Long-term effects of prescribed fire on vegetation structure, dynamics, and tree growth in red pine (*Pinus resinosa* Ait.) forests in north central Minnesota.

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Dedication

This thesis is dedicated to Jocelyn Rose Scherer.

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. 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. Further, burning altered shrub layer dynamics and community composition both in the short- and long-term. Both season and frequency of burning were important drivers of the response of the understory, with frequent summer season burns having the largest impact, including the greatest control of hazel brush.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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Chapter 1: Introduction

Across North America, the ecological effects of decades of fire suppression have become apparent within fire-depended forested ecosystems (Nowacki and Abrams 2008). The absence of fire in these ecosystems has drastically altered their composition, structure, and dynamics. Prescribed fire represents one tool available to forest managers to reincorporate fire into these stands in an effort to restore fire related processes and conditions. Prescribed fire has been evaluated extensively in some fire-depended forested ecosystems such as *Pinus*-dominated forests in the southwestern (e.g. Monleon and Cromack 1996, Hatten et al. 2012) and southeastern USA (e.g. Waldrop et al. 1992, Brockway and Lewis 1997), however long-term studies are non-existent for north temperate conifer forests, including the red pine (*Pinus resinosa*)-dominated forests of the Great Lakes region. This economically and ecologically important forest type has been greatly impacted by the absence of fire, including the development of high density stands, reduced levels of pine regeneration and recruitment, and decreased species diversity in the understory layer (Nyamai et al. 2014, Weyenberg et al. 2014, Fraver and Palik 2012). Given the historic role of mixed severity fire regimes in structuring these communities, red pine-dominated ecosystems appear well suited to the application of prescribed fire; however, responses have thus far been inconclusive and have only been evaluated in the short-term. This thesis attempts to explore the long-term effects that prescribed fire has on treated red pine stands. By revisiting an existing prescribed fire experiment established in 1959, this research provides a unique investigation of long-term prescribed fire effects in a controlled and replicated experiment.

Upon returning to the study we quantified the long-term effects of prescribed burning on ecosystem attributes including overstory structure, tree growth, mortality, as well as the abundance and composition of understory vegetation, including woody shrubs, tree regeneration, and herbaceous plants to address the following questions: 1) How does prescribed fire impact stand-level overstory structural, growth, and mortality patterns within red pine (*Pinus resinosa*) forests in the long-term, and do these effects vary between season and/or frequency of burning? 2) How persistent are the effects of prescribed fire season and frequency on understory plant communities (both woody and herbaceous) 40+ years after treatment? This thesis addresses these questions in two respective research chapters.

The first of these research chapters (Chapter 2) addresses the overstory structural dynamics, stand level growth, and mortality of red pine over a ~50 year period following fire. We used permanent plot records to evaluate the development of these stands in response to burning from 1959 through 2014. In addition, dendrochronological techniques were used to evaluate growth efficiency of the residual overstory red pine stems allowing an assessment of the cumulative effect of prescribed burning on the vigor of those residual trees.

The second research chapter (Chapter 3) quantifies the long-term trends in attributes of the woody and herbaceous understory communities, including abundance, diversity, and community composition over a multi-decade period following repeated burning. Again, permanent plot records enabled us to evaluate changes in the abundance, composition, and diversity of woody understory species for the period 1959 through 2014. Further, long-term effects on the herbaceous plant community were investigated through the use of an expanded survey design implemented in 2014.

The fourth and final chapter aims to synthesize the findings and conclusions from both research chapters, while placing them in the context of contemporary resource management concerns. Implications for silvicultural applications are expanded upon, future research directions suggested, and limitations of this particular study are discussed.

Chapter 2: Long-term impacts of prescribed fire on stand structure, growth, mortality, and individual tree vigor in *Pinus resinosa* forests.

2.1. 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 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, Frissel 1973, Heinselman 1973). Repeated surface fires along with higher severity fires occurring at intervals of 150 to 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, Drobyshev 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 (Frissel 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 towards non-pine species (Methven and Murray 1974, Drobyshev 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 1965, 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 1965, 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 1965, Peterson et al. 1994, Monleon and Cromack 1996, Sala et al. 2005, Battipaglia 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.

2.2. Methods

2.2.1. 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 – 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 juneberries (*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 m^2 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.

2.2.2. 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 6-12 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 – 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.

2.2.3. 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 1959-2010 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; m^2 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:

$$PAI = (\mathrm{BA}_{t0} - \mathrm{BA}_{t\text{-}1}) / (t_0 - t_{-1})$$

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:

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

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.

2.2.4. 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 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 α = 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 α = 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 α = 0.05.

2.3. Results

2.3.1. 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 2.1). 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 (Figure 2.1). 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 2.2).

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 (Figure 2.1). Season of burning impacted TPH and interacted with year to create the varied responses over the long-term (Table 2.2, Figure 2.1). 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 (Figure 2.2). Within the burned treatments, TPH did not significantly differ between summer and dormant season burning within a given burning frequency (Figure 2.1).

Basal area increased consistently over the duration of the study in all treatments (Figure 2.1). However, burned treatments maintained consistently lower basal areas than the unburned control throughout the study, particularly in later measurement periods (e.g., since 1997; Figure 2.1). The three-way interaction of season, frequency, and year (Table 2.2) created dynamic patterns among treatments throughout the duration of the study (Table 2.2, Figure 2.1). 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 (Figure 2.1).

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 (Figure 2.1). The three way interaction of season, frequency and year resulted in long-term differences in QMD among burned treatments and the control (Table 2.2, Figure 2.1). Significant differences between treatments were rare due to the increasing variability in tree size as small diameter stems were recruited over time (Figure 2.2, Appendix 1). In general, burned treatments had consistently higher QMD than untreated controls over the entirety of the study (Figure 2.1). Breakdown of tree size into diameter classes revealed that low QMDs were explained by the recruitment of small diameter stems into the unburned control (Figure 2.2). No differences in trends of QMD were found among burning treatments (Figure 2.1), which is corroborated by the similar composition and delay in the recruitment of smaller diameter stems between all burning treatments (Figure 2.2).

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 (Figure 2.2). Further, diameter class distributions revealed compositional differences in recent years. Small diameter 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 (Figure 2.2).

Snag density in 2014 was related to the application of fire (Table 2.3, Figure 2.3). 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 2.3). Snag densities were generally lower in burned treatments when compared to the control (Figure 2.3), 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 2.3, Figure 2.3). Snags consisted entirely of red pine, except in the unburned control, where small diameter hardwood snags were present in low numbers (results not shown).

2.3.2. 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 2.2). 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 (Figure 2.1). 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 (Figure 2.1).

Year and its interactions with season and frequency of burning were also found to be important in explaining mortality rates of red pine (Table 2.2). Mortality was low ranging from 0% to 0.47% until the year 2005, when the rate increased across several treatments (Figure 2.1). Mortality in the last two measurement periods increased significantly across the majority of treatments with mortality rates in 2014 ranging from 0.0 to 2.7% (Figure 2.1). 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 (Figure 2.1), and was significantly different from all burning treatments in 2014.

2.3.3. 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 review*). 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 2.4). Together, BAI and growth efficiency results indicate no persistent effect of burning on individual tree vigor ~45 years following treatment.

2.4. Discussion

2.4.1. 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) 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 towards 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), southeastern USA pine forests (Waldrop 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 m^2ha^{-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 m^2ha^{-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 m^2 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. 1996). 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).

2.4.2. 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 thinnings 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 1965), 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 m^2ha^{-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.

2.4.3. 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. *in prep*), 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 1965) 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.

2.5. 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 (*P. 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.

2.6. Tables and Figures

Table 2.1 Mean (± 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)

Table 2.2 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 1960-1970.

	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

Table 2.3 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 1960-1970.

	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

Table 2.4 Analysis of variance results for growth efficiency in 2014 at the *Red Pine Prescribed Burning Experiment* in north-central Minnesota, U.S.A. Burning treatments were applied from 1960-1970.

	growth efficiency		
	F	***df***	***p-value***
season	0.123	2	0.8849
frequency	0.4135	2	0.6666
season × frequency	0.4906	2	0.6191

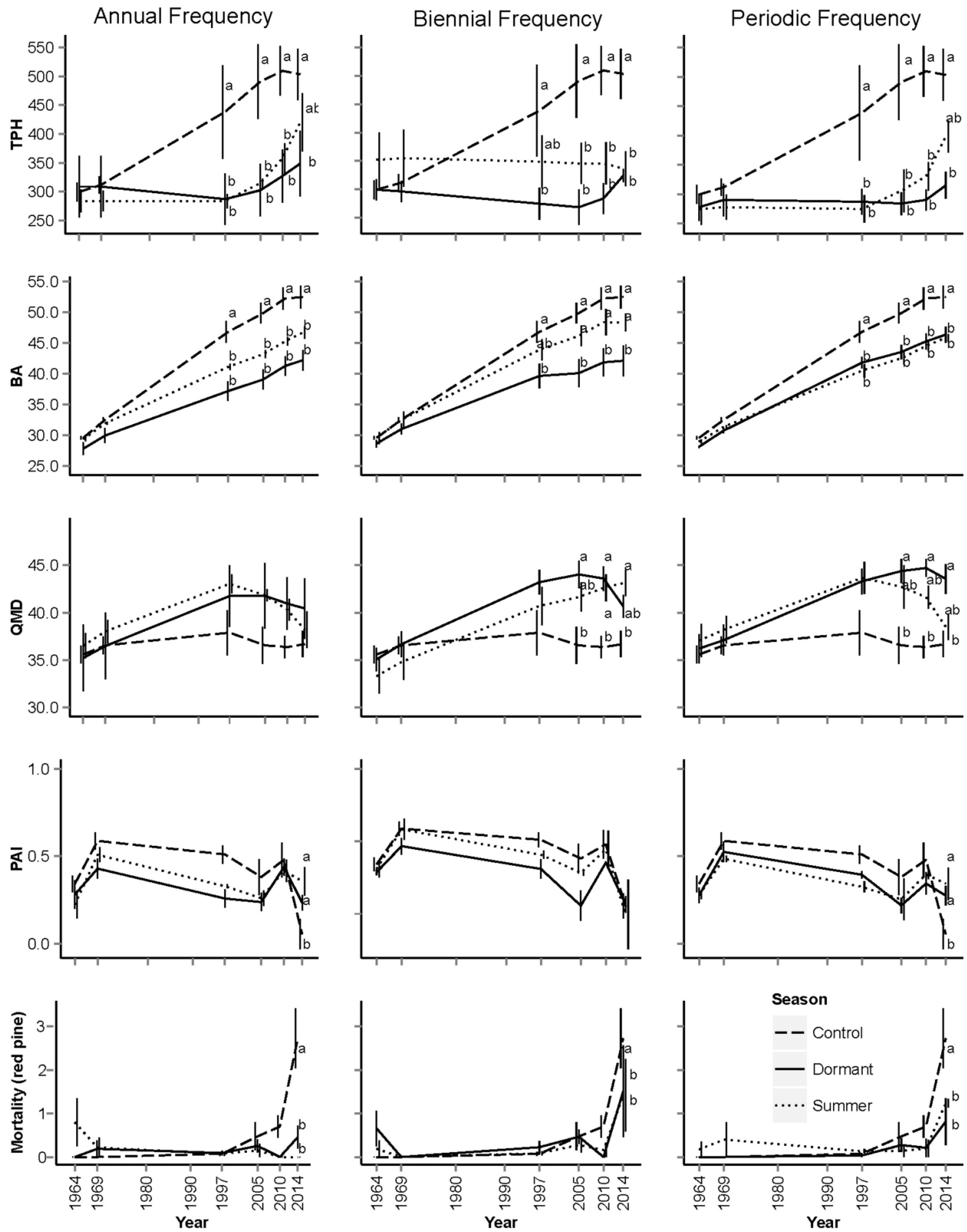

Figure 2.1 Tree density (TPH, trees ha^{-1}), basal area (BA, m^2 ha^{-1}), quadratic mean diameter (QMD, cm), periodic annual increment (PAI, m^2 ha^{-1}yr^{-1}) , and mortality (% of trees year^{-1}) for a 50 year period at the Red Pine Prescribed Burning Experiment in north-central Minnesota, U.S.A. Burning treatments were applied from 1960-1970. Letters indicate statistical difference from pairwise comparisons of burning season within a given fire frequency and year at α = 0.05. Control treatment is replicated in each frequency panel. Error bars are ± one standard error.

