation and ranged from high CWD

volume, high *P. resinosa* IV, and high maximum DBH in the negative portion of the axis

to low CWD volume in decay class three, low snag density, and lower maximum DBH

in the positive portion of the axis (Figure 2, see Table B2 in Appendix B).

Table 2: Characteristics of coarse woody debris (CWD) and snags in *Pinus resinosa* stands in northern Minnesota (*n* = sites for old growth and second growth, *n* = basal area treatments for extended rotation).

Structural attribute	Old growth (*n* = 8)		Second growth (*n* = 6)		Extended rotation (*n* = 5)	
	Mean ± SE	Range	Mean ± SE	Range	Mean ± SE	Range
Downed CWD volume (m^3/ha)	70.7 ± 8.8^a	37.2 – 124.1	11.5 ± 3.5^b	0 – 25.4	4.7 ± 1.6^b	1.4 – 10.5
Snag basal area (m^2/ha)	6.9 ± 1.2^a	2.7 – 14.2	2.9 ± 1.8^b	0.6 – 11.7	0.5 ± 0.3^b	0 – 1.6
Snag density (no./ha)	84.2 ± 6.9^a	24.0 – 166.0	75.0 ± 27.5^a	16.6 – 200.0	10.8 ± 0.5^b	0 – 12.5

Note: Statistically significant differences (P ≤ 0.05; Wilcoxon rank sum test) between groups are denoted by lowercase letters.
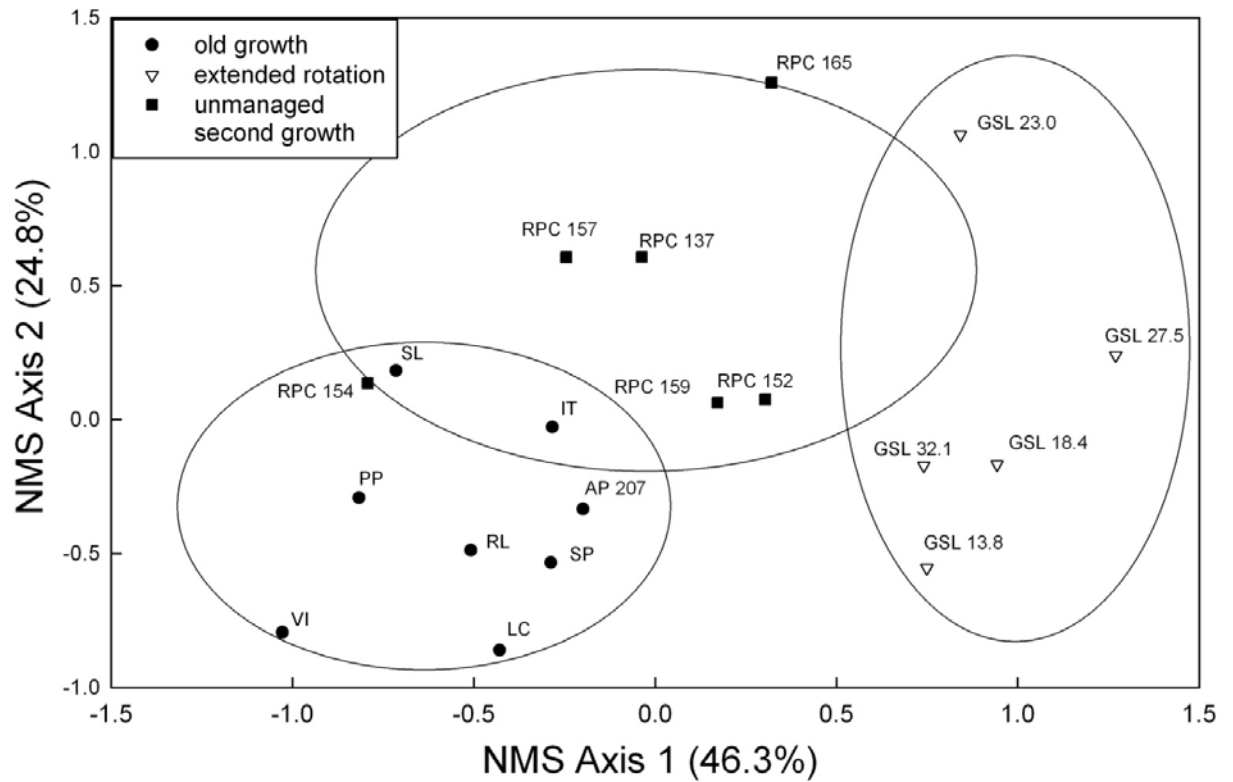
Figure 2: NMS Ordination of size distribution and CWD characteristics of all sites considered in the study. RPC = red pine chronosequence or unmanaged second growth, followed by a stand age suffix; GSL = Growing-Stock-Levels or extended rotation, followed by a basal area treatment suffix; AP = Allison plot, also followed by a stand age suffix. See Table B2 in Appendix B for structural characteristic correlations with Axes 1 and 2.

3.2 Structural development through time

The patterns in live-tree size distributions varied over time within and between the old-growth Allison plot, extended rotation, and unmanaged second-growth stands (Figure 3). The Allison plot size distributions ranged from unimodal to increasing-q, while the extended rotation size distributions were primarily unimodal or variable curve shapes

(Table 3). Upon visual inspection, the variable curves for the extended rotation size

distributions were largely right-skewed unimodal curves. Similarly, distributions for the

unmanaged second-growth stands were categorized as variable (Table 3), but visually

resembled right-skewed unimodal distributions (Figure 3). The intermediate and lower

basal area treatments for the extended rotation site had much flatter live-tree distribution

as would be expected for these stocking levels over time (Figure 3). Although the

extended rotation stands and Allison plot had similar live-tree distributions during stand

development (Figure 4), the Allison plot distribution had trees in a wider range of

diameters. In the final sampling period, ingrowth was reflected in the smaller size classes

at the Allison plot and extended rotation sites (Figure 4, 7.5 – 12.5 cm), most notably the

13.8 and 23.0 m^2/ha basal-area treatments.

The arrangement of sampling periods for the Allison plot and extended-rotation

sites in ordination space suggested distinct patterns of development over time (Figure 5).

All sampling periods grouped closely together by site type and basal area treatment, as

illustrated by the ordination diagram, which explained 72.1 % of the variation in the data

(Figure 5, final stress = 5.48, final instability < 0.001). The configuration of sites and

sampling periods along axis 1, which explained 41.0% of the variation, represented a

temporal progression from younger stand ages in the negative portion of the axis to older

ages in the positive portion. The structural attributes correlated with this axis reflected

stand development over time, with low large tree density, but high overall density in the

negative portion to high average, maximum, and minimum DBH in the positive portion

of the axis (Figure 5, see Table B2 in Appendix B). The distribution of sites along axis 2

(31.1% variation explained) generally reflected site differences and thinning treatments

and ranged from low minimum DBH, low density, and more equal distributions in the

negative portion of the axis to high large-tree density, *P. resinosa* basal area and IV in the

positive portion (Figure 5, Table B2). Additional variation in extended rotation stand

development visually coincides with thinning treatments. For example, thinning at stand

age 110 in the 13.8 m^2/ha treatment resulted in a structural shift in multidimensional

space (Figure 5).

Table 3: Tree diameter distribution shapes for the extended rotation, old-growth, and unmanaged second-growth *Pinus resinosa* stands over time (stand age in years given above each distribution shape). Letters indicate the shape as determined from sign and significance of regression parameters . UNI=Unimodal, V= Variable, IQ= Increasing-q (see Methods).

