THE EFFECT OF FIRE SEVERITY ON EARLY DEVELOPMENT OF UNDERSTORY VEGETATION FOLLOWING A STAND REPLACING WILDFIRE

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ABSTRACT

Four boreal mixedwood stands burned by the 1999 Black River wildfire in the southeastern Manitoba were sampled to study the effect of fire severity on the early (1999 to 2002) development of understory vegetation. Three fire severity classes (scorched, lightly burned, and severely burned) were identified on each stand based on the degree of forest floor consumption. Six plots per severity class were randomly selected on each stand. It was found that fire severity significantly affected post-fire vegetation response. Changes in the plant community over time also depended on fire severity. Among the three major life form groups, abundance of woody plants decreased while abundance of moss and liverwort increased with fire severity. Abundance of forbs and grass was highest on lightly burned severity class. As expected, invasive species cover increased while sprouting species cover decreased with fire severity. Coverage of seed banking species was greatest on lightly burned plots. Only in the 1st post-fire year was species richness and diversity reduced by fire severity. The rate of plant community recovery, in reference to mature stands, decreased with fire severity. Nevertheless, most species found in mature stands were currently present on each fire severity class. Unique species, especially those unique to lightly and/or severely burned plots, were not found in mature stands. Within the four post-fire years, rapid changes were observed only during the initial three post-fire years regardless of fire severity. As most differences observed among the three fire severity classes remained significant at the 4th post-fire year, how long it would take for plant communities developed on these fire severity classes to converge is not clear and further monitoring is required.

INTRODUCTION

Fire is one of the dominant ecological forces affecting the pattern and dynamics of boreal forests in North America (Rowe and Scotter 1973, Heinselman 1981, Van Wagner 1983, Rowe 1983, Johnson 1992). Interactions between fire regime and species life history traits are believed to determine post-fire vegetation development (e.g., Noble and Slatyer 1980, Rowe 1983, Halpern 1989). Among the three variables of the fire regime (cycle or frequency, intensity, severity or depth of burn) that affect plant regeneration, fire severity is of the greatest ecological importance (Van Wagner 1983) but subjected to few studies (Whittle et al. 1997a). Although boreal forest fires are typically high-intensity crown fires that kill all aboveground vegetation (Rowe and Scotter 1973, Van Wagner 1978, Heinselman 1981), their impact on the forest floor is extremely variable among or within burned stands (Dyrness and Norum 1983, Zasada et al. 1983, Wang 2002). The degree of duff consumption, measured by weight (kg/m^2), depth (cm) or % removal, is commonly referred to as fire severity (Van Wagner 1972, Albini 1976, Alexander 1982). Because lethal temperatures can only penetrate 2-3 cm below the burn boundary (e.g., Shimmel and Granstrom 1996), the degree of duff consumption serves as a good field indicator of below ground biological impact (Van Wagner 1983). Directly, fire severity determines availability of post-burn *in situ* propagules (buried seeds and spores or regenerating underground parts) through consumption or lethal heating during burning (Moore and Wein 1977, Flinn and Wein 1977, Johnson 1979, Rowe 1983, Johnston and Woodard 1985). Indirectly, fire severity influences the receptivity of post-fire seedbeds by altering physical, chemical, and biological conditions of the regeneration substrate (Dyrness and Norum 1983, Ahlgren and Ahlgren 1960, Christensen and Miller 1975, Thomas and Wein 1985, 1990, Herr and Duchesne 1995). Although the critical importance of fire severity to post-fire vegetation recovery has been commonly recognized (e.g., Rowe 1983, Johnson 1992), few studies have directly linked vegetation recovery to different severities (Johnston and Woodard 1985, Whittle et al. 1997a, Shimmel and Granstrom 1996).

Plant species of boreal forests are well adapted to frequent disturbance (Shafi and Yarranton 1973, Rowe 1983, Whittle et al. 1997b). Post-disturbance success of many boreal species has been largely attributed to their sprouting (Buse and Bell 1992, Arnup et al. 1995) and/or seed banking ability (Halpern 1988, Morgan and Neuenschwander 1988, Whittle et al. 1997b, Qi and Scarratt 1998). This dependence on *in-situ* propagules suggests the critical importance of fire severity. For sprouters, increased heat penetration should eliminate progressively more of the bud bank buried in the soil. For seed bankers, fire may both kill seeds and affect germination of surviving seeds. Severe fire tends to lower total plant coverage (Dyrness 1973, Johnston and Woodard 1985) and species richness (Halpern and Spies 1995) because *in-situ* propagules are either consumed or killed by lethal heating. On the other hand, severe fire also facilitates the colonization of invasive species, which usually disappear quickly (Dyrness 1973, Johnston and Woodard 1985, Halpern 1988, Halpern 1989, Qi and Scarratt 1998), especially on mesic to

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hygric and rich sites (De Grandpre and Bergeron 1997). Therefore, fire severity dictates the early regeneration dynamics and the rate of recovery to the pre-fire community.

The objective of this study was to investigate the effect of fire severity on the early dynamics of understory vegetation recovery on four burned boreal mixedwood stands in southeastern Manitoba. We hypothesize that (1) sprouting species decrease with fire severity while invasive species increase with fire severity, (2) species diversity decrease with fire severity, and (3) the rate of vegetation recovery towards the pre-fire plant community decreases with fire severity. The study was a part of a large research project aimed to understand post-fire regeneration dynamics of boreal mixedwoods in response to fire severity within the 1999 Black River fire. So far, we have described fire severity classes (Wang 2002) and reported density and growth of aspen (*Populus tremuloidies*) suckers in response to fire severity (Wang, in press).

