



Long-term impacts of prescribed fire on stand structure, growth, mortality, and individual tree vigor in *Pinus resinosa* forests



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ABSTRACT

Prescribed fire is increasingly being viewed as a valuable tool for mitigating the ecological consequences of long-term fire suppression within fire-adapted forest ecosystems. While the use of burning treatments in northern temperate conifer forests has at times received considerable attention, the long-term (>10 years) effects on forest structure and development have not been quantified. We describe the persistence of prescribed fire effects in a mature red pine (*Pinus resinosa* Ait.)-dominated forest in northern Minnesota, USA over a ~50 year period, as well as the relative roles of fire season and frequency in affecting individual tree and stand-level structural responses. Burning treatments were applied on 0.4 ha compartments arranged in a randomized block design with four blocks. Burning treatments crossed fire season (dormant, summer) and frequency (annual, biennial, and periodic), and include an unburned control for comparison. Treatments were applied from 1960 to 1970, with no further management interventions occurring since. Data were collected periodically from 1960 to 2014.

Forest structural development trajectories were significantly altered by the application of fire treatments. Burning treatments led to lower overstory densities, lower stand basal area, and larger tree diameters when compared to the unburned control over the study period. Differences between burning treatments were less apparent suggesting that the application of burning itself rather than a particular season and/or frequency of burning drives this long-term response. Overstory tree mortality and stand growth showed little or no response to burning treatments. In addition, we detected no impact of burning on long-term overstory tree growth efficiency (based on assessments >40 years post burning) suggesting these treatments had little cumulative effect on tree vigor. Our results indicate that the effects of burning treatments on structural dynamics are not ephemeral, but rather alter stand development trajectories in the long-term. The persistent nature of these effects highlights their potential as a tool for long-lasting structural alterations in treated stands without compromising overstory tree growth and vigor. The lack of red pine recruitment throughout the duration of the study suggests that prescribed fire alone cannot regenerate this species, and that further alteration to overstory and seedbed conditions would be needed to secure new cohorts of this species.

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1. Introduction

Prior to European settlement fire played a central role in the dynamics and functioning of many forested ecosystems across North America (Pyne, 1982). Historically, fires strongly influenced forest structure, species composition, and stand dynamics generally associated with fire-adapted ecosystems (Drobyshev et al.,

2008a; Nowacki and Abrams, 2008). In particular, low- and mixed-severity fire regimes maintained vast expanses of pyrophytic pine and oak forests across much of the eastern USA (Nowacki and Abrams, 2008; Frelich, 2002; Waldrop and Goodrick, 2012). Red pine (*Pinus resinosa* Ait.) dominated forests across the Great Lakes region represent an expansive example of these ecosystems with fire affecting patterns of structural dynamics, species composition, and regeneration (Heinselman, 1973; Drobyshev et al., 2008a; Fraver and Palik, 2012). Prior to European settlement, these ecosystems were characterized by a mixed-severity fire regime with low- to moderate-intensity surface fires

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occurring at intervals ranging from 5 to 50 years (Heinselman, 1973). These repeated understory fires were influential in the development and structure of these forests (Spurr, 1954; Frissell, 1973; Heinselman, 1973). Repeated surface fires along with higher severity fires occurring at intervals of 150–300 years, have been cited as contributing to the generation of a range of age structures from even-aged to multi-aged conditions (Frelich, 2002; Fraver and Palik, 2012).

Following several decades of devastating fires, policies enacted during the early 20th century and associated fire detection, prevention, and suppression efforts led to a dramatic decrease in the frequency and extent of burned area across the USA (Pyne, 1982; Nowacki and Abrams, 2008; Drobyshv et al., 2008b). Fire suppression efforts across the Great Lakes region beginning around 1920 have greatly limited the extent to which contemporary fires impact these ecosystems (Frissell, 1973; Heinselman, 1973; Hanberry et al., 2012). The extended absence of fire has greatly altered the structure and dynamics of these ecosystems, often resulting in buildups of woody understories, increased tree densities, lack of *Pinus* spp. regeneration, and changes in the species composition of forest canopies toward non-pine species (Methven and Murray, 1974; Drobyshv et al., 2008a; Hanberry et al., 2012). Given heightened interest in ecologically-grounded management, prescribed fire has increasingly been suggested as a tool to restore structural conditions in fire-adapted forest ecosystems while maintaining forest productivity (Vose, 2000; Agee and Skinner, 2005; Waldrop and Goodrick, 2012).

The potential for the use of prescribed fire was recognized early in the development of management strategies for red pine forests and has received considerable attention from researchers and practitioners since the 1960s. Initial interest in using prescribed fire to manage red pine forests developed in response to early observations of pine regeneration following fire and the well-known resistance of mature individuals of this species to fire-related injury (Maissurow, 1935; Van Wagner, 1970). However, owing to the ubiquitous development of undesirable understory conditions caused by fire suppression, nearly all of this work has focused on the impacts of this practice on mid- and understory vegetation dynamics, particularly that of woody shrub species (e.g., Buckman, 1964; Henning and Dickmann, 1996; Neumann and Dickmann, 2001). In contrast, relatively little is known regarding how prescribed fire affects long-term patterns in overstory structure, composition, and tree growth. Previous studies investigating prescribed fire effects on overstory trees within red pine forests have been limited to short-term evaluations and have not fully investigated the cumulative effects of fire as stands develop (e.g., Van Wagner, 1963; Methven, 1973; Methven and Murray, 1974). In particular, evidence for the legacy of structural alterations exceeding 10 years is rare. Few results from long-term experiments exist that evaluate the effects of fire on long-term changes in the structure and composition of red pine forests particularly after fire treatments have ceased.