Site	Distribution shape											
extended rotation	85	90	95	100	105	110	115	120	125	131	139	143
32.1 m^2/ha	V	V	V	UNI	V	V	V	V	V	V	V	V
23.0 m^2/ha	V	V	UNI	V	V	V	V	V	V	V	UNI	V
13.8 m^2/ha	V	V	V	V	V	V	V	V	IQ	UNI	V	V
old growth	120	125	130	135	140	145	149	154	160	207		
	V	V	V	V	V	V	UNI	UNI	V	IQ		
second growth	137	152	154	157	159	165						
	V	V	V	V	V	V						
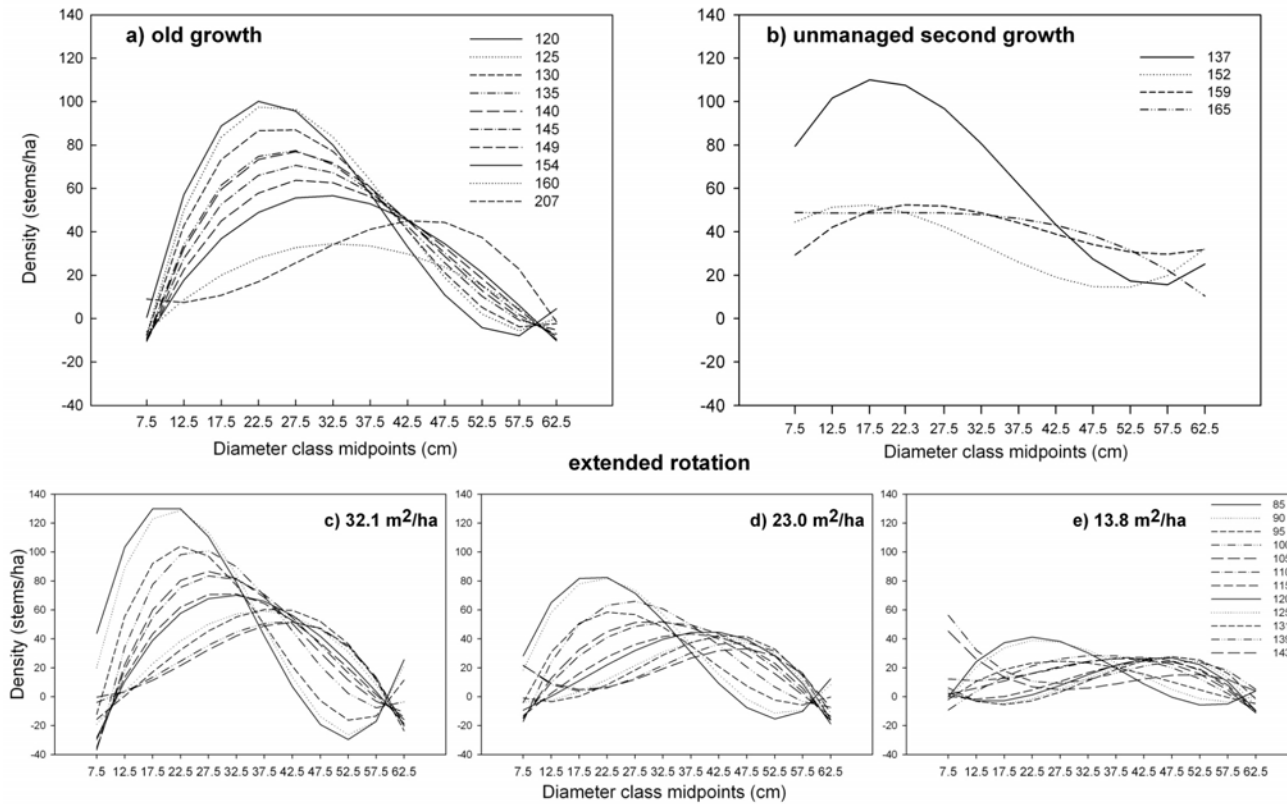
Figure 3: Changes in diameter distributions over time (legends refer to stand ages) for (a) old-growth *Pinus resinosa* from age 120-207, (b) unmanaged second-growth *P. resinosa* from age 137-165, and (c-e) extended rotation *P. resinosa* from age 85-143 years, shown at three basal area treatments: (c) the highest, 32.1 m²/ha, (d) the intermediate, 23.0 m²/ha, and (e) the lowest, 13.8 m²/ha. All sites show a general shift to higher diameter classes over time, though some also show an increase in smaller size classes over time due to ingrowth. These are fitted curves, and thus may be negative; for curve shape descriptions, see Table 3.
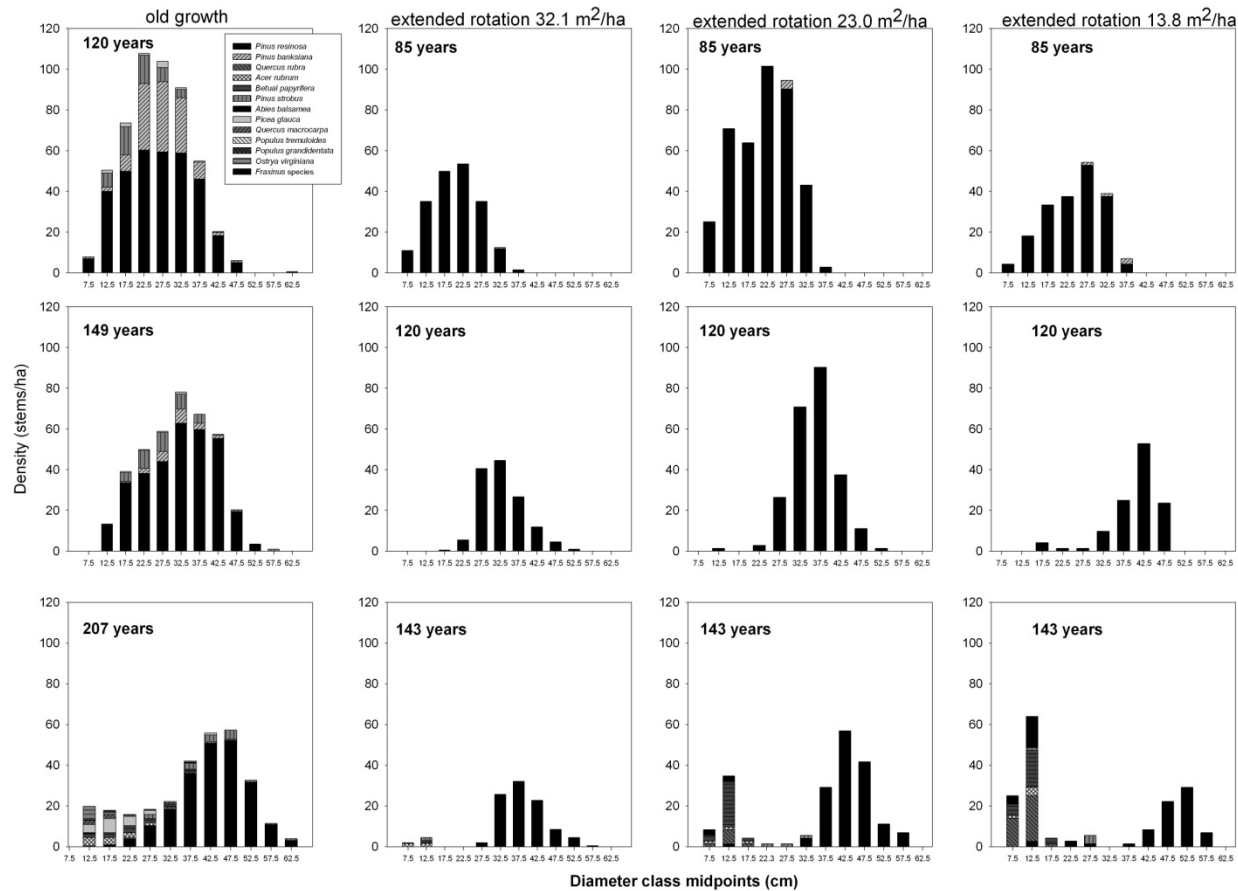
Figure 4: Diameter distributions from the first, middle, and most recent sampling period for the old-growth (Allison plot) and extended rotation sites. The extended rotation site data is split into the highest (32.1 m^2/ha), intermediate (23.0 m^2/ha), and lowest (13.8 m^2/ha) basal area treatments. All sites shift into larger size classes through time, and ingrowth appears in the smaller size classes by the final sampling period (bottom row).
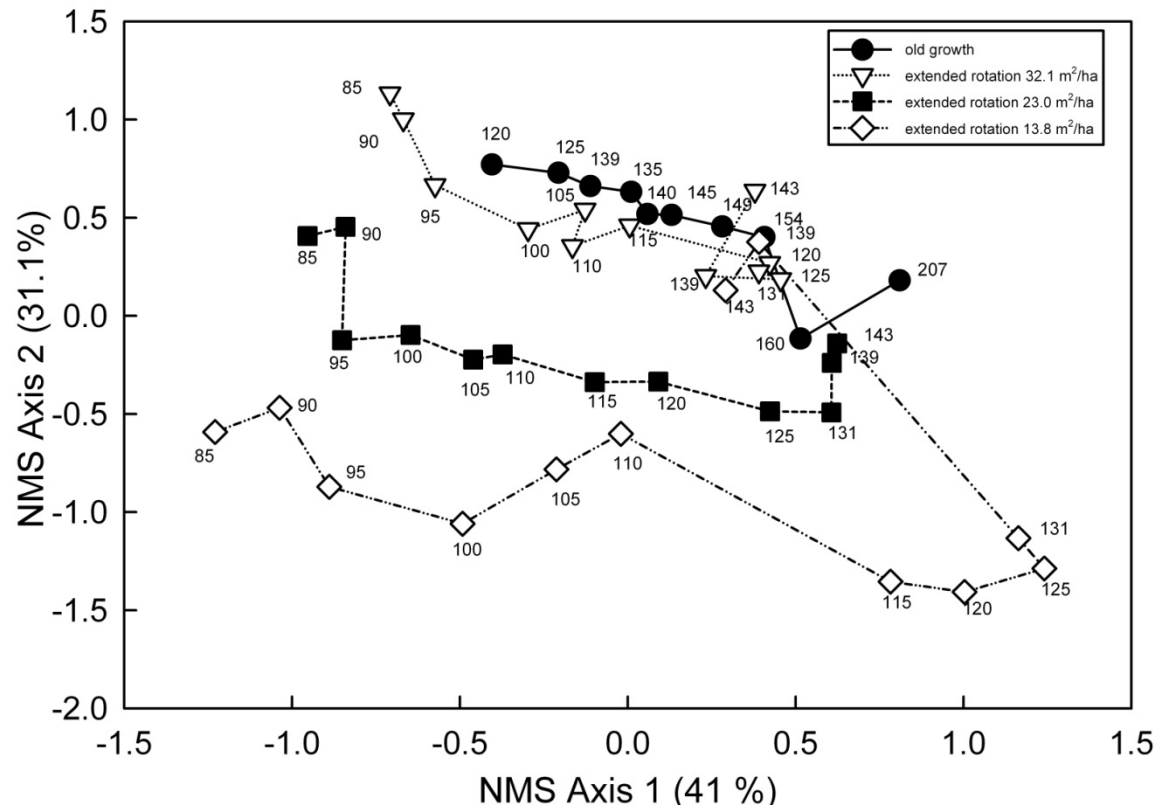
Figure 5: Non-metric multidimensional scaling (NMS) ordination of tree size distribution characteristics of the old-growth Allison plot (circles) and extended rotation stands at three basal area treatments: 32.1 m^2/ha (upside-down triangles), 23.0 m^2/ha (solid squares), 13.8 m^2/ha (diamonds). Each point on the graph represents a sampling period (and corresponding stand age) for the sites and treatment levels. See Table B2 for structural characteristic correlations with axes 1 and 2.

