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RESEARCH ARTICLE

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Old-Growth Southern Boreal Forest Stability and Response to a Stand-Replacing Wildfire

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ABSTRACT: Half of a 400-year-old forest in northeastern Minnesota, USA, burned in autumn 2006 providing a unique opportunity to examine stability and response to stand-replacing fire in a region where the historic mean fire return interval was about 100 y. We installed 18 permanent 50-m transects in 1977 and 18 more in 1997. In 2008, 18 additional transects were surveyed along with the initial transects; half were in the burned portion of the forest and half remained unburned. In 2010 and 2014, all transects were again inventoried. Before the fire, eastern white pine (*Pinus strobus*), historically the dominant tree, represented less than 4% of the canopy in which northern white cedar (*Thuja occidentalis*), balsam fir (*Abies balsamea*), and paper birch (*Betula papyrifera*) had become dominants. In 37 y of observation, few significant changes occurred in the unburned forest. In the burned forest, however, the intense fire killed virtually all trees on the upland, and reduced tree cover from near 90% to just over 10%, with survival primarily in wet draws. There was no nearby seed source for jack pine (*Pinus banksiana*) or quaking (*Populus tremuloides*) or big-toothed (*P. grandidentata*) aspen, the most frequent post-fire pioneers. Seedlings of aspen and paper birch established dominance in the small-tree layer within eight years, and dense white cedar established in mesic microsites near surviving seed sources. Stand-level diversity of vegetation after the fire was about the same as before the fire, but primarily as a result of species that survived in wet draws. Raspberry (*Rubus idaeus*), fire-weed (*Epilobium angustifolium*), and several sedges (*Carex* spp.) became temporarily abundant, peaking six years after fire. There was no post-fire white pine regeneration. Results indicate that in the long-term absence of fire there was a gradual shift in canopy composition with relatively little corresponding change in the understory. Results also underscore the importance of microsites in buffering change and driving landscape scale diversity, and how a shift in fire regime can initiate a different successional trajectory.

Index terms: old-growth, plant diversity, post-fire succession, southern boreal forest

INTRODUCTION

Old-growth, structurally complex forests in fire-maintained ecosystems typically are isolated in landscape positions that provide some degree of fire protection, such as on islands or land protected by wetlands or lakes. This study followed 17 y of post-fire response in a 1200-ha fragment of southern boreal forest that had persisted for over 400 y without fire, and eight years of post-fire response, in a region where the historic fire return interval averaged ~100 y. Pre-fire disturbance was largely limited to spruce budworm (*Choristoneura fumiferana* Clemens), wind, and mortality of once-dominant overstory pines. The severe wildfire burned about half of the forest in 2006, providing a unique opportunity to study the response in old-growth.

Dominance of white pine in the Upper Great Lakes region continues to decline because of changes in the fire regime—principally the loss of periodic low and moderately severe fire due to human fire suppression—coupled in many places with extensive logging (Frelich and Reich 1995; Abrams 2001; Friedman et al. 2001; Webb 2001; Frelich 2002). Kneeshaw and Gauthier (2003) suggested that the transition to old-growth in this region begins when the initial post-disturbance cohort, generally jack pine or aspen (Apfelbaum and Haney 1981), begins dying off. In southern boreal ecosystems, however, there is a long period of spruce-fir dominance that eventually begins to break up after ~250 y (Apfelbaum and Haney 1986). Where mature eastern white pine and red pine are present, they often survive fire, making old-growth less easily defined (Heinselman 1996). These long-lived pines can become super-canopy trees, overtopping associates such as balsam fir, white and black spruce, northern white cedar, and paper birch (Frelich and Reich 1995). While paper birch along with jack pine and aspen are early successional species, especially after fire, paper birch can perpetuate on tip-ups and nurse logs, usually in conjunction with gaps in the canopy in old-growth stands, where it commonly coexists with overstory pines. On mesic sites, in the long-term absence of fire, white cedar often becomes dominant over time (Frelich and Reich 1995). Not uncommonly, spruce budworm or repeated ground fire will disrupt development of the understory, including white cedar and birch, often fire-scarring but not killing mature white and red pines that can live for 400 or more years after which they gradually succumb to wind, insects, and disease (Heinselman 1973; Frelich and Reich 1995). The old-growth stands in this study had scattered surviving white and red

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pine that had once dominated the stand, leading Heinselman (1996) to classify it as an old-growth pine forest. Although heart-rot prevented accurate dating of many individual trees, we confirmed that the old pines were in excess of 400 y old. Within this old-growth forest were mixed-aged white cedar, some of which were nearly as old as the pines. The pines were not regenerating.

Throughout the Upper Great Lakes region, much of the old-growth white and red pine has been removed by logging, and most remaining stands have been severely reduced or eliminated by wind or fire (Heinselman 1996). There have been few opportunities to examine the vegetation of these rare old stands before and after wildfire. Because fire is a primary factor in shaping the southern boreal forest ecosystem (Frissell 1973; Heinselman 1973; Thomas-Van Gundy and Nowacki 2016), and many have noted that changes in the fire regime are leading to changes in composition (Clark 1988, 1990; Friedman and Reich 2005; Hanberry et al. 2012), we were interested in the ecological stability of the forest in the long-term absence of fire. Near the end of the 20th century, old-growth white and red pine communities represented about 6% of uplands in the Boundary Waters Canoe Area Wilderness (BWCAW) (Heinselman 1996). With climate change, old-growth forest is predicted to become increasingly rare as a result of increasing fire and greater weather extremes, including severe wind (Thompson et al. 1998). What happens when fire finally burns these isolated old-growth stands is largely unknown.

On 7 September 2006, a lightning strike ignited a fire on the southwest shore of Redeye Lake in the BWCAW in Superior National Forest, ~2.5 km south of the study area. On 14 September, when windy conditions developed, the fire expanded north over the Misquah Hills to the eastern end of Winchell Lake, then jumped ~0.6 km across the lake to the north shore. It continued north, burning through the old-growth between Winchell and Gaskin Lakes. Forest Service personnel used the portage trail between the lakes to contain the fire to the western half of the old-growth. Fire in the heavy fuels of the old-growth was intense, but it remained west of the portage. Cool, rainy weather on 16 September halted the fire.

Heinselman (1996), Frelich and Reich (1995), and Ohmann and Ream (1971) summarized the general ecological relationships and processes in old-growth southern boreal forests. Vegetation composition and structure reflect disturbance largely as combinations of fire, insects, logging, and wind (Van Wagner and Methven 1978; Bonan and Shugart 1989; Bergeron 1991; Heinselman 1996; Drapeau et al. 2000; Burris and Haney 2005, 2006). Fire and spruce budworm are the most prevalent natural disturbances in this region (Heinselman 1996). While spruce budworm normally has low-level impacts on forest community structure in the northern Great Lakes region, outbreaks periodically occur, affecting mostly balsam fir and white spruce.

Wind, insects, and mortality of overstory trees increase patchiness at a scale as small as 0.1 ha, which can favor alpha and beta diversity (Bazzaz 1983; Denslow 1985; Webb 1988; Drapeau et al. 2000; Peltzer et al. 2000). Recruitment of plant species following stand-replacing fire or blowdown are strongly influenced by microsite characteristics (Webb 1988; Bazzaz 1996; Carlten 1998; Elliott et al. 2002), whereas responses of birds and small mammals (e.g., microtines) reflect both habitat structure and patchiness (Herrando et al. 2003; Burris and Haney 2005, 2006). Diverse, spatially heterogeneous old-growth stands usually convert to more homogeneous, sometimes monotypic, stands after landscape-scale disturbance such as stand-replacing fire or severe wind (Frelich and Reich 1995; Lorimer 2001; Burris and Haney 2005, 2006). Neither landscape scale nor microsite dynamics of old-growth forests are well documented, especially where gap-phase replacement of senescing overstory trees is a primary disturbance (Frelich and Reich 1995; Scheller and Mladenoff 2002; Harper et al. 2003; Carlson et al. 2011). We expected severe fire to reduce patchiness associated with tree mortality and spruce budworm, but not microsite diversity associated with edaphic variation. Stand-replacing fire, we expected, would sharpen contrasts between upland and lowland communities, and temporarily reduce variation between edaphic microsites within each.

