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RESEARCH ARTICLE

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Vegetation Dynamics after Spring and Summer Fires in Red and White Pine Stands at Voyageurs National Park

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ABSTRACT: Conducting dormant season or springtime prescribed fire treatments has become a common practice in many regions of the United States to restore ecosystems to their natural state. Despite the knowledge that historically, fires often occurred during the summer, the application of summer burns has been deterred, in part, by a lack of understanding of fire season effects on vegetation. We explored the differences in fire effects between spring and summer burns at Voyageurs National Park, Minnesota. The fire season effects on the ground layer vegetation were clearly different among the treatments: pre-burn, spring, and summer. Vegetation composition of pre-burn and after spring fires was similar, but differed significantly from the summer fires. Spring fires propagated the same species that were present prior to the fire, whereas summer fires promoted a new suite of species through the germination of seedbank and high seed dispersal species. Cover and richness of seed bank and intolerant species were greatest after the summer fires, which contributed to the peak in richness found across all reproductive and tolerance attributes five years after these fires. Post summer fire composition showed shifts in composition through time. Substantial differences in the effects of burn seasonality on ground layer vegetation should be considered in long term restoration efforts to help maintain species diversity in red and white pine forest ecosystems.

Index terms: burn seasonality, ecosystem restoration, northern pine forests, prescribed fire, red pine, Voyageurs National Park, white pine

INTRODUCTION

Fire is a dominant disturbance agent in many ecosystems worldwide, originating from lightning strikes, volcanic eruptions, or humans (Pyne 1995). Regardless of origin, fires are characterized by the fire regime components: frequency (return interval), intensity, and seasonality (Gill and Groves 1981; Pickett and White 1985). The propagation, impact, or severity of fires is the result of the evolutionary interaction between fire as a disturbance process and the characteristics of the species impacted (Platt 1999; Gagnon et al. 2010). Of these components, the impacts of growing season fires are the least understood (Gill et al. 2002), likely due to the complex nature of the physical and biological environment during the growing season. Differences in the effects on vegetation due to fire season are related to the phenological stages of the plants, live and dead fuel moisture, and the state of the weather during and after the fire (Miller 2000). The effect on the plant community is, therefore, dependent on the state and interaction of these elements during the fire. In general, summer season fires tend to alter ecosystems more because plants are actively growing during this period and are more susceptible to damage (Miller 2000). Fuels tend to be drier, leading to increased fuel consumption, deeper soil heat penetration, and greater fire intensity, thereby increasing the damage to above- and below-ground plant parts. The wide variability in these components during the growing season makes effects from these fires far more difficult to predict. The type and degree of change wrought to a plant community is, therefore, greatly influenced by the season of fire, which comparatively speaking, may even result in different successional trajectories (Bond and van Wilgen 1996; Heinselman 1996).

The red and white pine forests (*Pinus resinosa* Aiton, *Pinus strobus* L.) of Northern Minnesota are considered by Heinselman (1973) to be "near-boreal." That is, they contain species of both the boreal forests to the north and the more temperate forests to the south. The ecosystem has a mixed fire regime dominated by frequent, low-intensity understory fires every 20–40 years with infrequent, stand replacing fires every 150–200 years (Heinselman 1981b). Historically, fires in this region were both human and lightning caused and, based on the climate, occurred from May through mid-October. Lightning fires typically occurred in July and August and were associated with short or long term droughts (Heinselman 1996). Anthropogenic fires may have taken place anytime throughout the fire season depending on the reason for lighting them. Nearly all prescribed fires in Northern Minnesota are conducted during a brief dry period in late spring. For a number of reasons, this is the most advantageous time to do so. Summers are usually wet and opportunities to conduct burns are limited, whereas during the

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spring, a brief dry period is almost a certainty. In addition, conducting fires during the summer requires a period of drought, which will increase fire intensity as well as the possibility of escape. However, these dry conditions are needed to achieve many of the desired fire effects resulting from summer fires.

Plant reproductive and survival characteristics, and their importance to post-burn species composition, have been well described (Keeley 1981; Rowe 1983; Bond and van Wilgen 1996; Miller 2000). These characteristics regulate how individual plants respond to fire-induced changes in the environment (Ahlgren 1960). Physical alterations to the site conditions caused by fire are numerous and include: changes in light and nutrient availability, soil pH, albedo, moisture availability, and mineral soil exposure (Ahlgren and Ahlgren 1960). Such changes favor certain plants based on their physiological and reproductive traits. The direct interaction of fire with plants triggers biological changes that vary from stimulation to mortality (Clarke et al. 2013). Some changes include: top-kill of the parent plant, or heat or chemical scarification of seeds causing sprouting and germination respectively (Miller 2000). The combination and degree of physical and biological changes caused by fire will dictate the post-burn community and the extent of its alteration. Differences in post-burn species composition are, therefore, reflective of the variability in burning conditions among seasons and the direct effects related to them (Ohmann and Grigal 1981).

Several studies have examined the post-burn understory revegetation in Northern Minnesota or nearby Canada (Ahlgren 1960; Methven 1973; Ohmann and Grigal 1979; Wang and Kemball 2005), while few have directly examined the effects of fire seasonality on the vegetation (Ohmann and Grigal 1981). In addition, the present study compares longer term effects within the red and white pine ecosystem and makes comparisons using eight separate burn treatments, while other studies examine one or two fires. The purpose of this study is to: (1) examine differences in ground layer species composition among pre-burn, spring, and summer fire treatments up to ten years post-burn, and (2) examine fire effects on species richness and diversity.

METHODS

Study Site

Our study was conducted at Voyageurs National Park (48°30’27”N, 92°41’43”W), approximately 56 km east of International Falls, Minnesota, along the Canadian border. Study sites are located on the Canadian Shield, where soils are thin, ranging from exposed bedrock to three meters deep in the depressions (Heinselman 1996). The climate is continental, with long cold winters and warm summers. The average winter and summer high temperatures are -8 ºC and 24 ºC, respectively. An average of 61 cm of precipitation is received annually, with 67% of it falling from May through September (NCDC 2013). The average leaf-on date is mid- to late-May (S. Weyenberg, pers. obser.). Our study sites were mixed red and white pine forests that fell within two very similar plant associations: White Pine/Mountain Maple Mesic Forest and Red Pine/Blueberry Dry Forest (Faber-Langendoen et al. 2007). Sites have an overstory dominated by *Pinus strobus* and *Pinus resinosa,* with scattered individuals of *Pinus banksiana* (Lambert) (jack pine), *Populus tremuloides* (Michx.), *P. grandidentata* (Michx.) (trembling and bigtooth aspen, respectively), *Betula paperifera* (Marshall) (paper birch), and *Picea glauca* (Moench) Voss (white spruce) (nomenclature follows the Integrated Taxonomic Information System 2014). *Thuja occidentalis* (L.) (northern white cedar), *Abies balsamea* (L.) (balsam fir), and *Acer rubrum* (L.) (red maple) are common in the midstory.

Since the initiation of the park’s prescribed fire program in 1989, 35 units have been burned in the red pine/white pine and mixed-wood forest types. In addition, the park also manages natural ignitions for resource benefit when appropriate. Until 2007, all prescribed fires took place in the spring, typically during the last two weeks in May, with the exception of one fall burn. Summer season burns were recently conducted in 2007 and 2009.

Sampling

Sampling occurred from 1997 through 2012, across six burn units (sites) (Table 1), which are located in relative close proximity to one another (Figure 1). Sites are characterized by open understories, dominated by herbs with occasional patches of dense shrubs and balsam fir. Repeated sampling was conducted in permanent plots, once from mid-June through July, at intervals of: one month to three years pre-burn, immediately post-burn, and 1, 2, 5, and 10 years post-burn. All sites have pre-burn data except for Section 33; otherwise, sites were sampled using the above time frame unless a fire treatment interrupted the cycle prematurely. Four summer fires and four spring fires occurred among the six sites. All spring fire treatments were prescribed fires, while summer treatments included one lightning fire, two prescribed fires, and one human caused wildfire, which burned two sites. Three sites (Tar Point, Mica Bay, and Alder Trail) were burned twice; first in the spring and then in the summer, with 5 to 10 years between fires. In summary, there were nine treatments on six sites and eight fires (Table 1).