4. Discussion

Our results indicate that old-growth forests are more structurally complex than their extended rotation and unmanaged second-growth counterparts. Old-growth *P. resinosa* forests are distinguished by higher volumes of CWD (including pieces in advanced decay), higher snag densities, and more complex tree size distributions (including larger trees), characteristics that have been widely recognized as distinct between managed and unmanaged systems (Hale et al. 1999, Kirby et al. 1998, McGee et al. 1999, Uotila et al. 2001, Crow et al. 2002) and second-growth and old-growth forests (Spies et al. 1991, Noel et al. 1997). Our results also indicate that extended rotation forestry (ERF) is effective at accelerating the structural characteristics of managed *P. resinosa* systems towards those found in old-growth forests, with the exception of CWD volumes and snag densities. As such, ERF may be a strategy to hasten the structural development of these second-growth systems to old-growth functional status, particularly if provisions are made for the deliberate creation and retention of CWD and snags.

4.1 Current structure of various Pinus resinosa *stands*

Volumes of CWD differed strongly among the old-growth, extended rotation, and unmanaged second-growth stands. Old-growth stands had the highest CWD volume (mean 70.7 m^3/ha), which was within the range of volumes reported for other coniferous old-growth systems (e.g., Sturtevant et al. 1997, Feller 2003, Fraver et al. 2008, Aakala 2010). The difference in CWD volumes between old-growth and unmanaged second-growth stands was reflective of larger CWD inputs in the old-growth stands, as well as the differences in mortality processes in the old-growth and unmanaged second-growth

stands (Jönsson et al. 2011). Coarse woody debris inputs can be more episodic, but typically old-growth sites have an increased 'background rate' of CWD input (Jönsson et al. 2011). In particular, much of the downed CWD within the unmanaged second-growth was smaller diameter material resulting from natural self-thinning mortality, whereas evidence of gap-scale disturbance resulting in mortality of large diameter overstory trees was prevalent in all of the old-growth systems examined. CWD volume was very low in the extended rotation stands and is likely due to the removal of potential CWD inputs during thinning entries and subsequent low mortality rates. Although harvesting activities cause increased inputs of small-diameter CWD inputs (Fraver et al. 2002), these materials decay rapidly resulting in lower volumes of CWD in managed stands relative to old-growth stands (Sippola et al. 1998, Siitonen et al. 2000). Similarly, Duvall and Grigal (1999) found that CWD inputs varied over time with thinning entries and concluded that extended rotation management will not restore old-growth structure unless increasing CWD volumes and snag densities are intentionally included as part of management prescription.

Snag density in the old-growth and unmanaged second-growth stands were similar, but were nearly seven times higher than that of extended rotation stands. Duvall and Grigal (1999) also observed higher snag density in unmanaged *P. resinosa* forests. Snag density is especially affected by timber management, as living trees are typically culled before they senesce or become more susceptible to disturbance. Snag basal area was not statistically different between old growth and unmanaged second growth, suggesting that snags occupied similar diameter classes in these forest types. However, snag basal area was significantly higher in old-growth compared to extended rotation

sites as well as between unmanaged second-growth and extended rotation sites. This result suggests that snags occupied smaller diameter classes in the extended rotation stands, possibly reflecting the preferential removal of larger diameter individuals.

Overall, old-growth, extended rotation, and unmanaged second-growth stands had similar live-tree size distribution characteristics by the final sampling period (Figures 3 and 4). Slight differences in size-distribution characteristics are not surprising given the difference in age between the old-growth, extended rotation, and unmanaged second-growth sites as maximum DBH values are expected to increase as a stand develops. However, all sites exhibited unimodal or left-skewed unimodal live-tree diameter distributions. Other studies have documented diameter distribution forms deviating from the negative exponential distribution commonly attributed to old-growth forest systems (Hett and Loucks 1976). Instead, temporal variability in disturbance leads to a wide variety of size distributions in older forests including rotated-sigmoid distributions and unimodal distributions (Coomes and Allen 2007).

