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Structure and development of old-growth, unmanaged second-growth, and extended rotation *Pinus resinosa* forests in Minnesota, USA

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The structure and developmental dynamics of old-growth forests often serve as important baselines for restoration prescriptions aimed at promoting more complex structural conditions in managed forest landscapes. Nonetheless, long-term information on natural patterns of development is rare for many commercially important and ecologically widespread forest types. Moreover, the effectiveness of approaches recommended for restoring old-growth structural conditions to managed forests, such as the application of extended rotation forestry, has been little studied. This study uses several long-term datasets from old growth, extended rotation, and unmanaged second growth *Pinus resinosa* (red pine) forests in northern Minnesota, USA, to quantify the range of variation in structural conditions for this forest type and to evaluate the effectiveness of extended rotation forestry at promoting the development of late-successional structural conditions. Long-term tree population data from permanent plots for one of the old-growth stands and the extended rotation stands (87 and 61 years, respectively) also allowed for an examination of the long-term structural dynamics of these systems.

Old-growth forests were more structurally complex than unmanaged second-growth and extended rotation red pine stands, due in large part to the significantly higher volumes of coarse woody debris (70.7 vs. 11.5 and 4.7 m^3/ha, respectively) and higher snag basal area (6.9 vs. 2.9 and 0.5 m^2/ha, respectively). In addition, old-growth forests, although red pine-dominated, contained a greater abundance of other species, including *Pinus strobus*, *Abies balsamea*, and *Picea glauca* relative to the other stand types examined. These differences between stand types largely reflect historic gap-scale disturbances within the old-growth systems and their corresponding structural and compositional legacies. Nonetheless, extended rotation thinning treatments, by accelerating advancement to larger tree diameter classes, generated diameter distributions more closely approximating those found in old growth within a shorter time frame than depicted in long-term examinations of old-growth structural development. These results suggest that extended rotation treatments may accelerate the development of old-growth structural characteristics, provided that coarse woody debris and snags are deliberately retained and created on site. These and other developmental characteristics of old-growth systems can inform forest management when objectives include the restoration of structural conditions found in late-successional forests.

1. Introduction

Old-growth forests are widely recognized as invaluable resources for guiding 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 old-growth structures and processes, with the goal of identifying reference conditions to which managed systems are compared (Foster et al., 1996; Stephenson, 1999; Spies, 2004). Concerns over declines in biodiversity in managed forest systems have also led to the expansion of management strategies to reduce the disparity between managed and unmanaged systems by managing for greater structural complexity. Such approaches typically use information on natural disturbances to guide harvest planning and implementation (Curtis, 1997; Palik et al., 2002; 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.

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A primary focus for studies of 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 influencing 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, as well as differences in functional traits among constituent tree species (Harmon et al., 1986; Vanderwel et al., 2006; D'Amato et al., 2008). Comparisons of structural conditions between old-growth and second-growth systems have emphasized the pervasive influence of anthropogenic disturbances, often evident as reduced heterogeneity, 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 harvesting of trees and stands before live tree and deadwood complexity and heterogeneity can develop (Franklin et al., 2007).

One management approach that has been proposed for restoring more complex 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, this approach assumes that extending the period of stand development and allowing for 'appropriate recovery periods' (Franklin et al., 2007) allows accrual of structural attributes (e.g., more age classes, variety of tree sizes, and large trees) characterizing old-growth forests (Curtis and Carey, 1996). In addition, extended rotation forestry typically includes repeated thinning treatments designed to emulate self-thinning processes and accelerate the development of understory communities and larger tree sizes (Bailey and Tappeiner, 1998). However, the ability of extended rotation forestry for restoring these critical structural elements in managed forests remains unknown (Hale et al., 1999).

To evaluate the efficacy of extended rotation forestry at restoring structural complexity, we compared the structure and development of old-growth, extended rotation, and unmanaged second-growth red pine (*Pinus resinosa* Ait.) stands in northern Minnesota, USA. *P. resinosa* has an extensive natural range in north-central and northeastern North America and is an ecologically and commercially important tree species occupying a significant proportion of the natural and managed forested landbase in this region. *P. resinosa* is typically managed with even-aged silvicutural methods such as clearcutting followed by planting (Gilmore and Palik, 2006). 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 logging and associated fires at the turn of the 20th century (Schulte et al., 2007). These changes to historic *P. resinosa* forests further highlight the need for a better understanding of forest structure and developmental pathways in these systems to inform restoration and ecological management approaches.