There is extensive evidence that prescribed fire can dramatically alter the structure of forested ecosystems by reducing tree densities, altering species composition, and reducing fuel loads (e.g., Thomas and Agee, 1986; Fajardo et al., 2007; Knapp et al., 2015). In addition, several studies have investigated the potential impacts of prescribed fire on individual tree growth and vigor caused by cambial injury, crown scorch, altered nutrient and water status of the soil, and modified competitive environment following burning (e.g., Van Wagner, 1963; Monleon and Cromack, 1996). The results of this work are inconclusive and have shown that prescribed fire can generate negative, positive, or no impact on individual tree growth and vigor depending on the intensity of fire applications and the physiological status of individual trees during the time of burning (e.g., Van Wagner, 1963; Peterson et al., 1994;

Monleon and Cromack, 1996; Sala et al., 2005; Battipaglia et al., 2014). Further, much of this work was conducted over limited time frames (i.e., <10 years), with a narrow set of experimental treatments from a limited set of ecosystems, leaving key knowledge gaps regarding the persistence of these effects on long-term tree vigor and the relative roles of frequency and season of fire applications in affecting these responses.

This study capitalizes on an existing long-term silvicultural experiment aimed at evaluating the effects of prescribed fire on red pine forests in north-central Minnesota, USA. Established in 1959, the *Red Pine Prescribed Burning Experiment* provides an unprecedented long-term record of vegetation dynamics following prescribed fire treatments and the relative effects of frequency and season of burning within a northern temperate conifer forest ecosystem. This study was initially designed to test the importance of both fire frequency (annual, biennial, periodic) and the season of burning (dormant, growing) on reducing woody encroachment in the understory, as well as investigating its efficacy in promoting suitable conditions for pine regeneration. Although prescribed burning treatments ceased in 1970, measurements have continued for over 50 years providing a unique opportunity to examine the legacy of prescribed fire management history on long-term forest development. Objectives of our study were to (1) evaluate the persistence of changes to overstory structure, growth, and mortality in red pine stands over a ~55 year period (i.e., 10 years of active fire treatment followed by 45 fire-free years), and (2) investigate the long-term cumulative effects of fire treatments on residual tree growth and growth efficiency to assess potential trade-offs between structural alterations and residual tree vigor. We hypothesize that (1) prescribed fire treatments would maintain lower overstory densities and more open structures by delaying the recruitment of fire sensitive species, and (2) that vigor of residual red pines would be unaffected by fire treatments given its known resistance to fire.

2. Methods

2.1. Site and experimental design

This study, initiated in 1959, is located within the Cutfoot Experimental Forest (CEF) on the Chippewa National Forest, in Itasca County in north-central Minnesota, USA (latitude 47°40'N, longitude 94°5'W). Climate at the CEF is cool continental with warm, humid summers often exceeding maximum temperatures of 32 °C, and cold winters with minimum temperatures falling below –35 °C. Growing season length ranges from 100 to 120 days and annual precipitation ranges from 500 to 640 mm with the majority falling as rain (U.S. Forest Service, 2009). Prolonged summer droughts are common. Soils are derived from glacial sandy outwash, weakly developed, very well drained, and classified as the Cutfoot series (Alban, 1977). Site index for red pine within the experiment averages 18.3 m at 50 years (range 17.7–18.8 m).

The study was established within a large complex of red pine-dominated stands on the CEF that were naturally regenerated after a stand replacing fire occurring in the late 1860s. The area has been classified as the Northern Dry-Mesic Mixed Woodland (FDn33) type using the local habitat type classification system (Minnesota Department of Natural Resources, 2003). This community is common across the region and typifies the greater western Great Lakes region pine forests with overstories dominated by mature red pine, with components of white pine (*Pinus strobus* L.), paper birch (*Betula papyrifera* Marsh), jack pine (*Pinus banksiana* Lamb.) and balsam fir (*Abies balsamea* (L.) Mill.). Understories were historically patchy shrub layers consisting of junberries (*Amelanchier* spp.),

bush honeysuckle (*Diervilla lonicera* P. Mill.), and hazel (*Corylus* spp.); however, alterations in historic disturbance regimes have resulted in the development of recalcitrant thickets of hazel.

Four replicate blocks were established in the study area in 1959 and thinned to a standard residual overstory basal area of 27–29 m² ha⁻¹ to homogenize overstory conditions. Standing dead trees, tree tops, and other non-merchantable materials were also removed following thinning in an effort to homogenize fuels across treatments units. No additional overstory manipulations have occurred since the initial thinning. In 1960, burning treatments were established and implemented within 0.4 ha treatment compartments assigned using a randomized block design to test the impacts of both season and frequency of fire applications. The seven treatments applied were as follows: summer annual (SA), summer biennial (SB), and summer periodic (SP), dormant annual (DA), dormant biennial (DB), and dormant periodic (DP), as well as an unburned control (CC). For the “summer” season factor, burning treatments were applied from late June through mid-August, while “dormant” treatments were applied in the spring (April and May), or fall (October). Annual frequencies correspond to burning every calendar year, biennial frequencies every other calendar year, and periodic frequencies every six to nine years.

2.2. Burning

In most cases burns were implemented 5–15 days following significant rain events (Alban, 1977). This resulted in forest floor fuel moisture that averaged roughly 100% of dry weight for dormant season burns and 40% for summer season burns (Buckman, 1964; Alban, 1977). Burns were applied using a combination of backing fires and headfires. Headfires varied in width from 6 to 12 m (Alban, 1977). Fuels were primarily pine litter and resulted in low to moderate fire intensity with flame heights generally less than 1 m. Fires resulted in a significant reduction of the forest floor litter layer, with losses greatest in the summer treatments (Alban, 1977). Burning treatments were applied from 1960 to 1970, after this time burning was halted resulting in 10–11 burns in annual treatments (1968 burn missed in dormant units due to lack of suitable burning conditions), 5 burns in biennial treatments, and 2 burns in periodic units. No further management entries have been made within the experimental blocks since 1970.

2.3. Field sampling

Within each 0.4 ha treatment compartment, a single 0.08 ha circular plot was placed near the center and permanently monumented prior to treatment in 1959. Within this plot all living trees larger than 9.1 cm dbh (diameter at breast height, 1.3 m) were recorded, identified to species and dbh measured to the nearest 0.25 cm. Dead trees were identified to species and recorded with no diameter measurement from 1959 to 2010 at which point diameter measurements for dead trees was added to inventory procedures (see below). Total height was measured to the nearest 0.3 m for the 6–8 red pine trees nearest plot center at the time of plot establishment. These measurements were collected in 1959, 1964, 1969, 1997, 2005, 2010, and 2014.