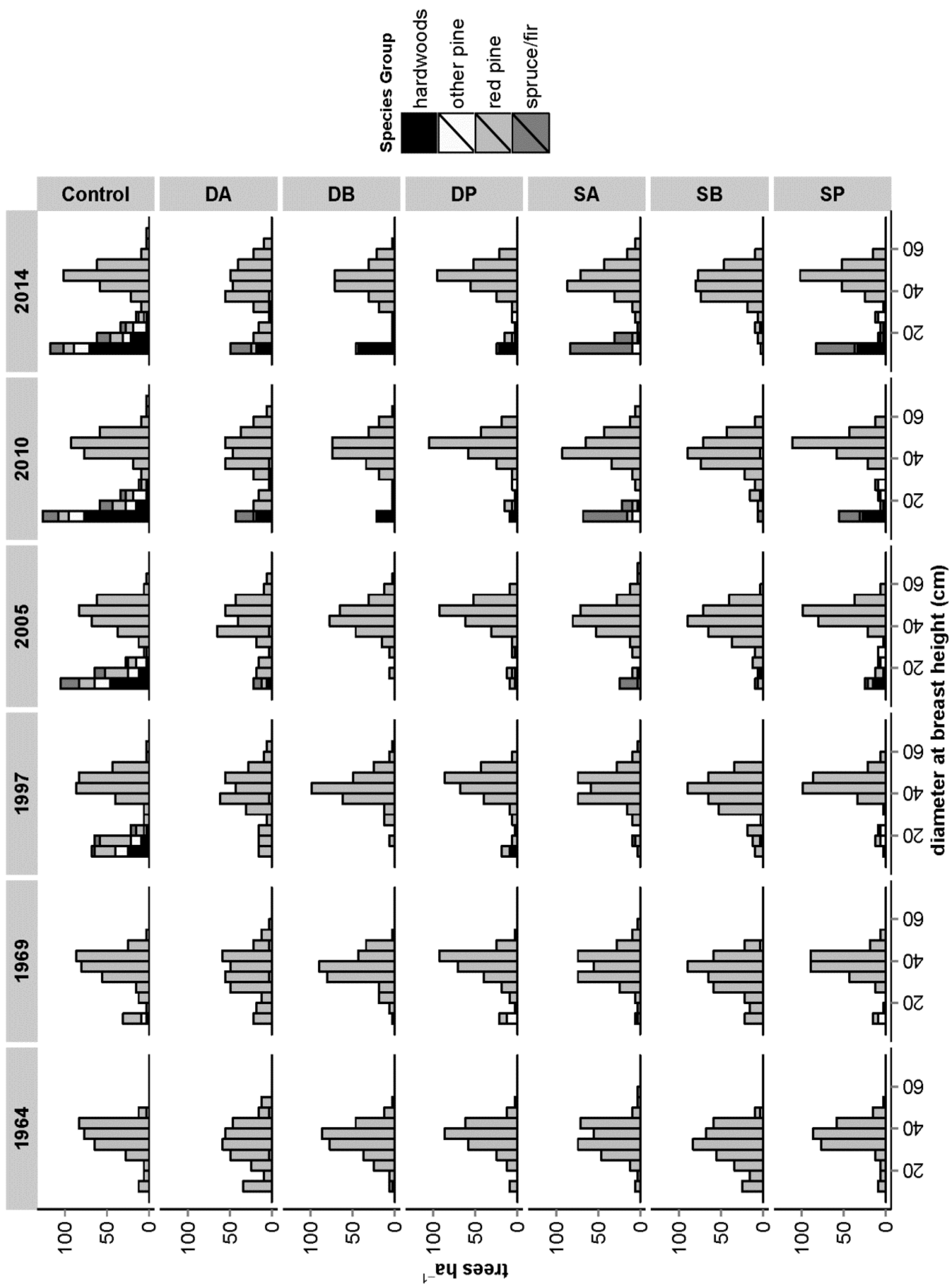

Figure 2.2 Diameter distributions by species group (treatment mean) for each measurement year at the Red Pine Prescribed Burning Experiment in north-central Minnesota, U.S.A. Burning treatments were applied from 1960-1970. Treatments are labeled as Control (unburned control), DA (dormant annual), DB (dormant biennial), DP (dormant periodic), SA (summer annual), SB (summer biennial), SP (summer periodic).

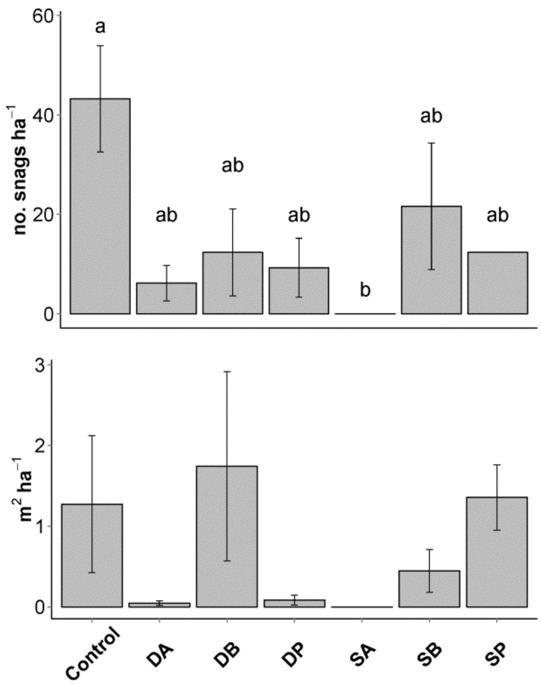

Figure 2.3 Mean snag density (upper panel, stems ha^{-1}) and snag basal area (lower panel, m^{2}ha^{-1}) for the Red Pine Prescribed Burning Experiment in north-central Minnesota, USA for the year 2014. Burning treatments were applied from 1960-1970. Letters indicate statistical differenences at *a = 0.05*.

Chapter 3: Long-term pine regeneration, shrub layer dynamics and understory community composition responses to prescribed fires in *Pinus resinosa* forests.

3.1. Introduction

Fire has been a dominant force shaping the historical development and dynamics of many forested ecosystems across North America and around the globe (Pyne 1982). For example, low- and mixed-severity fire regimes maintained a variety of pyrophytic pine and oak forests across much of eastern USA and adjacent Canada (Nowacki and Abrams 2008, Frelich 2002, Waldrop and Goodrick 2012). Red pine- (*Pinus resinosa* Ait.) dominated forests across the upper Great Lakes region are a classic example of these fire-adapted 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 occurring at intervals ranging from 5 to 50 years (Heinselman 1973). These repeated surface fires have been credited with reducing the abundance of woody shrubs and mesophytic tree species in the understory, facilitating pine regeneration through the creation of proper seedbed conditions, and maintaining composition and diversity of herbaceous ground-layer communities (Ahlgren 1976, Nyamai et al. 2014, Van Wagner 1970, Roberts 2004).

Wildfire suppression efforts have greatly limited the impact of fire effects within fire-dependent ecosystems across North America since the 1920s (Frissel 1973, Heinselman

1973, Waldrop et al. 1992). The extended absence of fire has greatly altered forest structure, often resulting in the development of dense understories of woody shrubs, which limit native tree regeneration and affect the composition of herbaceous ground-layer communities (Royo and Carson 2006, Waldrop et al. 1992). In red pine-dominated ecosystems, an important component of the Great Lakes region forests, the extended absence of surface fire is associated with dense understories of hazel (*Corylus cornuta* Marsh., *Corylus americana* Walt.) (Tappeiner 1971, Buckman 1964). Hazel species are highly competitive under these altered disturbance regimes due to their extended longevity, rhizomatous rooting habits, and ability to rapidly resprout vegetatively following stem mortality (Tappeiner 1971, Young and Peffer 2010). As such, the ubiquitous formation of dense shrub layers composed of hazel and other similar shrub species are associated with poor pine regeneration across much of the Great Lakes region (Tappeiner 1971, Dovčiak et al. 2003, Montgomery et al. 2010).

Prescribed fire has been proposed as a management tool for reducing woody stem densities in the understory and restoring vegetative communities in red pine forests and other fire dependent ecosystems across North America (Dickmann 1993, McRae 1994, Waldrop and Goodrick 2012). Earlier research has shown that fire affects the abundance, structure, and composition of red pine understories in the short term, often resulting in increased cover and richness of understory species (Cook et al. 2008, D'Amato et al. 2012). This response is dependent on the season and frequency of the fire and on the life history traits of the species present (Roberts 2004, Miller 2000).

While short-term effects of a limited set of fire prescriptions on understory vegetation have been well documented for red pine (e.g. Van Wagner 1963, Buckman 1964, Henning and Dickmann 1996), few studies have examined vegetation responses beyond 10 years and fail to assess the legacy of prescribed fire effects in the long-term (Henning and Dickmann 1996, Weyenberg and Pavlovic 2014). As a result, key knowledge gaps exist regarding prescribed fire and the long-term (i.e., > 10 years) vegetative outcomes within these ecosystems. In particular, information is lacking on the persistence of prescribed fire effects on vegetation after application of treatments has ceased.

This study takes advantage of an existing long-term silvicultural experiment located within a northern temperate conifer forest in north-central Minnesota, USA. The *Red Pine Prescribed Burning Experiment* was designed to examine the effectiveness of underburning mature red pine forests to reduce shrub (particularly hazel) abundance given the purported role of shrub competition in limiting natural regeneration of red pine in the region. Established in 1959, the study treatments were implemented between 1960 and 1970. Plot measurements were conducted during active treatment and were continued after cessation of the fires, creating a 50+ year data record. Consequently, this study provides an unprecedented short-term record of an initial 10-year burn period and a subsequent long-term record of fire-free vegetation development following various prescribed fire treatments. The fire treatments included combinations of fire frequency (annual, biennial, periodic) and fire season (dormant, summer) in a replicated design and include an unburned control for comparison.