Our objectives were to: (1) characterize and compare the range of variability in a set of structural attributes among old-growth, extended rotation, and unmanaged second-growth *P. resinosa* forests; and (2) contrast structural development through time among these forest conditions. To the best of our knowledge, the second objective has not been previously undertaken, although it is critical for a comprehensive evaluation of extended rotation forestry as a means of accelerating structural development toward that found in old-growth forests. By comparing extended rotation and old-growth *P. resinosa* at different developmental stages, 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. Moreover, many areas of second-growth forest around the globe are being set aside as ecological reserves that can contribute to conservation objectives, including increasing representation of older forest conditions on the landscape (e.g., Jönsson et al., 2009; Foster et al., 2010). By including the unmanaged second-growth systems in our comparisons we examined how this "passive" approach restored old-growth structural conditions vs. more "active" approaches like extended rotation forestry.

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 were located in Itasca and Scenic State Parks and the Chippewa and Superior National Forests of northern Minnesota. Temperatures range from −20 °C in January to 25 °C in July and mean annual precipitation from 53 to 81 cm (Silver, 2012). Stands occurred on a range of substrates, but all were fire-origin stands dominated by *P. resinosa* on well-drained, low-fertility, and 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 stands 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 in each stand; Fraver and Palik, 2012). A more detailed description of the stands can be found in Silver (2012) 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 (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. Recent disturbances affecting this plot included prescribed burns in 1998, 2000, and 2003, as well as a severe windstorm in 1995 that caused localized damage on the plot and significant pine mortality throughout Itasca State Park. Recent disturbance history for the seven remaining old-growth stands, including patchy windthrow from a 1999 storm, is summarized in Fraver and Palik (2012) and Aakala et al. (2012). These stands represent a variety of cohort structures, the oldest living trees having been established 201–317 years prior to sampling, depending on stand.

The extended rotation stands were part of the Red Pine Growing-Stock-Levels study, a long-term study on the Cutfoot Experimental Forest, within 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, and 32.1 m^2/ha retained post-treatment) that were maintained with repeated thinning every 5–10 years from 1954 to 2007. All treatment stands consisted of a single age cohort; stand age at the time of final sampling in 2007 was 143 years. Each basal area treatment was applied to three 1- to 2-ha stands 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 to 165 years at time of sampling in 2009, and each included three 0.02-ha plots. These

Table 1
Environmental characteristics and forest types for the four *Pinus resinosa* data sets used in this study.

Site	Stand 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 Stand, single 2.02-ha plot
Old-growth age-cohort study	Old growth	Well-drained sandy, nutrient-poor soils derived from glacial outwash	201–331	7 Stands, one 0.5-ha plot per stand
Red pine chronosequence	Unmanaged mature second growth	Well-drained sands derived from glacial outwash	137–165	6 Stands, three 0.02-ha plots per stand
Growing-Stock-Levels study	Extended rotation	Well-drained sands derived from glacial outwash	145	5 Treatments, 3 replicate stands per treatment, 3 0.08-ha plots per replicate

stand ages were comparable to those of the extended rotation stands (143 years), which allowed us to examine the effects of repeated thinning treatments on forest structure relative to second-growth systems with no thinning history (i.e., active vs. passive approaches to restoration).

The existence of repeatedly-measured, long-term datasets for both the Allison plot and the extended rotation stands provided an ideal 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.

2.2. Field methods

Detailed field-sampling protocols for the seven old-growth stands, 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 stands, species and diameter at breast height (DBH, 1.4 m) were recorded for all living and dead trees $\geqslant$10 cm between 2009 and 2011, depending on stand. Downed CWD pieces $\geqslant$10 cm diameter were inventoried at these stands 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 stand. For the extended rotation study, species and DBH were recorded for all living and dead trees >8.9 cm every 5–10 years from 1949 to 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 stands.

