NRC Research Press

ARTICLE

Long-term pine regeneration, shrub layer dynamics, and understory community composition responses to repeated prescribed fire in *Pinus resinosa* forests

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Abstract: Prescribed fire is increasingly viewed as a valuable tool for reversing ecological consequences of fire suppression within fire-adapted forests. While the use of burning treatments in northern temperate conifer forests has received considerable attention, the long-term (>10 year) effects on understory composition and dynamics have not been quantified. We describe the persistence of prescribed fire effects on the woody and herbaceous understory in a mature red pine (*Pinus resinosa* Ait.) forest in northern Minnesota, USA, over a ~50-year period, as well as the relative roles of fire season and frequency in affecting vegetation responses. Burning treatments were applied from 1960 to 1970 on 0.4 ha experimental units and crossed fire season and frequency in a randomized block design. Burning altered shrub layer dynamics and composition in both the short and long terms and was influenced by both fire season and frequency, with frequent summer season burns having the largest impact, including greatest control of hazel (*Corylus* spp.). The application of fire facilitated regeneration of pine; however, recruitment into the overstory was limited. Additionally, community composition of the herbaceous understory diverged 40+ years following burning. This study highlights the importance of continued burning in affecting vegetation responses and the potential of fire as a long-lasting vegetation management tool in these forests.

Key words: diversity, long-term study, controlled burn, vegetation control, *Corylus* spp.

Résumé : Le brûlage dirigé est de plus en plus considéré comme un outil précieux pour inverser les conséquences écologiques de la suppression des feux dans les forêts adaptées au feu. Bien qu'une attention considérable ait été accordée à l'utilisation des traitements de brûlage dans les forêts résineuses tempérées du nord, les effets à long terme (>10 ans) sur la composition et la dynamique de la végétation de sous-bois n'ont pas été quantifiés. Nous décrivons la persistance des effets du brûlage dirigé sur la végétation ligneuse et herbacée du sous-bois dans une forêt mature de pin rouge (*Pinus resinosa* Ait.) du nord du Minnesota, aux États-Unis, sur une période d'environ 50 ans en tenant compte du rôle relatif de la saison d'application et de la fréquence du feu sur la réaction de la végétation. Les traitements de brûlage ont été appliqués de 1960 à 1970 sur des unités expérimentales de 0,4 ha en distribuant la saison d'application et la fréquence des feux selon un dispositif en blocs aléatoires. La dynamique et la composition de la strate arbustive ont été influencées tant à court qu'à long terme par la saison d'application et la fréquence des feux. Les brûlages estivaux fréquents ont eu le plus d'impact, notamment pour maîtriser le noisetier (*Corylus* spp.). L'application du feu a facilité la régénération du pin bien que son accession au couvert dominant ait été limitée. De plus, la composition de la communauté herbacée du sous-bois a divergé plus de 40 ans après le brûlage. Cette étude met en évidence l'importance du brûlage continu sur la réaction de la végétation et le potentiel du feu comme outil d'aménagement durable de la végétation dans ces forêts. [Traduit par la Rédaction]

Mots-clés : diversité, étude de longue durée, brûlage dirigé, maîtrise de la végétation, *Corylus* spp.

Introduction

Fire has been a dominant force in shaping the historical development and dynamics of many forested ecosystems across North America and around the globe (Pyne 1982). Low- and mixed-severity fire regimes maintained a variety of pyrophytic forests across North America, most notably in forest types currently or historically dominated by pine and oak species (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. 2008; 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 exposed mineral soil seedbed conditions and more open growing space and maintaining composition and diversity of herbaceous ground-layer communities (Nyamai et al. 2014; Van Wagner 1970; Roberts 2004).

Received 14 September 2017. Accepted 6 December 2017.

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Wildfire suppression efforts have greatly limited the impact of fire within fire-dependent ecosystems across North America since the 1920s (Frissell 1973; Heinselman 1973; Waldrop et al. 1992). The extended absence of fire has greatly altered the composition and structure of pyrogenic forest ecosystems, allowing a shift from open- to closed-canopy conditions and development of dense understories of woody shrubs and trees that outcompete shade-intolerant, fire-adapted tree species and affect the composition of the herbaceous ground layer (Royo and Carson 2006; Waldrop et al. 1992). In red pine dominated ecosystems, an important and expansive forest type across the eastern United States (US) and adjacent Canada, 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 aggressively re-sprout following aboveground 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. 2013).

Prescribed fire has been proposed as a management tool for reducing woody stem densities in the understory and restoring vegetative communities in many fire-dependent ecosystems across North America, including ecosystems dominated by red pine (Dickmann 1993; McRae et al. 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 (Miller 2000; Roberts 2004; Weyenberg and Pavlovic 2014).

Although 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 red pine 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 the period of active treatment and were continued after cessation of the fires, creating a data record of 50+ years. 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 (*i*) abundance (density and biomass) of woody understory plants including pine regeneration in the short and long terms and (*ii*) composition and diversity of the woody and herbaceous understories in the long term. We hypothesized (1*a*) that prescribed fire would alter the abundance of woody shrubs in the short and long terms and, specifically, that summer season fires and higher frequency fires would result in reduced woody stem density and biomass at those time scales. We also hypothesized (1*b*) that pine regeneration would be enhanced by 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 vs. unburned controls.