The objectives of our study were to evaluate various prescribed fire season and frequency treatments and associated impacts on 1) abundance (density and biomass) of woody understory plants including pine regeneration in the short- and long-term and 2) composition and diversity of the woody and herbaceous understories in the long-term. We hypothesized (1a) that shrub abundance would be influenced by prescribed fire and reduced by summer season fires and higher frequency fires in the short- and long-term. We also hypothesized (1b) that pine regeneration and recruitment would be associated with prescribed fire treatments that effectively reduced shrub abundance in the long-term. Lastly, we hypothesized (2) that composition and diversity of the woody and herbaceous understories would be different in the long-term between plots treated with prescribed fire and unburned controls.

3.2. Methods

3.2.1. 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 – 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, are weakly developed and 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 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 sparse to patchy shrub layers consisting of juneberries (*Amelanchier* spp.), bush honeysuckle (*Diervilla lonicera* P. Mill.), and hazel (*Corylus* spp.). Fire history reconstruction for the Cutfoot experimental forest indicate that surface fires were once common in these ecosystems with fire return intervals ranging from 3-19 years (Guyette et al. 2015).

Four replicate blocks were established in the study area in 1959 and thinned to a standard residual overstory basal area of 27-29 m^2 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.

3.2.2. Burning

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 (Alban 1977). Fuels were primarily pine litter and resulted in low to moderate fire intensity with flame heights generally less than 1 m. Fires consumed the entire L horizon in burned units, and further consumed the F horizon in annually and biennially burned treatments (Alban 1977). Burning treatments were applied from 1960 – 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 activities have been conducted within the experimental blocks since 1970.

3.2.3. Field Sampling

Within each treatment compartment, a single 0.08 ha circular plot was established to monitor overstory conditions (see section 2.2.3 for details). Nested within this overstory plot were located eight smaller 4 m^2 circular sub-plots intended to track and monitor the response of understory woody species. The locations of these sub-plots were standardized and permanently monumented at 4.6 m and 10.7 m in each of the four cardinal directions (Figure 3.1). From 1959 through 1969, all live woody stems < 2.54 cm diameter at breast height (dbh) were tallied by species in 2.54 mm diameter (D12) classes, where D12 is the diameter ~30 cm (12 inches) above the ground. Beginning in 1997, sampling for stems < 2.54 cm dbh was updated to use metric diameter classes and measurements. From this point onward, all live woody stems > 15 cm in height were tallied in 2 mm diameter (D15) classes, where D15 is the diameter 15 cm above groundline. Additionally, all live woody saplings (stems 2.54 cm > dbh < 9.1 cm) were measured for dbh to the nearest 0.1 cm in each measurement year and were consistent for the entire study period.

An additional survey was conducted in 2014 to quantify long-term effects on the diversity and composition of the herbaceous ground layer. One meter square quadrats were established at each of the eight shrub sub-plots (Figure 3.1). In each quadrat, we assigned one of six foliage cover classes (<1%, 1-5%, 6-15%, 16-30%, 31-60%, 61-100%) for each herbaceous plant species rooted on the plot.

3.2.4. Statistical Analysis

First, abundance of woody species was evaluated as density and biomass. Density was calculated for each sub-plot and expressed as the number of woody stems ha^{-1} for each measurement year. Aboveground woody biomass of each living stem was calculated using published allometric equations from Perala and Alban (1993) developed from sites in close proximity to our study area. For stems < 2.54 cm DBH, diameter class midpoints for D12 and D15 were used when calculating biomass values. Stems within a sub-plot were summed to estimate biomass and expressed as Mg ha^{-1} for each sub-plot. Sub-plot data were averaged and summarized at the plot level before using for further analysis. Tree species capable of canopy status were categorized by their sensitivity of fire at maturity to investigate changes in the relative proportions of relevant functional groups over time using ratings from the Fire Effects Information System (Fischer et al. 1996).

To assess the short- and long-term effect of prescribed fire on woody species abundance, as well as the relative roles of fire season and frequency, we employed repeated measures mixed model analysis of variance. Separate models were developed for both stem density and aboveground stem biomass by species groups as responses and fire season, fire frequency, year, and all two- and three-way interactions as fixed effects. Four species groups categorized the responses: stem density and stem biomass for hazel (dominant understory shrub), red pine (overstory dominant), white pine (sapling dominant), and all woody shrub and tree species (total understory). A random intercept for each treatment compartment (Plot) was included. Basal area of overstory trees at the end of each sampling period was also included as a covariate in each model to control for the effect of overstory trees on resource availability. Models were fit using the “lme4” package in the R environment (Bates et al. 2013).

Planned mean contrasts for density and biomass 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). Associated *p*-values were adjusted using the false discovery rate (FDR) method for a family of three tests and significance is reported at $\alpha = 0.05$. Residual plots were used to visually assess homoscedasticity of variance. The natural logarithm or square root transformations was applied when necessary to normalize the distribution of residuals (Weisberg 2014).

Next, community composition patterns of understory plants among treatments over time were examined using nonmetric multidimensional scaling (NMS) for two datasets, one based on the abundance of woody species (biomass) and one based on herbaceous species abundance (cover). The woody dataset included the years 1959, 1969, and 2014 representing “before burning”, “end of burning”, and “long-after burning”. The herbaceous layer dataset included year 2014, providing a snapshot of the “long-after burning” effects. Both datasets were handled similarly. Only species which occurred on at least 5% of plots were included. NMS ordination was conducted using PC-ORD 6.0

(McCune and Mefford 2010) with 250 runs for both real and randomized data, and a maximum of 500 iterations per run. The response matrix consisted of species (columns) and plots (rows), and was analyzed using the Sørensens's distance measure for above ground biomass. Upon completion of the NMS ordination, Kendall rank correlation coefficients (τ) were calculated between species abundance and associated NMS axis scores with significance reported at $\alpha = 0.05$ following an FDR adjustment for multiple tests. Compositional differences among treatments were investigated using repeated measures distance-based multivariate analysis of variance (perMANOVA). Burning treatment (season/frequency combination), year, and their interaction were used as fixed effects, and a random intercept was included for each treatment compartment (Plot). In cases with a significant interaction, separate models were run for each fixed effect with the other held constant to facilitate pairwise comparisons of treatments. Significant differences among treatments were reported at $\alpha = 0.05$ following an FDR adjustment.

Finally, the effects of prescribed fire treatments on species diversity of the understory plants were evaluated using repeated measures mixed model analysis of variance on two datasets: one based on woody species abundance (biomass) and on based on herbaceous species cover. The woody dataset included the years 1959, 1969, and 2014; the herbaceous dataset included year 2014. Both datasets were handled similarly. Diversity indices (Shannon's entropy, evenness, species richness) were calculated per square meter in PC-ORD. Shannon's entropy was transformed to Shannon's diversity using an exponential function as suggested by Jost (2006) so that diversity is expressed as the effective number of commonly-dominant species. Given the presence of significant year by treatment interactions, pairwise comparisons of treatments were conducted for each year to assess treatment differences and report significance at $\alpha = 0.05$ following an FDR adjustment. Models were fit in R using the “lme4” package (Bates et al. 2013), with pairwise comparisons among treatments made using the package “lsmeans” (Lenth 2013).

3.3. Results

3.3.1. Woody understory density and abundance

The prescribed burning treatments implemented in the study affected the density and biomass of all species groups: hazel, white pine, red pine, and total woody understory species. For hazel, the three-way interaction of season, frequency, and year produced dynamic patterns in both the density and biomass over the duration of the study (Table 3.1, Figure 3.2a, Figure 3.3a). In terms of stem density, summer season burning decreased and dormant season burning increased hazel densities from the control particularly in the short term (i.e. 1964-1969, Figure 3.2a). Fire frequency had contrasting effects on hazel density as well. At the end of burning (1969), periodic burning, irrespective of season, resulted in hazel densities higher than the control in the periodic burning compared the control; Figure 3.2a). In contrast, summer-annual burning resulted in significantly low hazel densities in the short- and long-term (Figure 3.2a).

Hazel biomass revealed unique trends relative to those for stem density. All burning treatments displayed dramatic reductions in hazel biomass when compared to the unburned control near the end of the active burning period (i.e., 1969) (Figure 3.3a). Following the cessation of fire in 1970, biomass of hazel increased within all burning treatments until the mid-2000s; however, the rate of increase was not consistent across treatments (Figure 3.3a). Generally, dormant season burning resulted in much more rapid increases in hazel biomass following the cessation to fire, whereas summer burning resulted in a slower rate of increase (Figure 3.3a). As a result, hazel biomass in summer burning treatments was significantly lower than dormant season burning well into the 2000s for annual and biennially burned treatments (Figure 3.3a). Summer-annual burning displayed hazel biomass below that of the control through 1997, indicating a potential for a nearly three-decade delay of recolonization by woody shrubs (Figure 3.3a).

For white pine the three-way interaction of season, frequency, and year resulted in variable regeneration over the study (Table 3.1, Figure 3.2b, Figure 3.3b). In terms of both seedling density and biomass, only summer-annual and summer-biennial burning resulted in appreciable regeneration of white pine at any point throughout the study (Figure 3.2b, Figure 3.3b). White pine regeneration density and biomass (in the > 15cm height, < 9.1 cm DBH size class) peaked in the 1997 measurement period (Figure 3.2b) and has generally decreased since. White pine regeneration above that of the control in years since 1997 was significant for density in the summer-annual treatment and for biomass in summer-annual and summer-biennial treatments (Figure 3.2b).

Patterns of red pine regeneration were similar to that of white pine, but occurred at a lower absolute level. Density and biomass of red pine regeneration were affected by the interaction of season and frequency of burning (Table 3.1). Only the summer-annual treatment produced any measurable gains in red pine regeneration, with a small peak in both density and biomass occurring in the 1997 measurement year (Figure 3.2c, Figure 3.3c). Following a short peak in abundance in 1997, subsequent establishment of red pine has dissipated in the understory (Figure 3.2c, Figure 3.3c).

Total density and biomass of the woody understory (i.e., all species) were affected by the three-way interaction of season, frequency, and year (Table 3.1). Results and trends for stem density generally reflect that of hazel density (Figure 3.2d), the dominant species and lifeform in the understory (Figure 3.4). In contrast, results and trends for woody biomass were similar to hazel biomass in early measurement periods and influenced by pine biomass in later years (Figure 3.3d, Figure 3.4), because shrubs and fire resistant conifers (i.e. pine) dominated understory woody biomass during these time periods, respectively (Figure 3.4).

3.3.2. Woody understory community composition and diversity

NMS ordination of woody understory composition resulted in a two dimensional solution. The first axis explained 58.4% of the variation in composition for the years 1959, 1969, and 2014. A second axis explained an additional 11.4% of variation in those years (Figure 3.5). Prior to treatment in 1959, treatments occupied a similar portion of ordination space, including the unburned control. In 1969 following nine years of active burning, all burned treatments shifted positively along axis 1 away from the control and pre-treatment conditions (Figure 3.5). Following a 44-year fire-free period, burned treatments shifted back toward pre-treatment conditions in the negative portion of axis 1 with little separation from the control in 2014 (Figure 3.5). Species correlation's with NMS axis scores indicate that positive movement along axis 1 was associated with a decline in the abundance of several common woody shrub and tree species, particularly beaked hazel (Table 3.2).