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 $\geqslant$10 cm DBH, including 'ingrowth', i.e., trees that had become established since the initial inventory. Saplings (tree stems <10 cm DBH, height >1.4 m) were also tallied by species at this time within 14,400-m^2 circular plots systematically located within the larger 2-ha plot. We inventoried CWD throughout the entire 2-ha plot 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 structures were 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 ratios (cross-sectional height-to-width) developed from the old-growth *P. resinosa* stands used in this study (Fraver and Palik, 2012). For stands with multiple plots, volumes were averaged across plots and expressed on a per-ha basis. Coarse woody debris volume, snag density, and snag basal area were each compared between old-growth, extended rotation (treatments pooled), 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. Sites had a similar underlying distribution for each coarse woody debris and snag variable tested and therefore met the assumptions for Kruskal–Wallis tests.

For all stands, extended rotation treatments, and sampling periods, live-tree size-class distributions were constructed using 10-cm diameter classes. Regression equations were fit to the resulting distributions to determine the overall distribution form using PROC REG within SAS (SAS Institute Inc., 2012). The Gini coefficient (G) was used to examine the degree of size inequality within live-tree distributions between stands and extended rotation treatments over time. This coefficient ranges from zero (all individuals are equal in size) to one (maximum size inequality) 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:

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

where x = DBH and n = total trees, G = the Gini coefficient, i.e., the mean difference between each pair of individual sizes, divided by the total mean size. In addition, *P. resinosa* importance values (IV = [relative density + relative basal area]/2) were calculated for all stands and sampling periods using stems >10 cm DBH. We constrained our univariate comparisons of structural attributes to CWD to restrict experiment-wide error rates, but included live-tree size characteristics within ordinations examining structural variation among stands (see below).

Non-metric multidimensional scaling (NMS) ordination was used to examine patterns in structural variation among stands and treatments based on their current conditions, as well as over time for the Allison plot and extended rotation study (McCune and Grace, 2002). The primary matrix for comparisons among stands, based on current conditions, contained stand and treatment-level averages for structural attributes, including CWD volume, snag density, snag basal area, DBH attributes (average, standard deviation, minimum, and maximum), *P. resinosa* IV, *P. resinosa* relative basal area, total basal area, percentage of CWD volume in decay classes 2–5, total stem density, large tree density (trees >40 cm DBH), and degree of size inequality based on Gini coefficients. In contrast, the matrix used to examine structural development through time between the Allison plot and the extended rotation study contained only structural data based on live trees in each sampling period, due to the absence of long-term CWD data from these areas. For these temporal 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 to simplify 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 and Sørensen's distance measure. 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 conditions (McCune and Mefford, 1999).

3. Results

3.1. Current forest structure

CWD volumes were significantly higher in the old-growth stands 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); however, CWD volumes did not differ between unmanaged second-growth and extended rotation stands ($Z = -1.37$, $P = 0.178$). Old-growth and unmanaged second-growth stands also had significantly higher snag densities 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, based on multivariate patterns in live- and dead-tree attributes, differed significantly (MRPP, $A = 0.19$, $P < 0.0001$). This result was also illustrated by the grouping of stands in ordination space, which explained 71.1% of the variation in the data describing current structural conditions (Fig. 1, final stress = 9.8, final instability = 0.0). The greatest variation between these stand conditions was explained by axis 1 (46.3%), which represented a gradient from stands with high snag basal area and snag density and high

Table 2
Characteristics of coarse woody debris (CWD) and snags in *Pinus resinosa* stands in northern Minnesota (n = number of stands for old growth and second growth, n = number of basal area treatment replicates [plots pooled] for extended rotation).

Structural attribute	Old growth (n = 8)		Second growth (n = 6)		Extended rotation (n = 15)	
	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 ($P \leqslant 0.05$; Wilcoxon rank sum test) between stand types are denoted by lowercase letters.