MATERIALS AND METHODS

Study Area

The study was conducted in the Lac Seul Upland ecoregion of the Boreal Shield ecozone (Ecological Stratification Working Group 1995) of southeastern Manitoba, Canada. Four burned mixedwood stands (minimum 5 ha in size) were investigated within the 1999 Black River wildfire (Figure 1). These stands were selected to represent the range of sites that typically support aspen-conifer forests in the area. Before the burn, these stands were co-dominated by *Populus tremuloides* and a mixture of *Abies balsamea*, *Picea glauca*, *Picea mariana*, and/or *Pinus banksiana*. All stands are on flat terrain. Despite variation in texture, soil parent materials are of the same lacustrine origin. Historical fire records indicate that these stands had not been burned during the past 70 or more years. According to the fire status report from Manitoba Conservation Fire Program, the Black River wildfire started on 1 May 1999 and spread over the sampled area within two days. Fire weather conditions during the two days were very similar (Wang 2002). A brief summary of site and pre-disturbance stand composition is given in Table 1.

Study Design

Post-fire examination of the fire severity pattern within the burned boreal mixedwood stands suggested that three classes of fire severity were most appropriate in describing the impact of fire on the forest floor (depth-of-burn). As described by Wang (2002), the three severity classes are: scorched (SC) – litter not burned or partially burned; lightly burned (L) - litter burned but without or with very limited duff consumption; severely burned (S) - forest floor completely consumed, and organic matter in Ah horizon may also be partially consumed. Similar systems were also used to characterize fire severity classes elsewhere (Viereck et al. 1979, Ryan and Noste 1985). Although the exact amount of duff consumption could not be quantified due to lack of pre-fire measurements, the qualitatively defined fire severity classes reflected the degree of burning or heating on buried propogules in the forest floor or top mineral soil.

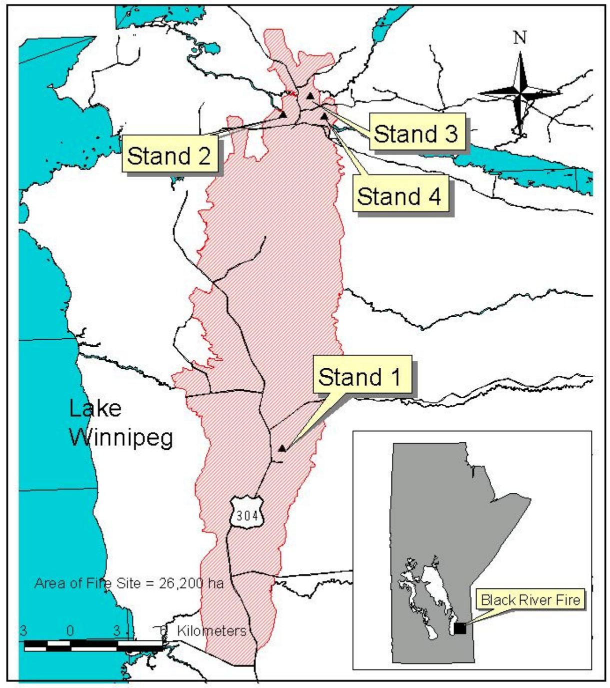

Figure 1. The boundary of the 1999 Black River wildfire and the locations of the four studied stands. Insert shows the location of the study area within province of Manitoba, Canada.

Table 1. A brief summary of pre-fire stand composition and site conditions for the four studied stands (Adopted from Wang, in press).

	1	2	3	4
BA (m^2/ha) [1]	29.2	30.6	34.2	38.2
Aspen	13.2	10.5	15.7	12.6
Conifer	15.8	18.7	18.0	25.3
Relative SMR[2]	5	5	4	4
SNR[3]	R	R	M	M
Soil texture[4]	C	CL	SL	LS

[1]BA = basal area.
[2]SMR = soil moisture regime (5 = hygric; 4 = mesic).
[3]SNR = soil nutrient regime (R = rich, M = medium).
[4]C = clay; CL = clay loam; SL = sandy loam; LS = loamy sand.

In each stand, areas subjected to each fire severity class were identified, flagged and numbered within one week after the burn. Among them, six areas > 3 m in radius were randomly selected for each fire severity class. Within each selected area, a 1-m radius (3.14 m^2) plot was set up with its center marked permanently by a PVC pipe painted orange at the top. As a result, a total of 72 plots, with 6 replicates per fire severity class per stand, were sampled in the study. The stand and plot selection was completed before the initiation of post-fire vegetation growth. It should be noted that six (one scorched and five lightly burned) plots were destroyed during the winter of 2000 because of unregulated firewood harvesting. As a result, replication for scorched and lightly burned classes reduced from the original 24 to 23 and 19, respectively.

Data Collection

On each plot, understory vegetation recovery was monitored in each of the four (1999 to 2002) post-fire years. Shrubs and forbs were identified to species, and the % cover of each identified species was estimated. The total % coverage of grass and mosses (including liverwort) were also estimated but were not identified to species. Vegetation monitoring was conducted between July and August of each year. In order to maintain consistency, % cover was visually estimated by one person (K. Kemball) over the entire study period. Grasses were not identified to species because accurate identification was not always possible due to lack of flowering at the time of sampling. Shoots of some moss species (e.g., *Polytrichum spp.*) were often intermingled, which made it impossible to quantify them separately in the cover estimates (Schimmel and Granstrom 1996). However, effort was made to identify grass and moss species during the 3rd post-fire year. The major grass species identified include *Carex spp.*, *Oryzopsis asperifolia*, *Luzula acuminata*, and *Calamagrostis canadensis*. The major moss and liverwort species identified include *Ceratodon purpureus*, *Polytrichum spp., Marchantia spp.* and *Pohilia nutans*.

To compare the rate of plant community recovery on different fire severity classes, data from plant communities of 20 young (10-years after fire) and 15 mature (> 70 years after fire) stands previously sampled (Kemball 2002) were also included in the study. In each young or mature stand, a 20 x 20 m plot was set up, within which five 2x2 m quadrants were randomly located. Understory vegetation on each quadrant was measured following the same procedure used in post-fire vegetation sampling.