Methods

Site and experimental design

This study is located within the Cutfoot Experimental Forest (CEF) on the Chippewa National Forest, in north-central Minnesota (latitude, 47°40′N; longitude, 94°5′W). Climate at the CEF is cool continental with warm, humid summers often exceeding maximum temperatures of 32 °C and cold winters with minimum temperatures falling below –35 °C. Growing-season length ranges from 100 to 120 days, and annual precipitation ranges from 500 to 640 mm with the majority falling as rain. Prolonged summer droughts are common. Soils are derived from glacial sandy outwash, weakly developed and very well drained, and classified as the Cutfoot series (Alban 1977).

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 and other similar communities are common across the western Great Lakes region, with overstories dominated by mature red pine and 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 CEF indicates that surface fires were once common in these ecosystems, with surface fire return intervals ranging from 3 to 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 $m^2 \cdot ha^{-1}$ to homogenize overstory conditions. Standing dead trees, tree tops, and logging slash were also removed following thinning in an effort to homogenize fuels across experimental units. No additional overstory manipulations have occurred since the initial thinning. Beginning in 1960, burning treatments were established and implemented within 0.4 ha experimental units 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), summer–periodic (SP), dormant–annual (DA), dormant–biennial (DB), and dormant–periodic (DP), as well as an unburned control (CTRL). Summer season burning treatments were applied from late June through mid-August, while dormant season burns were applied in the spring (April and May) or, when weather precluded spring burning (1965), late fall (October). Annual frequencies correspond to burning every year, biennial frequencies correspond to every other year, and periodic frequencies correspond to every six to nine years.

Burning

Burns were implemented 5–15 days following significant rain events and resulted in forest floor fuel moisture that averaged roughly 100% of dry mass 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 penetrated portions of the organic horizon, with the entire fibric layer consumed in all burned units, and further consumed the hemic layer in annually and biennially burned treatments, resulting in approximately 5% of the area with exposed mineral soil (Alban 1977). Burning treatments were applied from 1960 to 1970; after this time, burning was halted, resulting in 10–11 burns in annual treatments (the 1968 burn was missed in dormant units due to the lack of suitable burning conditions), five burns in biennial treatments, and two burns in periodic units. No further management activities have been conducted within the experimental blocks since 1970.

Field sampling

Within each experimental unit, a single 0.08 ha circular plot was established to monitor overstory conditions (for details, see Scherer et al. 2016). Nested within this overstory plot were eight smaller 4 m^2 circular subplots used to track and monitor the response of understory woody species. The locations of these subplots were standardized and permanently monumented at 4.6 m and 10.7 m from the plot center in each of the four cardinal directions. In the years 1959, 1964, and 1969, all live woody stems < 2.54 cm (1 in.) diameter at breast height (DBH) were tallied by species in 2.54 mm (0.1 in.) 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 the ground. All live woody saplings (2.54–9.1 cm DBH) were measured at breast height to the nearest 0.1 cm in each measurement year.

An additional survey was conducted in 2014 to quantify long-term effects on the diversity and composition of the herbaceous ground layer. Quadrats (1 m × 1 m) were established at each of the eight subplots mentioned above. 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.

Statistical analysis

First, abundance of woody species was evaluated as density and biomass. Density was calculated for each subplot and expressed as the number of woody stems per hectare for each measurement year. Aboveground woody biomass of each living stem was calculated using published allometric equations developed from sites in close proximity to our study area (Perala and Alban 1993). For stems < 2.54 cm DBH, diameter class midpoints for D12 and D15 were used when calculating biomass values. Stems within a subplot were summed to estimate biomass and expressed as $Mg \cdot ha^{-1}$ for each subplot. Subplot data were averaged and summarized at the plot level to develop better average stand-level characteristics before further analysis. Tree species capable of canopy status were categorized by their sensitivity of fire at maturity (Appendix Table A1) 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 effects 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 (ANOVA). Separate models were developed for both stem density and aboveground stem biomass by species groups as responses, with fire season, fire frequency, year, and all two- and three-way interactions as fixed effects. The unburned control was included as a level of season in all analyses. A random intercept for each experimental unit was included. Four focal species groups were chosen to analyze the response of stem density and stem biomass: hazel (dominant understory shrub), red pine (overstory dominant), white pine (sapling dominant), and all woody shrub and tree species (total understory). 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. Given that exploratory analysis revealed no significant differences in the pretreatment characteristics of response variables presented in this study (results not shown) and that our primary interest was to detect differences among treatments, pretreatment data were excluded from these analyses. 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. Natural logarithm or square root transformations were 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", "at the end of burning", and "long after burning". The herbaceous layer dataset included only year 2014, providing a snapshot of the "long after burning" effects. Both datasets were handled similarly. Only species that occurred on at least 5% of plots were included, resulting in a total of 42 species in the herbaceous dataset and 19 species in the woody dataset. In total, 28 experimental units (plots) were included in each analysis. NMS ordination was conducted using PC-ORD 6.0 (McCune and Medford 1999), 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 Sørensen distance measure for aboveground 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. The compositional differences identified through NMS among treatments were verified using repeated-measures distance-based multivariate ANOVA (perMANOVA). Burning treatment (season–frequency combination), year, and their interaction were used as fixed effects, and a random intercept was included for each experimental unit. 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 ANOVA on two datasets: one based on woody species biomass and the other based on herbaceous species cover. The woody dataset included the years 1959, 1969, and 2014; the herbaceous dataset included only data from 2014 as it was the only year in which measurements were taken. Both datasets were handled similarly. Diversity indices (Shannon's entropy, evenness, species richness) were calculated per square metre in PC-ORD (McCune and Medford 1999). 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 × 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.