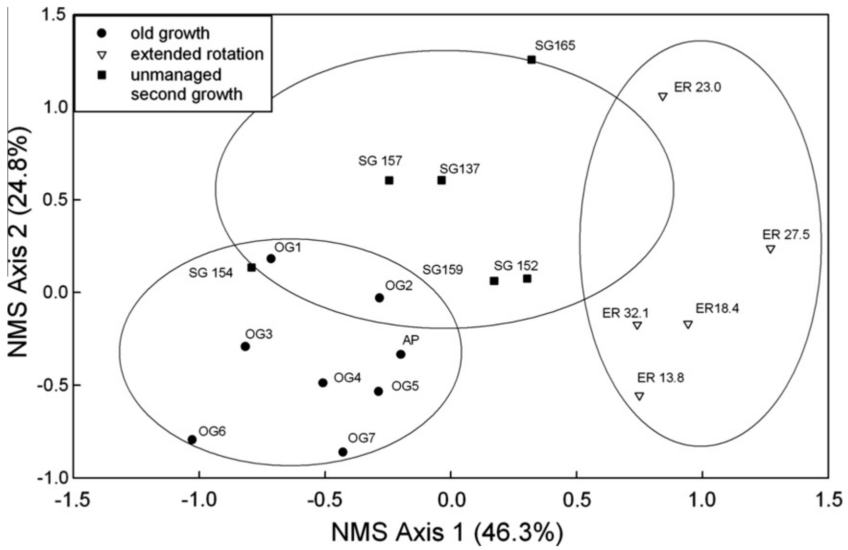

Fig. 1. NMS ordination of current structural conditions within old-growth, unmanaged second-growth, and extended rotation *Pinus resinosa* forests in Minnesota, USA. SG = unmanaged second growth, followed by stand age suffix; ER = extended rotation, followed by basal-area treatment suffix (m^2/ha); AP (Allison plot), OG 1–OG 7 = old growth stands.

Table 3
Selected structural and compositional characteristics in *Pinus resinosa* stands in northern Minnesota. Values for the extended rotation and old growth sites are from the final year of measurement only. OG = Old growth, SG = Second growth, and ER = extended rotation.

Stand	Gini coefficient	Average DBH (cm)	Maximum DBH (cm)	Percentage of trees with DBH >40 cm	*P. resinosa* relative basal area (%)
Allison plot	0.03	38.3	63.6	60.5	87.3
OG 1	0.06	27.5	70.0	11.5	36.0
OG 2	0.10	23.2	92.0	12.9	61.0
OG 3	0.03	39.7	78.2	60.0	50.4
OG 4	0.09	28.2	92.0	23.2	66.5
OG 5	0.07	31.2	77.2	33.9	55.3
OG 6	0.06	28.3	77.8	25.9	52.0
OG 7	0.06	28.7	67.4	21.5	49.1
SG 1	0.05	26.3	58.9	31.4	75.9
SG 2	0.04	28.8	60.5	36.8	89.0
SG 3	0.03	36.7	62.1	50.0	77.5
SG 4	0.05	22.9	56.8	15.2	73.3
SG 5	0.04	32.2	61.4	55.0	89.9
SG 6	0.03	30.9	55.5	25.0	86.7
ER 13.8 m^2/ha	0.08	27.7	58.2	39.4	41.0
ER 23.0 m^2/ha	0.03	36.0	56.9	58.0	69.2
ER 32.1 m^2/ha	0.06	37.2	55.6	33.2	97.9

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 (Fig. 1). Old-growth stands had high maximum DBH and low *P. resinosa* IV compared to the extended rotation stands (Table 3). 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 3, low snag density, and lower maximum DBH in the positive portion of the axis (Fig. 1, Table 4).

3.2. Structural development through time

The patterns in live-tree size distributions varied over time within and among the old-growth Allison plot, extended rotation, and unmanaged second-growth stands (Fig. 2). The Allison plot and extended rotation tree size distributions were primarily unimodal or skewed unimodal curves. Distributions for the unmanaged second-growth stands were right-skewed unimodal distributions (Fig. 2). The intermediate and lower basal area treatments for the extended rotation stands had much flatter live-tree distribution (Fig. 2). Although the extended rotation treatments and the Allison plot had similar live-tree distributions over time (Fig. 2), the Allison plot had trees in a wider range of diameters (Table 3). In the final sampling period, ingrowth was reflected in the smaller size classes at both the Allison plot and extended rotation stands (Fig. 2 and 7.5–12.5 cm), most notably the 13.8 and 23.0 m^2/ha basal-area treatments.