During the 2014 survey, additional measurements were taken to further examine the impacts of treatments on overstory tree vigor, and standing deadwood structures. First, dbh was measured for dead standing trees (snags) >1.4 m in height and at least 9.1 cm dbh. Also, increment cores were extracted at breast height from the subset of trees for which long-term height measurements were taken to examine inter-annual variability in tree growth and estimate sapwood depth for use in vigor assessments. Depth to the sapwood was identified on each core in the field by identifying the transition from translucent sapwood to opaque heartwood

and marked for later measurement. Cores were placed in plastic straws, labeled, and transported to the lab for processing.

Plot level measurements were used to calculate standard forest structural characteristics including stand density (TPH; trees ha⁻¹), basal area (BA; m² ha⁻¹), and quadratic mean diameter (QMD; cm). Quadratic mean diameter was used in place of the standard arithmetic mean as it is preferred for describing the effective size of the average tree competitor (Curtis and Marshall, 2000). Additionally, net periodic annual increment (PAI) of live tree basal area was calculated as:

$$\text{PAI} = (\text{BA}_{t_0} - \text{BA}_{t-1}) / (t_0 - t_{-1})$$

where t_0 is the year of interest, and t_{-1} is the prior measurement year. Also, annual mortality rates, expressed as a percent, were calculated using methods proposed by Sheil and May (1996) as:

$$\text{Mortality} = 1 - [1 - (M_1/N_0)]^{1/t}$$

where M_1 is the total number of stems that died during the sampling period, N_0 is the total number of live stems at the previous sampling date, and t is the number of years between sampling periods. Reineke's (1933) stand density index was calculated for each treatment unit using the summation method for irregular stands (Shaw, 2000). Further, relative density (RD) was calculated using methods proposed by Woodall et al. (2005) for mixed-species stands.

2.4. Laboratory and statistical analysis

Increment cores were oven dried overnight at 64 °C. Cores were then placed in wood mounts and sanded using progressively finer sand paper (up to 800 grit) until individual cells could be clearly identified. Annual growth rings and depth to the sapwood as described above were measured to the nearest 0.001 mm using a Velmex sliding-stage micrometer (Velmex Inc., Bloomfield, NY). In cases where the core did not pass directly through the pith, the number of missing annual rings was estimated using methods proposed by Applequist (1958). Cores were cross-dated visually using marker rings (Yamaguchi, 1991) to ensure proper dating of individual annual rings. Cross dating was statistically confirmed using the program COFECHA (Holmes, 1983). Individual tree ring width chronologies were converted to annual basal area increment chronologies using backwards reconstructed dbh values derived from inside bark dbh values at the time of increment core extraction and radial increments measured over time (Bunn, 2008). Inside bark dbh at the time of coring was estimated using bark factor equations presented by Fowler and Damschroder (1988).

Sapwood basal area (SWBA) was used as an index of leaf area (LA; Waring et al., 1982) and was calculated as basal area inside bark minus the heartwood basal area for each cored tree. Sapwood basal area was used in place of leaf area because available SWBA: LA allometric equations (Penner and Deblonde, 1996) were developed using trees of smaller size and ages less than those sampled in this study. Five year periodic volume increment (VINC) for the five year period ending in 2013 was calculated using the equation presented by Gilmore et al. (2005):

$$V = 0.1202D^{2.0565}$$

where V is stem volume in cubic feet and D is outside bark dbh in inches. Because of the mid-growing season sampling, current growing season growth was not included in analysis (Maguire et al., 1998). Individual tree volume increments were converted to cubic meters prior to further analysis. Growth efficiency (GE) was calculated as VINC divided by SWBA (McDowell et al., 2007).

Assessment of the impacts of burning season and frequency on forest structure (i.e., BA, TPH, and QMD), mortality, and growth

(PAI) were carried out using mixed model repeated measures analysis of variance (ANOVA) with season and frequency of burn, year, and their two-way and three-way interactions as fixed effects and measurement plot as a random effect. The unburned control was included as a level of season in all analyses. Plot (each plot corresponds to an individual treatment compartment) was chosen as the random effect over block given its generally superior performance as assessed by Akaike Information Criteria (AIC; Akaike, 1974). Given that our primary interest was in assessing the long-term persistence of treatment effects, pre-treatment data were not used in the repeated measures procedures. Pre-treatment data was tested for differences using ANOVA with burning treatment (season and frequency combination) as a fixed effect. Relative density at the end of each sampling period was also included as a covariate in the model of PAI to control for growth–growing stock relationships. Models were fit using the “lme4” package in the R environment (Bates et al., 2013).

Planned mean contrasts for structural characteristics were carried out to compare differences between season of burning (dormant, summer, control) within a given burning frequency (annual, biennial, periodic) for each sampling year using the package “lsmeans” (Lenth, 2013), with Bonferroni adjustments for a family of three tests. Significance is reported at the $\alpha = 0.05$ level. Residual plots were used to visually assess homoscedasticity of variance, and natural logarithm transformations applied when necessary to normalize the distribution of residuals (Weisberg, 2014).

Because measurements were not collected for standing dead trees until 2014, comparisons of the density and basal area of standing dead trees (“snags”) were carried out using linear model analysis of variance with season, frequency and their interaction as model predictors for year 2014 data only. Tukey’s pairwise contrasts were used to examine treatment level differences and report significance at $\alpha = 0.05$.

Alterations to the growth of residual trees were assessed using repeated measures linear mixed model analysis of variance with individual tree basal area increment (BAI) as a response, and season, frequency, year and their two- and tree-way interactions as predictors. Both measurement plot and block were included as random effects. Further we investigated the potential for persistent alterations to tree vigor by using growth efficiency as an index. Growth efficiency was compared using linear mixed model analysis of variance with season, frequency, and their interaction as independent variables, and measurement plot as a random effect. Because vigor measurements were only available for the year 2014, comparisons were limited to a single year. Multiple comparisons using a Tukey’s adjustment for multiplicity were conducted, with significance reported at $\alpha = 0.05$.

