Stand and cohort structures of old-growth *Pinus resinosa*-dominated forests of northern Minnesota, USA

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Abstract

Questions: What is the natural range of variability in stand and age structure of old-growth *Pinus resinosa*-dominated forests? Does the spatial pattern of tree ages provide insights into past disturbances that structured these forests?

Location: Old-growth *P. resinosa* forests at seven sites in Minnesota, USA.

Methods: We applied detailed dendrochronological methods to living and dead material to reconstruct stand and age structures prior to European settlement of the region. We linked dendrochronological data to mapped stem locations to shed light on spatial patterns of past disturbance.

Results: Data pooled across sites revealed a mean living tree basal area of 34.8 m^2·ha^{-1}, snag basal area of 6.9 m^2·ha^{-1} and down woody debris (DWD) volume of 100 m^3·ha^{-1}. Living tree diameter distributions varied between sites; however, at all sites, smaller diameter classes were dominated by non-pines, many pre-dating the onset of fire suppression in the 1920s. There were a variety of *P. resinosa* age structures, including one-cohort, two-cohort (at times with additional sporadic recruitment) and three-cohort stands. For multi-cohort stands, the spatial pattern of cohorts shows considerable within-stand patchiness.

Conclusions: The wide range of stand and age-cohort structures in these old-growth *P. resinosa* stands depicts pre-settlement forests more complex than those of the single-cohort, post-stand-replacing-fire model that has guided regional forest management. Within-stand patchiness of cohort age structures implies disturbances operating at scales smaller than typically associated with this regional forest type. Presence of non-pine 'ingrowth' on all sites might suggest that *P. resinosa* stands supporting these species lie within the natural range of variability for this community type, representing situations in which surface fires did not occur for extended periods or were spatially patchy at the stand scale. The diversity of reference conditions documented here suggests targets that might guide ecological restoration prescriptions for these ecosystems, with the goal of reintroducing structural and compositional complexity reflecting natural disturbance and stand development.

Introduction

Forest ecologists have long relied on old-growth forests to provide benchmark conditions regarding forest structure, composition and natural disturbance regimes. Such information allows us to assess the role of anthropogenic influences in actively managed or secondary forests, and thus can guide forest management and conservation decisions, as well as provide targets for restoration efforts (Foster et al. 1996). Setting restoration targets, however, remains a problematic task, in part because of uncertainties regarding historical conditions for a given ecosystem (Moore et al. 1999). Further, such targets must be viewed in the context of dynamic systems with myriad successional and developmental pathways, as well as potentially large natural ranges of variability for a given community type (Pickett & Parker 1994; Moore et al. 1999).

Throughout the northern hemisphere, there has been increasing interest in restoring the diversity of tree size and age structures in managed pine forests, many of which have been greatly altered from their natural state by harvesting, fire suppression and/or livestock grazing (Moore et al. 1999; Kuuluvainen 2002). Restoration efforts often include management prescriptions that emulate natural disturbances and stand development processes, producing structural and composition outcomes that fall within the natural range of variability for the system (Seymour & Hunter 1999; Franklin et al. 2007). Successful implementation of such approaches requires quantifiable reference conditions, which are often lacking.

Pinus resinosa Ait. (red pine) forests of the western Great Lakes region, USA, exemplify the challenges of setting targets for restoration. First, quantitative data from primary *P. resinosa* forests are quite rare. Second, decades of fire suppression in extant old-growth remnants may have shifted structure and composition outside the natural range of variability, thus limiting their use as references. Third, old-growth remnants of this forest type are extremely rare, given the extensive harvesting of Great Lakes pine forests that began in the late 1800s. This logging, as well as the frequent associated slash fires, has shifted dominance in these former pine forests to *Populus* or *Quercus* species (Palik & Pregitzer 1992; Schulte et al. 2007). Only through plantations established since the 1930s has *P. resinosa* maintained its status as one of the principal commercial timber species in the region.

Further, a close reading of the literature reveals divergent views regarding natural disturbances and the resulting age structures of *P. resinosa* stands. For example, early authors reported that *P. resinosa* regenerates in large canopy gaps created by windthrow (e.g. Bergman & Stallard 1916; Bergman 1924), and through this process *P. resinosa* stands can be self-perpetuating (Harvey 1922). At the other extreme, authors report that successful regeneration of this species depends on wildfire (e.g. Cook et al. 1952; Spurr 1954), with occasional severe fires shaping *P. resinosa* age structures across large landscapes (Heinselman 1973). In fact, Buckman et al. (2006) consider *P. resinosa* to be one of the most fire-dependent pines on Earth. The disturbance conditions fostering successful recruitment of this species have important implications for stand structure and composition, as a disturbance regime dominated by non-stand-replacing events may result in two- to multi-cohort stands that could persist over time (Seymour & Hunter 1999). Conversely, a regime dominated by stand-replacing events, such as crown fires, would result in single-cohort stands that require subsequent fire for renewal (Frelich 2002). A better understanding of these dynamics is critical for designing restoration prescriptions for *P. resinosa*-dominated forests, as well as for developing management approaches intended to sustain stand structures that fall within the natural range of variability for this system. Moreover, closer examination of structural conditions in reference *P. resinosa* systems can serve as a model framework for assessing other fire-influenced conifer forests.