The interaction of burning treatment and time in the perMANOVA of woody understory composition resulted in dynamic compositional patterns in the woody understory throughout the study ($F = 4.38$, $p = 0.006$). No significant differences among treatments were observed prior to treatment in 1959 (Figure 3.5). In 1969, woody compositions were significantly different between burned treatments and the control and among several burned treatments (Figure 3.5). No significant differences among treatments were observed in 2014 and indicate a return to pre-treatment composition.

In terms of woody species diversity, Shannon's diversity (richness of commonly-dominant species) and evenness resulted in a significant interaction of treatment and time ($F = 2.04$, $p = 0.044$ and $F = 4.03$, $p < 0.001$, respectively). Similar to woody composition, Shannon's diversity and evenness of woody species did not differ among treatments prior to treatment in 1959 or decades after burning in 2014, but was significantly lower in 1969 in the summer-annual burning treatment for Shannon's diversity and in all summer burned treatments for evenness (Table 3.3). Species richness of the woody understory showed no significant differences among treatments throughout the duration of the study (Table 3.3).

3.3.3. Ground-layer plant community composition and diversity

NMS ordination converged on a three dimensional solution for ground layer community composition in 2014. The first axis explained 53.9% of the variability, with axis 2 and axis 3 explaining 19.4% and 8.4% of the variability in composition, respectively (Figure 3.6). Results of perMANOVA indicate that burning treatment significantly affected (F = 1.29, p = 0.02) ground-layer composition in 2014. After adjusting for multiple tests, no significant differences among individual treatments were identified; however, arrangement of treatments in ordination space suggest that the composition of the summer-annual treatment is likely a driver of the significant burning treatment in the perMANOVA. The summer-annual treatment displayed more positive axis 1 scores than the other treatments (Figure 3.6). Species correlations with NMS axis scores indicate that positive axis 1 scores were associated with *Anenome quinquefolia, Aster macrophyllus,* and *Pteridium aquilinum* (Table 3.4).

Burning treatment was marginally significant in explaining Shannon's diversity and evenness of the herbaceous species in 2014 (F = 2.39, p = 0.07 and F =2.65, p = 0.051, respectively) (Table 3.5). After adjusting for multiple tests, no significant differences between treatments were found for Shannon’s diversity, evenness, or species richness (Table 3.5).

3.4. Discussion

3.4.1. Woody understory density and abundance

Prescribed fire resulted in dramatic alterations to both short- and long- term dynamics of woody shrub abundance. In the short-term (i.e.,1964-1969), prescribed fire, irrespective of fire season, resulted in dramatic reduction or near elimination of woody species biomass in the understory, a result consistent with early results from this experiment (Buckman 1964) and other studies in the region (Henning and Dickmann 1996, Neumann and Dickmann 2001, Van Wagner 1963). However, in the long-term, the influence of season and frequency of burning emerged and resulted in long-lasting changes to woody shrub density and abundance.

Season of burn affected woody vegetation density and biomass, even decades after burning ceased. For instance, dormant season burning led to large increases in hazel biomass over the entirety of the 50+ year study. The wide range of observed hazel biomass is likely attributed to the prolific sprouting of hazel initiated by the dormant season burning treatment that top-killed aerial stems, but not belowground rhizomes, as documented by other studies (Buckman 1964, Tappeiner 1979, Van Wagner 1963).

On the other hand, summer season burning, particularly at high frequency, was associated with low hazel biomass, even 40+ years after the last burning treatment. This finding supports early results from this study reported by Buckman (1964) who predicted that multiple summer burns would be needed to reduce hazel abundance in the long-term. Summer season burns generally burn hotter, penetrate deeper into organic soil layers (Alban 1977) and may cause more damage to the extensive rhizomatous root system of hazel, which is generally limited to the organic layer (Tappeiner 1971). Further, summer burns affect the stems of plants at a time when deciduous shrubs are particularly vulnerable. Following leaf out these species have reduced belowground carbohydrate stores, lowering their re-sprouting capability following top-kill (Miller 2000, Pelc et al. 2010). The responses observed in our study are similar to studies in the southeastern US where annual summer burning lead to a near-complete elimination of woody stems in the understory of a loblolly pine (*Pinus taeda* L.) stand after 40 years of continuous burning (White et al. 1990).

Although several studies have shown that prescribed fire may result in regeneration of both red and white pine (Van Wagner 1963, D'Amato et al. 2012, Methven and Murray 1974), the effects of the prescribed fire treatments we examined on red and white pine regeneration were not as clear as the effects on hazel. In general, pine regeneration was low throughout the study and among all treatments suggesting that prescribed fire, as implemented here, cannot establish a new cohort for either species. A low density of pine regeneration did exist early in the study (i.e., 1964), but did not persist. We assume burning caused direct mortality of regeneration, because seedlings of both species are easily killed by exposure to fire (Heinselman 1973). Around 1997, about 25+ years after burning ceased, we detected a pulse of pine regeneration in the units that were treated with summer-annual and summer-biennial treatments applied during the active burn period, 1960-1970. We speculate that this post-burning cohort established under suitable conditions that were associated with those treatments long after they were applied.

However, the 1997 cohort of pine densities declined for several possible reasons. First, the pine may have outgrown this size class (>15 cm tall to < 9.1 cm DBH) and recruited into the overstory size class (see Figure 2.2 in previous chapter). Second, the abundance of hazel (and overstory trees (see Figure 2.1 in previous chapter) increased, potentially creating unsuitable conditions for pine seedling survival. A nearby study found that hazel severely reduced the survivorship of planted pine seedlings, especially for red pine (Montgomery et al. 2013). Further, in a similar investigation, Methven (1973) concluded that, without subsequent alteration of the overstory through partial cutting, understories in stands treated with prescribed fire would revert to pre-fire conditions with little or no pine regeneration. Lastly, given the presence of an intact red pine overstory, red pine seedlings were likely infected by shoot blight caused by the fungal pathogens *Diplodia pinea* and *Sirococcus conigenus* (personal observation). Although these two pathogens can persist without major consequences in mature red pine, infection of red pine seedlings is lethal and poses a substantial barrier to natural regeneration of red pine across the region (Ostry et al. 2012).

3.4.2. Woody understory community composition and diversity

Prescribed fire led to divergence of community assemblages of the woody understory in the short-term. Near the end of burning treatments in 1969, near elimination of hazel and other shrub biomass in the understory led to a large change from pre-treatment and control conditions in all burning treatments and is similar to the results in other studies (e.g., Henning and Dickmann 1993, Neumann and Dickmann 2001). Reduction of abundant species such as hazel following fire was a main driver in the divergence of the woody shrub community composition. However, several decades after burning has ceased, burned treatments returned toward their pre-treatment conditions, demonstrating the resistance of those species present. While our study showed no persistent changes, a long-term study of the role of burning on understory vegetation in a loblolly pine ecosystem showed that burning treatments resulted in distinct community assemblages after 40 years (White et al. 1990). The ecosystem studied by White et al. (1990) differs from ours however with recolonization of the woody understory dominated by basal sprouting species rather than rhizomatous shrubs, and further burning was applied continuously in that study with no fire-free period (White et al. 1990).

The effect of the prescribed fire treatments on woody species diversity appears minimal, particularly in the long-term. Short-term differences in Shannon's diversity and evenness that emerged in 1969 can be attributed to the near elimination of woody biomass following nine years of active burning. This finding is consistent with Henning and Dickmann (1993) who found that species richness of the woody understory declined with fire frequency in the short-term. Similarly, burning, particularly at annual and biennial intervals, led to a decrease in richness and diversity of the woody understory in a South Carolina loblolly pine forest following 40 years of continuous burning (White et al. 1990). Overall, the diversity changes are attributed to alterations in relative abundance of species present on site rather than any losses or gains of species due to treatment. In the long-term, biomass had sufficient time to recover such that species diversity differences were no longer detectable among the treatments.

3.4.3. Ground-layer plant community composition and diversity

Investigation of the ground-layer plant community provides evidence that prescribed fire can have lasting effects on community composition. While our results are limited to only the recent measurement (2014), they provide evidence for distinct community assemblages in the long-term with high moss abundance for summer-annual burning that occurred more than four decades prior. While mosses and other bryophytes are often killed initially by fire, they are important post fire colonizers and can provide suitable seedbed conditions for many conifers (Ahlgren and Ahlgren 1960, Ryömä and Laaka-Linberg 2007). Several species of bryophytes have been found to colonize post fire ash effectively and in some cases are associated with areas where humus has been consumed (Ryömä and Laaka-Linberg 2007). Post fire investigation of soil properties in our experimental units indicate that summer-annual burning resulted in considerable consumption of humus and may have created conditions suitable for the establishment of post-fire bryophyte colonization (Alban 1977). Further, the summer-annual treatment was most effective in reducing the abundance of woody understory species (see 3.4.1 above), which may have created increased light levels and better microsite conditions for the persistence of moss species. The increased cover of moss in the summer-annual treatment may have facilitated the regeneration of both red and white pine in that treatment (Ahlgren 1976). Our results add to a body of literature documenting compositional shifts following the use of prescribed burning in Great Lakes region pine forests (e.g. Cook et al. 2008, D'Amato et al. 2012, Neumann and Dickmann 2001, Methven 1973) and provide evidence for significant ecological legacies created by prescribed fire management.

In terms of diversity, the ground layer showed minimal long-term impact from the burning treatments. We did not have data on short-term effects of fire on herbaceous diversity, but, if there were, the effects did not persist in the long-term. In comparison, regional, short-term (< 5 year) studies show a ~25% increase in the species richness (Neumann and Dickmann 2001), and a decrease in evenness of the ground layer (Cook et al. 2008). Long-term evaluations of the ground-layer response to prescribed fire are largely limited to pine ecosystems of the southeastern USA and in studies using continuous fire treatments (without extended fire-free periods). Species richness was positively associated with the frequency of fires in a Florida longleaf pine (*Pinus palustris* Mill.) forest after nearly 50 years of continued fire treatments (Glitzenstein et al. 2011). Further, Brockway and Lewis (1997) demonstrated that periodic growing-season burning led to increases in diversity and richness of the ground layer following 39 years of repeated burning.

3.5. Conclusions and Management Implications

While the short-term efficacy of prescribed fire as a method for restoring understory conditions has been well investigated, this study presents the only long-term post-fire evaluation for the red pine forests and woodlands that once dominated much of the Great Lakes region across both the United States and Canada. Results from this study suggest that prescribed fire can be used to reduce the abundance of woody shrubs in the understory and may result in unique understory plant community assemblages. Our findings provide evidence that these alterations are sustained for several decades following the cessation of prescribed fire treatments indicating long-term legacies of prescribed fire management within fire-dependent ecosystems.

As has been shown in earlier results from our study (Buckman 1964), season of burning appears to be the driving factor in affecting the response of the understory, and further that multiple burns will be needed to achieve satisfactory reductions in woody shrub abundance. Although the frequency of burning treatments (particularly annual burning) examined in this study are likely not practicable, it is clear that multiple growing-season burns will be needed in most stands to reduce the shrub layer. Specific burning intervals needed to maintain desired understory conditions will need further investigation.