Table 1. Repeated-measures analysis of variance (ANOVA) 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.

	Corylus cornuta			*Pinus strobus*			*Pinus resinosa*			All species		
	F	df	*p* value	*F*	df	*p* value	*F*	df	*p* value	*F*	df	*p* value
Aboveground woody biomass (Mg·ha⁻¹)												
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. of stems·ha⁻¹)												
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

Results

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. 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 1; Figs. 1A and 2A). Summer season burning decreased and dormant season burning increased hazel densities from the control, particularly in the short term (i.e., 1964–1969; Fig. 1A). Fire frequency had contrasting effects on hazel density as well. At the end of the treatment period (1969), periodic burning, irrespective of season, resulted in hazel densities higher than that of the control (Fig. 1A). In contrast, summer–annual burning resulted in significantly lower hazel densities in the short and long terms (Fig. 1A).

Hazel biomass revealed unique trends relative to those for stem density. All burning treatments displayed dramatic reductions in hazel biomass when compared with the unburned control near the end of the active burning period (i.e., 1969; Fig. 2A). 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 (Fig. 2A). 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 (Fig. 2A). 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; however, periodic treatments did not differ from the control beyond 1969 (Fig. 2A). 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 (Fig. 2A).

For white pine, the three-way interaction of season, frequency, and year resulted in variable regeneration over the study (Table 1; Figs. 1B and 2B). Trends in seedling density and biomass revealed that only summer–annual and summer–biennial burning resulted in appreciable regeneration of white pine at any point throughout the study (Figs. 1B and 2B). White pine regeneration density and biomass (in the sampled size classes) peaked in the 1997 measurement period (Fig. 1B) and has generally decreased since then. White pine regeneration in years since 1997 was significantly higher than the control in terms of density in the summer–annual treatment and for biomass in summer–annual and summer–biennial treatments (Fig. 1B).

Patterns of red pine regeneration were similar to those 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 year of burning (Table 1). Only the summer–annual treatment produced any measurable gains in red pine regeneration, with density and biomass of the species peaking in the 1997 measurement year (Figs. 1C and 2C). Red pine regeneration has since dissipated in the understory, with little or no regeneration present in later measurement periods (Figs. 1C and 2C).

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 1). Results and trends for stem density generally reflect that of hazel density (Fig. 1D), the dominant species and life-form in the understory (Fig. 3). In contrast, results and trends for woody biomass were similar to those for hazel biomass in early measurement periods and influenced by pine biomass in later years (Figs. 2D and 3), because shrubs and fire-resistant conifers (i.e., pine) dominated understory woody biomass during these time periods, respectively (Fig. 3).

Woody understory community composition and diversity

NMS ordination of woody understory composition resulted in a two-dimensional solution. The first axis explained 60.1% of the variation in composition for the years 1959, 1969, and 2014. A second axis explained an additional 8.6% of variation in those years (Fig. 4). Prior to treatment in 1959, all 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 pretreatment conditions (Fig. 4). Following a 44-year fire-free period, burned treatments shifted back toward pretreatment conditions in the negative portion of axis 1 with little separation from the control in 2014 (Fig. 4). Species' correlations 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 2).

A significant interaction between burning treatment and time, identified through perMANOVA, resulted in dynamic compositional patterns in the woody understory throughout the study

Fig. 1. Stem density (no. of stems·ha⁻¹) 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 were applied from 1960 to 1970. Lowercase letters indicate pairwise comparisons of burning season within a given fire frequency and year at $\alpha = 0.05$ following a false discovery rate adjustment. Control treatment is replicated within each frequency panel. Error bars are ±1 standard error. Note scale differences among *y* axes.

