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Response of overstory and understory vegetation 37 years after prescribed burning in an aspen-dominated forest in northern Minnesota, USA – A case study

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Abstract

Many studies have examined short-term changes in understory vegetation following prescribed burning. However, knowledge concerning longer term effects on both forest understory and overstory vegetation is lacking. This investigation was initiated to examine changes in understory (herbaceous and shrub) and overstory species composition almost four decades after logging and prescribed burning at the Pike Bay Experimental Forest in Minnesota. The experiment was established in 1964 with a randomized block design with four treatments: control (c); burned in spring 1967 (S0); burned in spring 1967 + repeat burn spring 1969 (S2); and burned in spring 1967 + repeat burn fall 1970 (F4). Overstory and understory species diversity indices and richness varied within and among treatments but were not strongly or consistently affected by the treatments. Multivariate analyses (multi-response block permutation procedures and non-metric multidimensional scaling) reveal some lingering effects of burning intensity and seasonal variation as well as some compositional differentiation among treatments, but only in the herb layer. In this environment, the effects of two repeated burnings (fire) have essentially disappeared for overstory and understory species diversity and community composition and have failed to convert an aspen-dominated stand to a coniferous stand (an original goal of the study).

Keywords: *community composition, disturbance, multi-response block permutation procedures (MRBP), non-metric multidimensional scaling (NMS), restoration, species diversity*

Introduction

Understory vegetation has a key role to play in the ecological dynamics within forests and is a critical component of nutrient cycling, soil building processes, soil fertility, water quality, and biodiversity (Chastain Jr. et al. 2006; Hart & Chen 2006; Gilliam 2007; Lencinas et al. 2011; Hawkins et al. 2013). Understory vegetation also provides critical habitat and resources to both animals and micro-organisms, and is important in the development of microsites for germinating tree seedlings (Craig & Macdonald 2009; Lencinas et al. 2011; Dhar et al. 2016). Understory development is altered by disturbances and management interventions such as prescribed burning.

The benefits of using prescribed burning in a forest management context are well documented. As a tool, it has been used to manipulate forest structure and function, through conversion of low-quality under-stocked stands, to stands with preferred species of acceptable density (Vose 2000), as well as help create forests which are diverse and/or are more resilient to disturbance (Knapp et al. 2007). Applied alone or in conjunction with other treatments such as harvesting, the removal of some portion of the organic soil layer through prescribed burning has been used to enhance forest productivity by improving seedbeds for many forest ecosystems including aspen-dominated stands (Kill 1970; Perala 1974; Hawkes et al. 1990; Swift et al. 1993; Kemball et al. 2006), and decreasing or delaying competition by brush species (Perala 1974; Vose 2000). In restoration projects, prescribed fire has been used to create conditions that help return desired species to forest ecosystems (Delcourt & Delcourt 1997; Brose & Van Lear 1998), including wildlife species which may have been extirpated as a result of fire suppression and the resultant shift in browse species (Klinger et al. 1989; Blake 2005). In drier Western North American forests, prescribed burning in recent years

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has proven to be extremely important, decreasing the risk of wildfire by reducing the amount of fuel build-up in forests (Vose 2000).

A number of studies have examined short-term changes in understory vegetation following prescribed burning on different forest ecosystems (conifer or mixed conifer–hardwood ecosystems) in North America, Europe, and Australia (McGee et al. 1995; Knapp et al. 2007; Penman et al. 2008; Arévalo et al. 2014). Some authors have concluded that many plant species respond strongly to differences in fire intensity and severity rather than the timing of the burn (Knapp et al. 2007), while other reported community composition was unaffected 12 years after springtime prescribed burning (McGee et al. 1995) or no compositional difference between control and burned plots (Arévalo et al. 2014). These observations imply that it is very difficult to make general assumptions about the impact of prescribed burning on understory vegetation. Therefore, studies on long-term effects of prescribed burning on forest vegetation are needed for sounder forest management strategies.

Most of these aforementioned studies were based on conifer or mixed conifer–hardwood ecosystems, as research related to prescribed burning in aspen-dominated stands is rather scarce. The response of understory vegetation to season of burning is complex (Knapp et al. 2007) as fire survival mechanism varies among the species, season of fire and the amount of consumable fuel stored on the forest floor (Kauffman & Martin 1989; Main & Barry 2002; Knapp et al. 2007). In addition, fuel moisture condition may also have a significant role on seasonal variability in prescribed fire. Spring burning is often conducted under higher fuel moisture conditions than fall burns, leading to reduced fuel consumption and fire severity (Kauffman & Martin 1989). Therefore, less plant mortality occurs in spring burns while more unburned patches are retained where fire sensitive species can easily survive and contribute to post-fire colonization (Lee 2004). This study was therefore undertaken to enhance our level of understanding about responses of understory and overstory vegetation to seasonal variation of prescribed burning for aspen-dominated stands.

Burning of coniferous slash fuels has successfully reduced conifer overstory and stimulated aspen suckering in harvested spruce–aspen stands (Kill 1970; Perala 1974). However, Guedo and Lamb (2013) reported that prescribed burning had limited long-term effectiveness in controlling aspen encroachment in Fescue grassland. In other studies, Bartos et al. (1991) mentioned that 96 % of the site variability in sixth-year aspen sucker numbers was due to the timing of burning (season) and number of old suckers present after burning, while Kay (2001) reported that a combination of fire and continued elk use may eliminate many aspen clones.

In general, the silvicultural use of prescribed burning in aspen-mixed hardwood forest is limited and short-termed, and long-term effects of fire on aspen sucker growth are undocumented (Perala 1974). Perala (1974) further stated that, in spite of unknown long-term effects, fire can certainly be considered for preparation of aspen regeneration sites when other methods are unavailable. Therefore, the current follow-up study, based on Perala's (1974) experimental design, provides an opportunity to answer questions regarding the implementation of prescribed burning and how this may impact aspen-dominated forest management strategies. In addition, this study also investigated the impact of prescribed fire on understory vegetation, an aspect not considered in the previous studies (Perala 1974, 1975, 1995). Therefore, the main objectives of our study were (i) to describe the response of understory vegetation > 37 years after prescribed burning treatments, with a focus on species diversity including both richness (presence) and evenness (relative abundance) and, (ii) to measure and analyze various metrics of the overstory as it has a great influence on understory growth, diversity, and species composition.