Data Analysis

Three general life form groups were organized in the study: mosses and liverworts, forbs and grasses, and woody plants (shrubs). Percent covers of woody plants and forbs were calculated by adding % covers of individual species. Based on information available from literature (e.g., Ahlgren and Ahlgren 1960, Rowe 1983, Haeussler et al. 1990, Buse and Bell 1992, Arnup et al. 1995, Fire Effects Information System 2003), each woody plant and forb species was classified into one of the three regeneration strategy groups: invader – species regenerated from post-fire transported seeds or spores, seed bankers – species regenerated from buried seeds, or sprouters – species regenerated from surface or buried vegetative parts. When a species was given more than one regeneration strategies or when assignments from different sources conflict with each other, a more probable regeneration strategy was assigned to the species based on our field observations. Percent cover of each regeneration strategy group was calculated by adding % cover of all species belonging to the group. Based on the presence and abundance of woody plant and forb species, richness and Shannon's diversity index was calculated for each plot.

Repeated measures analysis of variance was used to examine the effect of fire severity on % cover of each life form and regeneration strategy group as well as changes in % cover of each life form and regeneration strategy group over the four post-fire years. Similarly, repeated measures analysis of variance was also used to examine the effect of fire severity on species richness and diversity as well as changes in species richness and diversity over the four post-fire years. Whenever significant interaction between fire severity and post-fire year was found, change over the four post-fire years was analyzed separately for each fire severity class using one-way analysis of variance. Similarly, differences among fire severity classes were analyzed separately for each post-fire year using one-way analysis of variance.

Detrended correspondence analysis (DCA) with down-weighting of rare species was used to compare understory vegetation of the three fire severity classes to 10-year old and mature (>70 years old) stands using CANOCO 4 software (Ter Braak and Smilauer 1998). The averages of the three severity classes and 10-year old and mature stands were displayed in the ordination along with individual plots. Averages were added supplementary to diagrams so as not to affect ordination. Only the 3rd post-fire year data were used in this comparison to avoid over crowding. Percent similarity (PS) was also calculated as $PS = 200\sum \min(P_{ix}, P_{iy})$, where P_{ix} and P_{iy} are the percent cover of i_{th} species in sample x and y, expressed as proportions of the quantity of all species in sample x and y (Pielou 1975). PS is 0 if no species are in common and 100 if all species are in common and in the same proportion.

All statistical analyses except DCA were conducted using SYSTAT version 10.2 (SYSTAT Software Inc. 2002).

RESULTS

A total of 103 (23 shrubs and 80 forbs) species were found during the four post-fire years (Table 2). Among them, 50 (nine shrubs and 41 forbs) were common among the three fire severity classes. Twenty (eight shrubs and 12 forbs) species were shared by scorched and lightly burned while only nine (all forbs) shared by lightly and severely burned. There were eight (3 shrubs and 5 forbs), nine (2 shrubs and 7 forbs), and nine (2 shrubs and 7 forbs) species unique to scorched, lightly burned and severely burned, respectively. Most species common to all three fire severity classes were also abundant (up to 17% cover) and frequently found (up to 70% of the plots) species (Table 2). Except for *Clintonia borealis* and *Streptopus roseus*, however, all species that occurred on only two fire severity classes or were unique to one fire severity class had less than 1% cover and were found on less than 12% of all plots. With the exception of *Actaea rubra* and *Stretopus roseus* all forb species shared by slightly and severely burned plots, or unique to either slightly or severely burned plots, were not present on any of the 20 young (10-years old) or 15 mature (> 70 years old) fire origin stands used for comparison.

Table 2. Mean % cover and frequency of shrub and forb species that occurred on each fire severity class (SC = scorched, L = lightly burned, S = severely burned) during the first four post-fire years. Species were listed alphabetically, separately for shrubs and forbs. Species common to all fire severity classes listed first and species unique to one severity class listed last. Only the first 4 letters of species name are shown. Species with % cover < 0.1 are denoted as asterisk (*). Post-fire regeneration strategy of each species was assigned (I = invader or species regenerated from post-fire transported seeds or spores, S = seed bankers or species regenerated from buried seeds, V = sprouters or species regenerated from surface or buried vegetative parts).