The NMS ordination of live-tree structural characteristics over time for the Allison plot and extended-rotation stands suggested distinct patterns of development (Fig. 3). All sampling periods grouped closely together by stand type and basal-area treatment, as illustrated by the ordination diagram, which explained 72.1% of the variation in the data (Fig. 3, final stress = 5.48, final instability <0.001). The configuration of stand types 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

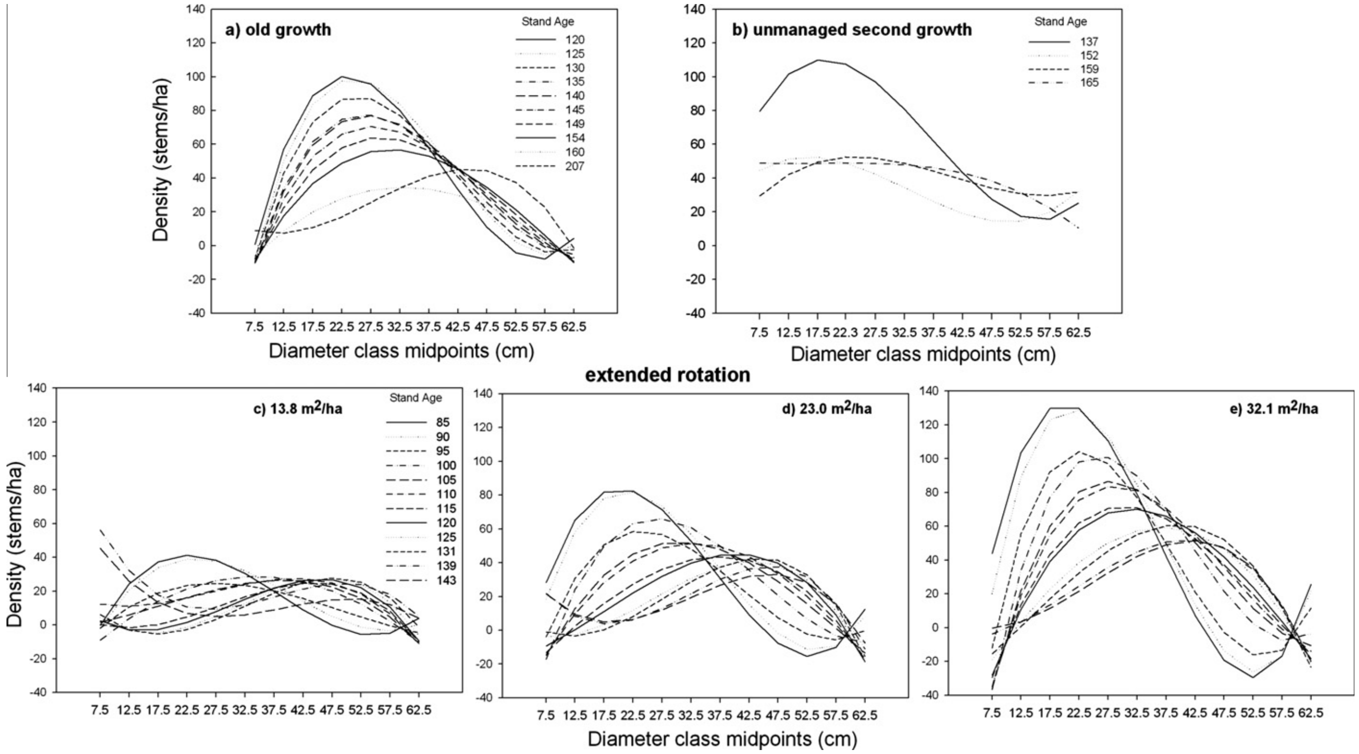

Fig. 2. Changes in diameter distributions over time for (a) old-growth *Pinus resinosa* Allison plot from age 120–207, (b) unmanaged second-growth *P. resinosa* from age 137–165 (four of the six stands shown here for visual clarity), and (c–e) extended rotation *P. resinosa* from age 85–143 years for three basal-area treatments: (c) the lowest, 13.8 m^2/ha, (d) the intermediate, 23.0 m^2/ha, and (e) the highest, 32.1 m^2/ha. All stands show a general shift to larger 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.