The sites were also differentiated by *P. resinosa* dominance based on importance values (IV) and relative basal areas. Specifically, old-growth sites had lower IV and lower relative basal areas than the extended rotation and unmanaged second-growth sites. This finding indicates that species composition shifted as the stands aged, thereby lowering the relative importance of *P. resinosa*. These shifts likely reflect ingrowth of other species, leading to the development of a lower canopy stratum that contains species such as *Betula papyrifera, Ostrya virginiana, Acer rubrum,* and *Abies balsamea* (Zenner and Peck 2009a, Fraver and Palik 2012).

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4.2 Structural development of old-growth and extended rotation Pinus resinosa *stands*

Tree basal area and density on the old-growth Allison plot during the entire 87-year study period were within the range of values reported in other studies of old-growth *P. resinosa* stands (Day and Carter 1990, Tyrrell et al. 1998, Zenner and Peck 2009a, Fraver and Palik 2012). Basal area remained constant from 1923-1957, declined in 1963, and then increased again by the most recent sampling period (see Table B1 in Appendix B). The basal area increase is accounted for by ingrowth of new species (above), as well as existing stem growth, enhanced in some trees in response to multiple canopy disturbances following wind events in 1941, 1983, and 1995 (Buckman 1953, Webb 1988). The extended rotation stand-level basal area fluctuated over time in response to thinning treatments. For both sites, the observed decrease in stand density over time is largely attributable to either mortality or thinning, and lack of *P. resinosa* regeneration, despite the ingrowth of several other species.

Owing to its shade intolerant nature, *P. resinosa* forests do not typically undergo the gap-forming multi-cohort processes of old-growth forests dominated by shade tolerant species. In many cases, these shade-tolerant systems originate as even-aged communities with self-thinning dominating size distribution (Ford 1975, Oliver and Larson 1996, Svoboda et al. 2010), leading to a unimodal curve similar to those observed in this study. Additionally, the scarcity of saplings and tree regeneration observed in the 32.1 m^2/ha extended rotation stands and at the Allison plot may have maintained the unimodal or right-skewed unimodal distributions over time (Figure 5). In contrast, the lower overstory densities in the 13.8 and 23.0 m^2/ha extended rotation treatments allowed

for greater ingrowth of intermediate and shade tolerant species leading to highly left-skewed and more complex distribution by the final sampling period. Moreover, the unimodal distributions observed in both the Allison plot and extended forests shifted to larger size classes over time; a finding consistent with other long-term studies examining size distributions of shade intolerant species (Harcombe et al. 2002).

Our results suggest that ERF accelerates old-growth structural development for some, but not all, structural attributes. The temporal development we characterized for the extended rotation stands demonstrates that these systems began to approximate the old-growth conditions found within the Allison plot 10-70 years sooner than had occurred through natural stand development (Figure 5). This acceleration varied between the stocking levels and was due to increases in maximum DBH, tree density, and standard deviation of DBH, as well as decreases in *P. resinosa* dominance and relative basal area with time and continued management. Other studies have found that management for late-successional attributes is successful for only a portion of the structural characteristics of old-growth forests (Davis et al. 2007, Jönsson et al. 2009). Similarly, we concluded that ERF restores characteristics of live-tree distributions found in old-growth systems, but does not maintain CWD and snag attributes.

4.3 Conclusions and management implications

There has been great interest in restoring structural conditions and functional attributes of old-growth forests in the Great Lakes region (Vora 1994, Fraver and Palik 2011), and these management goals often incorporate structural targets (Keeton 2006, Bauhus et al. 2009, D'Amato et al. 2011). The importance of forest structure in driving

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ecosystem processes and biodiversity has been well studied (Spies 1998), but few studies have directly assessed management goals that restore old-growth structure to a forest system. By utilizing two rare long-term studies, we determined that stand development patterns such as mortality, competition, and regeneration (or lack thereof) are likely influencing the structural differences between old-growth and extended rotation stands. Furthermore, by incorporating old-growth replicate sites and data from second-growth forests, we were able to place the stand development of extended rotation and old-growth *P. resinosa* into the range of variability inherent to these systems. More specifically, we were able to compare structural attributes such as the abundance of snags and volume of CWD to determine that old-growth forests contain a greater abundance of snags and higher volume of CWD than their extended rotation and unmanaged second-growth counterparts. These attributes are critical for deadwood-dependent organisms and should be a focus of management prescriptions aimed at restoring aspects of the range of structural conditions in old-growth to managed systems (Jonsson et al. 2005, Franklin et al. 2007, Bunnell and Houde 2010, Riffell et al. 2011).

The structural comparisons we made between old-growth, extended rotation, and unmanaged second-growth *P. resinosa* forests underscore the importance of empirical evaluations of emerging management strategies for restoring old-growth structure before wide implementation. While ERF has been widely suggesting and adopted for achieving old-growth structural conditions (Curtis and Carey 1996, Hale et al. 1999), we found that in practice, it leads to a deficit in CWD and snag retention. To account for the lack of CWD, extended rotation management plans could include deliberate creation of CWD and snag or cavity tree retention whenever feasible. In contrast to CWD volume

differences, the extended rotation sites had living tree size distributions similar to those of old-growth sites. To further approximate old-growth structure with ERF, a wider range of size classes need to be encouraged, and ingrowth and tree regeneration should be protected. Additionally, management plans should continue incorporating either thinning from below to allow canopy trees to grow into larger size classes or variable density thinning to maintain structural complexity at a stand and landscape scales (Carey and Curtis 1996, Franklin et al. 2007).

Despite these old-growth structural restoration goals, maintaining *P. resinosa* dominance may be difficult without some type of management. *P. resinosa* in the Great Lakes region has been experiencing a regeneration failure due to fire suppression and shoot blights *Diplodia pinea* and *Sirrococcus conigenus* (Hansen 1974, Stanosz et al. 1997, Bronson and Stanosz 2006). Without management intervention it has been hypothesized that these systems will shift to northern hardwood communities (Kurmis 1985) or that *P. resinosa* will no longer be a dominant species (Scheller et al. 2005). Many landowners and managers are using prescribed fire as a strategy for regenerating pine with varying success. *P. resinosa* is well adapted to surface fires (Bergeron and Brisson 1990), but in some sites existing shade-tolerant shrubs such as hazel (*Corylus* species*)* out-compete pine regeneration (Tappeiner 1971). Thus, if maintaining *P. resinosa* in old-growth conditions is a goal, careful attention to planting or promoting natural regeneration of this species will be necessary.

Long-term demographic data from old-growth and managed systems are invaluable resources for documenting structural development and determining the efficacy of a management regime. Our study made use of four *P. resinosa* studies, two

with historic structural records, to quantify and compare structural characteristics and to determine if ERF restored old-growth structure. Although ERF did begin to approximate old-growth structure (complexity was highest at the lowest stocking level), this study indicated that incorporating higher volumes of CWD and higher densities of snags into the management plans for these systems would be necessary to provide the full range of structural attributes in *P. resinosa* systems. Furthermore, ERF accelerated the development of live-tree distributions towards those found in old-growth forests at lower stocking levels, and it added complexity to live-tree distributions over time regardless of stocking level. Given this, it may still be a viable option to restore old-growth structure and simultaneously remove merchantable timber. Future monitoring of the old-growth and extended rotation stand structure will be necessary to critically evaluate ERF as these systems further develop.