Species	RS	SC	L	S
Woody plant				
Acer spic	V	6.1/17	1.1/7	0.1/3
Corylus corn	V	10.7/43	1.8/26	0.4/4
Diervilla lon.	V	14.1/51	8.6/35	4.1/26
Lonicera dioi[2]	V	0.1/1	0.1/1	0.1/1
Prunus pens[1,2]	S	0.3/5	1.2/9	1.1/4
Ribes glan	S	0.2/4	0.2/5	*/1
Rosa acic	V	1.6/31	1.9/22	1.4/15
Rubus idea	S	8.2/47	16.6/70	4.6/19
Vaccinium myrt[2]	V	0.7/12	0.1/2	0.1/1
Amelanchier alni	V	0.3/3	0.2/2	
Ribes oxy	S	0.1/4	*/3	
Ribes huds	S	*/1	0.1/2	
Ribes tris	S	0.2/3	*/2	
Viburnum edul[1,2]	S	*/1	0.8/12	
Viburnum rafi	S	1.0/5	*/1	
Symphoricarpus albu	V	*/1	*/1	
Alnus cris	V	0.4/3		
Lonicera vill[2]	V	0.1/1		
Ribes lacu	S	0.1/2		
Cornus stol	V		0.2/2	
Vaccinium angu[2]	V		*/1	
Sorbus canas[1]	S			0.1/1
Salix sp.	I			0.4/7
Forbs				
Aster cili	I	0.5/17	0.7/16	1.5/30
Cirsium arve[2]	I	4.3/28	6.3/31	1.5/23
Convolvulus sepi[1,2]	I	0.6/7	0.2/3	0.1/3
Cornus cana	V	4.3/60	6.9/73	0.9/26
Dracocephalum parv[1,2]	S	0.1/2	0.4/9	2.2/14
Epilobium angu	I	1.1/16	1.3/29	5.6/60
Equisetum prat	V	0.2/3	0.2/5	1.9/13
Equisetum sylv	V	0.4/8	1.1/20	5.1/46
Fragaria virg	V	1.0/26	0.6/10	0.2/5
Galium bore	V	1.4/20	0.4/14	0.1/3
Galium trif	V	1.4/24	0.3/9	0.1/3
Geranum bicki[1,2]	S	0.7/16	5.3/44	4.5/59
Impatiens cape[1,2]	I	0.9/11	0.3/7	0.4/9
Lathyrus ochr	I	0.8/19	0.5/15	3.3/44
Lathyrus veno[2]	I	0.8/10	0.6/10	2.4/34
Petasites palm	I	1.8/19	1.0/21	0.5/20
Rubus pube	V	3.4/66	2.8/57	1.6/29
Solidago cana	I	0.2/1	0.1/2	0.2/4
Sonchus arve[1,2]	I	1.8/25	2.5/24	4.4/36
Sonchus oler[1,2]	I	0.1/1	0.4/2	0.1/2
Taraxacum offi[2]	I	1.2/26	1.3/33	5.5/60
Vicia amer[2]	I	0.1/6	0.3/16	2.7/42
Apocynum andr	V	0.1/3	*/1	0.1/1
Aralia nudi	V	0.6/10	0.9/24	*/2
Asarum cana	I	0.1/1	0.1/1	*/2
Aster cons[1,2]	I	0.1/2	*/1	0.1/3
Aster puni[1,2]	I	0.4/4	*/2	1.4/18
Equisetum arve	V	*/1	0.1/2	0.7/1
Geum riva[1,2]	I	0.1/3	*/2	0.1/2
Mertensia pani	V	1.1/11	2.9/23	*/1
Mianthemum cana	V	1.1/38	0.8/27	*/2
Petasites sagi[2]	I	0.2/5	0.1/2	*/3
Pyrola secu[1,2]	V	0.1/4	0.1/8	*/2
Trientalis bore	I	*/6	0.4/14	0.1/7
Viola cana[2]	I	0.3/7	0.3/9	*/1
Viola reni	I	0.2/10	0.3/10	*/2
Ambrosia artea[1,2]	V	0.1/1	*/1	0.2/2
Viola neph[1,2]	I	*/1	*/5	*/1
Pteridium aqui	V	1.7/10	0.7/5	*/1
Clintonia bore	V	2.6/33	1.9/20	
Disporum trac[1]	V	0.4/9	0.1/2	
Mitella nuda	I	0.4/14	0.1/3	
Streptopus rose[2]	V	1.7/32	0.2/7	
Aquilegia brev[2]	V	*/1	0.2/3	
Circaea alpi[1]	I	0.1/3	*/1	
Coptis trif	V	0.1/11	*/2	
Fragaria vesc	V	*/3	0.1/1	
Galium trif[2]	V	0.5/11	*/3	
Melilotus indi[1,2]	I	*/1	0.5/2	
Pyrola asar	V	0.1/6	*/3	
Thalictrum venu	V	*/2	0.4/2	
Mentha arve[1,2]	I	*/2	*/1	
Adoxa mosc[1,2]	I	*/1	*/1	
Anaphales marg[1,2]	I		0.1/6	1.0/22
Aralia hisp[1,2]	S		0.8/7	0.1/2
Chenopodium albu[1,2]	I		0.5/6	0.1/4
Achillea mill[1,2]	I		*/1	0.2/5
Aster hesp[1,2]	I		*/1	0.5/10
Epilobium glan[1,2]	I		0.1/3	*/1
Senecio erem[1,2]	I		*/1	0.5/7

Heiracleum lana[2]	I		*/1	*/1
Aquilegia cana[1,2]	V	0.1/2		
Linnaea bore	V	0.1/4		
Anemone cana[1,2]	V	*/1		
Saniculua mari	I	*/1		
Athyrium feli	V	*/1		
Actaea rubr	V		0.1/3	
Corydalis semp[1,2]	S		0.1/1	
Urtica dioc[1,2]	I		0.1/1	
Agrimonia stri[1,2]	I		*/1	
Circaea quad[1,2]	I		*/1	
Corydalis aure[1,2]	S		*/1	
Geum macr[1,2]	I		*/1	
Senecio stre[1,2]	I		*/1	
Aster umbe[1,2]	I			0.1/1
Stellaria caly[1,2]	I			0.2/6
Melilotus alba[1,2]	I			*/1
Ranunculus lapp[1,2]	I			*/1
Ranunculus scel[1,2]	I			*/2
Trifolium hybr[1,2]	I			*/1

[1]Not found in 10-years old stand.
[2]Not found in mature stand.

Fire severity affected ($p < 0.001$) the abundance of mosses and liverworts. Also the changes in abundance of mosses and liverworts over the four post-fire years depended on fire severity ($p < 0.001$) (Table 3, Figure 2). In the 1st post-fire year, moss and liverwort coverage was minimal on scorched (0.2%) and lightly burned (0.3%) plots and almost absent on severely burned plots. In the 2nd post-fire year, moss and liverwort coverage was much more abundant on severely burned plots compared to either scorched ($p < 0.001$) or slightly burned ($p < 0.001$) plots. In the 3rd and 4th post fire years, severely burned plots had greater ($p = 0.011$) abundance of moss and liverwort than lightly burned plots, which, in turn, had greater ($p = 0.019$) abundance of moss and liverwort than scorched plots (Figure 2). Regardless of fire severity, the abundance of moss and liverwort increased during the initial three post fire years and slightly declined from 3rd to 4th year. Moss and liverwort reached and maintained greater abundance since the 2nd post fire year on severely burned plots ($p < 0.001$) and since 3rd post-fire year on lightly burned and scorched plots ($p < 0.05$).

Table 3. Results of repeated measures analyses of variance[1] with fire severity classes as treatments (TR), stands as blocks. Values shown are probabilities (n = 66).