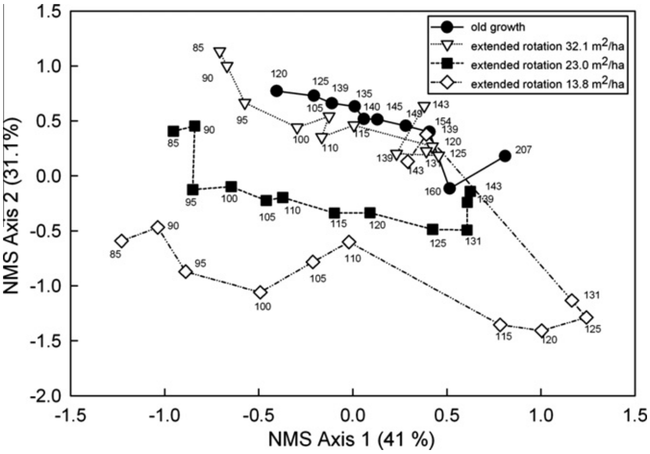

Fig. 3. NMS ordination of live-tree size distribution, density, and basal area characteristics of the old-growth Allison plot (10 re-measurement periods) and extended rotation stands for three basal area treatments: 32.1, 23.0, and 13.8 m^2/ha. Each point on the graph represents a sampling period (and corresponding stand age) for the stand and treatment levels. See Table 4 for structural characteristic correlations with axes 1 and 2.

DBH in the positive portion of the axis (Fig. 3). The distribution of stands along axis 2 (31.1% variation explained) generally reflected stand 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 and high *P. resinosa* basal area and IV in the positive portion (Fig. 3, Table 3, and Table 4). Additional variation in extended rotation stand development visually coincides with thinning treatments. For example, thinning just before the re-measurement at stand age 110 in the 13.8 m^2/ha treatment resulted in a structural shift in multidimensional space (Fig. 3).

4. Discussion

Our results indicate that when compared to unmanaged second-growth, extended rotation forestry was more effective at generating live-tree structural characteristics that approximated those found in old-growth *P. resinosa* systems, suggesting that active management may achieve these conditions more rapidly than passive approaches. Nonetheless, neither active nor passive approaches approximated the range of CWD volumes or snag basal areas found in old-growth systems. These findings suggest that extended rotation forestry may be a strategy to hasten the structural development of more complex conditions in currently unmanaged second-growth; however, provisions for the deliberate creation and retention of CWD and snags will be necessary if goals include restoring the full suite of structural conditions found in old growth. Our results also support a well-documented conclusion that old-growth forests are more structurally complex than their extended rotation and unmanaged mature second-growth counterparts. In particular, old-growth *P. resinosa* forests are distinguished by higher volumes of CWD (including pieces in advanced decay), higher snag basal areas, and more complex tree size distributions (including larger trees), characteristics that have been widely recognized as distinct between managed and unmanaged systems (Kirby et al., 1998; McGee et al.,1999; Uotila et al., 2001) and second-growth and old-growth forests (Spies and Franklin, 1991; Noel et al., 1998). The comparisons made in this study and the efficacy of extended rotation forestry are relevant to other forest types worldwide where dominant species are long-lived and shade intolerant.

4.1. Current forest structure

Downed CWD volumes 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; Fraver et al., 2008; Aakala, 2010). The difference in CWD volumes between old growth and unmanaged second growth 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). In particular, much of the downed CWD within the unmanaged second growth was smaller diameter material presumably resulting from natural self-thinning mortality, whereas CWD in all of the old-growth stands was larger diameter material, the result of canopy disturbance or senescence of overstory trees. CWD volume was very low in the extended rotation stands, likely due to the removal of potential CWD inputs during thinning entries and subsequent low mortality rates (Powers et al., 2012). Although harvesting activities often cause increased inputs of small-diameter CWD (Fraver et al., 2002), these materials decay rapidly, resulting in lower volumes of CWD in managed stands relative to old-growth stands (Sturtevant et al., 1997; 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 prescriptions.

Snag densities in the old-growth and unmanaged second-growth stands were similar, but were nearly seven times higher than that of extended rotation stands, suggesting that passive management over the time frame examined here allows the accrual of some structures characteristic of old growth. Duvall and Grigal (1999) also observed higher snag density in unmanaged *P. resinosa* forests. Snag density is especially affected by forest management, as low vigor and declining living trees are typically removed before they fully senesce or become more susceptible to disturbance, a long-term effect also found in other managed coniferous forest systems (Cline et al., 1980; Reid et al., 1996; Fridman and Walheim, 2000). Snag basal area was significantly higher in old growth compared to unmanaged second growth stands: diameters of snags within unmanaged second growth were generally smaller than those found in old growth (old growth = 31.3 ± 12.0 cm and second growth = 10.2 ± 5.4 cm). Snag basal area was significantly higher in old growth compared to extended rotation stands, as well, however unmanaged second-growth and extended rotation stands had statistically similar snag basal area. These trends reflected both the lower abundance of snags in extended rotation stands, as well as the small diameter of those few snags that remained in these systems, which likely reflects the preferential removal of larger diameter individuals.