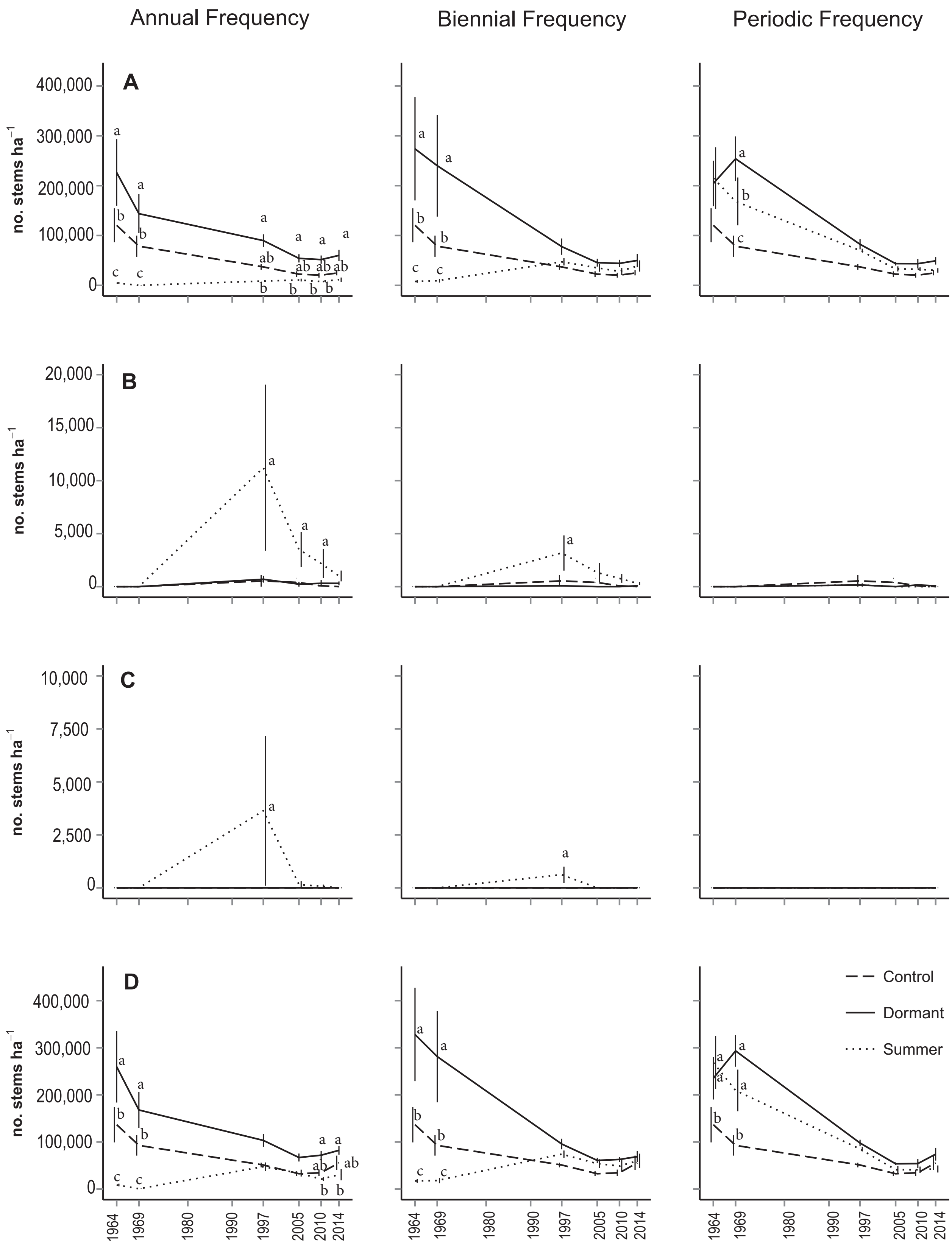
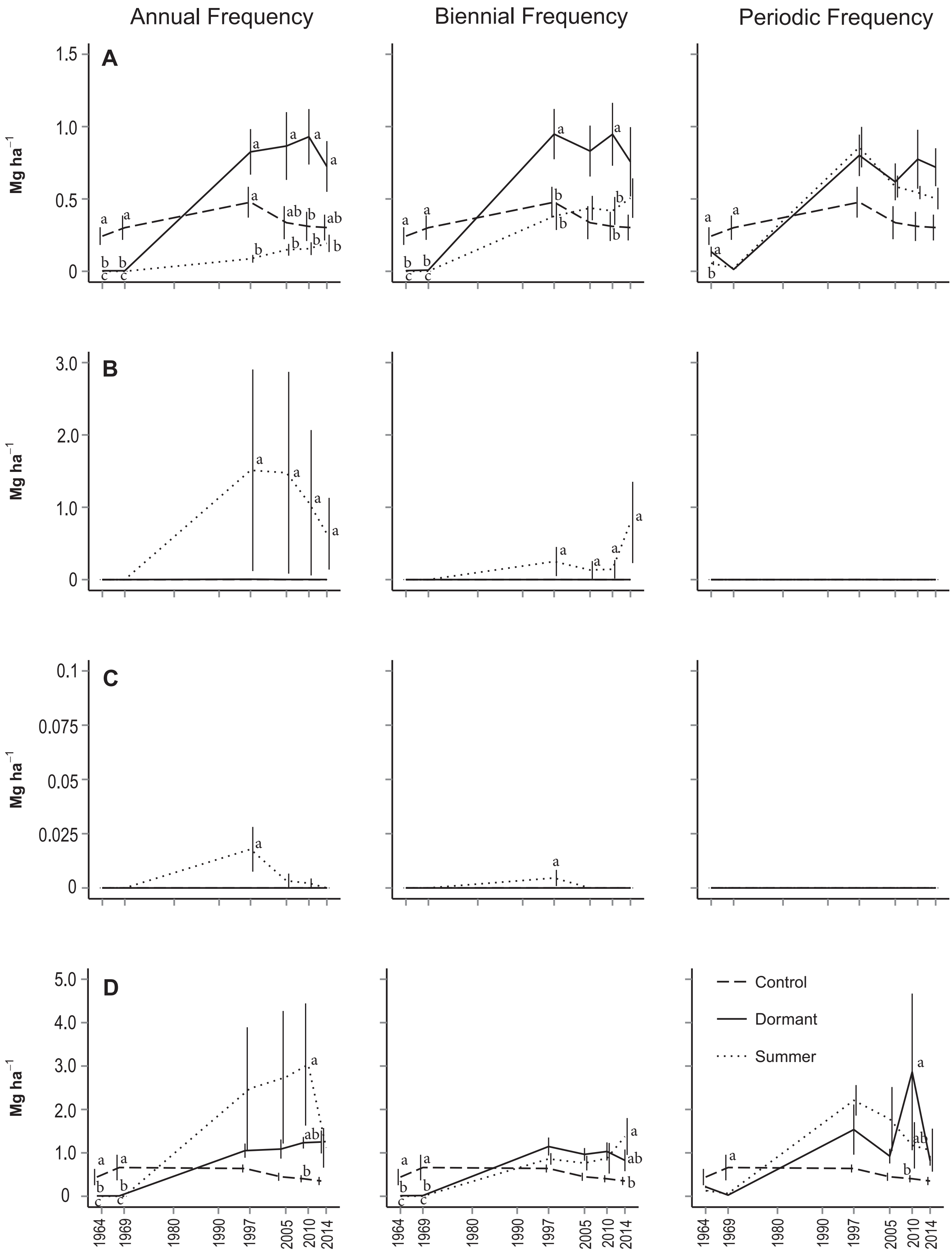