In areas where burning is not feasible (e.g., unsuitable weather, policy, etc.) (Melvin 2015), other management interventions may be used as surrogates to fire in the short- or long-term. Both mechanical and chemical methods have proven successful in achieving similar results, particularly related to the reduction of hazel density (Pelc et al. 2010, Tappeiner 1979). Season of mechanical removal ("brushing") of hazel show similar relations to season and frequency of treatments reported here for prescribed burning, but will likely require repeated treatments to maintain low hazel densities (Montgomery et al. 2013, Pelc et al. 2010).

Although periodic fires historically maintained red pine forests, prescribed fire alone appears unsuccessful in successfully establishing or recruiting a new cohort of red pine. If repeated summer burning or mechanical cutting were applied in conjunction with variants of the shelterwood method, we expect that regeneration of both red and white pine would improve markedly (D'Amato et al. 2012), although shoot blight infection may limit successful recruitment of established red pine seedlings (Ostry et al. 2012). White pine is not affected by these fungal pathogens, suggesting that natural regeneration of white pine may be a more attainable goal in these systems as long as that species is represented in the canopy as a seed source.

3.6. Tables and Figures

Table 3.1 Repeated measures analysis of variance results for aboveground woody biomass and stem density of woody shrubs and pine regeneration (>15 cm tall, <9.1 cm DBH) at the *Red Pine Prescribed Burning Experiment* in north-central Minnesota, USA. Burning treatments applied from 1960-1970.

	Aboveground woody biomass (Mg ha^{-1})											
	Corylus cornuta			*Pinus strobus*			*Pinus resinosa*			*all species*		
	F	***df***	***p-value***	***F***	***df***	***p-value***	***F***	***df***	***p-value***	***F***	***df***	***p-value***
Season	74.16	2	<0.001	20.71	2	<0.001	3.19	2	0.059	27.76	2	<0.001
Frequency	34.01	2	<0.001	12.69	2	<0.001	1.71	2	0.206	20.83	2	<0.001
Year	292.77	5	<0.001	5.61	5	<0.001	3.69	5	0.004	93.37	5	<0.001
Overstory Basal Area	0.35	1	0.553	0.01	1	0.931	0.01	1	0.929	0.02	1	0.879
Season × Frequency	12.86	2	<0.001	5.86	2	0.009	1.45	2	0.257	4.62	2	0.022
Season × Year	82.36	10	<0.001	7.71	10	<0.001	3.13	10	0.002	38.83	10	<0.001
Frequency × Year	59.88	10	<0.001	4.77	10	<0.001	1.49	10	0.153	23.08	10	<0.001
Season × Frequency × Year	5.78	10	<0.001	2.77	10	0.005	1.47	10	0.162	4.88	10	<0.001

	Density (no. stems ha^{-1})											
	Corylus cornuta			*Pinus strobus*			*Pinus resinosa*			*all species*		
	F	***df***	***p-value***	***F***	***df***	***p-value***	***F***	***df***	***p-value***	***F***	***df***	***p-value***
Season	22.29	2	<0.001	8.40	2	0.002	2.06	2	0.150	22.46	2	<0.001
Frequency	6.20	2	0.008	6.59	2	0.006	1.15	2	0.337	5.51	2	0.012
Year	12.75	5	<0.001	11.57	5	<0.001	2.81	5	0.020	16.01	5	<0.001
Overstory Basal Area	0.41	1	0.525	0.01	1	0.922	0.06	1	0.802	0.33	1	0.566
Season × Frequency	8.62	2	0.002	2.96	2	0.074	0.87	2	0.433	8.68	2	0.002
Season × Year	14.00	10	<0.001	6.30	10	<0.001	2.46	10	0.011	17.38	10	<0.001
Frequency × Year	9.65	10	<0.001	4.36	10	<0.001	1.14	10	0.344	14.38	10	<0.001
Season × Frequency × Year	5.43	10	<0.001	2.39	10	0.014	1.10	10	0.371	7.72	10	<0.001

Table 3.2 Species displaying significant ($\alpha = 0.05$) Kendall's rank order correlations with axes of NMS ordination of woody understory (>15 cm tall, <9.1 cm DBH) community composition at the *Red Pine Prescribed Burning Experiment* in northern Minnesota. *P*-values adjusted using FDR method for multiple tests.

	Species	relationship (+/-)	τ	*p*-value
Axis 1	*Amelanchier* spp.	–	-0.370	<0.001
	Abies balsamea	–	-0.264	0.007
	Acer rubrum	–	-0.245	0.010
	Corylus cornuta	–	-0.833	<0.001
	Diervilla lonicera	–	-0.372	<0.001
	Cornus spp.	–	-0.193	0.042
	Pinus strobus	–	-0.284	0.004
	Rubus spp.	–	-0.361	<0.001
	Vaccinium angustifolium	–	-0.400	<0.001
Axis 2	*Amelanchier* spp.	+	0.216	0.011
	Abies balsamea	+	0.348	0.001
	Acer rubrum	+	0.295	0.003
	Alnus spp.	–	-0.234	0.013
	Corylus cornuta	+	0.206	0.013
	Diervilla lonicera	+	0.224	0.020
	Pinus strobus	+	0.303	0.003
	Rubus spp.	+	0.283	0.003
	Salix spp.	–	-0.425	<0.001
	Vaccinium angustifolium	+	0.282	0.003

Table 3.3 Comparison of woody species diversity indices (+/- standard error) among burning treatments and an unburned control before burning (1959), end of burning (1969), and 44 years post burning (2014) at the *Red Pine Prescribed Burning Experiment* in north-central Minnesota, USA. Burning treatments applied from 1960-1970. Letters denote significant differences among treatments within a given year at α = 0.05 following an FDR adjustment for multiple tests.

	Shannon's Diversity (exp(H) or number of commonly-dominant species)						
	Control	Dormant Annual	Dormant Biennial	Dormant Periodic	Summer Annual	Summer Biennial	Summer Periodic
1959	2.3 (0.60)	1.8 (0.32)	2.3 (0.55)	2.0 (0.25)	2.2 (0.21)	2.3 (0.34)	2.4 (0.16)
1969	2.4 (0.58)a	3.4 (0.45)a	2.5 (0.44)a	2.8 (0.40)a	1.1 (0.09)b	2.7 (0.56)a	2.9 (0.21)a
2014	2.3 (0.57)	2.7 (0.23)	1.5 (0.10)	1.8 (0.26)	1.9 (0.33)	1.8 (0.30)	1.6 (0.28)

	Evenness (E, 0-1 where 0 indicates uneneven and 1 indicates even abundance of species)						
	Control	Dormant Annual	Dormant Biennial	Dormant Periodic	Summer Annual	Summer Biennial	Summer Periodic
1959	0.56 (0.15)	0.39 (0.13)	0.46 (0.16)	0.68 (0.14)	0.70 (0.14)	0.73 (0.05)	0.71 (0.09)
1969	0.53 (0.09)a	0.79 (0.05)ab	0.69 (0.05)ab	0.79 (0.08)ab	0.12 (0.12)c	0.85 (0.07)b	0.73 (0.06)b
2014	0.34 (0.08)	0.43 (0.05)	0.2 (0.03)	0.23 (0.05)	0.32 (0.08)	0.26 (0.08)	0.23 (0.07)

	Richness (S or number of species)						
	Control	Dormant Annual	Dormant Biennial	Dormant Periodic	Summer Annual	Summer Biennial	Summer Periodic
1959	3.5 (0.65)	3.8 (0.25)	4.2 (0.85)	3.2 (0.63)	3.5 (0.65)	3.0 (0.41)	3.5 (0.29)
1969	4.5 (0.87)	4.5 (0.29)	3.8 (0.63)	3.8 (0.63)	1.2 (0.25)	3.2 (0.63)	4.2 (0.25)
2014	4.2 (1.60)	5.5 (1.76)	6.2 (1.44)	5.2 (1.31)	7.0 (0.71)	5.8 (1.93)	5.0 (1.78)

Table 3.4 Species displaying significant ($\alpha = 0.05$) Kendall's rank order correlations with the two first axes of NMS ordination of ground layer community composition at the *Red Pine Prescribed Burning Experiment* in northern Minnesota. *P*-values adjusted using FDR method for multiple tests.

	Species	relationship (+/-)	τ	*p*-value
Axis 1	*Anenome quinquefolia*	+	0.416	0.049
	Aster macrophyllus	+	0.564	0.001
	Pteridium aquilinum	+	0.474	0.012
Axis 2	*Carex pennsylvanica*	–	-0.536	0.011
	Moss spp.	+	0.495	0.011

Table 3.5 Comparison of herbaceous species diversity indices (+/- standard error) among burning treatments and an unburned control 44 years post burning (2014) at the *Red Pine Prescribed Burning Experiment* in north-central Minnesota, USA. Burning treatments applied from 1960-1970. No significant differences among treatments were observed at $\alpha = 0.05$ following an FDR adjustment for multiple tests.

Treatment	Shannon's (H)	evenness (E)	Richness (S)
Control	13.5 (0.72)	0.87 (0.02)	20 (1.15)
Dormant Annual	12.5 (0.96)	0.87 (0.03)	18 (1.03)
Dormant Biennial	12.3 (1.17)	0.87 (0.01)	18 (1.49)
Dormant Periodic	14.5 (0.94)	0.87 (0.02)	22 (1.71)
Summer Annual	9.7 (1.39)	0.78 (0.03)	18 (1.38)
Summer Biennial	11.0 (0.77)	0.81 (0.01)	19 (0.85)
Summer Periodic	12.8 (1.04)	0.84 (0.03)	20 (0.50)

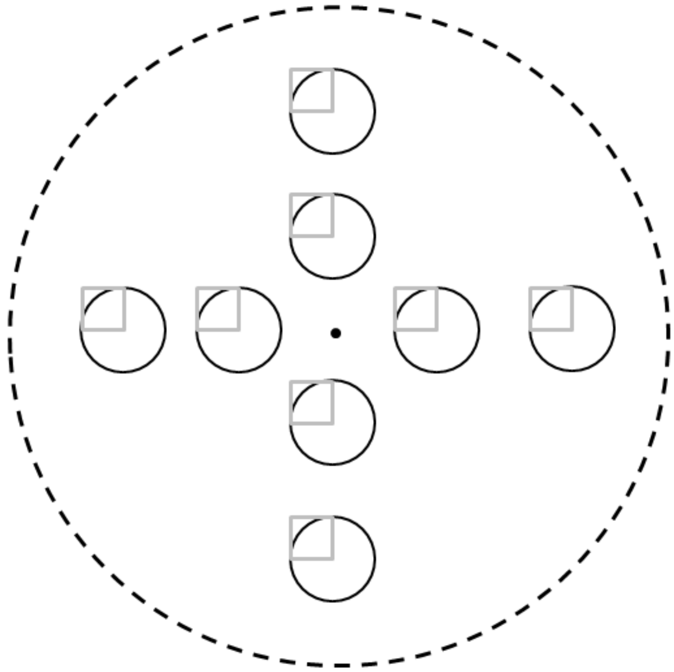

Figure 3.1 Understory sampling layout within each 0.08-ha overstory plot (dotted line) at the *Red Pine Prescribed Burning Experiment*, in northern Minnesota, USA. Small circles (solid line) depict the location of 4 m^2 woody understory species sampling plots at 4.6 m and 10.7m from plot center (dot) and small squares depict 1 m^2 herbaceous ground-layer sampling quadrats.