Vegetation sampling differed among sites depending on the objective of the initial sampling. Most sampling at the park is performed for long-term monitoring purposes (FMH, Fire Monitoring Handbook); however, alternate Project Level Monitoring (PLM) sampling is employed to assess more specific restoration objectives at Mica Island and Section 33. In FMH sampling, all woody, herbaceous, graminoid, and nonvascular species less than 2 m in height were sampled for percent cover from two 50-meter point intercept transects per 20 x 50 m plot plot (USDI National Park Service 2003). Additionally, any species observed within 2 m of each transect, but not encountered along either, was recorded as present in the plot. One or two FMH plots were established per burn unit. These plots were used for all spring fires and on two summer fires (Table 1). PLM sampling included visual estimates of cover at Section 33 and presence/absence (P/A) data

Table 1. Summary of sites by season of burn at Voyageurs National Park (1997–2009). Stand type: dominant overstory species by unit, RP – red pine, WP – white pine. Plot type: PLM$_1$ – Project Level Monitoring, FMH – Standard National Park Service fire effect monitoring protocols. Total number of plots at each site is indicated by *N* with the summarized number of plots in parentheses. Sample years (post): indicates the number of years following fire treatment in which the plot was sampled. All plots were sampled pre-burn except S33. Fire origin: W = Wildfire (* human caused), Rx = Prescribed fire. Where single fires burned multiple plots, the fire is listed once for all affected plots and/or units.

Fire season	Summer				Spring			
Burn unit	Section 33	Mica Island	Mica Bay & Alder Trail	Tar Point	Tar Point	Mica Bay	Alder Trail	Snake Island
Plot ID	S33	M25, M610	26, 27 & 41	48	48	26, 27	40, 41	42
Stand type	RP	RP	WP	WP	WP	WP	WP	WP
Plot type	PLM$_1$	PLM$_2$	FMH	FMH	FMH	FMH	FMH	FMH
N	6(1)	10(2)	2 & 1	1	1	2	2	1
Sample years (post)	1, 2, 5	1, 2, 5	1, 2, 5	1, 2	1, 2, 5	1, 2, 5, 10	1, 2, 5, 10	1, 2, 5, 10
Area sampled (m^2)	40.7	4	200	200	200	200	200	200
Fire origin	W	Rx	W*	Rx	Rx	Rx	Rx	Rx
Burn dates	8-28 July 2004	19 July 2007	2-4 Aug 2007	13 Aug 2009	26 June 2003	29 May 1997	17 June 1999	18 May 1999
Hectares	445	15	24	9	9	13	29	30
Fire danger	High	High	Extreme	High	Low/Mod.	Moderate	Moderate	Low
Duff moisture (%)	UNK	36	~15^{a}	27	85^{b}	85^{b}	85^{b}	85^{b}
Duff moisture code	39 – 55^{c}	31	74 – 81^{c}	30	7	33	31	17
Drought code	103 – 210^{c}	223	243 – 358^{c}	233	200	155	70	53
Mineral soil exp. (%)	43	13	45	20	17	6	6	0

[a] Moisture content estimated based on data taken within a week before and after the fire at nearby sites.

[b] Fuel moisture data collected at Voyageurs N.P. from 2007 through 2011 during the months of May and June give estimates of duff fuel moisture of 85 ± 27%, n = 14.

[c] Data selected for active burning dates only.

at Mica Island. Data at Section 33 were collected within a 3.6-m radius plot, while data at Mica Island were collected within four 1-m squares placed on the edge of a 3.6-m radius plot in the cardinal directions. Six to ten PLM plots were established per site. Individual plot data for Section 33 and Mica Island were aggregated. The six plots from Section 33 were averaged into one, and plots 2–5 and 6–10 from Mica Island were averaged to create two plots. Mica Island plots 1 and 8 did not burn and were excluded. Plots were summarized to avoid biasing the analyses toward the units with high numbers of plots. The analyses were run with, and without, the summarized plots without a substantial difference in conclusions. Using the summarized data is considered to be a more conservative approach and was used for all analyses.

All data were converted to P/A to create a dataset containing 146 species recorded in 50 samples from nine plots. It was necessary to delete species that occurred less than four times in the dataset, since they contribute a large number of zeros, thus making the analyses impossible to run. This is common to do in species datasets when one is interested in species redundancy rather than rare species, as is the case here (Peck 2010). After deleting uncommon species, the final matrix consisted of 60 species in 50 samples from nine plots. In cases where multiple species of the same genus were uncommon, the species were combined into a genus category instead of deleting them. When cover data were analyzed, Mica Island samples were excluded, resulting in a final dataset consisting of 46 species in 42 samples from seven plots.

Vital attributes, as described by Noble and Slatyer (1980), were assigned to each species, based on several sources (Ahlgren 1960; Heinselman 1981a; Rowe 1983; Kemball et al. 2006; USDA NRCS 2012; Fire Effects Information Sytems (FEIS) 2013). The assignments included the reproductive strategies: D – highly dispersed propagules; S – stored seed (seedbank); and V – vegetative (resprouter). A second category for community tolerances includes tolerant (T), intolerant (I), and tolerant with requirements (R) (Heinselman 1981a). In this context, tolerance refers to how tolerant a species is of competition and environmental gradients. The classification closely follows shade tolerance. Tolerant species thrive in a wide range of conditions, allowing immediate re-establishment after disturbance and continued persistence in the presence of competition. They are often regarded as generalists. Intolerant species are species that invade immediately after disturbance but are intolerant of competition and, therefore, disappear shortly thereafter. This group contains mainly pioneer species. The species "with requirements" are those that have some specific requirement(s) to their establishment; and, with the exception of lichens, they consist of mainly tolerant species. They tend to begin establishment after stands have reached maturity and, therefore, are often associated with older stands. The reproductive strategy assignments are based on the most dominant

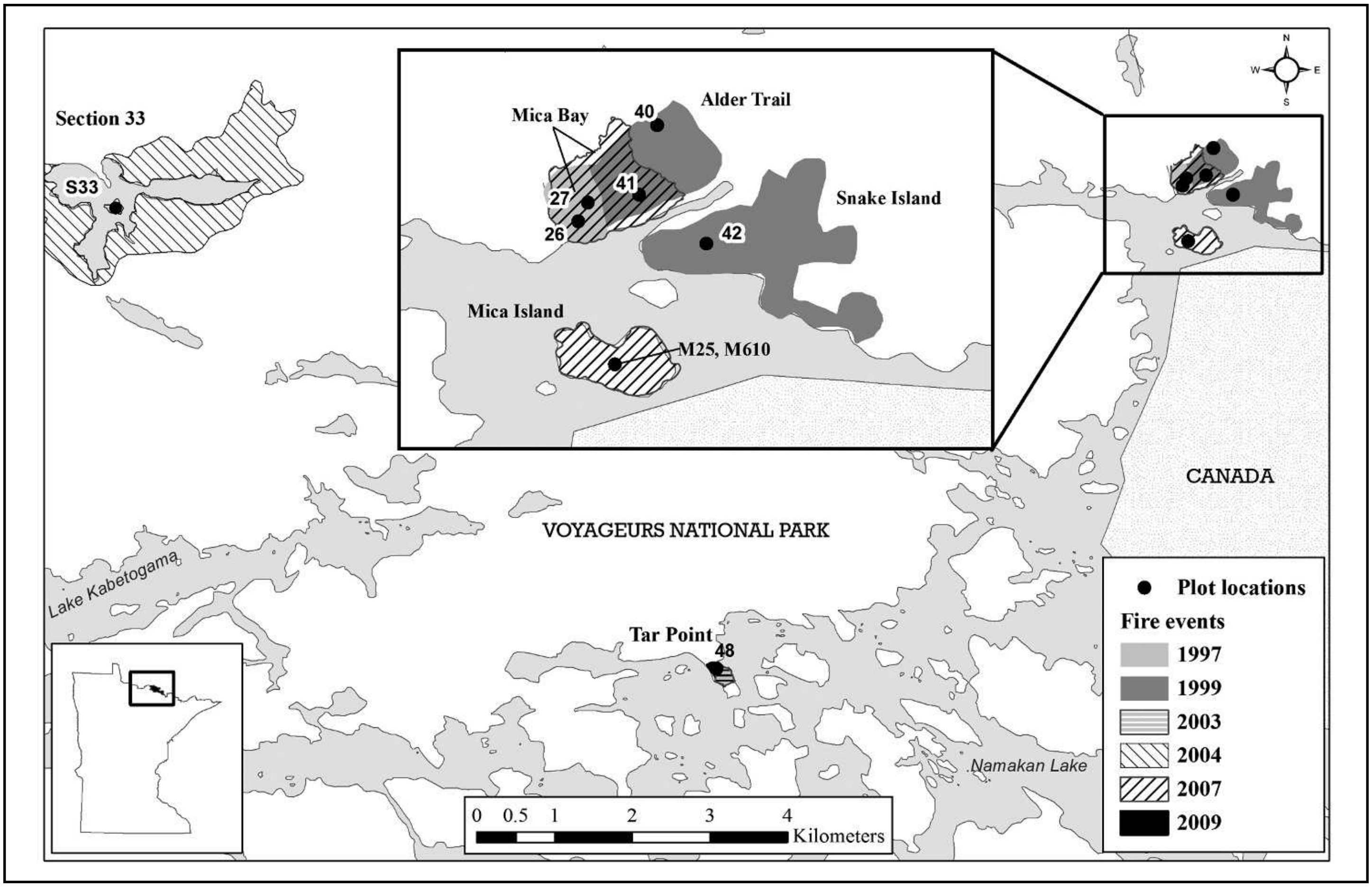

Figure 1. Voyageurs National Park site map including fire history from 1997 to 2009, and locations of burn units and plots.

attributes (Rowe 1983). More than one tolerance was listed when multiple species were clumped under one genus. Often a species may exhibit both intolerant and tolerant traits, such as *Ribes* spp. (currant) and *Fragaria* spp. (strawberry); in such cases it was listed as tolerant.