Materials and methods

Site description

The study area is located within the Chippewa National Forest, in the Pike Bay Experimental Forest, just east of Cass Lake about 87.48 km (54 miles) west of Grand Rapids, Minnesota, at approximately 47°19′43″ N and 94°30′54″ W. The climate is continental, with maximum summer temperatures of 32°C and winter minimum temperatures down to −35°C. The frost free growing season ranges from 100 to 120 days (Alban et al. 1991). Annual precipitation ranges from 50 to 60 cm (mean 57cm), with average snowfall of 88 cm. The study site lies on the Guthrie till (deposited from the last glaciation of the Wisconsin Ice Age). Soils are classified as Warba series silt loams with a 40-cm loess layer and are very productive (Alban et al. 1991). In 1965, mature aspen (60–85 years) dominated much of the forest, which contains some of the most productive aspen (*Populus tremuloides* Michx.) sites in northern Minnesota, with a site index of 22.9 m (75 feet) at 50 years. Historically, the forest at Pike Bay consisted of large diameter white pine (*Pinus strobus* L.), as well as northern hardwood species, including sugar maple (*Acer saccharum* Marshall.), red maple (*Acer rubrum* L.), basswood (*Tilia americana* L.), paper birch (*Betula papyrifera* Marsh), yellow birch (*Betula alleghaniensis* Britt), red oak (*Quercus rubra* L.), and bur oak (*Quercus macrocarpa* Michx.), and remnant examples of these species still exist within the study area (Perala 1974, 1975, 1995).

Sampling design

A randomized block design with three replicates per treatment (100 × 100 m plots) was established in 1964 prior to logging (complete clear-cut) in a 60-year-old aspen-dominated study area. After harvesting in 1965, four circular tree plots with an 11.35-m radius (404 m^2) were established in each treatment unit (plot). Plot centers were marked with a 1.0-m tall hexagonal aluminum pipe. Due to unsuitable burning conditions, the initial prescribed burn took place in 1967 (May) two years after harvest. The first spring re-burn was only partially effective and fire line intensity was 10 kW/m whereas the fall re-burn was highly effective and fire line intensity ranged from 20 to 100 kW/m and occasionally reaching up to 1000 kW/m (more details about burning treatments can be found in Perala 1974, 1995). Most of the coarse woody material up to 7.5-cm (three inches) diameter was consumed by the burn and much of the remaining hardwood species in the overstory were also killed. Hardwoods on the unburned treatment and those few not killed by the fire were also felled at this time, two years after logging. Two years after the initial burn, a repeat spring burn was done; three years after the initial burn, a repeated fall burn was applied to designated treatment units. These treatments, together with a clear-cut, are the four treatments of the experiment: (i) an unburned complete clear-cut (1967, control or C); (ii) burned spring 1967 (S0); (iii) burned spring 1967 + repeat burn spring 1969 (S2); and (iv) burned spring 1967 + repeat burn fall 1970 (F4) (for details see Perala 1974, 1975, 1995). In total, 12 (4 treatments × 3 replications) main plots and 48 tree plots (4 treatments × 3 replications × 4 tree plots) were established across the experimental area.

In June 2007, using original tree plot (48) centers as tie points, understory vegetation plot centers were established 5-m north and 5-m either west or east of the first understory vegetation plot. The north plot was always consistent; however, the second plot was determined depending on coarse woody debris; the location with the least amount of debris was favored. From the established vegetation plot center, two circular plots were measured: (i) a 0.562-m radius (1 m^2) herbaceous plot and (ii) a 1.262-m radius (5 m^2) shrub plot. For herbaceous and shrub layer, a total 96 (4 treatments × 3 replications × 4 tree plots × 2 herb and shrub plots) herbaceous and shrub plots were established across the experimental area.

Data collection

Overstory. All original treatment units and plot centers (pipe) from 1965, 1967, 1969, and 1970 were relocated in fall 2005 to initiate the current study. Overstory re-measurement was started in the fall-winter of 2005, and concluded in the very early spring of 2006, prior to the onset of the growing season. For overstory species, diameter at breast height (DBH > 2 cm and taller than 1.3 m), and heights (m) for all species within plots were measured. However, only basal area (BA) and stem density (stem ha^{-1}) were considered for this study. The data collection protocol was consistent with measurements made in the original study by Perala (1995) to compare tree layer changes over the last 15 years (1990 and 2005).

Understory. In June 2007, an understory vegetation inventory was carried out in the study area. In each shrub plot and herb plot, all vegetation was identified from genus to species level, and abundance (percent cover) of species. When species identification was uncertain, the specimens were collected for laboratory identification at the USDA Forest Service Northern Research Station Laboratory in Grand Rapids, MN. Digital photographs were taken for questionable or notable species. Mosses were not considered for this study. Woody plants (shrubs and tree regeneration) < 2 cm in diameter at breast height and >10 cm height were considered part of the shrub layer. This was also consistent within the herb layer, where both shrub and tree species were counted as part of the herb layer if they were <10 cm in height. The total number of sample plots was adequate as species numbers reached a plateau for all treatment plots (Supplementary material A).

Data analysis

Several diversity indices including species richness (S), Shannon–Weiner's index (H′), Simpson index (1/D), Shannon (E), and Simpson (E_D) evenness (Magurran 1988), were used to compare vegetation diversity among the four treatments for both understory and overstory. The stem density and BA for overstory species and species count for understory were used to calculate the diversity indices.

The overstory tree mean stand density, BA, quadratic mean diameter (QMD) and diversity data were analyzed with a linear mixed-effects model where blocks, and sampling plots, were treated as random factors and treatment, time, and their interactions were treated as fixed factors. For understory plant diversity indices, comparisons among the treatments were evaluated by blocked ANOVA using block and

Table I. Mean stand density, BA, and QMD (± SD) in 1990 and 2005 by prescribed burn treatment and the results of linear mixed-effects models.