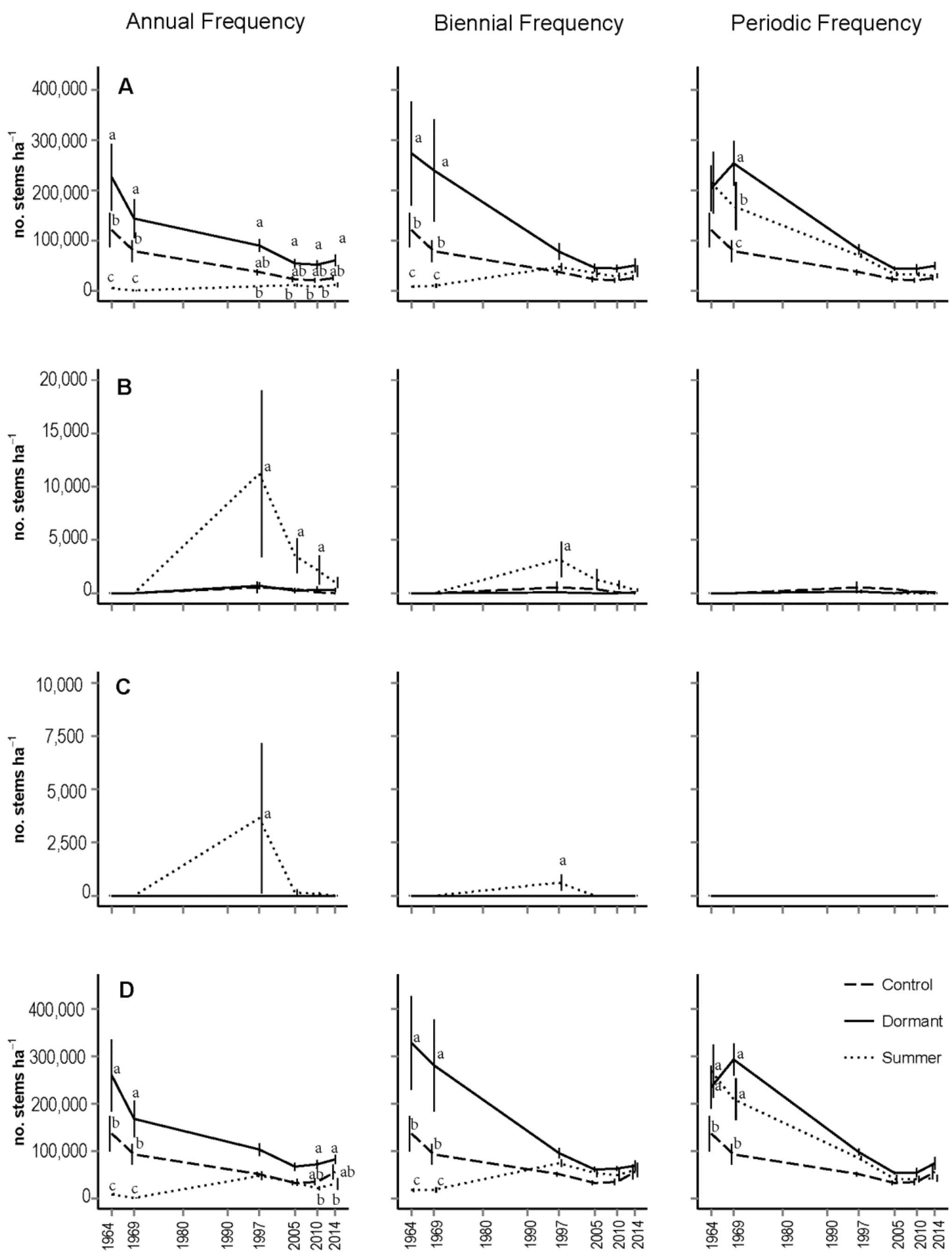

Figure 3.2 Stem density for hazel (row A), eastern white pine (row B), red pine (row C), and all woody species (row D) for a 50 year period at the *Red Pine Prescribed Burning Experiment* in north-central Minnesota, USA. Burning treatments applied from 1960-1970. Letters indicate pairwise comparisons of burning season within a given fire frequency and year at $\alpha = 0.05$ following an FDR adjustment. Control treatment is replicated within each frequency panel. Error bars are ± one standard error. Note scale differences among y-axes.

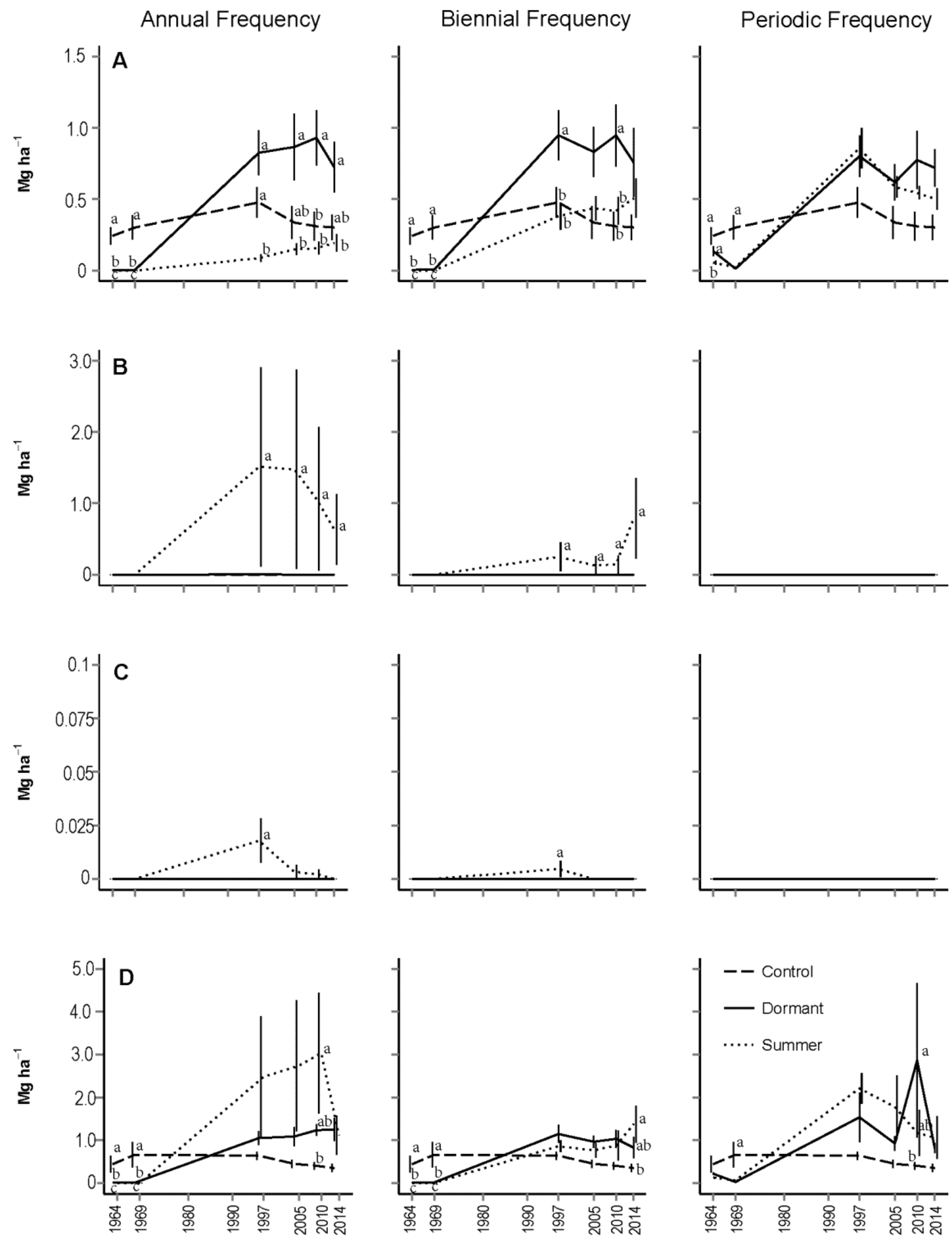

Figure 3.3 Aboveground biomass for hazel (row A), eastern white pine (row B), red pine (row C), and all woody species (row D) for a 50 year period at the *Red Pine Prescribed Burning Experiment* in north-central Minnesota, USA. Burning treatments applied from 1960-1970. Letters indicate pairwise comparisons of burning season within a given fire frequency and year at $\alpha = 0.05$ following an FDR adjustment. Control treatment is replicated within each frequency panel. Error bars are ± one standard error. Note scale differences among y-axes.

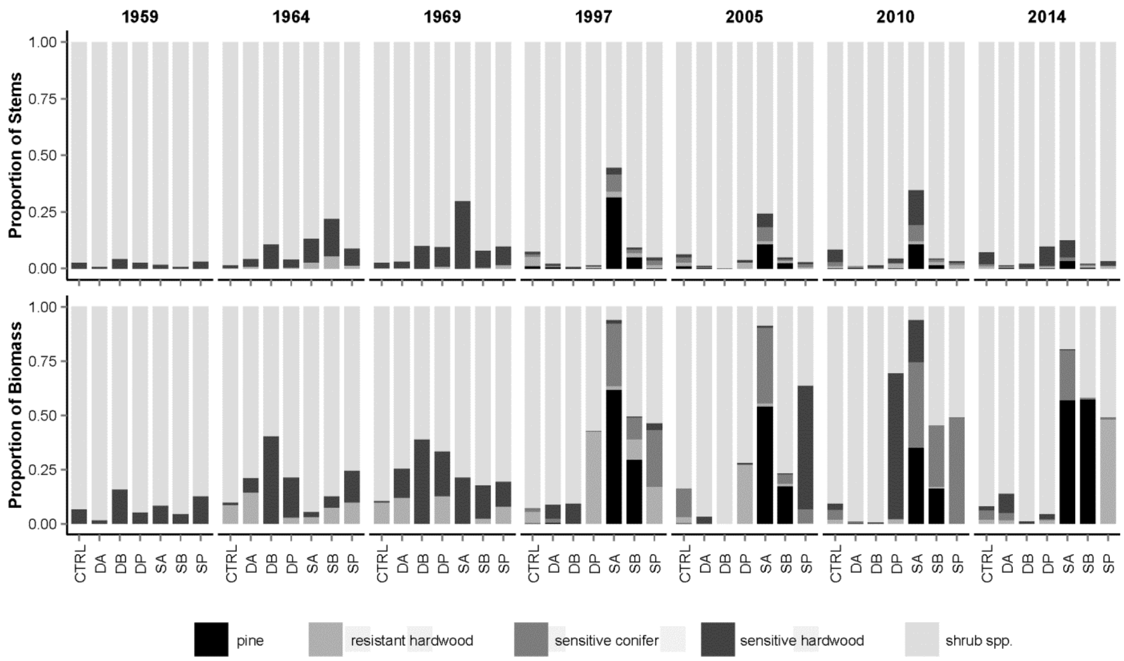

Figure 3.4 Proportional allocation of stem density (top row) and aboveground biomass (bottom row) in the woody understory at the *Red Pine Prescribed Burning Experiment* in north-central Minnesota, USA. Burning treatments were applied 1960-1970. Species groups defined by fire sensitivity at maturity from Fire Effects Information System (Fischer et al. 1996).