To address these needs, we devised a study to quantify the natural range of variability in stand and age structure of *P. resinosa*-dominated forests in Minnesota, USA, using old-growth remnants as reference guides. Specifically, we asked: (1) what is the natural range of variability in stand and age structure of old-growth *P. resinosa* stands; (2) does the spatial pattern of tree ages provide insights into the past disturbances that structured these old-growth forests? To address the concern that current structures may not represent pre-European settlement conditions, because of fire suppression, we apply detailed dendrochronological methods to living and dead material to reconstruct stand and age structures that were initiated well before fire suppression began.

Methods

Study area and sites

Our study sites all lie within the Laurentian Mixed Forest Province (Aaseng et al. 2003) of northern Minnesota, USA. The climate is cold-temperate continental, characterized by short cool summers and long, severe winters. Mean annual temperature ranges from 1 °C in the northern portion of the province to 4 °C in the south, and mean annual precipitation ranges from 53 cm in the western portion of the province to 81 cm in its eastern limit in Minnesota (Aaseng et al. 2003). The region is characterized by rolling topography associated with various Pleistocene glacial features. *Pinus resinosa* forests in this region typically occupy well drained, sandy and/or rocky and nutrient-poor soils (Aaseng et al. 2003). This forest type can exist as pure stands or in mixtures with *Pinus strobus* (white pine) and both tolerant and intolerant hardwoods (Horton & Brown 1960). *Pinus resinosa* is rated as intermediate (Horton & Brown 1960) to intolerant (Benzie 1977) of shade, and its maximum longevity is estimated at 400 yr (Johnson 1994).

Our research questions required that we locate mature *P. resinosa* sites in Minnesota that had no visible or historical evidence of timber harvesting. Seven sites, out of ca. 45 surveyed, met our criteria. Each was within currently protected areas, including Itasca State Park, Scenic State Park, Pine Point Research Natural Area, Sunken Lake Natural Area (both within Chippewa National Forest), Lac La Croix Research Natural Area, Ramshead Lake and Voyageurs Island (all three within Boundary Waters Canoe Area Wilderness) (Fig. 1).
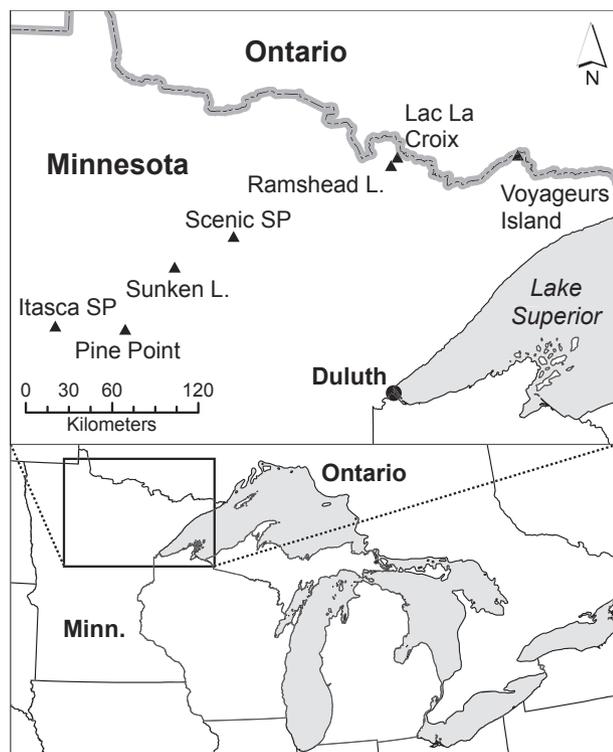
Fig. 1. Location of the seven old-growth *Pinus resinosa* study sites in northern Minnesota, USA.

Field sampling

One 70.7-m × 70.7-m plot (0.5 ha) was established at each of the seven sites. We selected this plot size following Zenner & Peck (2009a), who report that many descriptors, including spatial patterns, of mature *P. resinosa* forests stabilize when sampling area is increased to 0.5 ha. Busing & White (1993) report similar findings for old-growth mixed-species forests. The small stand size at several locations constrained our intent to randomize plot locations within stands. Thus, to reduce subjectivity in plot placement and to focus on forest interior conditions, we simply placed plots in the geographical centres of each old-growth stand. Within each plot, we recorded diameter at breast height (DBH, 1.37 m), species and *x* and *y* co-ordinates for all living and standing dead trees (stems ≥ 10 cm DBH). For the purpose of mapping stem locations, plots were divided into 5-m × 70.7-m transects, and within each transect, trees were uniquely numbered consecutively from south to north. For living pines, we extracted one increment core near the base of each tree to estimate age and determine growth patterns. Because of high tree density at the Pine Point site, we subsampled pine trees by coring every other numbered tree, thus ensuring representative sampling across diameter classes and throughout the plot, while eliminating bias in tree selection. In three

transects on each plot, we tallied all saplings (individuals >1.37 m in height, less than 10 cm DBH) by species. In these same transects, we cored all living non-pine trees to approximate age structures for these species.