Fuel moisture conditions and fire hazard were assessed via direct samples of the duff moisture and two parameters of the Canadian Fire Behavior Prediction System: Duff Moisture Code (DMC) and Drought Code (DC) (Van Wagner 1970). Duff moisture samples were taken prior to some burns and were estimated for others based on samples taken a few years later, but during the same time of year (Table 1). Both fire indices are numerical ratings of the amount of moisture in the duff layer. The DMC relates to the upper duff and gives an indication to its possible consumption. The DC relates to the lower, compact duff layers. Although lower duff layers are not present on our sample sites, DC is still used as an indicator of seasonal drought and related fire danger.

All sampled stands were underburned with surface fires. Portions of the overstory in some stands were killed; however, these areas did not happen to occur within our study plots. Stands subject to prescribed fires were burned within the range of predefined prescription parameters (temperature: 27 ºC–10 ºC; relative humidity: 50%–23%; Fine Fuel Moisture Code: 94–86; DMC: 40–4; DC: 250–40). The two wildfires burned at the hot end of this prescription and beyond.

Fire severity was visually assessed at all locations using qualitative criterion of the substrates and remaining vegetation. Severity was recorded on a scale of 0 through 5, with 0 being unburned and 5 being severely burned. Mineral soil exposure was assessed at 40 locations per site pre- and immediately post-burn (Table 1) (USDI National Park Service 2003). Preburn data collection was not possible at the Section 33 site.

Statistical Analyses

Fire Effects on Composition

Non-metric Multidimensional Scaling (NMS) and Multiple Response Permutation Procedure (MRPP) analyses were performed to determine how treatments differed in their effects on species composition, using PC-ORD 6 software (McCune and Mefford 2006). NMS gives a visual representation of the spatial pattern of the sample rank order from the distance matrix of the samples. It was used to diagnose the degree of similarity in species composition among the three treatments (pre-burn, and spring and summer post-burn). The NMS analysis was run in "slow and thorough" mode using a Sørnenson distance matrix, three axes, and a random starting configuration.

The MRPP analysis was used to test for compositional differences in the effect size among the seasonal treatments. MRPP determines if species samples within a group are more similar to each other than they would be if they belonged to a different group. This is reflected in the p-value derived from the test statistic T. Exactly how similar the samples are within a group is indicated by the effect size variable A, which increases with increasing similarity of the samples (Peck 2010). As A increases, the groups in the comparison become increasingly discrete (i.e., different from each other). Values for A less than 0.1 are common in ecological data (McCune and Grace 2002). A value of 1 indicates that within group, samples are identical. A Sørnenson distance matrix was used in the analysis.

Two-way Cluster Analysis (cluster analysis) was used to identify species and plot groups (clusters). The clusters were then classified based on similarities in species attributes or plot treatments. All treatments and time periods were included in the analysis. A Sørenson distance matrix and the flexible beta linkage method (β = -0.25) were used with PC-ORD 6 software (McCune and Mefford 2006).

Indicator Species Analysis (ISA) was used to determine indicator species for each treatment (PC-ORD 6) (McCune and Mefford 2006). All treatments and time periods were used in the analysis, with treatment as the grouping variable. The ISA analysis calculates an indicator value (IV) for each species, which is the product of the species' frequency (f) and relative frequency (RF) multiplied by 100. A value of 100 indicates that the species is present at all plots for one treatment but is not present in any others. A Monte Carlo test was performed using 4999 iterations of randomized data to test whether the observed indicator value was greater than expected by chance (Peck 2010). Species with significant indicator values are considered indicators for that treatment ($p < 0.05$) (Appendix). The frequency of each species (f) was calculated per treatment as the total number of occurrences of a species within a treatment divided by the number of plots in the treatment. Relative frequency (RF) was calculated as the frequency of a species (f) divided by the sum of frequencies for that species across all treatments (g) (Equation 1) (Dufrêne and Legendre 1997; McCune and Grace 2002). Dufrêne and Legendre (1997) suggest a slightly different equation for P/A data sets, which does not, however, account for the unequal sample sizes seen among our groups, as equation 1 does. Equation 1 moderates the differences in the indicator values between the groups. For example, *Maianthemum canadense* (Desf.) (Canada mayflower) is found on all plots in all treatment groups. Using Dufrêne and Legendre's equation for P/A data, the species has indicator values of 44 and 16 for the spring and pre-burn treatments, respectively. Using Equation 1, all three treatments have a value of 33.3, as one would expect.

Equation 1: $RF = \frac{f}{\sum_{i=1}^{g} f}$

Temporal Changes in Diversity after Fire

NMS and MRPP analyses were also used to identify temporal changes in composition. With the overlay of successional and temporal trajectories, NMS assisted in visualizing direction and degree of "movement," or change, in the plant communities through time (Figure 2a, b). An MRPP analysis was performed using "years since treatment" and "treatment type" for the grouping variables. For instance, one group consisting of all spring, year 1, post-burn samples was compared to another containing all spring year 2 samples. The pre-burn group was not subdivided by year since there was only one pre-burn measurement per plot. The analyses were performed in the same manner as described earlier.

Analysis of variance (ANOVA) was used with a Tukey's B significance test to check for differences in species vital attributes and diversity indices. Mean species cover and richness were calculated for each tolerance and reproductive attribute and compared among the eight treatment by year classes (SPSS 2003). Separate analyses were performed on P/A and cover data. Species evenness (E), Shannon's Diversity (H), and Simpson's Diversity (D) were calculated using the cover data, while the full P/A data set of 146 species was used to calculate Richness (S).

RESULTS

A total of 146 species were found among all the sampling plots across time (partial list in Appendix). Separated by lifeform, there were 6 lichens, 12 mosses/liverworts, 9 ferns and allies, 15 graminoides, 69 forbs, and 35 woody plants. Forty percent were dispersers, 50% were vegetative, and 10% persist in the seed bank. Forty-three percent were intolerant, 42% were tolerant, and 15% were species with requirements.

Fuel Conditions and Fire Severity

The DMC and DC fire indices ranged from low to moderate for spring treatments and from high to extreme from summer (Table 1). This corresponded well with the results of the gravimetric duff moisture sampling averaging 85% for the spring treatments and 26% for the summer (Table 1). Spring fires had an average fire severity rating of 1.3 or "Scorched," while the average for summer fires was 2 or "lightly burned." There was considerable variation in the severity of the summer fires, likely related to differences in relative humidity and wind speed on the days of the fires. The Tar Point summer fire was only assessed as scorched, while the Section 33 fire was of moderate to high severity. Mineral soil exposure ranged from 0% to 17% for the spring fires, 13% to 45% for the summer fires (Table 1), and was effectively zero in the pre-burn condition with mineral soil being found at only two of the 250 sample points.

Fire Effects on Composition

The NMS produced a final ordination with three axes (stress = 16.43), explaining 78% of the total variation, with the individual axes, in numerical order, explaining 13%, 38%, and 27% of the variation. Summer treatments were spatially separated in all views by composition in ordination space, while the pre-burn and spring treatments showed some overlap (Figure 2a, b).

The MRPP results for P/A data indicate that there are compositional differences among all three burn seasons ($A = 0.13$, $p < 0.001$). Pairwise comparisons indicate significant differences between summer treatments, and both the spring and pre-burn treatments. The comparison between pre-burn and spring treatments, though statistically significant ($p = 0.002$), reflected only minor differences in species composition as indicated by the low value of A (0.04).

The discreteness of the summer treatment group and the relative mixing of the spring and pre-burn plots were confirmed in the cluster analysis. Plots on the plot dendrogram were separated into three sets; the first consists almost entirely of summer treatments; the second a mixture of summer, spring, and pre-burn; and the third contains all plot 48 samples and one from plot 26. Given the repeated sampling method used, individual plots tended to cluster together as one drilled down through the dendrogram.