Chapter Four: Conclusions

The results presented in this thesis indicate that old-growth red pine is structurally complex, with spatially random mortality occurring at the stand level. Additionally, extended rotation management does restore some aspects of old-growth structure to red pine (*Pinus resinosa*) forests, but old-growth remains more complex largely due to coarse woody debris (CWD) and snag characteristics. ERF accelerated the development of old-growth structure anywhere from 10-70 years depending on stocking level. The old-growth stands had significantly higher coarse woody debris volume and snag basal area than their extended rotation, and unmanaged second-growth counterparts. Snag density was significantly higher in the old-growth and unmanaged second-growth stands than in the extended rotation stands. Tree diameter distributions among old-growth, extended rotation, and unmanaged second-growth stands were either unimodal or right-skewed unimodal with varying degrees of complexity as ingrowth species grew into the smaller size classes.

One old-growth stand, the Allison plot, had spatially random mortality events during the 87-year study period. Mortality rates were within the range of values found in other conifer systems, and generally decreased with diameter. The spatially random pattern of mortality events over time differed from the clustered pattern of dead trees in the most recent sampling period, highlighting the difference in quantifying the spatial process of mortality versus the final pattern of dead trees. The dead trees on the plot were likely affected by an interaction of mortality agents including windthrow, root-rot fungi such as *Armillaria ostoyae*, insect damage, as well as senescence.

These results underscore the importance of mortality processes in creating coarse woody debris, and snags within old-growth forests. The intentional harvest of trees in the extended rotation stands precludes natural mortality, thereby preventing these stands from fully realizing old-growth structure. The Allison plot and extended rotation stands had similar development of size distributions, however, CWD and snag characteristics were enough to distinguish old-growth, extended rotation, and unmanaged second-growth stands in multi-dimensional ordination space. Although no direct spatial pattern comparisons were made, an analysis of spatial patterns of mortality suggested that mortality events occur randomly in the unmanaged red pine stands. This random pattern likely influenced many of the developmental patterns of tree growth in the old-growth Allison plot. The following sections provide management recommendations and future research possibilities based on these results.

Management recommendations

If restoration of late-successional structural characteristics is a management goal, these results suggest that some aspects of ERF will be effective.   First, allowing red pine to mature beyond the typical rotation age (60-80 years) promotes the growth of trees into larger size classes. Long-term thinning regimes are another approach beyond simply extending rotation age. These thinning treatments can mimic the random spatial pattern of mortality. Additionally, the thinning method applied (e.g. thinning from above or below) could vary at each tree removal location to emulate the size-specific patterns of mortality. Variable density thinning (VDT) early in stand development will also encourage tree growth into larger size classes as well as promote stand-level variability

and biodiversity (O'Hara et al. 2010), while VDT later in stand development can continue to promote biodiversity (Carey and Curtis 1996). Therefore, it is possible that long-term thinning is a suitable management approach to restoring late successional characteristics in red pine forests.

Despite the efficacy of repeated thinning and extended rotation ages, these management options will not mimic the deadwood dynamics of old-growth forests, as thinning typically captures mortality that would otherwise lead to CWD creation. Therefore, management prescriptions should include CWD volume and snag retention targets to fully restore late-successional characteristics to red pine forests. Results from this study reveal wide ranges of CWD volume and snag densities in old-growth red pine forests. CWD volumes of 37 to 124 m^3/ha were found in this study among all old-growth stands and provide a benchmark for target volumes in this forest type. Similarly, snag density ranged from 24 to 166 stems/ha, also offering a wide range of options for managers. Snag basal area was significantly higher in the old-growth stands, which suggests that snag retention should incorporate snags in larger size classes.

Future research

A unique aspect of this study was the use of long-term repeatedly-measured datasets. As of this writing, there is not a specific re-sampling plan for the Allison plot, but the Forest Service Northern Research Station has a re-sampling plan for the extended rotation stands. Given the usefulness of long-term data in determining spatial patterns of mortality and drivers of stand development, it is highly recommended that these stands be re-sampled in the future. In all future re-sampling efforts, CWD and snags should be

tallied, and size characteristics should be measured to track the temporal variability of these important structural elements. Furthermore, given the difficulty in relocating tagged trees on the Allison plot after 50 years of no sampling, it is recommended that sampling occur ever 5-10 years.

Future work on the Allison plot will include growth analyses as well as a more in-depth analysis of mortality rates and agents. Additionally, future research will investigate the role of competition in driving the developmental processes explored in this study. Itasca State Park is continuing to manage and regenerate their red pine resource, and research efforts should continue to help inform their management goals. Of particular importance is red-pine regeneration in response to surface fire. Currently, the Allison plot is experiencing a red pine regeneration failure largely due to competition from woody shrubs such as hazel (*Corylus* species). As the Allison plot ages, tracking stand development will yield more clues about the natural development and successional patterns of these ecosystems in the absence of timber harvesting.

There were a few limitations to the research presented in this thesis that should be addressed in future work on these sites. First, as noted in Chapter 1, we could not accurately map the locations of 32% of the originally mapped trees on the Allison plot. This uncertainty was incorporated into the spatial analysis of mortality events, but could be avoided by more frequent re-sampling efforts. Additionally, the Allison plot field notes, while providing an adequate record of mortality events, were at times difficult to interpret, thereby introducing uncertainty in mortality dates. Similarly, notation was not consistent regarding snags, so snag characteristics were not analyzed over time for the Allison plot, which precludes a detailed analysis of snag dynamics.

We were also limited by the variables and study designs of the other three red pine datasets. First, coarse woody debris was not historically measured in the extended rotation stands or the Allison plot, and size thresholds for measuring CWD in the most recent sampling period differed across the four datasets. Second, tree saplings and seedlings were not consistently measured across the three datasets, thus a thorough analysis of tree regeneration was not possible. Third, chronosequences are not the ideal method of tracking stand development (Johnson and Miyanishi 2008), but for the purposes of this study, allowed us to compare structural characteristics of similarly aged stands with those from the extended rotation site. Based on these limitations, we recommend tracking understory development by measuring saplings and seedlings, focusing sampling efforts on consistent CWD measurement, and measuring other unmanaged second-growth red pine stands in northern Minnesota to further evaluate the results presented in this thesis.

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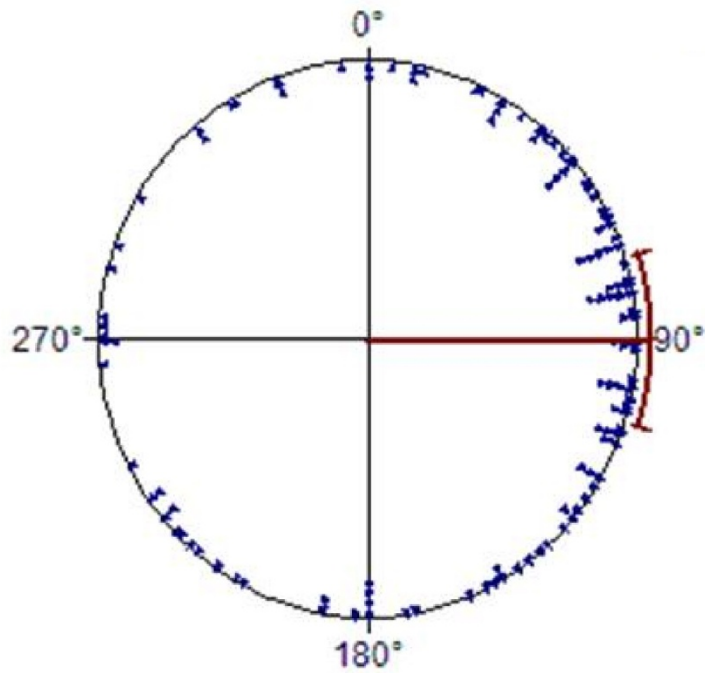
Figure A1. Fall directions of windthrown trees (small triangles). Solid red line indicates the mean fall direction (ca. 90°) with error bars representing standard deviation. The significant uniformity in fall directions corroborates the prevailing westerly wind storm tracks in this region.