Because vegetation structure as well as patchiness and microsite characteristics likely will be differentially affected by disturbance type, and vary according to pre-disturbance characteristics (Reich et al. 2001; Baker 2002), responses to wind, fire, and insect disturbances may differ in old-growth forests compared to younger stands where pines are more abundant (Dyer and Baird 1997). Also, response to disturbance is species-specific (Dunn et al. 1983; McIver and Starr 2001; Greene et al. 2006) and would be expected to vary from one cover type to another, resulting in different community responses. While these uncommon old-growth forests exist in several locations in the BWCAW, the opportunity to compare gap-replacement disturbance and response to stand-replacing fire is quite rare. Moreover, Heinselman (1996) documented tree cover in several of these old communities, as a part of stand-origin mapping, but gave little attention to understory succession, especially of the ground-layer species.

Although Carleton (2003) reported that plant diversity was primarily influenced by variation in the substrata, Carlson et al. (2011) demonstrated that stand-scale species richness was positively related to heterogeneity of the old-growth canopy, suggesting that gaps associated with gradual thinning of the old pines and spruce budworm mortality should lead to increased plant species richness at the stand scale. We hypothesized that in the continued absence of stand-replacing fire, forest composition would continue to change slowly as overstory pines died and white cedar increased. Spruce and fir were regenerating more or less independently of pine mortality, subject to periodic budworm outbreaks. Birch regeneration was largely dependent on nurse logs that will likely become less common within a few decades after the pines are gone. Thus, in several decades, birch regeneration will likely decrease. Stand-replacing fire generally results in a different suite of species with fewer distinct communities than in the old-growth (Johnson 1992). We predicted that intense fire associated with heavy fuel in the old-growth, that totally removed the canopy except in wet draws, would increase the homogeneity of post-fire communities.

Neither jack pine nor aspen was present in the studied forest, which was largely isolated from younger forests by lakes to the north and south (see Figure 1). We hypothesized that aspen and paper birch, more easily disseminated by wind, would be more likely to colonize the exposed soil after fire than jack pine. We expected white cedar would regenerate especially where nearby parent trees survived in wet draws. White pine and red pine, largely gone from this forest, might gain some presence after fire. We predicted a first-generation post-fire forest of aspen, paper birch, and scattered white pine, with white cedar in mesic areas. We expected ground-layer diversity to decrease.

METHODS

Our study site is located between Winchell and Gaskin Lakes (lat 48°00ě00.49ěN, long 90°33ě19.38ěW; Figure 1). This old-growth stand probably originated following a stand-replacing wildfire around 1610 (M.L. Heinselman, pers. comm.).

We first surveyed vegetation in 1977 with nine permanently marked 50-m transects, each separated by 50 m from the nearest transect. In 1997, we added nine additional transects in another area of the forest and initiated a standard sampling protocol that we then continued in all subsequent surveys. Each set of transects was part of a 250 × 250-m block that we used for

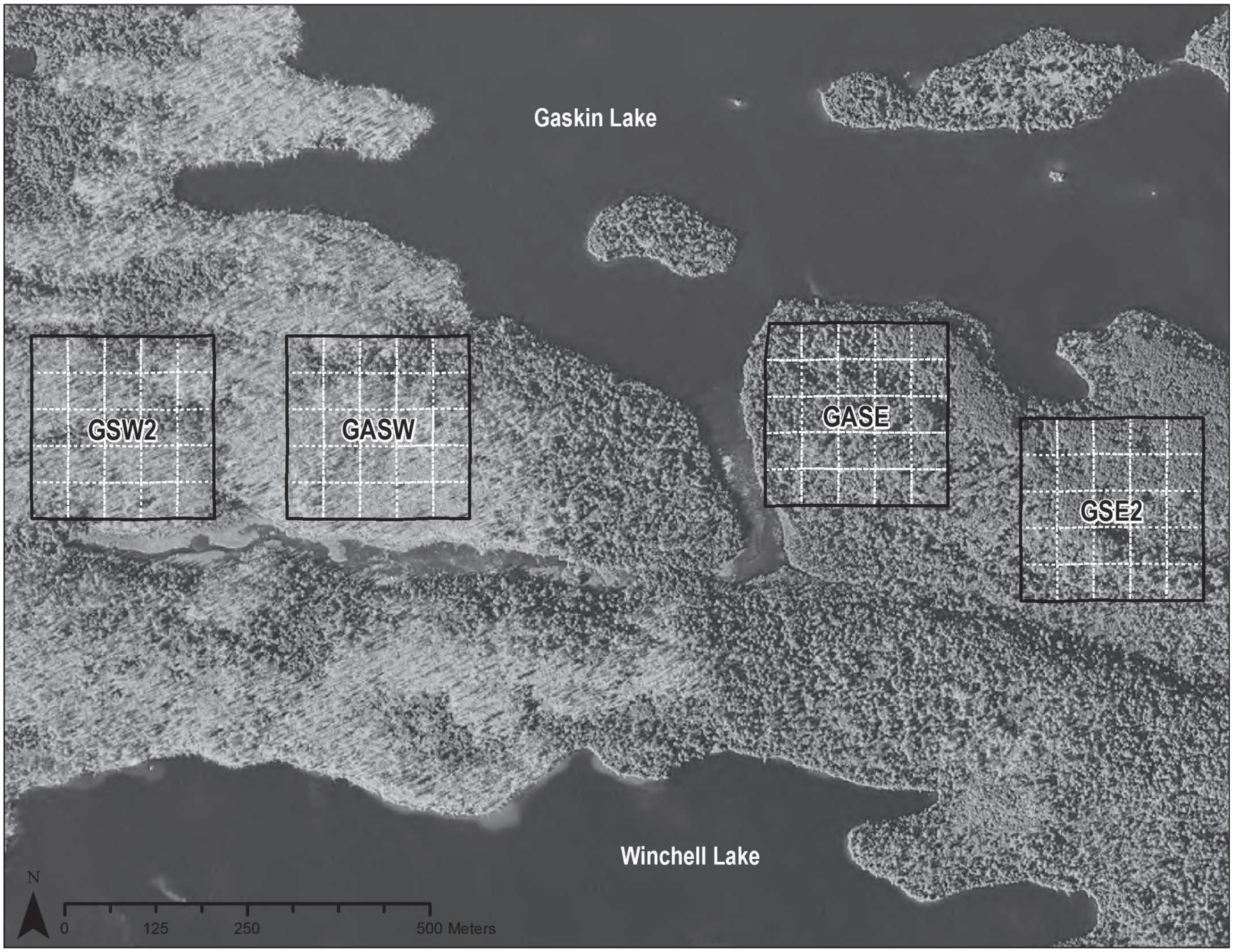

Figure 1. Aerial photograph from 2008 showing GASE, installed in 1977, and GASW, added in 1997. GSE2 and GSW2 were added in 2008. The burned western portion is light gray in contrast to the old-growth that did not burn. What appears to be unburned fragments on the north edges of GASW and GSW2 were wet areas that experienced only light ground fire, although many of the larger trees were blown over during the fire. The northeastern portion of GSE2 lacks large white pines, and may have had a fire more recently than 1610, although there is no evidence other than the somewhat different composition of the forest as mapped by Heinselman (http://cffe/cfans.umn.edu/).

sampling birds in a larger, long-term study (Apfelbaum and Haney 1986). Fortuitously, the 2006 fire burned across the second set of transects, but the initial set remained unburned. In 2008, we replicated each set with an addition nine transects (Figures 1 and 2) and surveyed all transects. To facilitate discussion, we refer to these sets of transects as follows: GASE and GSE2 were unburned; GASW and GSW2 were burned. We resurveyed the four sets of transects again in 2010 and 2014. This study compares the composition, structure, and change in ground layer, shrub and small-tree layer, and tree-layer vegetation with and without fire. To our knowledge there has been no quantitative study before and after stand-replacing fire in comparable old-growth forests in this region.