3. Results

3.1. Stand structure

Prescribed fire resulted in long-term alterations to stand structure. Prior to the implementation of burning treatments, overstory conditions among and within treatment blocks were comparable,

with no significant differences in structural conditions (BA, TPH, QMD) in 1959 (Table 1). Over the 54-year period since the initiation of burning treatments, prescribed fire modified the structural development of treated stands toward lower overstory density with larger average tree size (QMD) than unburned control stands (Fig. 1). Season and frequency of burning created dynamic temporal patterns within each live tree structural characteristic (BA, TPH, QMD), as was evident by the significant effect of year (time); year by frequency interaction; year by season interaction; and the three way interaction of year, season, and frequency in many of the ANOVAs (Table 2).

Tree density (TPH) consistently increased over the study period in the control, whereas all burned treatments show little change throughout the early measurement periods but rapidly increased since 2005 (Fig. 1). Season of burning impacted TPH and interacted with year to create the varied responses over the long-term (Table 2, Fig. 1). Differences between burned treatments and the control can largely be attributed to the recruitment of small diameter non-pine trees into the overstory since 1997 within the control, whereas appreciable recruitment in burned treatments was largely delayed until 2010 (Fig. 2). Within the burned treatments, TPH did not significantly differ between summer and dormant season burning within a given burning frequency (Fig. 1).

Basal area increased consistently over the duration of the study in all treatments (Fig. 1). However, burned treatments maintained consistently lower basal areas than the unburned control throughout the study, particularly in later measurement periods (e.g., since 1997; Fig. 1). The three-way interaction of season, frequency, and year (Table 2) created dynamic patterns among treatments throughout the duration of the study (Table 2, Fig. 1). Differences within the burned treatments were less pronounced, with differences existing only between burning seasons in biennially burned treatments for the three most recent measurement periods (Fig. 1).

Quadratic mean diameter remained relatively constant throughout the study period within the control. In contrast, the burning treatments showed a consistent increase until the 2000s, at which point there was a marked decline in QMD for these treatments (Fig. 1). The three way interaction of season, frequency and year resulted in long-term differences in QMD among burned treatments and the control (Table 2, Fig. 1). Significant differences between treatments were rare due to the increasing variability in tree size as small diameter stems were recruited over time (Figs. 2 and A1). In general, burned treatments had consistently higher QMD than untreated controls over the entirety of the study (Fig. 1). Breakdown of tree size into diameter classes revealed that low QMDs were explained by the recruitment of small diameter stems into the unburned control (Fig. 2). No differences in trends of QMD were found among burning treatments (Fig. 1), which is corroborated by the similar composition and delay in the recruitment of smaller diameter stems between all burning treatments (Fig. 2).

There was substantial development of smaller diameter classes beginning in 1997 in the control treatments, whereas these size classes did not develop until the 2010 measurement period in burned treatments (Fig. 2). Further, diameter class distributions revealed compositional differences in recent years. Small diameter

Table 1
Mean (\pm standard error) overstory (trees >9.1 cm dbh) structural characteristics prior to the implementation of burning treatments, and an unburned control for the Red Pine Prescribed Burning Experiment in north-central Minnesota, USA. Analysis of variance of pretreatment conditions indicates no significant differences among treatments at $\alpha = 0.05$, results not shown.

	Control	Dormant annual	Dormant biennial	Dormant periodic	Summer annual	Summer biennial	Summer periodic
TPH	299.5 (16.2)	308.8 (53.6)	308.8 (17.5)	274.8 (21.0)	299.5 (23.3)	361.2 (47.1)	284.1 (33.1)
BA	27.90 (0.5)	26.43 (0.7)	27.25 (0.7)	26.79 (0.2)	28.30 (0.2)	28.06 (0.7)	27.60 (0.3)
QMD	34.55 (0.8)	34.40 (3.6)	33.66 (1.1)	35.49 (1.5)	34.94 (1.4)	32.03 (1.8)	35.72 (2.1)