Four broad species compositional clusters were identified in the cluster analysis. The broad groupings include: species common to summer treatments (clusters 1 and 2), species common to pre-burn treatments (3) and species common to all treatments (4). Species are tabled in the Appendix using the four species divisions identified here. Cluster 1 is split between tolerant and intolerant species with most reproducing vegetatively (Figure 3a, b). Cluster 2 contains mainly intolerant species of seedbank or dispersed propagule origin. Species clusters 1 and 2 contain a unique set of 37 species that most frequently occurred in the summer treatment and often were absent from the other two treatments (Appendix). Within these two clusters, the summer treatment had 22 significant indicator species, 11 exclusive species, and 24 that were not found at all in the pre-burn treatment. Sixty-seven percent of all seed-banking species and 46% of all intolerant species were significant indicators of the summer treatment. Three species, *Fragaria vesca* (L.) (woodland strawberry), *Galium boreale* (L.) (northern bedstraw), and *Galium triflorum* (Michx.) (fragrant bedstraw), were more frequent in the pre-burn condition and appear to be miscategorized, while *Symphyotrichum* spp. (*S. ciliolatum* (Lindl.) Á. Löve & D. Löve (Lindley's aster), *S. puniceum* (L.) Á. Löve & D. Löve (purplestem aster), and *S. lateriflorum* (L.) Á. Löve & D. Löve (calico aster)), placed in Cluster

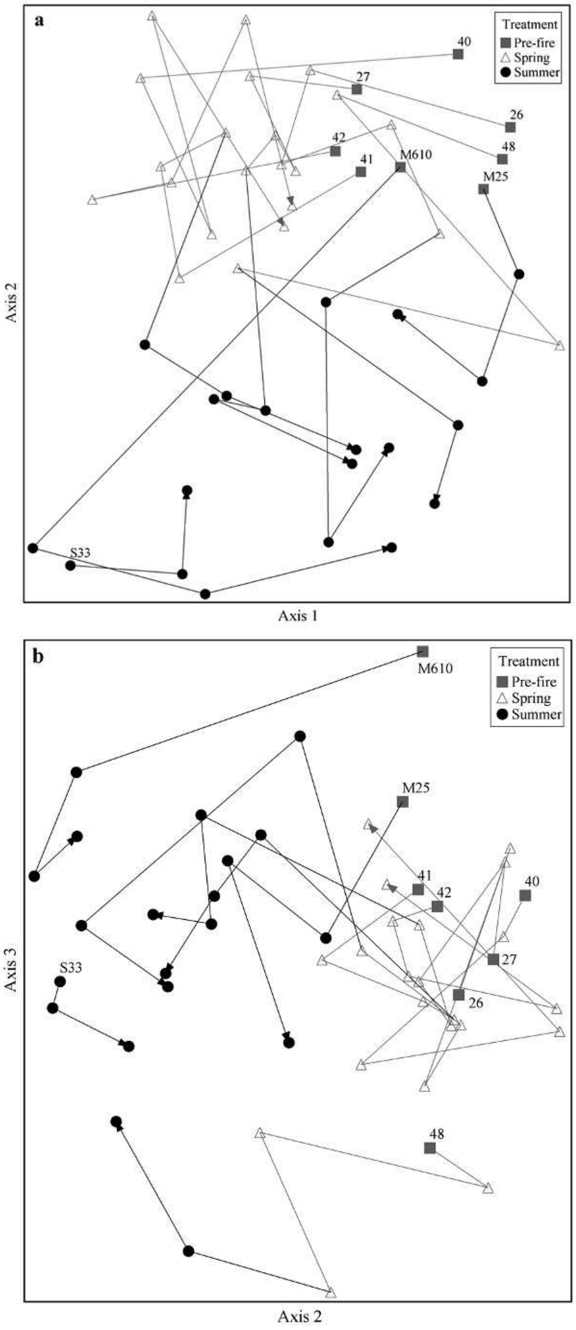

Figure 2. NMS analysis showing two axes combinations (a, b) at Voyageurs National Park (1997–2009). Successional trajectories connect the individual plot samples through time. Each trajectory starts with the pre-burn and ends with the five- or ten-year post-burn sample. The samples taken at Section 33 (S33) start with the first year post-burn as no pre-burn samples were taken.

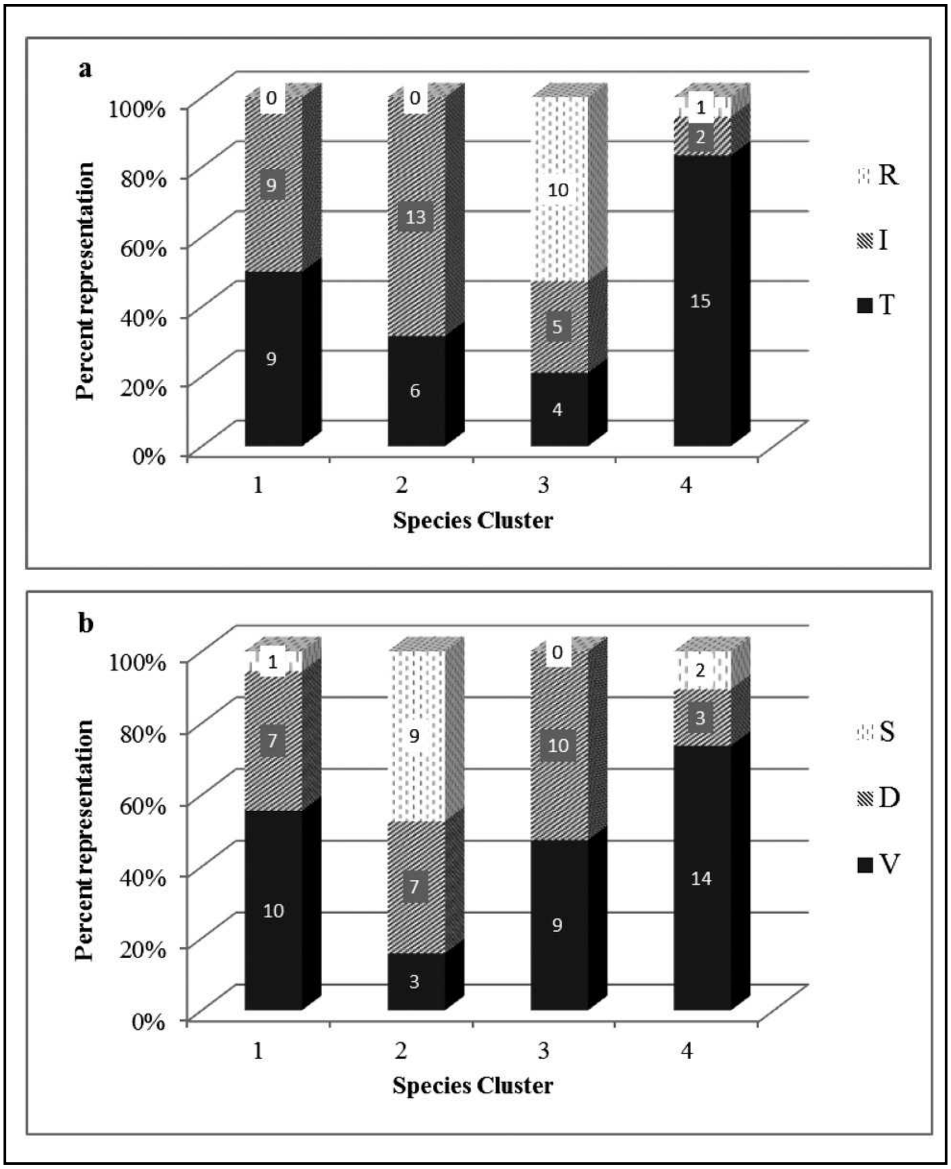

Figure 3. Summary of species tolerances (a) and reproductive strategies (b) for species clusters found in Appendix at Voyageurs National Park (1997–2009). Tolerance codes are: R = species with requirements, I = intolerant, and T = tolerant. Reproductive strategy codes are: S = seedbank, D = dispersal, and V = vegetative resprouting.

3, were identified as indicator species for the summer group, also appear to be miscategorized. Cluster 3 is dominated by species with requirements (Figure 3a) and contains three indicator species of the pre-burn treatment; *Pleurozium schreberi* (Brid.) Mitt. (Schreber's big red stem moss), *Linnaea borealis (*L.) (twinflower), and *Chimaphila umbellata* (L.) W.P.C. Barton (pipsissewa), and three for the summer set, *Symphyotrichum* spp. Several other species of lichens and mosses were common to the pre-burn treatment but not indicators of it, since they were also well represented in the other treatments. Species in Cluster 3 are relatively infrequent among all treatments. The cluster contains many species that are either fire sensitive or take a long period of time to reestablish following fire. Cluster 4 is distinguished by tolerant species of vegetative origin (Figure 3a, b). These species are very common to all treatments (average frequency = 78%) with minimal differences in the species frequency among the treatments. Cluster 4 contains a "core" group of at least 15 generalist species and a secondary group of five species that were encountered less frequently, but equally distributed among the treatments. Of the species found in Cluster 4, 75% are classified as tolerant or generalists. Two species were identified as significant indicator species for a particular treatment; however, given their high frequencies in the other groups, this does not appear to be biologically significant. To help visualize these compositional differences, the composition of each treatment was condensed using the most frequently occurring species (Figure 4).