	Between		Within	
	B	TR	YEAR	YEAR*TR
Life from				
Moss/livewort	0.024	0.000	0.000	0.000
Forbs and Grass	0.014	0.025	0.000	0.870
Woody plants	0.001	0.000	0.000	0.000
Regeneration strategy				
Invader	0.000	0.000	0.000	0.000
Seed banker	0.361	0.000	0.000	0.001
Sprouter	0.000	0.000	0.000	0.000
Species diversity				
Richness	0.005	0.006	0.000	0.004
Shannon's index	0.001	0.021	0.000	0.000

[1]$Y_{ijkl} = u + TR_i + B_j + EB_{ijk} + YEAR_l + (YEAR*TR)_{il} + EW_{ijkl}$ is the model used for the analysis, where i = 1, 2, and 3 (severity classes); j = 1, 2, 3, and 4 (blocks); k = 1, 2, 3, 4, 5, and 6 (replicates); and l = 1, 2 and 3 (years); B = block (stand); TR = treatment (fire severity); YEAR = post-fire year; EB and EW are errors between subject and within subject, respectively.

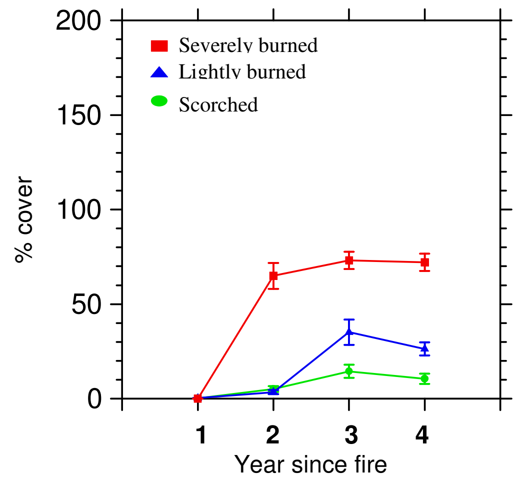

Figure 2. Mean % cover of mosses and liverworts for each fire severity class in each of the four post-fire years. Error bars shown are standard errors.

The abundance of forbs and grass was affected by fire severity ($p < 0.025$) (Table 3, Figure 3). In the 1st post-

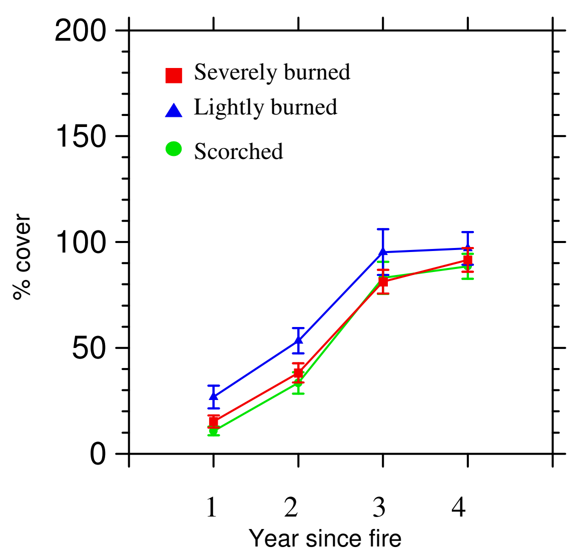

Figure 3. Mean % cover of forbs and grasses for each fire severity class in each of the four post-fire years. Error bars shown are standard errors.

fire year, forbs and grass were more abundant on slightly burned plots than those on scorched ($p = 0.001$) or severely burned ($p = 0.022$) plots. In the 2nd post-fire year, forbs and grass on slightly burned plots were only more ($p = 0.019$) abundant than those on scorched plots. Differences in the abundance of forbs and grass were not found ($p \geq 0.214$) in the 3rd or 4th post fire year (Figure 3). Regardless of fire severity, the abundance of forbs and grass increased ($p \leq 0.012$) over the initial three post fire years and remained approximately the same ($p \geq 0.720$) from 3rd to 4th post-fire years.

Fire severity affected ($p < 0.001$) the abundance of woody plants. Also the changes in woody plant abundance over the four post-fire years depended on fire severity ($p < 0.000$) (Table 3, Figure 4). In the 1st post-fire year, shrub cover was higher ($p < 0.001$) on scorched plots compared to lightly and severely burned plots. Since the 2nd post-fire year, both scorched and lightly burned plots had higher ($p \leq 0.003$) shrub cover compared to severely burned plots. On scorched and lightly burned plots, shrub cover increased ($p \leq 0.014$) over the first three post-fire years and remained the same ($p = 0.999$) between the 3rd and 4th post-fire years. On severely burned plots, woody plant cover remained the same during the 1st and 2nd post-fire years ($p = 0.318$) as well as during the 3rd and 4th post-fire years ($p = 0.999$). However, shrub cover in the 3rd and 4th post-fire years was higher ($p \leq 0.030$) than that in the 1st and 2nd post-fire years (Figure 4).

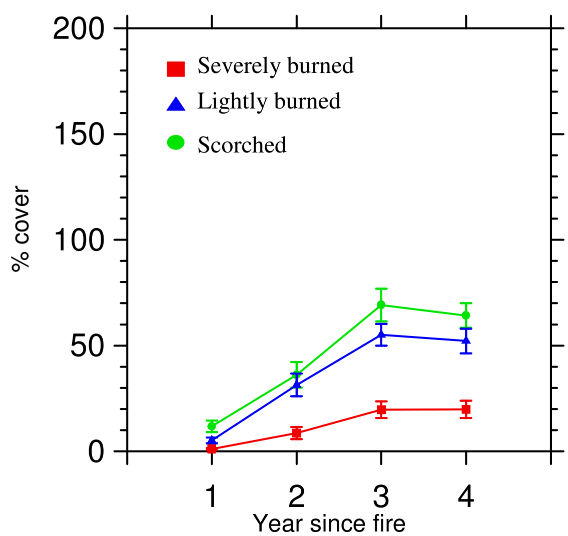

Figure 4. Mean % cover of woody plants for each fire severity class in each of the four post-fire years. Error bars shown are standard errors.