Response	Year	C	S0	S2	F4	*P* Treat	*P* Year	*P* Treat : year
Tree density [stems ha^{-1}]	1990	2437 (348)*b*	2480 (199)*b*	2134 (241)*b*	2908 (177)*c*	**0.027**	**<0.001**	**0.020**
	2005	1301 (132)*a*	1928 (94)*b*	2270 (118)*b*	1987 (105)*b*			
Basal area [m^2 ha^{-1}]	1990	4.58 (0.67)	3.65 (0.33)	3.10 (0.89)	4.73 (0.43)	0.185	**<0.001**	0.398
	2005	5.59 (0.83)	6.86 (0.66)	5.26 (0.54)	6.77 (0.78)			
Quadratic mean diameter [cm]	1990	4.87 (0.18)*y*	4.32 (0.11)*xy*	4.07 (0.40)*x*	4.50 (0.13)*xy*	**<0.001**	**<0.001**	0.137
	2005	7.29 (0.27)*y*	6.65 (0.24)*y*	5.42 (0.30)*x*	6.47 (0.41)*y*			

Notes: C: control, S0: burned spring 1967, S2: burned spring 1967 + repeat burn spring 1969 and F4: burned spring 1967 + repeat burn fall 1970; significant effects in bold; values followed by the same letter were not significantly ($\alpha = 0.05$, Tukey's test for multiple comparison) different for treatment effect for individual years (for density: *a*, *b*, *c* and for quadratic mean diameter: *x*, *y*).

plot as random factors (Schmiedinger et al. 2012). Analyses were conducted using the function "lme" from the package "nlme" in the R statistics system version 3.1.0 (R Core Team 2014). Tukey HSD post hoc comparisons ($\alpha = 0.05$) were carried out using the function "glht" from the package "multicomp" 1.3 − 2 if significant mean differences were found.

Normality and homogeneity of variances were tested by examining the residuals versus the fitted plots and the normal q–q plots of the models. No transformations were necessary.

A nonparametric multivariate test "multi-response permutation procedure for randomized blocks (MRBP)" was used to differentiate understory species composition among treatments. The statistic "A" represents within-group homogeneity compared to the random expectation and the test statistic "T" indicates separation between groups. MRBP and treatment contrasts were conducted using Blossom Statistical Software. An unconstrained ordination non-metric multidimensional scaling (NMS) was used to illustrate variation in community composition among the treatments (McCune & Grace 2002). The ordination analysis was conducted using the package "ecodist" within the package "vegan 2.0-5" (Oksanen et al. 2012) in the R statistics system.

The affinity of species to particular treatment units was evaluated by an indicator species analysis (Dufrêne & Legendre 1997; De Cáceres 2013) on abundance data with the function "multipatt" of the package "indicspecies" version 1.7.5 for the R statistics system (De Cáceres 2013). Function "multipatt" is the most commonly used function of "indicspecies"; it allows the determination of species lists associated to particular groups of sites (or combinations of those) (De Cáceres et al. 2012). In addition, rank abundance and proportional abundance were used to examine understory species distributions as they occurred within treatments and among treatments. These were useful for identifying common and rare or uncommon species.

Results

Overstory

The mixed model analysis indicated that the QMD ($p < 0.001$) and tree stem density (stems ha^{-1}) ($p = 0.027$) were significantly different among treatments while BA (m^2 ha^{-1}) ($p = 0.185$) was not significantly different (Table I). When the year by treatment interaction was considered, only tree density showed significant effect ($p = 0.020$). Tree density decreased in all treatments over the 15 years except treatment S2 where density slightly increased from 2134 to 2270 stems ha^{-1} although change was not significant (Table I). The amount of density decrease between the two measurements ranged from 552 to 1136 stems ha^{-1} for the treatments C, F4, and S0. BA and QMD increased in all treatments between 1990 and 2005. Tukey's test for multiple comparisons ($\alpha = 0.05$) for tree density showed treatment F4 (in 1990) and treatment C (in 2005) were significantly ($p < 0.001$) different from the other treatments while only treatment S2 was significantly different for QMD in 2005 (Table I).

Overstory species richness was not significantly different among treatments ($p = 0.828$), year ($p = 0.296$) or their interactions ($p = 0.689$). For both 1990 and 2005 measurements, mean richness was similar across the treatments. In total, 14 tree species were counted in the sampled plots and the most abundant species across all treatments were aspen, sugar maple, red maple, and ironwood (*Ostrya virginiana* (Mill.) K. Koch). However, other species such as basswood, paper birch, red oak, green ash (*Fraxinus pennsylvanica* Marshall), and bur oak were also found. In addition, three uncommon species (white spruce: *Picea glauca* (Moench) Voss, balsam fir: *Abies balsamea* (L.) Mill., and American elm: *Ulmus americana* L.) were also found in the F4 (fall burn) and S0 (spring burn) treatments.

Considering the diversity indices based on tree BA and density, none of the treatments were significantly different from each other whereas a significant

Table II. Results of linear mixed-effects models based on density and BA of the overstory diversity in 2005.

Diversity indices	Source	Based on density [stems ha^{-1}]		Based on basal area [m^2 ha^{-1}]	
		F stat	*P* value	*F* stat	*P* value
Shannon [H′]	Treatment	0.098	0.958	0.746	0.562
	Year	21.550	**0.002**	142.055	**<0.001**
	Interaction	7.676	**0.009**	3.175	0.085
Shannon evenness [E′]	Treatment	1.024	0.445	4.610	0.053
	Year	5.455	**0.047**	6.287	**0.036**
	Interaction	0.421	0.743	34.977	**<0.001**
Simpson [1/D]	Treatment	0.332	0.803	1.327	0.350
	Year	18.612	**0.002**	69.706	**<0.001**
	Interaction	4.229	**0.045**	3.998	0.051
Simpson evenness [$E_{1/D}$]	Treatment	2.798	1.311	1.044	0.439
	Year	13.996	**0.005**	85.107	**<0.001**
	Interaction	1.148	0.386	3.214	0.082

Note: Significant effects in bold.

year effect was observed (Table II). When the year by treatment interaction was considered, significant effects were observed in Shannon evenness ($p < 0.009$) for tree BA and in Simpson diversity ($p = 0.045$) for tree density. Shannon and Simpson diversity indices showed a variable response among the treatments but the value of both diversity indices decreased from 1990 to 2005 when BA was considered while the opposite trend was observed for density based indices (Figures 1 and 2).