Although absolute tree sizes differed between old-growth, extended rotation, and unmanaged second-growth stands (Table 3), the live-tree size distribution forms were quite similar among the three stand types by the final sampling period (Fig. 2). Slight differences in size-distribution characteristics are not surprising given the difference in age between these stand types, as maximum DBH values are expected to increase as stands develop. However, despite differences in tree size, all stand types exhibited unimodal or skewed unimodal live-tree diameter distributions. Other studies have documented diameter distribution forms deviating from the negative exponential distribution commonly attributed to old-growth forests (Hett and Loucks, 1976), particularly in systems dominated primarily by long-lived, shade intolerant overstory species (Zenner, 2005; Fraver et al., 2008). Instead, temporal variability in disturbance leads to a wide variety of size distributions in older forests, including rotated-sigmoid and unimodal distributions (Coomes and Allen, 2007).

Our study stands were also differentiated by *P. resinosa* dominance based on importance values (IVs) and relative basal areas. Specifically, old-growth stands had lower *P. resinosa* IVs and lower relative basal areas than the extended rotation (23.0 and 32.1 m^2/ha stocking levels) and unmanaged second-growth stands (Table 3). This finding indicates that species composition shifted as the stands aged, reflecting the ingrowth of non-pine species, and leading to the development of a lower canopy stratum that includes *Betula papyrifera*, *Ostrya virginiana*, *Acer rubrum*, and *Abies balsamea* (Zenner and Peck, 2009; Fraver and Palik, 2012).

4.2. Structural development through time

Our approach of tracking the development of tree size distributions through time provided insights into the long-term effects of extended rotation treatments. In general, the tree-size distributions for *P. resinosa* in extended rotation treatments, as well as old-growth Allison plot, were unimodal through age 120 years, after which ingrowth of largely intermediate and shade-tolerant tree species created highly left-skewed and more complex distributions (Fig. 2). By age 143 years, this difference had become more pronounced with decreasing basal-area retained (Fig. 3), as the more open conditions and cessation of understory removal on the 13.8 and 23.0 m^2/ha treatments apparently fostered recruitment of other, more tolerant species. The scarcity of ingrowth observed in the 32.1 m^2/ha treatments and at the old-growth Allison plot at this time resulted in unimodal or right-skewed unimodal distributions. Ingrowth had appeared on the old-growth plot by the time of the most recent inventory at stand age 207 years (Fig. 2), presumably the result of more recent canopy openings following patchy overstory mortality as well as the recent prescribed burning in the stand (pers. obs.). The largely unimodal distributions for *P. resinosa* is readily explained by its shade intolerance. Systems dominated by shade intolerant tree species may often establish as single cohort stands, with self-thinning processes primarily shaping the development of size distributions (Ford, 1975; Oliver and Larson, 1996), a process typically leading to unimodal distributions similar to those observed in this study. In some cases, more complex composite distributions may develop due to the ingrowth of more shade tolerant species (e.g., Zenner, 2005; Fraver and Palik, 2012); however, the distribution of the intolerant, overstory species generally maintains a unimodal pattern over time. This pattern has been shown, for example, in Scots pine (*Pinus sylvestris* L.) forests of Fennoscandia (Rouvinen and Kuuluvainen, 2005) and in Douglas-fir (*Pseudotsuga menziesii* Mirbel) forests of the western United States (Zenner, 2005). Moreover, the unimodal distributions observed in both the Allison plot and extended rotation 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; Zenner, 2005).