Fig. 2. Aboveground biomass (Mg·ha⁻¹) for hazel (row A), eastern white pine (row B), red pine (row C), and all woody species (row D) for a 50-year period at the Red Pine Prescribed Burning Experiment in north-central Minnesota, USA. Burning treatments were applied from 1960 to 1970. Lowercase letters indicate pairwise comparisons of burning season within a given fire frequency and year at $\alpha = 0.05$ following a false discovery rate adjustment. Control treatment is replicated within each frequency panel. Error bars are ±1 standard error. Note scale differences among y axes.



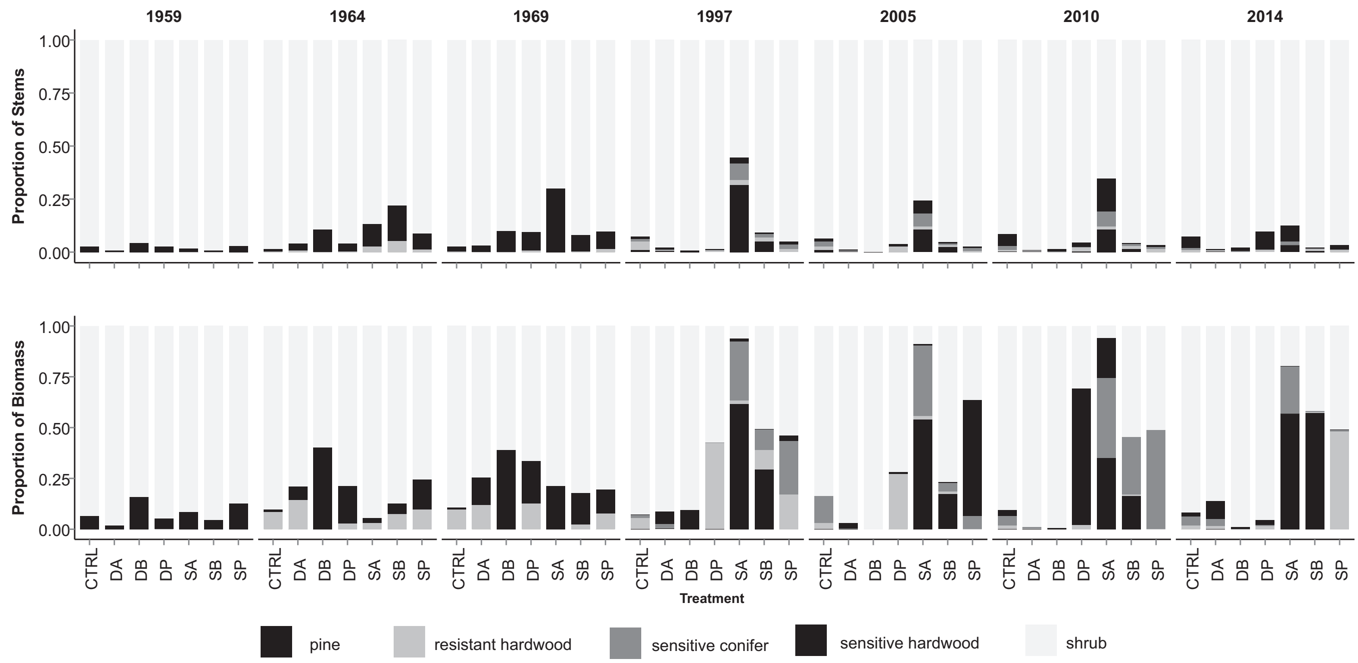


Fig. 3. Proportional allocation of stem density (top row) and aboveground biomass (bottom row) in the woody understory at the Red Pine Prescribed Burning Experiment in north-central Minnesota, USA. Burning treatments were applied from 1960 to 1970. Species groups are defined by fire sensitivity at maturity from Fire Effects Information System (Fischer et al. 1996; Fire Effects Information System Database found at http://www.feis-crs.org).