Although we located sets of transects to favor upland and minimize lowland forest types (Heinselman 1996), the diverse landscape is a significant potential source of experimental error when comparing vegetation on different sets of transects and their response to fire. Based on ground-truthed aerial photograph image analysis, the % of lowland mesic draws and associated vegetation, including white cedar cover types, surrounding the four sets was GASW (7%), GSW2 (30%), GASE (30%), GSE2 (33%).

Initial transects were located by tape and compass; GPS was used beginning in 2008. Vegetation was systematically sampled along each 50-m transect (Figure 2). Cover for each tree and shrub species was estimated using the line-intercept method. Trees were defined as stems standing more than 45° above the horizontal with a dbh (diameter at breast height) of at least 5 cm. Shrubs were identified as all stems with a height >1 m and a dbh <5 cm; trees meeting these size standards were analyzed as part of the shrub layer. Details of our field methods have been previously published (Burris and Haney 2005, 2006).

The numbers of live and dead shrub stems within 1 m of the right side of transects were tallied by species (Figure 2). Diameter, rounded to the nearest inch (2.54 cm), of all live and dead trees within 1 m of transects was measured. Five 1-m^2 circular quadrats centered at 5, 15, 25, 35, and 45 m along each transect were used to ocularly estimate percent cover of ground-layer species (vegetation <1 m tall), exposed mineral substrate, bryophytes, coarse litter (diameter >2.5 cm), and fine litter (diameter <2.5 cm). The sum of individual species cover within a stratum commonly exceeded 100%. Raspberry, with individual stems above and below 1 m in height, was analyzed in the herb layer. Coarse litter was often suspended over the fine litter, resulting in a combined litter estimate frequently >100%.

Ground-layer flora frequency was calculated as the percentage of the 1-m^2 quadrats occupied by a given species on each transect; species cover per transect was obtained by averaging across the five quadrats for each transect. Species richness was the number of species found along each transect. Overall richness was expressed as the total number of species recorded among the 18 transects in the burned and unburned areas we sampled.

We also explored potential differences in how functional groups of plant species responded to fire using the sum of percent cover of all species within a functional group and the SAS GLM procedure with data from 2008, 2010, and 2014. Ground-layer species were assigned to a functional group according to four criteria: life form (tree, shrub, grass, sedge, forb, etc.), pollinator mode (wind, insect, bird, mammal, etc.), seed/fruit dissemination modes (bird, mammal, wind, etc.), plant species fire-response mechanism at the

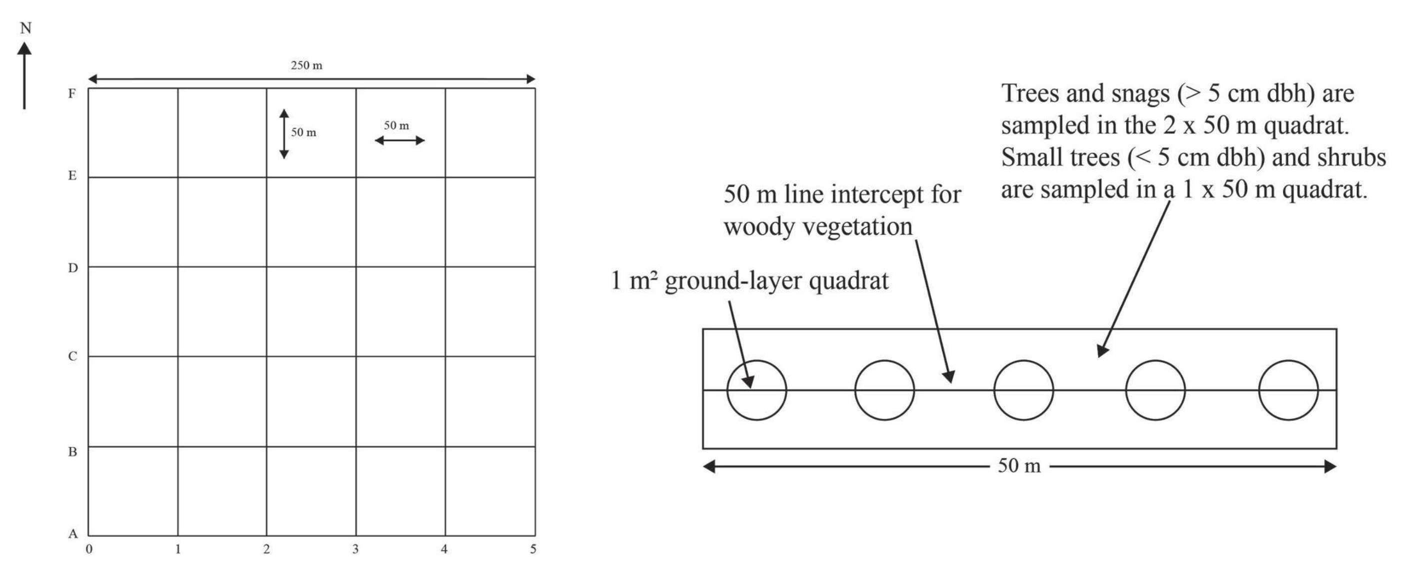

Figure 2. Layout of transects at each site. Transects were placed through the center of 9 of the 25 segments, three each in the first, middle, and right rows, so that each transect was separated from the nearest transect by 50 m.

propagule and whole-plant levels (serotiny, fire scarification, fire chemical alteration, long lived subterranean structure, seed bank responder, etc.). All plant species nomenclature and functional group allocations are based on species descriptions using descriptions by Gleason and Cronquist (1991), field observations, and prior studies (Apfelbaum and Haney 1986).

Data Analyses

After evaluating data distributions and testing assumptions, all but the zero values in multivariate analyses met requirements without requiring transformations. The stability and characteristics of the old-growth forest were evaluated with one-way ANOVA of pre-burn data from GASE and GASW (1997), and the GASE and GSE2 unburned transects sampled in 2014.

To evaluate shifts in vegetation after fire, we ordinated herbaceous vegetation transect data using nonmetric multidimensional scaling (NMDS) with Sørensen distance analyzed as time series ordination with PCORD. This required a transformation for zero values by adding a constant to all data, following the standard methods in McCune and Mefford (1999). Herbaceous cover was summarized by species, survey year, and transect. Only species with mean cover >0.5% were included in the ordination analysis. Relativized absolute species cover was classified using TWINSPAN in PCORD (McCune et al. 2002).

We repeatedly sampled transects to evaluate the stability of the unburned forest, so autocorrelation and unequal variance in unburned versus burned data limited our opportunity to statistically examine vegetation response over time. Repeated measures analysis could only be interpreted with such conservative restraints that, on advice of two statisticians, we elected to describe post-fire changes by comparing means with standard deviations. To test if total plant species richness was different before and after fire, we used chi square analysis. All statistical tests were evaluated at $P<0.05$.

RESULTS

We observed little change in the unburned old-growth from 1977 through 1997 when we initiated a standardized sampling protocol. Changes were primarily in balsam fir cover that decreased following spruce budworm outbreaks, and increased between outbreaks and, to a much lesser extent, after periodic death of large overstory pines. Wind damage, other than occasional breakage of large limbs from old pines, was negligible during the 37 y of observation. For a statistical analysis of stability in the unburned old-growth, we compared 1997 pre-fire surveys of GASE and GASW transects to the unburned transects (GASE and GSE2) in 2014.

Unburned Old-Growth Forest

Historic fire was evidenced only by charcoal in the soil; none of the big pines had visible fire scars, indicating that no fire had occurred in most of the study area since the white pines began growth over 400 y ago. A historical fire probably had burned the northeast third of GSE2 as indicated by the lack of trees older than 250 y. Scattered throughout the rest of the study area were fallen trees up to a meter or more in diameter, many of which were well decayed, suggesting that the old pines had been dying for many decades. Only one big pine died in the two unburned blocks we studied in detail, providing a very rough estimate of one death per 10 ha per decade.

Total tree cover increased nearly 22% from 1997 to 2014, but the difference was not statistically significant. Among species, paper birch and balsam fir both increased whereas white cedar and white pine decreased. Only the three-fold increase in balsam fir tree cover was significant. In many instances birch trees up to 40 or more years old were pedestalled on exposed roots as much as a meter above the ground. Although the two-fold increase in paper birch tree cover was not significant, birch accounted for 40% of the total canopy. White cedar accounted for nearly one-fourth of total tree cover. White pine represented about 5% of total tree cover in 2014, a decrease from 10% of total tree cover in 1997.