Understory

Like the overstory, understory shrub and herb layer richness was not significantly different among the treatments although the treatment F4 (burned spring 1967 + repeat burn fall 1970) had slightly higher species richness compared to the other treatments. A total of 32 species were counted across the experimental area in the shrub layer where 21, 18, 21, and 22 species were found in the C, S0, S2, and F4 treatments, respectively. Among them *A. rubrum, A. saccharum*, *B. alleghaniensis*, *Populus spp*., *Quercus* spp., and *T. americana* were the most common species and *A. rubrum* and *A. saccharum* were the most abundant species found across all treatments. Four species (*Cornus stolonifera* L., and *Corylus americana* Marshall, in S0, *Picea glauca* (Moench) Voss in F4, and *Rosa spp.* in the C) were found only in a single treatment. For the herbaceous layer, the greatest number of species was found in the F4 (42 species) treatment which was followed by the C (41), S0 (38), and S2 (37) treatments.

There were no significant differences among the treatments for any diversity indices in the understory and all the indices showed almost similar treatment responses except for Shannon and Shannon evenness in the control treatment's shrub layer (Figure 3). Shannon and Shannon evenness of the shrub layer in control treatment were lower compare to all other treatments.

Compositional change in the understory layer

NMS ordination for understory layer data yielded a two-dimensional solution which explained 60.6 % for shrubs and 79.1% for herb layer variability in the original data matrix. For the shrub layer, the ordination and MRBP ($p = 0.832$) analyses ($n = 12$) did not detect differences in community composition among treatments (Figure 4 and Table III).

In the herb layer, ordination showed differentiation for species composition among treatments and a clear distinction in community composition between F4 (burned spring 1967 + repeat burn fall 1970) with all other treatments (Figure 4). The multi-response block permutation procedures (MRBP) analysis indicated that community composition significantly differed ($p = 0.013$, $T = -2.994$) among treatments (Table III), but pair-wise comparisons did not show any significant difference among the treatments ($\alpha = 0.05$). This suggests that although seasonality of prescribed burning may still have some impact on the herb layer when treatments were compared as a whole, at an individual treatment level however, they did not show any significant impact.

Out of 10 rare or uncommon species, 4 (*Apocynum androsaemifolium* L., *Sambucus racemosa* L., *Lonicera canadensis* Bartram., and *Carpinus caroliniana* Walter) were found in F4, 2 each in S2 (*Abies balsamea* L. and *Rosa spp.*), S0 (*Prunus serotina* Ehrh. and *Pteridium aquilinum* (L.) Kuhn) and C (*Equisetum sylvaticum* L. and *Dicentra cucullaria* (L.) Bernh.) treatment (data not shown). Among the 10 most abundant species for each treatment, 6 species (*Anemone quinquefolia* L., *Aralia nudicaulis* L., *Fragaria virginiana* Duchesne, *Maianthemum canadense* Desf., *Trientalis borealis* Raf., and *Uvularia grandiflora* Sm) were not found in F4 treatment. However, the most abundant species (*Matteuccia struthiopteris* (L.) Todaro) in F4 treatment was not found in treatment C and had the lowest species abundance in treatment S0 and S2.

Based on the indicator species analysis, our study also revealed that four species (*A. androsaemifolium*,

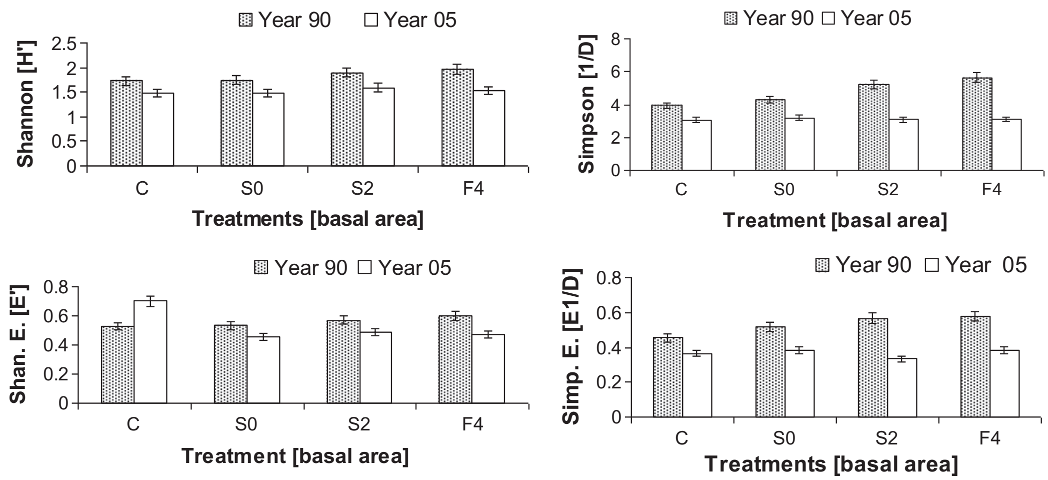

Figure 1. BA-based on overstory tree species' diversity indices (± SEM) by treatment in 1990 and 2005.
Note: [C: control, S0: burned spring 1967, S2: burned spring 1967 + repeat burn spring 1969 and F4: burned spring 1967 + repeat burn fall 1970].

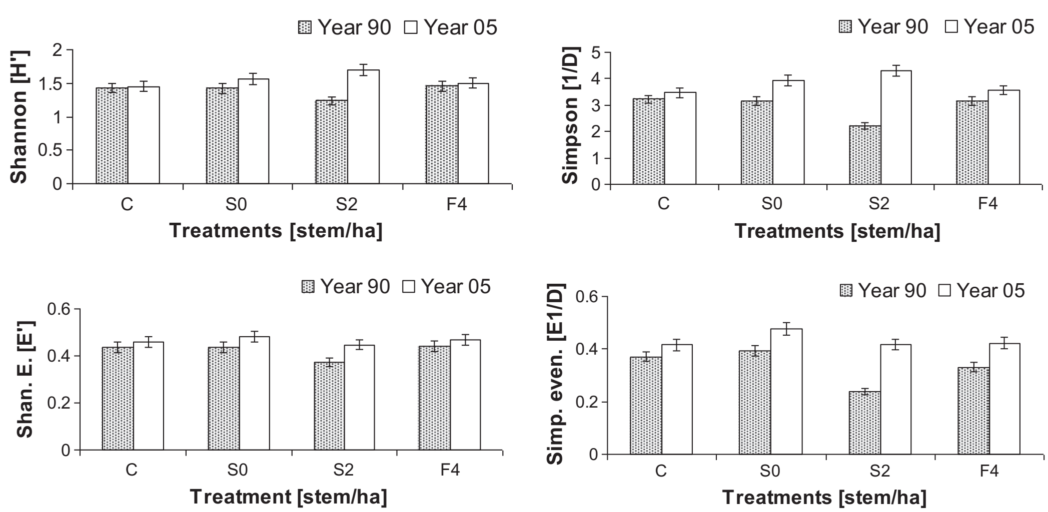

Figure 2. Density-based on overstory tree species' diversity indices (± SEM) by treatment in 1990 and 2005.
Note: [C: control, S0: burned spring 1967, S2: burned spring 1967 + repeat burn spring 1969 and F4: burned spring 1967 + repeat burn fall 1970].