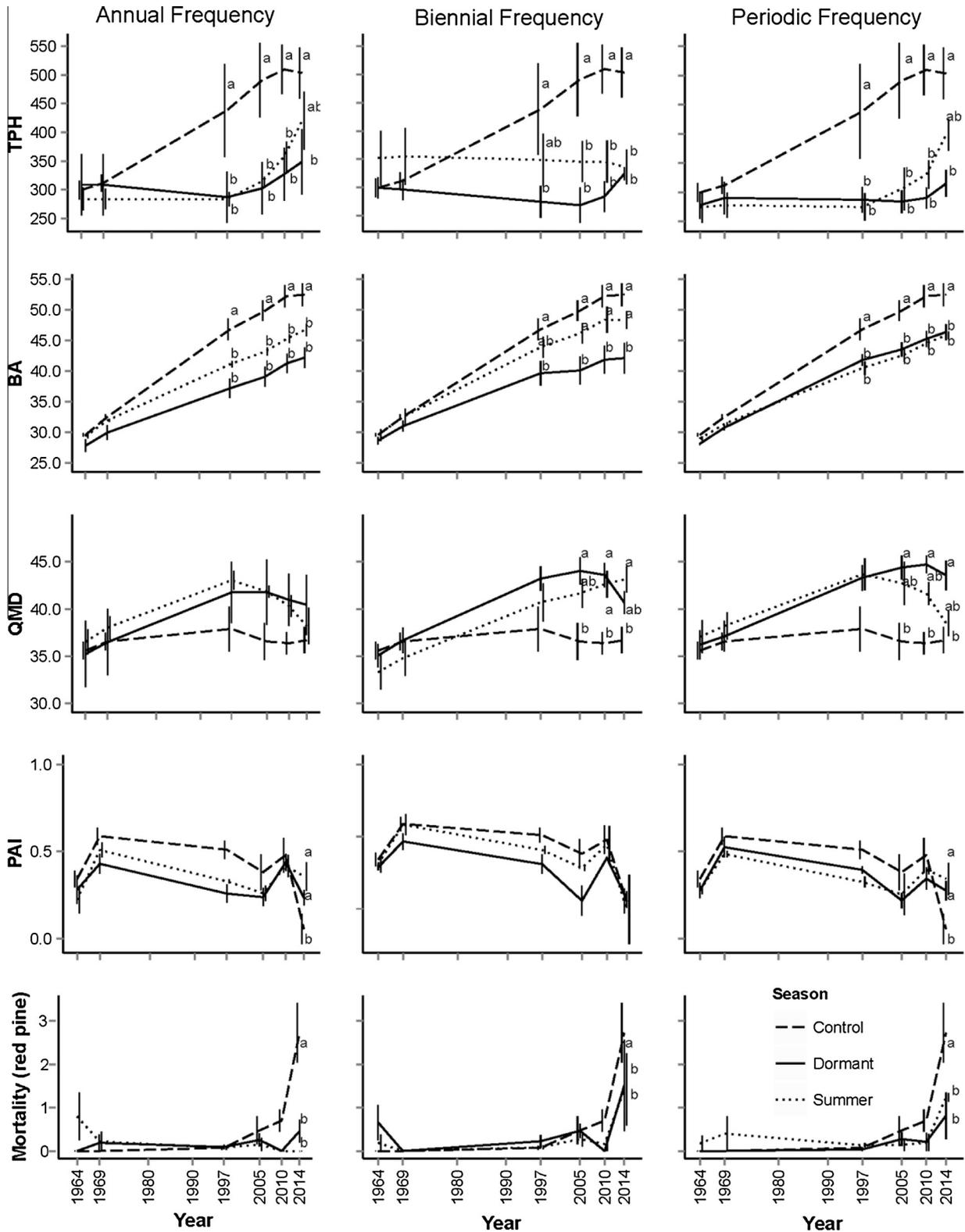


Fig. 1. Tree density (TPH, trees ha⁻¹), basal area (BA, m² ha⁻¹), quadratic mean diameter (QMD, cm), periodic annual increment (PAI, m² ha⁻¹ yr⁻¹), and mortality (% of trees year⁻¹) for a 50 year period at the Red Pine Prescribed Burning Experiment in north-central Minnesota, USA. Burning treatments were applied from 1960 to 1970. Letters indicate statistical difference from pairwise comparisons of burning season within a given fire frequency and year at $\alpha = 0.05$. Control treatment is replicated in each frequency panel. Error bars are \pm one standard error.

stems were dominated by hardwood species in the unburned control with considerable components of all species groups. Burned treatments showed a general trend toward conifer recruitment in smaller diameter classes (Fig. 2).

Snag density in 2014 was related to the application of fire (Table 3, Fig. 3). Specifically, season of fire was found to be important in explaining the abundance of snags, while frequency and its interaction with season were not (Table 3). Snag densities were

Table 2
Repeated measures analysis of variance results for basal area (BA), tree density (TPH), quadratic mean diameter (QMD), Mortality of red pine, and periodic annual increment (PAI) for the Red Pine Prescribed Burning Experiment in north-central Minnesota, USA. Burning treatments were applied from 1960 to 1970.

	BA			TPH			QMD			Mortality			PAI		
	F	df	p-value	F	df	p-value	F	df	p-value	F	df	p-value	F	df	p-value
Season	11.54	2	<0.001	4.523	2	0.023	1.226	2	0.314	5.872	2	0.053	0.425	2	0.659
Frequency	0.89	2	0.426	0.239	2	0.790	0.373	2	0.693	2.385	2	0.304	2.251	2	0.131
Year	1026.21	5	<0.001	15.342	5	<0.001	59.167	5	<0.001	66.969	5	<0.001	20.328	5	<0.001
Season × frequency	2.19	2	0.137	0.302	2	0.743	0.127	2	0.881	0.375	2	0.829	0.051	2	0.950
Season × year	7.1	10	<0.001	5.609	10	<0.001	2.222	10	0.022	40.437	10	<0.001	2.315	10	0.017
Frequency × year	1.3	10	0.240	1.678	10	0.095	2.115	10	0.029	20.752	10	0.023	2.267	10	0.019
Season × frequency × year	2.58	10	0.008	1.261	10	0.262	2.609	10	0.007	6.014	10	0.810	0.682	10	0.739