Total shrub cover decreased slightly over the 17 y. Only balsam fir significantly changed in the shrub layer with a nearly 10-fold increase (Table 1). Mountain maple decreased from about 61% of total shrub layer to 37%, as balsam fir increased from about 5% of the shrub layer to over 29%. White pine averaged <0.1% in the shrub layer. Patchiness resulted in very high variance. White and black spruce were both present in the tree layer and shrub layer, but averaged <1% cover.

There were also few significant changes in the herb and ground layers from 1997 to 2014 (Table 1). There were nonsignificant decreases in herb layer species richness and nonsignificant increases in exposed mineral soil and coarse litter. Raspberry and *Carex* spp. were the only taxa with significant changes, both decreasing. Although not significant, the three-fold increase in white cedar seedlings may be noteworthy.

When considering all post-fire data from the unburned transects, we gain a little additional insight into the stability of the old-growth forest. All changes were small relative to standard deviations, from 2008 through 2014. There was a 30% increase in total tree cover from 2008 through 2014 (Table 1). Paper birch, balsam fir, white cedar, and even white pine all increased in the tree layer. There were only small changes in the shrub layer. In the herb and ground layers there were increases in white cedar and coarse litter, nearly all from fallen limbs of old pines. Total herb-layer cover was twice as high in 2010 as in the other two years, probably because that spring was warmer than normal, allowing vegetation to be more advanced than usual in late May–early June when we collected data. (According to the National Weather Service, for the Ely, Minnesota, airport for March, April, and May, total heating degree days were 35% higher than in 2008 and 37% higher than in 2014.) Raspberry, while locally important, was restricted to spruce budworm mortality areas, with a ten-fold variation among sample years. Paper birch, *Lonicera canadensis*, *Maianthemum canadensis*, *Lycopodium obscurum*, *Aralia nudicaulis*, and *Clintonia borealis*

Table 1. Means for all metrics are based on 18 transects except for total plot richness, which is the total of the species recorded on each set of 18 transects. Average cover for pre-fire transects sampled in 1997 (GASE and GASW) are compared to unburned transects sampled in 2014 (GASE and GSE2) with one-way ANOVA. An asterisk on the 1997 mean indicates a significant difference ($P < 0.05$) from the 2014 mean. Each of the other means also are averages for 18 transects sampled in burned or unburned plots in the year indicated. One standard deviation is given in parentheses for the 2008–2014 means.

		Preburn	Unburned control transects			Burned transects		
	Metric (% cover)	**1997**	**2008**	**2010**	**2014**	**2008**	**2010**	**2014**
Tree layer	Total tree cover	68.8	61.9(33.8)	75.1(37.1)	87.9(28.7)	6.8(8.8)	12.4(19.2)	12.6(22.2)
	Paper birch tree cover	15.9	29.0(32.9)	32.2(28.3)	36.1(33.3)	<0.1(0.1)	3.2(9.7)	2.2(5.4)
	Balsam fir tree cover	6.6*	11.2(10.7)	15.7(14.2)	21.8(11.1)	2.2(3.8)	3.3(5.1)	1.6(3.5)
	White cedar tree cover	33.3	18.7(13.6)	17.7(19.5)	21.2(24.3)	2.5(4.4)	2.5(5.6)	5.5(12.1)
	White pine tree cover	7.2	1.4(4.4)	1.7(4.1)	4.5(10.2)	1.6(4.7)	0.0(0.0)	<0.1(0.1)
Shrub layer	Total shrub cover	51.3	74.6(27.3)	70.6(18.9)	65.2(21.2)	12.6(14.1)	41.4(21.6)	60.6(18.3)
	Mountain maple cover	31.2	30.4(19.5)	32.6(15.9)	24.6(16.9)	3.1(5.6)	7.6(9.7)	6.0(6.4)
	Balsam fir shrub cover	2.5*	15.6(13.1)	13.3(9.0)	19.2(11.9)	<0.1(1.3)	1.4(2.8)	1.7(4.3)
	Corylus shrub cover	8.8	12.4(16.1)	11.2(9.8)	8.4(10.5)	3.0(5.6)	7.7(10.5)	8.8(9.1)
	White cedar shrub cover	2.1	5.8(6.7)	5.7(4.9)	5.5(6.9)	<0.1(0.9)	1.4(2.6)	2.2(4.3)
	Aspen shrub cover	0.0	0.0(0.0)	0.0(0.0)	0.0(0.0)	0.0(0.0)	7.1(6.5)	9.5(9.6)
	Paper birch shrub cover	0.2	4.3(7.7)	2.5(3.4)	1.3(3.1)	0.0(0.0)	7.6(8.3)	24.2(17.9)
Herb and ground layers	Total ground-layer cover	47.0	30.7(16.7)	70.4(22.7)	38.8(18.3)	45.4(21.5)	111.2(32.6)	48.4(12.6)
	Total plot richness	97.0	46.0	51.0	49.0	56.0	53.0	55.0
	Avg. transect richness	19.9*	11.3(3.4)	15.2(3.9)	11.4(3.1)	16.7(5.7)	16.1(4.6)	13.6(3.7)
	Percent exposed mineral	0.8	1.3(2.7)	0.6(1.5)	3.4(9.6)	18.7(13.9)	7.1(7.6)	5.9(6.6)
	Percent coarse litter	22.7	26.7(10.8)	25.9(14.5)	33.1(11.7)	19.0(9.4)	21.7(11.5)	32.3(17.0)
	Raspberry cover	8.9*	3.9(6.4)	5.8(8.9)	0.8(1.6)	10.8(9.9)	32.6(18.9)	18.9(14.6)
	White cedar cover	2.4	3.8(7.2)	4.2(6.6)	8.2(11.8)	2.2(3.2)	1.7(2.0)	4.7(5.8)
	Aspen cover	0.0	0.0(0.0)	0.0(0.0)	0.0(0.0)	1.3(1.2)	7.3(5.1)	0.5(0.6)
	Mountain maple cover	2.4	0.7(1.1)	10.2(12.3)	3.0(4.4)	1.2(1.9)	3.9(5.4)	1.8(2.3)
	Balsam fir cover	3.2	5.4(6.6)	12.0(9.3)	3.1(5.7)	0.6(2.2)	1.2(3.8)	0.6(1.1)
	Paper birch cover	<0.1	<0.1(0.2)	1.0(2.6)	0.3(0.8)	5.8(7.4)	10.1(8.2)	3.6(3.1)
	Carex spp. cover	3.5*	1.0(1.9)	0.7(1.0)	0.6(1.3)	8.0(9.9)	13.4(9.7)	0.9(1.6)
	Fireweed cover	0.0	0.0(0.0)	<0.1(0.1)	0.0(0)	1.2(1.7)	4.6(3.5)	0.6(0.9)
	Corylus cover	0.3	0.6(1.5)	9.0(15.8)	1.1(2.5)	0.9(1.5)	10.3(15.0)	3.5(8.1)

exceeded 1% on some transects, but averaged <1% for any transect-year (Table 2). Tree seedlings, primarily balsam fir, paper birch, and white cedar, were nearly always limited to decayed nurse logs. Herb cover was especially sparse under white cedar and, to a lesser extent, under mountain maple. A total of 88 species were recorded on unburned transects from 1997 through the 2014 sampling year. Although richness decreased greatly from 1997–2008 through 2014, the difference was not significant because of high variance.

Exposed mineral surface averaged less than 2% and, correspondingly, the measured fine litter cover averaged over 98%. Coarse litter, primarily fallen limbs from the pines and decaying trunks of trees, averaged over 27% cover.

In addition to past death of large pines, the other primary disturbance was spruce budworm mortality of balsam fir. Patches, up to 1.0 ha, frequently coincided with mortality of overstory pines, as evidenced by decaying remnants and snags left when tops of old pines were broken off. During the 17 y of this study, we found steady increase in balsam fir tree and shrub-layer cover. In older gaps that apparently developed from prior budworm outbreaks, mountain maple was, by far, the most responsive species, often expanding to over 70% cover. Mountain maple with 5–6-m height grew in clumps with as many as a dozen stems, some as large as 20-cm dbh.