Appendix B

Table B1: Primary matrix constructed for the NMS ordinations comparing 1) current structural characteristics of the old-growth, unmanaged second-growth, and extended rotation stands and; 2) structural development of old-growth and extended rotation stands over time. Prefixes denote stand type: AP is Allison plot or old-growth, GSL is Growing-Stock-Levels or extended rotation, PP-SL are old-growth stands, and RPC are Red Pine Chronosequence or unmanaged second-growth stands. All GSL sampling stands are affixed with the sampling year and basal area treatment level. Variables that could not be measured over time (e.g. CWD volume) are denoted by an "M" for missing. Anything not designated as RP, or red pine, specifically includes all other species present on the site. DBH characteristics do not contain stems under 10 cm. Stems/hectare are average across the three plots in each RPC stand. CWD decay class percentages are expressed as volume, not number of pieces.

Site	Gini	AvgDBH	MaxDBH	MinDBH	CWD	RPImpVa	RPRELBA	LIVEBA	StemsHA	DiamOver4	DC2Pct	DC3Pct	DC4Pct	DC5Pct	DBHSD	SnagDens	SnagBA
AP1923	0.05	26.03	61.21	7.82	M	64.59	69.49	30.42	517.00	15.60	M	M	M	M	8.55	M	M
AP1928	0.05	27.52	65.28	8.89	M	68.38	73.48	32.93	498.00	21.60	M	M	M	M	8.76	M	M
AP1933	0.05	28.50	65.28	8.64	M	71.81	77.84	31.37	449.00	24.50	M	M	M	M	8.89	M	M
AP1938	0.05	29.50	66.04	8.63	M	73.96	80.53	32.14	428.00	30.00	M	M	M	M	9.03	M	M
AP1943	0.04	29.90	66.55	8.63	M	76.11	82.82	32.25	420.00	32.00	M	M	M	M	9.09	M	M
AP1948	0.04	30.52	67.56	8.63	M	78.43	85.62	32.61	404.00	34.00	M	M	M	M	9.33	M	M
AP1952	0.04	31.62	67.82	11.43	M	79.70	87.13	33.26	390.00	38.00	M	M	M	M	9.45	M	M
AP1957	0.04	32.68	68.07	11.43	M	82.24	90.92	32.48	357.00	44.00	M	M	M	M	9.51	M	M
AP1963	0.03	33.65	60.71	11.94	M	80.91	87.97	20.67	216.00	47.40	M	M	M	M	9.16	M	M
AP2010	0.03	38.34	63.60	10.30	77.65	80.40	87.35	37.98	298.00	60.50	25.07	40.13	16.80	12.61	12.51	77.59	6.35
G49_32	0.06	20.62	39.37	9.14	M	93.25	97.14	34.45	605	0.68	M	M	M	M	6.4	M	M
G49_23	0.04	21.34	36.32	9.14	M	73.62	69.17	24.57	401	0	M	M	M	M	7.1	M	M
G49_13	0.03	24.25	38.35	9.65	M	49.17	40.43	16	193	0	M	M	M	M	6.89	M	M
G54_32	0.05	22.15	41.56	9.1	M	93.1	97.2	38.19	586	0.24	M	M	M	M	6.59	M	M
G54_23	0.04	22.92	37.85	8.89	M	76	72.46	28.49	404	0	M	M	M	M	7.6	M	M
G54_13	0.03	26.4	41.4	9.4	M	52.56	45.94	18.6	199	0.7	M	M	M	M	7.72	M	M
G59_32	0.04	24.79	42.93	9.4	M	93.7	100	36.08	464	0.6	M	M	M	M	6.16	M	M
G59_23	0.02	26.29	38.86	9.14	M	74.88	72.92	26.31	296	0	M	M	M	M	7.44	M	M
G59_13	0.02	29.22	43.94	9.65	M	52.11	44.15	15.93	144	2.88	M	M	M	M	8.48	M	M
G64_32	0.03	29.4	50.04	12.95	M	94.05	100	35.28	492	6.5	M	M	M	M	6.22	M	M
G64_23	0.02	29.69	45.47	9.4	M	75.8	73.3	25.86	349	3.98	M	M	M	M	7.26	M	M
G64_13	0.02	34.24	45.72	11.68	M	51	44.13	15.57	163	12.82	M	M	M	M	5.82	M	M
G69_32	0.04	31.08	50.55	16	M	94.37	100	35.09	442	9.12	M	M	M	M	5.82	M	M
G69_23	0.02	32.26	46.99	9.14	M	74.48	73.5	25.8	299	9.77	M	M	M	M	6.84	M	M
G69_13	0.02	33.8	48.26	9.65	M	52.26	45.64	16.45	164	26.27	M	M	M	M	9.64	M	M
G74_32	0.03	31.93	51.31	12.19	M	94.5	99.6	37.24	443	11.25	M	M	M	M	5.87	M	M
G74_23	0.02	33.43	48.26	9.4	M	76.03	74.32	27.68	299	12.09	M	M	M	M	7.02	M	M
G74_13	0.02	32.52	49.28	9.14	M	52.82	47.74	18.65	189	34.56	M	M	M	M	11.93	M	M
G79_32	0.04	33.06	52.07	17.02	M	94.7	100	34.94	390	12.81	M	M	M	M	5.83	M	M
G79_23	0.02	35.93	50.04	10.16	M	74.7	72.6	30.39	242	20.69	M	M	M	M	5.538	M	M
G79_13	0.01	40.23	49.78	15.49	M	50	45	15.58	118	64.71	M	M	M	M	6.57	M	M
G84_32	0.03	34.1	52.57	17.78	M	94.7	100	37.1	390	35.9	M	M	M	M	5.8	M	M
G84_23	0.02	37.22	51.56	10.4	M	76	74	27.41	243	30.29	M	M	M	M	5.87	M	M
G84_13	0.01	42.29	51.82	18.29	M	52.34	46.78	17.35	119	76.74	M	M	M	M	6.37	M	M
G89_32	0.03	35.96	53.85	19.3	M	94.3	100	35.16	333	22.5	M	M	M	M	2.3	M	M
G89_23	0.02	39.6	53.85	11.68	M	75.97	73.36	25.79	203	46.58	M	M	M	M	5.72	M	M
G89_13	0.01	44.68	54.36	20.83	M	58.16	54.32	19.1	118	84.7	M	M	M	M	6.33	M	M
G95_32	0.03	37.13	54.1	21.34	M	94	100	37.23	332	29.29	M	M	M	M	5.76	M	M
G95_23	0.02	41.04	55.12	12.7	M	76.48	74.78	28.3	204	55.78	M	M	M	M	5.96	M	M
G95_13	0.01	45.98	56.13	14.73	M	56.87	55.75	21.43	121	86.2	M	M	M	M	7.47	M	M
G03_32	0.03	36.98	55.37	9.4	M	93.47	98.23	33.56	294	31.53	M	M	M	M	8.17	M	M
G03_23	0.02	36.74	56.13	8.89	M	76.68	74.29	28.56	215	55.48	M	M	M	M	13.59	M	M
G03_13	0.06	29.46	57.91	8.89	M	63.42	65.26	24.84	247	44.38	M	M	M	M	18.54	M	M
G07_32	0.06	37.15	55.63	9.14	10.64	93.75	97.92	33.8	287	33.18	45.5735	50.5812	1.79761	2.04762	8.75	12.49028	0.68085
G07_23	0.03	36.03	56.9	9.14	1.91	73.25	69.17	27.13	201	57.93	10.1856	0	14.2936	68.6765	14.55	12.49028	0.14764
G07_13	0.08	27.71	58.17	9.14	3.53	47	40.97	16.6	169	39.34	34.4391	42.8087	22.7522	0	18.82	16.6537	0.18612
PP	0.06	27.49	70.00	10.00	65.54	32.00	36.00	36.20	520.00	11.50	21.99	41.70	11.33	24.97	11.45	92.00	8.15
SP	0.10	23.16	92.00	10.00	56.73	44.50	61.00	39.30	564.00	12.90	12.62	60.67	18.62	8.08	18.76	24.00	2.74
LC	0.03	39.67	78.20	10.30	81.47	39.20	50.40	27.30	184.00	60.00	7.93	67.81	18.72	5.54	17.80	56.00	7.42
IT	0.09	28.15	92.00	7.70	37.19	47.20	66.50	43.10	494.00	23.20	16.76	28.99	9.42	44.82	18.70	54.00	3.63
RL	0.07	31.21	77.20	10.00	68.02	41.60	55.30	33.70	320.00	33.97	2.09	51.65	33.10	13.16	19.19	78.00	7.03
VI	0.06	28.34	77.80	10.00	124.14	40.00	52.00	25.60	292.00	25.87	6.48	58.48	23.53	11.51	17.78	126.00	14.22
SL	0.06	28.66	67.40	7.70	64.55	38.80	49.10	38.60	482.00	21.46	16.90	20.91	46.04	16.15	13.79	166.00	6.00
RPC1875	0.05	26.31	58.90	10.30	23.17	61.85	75.87	54.00	633.00	31.43	0.00	23.03	54.21	22.76	14.46	33.33	0.83
RPC1860	0.04	28.80	60.50	10.30	16.89	68.43	89.04	37.30	433.00	36.84	26.65	42.25	31.10	0.00	16.68	33.33	0.44
RPC1858	0.03	36.65	62.10	10.20	0.00	62.67	77.51	48.60	400.00	50.00	0.00	0.00	0.00	0.00	13.72	200.00	11.73
RPC1855	0.05	22.87	56.80	10.10	27.19	60.56	73.30	35.13	633.00	15.15	88.68	0.00	11.32	0.00	15.49	83.33	2.33
RPC1853	0.04	32.24	61.40	11.00	7.54	68.80	89.78	51.60	533.00	55.00	50.23	49.77	0.00	0.00	14.54	83.33	1.72
RPC1847	0.03	30.91	55.50	10.90	14.21	67.27	86.71	46.11	500.00	25.00	6.03	0.00	33.88	60.08	15.04	16.67	0.60