S. racemosa, *Viola canadensis*, and *Cornus alternifolia* L.) were significantly (α = 0.05) associated with treatment F4. Conversely, none of the species showed any association with any other treatments individually (Table IV). In addition, there are some species whose patterns of abundance are more associated with a combination of treatments: for example, *Onoclea sensibilis* L. and *Actaea rubra* (Ait.) Willd. were associated with the combination of treatments F4 + C2 and C + S0, respectively; in addition, 10 species were found in all treatment (Table IV).

Discussion

Considering the overstory diversity, this study suggests that, after almost 40 years, none of the burning treatments resulted in significant differences. In the tree layer, aspen, sugar maple, ironwood, and balsam poplar were the most abundant species, which is similar to what was documented by Perala (1975) 30 years ago. This finding demonstrated that burning treatments did not foster ingress of conifers, failed to convert the former aspen stand to a conifer stand, and that the treated sites were rapidly occupied by aspen as well as associated hardwoods, without opportunity for the less competitive conifers to become established (Perala 1975). The Pike Bay site, primarily an aspen stand prior to logging in 1965, had an established aspen root system and seedbed. Where burning was intense enough to expose mineral soil and create free space, aspen seeded in along with birch, thereby impeding the regeneration of conifers

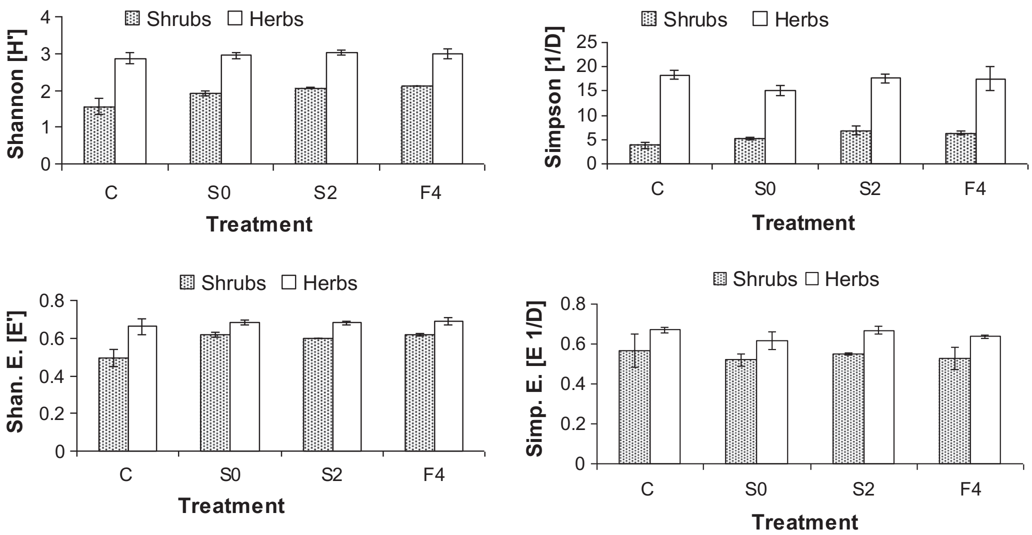

Figure 3. Herb and shrub species' diversity indices (± SEM) by treatment in 2005.
Note: [C: control, S0: burned spring 1967, S2: burned spring 1967 + repeat burn spring 1969 and F4: burned spring 1967 + repeat burn fall 1970].

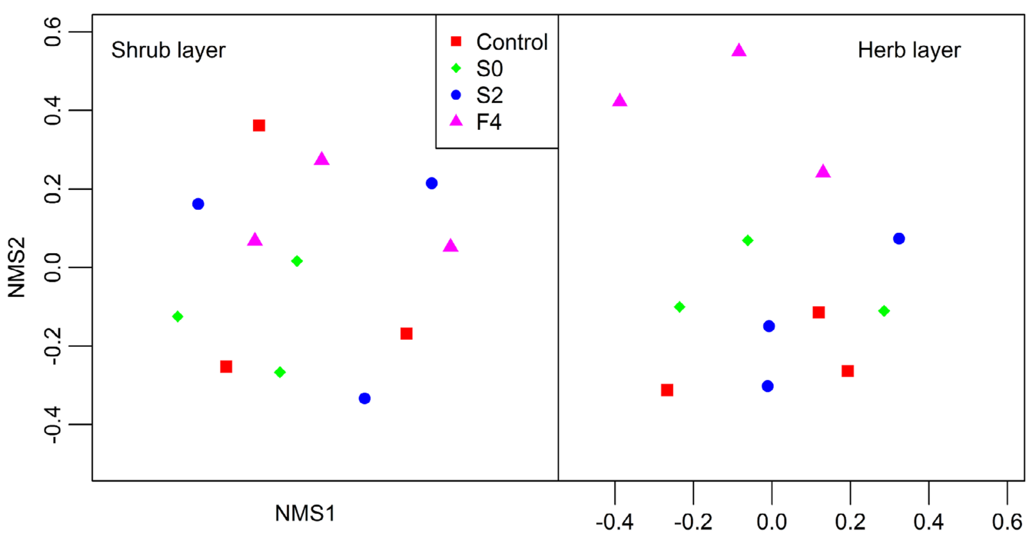

Figure 4. NMS ordination for shrub and herb layers.
Note: [C: control, S0: burned spring 1967, S2: burned spring 1967 + repeat burn spring 1969 and F4: burned spring 1967 + repeat burn fall 1970].

(Wang & Kemball 2005). A similar observation by Perala (1975) indicated that paper birch and aspen seeds germinated vigorously in the patches of exposed mineral soil. Where the fire burned less intensely, aspen and associated hardwoods and shrubs (e.g. maples, willows (*Salix spp.*), and hazelnut (*Corylus americana* Walt.)) were able to regenerate by vegetative means (Perala 1975).