The protected status of sample sites precluded any destructive sampling of living or dead material. Thus, we were unable to collect radial cross-sections or wedges that are sometimes used for dendrochronological analyses, particularly of dead material. Instead, we extracted large diameter (12 mm) increment cores from dead pines, both standing and fallen. Borers of this diameter greatly increase the likelihood of obtaining useable samples from partially decayed wood, while minimizing the visual impact of sampling. In nearly all cases, the sapwood had rotted from these samples; however, once cross-dated (below), establishment dates and growth patterns could be readily obtained.

We also inventoried down woody debris (DWD) volume to shed light on past disturbances and to augment the structural description for this old-growth forest type. For each DWD piece originating inside the plot, we recorded species (when possible), diameters at large and small ends, length, *x* and *y* co-ordinates (pines only) and decay class, using a five-class system (Sollins 1982), with class I being least and class V most decayed. Only pieces with a large-end diameter greater than 10 cm were inventoried.

Laboratory procedures

Increment cores were affixed to wooden mounts and sanded to a fine polish. Ring widths were measured to the nearest 0.01 mm using a Velmex (Bloomfield, New York, US) sliding-stage stereomicroscope. Cross-dating of both living and dead material was conducted using the marker year method of Yamaguchi (1991), with verification by COFECHA (Holmes 1983). Establishment dates from cross-dated deadwood were included in the age class distributions. All cohorts ultimately identified were based on living trees; the deadwood cores provided supporting information for earlier periods. To refine ring counts for cores that missed the pith, we applied Duncan's (1989) geometric pith location method and confirmed these corrections with Applequist's (1958) visual method. We also adjusted age estimates to account for coring height, using regression models that simultaneously consider coring height and growth rates from a tree's innermost rings (Fraver et al. 2011). These models were developed from stem sections of *P. resinosa* trees growing under various light conditions in this same region. Used in combination, these methods substantiate our estimated establishment dates, making them as close to the true establishment dates as possible without destructively sampling the study trees themselves (see Gutsell & Johnson 2002).

Table 1. Relative basal area (as a percentage) for tree species at each of the seven old-growth *Pinus resinosa* sites. Species with relative basal area < 2% at any site are not listed.

Tree species	Itasca S.P.	Sunken L.	L. La Croix	Scenic S.P.	Ramshead L.	Voyageurs Is.	Pine Pt.	Mean
Pinus resinosa	66.5	49.1	50.4	61.0	55.3	52.0	36.0	52.9
Pinus strobus	9.8	36.5	48.1	16.9	35.7	31.1	24.8	29.0
Betula papyrifera	3.3	9.7	1.3	10.4	3.5	8.1	7.0	6.2
Abies balsamea	–	1.3	–	5.0	3.5	4.2	–	2.0
Acer rubrum	7.9	1.1	–	4.2	< 1	–	2.0	2.2
Picea glauca	1.5	< 1	–	< 1	< 1	4.6	< 1	1.2
Populus spp.	3.5	< 1	< 1	1.8	–	–	10.1	2.4
Quercus spp.	4.9	< 1	–	–	–	–	19.6	3.6

We calculated the volume of each DWD piece using the conic-paraboloid formula, which has greater accuracy than traditional formulae (Fraver et al. 2007). Volumes of pieces in decay classes IV and V were multiplied by cross-sectional height–width ratios (0.82 and 0.42, respectively, determined in a concurrent study at these same sites) to account for their collapse during decay.

Results

Forest structure and composition

Pines clearly dominated the canopies of all seven old-growth sites (Table 1), with *Pinus resinosa* accounting for 53% of stand basal area and *Pinus strobus* accounting for 29% (plots pooled). At several sites, hardwoods also occupied canopy positions, but were more common in the subcanopy. Data pooled across sites revealed a mean living tree basal area of 34.8 $m^2 \cdot ha^{-1}$ and density of 408 $trees \cdot ha^{-1}$, with snag basal area at 6.9 $m^2 \cdot ha^{-1}$ and density of 81 $snags \cdot ha^{-1}$ (considering trees $\geq$ 10 cm DBH; Table 2). The seven sites showed a variety of diameter distributions (Fig. 2). Sapling abundance varied widely among sites (from 414 to 5111 $stems \cdot ha^{-1}$); however, *P. resinosa* saplings were extremely uncommon, ranging from 0 (on four sites) to 19 $stems \cdot ha^{-1}$ (Table 2). Mean DWD volume was 100.0 $m^3 \cdot ha^{-1}$, of which *P. resinosa* comprised 56% and *P. strobus* 20% on average (excluding pieces that could not be identified to species). On each site, DWD was distributed unequally among decay classes, and decay class distributions differed among sites (not shown). Additional structural characteristics of each plot are shown in Table 2.