Most of the large overstory pines had died prior to when we began our 1977 observations, and the scattered remaining trees were dying very slowly. White pine regeneration was essentially absent throughout the 37 y of observation. In the ground layer, only white cedar appeared to be increasing, although the increase was nearly all from layering of branches of established shrub-layer specimens.

Fire in the Old-Growth Forest

The effects of the stand-replacing fire were dramatic with noteworthy changes in nearly every measure. In 2008, near the beginning of the second growing season after the 2006 fire, total tree canopy was 62% in the unburned transects and less than 7% in the burned transects. Tree cover on burned transects increased to over 12% by 2010, and remained unchanged in 2014 (Table 1). Much of the change in canopy cover resulted from delayed mortality and recovery of some birch and white cedar that were damaged but not killed, growing primarily in wet draws where fire tended to burn as a low-intensity ground fire. For example, in 2008 paper birch had 29% cover in unburned transects but <0.1% in the burned plots, but had recovered to over 3% cover in burned transects by 2010. White pine, with an average of about 4% cover in the unburned forest, was reduced by fire with only widely scattered survivors in wet areas. In the burned uplands, some of the big pines were still alive in 2008, but all were dead by 2010, leaving no overstory.

We found a decrease in total shrub-layer cover from nearly 75% on the control transects to about 12% on burned transects the second spring after the fire (Table 1). In 2014, total shrub cover was 65% on unburned transects and had increased to over 60% on burned transects, primarily from paper birch and aspen that seeded in after the fire and grew into the shrub and small-tree layer by 2014. There was an average of 2200 stems/ha of paper birch in unburned transects and 14,100 stems/ha in burned transects. Similar response was found with aspen seedlings, present only in the ground layer in 2008, but with an average density of 7000/ha and over 9% cover in the shrub layer by 2014. No aspen was found in the unburned forest. Mountain maple, white cedar, and balsam fir had little recovery, but by 2014 *Corylus* shrub cover equaled that found in the unburned forest.

Total herb-layer vegetation cover was greater on burned transects in each of the three years we followed the fire, but with great year-to-year variation (Table 1). On both burned and unburned transects, peak cover in 2010, four years after the fire, was probably a result of an unusually warm spring. Slightly more species were found on burned transects. There was an increase in average transect richness in 2010 when we also found considerably higher total cover in the ground layer. We recorded 83 species in burned transects during the three sample years of 2008 through 2014, 55 of which were also found on unburned transects. Of the 28 species found only in burned transects, two-thirds were found only in lightly burned wet or mesic draws.

In the ground layer, there was a large increase in exposed mineral soil on burned transects, but it decreased steadily and, by 2014, remained only slightly higher than on unburned transects. Coarse litter was reduced by the fire as measured in 2008, but it increased as fire-killed trees fell and by 2014 was not appreciably different from the amount of coarse litter on unburned transects.

Raspberry increased by an order of magnitude in the ground layer after fire, and was three-fold higher in 2010 than 2008, before falling off in 2014. In addition to raspberry, aspen, paper birch, *Carex* spp., and fireweed increased after fire. All of these taxa peaked in 2010, then decreased in 2014, but for different reasons. *Carex* and fireweed died out, but aspen and paper birch grew from the herb layer (< 1 m) into the shrub layer as discussed previously. Balsam fir was completely eliminated in the herb layer by the fire. Other species in the herb layer (Table 2), such as fringed bindweed, may have increased temporarily after fire, but their frequency was too low for our sampling protocol to detect such subtle changes.

Herb-layer cover of cedar in unburned transects was largely a result of decumbent branches <1 m tall (our subjective criteria for defining the herb-layer flora) that had taken root, most of which remained connected to larger stems. In the upland, all such herb-layer cedar cover was eliminated by the fire. Shrub-layer cedar increased slowly on burned transects through 2014 as small trees in wet areas recovered. The increase in the herb layer was a result of growth of seedlings. Seedlings were established primarily on exposed soils on cooler slopes and in shaded or protected mesic microsites. In some areas, they nearly blanketed the ground.

NMDS highlighted the species changes in the herb layer, clearly separating vegetation

Table 2. Cover of herb-layer plant species. Data are means of 1-m^2 quadrat samples averaged across treatment-years.

Binomials (after Gleason and Cronquist 1991)	**Common name**	**Unburned 1997–2014**	**Burned 2008**	**Burned 2010**	**Burned 2014**
Dracocephalum parviflorum	American dragon-head	0.0	0.1	0.0	0.0
Sorbus americana	American mountain-ash	< 0.1	< 0.1	0.0	0.0
Taxus canadensis	American yew	0.8	0.0	0.0	0.4
Polygonum sagittatum	arrow-leaved tearthumb	0.0	0.00	0.00	< 0.1
Abies balsamea	balsam fir	5.9	0.7	1.2	0.6
Actaea pachypoda	baneberry	< 0.1	0.0	0.0	0.0
Corylus cornuta	beaked hazel	2.8	0.9	10.3	3.5
Salix bebbiana	beaked willow	0.0	0.0	< 0.1	0.2
Galium spp.	bedstraw	< 0.1	0.0	0.0	0.0
Trillium flexipes	bent trillium	< 0.1	0.0	0.0	0.0
Trillium grandiflorum	big white trillium	< 0.1	0.0	0.0	0.0
Aster macrophyllus	big-leafed aster	0.5	0.4	2.3	1.3
Populus grandidentata	big-toothed aspen	0.0	0.0	0.3	0.0
Fraxinus nigra	black ash	0.0	0.0	0.0	< 0.1
Rubus occidentalis	black raspberry	0.1	0.5	0.0	0.5
Picea mariana	black spruce	0.1	0.0	0.0	0.0
Poa spp.	bluegrass	< 0.1	0.0	0.0	0.3
Calmagrostis canadensis	bluejoint	0.1	0.6	2.3	0.9
Ribes odoratum	buffalo-currant	0.0	0.0	< 0.1	0.0
Cornus canadensis	bunchberry	0.9	1.4	1.4	1.5
Diervilla lonicera	bush-honeysuckle	0.0	< 0.1	0.0	< 0.1
Maianthemum canadense	Canada mayflower	1.0	0.3	0.1	0.7
Osmunda cinnamomea	cinnamon-fern	0.0	0.2	0.0	0.0
Clintonia borealis	Clinton's lily	1.2	0.3	2.0	0.6
Lycopodium spp.	clubmoss	0.0	0.0	< 0.1	0.1
Vaccinium angustifolium	common lowbush-blueberry	0.0	< 0.1	0.0	0.0
Gaultheria hispidula	creeping snowberry	< 0.1	0.0	0.0	0.0
Taraxacum spp.	dandelion	0.0	0.0	0.0	< 0.1
Ribes cynosbati	dogberry	0.1	0.0	0.0	0.0
Cinna latifolia	drooping woodreed	0.0	0.0	0.0	0.1
Rubus pubescens	dwarf raspberry	0.1	0.0	0.0	0.0
Ribes americanum	eastern black currant	0.0	0.3	0.0	0.0
Pinus strobus	eastern white pine	0.1	0.0	0.0	< 0.1
Epilobium coloratum	eastern willow-herb	0.0	< 0.1	0.2	0.0
Circaea alpina	enchanter's nightshade	< 0.1	0.0	0.1	0.0
Schizachne purpurascens	false melic	< 0.1	0.0	0.0	0.0
Epilobium angustifolium	fireweed	< 0.1	1.2	4.6	0.6
Erigeron spp.	fleabane	0.0	< 0.1	0.0	0.0
Lonicera canadensis	fly-honeysuckle	1.1	< 0.1	0.4	0.3
Polygonum cilinode	fringed bindweed	0.0	1.5	0.3	0.0
Coptis groenlandica	goldthread	0.2	< 0.1	< 0.1	< 0.1
Ribes spp.	gooseberry	0.0	0.1	0.0	0.0
Viola selkirkii	great-spurred violet	0.2	0.0	0.0	0.0
Lonicera spp.	honeysuckle	0.0	0.0	0.0	0.0
Conyza canadensis	horseweed	< 0.1	0.0	0.0	0.0
Viola renifolia	kidney-leaved violet	0.1	0.4	0.0	0.0
Cornus amomum	knob-styled dogwood	< 0.1	0.0	0.0	0.0
Athyrium filix-femina	lady fern	< 0.1	0.0	0.0	0.0
Chamaedaphne calyculata	leatherleaf	< 0.1	0.0	0.0	0.0

Continued

Table 2. (Cont'd.)