Prescribed burning had very little effect on shrub and herb layer diversity after 37 years, even though the burn treatments were quite different. Similar results were also reported in other studies (McGee et al. 1995; Glasgow & Matlack 2007: Knapp et al. 2007; Prévosto et al. 2011). According to Knapp et al. (2007), understory vegetation recovered rapidly after prescribed burning in a mixed conifer forest at Sequoia National Park, USA. Similarly, Glasgow and Matlack (2007) and Prévosto et al. (2011) reported a single prescribed burn had only a short-term effect on the understory.

For species composition, the shrub layer did not show any treatment effect whereas the herb layer showed significant differentiation among treatments. This might be due to fire behavior, burning intensities, seasonal variability of the prescribed burning or fuel moisture conditions. The Pike Bay site had several fire regimes of varying burning intensity (first spring re-burn fire line intensity was 10 kW/m and second fall re-burn fire line intensity ranged from 20 to100 kW/m) with seasonal variability (spring burn, and repeated spring and fall burn) (for detail about fire treatments, see Perala 1975), which likely resulted in different seedbeds. Fuel moisture conditions in the early season plays an important role in fuel consumption as spring burns consume less fuel than the fall burns (Kauffman & Martin 1989; Knapp et al. 2005). According to Knapp et al. (2005), fall burns consumed 19% more fuels from the forest floor than the spring burn in mixed conifer forest adjacent to the Giant Sequoia grove in Sequoia National Park, USA. A higher fuel moisture condition is typical in early season and can also result in more unburned patches where fire sensitive species are more likely to persist (Knapp et al. 2005).

The size and abundance of these unburned refugia relative to propagule dispersal distances may play in important role in post fire plant recolonization (Lee 2004). This might be the reason why treatment F4 (burned spring 1967 + repeat burn fall 1970) showed some compositional differentiation from all other treatments, although none of the treatments were significantly different from each other, using post hoc tests. In addition, the greatest number (42) of species and some level of compositional change (four rare or uncommon species, four indicator species, and changes in species abundance, compared to other treatments) were found in treatment F4. Several long-term, repeated fire studies in southeastern

Table III. Result of multi-response block permutation procedures (MRBP) procedures for understory layer community composition among treatments (main effect and treatment contrasts against control treatment) in 2005.

		A	*T*	*P*
Shrub layer	Main effect of treatment	−0.038	0.953	0.832
Herb layer	Main effect of treatment	0.219	−2.994	**0.013**
	C vs. S0	0.006	−0.343	0.366
	C vs. S2	0.010	−0.377	0.331
	C vs. F4	0.331	−1.721	0.062
	S0 vs. S2	0.002	−0.112	0.516
	S0 vs. F4	0.373	−1.723	0.062
	S2 vs. F4	0.367	−1.722	0.062

Notes: C: control or unburned, S0: burned spring 1967, S2: burned spring 1967 + repeat burn spring 1969 and F4: burned spring 1967 + repeat burn fall 1970; A: represents within-group homogeneity compared to the random expectation; T: indicates separation between groups; significant effects in bold.

Table IV. Indicator species analysis across all different treatments. Species with significant affinity to treatment F4 are shown in bold.

	Treatment							Treatment					
Herb layer	C	F4	S0	S2	Stat	*P*	Herb layer	C	F4	S0	S2	Stat	*P*
Abies balsamea	0	0	0	1	0.58	1.00	*Hepatica americana*	1	1	1	1	0.95	NA
Acer rubrum	1	0	0	0	0.57	1.00	*Lathyrus ochroleucus*	0	1	0	0	0.81	0.08
Acer saccharum	1	0	0	0	0.58	1.00	*Lonicera canadensis*	0	1	0	0	0.58	1.00
Acer spicatum	0	1	1	0	0.57	1.00	*Maianthemum canadense*	1	0	1	1	1.00	0.01
Actaea rubra	1	0	1	0	0.93	0.03	*Matteuccia struthiopteris*	0	1	1	1	0.87	0.12
Amphicarpa bracteata	0	0	0	1	0.81	0.12	*Mitella nuda*	1	0	1	1	0.82	0.38
Anemone quinquefolia	1	0	1	1	0.94	0.11	*Onoclea sensibilis*	1	1	0	0	0.91	0.04
Apocynum androsaemifolium	0	1	0	0	1.00	**0.02**	*Osmorhiza claytonii*	1	1	1	1	0.91	NA
Aquilegia formosa	0	1	1	0	0.57	1.00	*Osmunda claytoniana*	1	1	1	0	0.75	0.59
Aralia nudicaulis	1	0	1	1	0.94	0.13	*Prunus serotina*	0	0	1	0	0.58	1.00
Aralia racemosa	0	1	0	0	0.74	0.16	*Pteridium aquilinum*	0	0	1	0	0.57	1.00
Asarum canadense	1	0	0	1	0.79	0.34	*Pyrola asarifolia*	1	0	0	1	0.70	0.49
Aster macrophylla	1	1	1	1	1.00	NA	*Quercus spp.*	0	1	0	0	0.57	1.00
Aster spp.	1	1	1	1	0.87	NA	*Ranunculus spp.*	0	1	0	0	0.58	1.00
Athyrium filix-femina	1	1	1	1	0.96	NA	*Ribes* sp. *1* (armed)	0	1	1	0	0.71	0.52
Botrichium virginianum	0	0	1	0	0.82	0.17	*Ribes* sp. *2* (unarmed)	1	1	0	1	0.58	1.00
Carpinus caroliniana	0	1	0	0	0.82	0.16	*Rosa* spp	0	0	0	1	0.57	1.00
Carya laciniosa	0	1	1	0	0.58	1.00	*Rubus pubescens*	1	0	1	1	0.96	0.01
Circaea alpina	1	1	0	0	0.57	1.00	*Sambucus racemosa*	0	1	0	0	1.00	**0.02**
Clintonia borealis	1	0	1	1	1.00	0.02	*Sanguinaria canadensis*	0	0	1	0	0.57	1.00
Cornus alternifolia	0	1	0	0	0.92	**0.02**	*Smilax ecirrhata*	1	0	1	0	0.70	0.51
Cornus canadensis	1	1	0	1	0.67	0.82	*Solidago flexicaulis*	1	0	1	1	0.67	0.83
Corylus americana	0	1	1	0	0.58	1.00	*Staphylea trifolia*	1	1	0	0	0.58	1.00
Dicentra cucullaria	1	0	0	0	0.57	1.00	*Streptopus roseus*	1	1	1	1	0.98	NA
Epilobium angustifolium	1	0	0	1	0.71	0.52	*Thalictrum dioicum*	1	1	1	1	1.00	NA
Equisetum arvense	1	0	0	1	0.57	1.00	*Tilia americana*	0	1	0	0	0.86	0.05
Equisetum pratense	0	1	0	1	0.58	1.00	*Trientalis borealis*	1	0	1	1	0.94	0.07
Equisetum sylvaticum	1	0	0	0	0.58	1.00	*Trillium spp.*	1	1	1	1	0.76	NA
Fragaria virginiana	1	0	1	1	0.66	0.85	*Uvularia grandiflora*	1	0	1	1	0.98	0.02
Galium trientalis	1	1	1	1	0.76	NA	Unknown vine	0	1	1	0	0.85	0.33
Grass spp.	1	1	1	1	0.95	NA	*Viola canadensis*	0	1	0	0	1.00	**0.02**
Gymnocarpium dryopteris	0	1	0	0	0.89	0.07	*Viola* spp.	0	0	0	1	0.58	1.00