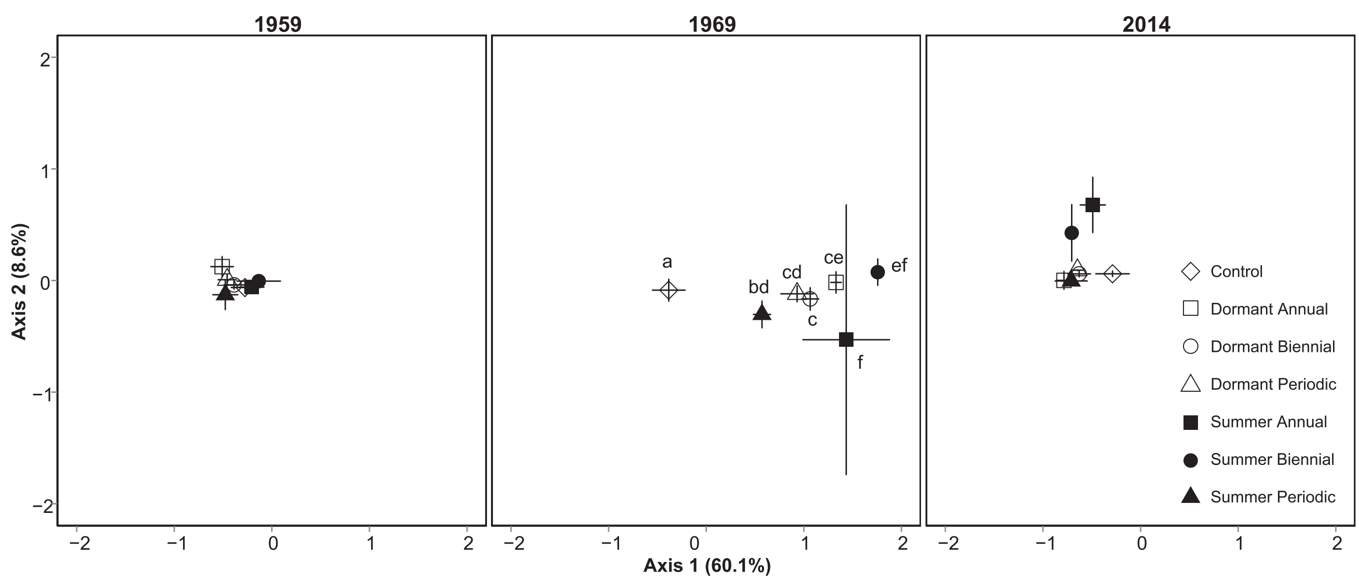


Fig. 4. Nonmetric multidimensional scaling ordination plot of woody understory composition (mean ± standard error) before burning (1959), at the end of active burning (1969), and 44 years after burning (2014). Treatments with different lowercase letters denote significant differences at $\alpha = 0.05$ after a false discovery rate adjustment for pairwise comparisons.

($F = 4.38$, $p = 0.006$). No significant differences among treatments were observed prior to treatment in 1959 (Fig. 4). In 1969, woody compositions were significantly different between burned treatments and the control, as well as among several burned treatments (Fig. 4). No significant differences among treatments were observed in 2014.

Shannon's diversity and evenness were effected by a significant interaction of treatment and time ($F = 2.04$, $p = 0.044$, and $F = 4.03$, $p < 0.001$, respectively). Shannon's diversity and evenness of woody species did not differ among treatments prior to burning 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). Species richness of the woody understory showed no significant differences among treatments throughout the duration of the study (Table 3).

Herbaceous plant community composition and diversity

NMS ordination converged on a three-dimensional solution for herbaceous 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 (Fig. 5). Results of perMANOVA indicate that burning treatment significantly affected ($F = 1.29$, $p = 0.02$) ground-layer composition

Table 2. Species displaying significant (α = 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 north-central Minnesota, USA.

Axis	Species	Relationship (+/–)	τ	p value
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
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

Note: p values adjusted using false discovery rate method for multiple tests.

in 2014. After adjusting for multiple tests, no significant differences among individual treatments were identified; however, arrangement of treatments in ordination space suggests that the composition of the summer–annual treatment is likely a driver of the significant burning treatment effect in the perMANOVA. The summer–annual treatment displayed more positive scores on both axes than the other treatments (Fig. 5). More positive scores along axis 2 are generally associated with higher intensity treatments and resultant control of hazel, as outlined in previous sections. Species correlations with NMS axis scores indicate that positive axis 1 scores were associated with *Anenome quinquefolia* L., *Eurybia macrophylla* L., and *Pteridium aquilinum* L., while axis 2 scores were negatively associated with *Carex pennsylvanica* Lam. and positively associated with moss species (Table 4).

Burning treatment (season × frequency combination) was not significant in explaining Shannon's diversity and evenness of the herbaceous layer in 2014 (F = 2.39, p = 0.07, and F = 2.65, p = 0.051, respectively) (Table 5). Further, after adjusting for multiple tests, no significant differences among treatments were found for Shannon's diversity, evenness, or species richness (Table 5). A complete list of the species identified in the herbaceous layer can be found in Appendix Table A2.

Discussion

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 during active burning (i.e., 1964–1969), prescribed fire, irrespective of fire season, resulted in dramatic reduction or near elimination of woody 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, after long-term fire removal, the interaction of season and frequency of burning emerged and resulted in long-lasting changes to woody shrub density and biomass.

Season of burn affected long-term 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 in the region (Buckman 1964; Tappeiner 1979; Van Wagner 1963).