Binomials (after Gleason and Cronquist 1991)	**Common name**	**Unburned 1997–2014**	**Burned 2008**	**Burned 2010**	**Burned 2014**
Dryopteris marginalis	marginal wood-fern	0.6	0.0	5.3	0.3
Thelypteris palustris	marsh-fern	0.0	0.0	< 0.1	0.1
Caltha palustris	marsh-marigold	< 0.1	0.0	0.9	0.2
Acer spicatum	mountain maple	4.1	1.2	3.9	1.8
Mitella nuda	naked mitrewort	0.2	0.0	0.0	0.0
Thelypteris phegopteris	narrow beech-fern	0.4	0.0	0.1	< 0.1
Mertensia paniculata	northern bluebell	< 0.1	0.0	0.6	0.0
Rubus flagellaris	northern dewberry	< 0.1	0.0	0.0	0.0
Lycopodium complanatum	northern ground-cedar	0.0	0.4	0.0	0.6
Viola palustris	northern marsh-violet	0.1	0.1	0.0	< 0.1
Cornus racemosa	northern swamp-dogwood	< 0.1	0.0	0.0	0.0
Galium triflorum	northern three-lobed bedstraw	0.2	0.4	0.1	0.6
Thuja occidentalis	northern white cedar	4.6	2.2	1.7	4.7
Oxalis acetosella	northern wood-sorrel	0.1	0.0	0.0	0.0
Gymnocarpium dryopteris	oak-fern	0.1	0.0	0.1	0.0
Impatiens capensis	orange jewel-weed	0.2	0.2	0.9	< 0.1
Betula papyrifera	paper birch	0.3	5.8	10.1	3.6
Anaphalis margaritacea	pearly everlasting	0.0	0.0	0.0	0.3
Prunus pensylvanica	pin-cherry	0.0	0.1	0.7	0.0
Pyrola asarifolia	pink shinleaf	0.1	0.0	0.0	0.0
Lycopodium obscurum	princess-pine	3.8	0.5	1.1	1.6
Populus tremuloides	quaking aspen	0.0	1.3	7.3	0.5
Acer rubrum	red maple	< 0.1	0.0	< 0.1	0.0
Rubus idaeus	red raspberry	4.9	10.8	32.6	19.1
Sambucus racemosa	red-berried elder	0.2	0.6	0.3	0.1
Rosa spp.	rose	< 0.1	0.0	0.0	0.0
Oryzopsis asperifolia	rough-leaved ricegrass	0.3	0.2	0.1	0.1
Lycopodium clavatum	running pine	0.0	0.0	0.0	0.0
Onoclea sensibilis	sensitive fern	0.1	0.0	0.0	0.0
Amelanchier spp.	serviceberry	< 0.1	0.0	0.0	< 0.1
Lycopodium lucidulum	shining clubmoss	3.1	2.0	1.1	0.7
Scutellaria sp.	skullcap	0.1	0.0	0.0	0.0
Vaccinium oxycoccos	small cranberry	0.0	0.0	< 0.1	0.0
Bromus inermis	smooth brome	< 0.1	0.0	0.0	0.0
Alnus incana	speckled alder	0.4	0.4	0.2	0.5
Dryopteris spinulosa	spinulose wood-fern	0.2	0.3	0.0	0.0
Apocynum androsaemifolium	spreading dogbane	0.0	0.0	4.2	0.0
Trientalis borealis	starflower	1.1	0.3	0.8	0.4
Lycopodium annotinum	stiff clubmoss	0.4	0.0	0.0	0.0
Ribes triste	swamp red currant	0.1	0.0	0.0	0.0
Rubus hispidus	swamp-dewberry	0.2	0.3	0.7	0.0
Viola blanda	sweet white violet	0.2	0.0	0.0	0.0
Rubus parviflorus	thimbleberry	0.4	0.1	0.9	0.0
Linnaea borealis	twinflower	0.6	0.1	< 0.1	0.1
Streptopus roseus	twisted stalk	0.7	0.0	0.3	0.1
Mitella diphylla	two-leaved mitrewort	0.1	0.2	0.0	< 0.1
Viola spp.	violet	0.2	0.0	0.0	< 0.1
Picea glauca	white spruce	0.3	0.1	0.1	< 0.1

Continued

Table 2. (Cont'd.)

Binomials (after Gleason and Cronquist 1991)	**Common name**	**Unburned 1997–2014**	**Burned 2008**	**Burned 2010**	**Burned 2014**
Lathyrus ochroleucus	white vetchling	0.0	< 0.1	0.0	0.0
Geranium bicknellii	wild geranium	0.0	0.2	< 0.1	0.0
Lonicera dioica	wild honeysuckle	0.1	0.0	0.0	0.0
Aralia nudicaulis	wild sarsaparilla	1.0	0.0	1.3	< 0.1
Viola macloskeyi	wild white violet	0.3	0.0	0.0	0.0
Gaultheria procumbens	wintergreen	< 0.1	0.0	0.0	0.0
Equisetum sylvaticum	woodland-horsetail	< 0.1	< 0.1	0.3	0.1
Luzula multiflora	wood-rush	0.0	0.0	0.0	0.1
Oxalis spp.	wood-sorrel	0.0	0.0	0.0	0.0
Athyrium spp.		< 0.1	0.0	0.0	0.0
Carex aurea		< 0.1	0.0	1.3	0.0
Carex communis		< 0.1	0.3	0.0	0.0
Carex debilis		< 0.1	0.0	0.0	0.0
Carex disperma		0.3	0.0	0.0	0.0
Carex intumescens		< 0.1	0.0	0.2	0.0
Carex pedunculata		0.7	0.0	0.1	0.3
Carex rossii		0.0	< 0.1	0.0	0.0
Carex spp.		0.2	7.7	11.8	0.5
Carex tenera		< 0.1	0.0	0.0	0.0
Carex trisperma		< 0.1	< 0.1	0.0	< 0.1
Carex umbellata		< 0.1	0.0	0.0	0.0
Fimbristylis spp.		0.0	0.2	0.0	0.0
Milium effusum		< 0.1	0.7	0.0	0.0

into pre- and post-fire clusters (Figure 3). Axis 1 explained 79% of the variance and Axis 2 explained an additional 18% with a total r^2 of 98%. Axis 1 was strongly negatively correlated with species found in the understory of unburned transects, especially ground pines (*Lycopodium lucidulum*, *L. obscurum*, *L. annotinum*), thimbleberry, balsam fir, mountain maple, white cedar, Canada yew (*Taxus canadensis*), Canada mayflower, *Carex pedunculata*, Clinton's lily, wild sarsaparilla, and fly-honeysuckle. Big-leafed aster, red raspberry, fireweed, seedlings of paper birch and quaking aspen, and various sedges were most strongly correlated with the burned transect trajectories after fire.

To further elucidate the extensive changes in the herb-layer vegetation following fire, TWINSPAN was used to identify groupings (not shown). In addition to clearly separating species that became prominent after the fire from those in the unburned forest, a group of 41 species was identified that was largely associated with wet and mesic microsites. Important species included Canada bluejoint grass, various sedges (especially *Carex rostrata*), and marsh-marigold.

We looked for post-fire responses in functional groups (Peterson et al. 2007). Only the graminoid group changed significantly ($P < 0.0001$) with an interaction between treatment (burned/unburned), and year (Table 3). Graminoid species, especially sedges, increased dramatically after the fire, but decreased nearly as abruptly from a peak four or five years after the fire.