Temporal Changes in Species Diversity after Fire

Temporal trajectories (pre-burn, 1, 2, 5, 10 years) overlaid on the NMS graph reveal successional patterns of change among the plots (Figure 2a, b). All spring treatment plots follow similar patterns of directional shift following the fire treatment. All trajectories shift strongly left after the initial summer fire treatment (Figure 2a, b). The overall magnitude of this shift is far greater than is seen following the spring fires. Trends for plots in units that were burned twice (plots 26, 27, 41, 48) were similar to those that were burned once. Plot 48 was spatially separated from all others because it lacks certain common species, but temporal trends are similar.

The MRPP analysis comparing the treatments by year group showed that all summer samples were significantly different from the pre-burn and spring treatments ($p \leq 0.003$). Within the summer treatment group, only years 1 and 5 were significantly different ($p \leq 0.001$). All spring samples were significantly different from the pre-burn condition ($p < 0.05$). Within the spring treatment, the only significant differences were the comparisons of year 10 with years 2 and 5 ($p < 0.05$).

The temporal shifts in the frequency of select species were most evident in the summer treatment (Figure 5). *Marchantia polymorpha* (L.) (common liverwort), *Geranium bicknellii (*Britton) (Bicknell's cranesbill), *Symphyotrichum* spp., and *Corydalis sempervirens* (L.) Pers. (rock harlequin) dominated the sites the first year post-burn, but declined greatly by

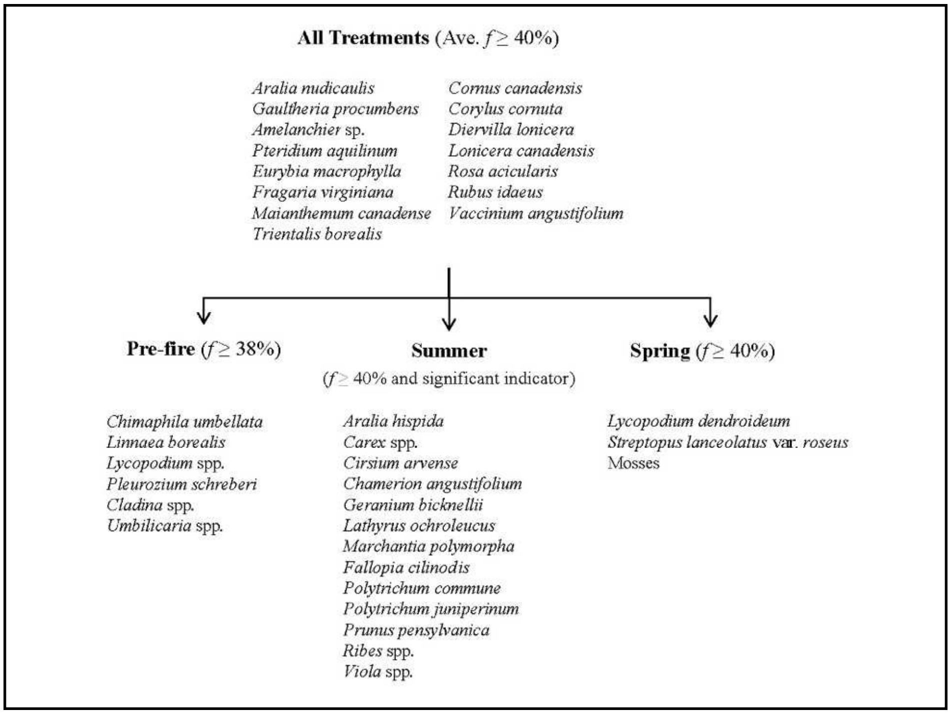

Figure 4. Primary species composition by treatment at Voyageurs National Park (1997–2009). Selected species have within treatment frequencies of ~40% or more. Summer treatment species were restricted to significant indicators. Species common to all treatments are grouped separately.

year 5. They were quickly displaced by species such as *Fallopia cilinodis* (Michx.) Hulob (fringed black bindweed), *Chamerion angustifolium* (L.) Holub (fireweed), *Rubus idaeus* (L.) (common red raspberry) and *Polytrichum* spp. (Hedw.) (hair cap mosses), many of which were already abundant in year 1. Some species took several years to proliferate and were not particularly frequent until year 5 (i.e., ferns, *Pleurozium schreberi, Lathyrus venosus* (Muhl. ex Willd.) (veiny pea), and *Carex pensylvanica* (Lam.) (penn sedge)). Of note, years 2 and 5 were not found to be significantly different in the MRPP analysis and this is well reflected by most species in Figure 5. Species such as *Eurybia macrophylla* (L.) Cass. (bigleaf aster), *Cornus canadensis* (L.) (Canadian bunchberry), and *Maianthemum canadense* did not show dramatic patterns of decline or expansion, but were abundant throughout the 5 year post-burn period. No substantial patterns of species replacement were seen following spring treatments (data not shown).

Reflecting the above shifts in species composition, reproductive and tolerance attributes showed partiality to certain treatment/time groups. Summer years 2 and 5 had significantly greater numbers of seed banking species as compared to the pre-burn and spring treatments (Figure 6a). Similarly, summer year 5 had a significantly greater number of dispersers than the pre-burn and spring treatments. Intolerant species had their highest richness after the summer burns as compared to the spring burns (Figure 6b). Species with requirements had their highest richness in the pre-burn, spring year 10, and summer year 5 treatments. Richness of tolerant species was greatest in summer year 5, which was significantly higher than the pre-burn and spring treatments. Total species richness (S) in summer year 5 was nearly twice that of the pre-burn and spring years 1 through 10 treatments (Figure 7a).

Total ground layer cover was significantly greater for summer years 2 and 5, and spring year 10, as compared to spring year 1 (Figure 7a). Seed banking species had the highest cover during summer year 1, a value significantly greater than all pre-burn and spring samples (Figure 7b). Cover of dispersing species was significantly greater for summer year 5 compared to spring years 1 and 5. Cover of intolerants was significantly greater in summer years 1, 2, and 5 than pre-burn and spring years 1 and 2 (Figure 7c). Except for spring year 10, cover of species with requirements was significantly greater in pre-burn than all other treatment year classes. There were no significant differences in mean cover for vegetative and tolerant species. Evenness (E) showed no significant differences among the treatment year classes. Shannon diversity was significantly greater in summer year 5, as compared to spring years 1 and 5 (Figure 7d). Simpson's diversity was significantly greater for summer years 2 and 5 as compared to spring year 1.

DISCUSSION

Fire Effects on Composition

All analyses showed a clear difference between the summer, and the pre-burn and spring treatments. Summer treatments resulted in a unique suite of species dominated by pioneer, or intolerant, species originating from seedbanks or highly dispersed propagules. The pre-burn treatments were characterized by species with requirements, which are more common in stands that are older and have not experienced fire for some time. Since none of the stands in the study had burned since 1936, there was ample time for such species to establish. Spring treatments resulted in species assemblages that were relatively similar to the pre-burn treatments, with a noted reduction in species with requirements and the addition of a few very infrequent pioneer species.

There were many species common to all treatments whose frequencies were not greatly changed by either seasonal fire treatment. These species, consisting of ~15 generalist species identified in Cluster 4, serve as foundational species in the red and white pine community types of our study. Algren (1960) concluded that many of these species, such as *Eurybia macrophylla*, *Maianthemum canadense,* and *Cornus canadensis*, have very high heat tolerances, allowing them to be rather ubiquitous, even in the presence of fire. Though common, the presence of these species should not be overlooked, for these species likely give stability to the community and provide unknown ecosystem services.