Fire severity affected ($p < 0.001$) the abundance of invasive species. Also, the changes in abundance of invasive species over the four post-fire years depended on fire severity ($p < 0.000$) (Table 3, Figure 5). No differences in the abundance of invasive species were observed in the 1st ($p = 0.177$) and 2nd ($p = 0.143$) post-fire years. Severely burned plots had much higher ($p \leq 0.011$) abundance of invasive species than lightly burned and scorched plots in the 3rd and 4th post fire years. On severely burned plots, significant differences were found between all post-fire years except between the 3rd and 4th post fire years. On lightly burned plots, significant differences were only observed only between the 1st and the 3rd ($p < 0.000$) and between the 1st and the 4th ($p < 0.000$) post fire years. On scorched plots, invasive species became more ($p \leq 0.0273$) abundant in the 3rd and 4th post fire years compared to the 1st and 2nd post-fire years.

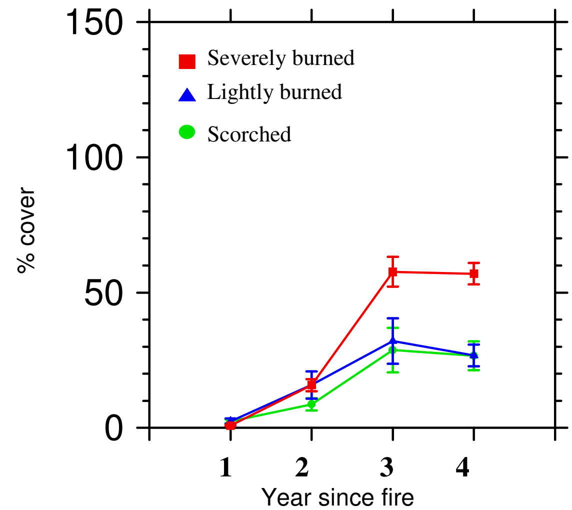

Figure 5. Mean % cover of invaders (species regenerated from post-fire transported seeds or spores) for each fire severity in each of the four post-fire years. Error bars shown are standard errors.

Fire severity affected ($p < 0.001$) the abundance of seed banking species. Also the changes in abundance of seed banking species over the four post-fire years depended on fire severity ($p = 0.001$) (Table 3, Figure 6). In the 1st post-fire year, scorched plots had lower abundance of seed banking species than lightly burned ($p < 0.001$) and severely burned ($p = 0.027$) plots. In the 2nd post fire year, abundance of seed banking species remained significantly lower on scorched plots compared to lightly burned plots ($p = 0.011$). In the 3rd and 4th post-fire years, both scorched and severely burned plots had lower abundance of seed banking species compared to lightly burned plots ($p \leq 0.003$). While the abundance of seed banking species changes over the four post-fire years on scorched ($p = 0.001$) and lightly burned ($p = 0.012$) plots, it remained the same ($p = 0.680$) on severely burned plots.

Fire severity affected ($p < 0.000$) the abundance of sprouting species. Also the changes in abundance of sprouting species over the four post-fire years depended on fire severity ($p < 0.000$) (Table 3, Figure 7). In the first two post-fire years, scorched plots had higher ($p = 0.000$) cover of sprouters than severely burned plots. In the 3rd and 4th post-fire year, both scorched and lightly burned plots had higher ($p < 0.017$) cover of sprouters than severely burned plots. On scorched and lightly burned plots, sprouters increased ($p \leq 0.008$) their abundance during the first three post-fire years and remained the same ($p = 0.999$).

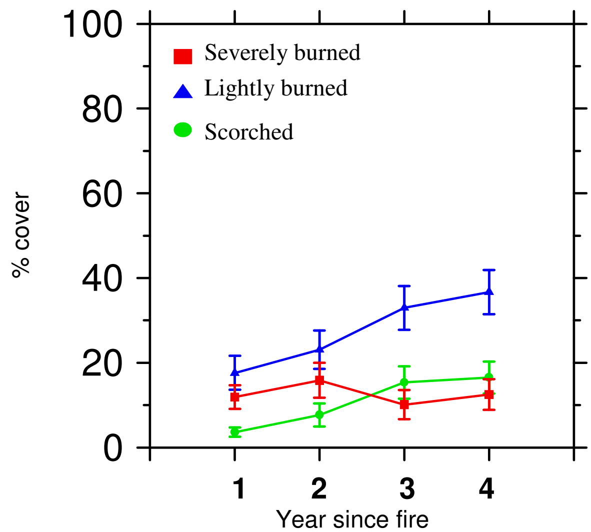

Figure 6. Mean % cover of seed bankers (species regenerated from buried seeds) for each fire severity in each of the four post-fire years. Error bars shown are standard errors.

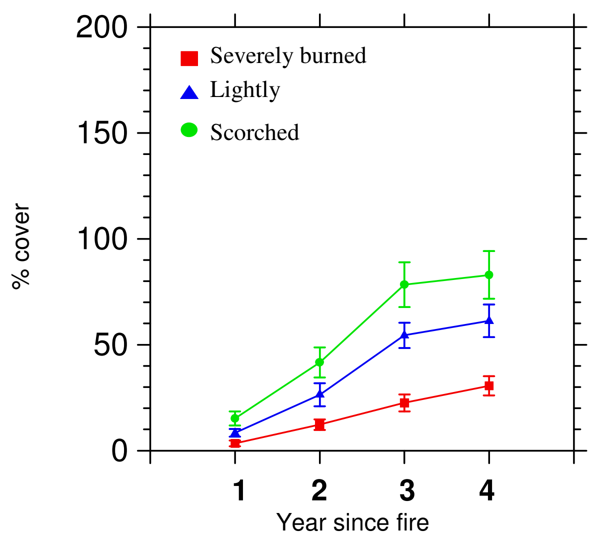

Figure 7. Mean % cover of sprouters (species regenerated from surface or buried vegetative parts) for each fire severity in each of the four post-fire years. Error bars shown are standard errors.

between the 3rd and 4th years. On severely burned plots, abundance of sprouting species remained the same during the 1st and 2nd post-fire years ($p = 0.189$) as well as during the 3rd and 4th post-fire years ($p = 0.295$). However, abundance in the 3rd or 4th post-fire years was higher ($p \leq 0.05$) than that in the 1st or 2nd post-fire years (Figure 7).