Allison Plot age structure

To determine tree-age structure of the Allison plot, 100 increment cores were collected in a stratified (by species) random manner in 2010. Cores were mounted, sanded, and aged according to standard dendrochronological methods (Stokes and Smiley 1968). Ring widths were measured to the nearest 0.005 mm resolution using a Velmex measuring system (East Bloomfield, New York, USA). Cores were visually (Yamaguchi 1991) as well as statistically cross-dated using COFECHA software (Holmes 1983). Cores for which the pith was missed were corrected using the geometric method outlined in Duncan (1989) or visually corrected using a pith locator (Applequist 1958). All pine cores were corrected for coring height using the methods outlined in Fraver et al. (2011). Ring counts for ingrowth species (*Betula papyrifera, Ostrya virginiana, Acer rubrum,* and *Picea glauca*) were corrected for missing pith using a pith locator, but not corrected for coring height. *P. resinosa* was the primary species recruited in the early 1800's (Figure B1). *Pinus banksiana* was also present at this time, but complete mortality by 2010 prevented us from determining age. Ingrowth species appeared around the 1890's and had two recruitment peaks from 1910-1930 and 1950 - 1980 (Figure B1).
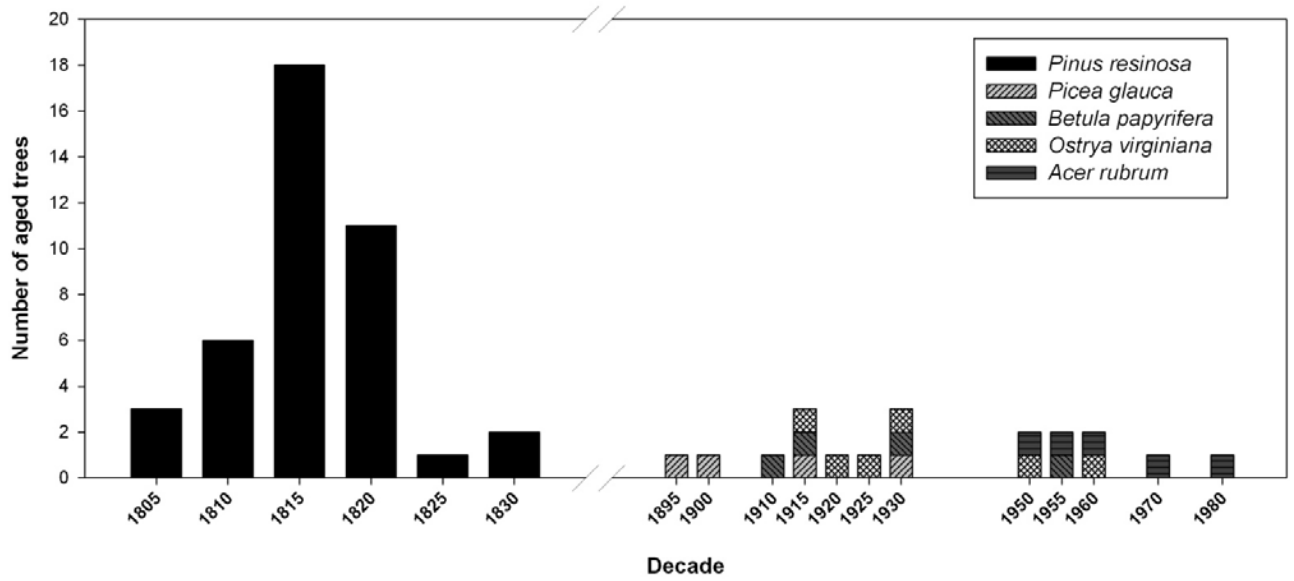
Figure B1: Tree-age structure of the Allison plot based on a sub-sample of increment cores. The stand was initiated following an 1803 fire and was largely dominated by *Pinus resinosa* and *Pinus banksiana*, though by the time of our sampling in 2010, there was no longer *Pinus banksiana* in the stand for age determination.

Table B2: Correlations (Kendall's τ) between structural characteristic variables and non-metric multidimensional scaling Axes 1 and 2. Bold correlations indicate significance (P < 0.05).

Ordination 1: All sites			Ordination 2: Old-growth and extended rotation sites over time		
Structural characteristic	Axis 1	Axis 2	Structural characteristic	Axis 1	Axis 2
Gini coefficient	**-0.336**	-0.299	Gini coefficient	**0.762**	0.185
Average DBH	0.24	-0.064	Average DBH	**-0.447**	**-0.621**
Maximum DBH	**-0.563**	**-0.446**	Maximum DBH	0.161	**-0.513**
Minimum DBH	0	0.037	Minimum DBH	**-0.332**	**-0.281**
CWD volume	**-0.567**	**-0.404**	*P. resinosa* importance value	**0.384**	-0.084
P. resinosa importance value	**0.544**	**0.333**	*P. resinosa* relative basal area	**0.439**	-0.091
P. resinosa relative basal area	**0.368**	0.298	Live tree basal area	**0.5**	-0.038
Live tree basal area	-0.181	0.263	Density	**0.801**	**0.319**
Density	-0.258	0.235	Large tree density	**-0.265**	**-0.828**
Large tree density	0.298	-0.099	DBH standard deviation	0.061	-0.088
% CWD decay class 2	**0.375**	0.07			
% CWD decay class 3	-0.28	**-0.673**			
% CWD decay class 4	0.012	0.118			
% CWD decay class 5	-0.066	0.199			
DBH standard deviation	-0.146	-0.216			
Snag density	**-0.736**	-0.107			
Snag basal area	**-0.778**	**-0.357**			