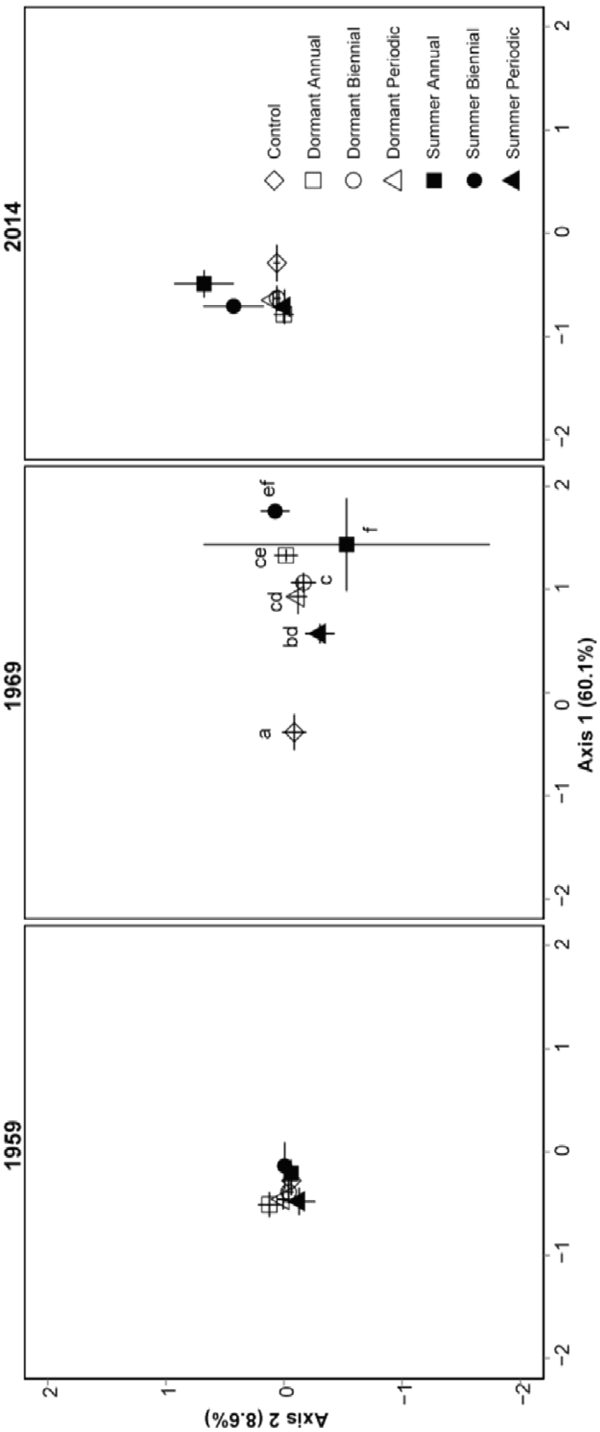

Figure 3.5 Non-metric multi-dimensional scaling ordination plot of woody understory composition (mean ± standard error) before burning (1959), end of active burning (1969), and 44 years post-burning (2014). Treatments with different letters denote significant differences at $\alpha = 0.05$ after an FDR adjustment for pairwise comparisons.

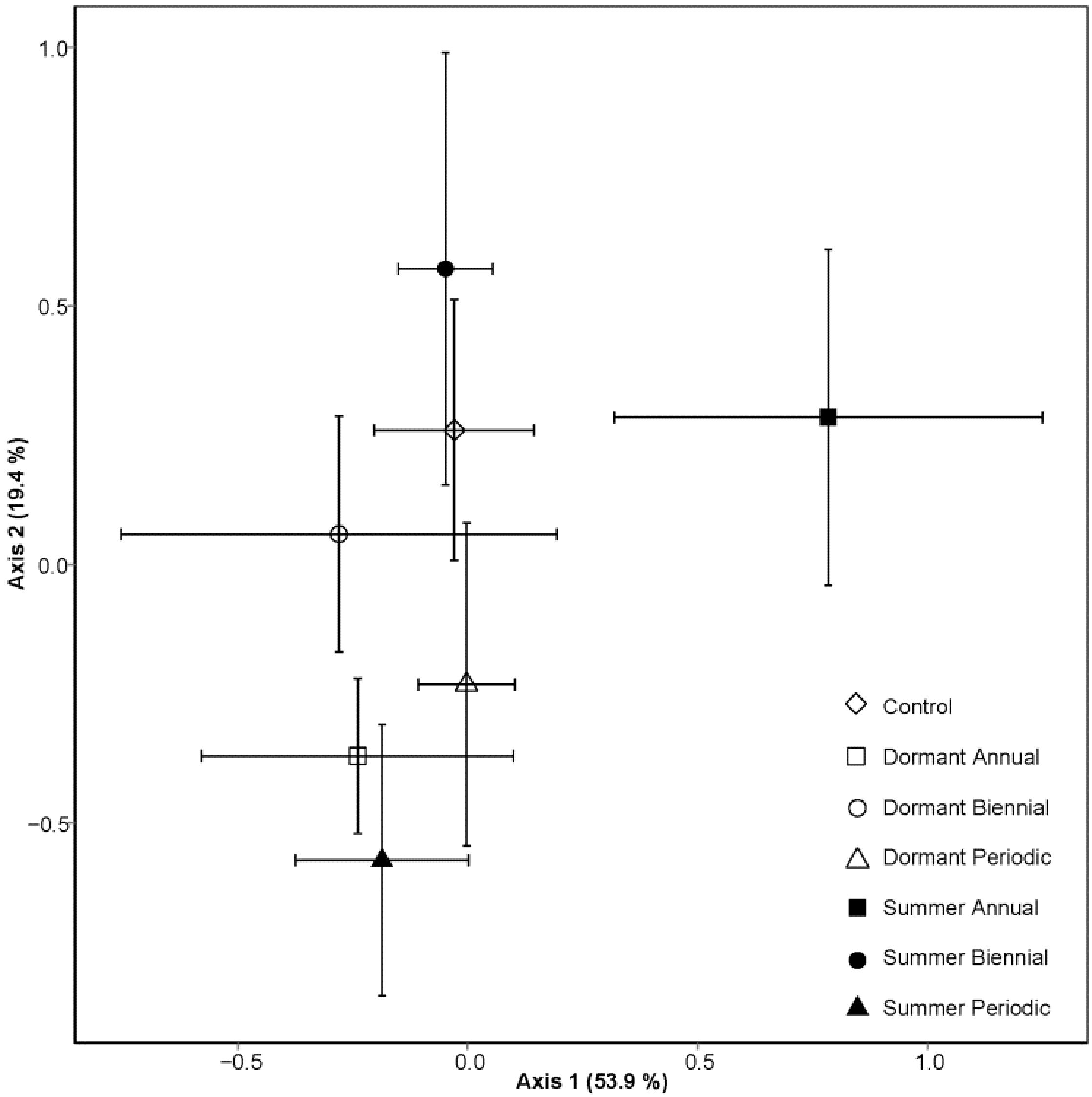

Figure 3.6 Non-metric multi-dimensional scaling ordination plot of herbaceous understory composition (mean ± standard error) 44 years post-burning (2014). Treatments with different letters denote significant differences at $\alpha = 0.05$ after an FDR adjustment for pairwise comparisons.

Chapter 4: Conclusions

This thesis adds to a body of literature examining the effects of prescribed fire when used as a silvicultural tool in pyrophytic forests. The result of this research has important implications for land managers who work in these ecosystems and wish to reincorporate fire as a means for vegetation management. Capitalizing on an established long-term silvicultural experiment, we were able to study the long-term effects of prescribed fire in a controlled and replicated experiment. The variety of experimental treatments applied, and the temporal duration of measurement make this an unprecedented record of prescribed fire management for a northern-temperate pine forest. The first research chapter of this thesis (Chapter 2) explored the long-term effects of prescribed fire on the overstory of a mature red pine forest. We found that fires dramatically altered the structural development trajectory of stands, even after a prolonged fire free period. Fire treated stands were less dense, had larger average tree size, and maintained more-open woodland structures for the 50+ year study period. Chapter 3 investigated the response of the understory to those prescribed fire treatments, including both the woody and herbaceous communities. Again, we found evidence, that prescribed fire dramatically impacted these stands in terms of the understory communities that would develop over time. Both season and frequency of burning affected the response of understory vegetation. In general, more frequent summer season burns were most effective in reducing the abundance of shrubs and promoting pine regeneration.

Amazingly many of these differences persisted for over 50 years, including several fire free decades. The findings of this thesis provide evidence that prescribed fire can have long-lasting impacts on both the understory, and the overstory of treated stands in the long-term, particularly when applied in successive years during the growing season.

4.1 Management Implications

Prescribed fire as implemented in this study effectively reduced the abundance of a recalcitrant woody understory of rhizomatous shrubs, and also resulted in reduced overstory tree density in the long-term. Descriptions of pre-settlement red pine ecosystems indicate these lower density forest conditions were likely a feature of old-growth pine forests in the region and reincorporating fire into these systems through careful prescribed burning may provide an opportunity to restore elements of pre-settlement overstory structures and understory compositions. Given the limited ability of managers to implement the full range of fire intensities that would have occurred naturally within these systems prescribed fire may not fully replicate the processes of a natural mixed-severity fire regime. For this reason, forest managers may need to further rely on other silvicultural methods to more fully achieve desired structural and regeneration conditions, including combining prescribed fire with regeneration and thinning methods that restore complex overstory conditions, including variable retention harvests systems, irregular shelterwood methods, and variable density thinning.

The results from Chapter 2 and 3 clearly demonstrate that both fire season and frequency are important considerations when considering the application of prescribed fire. If a reduction of shrubs or other woody plants in the understory is desired, fire must be applied during the growing season, and multiple fires must be implemented. The efficacy of treatments is controlled by these two factors, and will have dramatic short- and long-term implications for treated stands. In practice, most fires are applied during the dormant season, either as spring or fall burns, and are rarely applied in sequential seasons. This work strongly highlights the importance of increasing the use of growing season burns to reduce hazel densities. Such burns could be promoted through felling and leaving hazel stems in the early part of the growing season to serve as fuels when applying mid-season burns. While prescribed fire may result in conditions suitable for germination and establishment of pine seedlings, the fungal pathogens *Diplodia* and *Sirroccus* may greatly limit the ability to successfully recruit red pine regeneration under an existing canopy of red pine (Ostry et al. 2012). Alternating rotations of red and white pine in these systems may be a suitable long-term goal if natural regeneration is the objective, and may greatly reduce the risk of infection from the above mentioned shoot-blight pathogens.