Fire severity affected ($p = 0.006$) species richness. Also changes in richness over the four post-fire years depended on fire severity ($p < 0.000$) (Table 3, Figure 8). In the 1st post fire year, more species were found on scorched and lightly burned plots compared to severely burned plots ($p < 0.000$). No difference ($p \geq 0.075$) in species richness was found after the 1st post-fire year. On scorched plots, species richness remained the same during the 1st and 2nd post-fire years ($p = 0.266$) as well as during the 3rd and 4th post-fire years ($p = 0.999$). However, more species were found in the 3rd or 4th post-fire years compared to either 1st or 2nd post-fire years ($p < 0.000$). On lightly and severely burned plots, species richness increased ($p \leq 0.020$) over the first three post fire years and remained the same or slightly declined from the 3rd to the 4th post-fire year (Figure 8).

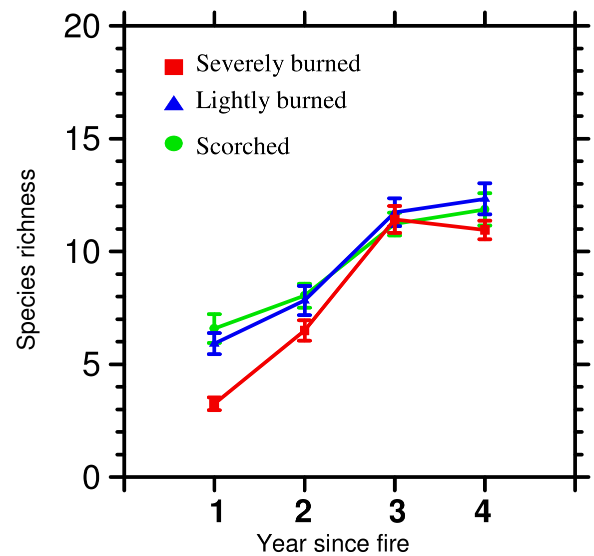

Figure 8. Species richness of each fire severity in each of the four post-fire years. Error bars shown are standard errors.

Fire severity affected ($p = 0.021$) the Shannon's diversity index. Also changes in the Shannon's diversity index over the four post-fire years depended on fire severity ($p < 0.001$) (Table 3, Figure 9). In the 1st post fire year, species diversity was higher on scorched and lightly burned plots compared to severely burned plots ($p < 0.001$). No difference ($p \geq 0.179$) in species diversity was found after the 1st post-fire year. On scorched and lightly burned plots, species diversity remained the same during the 1st and 2nd post-fire years ($p \geq 0.522$) as well as during the 3rd and 4th post-fire years ($p \geq 0.174$). However, species diversity was higher in the 3rd or 4th post-fire years compared to either 1st or 2nd post-fire years ($p \leq 0.000$). On severely burned plots, species diversity increased ($p < 0.001$) over the first three post-fire years and remained the same from the 3rd to the 4th post-fire year (Figure 9).

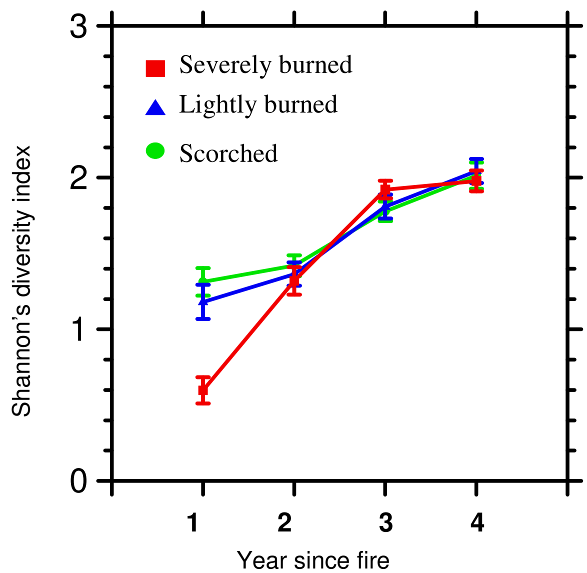

Figure 9. Species diversity (Shannon's diversity index) of each fire severity in each of the four post-fire years. Error bars shown are standard errors.

DCA ordination displayed the relative position of fire severity plots in relation to plots sampled from 10-years old and mature stands (Figure 10). At the 3rd post fire year, the recovery to pre-fire condition was negatively affected by fire severity. Percent similarity values, which and decreased from 48 to 25 to 13% from scorched to lightly to severely burned plots compared to mature stands, reinforced the ordination results. Compared to 10-years old stands, percent similarity values decreased from 57 to 39 to 27% from scorched to lightly to severely burned plots.

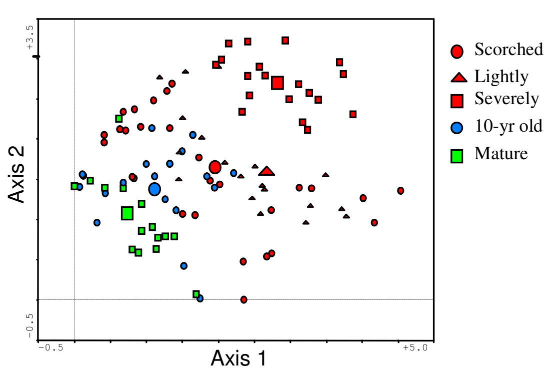

Figure 10. DCA ordination of fire severity plots at the 3rd post fire year, 10-year old stands and mature stands. Small symbols are individual plots or stands, and large symbols are plot or stand means.