Cohort structure and disturbance

Two of the seven old-growth sites (Itasca, Scenic State Parks) showed primarily single-cohort *P. resinosa* age structures; two showed double cohorts (Lac La Croix, Pine Point); two showed double cohorts with sporadic additional recruitment (Ramshead Lake, Voyageurs Island); and one showed three cohorts (Sunken Lake) (Fig. 3). We define cohort as a group of trees of similar age, presumed to have recruited following a single disturbance. Figure 3 includes establishment dates derived from deadwood, which bolstered these age data, particularly for the earlier time periods. However, none of the cohorts shown consists entirely of dead trees. Within a cohort, establishment often occurred over protracted periods, spanning from 9 to 32 yr. On all sites, *P. resinosa* were consistently the oldest trees; *P. strobus* and non-pines, when present, became established long after the earliest *P. resinosa* cohorts (Fig. 3).

On sites with more than one *P. resinosa* cohort, the spatial distribution of cohorts may provide insights into the scale at which past disturbances operated. Four such sites with sufficient numbers of trees in each cohort demonstrate various patterns of interspersion and/or segregation (Fig. 4). The oldest trees were generally scattered throughout the sites, with the younger cohorts interspersed. On the sites with more than two cohorts (Sunken Lake, Ramshead Lake), the youngest two cohorts appear to be somewhat segregated, although low numbers of trees per cohort confounded any rigorous assessment of spatial patterns.

Plots showed abundant visual evidence of past disturbance in the form of fire scars on living and dead trees, as well as uprootings (relatively recent trees plus soil pits and mounds from long-past wind storms; Table 2). The mean number of fire-scarred pine trees (living or dead) was 17 ha^{-1}. Most fire-scarred pines had multiple scars.

Wind damage was common on all plots, with a mean of 19 $uprooted trees \cdot ha^{-1}$ (old and recent). The varied decay states of uprooted trees suggest multiple wind storms at six of the seven sites.
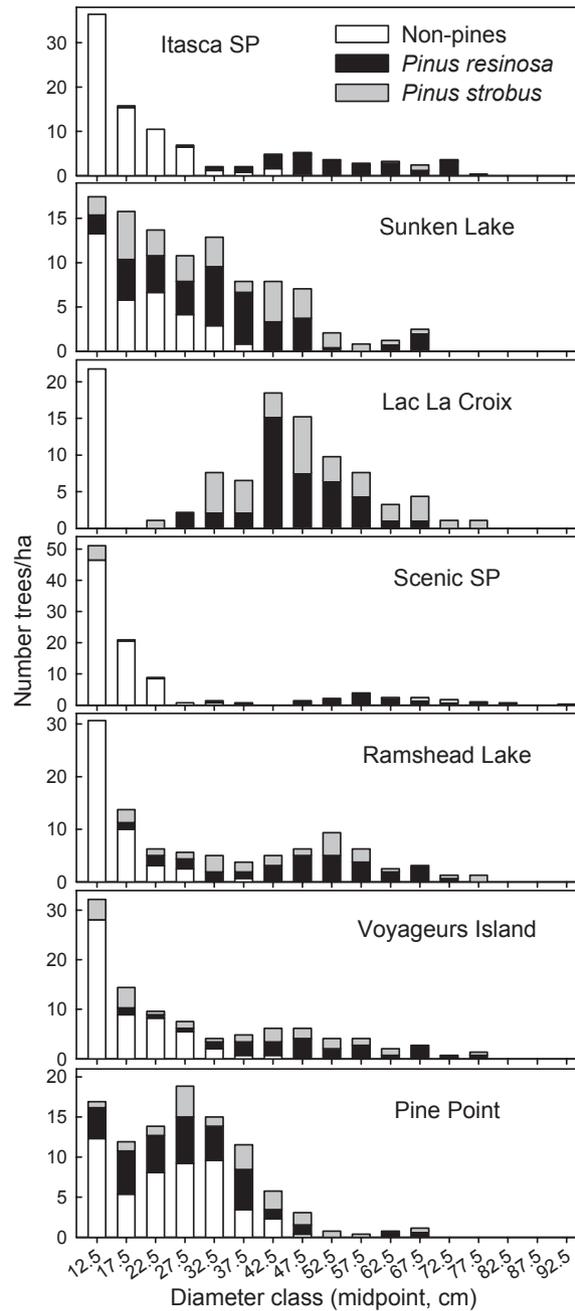
Discussion

Forest structure and composition

Tree size distributions found here generally lie within the ranges reported from the few studies of old-growth *Pinus resinosa* in this region. Diameter ranges are similar to those inferred from Bergman (1924) and calculated from Harvey's (1922) data for old-growth *P. resinosa* stands in

Table 2. Structural characteristics of the seven old-growth *Pinus resinosa* sites, demonstrating a wide range of variability among sites. BA = basal area (m²); DWD = down woody debris (m³); saplings = stems > 1.4 m in height, less than 10 cm DBH. Trees and snags refer to stems ≥ 10 cm DBH.