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. 2011). The responses observed in our study are similar to those of studies in pine forests of the southeastern US where annual summer burning led 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 that 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 without additional silvicultural treatments to assist recruitment of this species into the canopy (e.g., overstory density reduction). A modest pulse of pine regeneration was detected in 1997 in the units that were treated with summer–annual and summer–biennial burning. We speculate that this postburning cohort established under suitable seedbed conditions (i.e., exposed mineral soil) and that reduced abundance of shrubs in those treatments facilitated this response.

While a cohort of pine regeneration was detected in 1997, the density has since 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, although there is limited evidence that large amounts of pine regeneration were recruited into the upper strata or lost to stem exclusion processes (see figs. 1 and 2 of Scherer et al. 2016). Second, the abundance of hazel and overstory trees (see fig. 1 of Scherer et al. 2016) increased, potentially creating unsuitable conditions for pine seedling survival through increased competition and shading. 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 prefire conditions with little or no pine regeneration. Red pine, much like long-leaf pine (*Pinus palustris* Mill.), can persist in low to moderate light environments but requires small- to large-scale release from overhead competitors to recruit into overstory positions (Fraver and Palik 2012; Gilmore and Palik 2006; Pederson et al. 2008). Lastly, given the presence of an intact red pine overstory, red pine seedlings were likely infected by shoot blight (personal observation) caused by the fungal pathogens *Diplodia pinea* Desm. and *Sirococcus conigenus* Dc. Although these two pathogens can persist without major consequences in mature stands, 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).

Table 3. Comparison of woody species diversity indices (± standard error) among burning treatments and an unburned control before burning (1959), at the end of burning (1969), and 44 years after burning (2014) at the Red Pine Prescribed Burning Experiment in north-central Minnesota, USA.

Year	Control	Dormant–annual	Dormant–biennial	Dormant–periodic	Summer–annual	Summer–biennial	Summer–periodic
Shannon's diversity (exp(*H*) or number of commonly dominant species)							
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 uneven and 1 indicates even abundance of species)							
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)							
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)

Note: Lowercase letters denote significant differences among treatments within a given year at $\alpha = 0.05$ following a false discovery rate adjustment for multiple tests.

Fig. 5. Nonmetric multidimensional scaling ordination plot of herbaceous understory composition (mean ± standard error) 44 years after burning (2014).

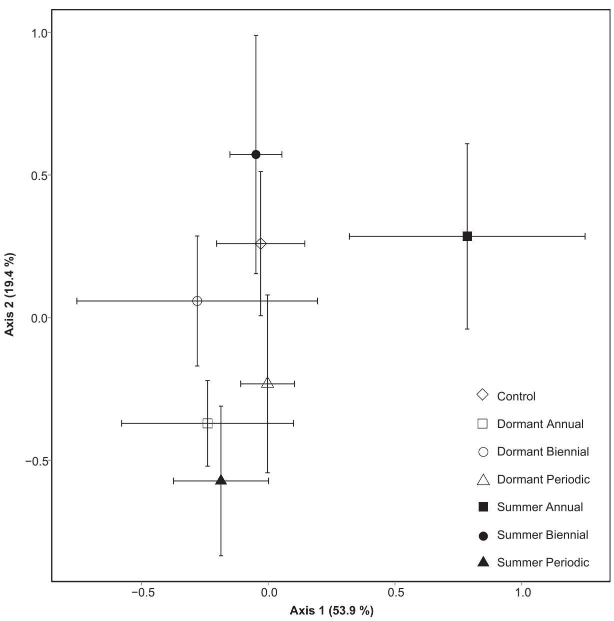


Table 4. Species displaying significant ($\alpha = 0.05$) Kendall's rank order correlations with the two first axes of NMS ordination of ground-layer community composition at the Red Pine Prescribed Burning Experiment in northern Minnesota.

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

Note: *p* values adjusted using false discovery rate method for multiple tests.

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 pretreatment and control conditions in all burning treatments and is similar to the results in other studies (e.g., Henning and Dickmann 1996; 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, community composition of burned treatments promptly returned toward their pretreatment conditions, demonstrating the resilience of those species present. While our study showed no persistent changes, similar studies have shown that burning can have long-term impacts on understory vegetation in loblolly pine (*Pinus taeda* L.) and mixed oak ecosystems (Bowles et al. 2007; White et al. 1990). However, the ecosystem studied by White et al. (1990) differs from ours, with recolonization of the woody understory dominated by basal sprouting species rather than rhizomatous shrubs. Further burning was applied continuously in both of these studies with no fire-free period (White et al. 1990; Bowles et al. 2007). In a mixed oak–pine ecosystem, Dumas et al. (2007) showed that fire can generate persistent changes in the understory community, with a reduction in the dominant shrub species by repeated burning as one of the primary factors driving these changes.

Table 5. Comparison of herbaceous species diversity indices (± standard error) among burning treatments and an unburned control 44 years after burning (2014) at the Red Pine Prescribed Burning Experiment in north-central Minnesota, USA.

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)

Note: No significant differences among treatments were observed at $\alpha = 0.05$ following a false discovery rate adjustment for multiple tests.

The effect of the prescribed fire treatments on woody species diversity appears minimal, particularly after the long-term cessation of fire. 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 that of Henning and Dickmann (1996), who found that species richness of the woody understory declined with fire frequency in the short term. Peterson and Reich (2008) demonstrated that disturbance alters diversity by changing the abundance of dominant understory species. As hazel regained dominance following burning in our treatments, it is likely that the understory reverted back to pretreatment conditions due to competitive exclusion of other species. Further, 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), suggesting that high-frequency disturbance may eliminate some species that contribute to overall diversity. 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, after an extended period without fire, species had sufficient time to recover biomass such that species diversity differences were no longer detectable among the treatments.