DISCUSSION

In the long-term and continued absence of fire, white and red pines in the old-growth southern boreal forest eventually succumb to wind, insects, and disease with minimal regeneration, and are replaced by northern white cedar, balsam fir, white spruce, and paper birch (Heinselman 1973). Heinselman's conclusions were based on his study of old-growth remnants throughout the Quetico–Superior region, which included the old-growth forest that was the object of this study, the largest remnant he examined. Most of the old pines could not be accurately dated because of advanced heart-rot, although Heinselman dated one 41-in (104 cm) dbh white pine at 360 y in 1969. None of the old pines that we examined in 1977, eight years after Heinselman's study, had visible fire scars, however charcoal occurred in the upper soil horizon. The subtle change in unburned old-growth that we observed over 37 y was consistent with Heinselman's (1996) conclusions.

Both our observations as well as quantitative examination of vegetation indicate that in this old-growth forest the pines had been nearly all replaced and a different forest ecosystem was established. The increase in balsam fir, both in the canopy and small-tree layer, was likely a result of rebound from a previous spruce budworm outbreak prior to 1997 (Heinselman 1996). As balsam fir increased, there was

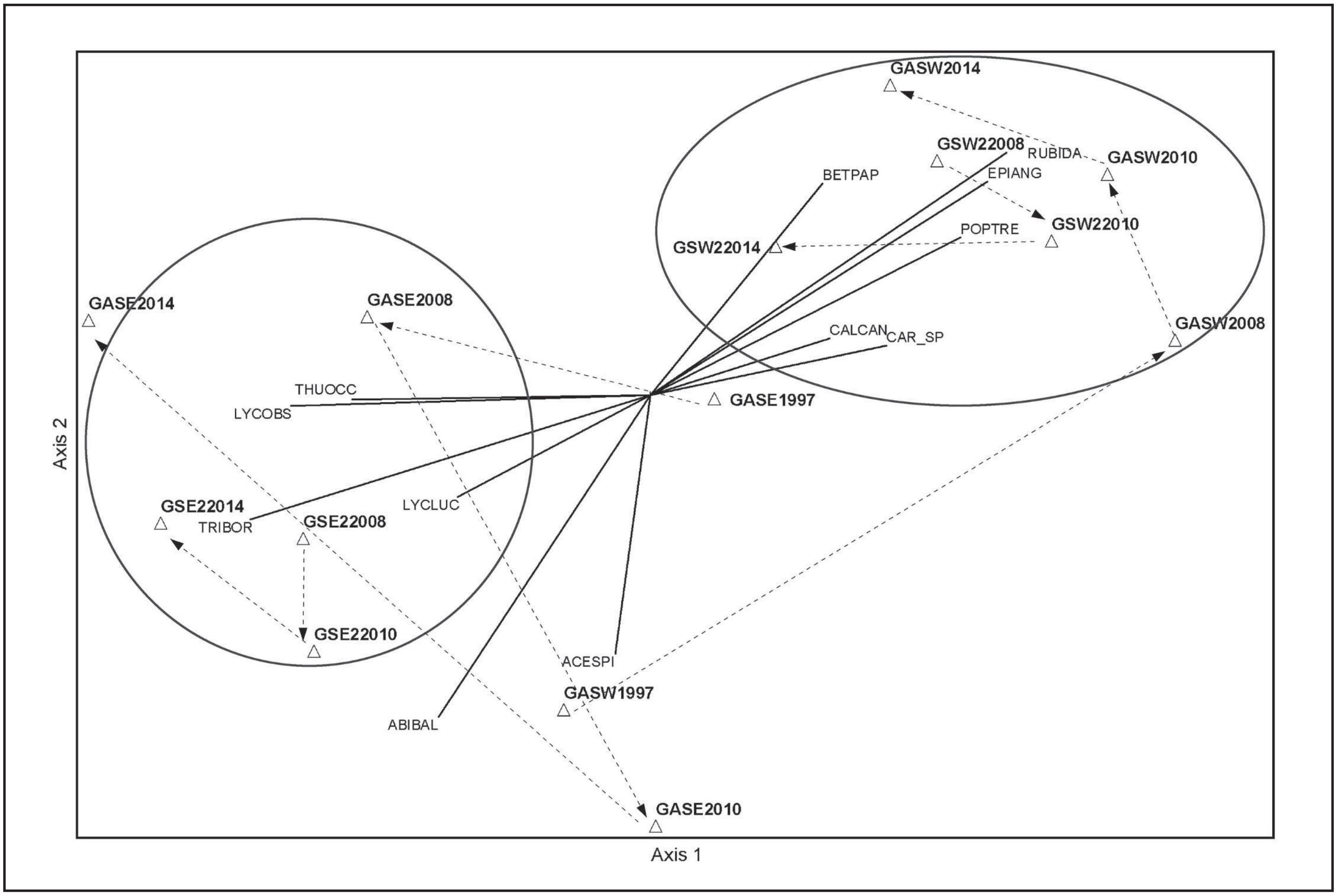

Figure 3. Nonmetric multidimensional scaling (NMDS) analysis comparison of burned and unburned herb-layer plant communities measured along transects. Arrows indicate trajectories of burned (GASW/GSW2 2008–2014) and unburned (GASE 1997; GASE and GSE2 2008–2014) plant communities. Only plant species with cover values >0.5% were used to evaluate shifts in plant communities.

a corresponding decrease in herb-layer richness, but only a modest decrease in total herb-layer cover. Periodic outbreaks of spruce budworm modify the abundance of balsam fir and this contributes some of the variation in herb-layer diversity and cover. Although the old-growth appears stable, some changes may yet occur. For example, in the absence of fire, paper birch recruitment depends on nurse logs and light gaps. As the remaining old pines die, paper birch may gradually decrease as nurse logs decay and canopy gaps close.

Loehle (1988) suggested that eastern white pine can live for ~450 y. In this stand, most exceeded 400 y, and nearly all evidenced advanced decay. Fire burned out the centers of many of the remaining pines, leaving temporary structures that provided nesting and roosting habitat for chimney swifts (*Chaetura pelagica* L.), among other animal species. Fallen trunks of large white and red pine, in various stages of decay, indicated that the stand had been dominated by pines, perhaps as recently as 1950, but was in the final stage of decline—what Heinselman (1973) called the "senescence period." Only one large red pine remained in our study area in 2014 and white pine canopy cover was reduced to just over 4%. None of the old pine stems had been felled by wind, but appeared to have died standing, then fallen after some initial decay.

We found no white pine, spruce, or balsam fir seedlings through eight years post-fire. While the latter would not have been expected, we did expect at least some white pine would regenerate from surviving trees in moist draws and the few remaining overstory old trees that survived for at least two years after the fire. At least some old-growth white pines can provide seeds for regeneration during 10–20 y following stand-replacing fire (Heinselman 1996). Abrams (2001), however, concluded that white pine was probably more likely to be recruited by moderate fire rather than high-intensity fire, and likely more in forests where trees are not so old. In this forest, with the dense understory and heavy litter accumulation, the fire was especially intense, and the old pines, with advanced heart-rot, may have been more susceptible to fire. No white pine individuals on uplands survived beyond two years after fire.

In mesic draws, white cedar dominated the

Table 3. Summed % absolute cover of graminoid species averaged across each transect.

	2008	2010	2014
Unburned	2.5	2.3	2.0
Burned	72.1	106.9	5.9

canopy with a sparse understory of birch or balsam fir. The age of cedars averaged 250–300 y, somewhat younger than the estimated age of the pines, suggesting they had become established during succession after the initial fire, ~1610. In the unburned old-growth, cedar was recruited primarily through vegetative layering; cedar tree and shrub-layer cover was not increasing. Where gaps occurred in the balsam fir canopy, following spruce budworm mortality, mountain maple had increased and in places formed an open canopy at 5–6-m height, consistent with the conclusions of Aubin et al. (2005). Mountain maple did not increase, however, over the 17 y we monitored the stand, and it was scarce under the cedar canopy. Shrub-layer balsam fir was sparse under mountain maple.