DISCUSSION

Boreal forests typically accumulate a thick forest floor because of slow decomposition due primarily to cold climate. Except for loose litter on the surface the boreal forest floor (i.e., duff layer) is too compact to be much involved in flaming combustion. However, duff may be consumed to a variable degree by smoldering combustion after the main fire front has passed (Van Wagner 1972, Alexander 1982, Weber et al. 1987, Johnson 1992). Therefore, the depth of burn and its spatial variation bear no relationship with the intensity of the fire front, despite fire intensity is a useful predictor for aboveground effect. In fact, spatial variation in depth of burn has been frequently observed (Dyrness and Norum 1983, Zasada et al 1983, Wang 2002) although its implication to vegetation recovery has seldom been studied explicitly. The 1999 Black River wildfire of our study killed all aboveground vegetation on each of the four study stands but its impact on forest floor ranged from 0 to 100% consumption. Three distinctive fire severity classes have been identified and used to describe duff consumption pattern (Wang 2002). In the context of this study, the three fire severity classes were used as treatment variables, each stand as a block, and the six plots within each fire severity class and each stand as replicates. Compared to a true manipulative experiment, however, each "treatment" level (i.e., fire severity class) of this study could not be randomly assigned to each experimental unit (i.e., plot). Consequently, variables intrinsic to each plot, especially the local variation in the pre-fire species composition, could potentially confound the effect of fire severity. Because of this confounding effect, our study focused mainly on species groupings instead of individual species in response to fire severity and time since fire. We believe that this approach can, at least in part, circumvent the deficiency of our study design based on an uncontrolled wildfire.

Previous studies have shown that, after an initial increase of weedy invaders, disturbed boreal forest communities vary little in species composition from pre-disturbance communities (Dyrness 1973, Johnston and Woodard 1985, Halpern 1988, Halpern 1989, Qi and Scarratt 1998). This is especially true on mesic to hygric and rich sites (De Grandpre and Bergeron 1997) such as ours. Despite their distinctive difference, the three fire severity classes shared a large number (48 out of 103) of species that were also most abundant and frequently found (Table 2). Those species unique to any one or two severity classes were neither as abundant nor as frequently found, and a large portion would only likely persist for less than 10 years (Table 2). These results suggest that boreal forest plants are well adapted to fire disturbances of different severity, which supports the conclusion that nearly all successional species are present at the early stage of post-fire succession (Rowe 1961, Dix and Swan 1971, Carleton and Maycock 1978). The larger number of species shared by scorched and lightly burned plots compared to the number of species common to lightly and severely burned plots, and no species being shared between scorched and severely burned plots, suggests lightly burned plots are more similar to scorched plots. As described by Wang (2002) both scorched and lightly burned plots maintained an intact or almost intact duff layer that was entirely absent on severely burned plots due to smoldering consumption. Moreover, all species shared by or unique to slightly and severely burned plots would only likely persist for less than 10 years while more than half of the species shared by scorched and lightly burned plots would likely persist to the mature stage (Table 3). Clearly, severe fire does eliminate the early occurrence of some residual species. If or when these species will return to severely burned plots requires further monitoring.

Our results showed that species differed in their ability to respond to fire of different severity (or depth of burn) because of their inherent differences in regeneration strategy. Given that fire intensity per se has no selective impact because it uniformly kills all aboveground vegetation, it is reasonable to argue that fire severity largely determines post-fire vegetation response through affecting *in situ* propagules as well as physical, chemical and biological characteristics of the post-fire seedbed. Complete consumption of forest floor by smoldering combustion on severely burned plots would have eliminated most *in situ* propagules while lack of and very limited duff consumption, respectively, on scorched and lightly burned plots would have preserved most *in situ* propagules. As expected, invasive species were clearly favored in all but the 1st post-fire year (Figure 5) while sprouters were much lower in each of the four post-fire years on severely burned plots (Figure 7). The lack of difference in the 1st year for invaders could, at least in part, be attributed to lack of seed input because most plants disperse their seeds in the fall. Ash deposits may have also negatively affected germination of seeds or spores imported during the growing season. Our field measurements suggested ash deposits averaged 3-4 cm in depth on severely burned plots (unpublished data) and previous studies have shown that ash, particularly of *Populus tremuloides* origin, is toxic to conifer germination (Thomas and Wein 1990). Seed bankers performed best on lightly burned plots (Figure 6). Scorching may not have be sufficient to stimulate germination of seeds while severe burning would have resulted in consumption of most buried seeds. Overall, the response of species with different regeneration strategies fits well with the simple conceptual model of Schimmel and Granstrom (1996). Although assignment of some species into a regeneration strategy group was not in agreement by all sources of literature, eliminating those species from the analysis did not change our findings.

Among the three life form groups, the moss and liverwort group and the woody plant groups were much more responsive to fire severity compared to the forbs and grass group. This is likely due to the regeneration strategy of species within each group. Most species in the moss and liverwort group, according the species identification made in the third year, are invasive species dominated by *Ceratodon purpureus* and *Polytrichum spp*. Therefore, the increase abundance of mosses and liverworts with fire severity would be expected. The lack of differences among fire severity classes during the 1st post-fire year are likely due both to less amount of spores blown in and the possible toxic effect of ash. Woody plants, on the other hand, were dominated by sprouting species (Table 3). Consequently a decrease in their cover with fire severity was expected. Unlike moss-liverwort or woody plants, species of forbs and grass group are much more diverse in their regeneration strategies. Although grass species found in this study are largely sprouting species, the 80 forbs consisted of species with different regeneration strategies. Consequently, the forbs and grass group responded less to fire severity.

A general trend that emerged from this study is that species richness and abundance rapidly increased during the initial three years and remained relatively stable from the 3rd to 4th year. Similarly, Dyrness (1973) also found that most increases in plant species richness occurred during the first three years following slash burning. Rapid recovery of plant communities following fire has been frequently observed in boreal forest (Rowe 1961, Dix and Swan 1971, Carleton and Maycock 1978) as well as Miditerranean forest (Trabaud and Prodon 2002). However, differences in the composition and abundance of understory plants remained among fire severity classes four years after fire. How long it would take for understory vegetation on the three fire severity classes to converge is not clear, though the canopy is and will be continuously dominated by aspen. At the current stage of development, vegetation on scorched plots was the most similar while vegetation on severely burned plots was the least similar to mature stands. As expected, succession has been set back much more on severely burned plots.

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