Herbaceous plant community composition and diversity

Investigation of the herbaceous 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, even during a prolonged period without fire. Higher cover of moss species and reduced cover of *Carex pennsylvanica* was observed 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 postfire colonizers and can provide suitable seedbed conditions for many conifers (Ahlgren and Ahlgren 1960; Ryömä and Laaka-Linberg 2005). Several species of bryophytes have been found to colonize postfire ash effectively and, in some cases, are associated with areas where humus has been consumed (Ryömä and Laaka-Linberg 2005). Postfire investigation of soil properties in our experimental units indicate that summer–annual burning resulted in a 47% reduction of humus and may have created conditions suitable for postfire bryophyte colonization (Alban 1977). Further, the summer–annual treatment was most effective in reducing the abundance of woody understory species, which may have created increased light levels and better microsite conditions for the persistence of moss species and other postfire colonizers, including pine 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 through the creation of a suitable organic seedbed (Ahlgren and Ahlgren 1960). 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 alteration to vegetative communities through the continual use of prescribed fire. However, with a prolonged absence of fire, many community components revert to prefire conditions relatively quickly.

In terms of diversity, the ground layer showed minimal long-term impacts from the burning treatments. Because of the limited temporal scale of our herbaceous layer data, we cannot speculate to any short-term responses; however, previous studies have shown that prescribed fire can have short-term impacts on diversity measures within red pine forests. For example, short-term (<5 year) studies show a $\sim$25% increase in species richness (Neumann and Dickmann 2001) and a decrease in evenness of the ground layer (Cook et al. 2008). Additionally, Weyenberg and Pavlovic (2014) showed that postfire community assemblages in a similar ecosystem can diverge substantially in the short term but return to prefire conditions relatively quickly. Long-term evaluations of the herbaceous response to prescribed fire are largely limited to pine ecosystems of the southeastern US 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. 2012). Further, Brockway and Lewis (1997) demonstrated that periodic growing-season burning led to increases in diversity and richness of the herbaceous layer following 39 years of repeated burning.

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 postfire evaluation for the red pine forests and woodlands that once dominated much of the Great Lakes region in both the US and Canada. Results from this study suggest that prescribed fire can be used to reduce the abundance of woody shrubs in the understory and initiate pine regeneration 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 that are dependent on the season and frequency of burning. Further, this work demonstrates that without proper season and frequency of fire application, vegetation can quickly revert back to pretreatment conditions.

As has been shown in earlier results from this study (Buckman 1964), season of burning appears to be the driving factor in affecting the response of the understory, and further, 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. Our findings suggest that to maintain the open understories and community assemblages created by fire, continual use of prescribed burning throughout the life of the stand will be needed; however, specific burning intervals should be established through further investigation.

In areas where unsuitable weather and (or) policies limit the use of burning (e.g., Melvin 2012), other management interventions may be useful 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. 2011; Tappeiner 1979). A season of mechanical removal ("brushing") of hazel results in 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. 2011).

Although periodic fires historically maintained red pine forests, prescribed fire alone appears unsuccessful in establishing or recruiting a new cohort of red pine. Prescribed fire, as applied here, did not effectively reduce overstory stocking (Scherer et al. 2016), resulting in stocking levels consistently at or above recommended stocking levels for red pine in the region (i.e., maximum stocking or "A-line" from stocking chart for red pine; Benzie 1977). Red pine is a relatively shade intolerant species that requires significant exposure to light for regeneration (Gilmore and Palik 2006). If repeated summer burning or mechanical shrub cutting were subsequently followed by regeneration harvests such as 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.

Acknowledgements

We would like to thank Robert Buckman for envisioning and establishing this study in 1959 and Doug Kastendick and many other scientists and technicians at the USDA Forest Service (USFS) Northern Research Station for collecting and maintaining inventory records throughout the duration of the study. Valuable field assistance in 2014 was provided by Bryten Felix. Discussion and comments from members of the University of Minnesota's Silviculture and Applied Forest Ecology Lab have greatly improved the scope and direction of this work. Scott Weyenberg, Jessica Miesel, and Laura Kenefic provided comments on an earlier draft of this article that greatly clarified and strengthened this work. Funding that made this work possible was provided by the USFS Northern Research Station and USFS State and Private Forestry Evaluation Monitoring Program. Additional financial support was provided by the University of Minnesota's Department of Forest Resources through the Henry Hansen Forest Ecology Fellowship and the Catherine Hill Fellowship in Forest Resources and the Minnesota Agricultural Experiment Station.

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Appendix A

Table A1. Woody understory survey species list before burning (1959), at the end of burning (1969), and 44 years after burning (2014) at the Red Pine Prescribed Burning Experiment in north-central Minnesota, USA.

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.

Table A2. Ground-layer plant survey species list 44 years after burning (2014) at the Red Pine Prescribed Burning Experiment in north-central Minnesota, USA.

Species	Frequency	Treatments	Life-form
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

Table A2. (*concluded*).

Species	Frequency	Treatments	Life-form
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