Graminoid species were the only functional group that responded significantly to fire, a response we also observed following salvage logging after severe wind disturbance (Lain et al. 2008). Following the fire, total sedge cover, including several species not previously found in the unburned forest, increased ten-fold within four years over much of the upland, suggesting that these may have developed from dormant seeds in the seed bank. We have previously documented seedbank responses in nearby 70- to 90-year-old forests sampled before and after fire (Apfelbaum and Haney 1981) to include many of the plant species that typically increase after fire, such as fringed bindweed and wild geranium. However, geranium was not present in this forest after fire. It apparently did not survive as well in the seed bank since the fire event that gave rise to the old-growth. Similarly, jack pine, if it ever occurred, was completely eliminated through succession and, therefore, was not present in post-fire regrowth.

The fire exaggerated differences among transects. Vegetation composition and structure on upland transects changed greatly whereas transects that crossed wet or mesic draws experienced, on average, far less change. Thus, variance in vegetation metrics increased among samples after fire. Much of the differences between transects were attributable to the different proportions of wet and mesic draws compared to upland transects. Within eight years after fire, however, the differences diminished.

Future without Fire

The probability of fire will likely increase with climate change that also will likely increase severe wind events and, perhaps, more severe spruce budworm outbreaks (Clark 1988). Many researchers have observed that white cedar, birch, spruce, and balsam generally replace white pine in the long-term absence of fire (Heinselman 1973, 1996; Frelich and Reich 1995; Leithead et al. 2012). This is certainly what we observed, although spruce was a very minor component of this forest. The change was largely completed by 400 y and the forest now seems stable. Nevertheless, the composition of mature forests in this region can change suddenly with severe wind events (Canham and Loucks 1984; Burris and Haney 2005, 2006) or spruce budworm defoliation (Batzer and Popp 1985), which would temporarily open gaps that might allow increases in paper birch or mountain maple. We saw evidence of wind disturbance during the 37 y of direct observation, but it primarily resulted in loss of large limbs and occasional tops from overstory trees. Tip-ups, exposed root masses with associated soil when trees are blown over, were rare, but may become more common with stronger wind events and, if so, favor paper birch or white cedar. Our data suggest that balsam fir and white cedar will continue to dominate until either fire or an unusual outbreak of spruce budworm, consistent with conclusions of Heinselman (1996). Heinselman (1996) also predicted that paper birch, which is mostly an early seral species, would remain a strong component of old-growth by getting started on nurse logs. To the extent that tip-ups offset loss of nurse logs, we agree. Heinselman also concluded that the absence of fire would result in the loss of aspen. While we generally agree at the stand scale, the ability for long-range seed dispersal allows aspen to reinvade from parent trees far removed from individual stands if there is severe wind disturbance.

Future Trajectory with Fire

In the Quetico–Superior region, it seems unlikely that any stand would be so isolated as to not have aspen following stand-replacing fire. Aspen, which was completely absent in unburned old-growth, was present in virtually every square meter on burned upland two years following the fire. The nearest stands of aspen were approximately 1 km away; wind dissemination can easily carry aspen seeds many times that distance (Perala 1990). Paper birch regenerated nearly twice as successfully as aspen based on stem counts in the shrub layer. While paper birch was abundant in the unburned forest, it will be even more so in the first-generation post-fire forest.

Although it will take several decades to attain maturity, white cedar will probably maintain about the same distribution and abundance as was present in the pre-fire old-growth. While seed dispersal is effectively limited to within 45–60 m of parent trees (Johnson 1990), mature white cedar survived in wet draws. It also is possible for catkins to survive the fire and release viable seed the following winter (Lee Frelich, pers. comm.). Recruitment well beyond 60 m of surviving trees suggests that some northern white cedar cones on fire-killed trees survived fire. White cedar seedlings, restricted to old nurse logs and tip-ups in the unburned forest, carpeted most mesic microsites after fire. White cedar will grow on uplands with adequate moisture, best on deeper soils with good nutrient content (Johnson 1990; Heinselman 1996). We found no seedlings of white cedar in wet draws, but they were abundant on lower slopes and even uplands in microsites shaded by coarse woody debris or aspen and birch regrowth.

White cedar is slow-growing, especially on acidic soils such as these; seedlings were less than 15-cm tall eight years after the fire. White cedar, however, is sufficiently tolerant (Johnson 1990) to persist under developing aspen, at least on mesic sites.

Birch and aspen seedlings had reached over 2 m tall by 2014. Heinselman (1996) estimated that the aspen–birch community type occupied 6.3% of the unlogged areas in BWCAW. He did not mention, however, that this community type probably was a result of intense fire in stands without pine, or that under some conditions, white cedar could be recruited along with the aspen and birch.

The few surviving white pines in mesic and borders of wet draws that were not blown down by the high winds during fire may provide a source for some pine recruitment in surrounding uplands in the next decade or two. White pines, even on favorable sites, produce good seed crops irregularly and regeneration is often sporadic after fire even when some parent trees survive. White pine cone beetle (*Conophthorus coniperda* Schwarz) may result in failure of white pine seed production and good seed crops often occur only every decade (Wendell and Smith 1990). Thus, it is possible that white pine might still gain some presence in the post-fire succession, but clearly white pine will not regain dominance in the next generation of this forest.

The potential for landscape topography to influence successional patterns should not be overlooked (Fahey 2012). Variation in topography, and even microsite variation, was important for maintaining not only herb-layer species diversity at the stand scale but was important in post-fire tree recruitment, especially northern white cedar. Whereas intense fire occurred through the uplands, it skipped lightly across wet draws and depressions where different species resided and where herbaceous vegetation was relatively little impacted. As a consequence, the fire greatly sharpened the contrast between the vegetation of uplands and depressions.

In the absence of future severe disturbance, a new aspen–birch forest with a patchy understory of white cedar will develop, perhaps with scattered white pine limited to wetland margins. Over time, we predict a slow increase in balsam fir, recruited primarily from surviving trees in wet draws. For at least the next several decades, the decaying logs of fallen white pines will continue to serve as potential nurse logs for birch, white cedar, and perhaps white pine, although white cedar and especially birch already are well represented in the next generation.

The progressive loss of fire-tolerant pines from US forests is a common story. For example, California and Southwestern forests, once dominated by fire-tolerant pines like ponderosa (*Pinus ponderosa*), Jeffrey (*P. jeffreyi*), and sugar (*P. lambertiana*), have been replaced by fire-intolerant, shade-tolerant species such as white fir (*Abies concolor*) and incense cedar (*Calocedrus decurrens*) following logging of the pine and a century of fire suppression (North et al. 2016). When fires occur today, they are commonly severe events that create large patches of mortality that are not easily recolonized by the heavy-seeded pines. As in the forest we studied, the low density of pines in the modern forest also greatly reduces pine reproduction (Welch et al. 2016). In these forests, multiple moderately severe fires, mechanical reduction, and supplemental planting are often necessary to reduce the fir and cedar and regenerate the pines (Walker 1999; Bailey and Covington 2002). Longleaf pine (*P. palustris*) is another fire-tolerant species that once dominated southeastern US landscapes but is now rare due to logging and fire suppression (Landers et al. 1995).

SUMMARY

In a landscape where the natural fire return interval is about a century, this southern boreal forest escaped fire for ~400 y, eventually exceeding the regeneration cycle of white pine. The slow loss of pines corresponded with an increase in balsam fir, paper birch, and northern white cedar, and accumulation of fine and coarse litter. Spruce budworm and wind, along with periodic death of large pines, maintained gaps in the canopy that permitted persistence of paper birch, but not white pine. Periodic gaps were likely also important for maintaining understory diversity, which remained stable over the 17 y of the study, with local decreases during periods of balsam fir increase. Dense old-growth conditions resulting from four centuries without fire increased the forest's vulnerability. When fire occurred, it burned with unusual intensity resulting in complete mortality of remaining old pines along with upland balsam fir, paper birch, and white cedar. Aspen, with its excellent wind dissemination, became established quickly from distant seed sources. Paper birch was even more successful than aspen, but likely from catkins on fire-killed trees. White cedar became established in mesic microsites from seeds from fire-killed trees or trees surviving along wet draws. The next generation will be a birch–aspen–northern white cedar forest with few white pines. Understory diversity was not affected greatly by fire, but composition changed dramatically; eight years after fire, the herb layer was beginning to return to its pre-fire state, however. At the landscape scale, moist topographic depressions buffered fire effects and were important contributors to post-fire composition of the understory as well as tree species recruitment.

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