Site	Live trees BA·ha⁻¹	Live trees Stems·ha⁻¹	Trees >40 cm·DBH·ha⁻¹	Snags BA·ha⁻¹	Snags Stems·ha⁻¹	Snags >40 cm·DBH·ha⁻¹	Fire scars No.·ha⁻¹	Uprootings No.·ha⁻¹	Saplings·ha⁻¹ *Pinus resinosa*	Saplings·ha⁻¹ *Pinus strobus*	Saplings·ha⁻¹ Non-pine	DWD Vol·ha⁻¹
Itasca S.P.	43.1	494	130	3.6	54	10	20	24	0	0	773	61.6
Sunken L.	38.6	482	104	5.4	140	2	6	15	0	0	943	74.5
Lac La Croix	27.3	184	112	7.4	56	24	8	16	0	1405	3706	127.6
Scenic S.P.	39.3	564	92	2.7	24	6	28	30	0	802	236	82.4
Ramshead L.	33.7	320	114	7.0	78	22	18	2	19	405	1556	120.4
Voyageurs Is.	25.6	292	80	14.2	126	54	26	24	9	858	3404	157.8
Pine Point	36.2	520	62	8.1	88	20	16	22	9	0	405	75.5
Mean	34.8	408	99	6.9	81	20	17	19	5	496	1575	100.0

Fig. 2. Tree diameter distributions for the seven old-growth *Pinus resinosa* sites, showing a range of forms. Non-pines include *Abies balsamea*, *Picea glauca*, *Acer rubrum*, *Betula papyrifera*, *Populus* spp. and *Quercus* spp.

this region, but are larger than those reported by Frelich & Reich (1995) and Zenner & Peck (2009a) for contemporary old-growth *P. resinosa* in this same region. Although the diameter distributions vary from site to site (Fig. 2), three distinct distributions, each associated with a species or species group, can be recognized across sites: (1) abundant
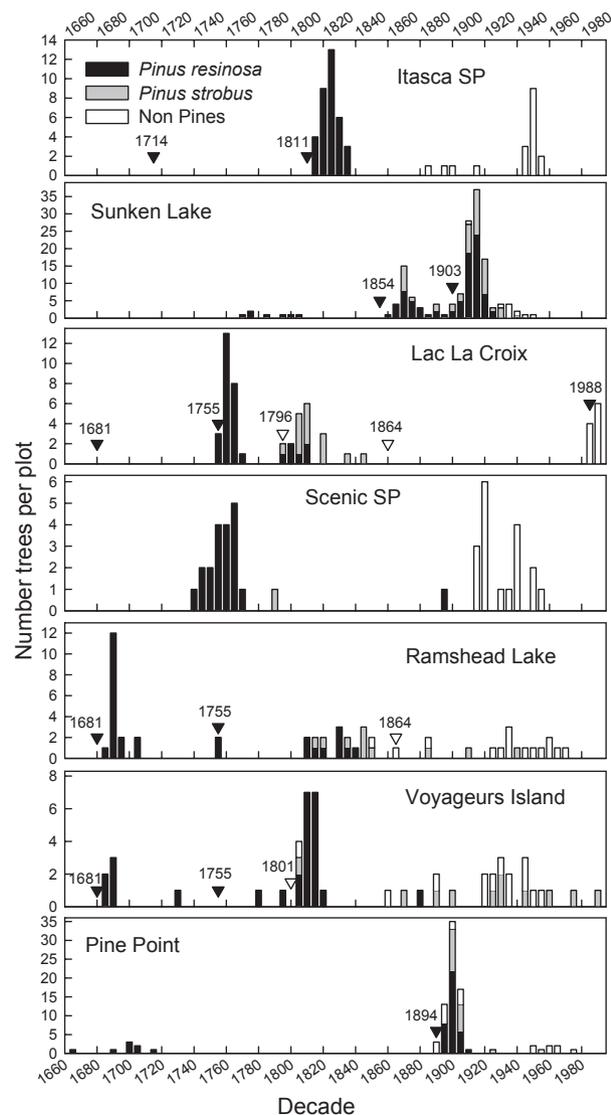
Fig. 3. Age structures of the seven old-growth *Pinus resinosa* sites showing a variety of forms, including one-cohort, two-cohort (at times with sporadic recruitment) and three-cohort age structures. Solid triangles denote known fire dates at each site; open triangles denote known fire dates on nearby sites.

small-diameter and younger non-pines that generally create a reverse-J form; (2) older *P. resinosa* that form large, broad peaks or plateaus reflecting prolonged establishment periods (Fig. 3), as well as variability in individual tree growth; and (3) *Pinus strobus* which, like *P. resinosa*, forms broad peaks, but unlike *P. resinosa*, is typically also found in the smaller diameter classes. Together, these patterns produce a range of diameters contributing to the structural diversity of the stands. All sites have relatively large numbers of trees ≥ 40 cm DBH (Table 2), a size threshold indicative of late-successional *P. resinosa* forests in this region (D'Amato et al. 2010).