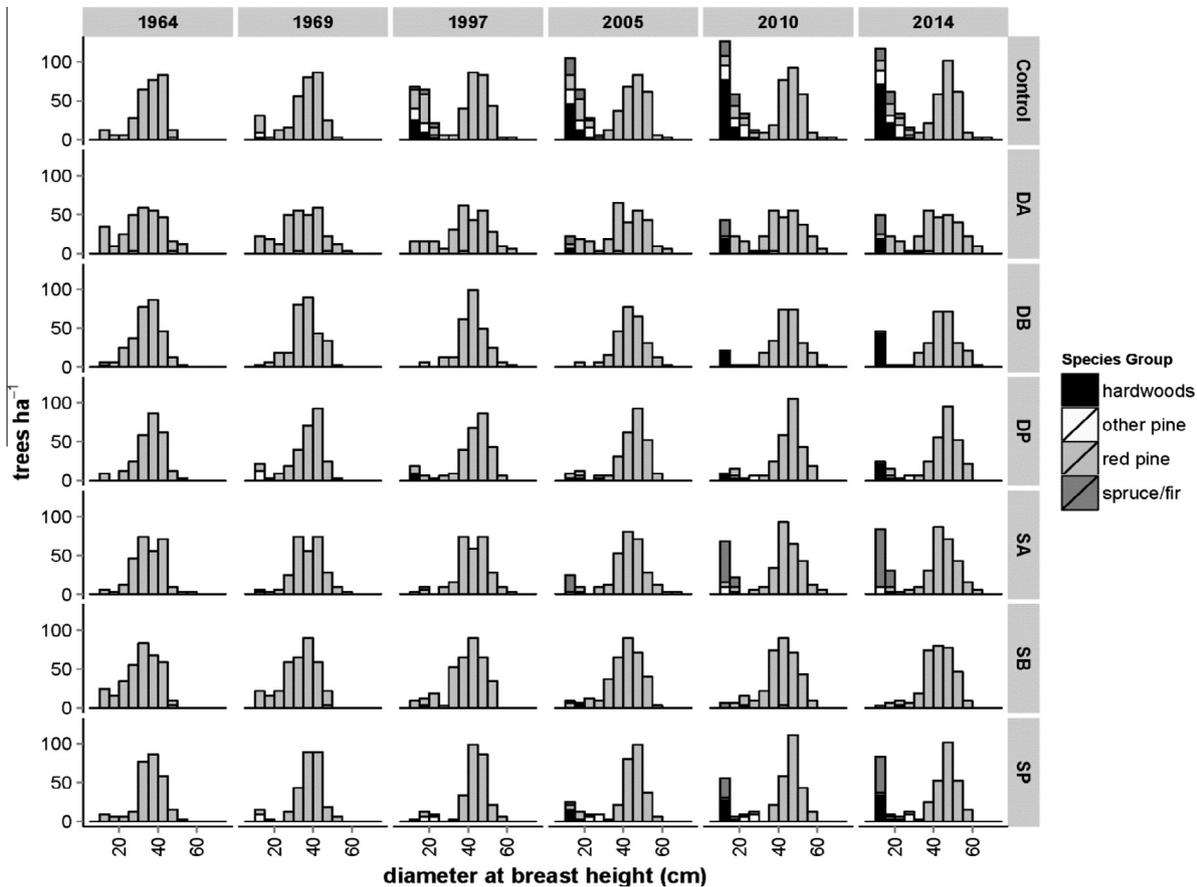


Fig. 2. Diameter distributions by species group (treatment mean) for each measurement year at the Red Pine Prescribed Burning Experiment in north-central Minnesota, USA. Burning treatments were applied from 1960 to 1970. Treatments are labeled as Control (unburned control), DA (dormant annual), DB (dormant biennial), DP (dormant periodic), SA (summer annual), SB (summer biennial), SP (summer periodic).

Table 3
Analysis of variance results for snag density and snag basal area for the year 2014 at the Red Pine Prescribed Burning Experiment in north-central Minnesota, USA. Burning treatments were applied from 1960 to 1970.

	No. snags ha ⁻¹			Snag basal area		
	F	df	p-value	F	df	p-value
Season	9.44	2	0.001	1.56	2	0.234
Frequency	1.69	2	0.208	1.77	2	0.195
Season × frequency	0.53	2	0.598	2.47	2	0.109

generally lower in burned treatments when compared to the control (Fig. 3), and the summer annual treatment had no snags in the 2014 sampling year. Snag basal area in 2014 was not related to the application of fire (Table 3, Fig. 3). Snags consisted entirely of red pine, except in the unburned control, where small diameter hardwood snags were present in low numbers (results not shown).

3.2. Stand level growth and mortality

After controlling for relative density, periodic annual increment was affected by interactions of both season and frequency with year (Table 2). Except for a rapid increase in PAI from 1964 to 1969, following the initial thinning prior to the study establishment, basal area growth declined slightly over the study period across all treatments (Fig. 1). PAI was consistent across all treatments, with no significant differences until the most recent measurement period, where the control displayed values lower than that of the treated units (Fig. 1).

Year and its interactions with season and frequency of burning were also found to be important in explaining mortality rates of red pine (Table 2). Mortality was low ranging from 0% to 0.47% until the year 2005, when the rate increased across several treatments (Fig. 1). Mortality in the last two measurement periods

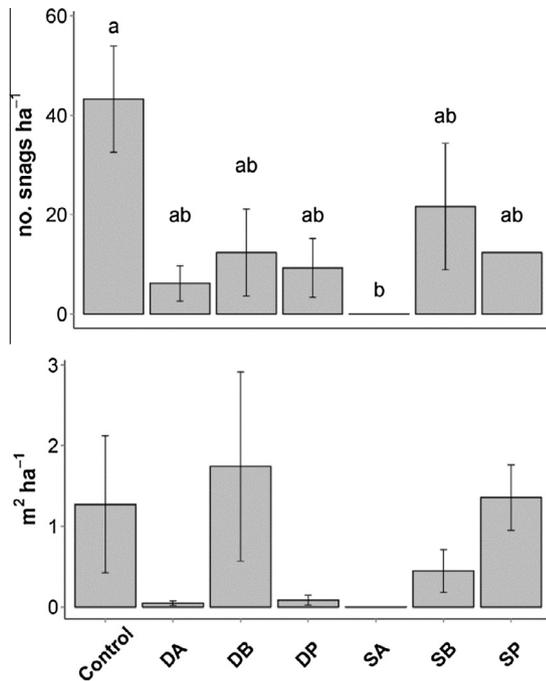


Fig. 3. Mean snag density (upper panel, stems ha⁻¹) and snag basal area (lower panel, m² ha⁻¹) for the Red Pine Prescribed Burning Experiment in north-central Minnesota, USA for the year 2014. Burning treatments were applied from 1960 to 1970. Letters indicate statistical difference from pairwise comparisons of burning treatment (season and frequency combination) $\alpha = 0.05$. Error bars represent \pm one standard error ($N = 4$). Snags defined as standing dead trees > 1.37 m tall, and > 9.1 cm DBH. See Fig. 2 for treatment labels.

increased significantly across the majority of treatments with mortality rates in 2014 ranging from 0.0% to 2.7% (Fig. 1). The summer annual treatment was an exception to this trend, with a mortality rate of 0% in 2014. This recent increase was most pronounced in the control (Fig. 1), and was significantly different from all burning treatments in 2014.

3.3. Individual tree growth and efficiency

Overall, individual tree basal area growth (BAI) for residual red pines was unaffected by burning treatments over the duration of the study (results not shown; see also Bottero et al., in preparation). Season and frequency of burning were found to be unrelated to BAI. Year was the only factor significantly associated with BAI across all treatments ($p < 0.001$). Further, analysis of variance results for growth efficiency in 2014 indicate no treatment effect for the subset of residual red pines sampled (Table 4). Together, BAI and growth efficiency results indicate no persistent effect of burning on individual tree vigor ~ 45 years following treatment.

4. Discussion

4.1. Stand structure

This study provides evidence that prescribed fire has long-term impacts on the stand development trajectories of red pine-dominated forest ecosystems. In particular, the long-term nature of the study provides evidence that the impacts of prescribed fire are not ephemeral, as differences in stand structure persisted over a 45-year fire-free period following the cessation of a 10-year active burning period due in large part to delayed recruitment of fire-sensitive species in these areas supporting our first hypothesis. These results largely corroborate earlier short-term (i.e., < 10 year)

Table 4

Analysis of variance results for growth efficiency in 2014 at the Red Pine Prescribed Burning Experiment in north-central Minnesota, USA. Burning treatments were applied from 1960 to 1970.