Our results suggest that extended rotation forestry accelerates old-growth structural development for some, but not all, structural attributes; large-tree density, overall density, average DBH, and maximum DBH were characteristics accelerated by extended rotation forestry. 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 (Fig. 3). This acceleration varied between the stocking levels and the variation was due to differing 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. Several previous 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), and that particular attributes such as the accrual of large trees and CWD in advanced stages of decay are especially time demanding, taking many decades to develop (Jönsson et al., 2009). Similarly, we concluded that extended rotation forestry restores characteristics of live-tree distributions found in old-growth systems, but does not maintain CWD and snag attributes. We note that the old-growth Allison plot used in this developmental comparison contains smaller trees and fewer age cohorts than the seven other old growth site, placing it at the low end of the natural range of structural variability for old-growth *P. resinosa* systems. As a result, restoring the full range of structural conditions found in old-growth stands may require much longer recovery intervals and greater provisions for retention of large living and dead trees as part of extended rotation forestry prescriptions.

4.3. Conclusions and management implications

There is an increasing interest in restoring more complex structural features characteristic of old-growth in managed forests (Millar et al., 2007; Fraver and Palik, 2012), and these management goals often incorporate specific structural targets (Keeton, 2006; Bauhus et al., 2009; D'Amato et al., 2011). The importance of forest structure in driving ecosystem processes and biodiversity has been well documented (Spies, 1998), but few studies have directly assessed forest management approaches recommended for restoring complex structure. By utilizing two rare long-term, permanent-plot studies, our work highlights the importance of stand development processes such as mortality, competition, and regeneration (or lack thereof) in influencing structural differences between old-growth and extended rotation stands, a finding found in other studies of *P. resinosa* systems (D'Amato et al., 2010; Aakala et al., 2012; Fraver and Palik, 2012). Furthermore, by incorporating additional old-growth stands and data from managed 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, by comparing structural attributes, we determined that old-growth forests contain greater snag basal area and CWD volume 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; Bunnell and Houde, 2010).

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 increasing structural complexity before wide implementation. While extended rotation forestry has been widely suggested and adopted for achieving structural conditions similar to old-growth (e.g., Curtis and Carey, 1996; Hale et al., 1999), we found that in practice, it leads to a deficit in CWD volumes and snag basal areas. To account for the deficit 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 stands had living-tree size distributions similar to those of old-growth stands. To further approximate old-growth structure with extended rotation forestry, a wider range of tree size classes should be encouraged, and ingrowth and tree regeneration should be protected. Additionally, management plans should continue to incorporate either thinning from below to allow dominant canopy trees to grow into larger size classes or variable density thinning to maintain structural complexity and increase stand heterogeneity at stand and landscape scales (Curtis and Carey, 1996; Franklin et al., 2007). Deliberately creating snags and downed logs from a portion of trees traditionally removed by these thinning

Table 4
Correlations (Kendall's τ) between structural characteristic variables and non-metric multidimensional scaling axes 1 and 2 for Figs. 1 and 3. Bold correlations indicate significance ($P < 0.05$).

Ordination 1: all stands (Fig. 1)			Ordination 2: old-growth and extended rotation over time (Fig. 3)		
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**	CWD volume	–	–
P. resinosa importance value	**0.544**	**0.333**	*P. resinosa* importance value	**0.384**	−0.084
P. resinosa relative basal area	**0.368**	0.298	*P. resinosa* relative basal area	**0.439**	−0.091
Live tree basal area	−0.181	0.263	Live tree basal area	**0.5**	−0.038
Density	−0.258	0.235	Density	**0.801**	**0.319**
Large tree density	0.298	−0.099	Large tree density	**−0.265**	**−0.828**
% CWD decay class 2	**0.375**	0.07	% CWD decay class 2	–	–
% CWD decay class 3	−0.28	**−0.673**	% CWD decay class 3	–	–
% CWD decay class 4	0.012	0.118	% CWD decay class 4	–	–
% CWD decay class 5	−0.066	0.199	% CWD decay class 5	–	–
DBH standard deviation	−0.146	−0.216	DBH standard deviation	0.061	−0.088
Snag density	**−0.736**	−0.107	Snag density	–	–
Snag basal area	**−0.778**	**−0.357**	Snag basal area	–	–

treatments would allow for the recruitment of deadwood, while also accelerating the development of large, living trees. We also found that passive management over the time frame examined here allows the accrual of some old-growth structural characteristics, such as snag densities and large trees, in developing second-growth stands. Inclusion of additional study stands, measurement of stand heterogeneity, and future monitoring of the old-growth and extended rotation stand structure will be necessary to further critically evaluate extended rotation forestry as these systems develop.

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