One striking feature of the diameter distribution is the absence of small-diameter, or younger, *P. resinosa* and the abundance of small stems of non-pine species. This same disparity is clearly evident in the sapling layer, where *P. resinosa* is uncommon or absent (Table 2). Without disturbance, such as fire, to reduce the abundance of non-pines and promote pine regeneration, these sites will likely convert to mixed-species forests in which *P. resinosa* is virtually absent. This lack of pine recruitment is commonly attributed to fire suppression, which began in this region in ca. 1920. On our sites, non-pines include shade-intolerants (*Betula papyrifera*, *Populus* spp.), mid-tolerants (*Quercus* spp., *Acer rubrum*) and shade-tolerant species (*Abies balsamea*, *Picea glauca*). However, these species may have occupied sub-canopy positions in pine forests of the pre-settlement (i.e. pre-fire suppression) period as well, simply as a result of lengthy periods devoid of surface fires. Using early Government Land Office surveys from the late 1800s, Whitney (1986) found that more than 88% of pine stands included hardwoods and tolerant conifers in sub-canopy positions. Similar findings have been reported by Harvey (1922) and Kittredge (1934) for pre-settlement conditions in this region. These findings suggest that more contemporary inventories of old-growth *P. resinosa* remnants (Grigal & Ohmann 1975; Frelich & Reich 1995; Zenner & Peck 2009a) may depict tree compositions that lie within the natural range of variability for this community type, representing situations in which surface fires had not occurred for extended periods. However, the diameter structure of such forests may fall outside the natural range if lengthy fire-free periods allow non-pines to achieve sizes potentially larger than those of pre-settlement forests.

To the best of our knowledge, no published DWD volume data for old-growth *P. resinosa* systems are available for comparison to our 100 m³·ha⁻¹. Our finding that *P. resinosa* and *P. strobus* comprised portions of DWD abundance similar to their relative abundance as living trees suggests some consistency in tree species composition over the past century or more. Uneven within-site distribution of DWD pieces among decay classes (not shown) suggests pulses in disturbance and deadwood inputs over perhaps the past century or more. Differences in decay class distributions among sites suggest dissimilar histories of low- to moderate-severity disturbances.

Cohort structure and disturbance

Our results clearly show a variety of *P. resinosa* age structures, including one-cohort, two-cohort (at times with additional sporadic recruitment) and three-cohort stands (Fig. 3). Although a number of workers mention multi-cohort *P. resinosa* stands in the US Lake States (Heinselman 1973, 1996; Frissell 1973; Frelich 2002; Drobyshev et al.
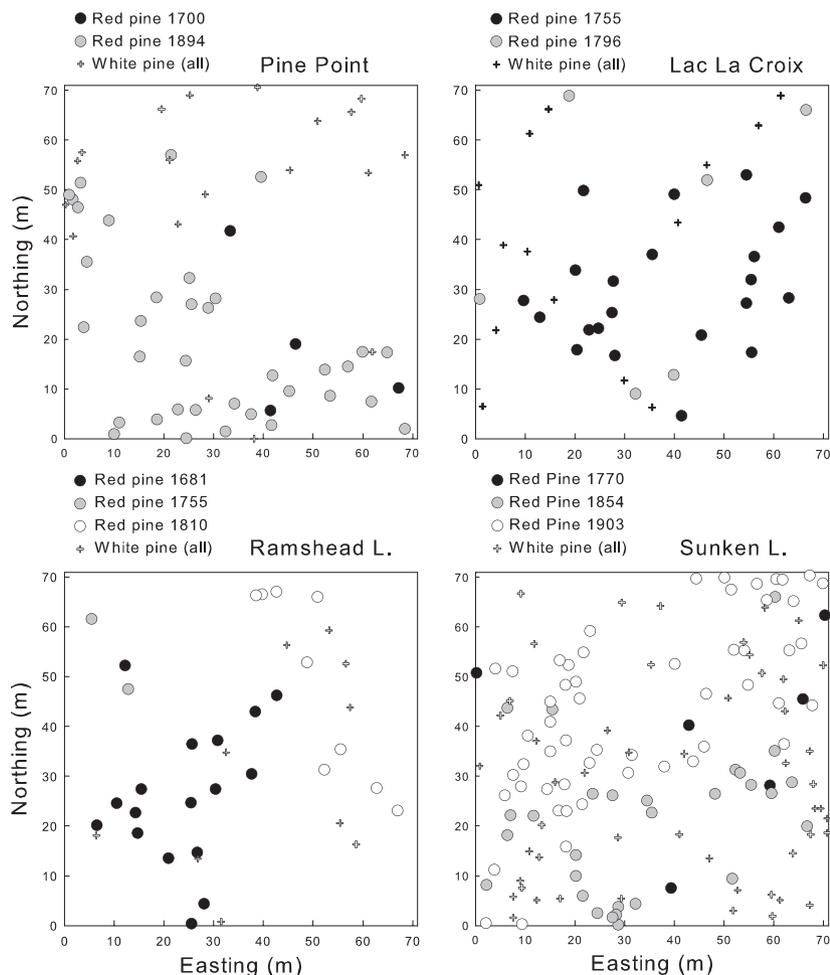
Fig. 4. Spatial arrangement of trees on four old-growth *Pinus resinosa* multi-cohort plots with sufficient numbers of trees in each cohort to warrant mapping. *Pinus resinosa* trees are listed according to cohort establishment dates; *Pinus strobus* are not listed as such. Plot size is 0.5 ha.