Notes: C: control, S0: burned spring 1967, S2: burned spring 1967 + repeat burn spring 1969 and F4: burned spring 1967 + repeat burn fall 1970; the first four columns indicate (with 1 and 0) which treatments were included in the combination preferred by the species. The last two columns are the association statistic and the p-value of the permutational test. NA indicates the highest indicator value components and those species which can be found across all treatments.

USA documented relatively subtle effects on understory abundance and richness as well (Waldrop et al. 1992; Glitzenstein et al. 2003). Based on a study by Glitzenstein et al. (2003), understory vegetation shifted from woody to herbaceous-dominated communities with increasing fire frequency but only at one of two sites. A similar shift has also been reported by Waldrop et al. (1992) but only with annual burning. This suggests without fire, these systems were invaded by woody species and frequent burning with seasonal variability could reduce the woody sprouts and shrubs, allowing increased herbaceous species abundance (Knapp et al. 2007; Glasgow & Matlack 2007). In another study, McGee et al. (1995) mentioned that community composition remained unaffected 12 years after springtime prescribed burning, while Dodson et al. (2008) reported that species composition varied within and among burning treatments but was not strongly or consistently affected by burning treatment. After considering certain limitations (e.g. no pre-treatment understory vegetation data, small number of replication, lack of repeated fall burning treatment), our study overall indicates that burning treatments to modify forest structure may have very little impact on overstory and long-term understory species composition. This is an important insight with regards to forest management (tree species conversion). Future work should focus on documenting critically the fire intensity, seasonal variation, proximity of seed sources, etc.

Although the findings of this study did not show any significant difference among treatments on understory vegetation diversity other than some lingering effects on species composition in the herbaceous layer, it does not mean that the ecosystem has been stable and unchanging. Likely, in the 37 years since Perala first began to examine the fire study at Pike Bay, there have been changes in species due to succession. In the life of an ecosystem, 37 years is a short time, and it is fascinating to think that in such a relatively short span of time (duration of experiment), effects of a considerable disturbance, such as repeated fire events, can disappear, at least from an above ground standpoint. With the looming impacts of climate change upon us, it will be interesting to examine these stands again in 20 years and see if vegetation patterns and current condition are still maintained. In addition, we also recommend that forest managers and practitioners consider these results, with some caution, due to our limited number of replication and treatment size.

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Supplemental data

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References

Alban DH, Perala DA, Ostry MA, Probst JR. 1991. Aspen ecosystem properties in the Upper Great Lakes. Research Paper NC-300. USDA. p. 47.

Arévalo JR, Fernández-Lugo S, García-Domínguez C, Naranjo-Cigala A, Grillo F, Calvo L. 2014. Prescribed burning and clear-cutting effects on understory vegetation in a *Pinus canariensis* stand (Gran Canaria). Sci World J 2014. Article ID 215418. Available: http://dx.doi.org/10.1155/2014/215418

Bartos DL, Mueggler WF, Campbell Jr RB. 1991. Regeneration of aspen by suckering on burned sites in Western Wyoming. US Forest Service, Research Paper INT-448, pp. 1–14. Available: http://www.fs.fed.us/rm/pubs_int/int_rp448.pdf. Accessed May 08 2016.

Blake JG. 2005. Effects of prescribed burning on distribution and abundance of birds in a closed-canopy oak-dominated forest, Missouri, USA. Biol Cons 121: 519–531.

Brose PG, Van Lear DH. 1998. Responses of hardwood advance regeneration to seasonal prescribed fires in oak-dominated shelterwood stands. Can J For Res 28: 331–339.

Chastain Jr RA, Currie WS, Townsend PA. 2006. Carbon sequestration and nutrient cycling implications of the evergreen understory layer in Appalachian forests. For Ecol Manage 231: 63–77.

Craig A, Macdonald SE. 2009. Threshold effects of variable retention harvesting on understory plant communities in the boreal mixedwood forest. For Ecol Manage 258: 2619–2627.

De Cáceres M, Legendre P, Wiser SK, Brotons L. 2012. Using species combinations in indicator value analyses. Methods Ecol Evol 3(6): 973–982.

De Cáceres M. 2013. How to use the indicspecies package (ver. 1.7.5). Available: http://cran.rproject.org/web/packages/indicspecies/vignettes/indicspeciesTutorial.pdf. Accessed May 4 2016.

Delcourt HR, Delcourt PA. 1997. Pre-Columbian native American use of fire on southern Appalachian landscapes. Cons Biol 11: 1010–1014.

Dhar A, Parrott L, Hawkins CD. 2016. Aftermath of mountain pine beetle outbreak in British Columbia: Stand dynamics, management response and ecosystem resilience. Forests 7(8): 1–19.

Dufrêne M, Legendre P. 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. Ecol Monogr 67(3): 345–366.

Dodson EK, Peterson DW, Harrod RJ. 2008. Understory vegetation response to thinning and burning restoration treatments in dry conifer forests of the eastern Cascades, USA. For Ecol Manage 255: 3130–3140.

Gilliam FS. 2007. The ecological significance of the herbaceous layer in temperate forest ecosystems. BioScience 57: 845–858.