Differences in the frequencies of seedbank and high seed dispersal species found between the seasonal treatments were likely due to differences in seedbed

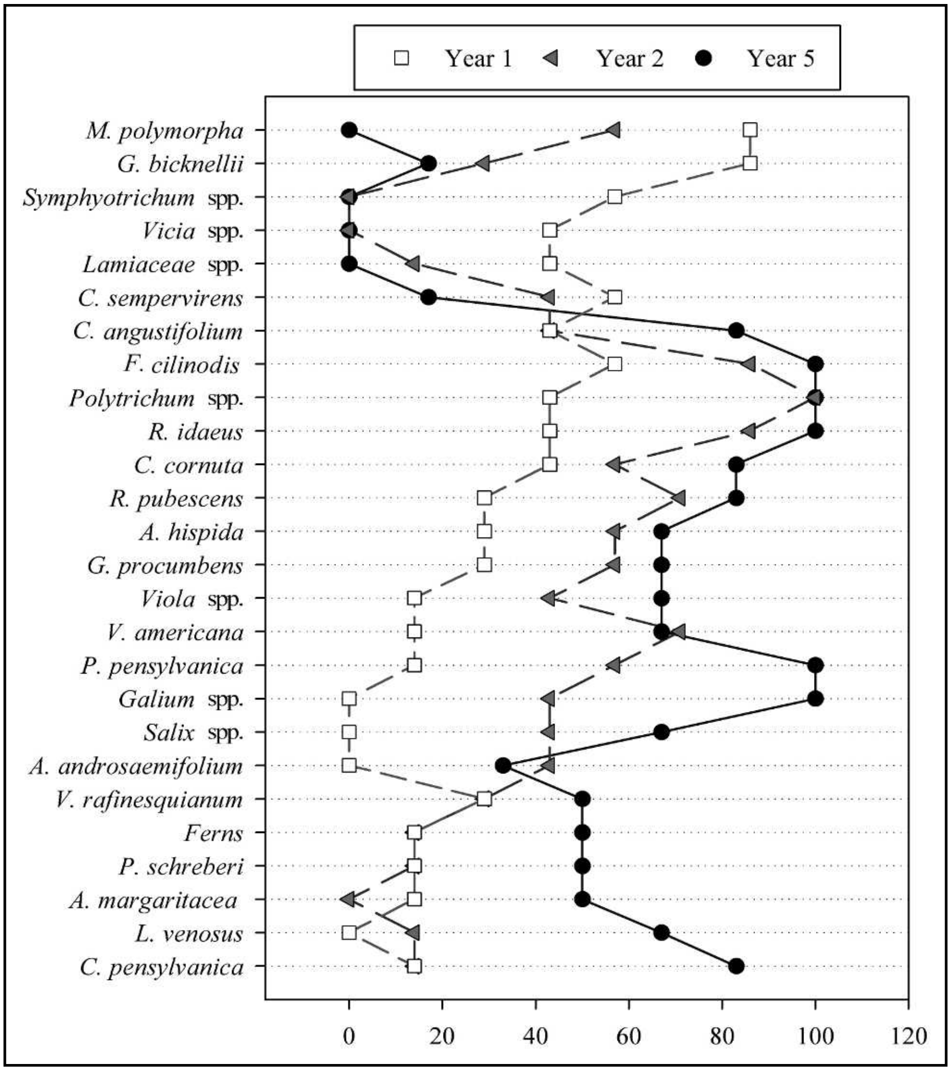

Figure 5. Frequencies of the 26 most recurrent species found in the summer treatment group for 1, 2, and 5 years since fire at Voyageurs National Park (1997–2009). Species that were most frequent in year 1 appear at the top, relatively frequent in all years in the center, and mainly frequent in years 2 or 5 toward the bottom.

preparation and seed heat scarification. This is a consequence of differences in the depth of burn and soil heat penetration between the two seasonal treatments (Ahlgren 1960; Ohmann and Grigal 1981; Abrams and Dickmann 1984; Keeley and Fotheringham 2000; Miller 2000; Knapp et al. 2009). The fuel moisture of larger surface fuels and duff varies widely, but tends to be relatively high during the spring in Northern Minnesota, since fuels have not had time to dry from the recent snow melt (Alban 1977; Heinselman 1996). High fuel moistures inhibit duff consumption and soil heat penetration (DeBano et al. 1998; Busse et al. 2006), and prevent seedbed preparation and heat scarification of seedbank species (Miller 2000; Knapp et al. 2009). In contrast, the duff moisture content during summer fires tends to be fairly low (Alban 1977) and soil temperatures are near their maximum, leading to greater duff consumption (Van Wagner 1963; Weyenberg, unpubl. data) and soil heat penetration. Ohmann and Gigal (1981) found that differences in revegetation between the spring and summer fires can be explained by differences in forest floor removal. Indeed, our summer fires resulted in greater mineral soil exposure than the spring fires, certainly due to the differences in soil and duff moistures between the two seasons. Species, such as *F. cilinodis* and *Geranium bicknellii*, which require mineral soil exposure and/or heat scarification for germination, were invariably favored (Ahlgren 1960; Abrams and Dickmann 1984; Granström and Schimmel 1993).

Bryophyte frequencies varied by treatment and time depending on their site requirements. The liverwort *Marchantia polymorpha* was very abundant following summer treatments, especially on the severely burned areas. It was later supplanted by mosses. Both species are common pioneers to newly burned sites where the organic layer is consumed and competition is minimal (Ahlgren 1974; Heinselman 1981a; Glime 1993). Mosses such as *Pleurozium schreberi* and *Dicranum* spp. (Hedw.) can take several decades to re-establish following disturbance (Uggla 1959; Heinselman 1981a), and were, therefore, uncommon in the summer treatment but found more frequently in the pre-burn condition.

Our findings coincide well with the findings of other authors. Ahlgren (1960) found similar groupings of species when examining post-burn reproduction in northeastern Minnesota in similar plant communities. A large abundance of pioneer species was reported by Ohmann and Grigal (1981) on the summer treatment as compared to the spring, and the sprouting of low shrubs and herbs was found to be more vigorous, in general, following the spring treatment. Similar to Wang and Kemball (2005), who compared the understory response from a May wildfire with varying severity, we found dispersers (invaders) to be more frequent on the higher severity (summer) treatments. In contrast, however, we found the seedbank and vegetative species to have a greater affinity toward the higher severity treatments, and found greater species richness in those areas as well. The differences between our findings may be due to differences in season of burn, degree of severity, and/or ecosystem type.

Temporal Changes in Diversity after Fire

Within the summer treatment group, there was a clear pattern of species dominance and replacement through time. Pioneer species, such as *Geranium bicknellii* and *Marchantia polymorpha*, were especially frequent immediately following the disturbance. These species quickly declined by year 2 and were replaced by others that