	Growth efficiency		
	F	df	p-value
Season	0.123	2	0.8849
Frequency	0.4135	2	0.6666
Season \times frequency	0.4906	2	0.6191

findings in red pine ecosystems (Alban, 1977; Methven, 1973), but further extend our understanding of the long-term dynamics following burning treatments and highlight the ability for sustained alteration to stand development resulting from low-severity under-burning. Further, investigations of stand growth, red pine mortality, and efficiency confirm our second hypothesis and reveal that there are little or no long-term trade-offs between structural alteration and productivity as a result of burning treatments within these fire-adapted ecosystems.

The application of fire effectively delayed recruitment of a shade-tolerant midstory for several decades and altered the composition of midstory ingrowth toward conifer dominance resulting in differing stand development trajectories in burned versus unburned stands. As a result, the size structure of burned stands was dramatically altered over the long-term, extending earlier short term findings in red pine systems which indicate that understory and midstory trees can be eliminated with little to no effect on the fire-resistant residual red pine (Methven and Murray, 1974; Henning and Dickmann, 1996; Neumann and Dickmann, 2001). Diameter distributions of burned stands were similar to those observed following multiple burns in an old-growth red pine stand at Itasca State Park located approximately 90 km to the southwest (Zenner and Peck, 2009). In contrast, similarly-aged, managed stands in the study region without a history of burning treatments show a higher degree of development in smaller size classes (D'Amato et al., 2010). The diameter distributions observed fit within the range of size structures outlined by several old-growth sites across northern Minnesota by Fraver and Palik (2012) who suggest that mixed severity fire was an integral process in creating the diversity in stand structures in pre-settlement red pine forests. Interestingly, the unburned control is also well represented in the range of structures outlined by Fraver and Palik (2012), suggesting that prolonged fire-free periods may have been important in creating the diversity of stand structures present prior to European settlement. Further, the development of burned stands in this study more closely reflect the conditions described in early accounts for the area (Spurr, 1954), which describe much lower tree densities with open and/or patchy midstory development.

The trends observed in overstory live-tree structures mirror those found in other fire-dependent temperate forest systems in North America where the use of prescribed fire has been more widely accepted as a silvicultural and restorative tool. For example, burning experiments in oak forests and woodlands (Peterson and Reich, 2001; Hutchinson et al., 2005; Knapp et al., 2015), south-eastern USA pine forests (Waldrup et al., 1992; Brockway and Lewis, 1997; Varner et al., 2005), and western USA ponderosa pine (*Pinus ponderosa* Dougl.) forests (Thomas and Agee, 1986; Sackett et al., 1994; Sackett and Haase, 1998; Fajardo et al., 2007) have found that repeated burning reduces the density of the overstory by reducing numbers of small diameter and thin barked trees. The resultant stands typically display changes to the distribution of tree sizes with diameter distributions shifting from negative exponential forms in unburned controls to Gaussian forms in repeatedly burned treatments (Peterson and Reich, 2001; Knapp et al., 2015). While the diameter distributions found in unburned

controls were not of a negative exponential form, the increased presence of mesophytic and small diameter stems indicate similar recruitment processes and development in the absence of fire, a well-documented phenomenon within eastern oak and pine forests (Nowacki and Abrams, 2008). This change in the density of smaller trees is also quite evident in the trends of quadratic mean diameter where decreases in tree density were associated with larger quadratic mean diameter. In other investigations of repeated prescribed under-burning, the reduced densities described above were associated with increases in the average tree size (Knapp et al., 2015), similar to the patterns observed in the present study. The long-term differentiation of basal area levels between burned treatments and the unburned control is similar to the multi-decade findings from oak-dominated systems in Missouri where unburned controls resulted in higher densities, higher basal areas, and smaller diameters when compared to repeatedly burned treatments (Knapp et al., 2015).

The long-term dataset use in our study provided an interesting contrast to other long-term prescribed fire studies in North America (e.g., Peterson and Reich, 2001; Brockway and Lewis, 1997; Knapp et al., 2015) in that our study does not have continuous treatment. Despite a 45-year fire-free period, burned stands within our study show similar structural responses to studies experiencing continued burning. The multi-decade fire-free period following active burning in our study uniquely shows the temporal persistence of structural alterations, and suggests that extended fire-free periods could be incorporated into prescribed burning regimes without setbacks to structural alterations.

In terms of standing deadwood structures, the average density and basal area of snags in 2014 across all treatments (i.e., 15 snags ha⁻¹ and 0.71 m² ha⁻¹) were comparable to levels found in similarly aged managed forests in the region reported by Silver et al. (2013a; 10.8 snags ha⁻¹ and 0.5 m² ha⁻¹). However levels were considerably lower than those reported for old-growth stands within the region (Fraver and Palik, 2012; 81 snags ha⁻¹ and 6.9 m² ha⁻¹), likely due to the preferential removal of dead standing trees during thinnings prior to the establishment of the study. We do, however, see evidence that the abundance of snags is increasing in the unburned controls due to competition-induced mortality (see below) of small diameter understory stems, a likely secondary effect of the higher densities observed in those treatments. The higher snag densities in the control may not be biologically important given that the smaller snag size contributes comparatively less to services provided by standing deadwood including habitat for local snag inhabiting fauna (Harmon et al., 1986). In addition, the accumulation of smaller diameter standing dead trees undoubtedly increases the buildup of fuels, potentially placing these unburned areas at higher risk for high severity fire (Vose, 2000).

4.2. Stand level growth and mortality

Stand level growth was low throughout the study when compared to repeatedly thinned red pine stands in the region (Buckman et al., 2006; Bradford and Palik, 2009; D'Amato et al., 2010). Basal area growth (PAI) differed little between treatments, even with the significant differences in stocking (TPH, BA) levels, and is consistent with earlier work suggesting that growth is relatively constant over a wide range of basal area stocking levels in red pine systems (Gilmore et al., 2005; D'Amato et al., 2010). Recent differences between the unburned control and burned treatments are likely related to increased mortality rates in the control during this time period (see below). The slight decline in PAI over time observed across all treatments is likely an effect of the high basal area stocking observed throughout the study, which exceed typical targets within the region for managing red pine

dominated stands (Gilmore and Palik, 2006; Wyckoff and Lauer, 2014). If burning treatments were accompanied by thinning or other partial harvests at this advanced stand age, basal area growth rates may increase to levels more typical of managed red pine forests in the region (D'Amato et al., 2010).