CWD decay class distributions

    CWD decay class distributions were averaged for each study type and

compared using two-sample Kolmogorov-Smirnov goodness of fit tests. Distributions

were similar between old growth and unmanaged second growth (Figure B2,

Kolmogorov-Smirnov test P = 0.08), unmanaged second-growth and extended rotation

(Kolmogorov-Smirnov test P = 0.82), but differed slightly for old-growth and extended

rotation stands (Figure B2, Kolmogorov-Smirnov test P = 0.01). The unmanaged second-

growth type had fairly even distribution across all decay classes (Figure B2). The old-

growth and extended rotation types had unimodal distributions with the highest
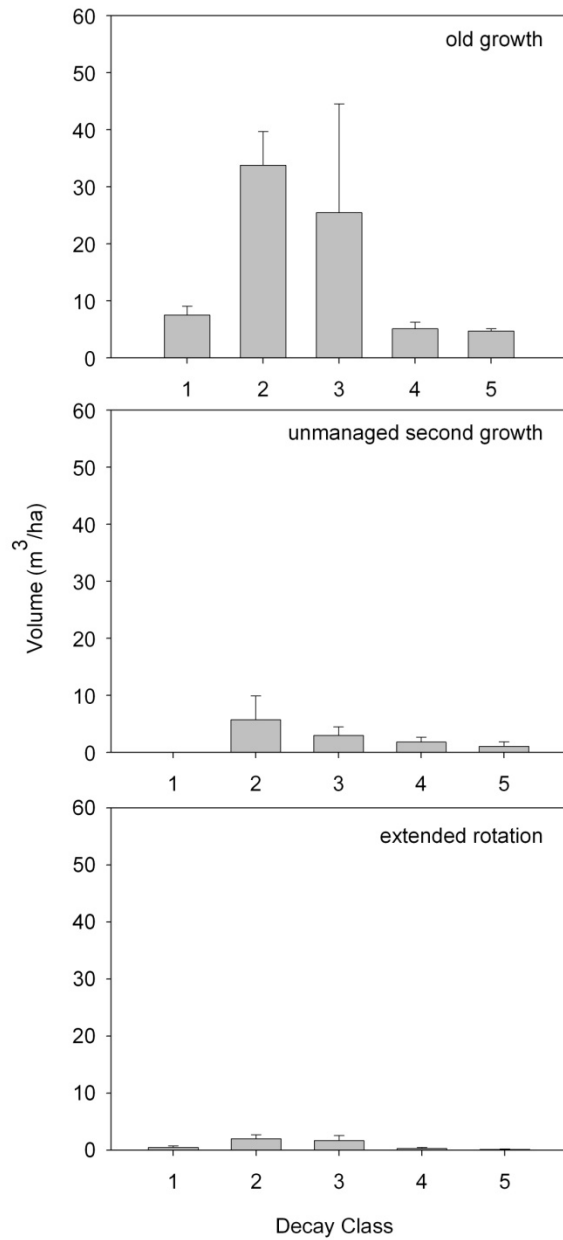
proportion of CWD volume in decay class 3.

Figure B2: Downed coarse woody debris decay class distribution for each study type. All stands within sites were averaged and bars represent standard errors.

Allison plot ingrowth and saplings

In 1948, ingrowth species, that is, trees not tagged in the initial 1923 sampling with DBH ≥ 10 cm, were tallied and DBH measurements were taken. Trees were not tagged and mapped for future measurement, meaning that some of the ingrowth from the 2010 sampling may include those first measured in 1948. Saplings (trees with DBH < 10 cm and height > 4.5 meters), were also tallied in 1948 in a complete inventory. In 2010, saplings were tallied using 14 400 m^2 circular plots. Ingrowth appeared to decrease overall, and shift into higher diameter classes from 1948 to 2010 (Figure B3). Sapling density decreased from 1948 to 2010.
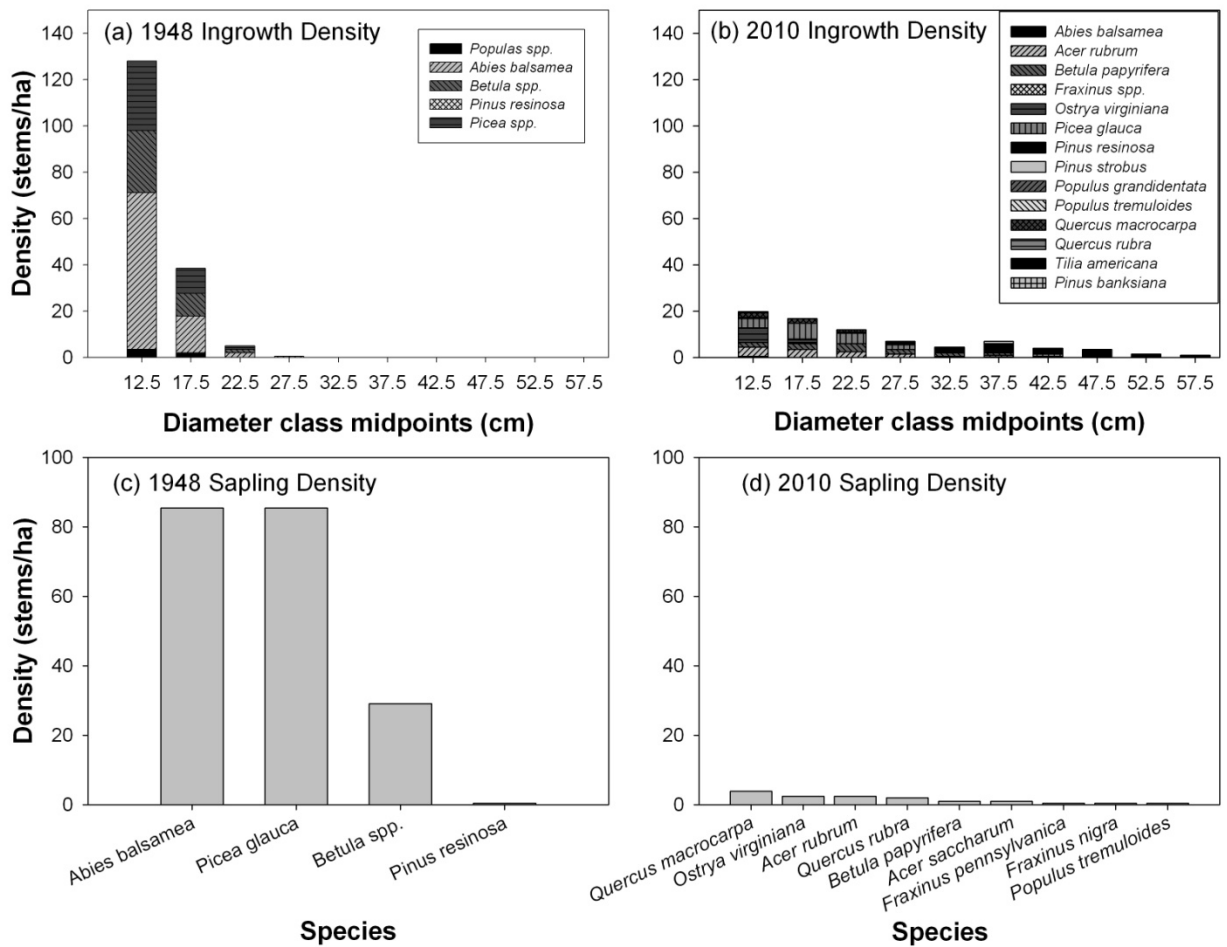
Figure B3: Ingrowth and sapling density for the old-growth Allison plot. (a) density of ingrowth species (stems not present during initial plot establishment in 1923) during the 1948 sampling, (b) density of ingrowth species during the most current sampling period; c) saplings (trees < 10 cm) measured in 1948, and (d) in 2010.