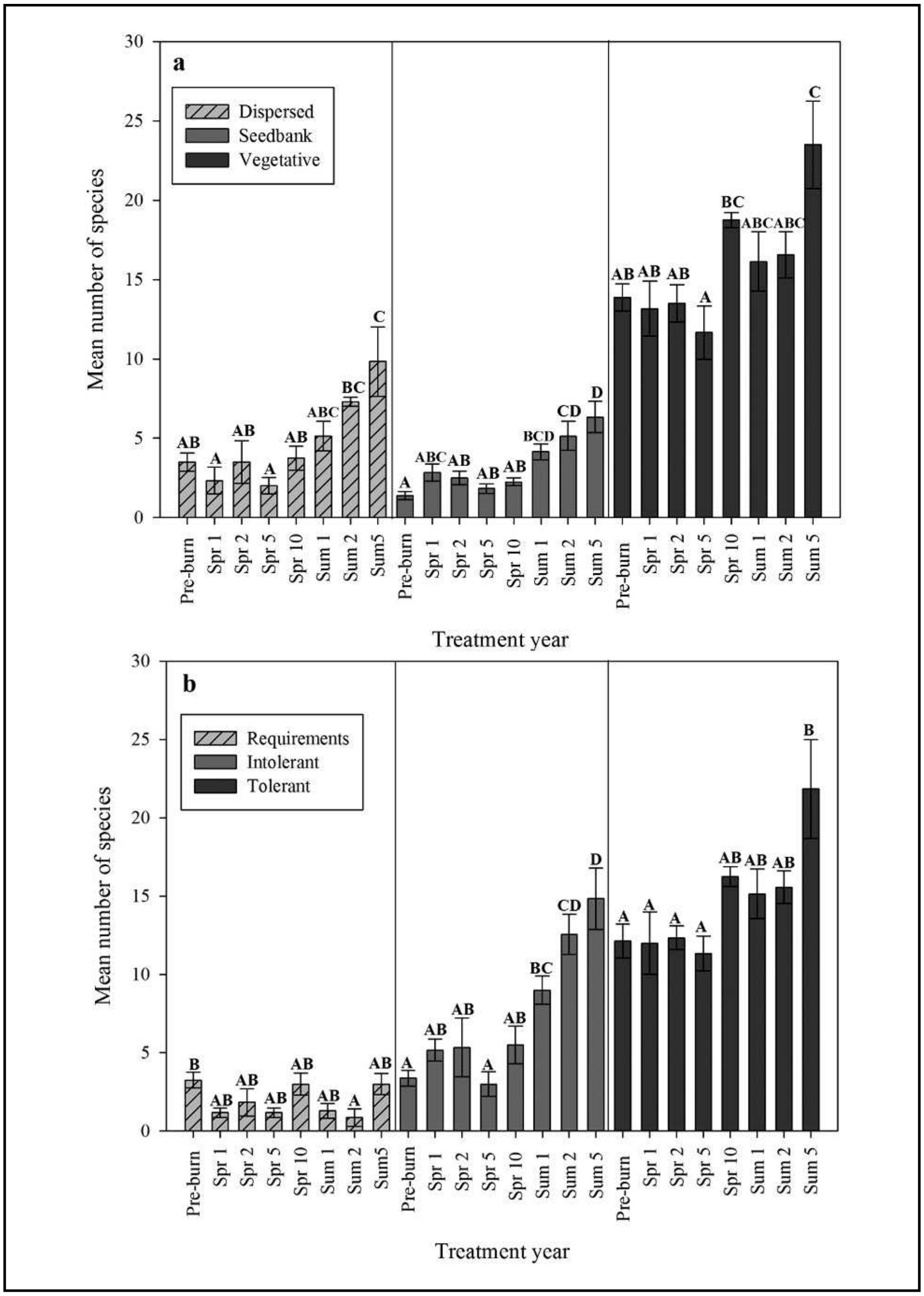

Figure 6. Species richness for each reproductive (a) and tolerance (b) attribute by treatment year at Voyageurs National Park (1997–2009). P/A data from all treatments was used in all calculations. Tukey's B significance test was used to compare treatment years per attribute.

take slightly longer to establish or reach the site. In turn, many of these species will be shaded out by the tree canopy and replaced by the generalist species of Cluster 4, most of which were already dominant by year 5. Ahlgren (1974) found similar patterns of species replacement in the post-burn recovery of jack pine-black spruce stands in northeastern Minnesota.

Changes in species diversity can be traced back to the individual species tolerance traits and reproductive attributes, and their interaction with fire severity. These changes were most dramatic following the summer fire treatments, which were more severe. Seedbankers and dispersers were highly abundant immediately after fire. Though the number of these species was initially relatively low, they increased dramatically by year 5, an increase that was coincident with that of resprouters and tolerants from years 2 to 5. This marks a transition period where both tolerant and intolerant species are present simultaneously, leading to a significant peak in species richness at year 5. We expect diversity to decrease as the tolerant species become increasingly dominant and the intolerant species slowly die off.

Diversity following the spring treatments remained relatively constant, except for a mild increase in year 10, which can be attributed to an increase in species with requirements. This is in contrast to Cook et al. (2008), who found increases in herbaceous layer diversity following a low intensity spring prescribed fire in a Wisconsin white pine forest. Although the changes in diversity following our spring treatments were not significant, there were additions of pioneer species seen following the treatment. There were, in fact, nine species found in the spring treatment that did not occur in the pre-burn treatment. The species were all components of species Clusters 1 and 2, which were indicative of the burned treatments. The frequencies of these species in the spring treatment were all less than 20%, indicating only a mild facilitation of these species as compared to the summer treatment. This further suggests that severity of the spring treatments was minimal and insufficient to bring about substantial change to the plant community. It follows that repeated spring treatments, though useful for added reduction of woody fuels and small diameter woody species, will likely only result in changes to understory species abundance, but not in species composition (Methven 1973). Using duff consumption as a surrogate for fire severity, the severity required for an appreciable change in species composition might only be obtained when the duff moisture content is below 40% (Van Wagner 1963). Only below this threshold can appreciable duff consumption be achieved – a necessary precursor to the germination and establishment of many pioneer species.

CONCLUSION

The main changes that can be attributed to

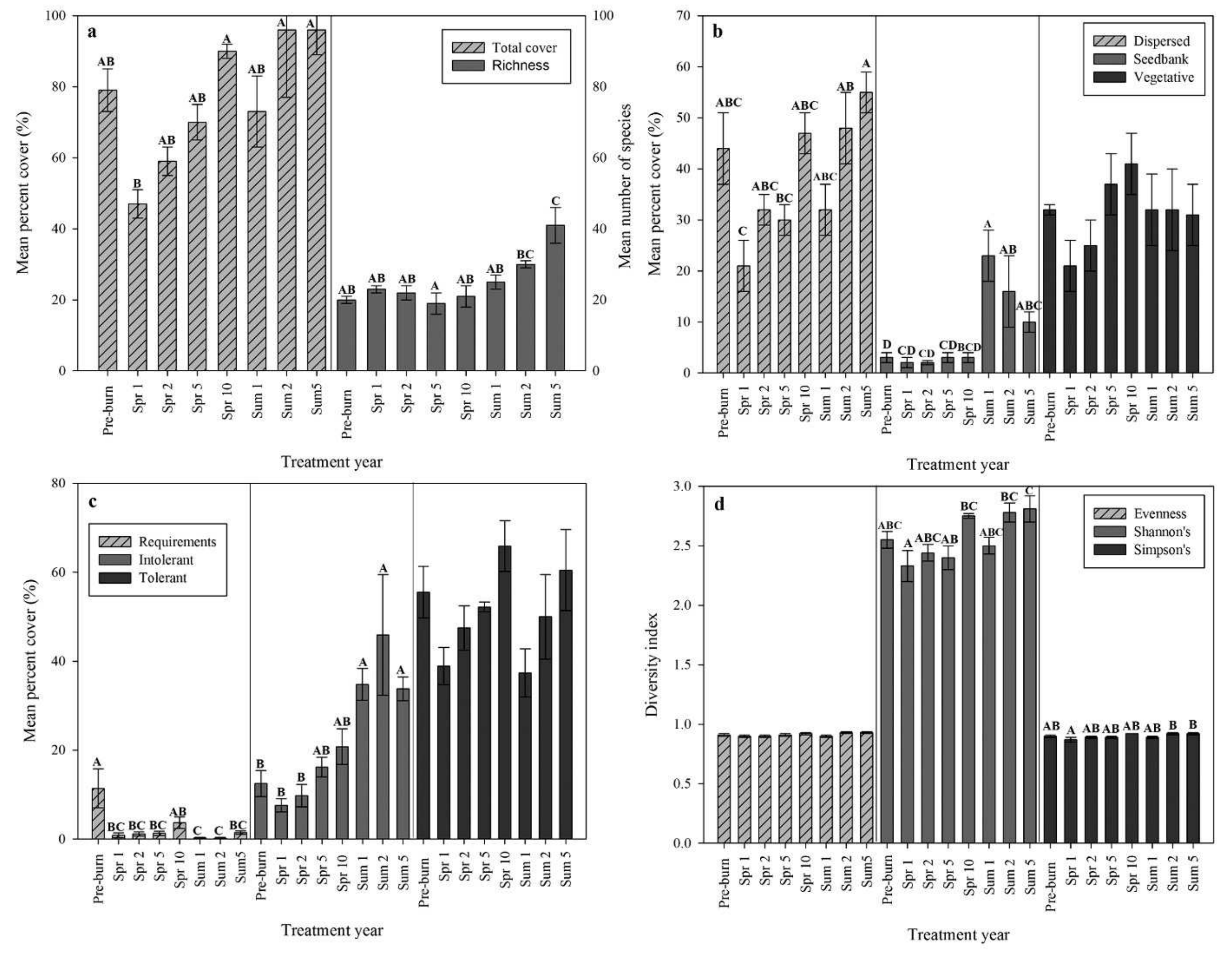

Figure 7. Temporal trends of mean percent cover for total cover and richness (a), reproductive attributes (b) and tolerance (c), and diversity indices (d) at Voyageurs National Park (1997-2009). Species richness was calculated using the P/A dataset; all other comparisons use the cover dataset. Tukey's B was used for significance tests. Graphs without significance labels were not significant.

summer burn treatments include a dramatic reduction in the frequency of species associated with older, unburned stands, and the addition of numerous pioneer species, which dominate the site for the first five years post-burn. This treatment was, by far, the most species-diverse. Spring fires, in contrast, contained species that were often found in one, or both, of the other treatments and, therefore, essentially no species serve as indicators of this treatment. Though the spring treatment was found statistically different from the other two (MRPP analysis), significant biological changes were not evident. The types of compositional changes seen after a spring fire are similar to that of a summer fire (i.e., the reduction of species with requirements and the addition of pioneer species), but are orders of magnitude less, with any changes being very short-lived. In general, pioneer species are lacking in the spring treatment, resulting in very little change in species composition from the pre-burn condition.

The substantial increase in diversity alone makes summer treatments a desirable consideration for red and white pine forest restoration projects. In addition, summer treatments fulfill stand maintenance requirements by controlling invading hardwoods and underbrush (Buckman 1964), and maintaining a receptive seedbed for pine regeneration, making them vital for stand persistence on many sites.