2008), none provide detailed stand-level data. Similarly, studies from other regions report *P. resinosa* stands consisting of more than one cohort. Engstrom & Mann (1991) and Mann et al. (1994) report multi-cohorts located on steep, rocky slopes in Vermont, and Butson et al. (1987) and Bergeron & Brisson (1990) report multi-cohorts at the species' northern limit in Ontario and Quebec, respectively. Our study documents such age structures for additional *P. resinosa* site types in the western portion of the species' range where this had not been definitively shown.

The protected designation of the study sites precluded destructive sampling necessary to reconstruct detailed fire histories. Nevertheless, our data along with previous studies in the region, allow us to make inferences concerning the nature of past disturbances. The fire scars noted on pine trees at all study sites provide clear evidence of occasional non-stand-replacing fires, some of which may have fostered *P. resinosa* regeneration. Six of the 13 cohorts identified across all sites became established immediately

following a locally documented fire (Fig. 3), using fire dates obtained from published local accounts for Itasca State Park (Spurr 1954; Frissell 1973), Pine Point (Kurmis & Ness 1966), Lac La Croix, Ramshead Lake and Voyageurs Island (Heinselman 1996), as well as our own dated fire scars from Sunken Lake. For the three Boundary Waters sites, if we include fire dates shown in adjacent mapped stands (Heinselman 1996), three additional cohorts can be attributed to fire (Fig. 3). The lack of any known fire dates for Scenic State Park precludes making inferences there.

Two sites where two pine cohorts established in rapid succession require special consideration. The ca. 1796 cohort at Lac La Croix and the ca. 1903 cohort at Sunken Lake (Fig. 3) became established at a time when many trees of the previous cohorts, given their ages of 25–35 yr, would have had bark too thin to afford protection from fire (Bergeron & Brisson 1990; Heinselman 1996). The establishment of the more recent cohorts may be explained by very patchy fire, which would have caused partial canopy

removal, yet allowed young trees to survive elsewhere in the stand. The patchiness of fires may be controlled in part by moderate severity wind storms, which in this system often create multiple tree-fall gaps (Bergman 1924), resulting in canopy openings up to 30 m in diameter (Frelich & Reich 1995), and thus creating fuel concentrations of a corresponding size. Such localized fuel loads may increase surface fire intensity to the point of crowning out in adjacent edge trees, causing additional local tree mortality and further opening the canopy.

For our sites with more than one *P. resinosa* cohort, the spatial distribution of cohorts may shed additional light on the nature and size of past disturbances. The oldest cohorts at the multi-cohort sites survived documented fires, and they appear to have provided seed for the next cohort, which was scattered among or surrounding the older trees (Fig. 4). Both Ramshead and Sunken Lake show the oldest trees to be similarly scattered about the plot, with the two younger cohorts loosely segregated from each other. Such patterns could be generated by environmental boundaries, but there was no evidence of this in the field, nor on US Forest Service stand maps. We suggest that loose segregation and inter-digitation (Sunken Lake) of younger cohorts reflects within-stand patchiness of fire intense enough to kill overstorey trees and foster *P. resinosa* establishment in canopy openings.

The historical fire regime for *P. resinosa* systems in northern Minnesota has been described as mixed severity, with frequent low-intensity surface fires occurring on average every 5–50 yr and high-intensity crown fires occurring every 150–250 yr (Heinselman 1996). Frissell's (1973) results from north-central Minnesota also point to a mixed-severity regime, although with slightly higher frequencies. Although our data are insufficient to make claims concerning regional fire frequencies, they do support the notion of a mixed-severity regime. However, our stand-level results suggest that mixed severity may occur within single fires, resulting in patchy cohort structures seen in several of our sites. Under this scenario, *P. resinosa* forests could persist in the absence of stand-replacing fire, with regeneration occurring in disturbance patches, as has been suggested by Harvey (1922), Bergeron & Brisson (1990) and Frelich (2002). Patchiness of cohort structures similar in scale to those seen here and attributed to fire has been reported by Bergeron & Brisson (1990) for *P. resinosa* forests in Quebec, and by Wallenius et al. (2002) for the ecologically similar *Pinus sylvestris* forests in Fennoscandia.