4.2 Study Limitations and Recommendations for Future Research

This study has allowed for a unique investigation of the role of prescribed fire as a management tool in fire-adapted forest communities. The design of the experiment allowed for a direct investigation of the importance of both season and frequency of burning, something that previous studies in the region have failed to do. Further, the 50+

year duration of the study provides one of the longest records of prescribed fire management in a forested ecosystem globally. While this design allowed for unique investigations into the relative roles of fire season and frequency in the long-term, the treatments applied in the experiment are impractical for most operational level management schemes. The fire frequencies employed in this study, particularly annual burning, would be difficult to apply on an operational level due to operational constraints including cost, weather, and stand fuel levels. The research has elucidated the importance of burning in the growing season when control of the woody understory is a management objective, but future research and experimental trials will be needed to identify optimal burning intervals for operational use.

Regeneration of pine species is a common objective of prescribed fire treatment in many pine dominated ecosystems. Our study tested the role of burning in achieving regeneration of pine species and although some pine regeneration was observed following fire, it was clear that further alterations to stand structural conditions would be needed to successfully regenerate these stands. If natural regeneration of pine species is a desired outcome of prescribed fire, future research will need to combine other overstory manipulations with burning treatments such that established seedlings can be released from overstory shade. Following successful control of the understory through burning, variants of the seed tree or shelterwood methods may provide a suitable option as silvicultural systems for these ecosystems.

Prescribed burning can be an important tool for reducing fuel levels in fire prone ecosystems (Agee and Skinner 2005). This aspect was not assessed in our study; however an assessment of the efficacy of burning as a fuel reduction treatment in red pine ecosystems is merited.

Lastly, this study utilizes relatively small (0.4 ha) treatment units, and considerable care was taken to burn each unit completely. On a larger more operational scale a wider range of burning intensities would occur and may lead to increased variability in responses. Such variability was likely a feature of natural fire regimes in these systems andfuture research should aim to treat larger areas that would be more representative of an operational scale project so as to evaluate ecological responses.

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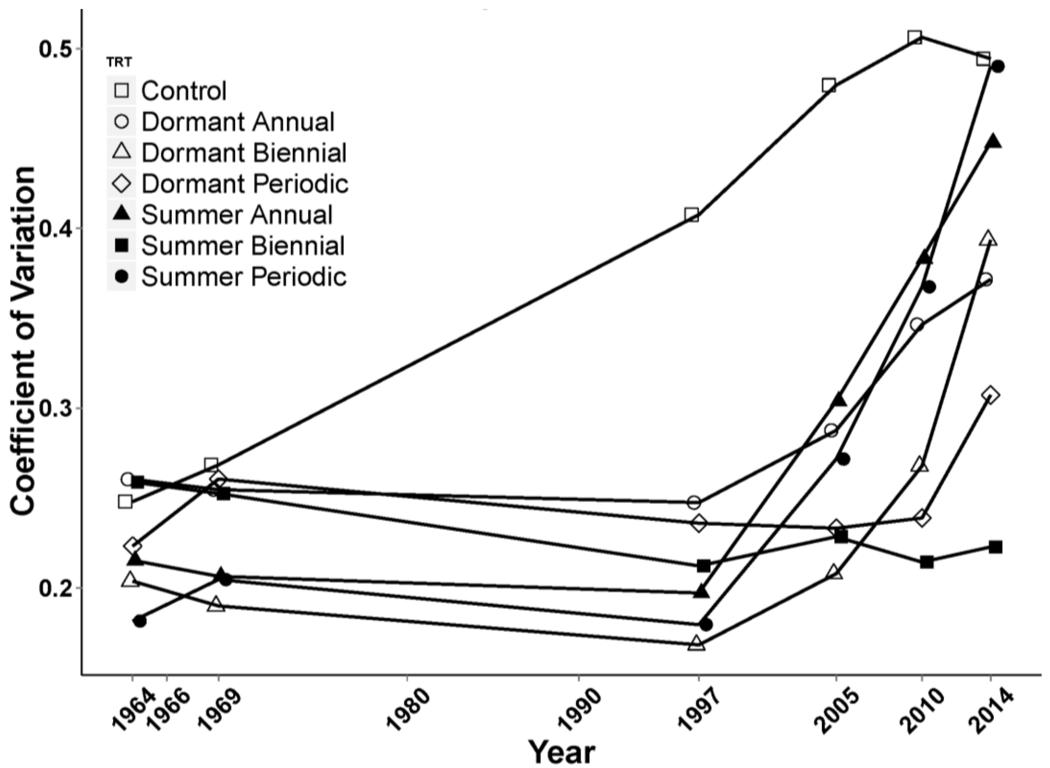
Appendices



Appendix 1 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, U.S.A. Burning treatments applied from 1960-1970.

Appendix 2 Woody understory survey species list for (1959), end of burning (1969), and 44 years post burning (2014) at the *Red Pine Prescribed Burning Experiment* in north-central Minnesota, USA. Burning treatments applied from 1960-1970.

Species	frequency	treatments	life form	FEIS fire rating*
Abies balsamea	0.14	CC, DA, DB, DP, SA, SB	tree	sensitive conifer
Acer rubrum	0.23	CC, DA, DB, DP, SA, SB, SP	tree	sensitive hardwood
Alnus spp.	0.23	CC, DA, DB, DP, SA, SP	shrub	--
Amelanchier spp.	0.86	CC, DA, DB, DP, SA, SB, SP	shrub	--
Betula papyrifera	0.07	CC, DA, DB, SA, SP	tree	sensitive hardwood
Celastrus scandens	0.02	DP, SB	shrub	--
Cornus spp.	0.35	CC, DA, DB, DP, SA, SB, SP	shrub	--
Corylus cornuta	0.96	CC, DA, DB, DP, SA, SB, SP	shrub	--
Diervilla lonicera	0.17	DA, DB, DP, SA, SB, SP	shrub	--
Fraxinus nigra	0.01	DP	tree	sensitive hardwood
Lonicera canadensis	0.13	CC, DA, DP, SA, SB, SP	shrub	--
Lonicera dioica	0.05	CC, DB	shrub	--
Lonicera hirsuta	0.10	CC, DA, DB, DP, SB	shrub	--
Parthenocissus vitacea	0.02	DA, DP	vine	--
Picea glauca	0.01	SP	tree	sensitive conifer
Picea mariana	0.01	CC	tree	sensitive conifer
Pinus strobus	0.13	DA, DB, DP, SA, SB	tree	resistant conifer (pine)
Populus grandidentata	0.01	DB	tree	sensitive hardwood
Populus tremuloides	0.01	DA	tree	sensitive hardwood
Prunus pensylvanica	0.02	DB	shrub	--
Prunus serotina	0.01	SA	tree	sensitive hardwood
Prunus virginiana	0.19	CC, DB, DP, SA, SB, SP	shrub	--
Quercus macrocarpa	0.02	DA, DP	tree	resistant hardwood
Quercus rubra	0.23	CC, DA, DP, SB, SP	tree	resistant hardwood
Rosa spp.	0.10	CC, DA, DP, SB, SP	shrub	--
Rubus spp.	0.25	CC, DA, DB, DP, SA, SB, SP	shrub	--
Salix spp.	0.50	CC, DA, DB, DP, SA, SB, SP	shrub	--
Sorbus decora	0.01	DA	shrub	sensitive hardwood
Symphoriocarpus alba	0.04	DA, DB, SP	shrub	--
Vaccinium angustifolium	0.32	CC, DA, DB, DP, SA, SB, SP	shrub	--
Viburnum lentago	0.01	CC	shrub	--
Viburnum rafinesquianum	0.11	CC, DA, DB SA, SB	shrub	--

* Fire Effects Information System Database found at: http://www.feis-crs.org

Appendix 3 Ground-layer plant survey species list 44 years post burning (2014) at the *Red Pine Prescribed Burning Experiment* in north-central Minnesota, USA. Burning treatments applied from 1960-1970.

Species	frequency	treatments	lifeform
Anenome quinquefolia	1.00	CC, DA, DB, DP, SA, SB, SP	forb
Apocynum androsaemifolia	0.39	CC, DA, SA, SB, SP	forb
Aralia nudicaulis	0.89	CC, DA, DB, DP, SA, SB, SP	forb
Aster macrophyllus	1.00	CC, DA, DB, DP, SA, SB, SP	forb
Aster spp.	0.14	DA, DB, SP	forb
Carex pensylvanica	0.21	DA, DB, DP, SA, SP	graminoid
Chimiphila umbellata	0.07	DA, SP	forb
Circea alpina	0.11	CC, DB, DP	forb
Clintonia borealis	0.89	CC, DA, DB, DP, SA, SB, SP	forb
Convulvulus spithamaeus	0.07	SA, SB	forb
Cornus canadensis	0.29	CC, DA, DB, DP, SA, SB, SP	forb
Dryopteris carthusiana	0.07	CC, DP	forb
Fragaria virginiana	0.54	CC, DA, DB, DP, SA, SB	forb
Gallium borealis	0.96	CC, DA, DB, DP, SA, SB, SP	forb
Gallium triflorum	0.93	CC, DA, DB, DP, SA, SB, SP	forb
Gaultherium procumbens	0.46	CC, DA, DB, DP, SB, SP	forb
Goodyera tesselata	0.14	CC, SA, SP	forb
grass spp.	0.07	CC, DA, DB, DP, SA, SB, SP	graminoid
Helianthus spp.	0.07	DB, DP	forb
Hepatica americana	0.14	DA, DB, SA, SB	forb
Lathyrus ochroleucus	0.82	CC, DA, DB, DP, SA, SB, SP	forb
Lathyrus venosus	0.11	DP, SA, SB	forb
Linnea boreale	0.46	CC, DA, DB, DP, SA, SB, SP	forb
Lycopodium clavatum	0.11	CC, SB	forb
Lycopodium complanatum	0.07	CC, SP	forb
Maianthemum canadensis	1.00	CC, DA, DB, DP, SA, SB, SP	forb
Monensis uniflora	0.36	CC, DA, DB, DP, SA, SB, SP	forb
moss spp.	1.00	CC, DA, DB, DP, SA, SB, SP	moss/bryophyte
Osmorhiza longistylis	0.07	DB, DP	forb
Piptatheropis pungens	1.00	CC, DA, DB, DP, SA, SB, SP	graminoid
Polygala paucifolia	0.32	CC, DB, DP, SA, SB, SP	forb
Pteridium aquillinum	0.86	CC, DA, DB, DP, SA, SB, SP	forb
Pyrola americana	0.29	CC, DB, DP, SB, SP	forb
Rubus pubescens	0.89	CC, DA, DB, DP, SA, SB, SP	forb
Sanicula marilandica	0.21	DP, sA, SP	forb
Streptopus roseus	0.64	CC, DA, DB, DP, SA, SB, SP	forb
Taraxacum spp.	0.07	SA	forb
Thalictrum dioica	0.39	CC, DB, DP, SA, SB, SP	forb
Trientalis borealis	0.82	CC, DA, DB, DP, SA, SB, SP	forb
Uvularia sessilifolia	0.71	CC, DA, DB, DP, SA, SB, SP	forb
Vicia americana	0.07	DP, SP	forb
Viola spp.	0.54	CC, DA, DB, DP, SA, SB, SP	forb