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Appendix. Within treatment frequency for each species at Voyageurs National Park (1997–2009). Species clusters are defined based on the two-way cluster analysis. Where species were combined into one genus, multiple species are listed to document the included species. Reproductive attributes include: S = seedbank, D = dispersal, and V = vegetative. Tolerance attributes include: T = tolerant, I = intolerant, and R = species with requirements. The most dominate traits are listed first. Where multiple species are listed, each species' traits are indicated with a superscript. If a species is a statistically significant indicator for the group listed, it is identified as follows: * = significant ($p < 0.05$), or ** = highly significant ($p < 0.01$.) Treatment groups are listed with the sample number in parentheses. Bold font indicates the maximum value.

Species clusters	Attributes	Scientific name	Common name	Significant indicator	Frequency		
					Pre-burn (8)	**Spring (22)**	**Summer (20)**
1	S, I	*Prunus pensylvanica* (L.f.)	Pin cherry	Summer**	13	9	**55**
1	D, S, I	*Vicia americana* Muhl. ex Willd.	American vetch		25	18	**50**
1	D, S, T/I	*Viola* spp. (L.)	Violet species	Summer**	0	0	**40**
1	V, T	*Carex pensylvanica* (Lam.)	Penn sedge	Summer*	0	0	**35**
1	D, T	*Galium asprellum* (Michx.)	Rough bedstraw	Summer*	0	5	**35**
1	V, D, I	*Salix* spp. (L.)	Willow species		13	14	**35**
1	V, T	*Viburnum rafinesquianum* (Schultes)	Downy arrow-wood		13	32	**35**
1	V, D, I	*Apocynum androsaemifolium* (L.)	Spreading dogbane		0	5	**25**
1	V, T	*Athyrium filix-femina* ^{V,T} (L.) Roth *Dryopteris carthusiana* ^{V,T} (Vill.) H.P. Fuchs *Gymnocarpium dryopteris* ^{V,T} (L.) Newman	Fern species	Summer*	0	0	**25**
1	V, T	*Cornus rugosa* (Lam.)	Round leaf dogwood		13	18	**25**
1	D, V, I	*Lathyrus venosus* Muhl. ex Willd.	Veiny pea		0	5	**25**
1	D, I	*Melampyrum lineare* (Desr.)	Narrowleaf cowwheat		13	5	**25**
1	D, I	*Anaphalis margaritacea* (L.) Benth.	Pearly everlasting	Summer *	0	0	**20**
1	V, T	*Fragaria vesca* (L.)	Woodland strawberry		**25**	14	15
1	V, D, I	*Galium boreale* ^{V,I} (L.) *G. triflorum* ^{D,I} (Michx.)	Bedstraw		**25**	9	10
2	S, I	*Fallopia cilinodis* (Michx.) Holub	Fringed black bindweed	Summer**	0	9	**80**
2	D, V, I	*Polytrichum commune* ^{D,I} (Hedw.) *P. juniperinum* ^{D,I} (Hedw.)	Hair cap mosses	Summer**	25	5	**80**
2	D, S, I	*Cirsium arvense* (L.) Scop.	Canada thistle	Summer**	0	0	**75**
2	V, S, T/I	*Carex houghtoniana* ^{S,I} Torey ex Dewey *C. intumescens* ^{V,T} (Rudge) *C. pellita* ^{V,I} Muhl. ex Willd.	Sedges	Summer**	0	5	**70**

Continued

Appendix. (Continued)

Species clusters	Attributes	Scientific name	Common name	Significant indicator	Frequency Pre-burn (8)	Frequency Spring (22)	Frequency Summer (20)
2	S, T	*Ribes glanulosum*^{S,T} (Grauer) *R. hirtellum*^{S,T} (Michx.) *R. lacustre*^{S,T} (Pers.) Poir.	Currants	Summer**	0	14	**60**
2	S, V, T	*Rubus pubescens* (Raf.)	Dwarf red raspberry	Summer*	38	18	**60**
2	D, V, I	*Chamerion angustifolium* (L.) Holub	Fireweed	Summer**	0	0	**55**
2	V, S, T	*Anemone quinquefolia* (L.)	Wood anemone		13	18	**50**
2	S, V, I	*Aralia hispida* (Vent.)	Bristly sarsaparilla	Summer**	0	0	**50**
2	D, V, I	*Lathyrus ochroleucus* (Hook.)	Cream peavine	Summer*	0	18	**45**
2	S, I	*Corydalis sempervirens* (L.) Pers.	Rock harlequin		0	14	**40**
2	D, I	*Marchantia polymorpha* (L.)	Common liverwort	Summer**	0	0	**50**
2	S, I	*Geranium bicknellii* (Britton)	Bicknell's cranesbill	Summer*	0	18	**45**
2	D, I	*Lamiaceae* spp. (L.)	Mint	Summer*	0	0	**20**
3	D, R	*Pleurozium schreberi* (Brid.) Mitt.	Schreber's big red stem moss	Pre-burn**	**100**	18	25
3	V, D, R	*Linnaea borealis* (L.)	Twinflower	Pre-burn*	**88**	36	45
3	V, T	*Chimaphila umbellate* (L.) W.P.C. Barton	Pipsissewa	Pre-burn**	**63**	9	10
3	V, R	*Cladonia cristatella*^{V,R} (Tuck) *Cladina stellaris*^{V,R} (Opiz) Brodo *Cladina mitis*^{V,R} (Sandst) Hustich *Cladina rangiferina*^{V,R} (L.) Nyl. *Umbilicaria*^{V,R} spp. (Hoffm.)	Lichens		**38**	14	10
3	D, T	*Lycopodium annotinum*^{D,T} (L.) *L. clavatum*^{D,T} (L.) *L. complanatum*^{D,T} (L.)	Clubmosses		**38**	5	15
3	V, I	*Vaccinium myrtilloides* (Michx.)	Velvetleaf blueberry		25	**45**	20
3	D, R	*Dicranum* spp. (Hedw.)	Dicranum mosses		13	**14**	0
3	D, R	*Juniperus communis* (L.)	Common juniper		13	0	**15**
3	V, R	*Polypodium virginianum* (L.)	Rock polypody		13	5	**20**
3	D, I	*Vicia spp.* (L.)	Vetch		13	0	**15**
3	D, I	*Symphyotrichum ciliolatum*^{D,I} (Lindl.) *Á. Löve & D. Löve* *S. puniceum*^{D,I} (L.) Á. Löve & D. Löve *S. lateriflorum*^{D,I} (L.) Á. Löve & D. Löve	Aster	Summer*	0	0	**20**

Continued

Appendix. (Continued)

Species clusters	Attributes	Scientific name	Common name	Significant indicator	Frequency		
					Pre-burn (8)	**Spring (22)**	**Summer (20)**
4	D, R	Numerous genera	Moss		25	**55**	20
4	V, T	*Streptopus lanceolatus* var. *roseus*	Rose twisted stalk		13	**50**	35
4	D, T	*Lycopodium dendroideum* (Michx.)	Tree groundpine		13	**41**	30
4	V, D, T	*Trientalis borealis* (Raf.)	Starflower		38	41	**55**
4	V, T	*Clintonia borealis* (Aiton) Raf.	Bluebead lily		**38**	32	20
4	V, T	*Corylus cornuta* (Marshall)	Beaked hazel	Spring*	75	**100**	60
4	D, T	*Eurybia macrophylla* (L.) Cass.	Largeleaved aster		88	**100**	95
4	V, T	*Maianthemum canadense* (Desf.)	Canada mayflower		100	100	100
4	D, V, T/I	Numerous genera	Grass		100	100	100
4	V, T	*Aralia nudicaulis* (L.)	Wild sarsaparilla		88	**95**	**95**
4	V, I	*Vaccinium angustifolium* (Aiton)	Lowbush blueberry		**100**	91	95
4	V, T	*Pteridium aquilinum* (L.) Kuhn	Bracken fern		75	**82**	75
4	S, T	*Gaultheria procumbens* (L.)	Eastern wintergreen		75	**77**	50
4	S, V, I	*Rubus idaeus* (L.)	Common red raspberry		38	**77**	75
4	V, T	*Cornus canadensis* (L.)	Canadian bunchberry		63	73	**75**
4	V, S, T	*Amelanchier* spp. (Medik.)	Serviceberry		63	**68**	65
4	V, I	*Rosa acicularis* (Lindl.)	Prickly rose		50	68	**75**
4	V, T	*Fragaria virginiana* (Duchesne)	Virginia strawberry		63	**64**	55
4	V, T	*Lonicera canadensis* W. Bartram ex Marshall	American fly honeysuckle		88	59	65
4	V, T	*Diervilla lonicera* (Mill.)	Northern bush honeysuckle	Summer*	63	50	**90**