The presence of uprootings and pit-and-mound microtopography on all sites points to wind as an additional significant disturbance agent. Although *P. resinosa* is widely considered as fire-dependent (Spurr 1954; Frissell 1973; Buckman et al. 2006), a close reading of the literature, particularly early literature, also points to *P. resinosa* regen-

eration following windstorms (Sherrard 1903; Bergman & Stallard 1916; Bergman 1924; Ahlgren 1976; Bergeron & Gagnon 1987). Further, although it is generally accepted that successful *P. resinosa* seedling establishment requires exposed mineral soil, as from fire (Cook et al. 1952; Frissell 1973), a number of workers (e.g. Van Wagner 1971; Burns & Honkala 1990), as well as our own observations, confirm that establishment can occur in moss or thin litter. Thus, for cohort establishments not coinciding with documented fires (e.g. the ca. 1805 cohort at Ramshead Lake), as well as sporadic recruitment between cohorts, we suggest that windstorms may have promoted *P. resinosa* establishment or recruitment.

We acknowledge that our results and interpretation are drawn from only seven sites; however, to our knowledge these seven sites represent the near complete population of intact old-growth *P. resinosa* forests in Minnesota (another site exists in the Scientific and Natural Area at Itasca State Park, but its strict protection precludes extensive increment coring). We believe that these seven sites document stand and age structures representing at least a portion of the natural range of variability exhibited by this forest type in Minnesota.

Application to restoration and ecological management

Scientists and forest managers worldwide are embracing the concept of forest management based on natural disturbances and stand development processes (e.g. Seymour & Hunter 1999; Palik et al. 2002; Bauhus et al. 2009; Puettmann et al. 2009). These approaches intend to manage stands within the historic range of structure and composition that result from natural processes (Seymour & Hunter 1999; Franklin et al. 2007). The use of ecological approaches requires quantitative information on structural targets for management, namely by identifying reference conditions in unmanaged stands. Adequate information exists for several major pine-dominated forest types (e.g. Fulé et al. 1997; Moore et al. 1999; Kuuluvainen 2002), but is lacking for others, particularly where old-growth and mature unmanaged examples are rare.

Our results reveal a wide range of stand and age-cohort structures for old-growth *P. resinosa* sites in northern Minnesota, indicating a diversity of conditions suitable as restoration targets and guides for ecological management, and suggesting much flexibility in the types and timing of the various interventions aimed at restoring these systems. Documented reference conditions include one- to three-cohort age structures (the latter including cohort patchiness), a range of tree sizes including large-diameter living and dead trees, and a mix of sub-dominant tree species. These conditions differ markedly from those of most

contemporary *P. resinosa* forests, which are often plantations or actively managed even-aged stands. Traditional management strategies tend to result in single-cohort stands lacking large-diameter living and dead trees and composed almost exclusively of *P. resinosa*. Forest managers may choose to develop prescriptions designed to move stands closer to reference conditions by restoring, to varying degrees, the structural targets we have identified. However, this does not imply managing for old-growth conditions *per se*, but rather an attempt to reduce disparities between reference and managed conditions in working forests (Franklin et al. 2007). We note also that in areas where shoot blights of the genera *Sirococcus* and *Diplodia* are present, creating stands with younger or smaller *P. resinosa* under mature infected trees may be counterproductive, as smaller trees in this situation exhibit high rates of infection and subsequent mortality (Bronson & Stanosz 2006). However, shoot blight infestation is not ubiquitous across the range of red pine ecosystems, suggesting that multi-cohort stands are not universally problematic.

Given the importance of wildfire in maintaining this forest type, prescribed fire has long been recommended as a restoration tool, with the intent of eliminating competition from established non-pines, as well as promoting pine regeneration (Spurr 1954; Van Wagner 1971; Frissell 1973). Although it has clearly been shown to reduce the density of non-pine understories (Buckman 1964; Methven & Murray 1974), concerns exist that prescribed fire may cause a shift in dominance toward *Populus* or *Pinus banksiana* (Ahlgren 1976) or northern hardwoods (Zenner & Peck 2009b).

The *P. resinosa* situation in the US Lake States directly mirrors that of northern Europe, where recent emphasis on multi-purpose forest management, as well as emergence of forest certification, has created pressure to diversify plantations such that they more closely resemble their unmanaged counterparts (Cameron et al. 2001; Bauhus et al. 2009), in what has come to be called 'transformation silviculture' (O'Hara 2001). Achieving such structural objectives, however, may take many decades. For example, the formation of DWD in advanced stages of decay and the development of tree size differentiation, particularly including large trees, have been shown to be among the more time-demanding objectives in the conversion of managed forests to more complex conditions (Storaunet et al. 2000; Jönsson et al. 2009).

Acknowledgements

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