Glasgow SL, Matlack RG. 2007. Prescribed burning and understory composition in a temperate deciduous forest, Ohio, USA. For Ecol Manage 238: 54–64.

Glitzenstein JS, Streng DR, Wade DD. 2003. Fire frequency effects on longleaf pine (*Pinus palustris* P. miller) vegetation in South Carolina and northeast Florida. USA Nat Area J 23: 22–37.

Guedo DD, Lamb EG. 2013. Prescribed burning has limited long-term effectiveness in controlling Trembling Aspen (*Populus tremuloides*) encroachment into fescue grassland in Prince Albert National Park. Can Field Nat 127(1): 50–56.

Hart SA, Chen HYH. 2006. Understory vegetation dynamics of North American boreal forests. Crit Rev Plant Sci 25(4): 381–397.

Hawkins CDB, Dhar A, Lange J. 2013. Vegetation management with glyphosate has little impact on understory species diversity or tree growth in a sub boreal spruce plantation – A case study. Plant Biosyst 147(1): 105–114.

Hawkes BC, Feller MC, Meehan D. 1990. Site preparation: Fire. In: Lavender DP, Parish R, Johnson CM, Montgomery G, Vyse A, Willis RA, Winston D, editors. Regenerating British Columbia's forests. Vancouver, BC: UBC Press. pp. 131–149.

Kauffman JB, Martin RE. 1989. Fire behavior, fuel consumption, and forest-floor changes following prescribed understory fires in Sierra Nevada mixed conifer forests. Can J For Res 19: 455–462.

Kay CE. 2001. Evaluation of burning aspen communities in Jackson Hole, Wyoming. In: Shepperd WD, Binkley D, Bartos DL, Stohlgren TJ, Eskew LG, editors. Sustaining aspen in western landscapes: Symposium proceedings, 13–15 June 2000, Proceedings RMRS-P-18. Fort Collins: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. pp. 215–224.

Kemball KJ, Wang GG, Westwood AR. 2006. Are mineral soils exposed by severe wildfire better seedbeds for conifer regeneration? Can J For Res 36: 1943–1950.

Kill AD. 1970. Effects of spring burning on vegetation in old partially cut spruce-aspen stands in east-central Alberta. Department of Fisheries and Forestry, Canadian Forestry Service, Forest Research Laboratory, Edmonton, Alberta. Information Report A-X-33. 12 p.

Klinger RC, Kutilek MJ, Shellhammer HS. 1989. Population responses of black-tailed deer to prescribed burning. J Wildl Manage 53: 563–571.

Knapp EE, Keeley JE, Ballenger EA, Brennan TJ. 2005. Fuel reduction and coarse woody debris dynamics with early season and late season prescribed fires in a Sierra Nevada mixed conifer forest. For. Ecol. Manage. 208: 383–397.

Knapp EE, Schwilk DW, Kane JM, Keeley JE. 2007. Role of burning season on initial understory vegetation response to prescribed fire in a mixed conifer forest. Can J For Res 37: 11–22.

Lee P. 2004. The impact of burn intensity from wildfires on seed and vegetative banks and emergent understory in aspen-dominated boreal forests. Can J Bot 82: 1468–1480.

Lencinas MV, Pastur GM, Gallo E, Cellini JM. 2011. Alternative silvicultural practices with variable retention to improve understory plant diversity conservation in southern Patagonian forests. For Ecol Manage 262: 1236–1250.

Magurran AE. 1988. Ecological diversity and its measurement. Princeton, NJ: Princeton University Press.

Main MB, Barry MJ. 2002. Influence of season of fire on flowering of wet prairie grasses in south Florida, USA. Wetlands 22: 430–434.

McCune B, Grace JB. 2002. Analysis of ecological communities. Gleneden Beach, OR: MjM Software Design.

McGee GG, Leopold DJ, Nyland RD. 1995. Understory response to springtime prescribed fire in two New York transition oak forests. For Ecol Manage 76: 149–168.

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, et al. 2012. Vegan: Community ecology package. R package version 2.0-5. Available: http://CRAN.R-project.org/package=vegan

Penman TD, Binns LD, Shiels RJ, Allen RT, Kavanagh RP. 2008. Changes in understorey plant species richness following logging and prescribed burning in shrubby dry sclerophyll forests of south-eastern Australia. Austral Ecol 33: 197–210.

Perala DA. 1974. Prescribed burning in an Aspen – Mixed hardwood forest. Can J For Res 4: 222–228.

Perala DA. 1975. Repeated prescribed burning in aspen. USDA Research Note NC-171. U.S. Department of Agriculture, Forest Service, N. C. Forest Experiment Station, Minnesota.

Perala DA. 1995. Quaking aspen productivity recovers after repeated prescribed fire. Research Paper NC-324. U.S. Department of Agriculture, Forest Service, N. C. Forest Experiment Station, Minnesota.

Prévosto B, Bousquet-Mélou A, Ripert C, Fernandez C. 2011. Effects of different site preparation treatments on species diversity, composition, and plant traits in *Pinus halepensis* woodlands. Plant Ecol 212: 627–638.

R Core Team. 2014. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. ISBN 3-900051-07-0. Available: http://www.R-project.org/

Schmiedinger A, Kreyling J, Steinbauer MJ, Macdonald SE, Jentsch A, Beierkuhnlein C. 2012. A continental comparison indicates long-term effects of forest management on understory diversity in coniferous forests. Can J For Res 42: 1239–1252.

Swift LW, Elliott KJ, Ottmar RD, Vihnanei E. 1993. Site preparation burning to improve southern Appalachian pine-hardwood stands: fire characteristics and soil erosion, moisture, and temperature. Can J For Res 23: 2242–2254.

Vose JM. 2000. Perspectives on using prescribed fire to achieve desired ecosystem conditions. In: Moser WK, Moser SM, editors. Fire and forest ecology: innovative silviculture and vegetation management. Tall timbers fire ecology conference proceedings, No. 21. Tallahassee, FL: Tall Timbers Research Station. pp. 12–17.

Waldrop T, White DL, Jones SM. 1992. Fire regimes for pine-grassland communities in the southeastern United States. For Ecol Manage 47: 195–210.

Wang GG, Kemball KJ. 2005. Balsam fir and white spruce seedling recruitment in response to understory release, seedbed type, and litter exclusion in trembling aspen stands. Can J For Res 35: 667–673.