While effective in eliminating small diameter stems and delaying recruitment, prescribed fire as implemented here has no effect on the mortality of the residual overstory. Mortality rates over the study period are comparable to values reported for managed and old-growth red pine stands in the region (Powers et al., 2010; Silver et al., 2013b). The relatively low and stable mortality rates extend earlier short-term findings from prescribed burning experiments in red pine forests in Ontario (Van Wagner, 1963), as well as those reported by Alban (1977) for the same study reported on here and suggest that fire can be applied with little or no impact on overstory pine supporting our second hypothesis. The recent rapid increases in mortality since 2010 be partially explained by the presence of root disease caused by the fungus *Armillaria* spp. within treatment blocks (personal observation), a phenomenon well documented in the region and known to impact mortality rates in older (e.g., >100) red pine stands (Kromroy, 2004; Gilmore and Palik, 2006; Silver et al., 2013b). Further, we believe recent increases in mortality and associated differentiation between burned treatments and the control to be related to competition-induced mortality in response to increasing density over time (see previous section). In a region-wide analysis of several growth and yield studies Buckman et al. (2006) reported that mortality rates may increase to 15.3% of basal area growth for stands with stocking over 46 m² ha⁻¹, a level being approached and/or exceeded by stands included in this study. Higher mortality in the unburned control, where build-up of a woody midstory resulted in higher densities, further corroborates this and suggests higher mortality may be a secondary effect of increased density caused by the lack of fire.

4.3. Individual tree growth and vigor

Individual tree growth over the long-term for residual red pines appears to be unaffected by the wide range of fire prescriptions employed in our study. While small growth reductions within this experiment have been associated with the application of fire in the short term (Bottero et al., submitted for publication), no measurable effect is present after several fire-free decades. Similarly, fire was found to have no significant effect on growth in a ponderosa pine forest in Oregon following repeated burning (Hatten et al., 2012). Further, no differences in growth efficiency were found among burning treatments suggesting that no long-term physiological changes occurred within residual trees exposed to prescribed fires. While fire has been shown to substantially reduce the size of individual tree crowns, and cause cambial injury to residual red pines (Van Wagner, 1963) these effects and associated impacts on growth are apparently short-lived and no longer persistent in stands after several fire-free decades. In addition, careful application of prescribed fires on these sites, including the removal of excess logging slash and fuels likely minimized fire-related injuries to residual trees. The long-term stability of individual tree vigor and mortality (above) illustrate the well-known fire resistance of red pine (Van Wagner, 1970), and indicate no consequences for the use of burning treatments in terms of overstory productivity, particularly of residual overstory red pines.

5. Conclusions and management implications

Results from this study suggest that prescribed fire can be used to alter the structural development trajectory of red pine stands. Our

findings provide evidence that these alterations are sustained for several decades following the cessation of prescribed fire treatments. Although the frequency of burning examined in this study are likely not practicable, the structural outcomes described in this work can serve as useful point of reference for assisting managers in achieving a wide range of forest and woodland management objectives in northern temperate pine ecosystems. These objectives include the restoration of pre-settlement woodland structure, the reduction of live woody fuels, creating open park-like aesthetics, and increasing light penetration to the forest floor to facilitate the establishment of pine seedlings. While the long-term efficacy of prescribed fire has been demonstrated in other ecosystems, including longleaf pine (*Pinus palustris*), ponderosa pine, and eastern oak (*Quercus* spp.) forests, this study presents the only long-term evaluation for the red pine forests and woodlands that once dominated much of the Great Lakes region across both the United States and Canada.

Although red pine were historically maintained by periodic fires, prescribed fire alone appears unsuccessful in successfully establishing or recruiting a new cohort of red pine, as is evident by the lack of red pine in lower diameter classes throughout the study. It is likely that the pre-settlement fire regime may have been more heterogeneous in severity resulting in more dramatic density reductions (Fraver and Palik, 2012), and that fires likely interacted with other disturbances (i.e., windthrow events) to further alter overstory and seedbed conditions. While this study provides evidence that prescribed fire alone can significantly impact the successional trajectory of these forests, fire-induced structural modifications could further satisfy the objectives of managers if used in conjunction with more conventional silvicultural treatments including forests thinnings and variants of seed-tree and shelterwood harvests. Fire-treated stands were lower in tree density and basal area throughout the study, but, because mortality of the residual pine overstory was minimal, they remained at or above recommended stocking levels for this species in the region (i.e., maximum stocking or “A-line” from stocking chart for red pine [Benzie, 1977]). If these fires were applied in concert with typical thinning schedules for the region we would expect refined development of woodland structural characteristics of these ecosystems, including lower densities, larger residual pines, and improved regeneration conditions.

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Appendix A

See Fig. A1.

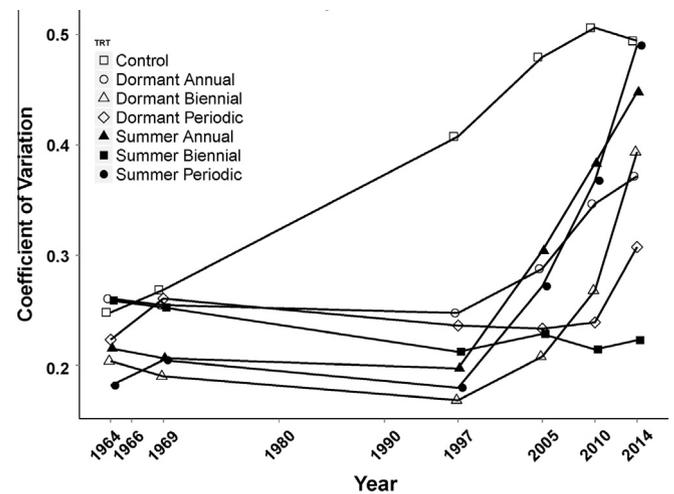


Fig. A1. Variability in tree diameters as expressed by the coefficient of variation in diameters over a 50 year period for the Red Pine Prescribed Burning Experiment in north-central Minnesota, USA. Burning treatments applied from 1960 to 1970.

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