NRC Research Press

ARTICLE

Prescribed burning of harvested boreal black spruce forests in eastern Canada: effect on understory vegetation

Nicolas Faivre, Catherine Boudreault, Sébastien Renard, Nicole J. Fenton, Sylvie Gauthier, and Yves Bergeron

Abstract: Ecosystem-based management advocates that forestry disturbances should aim to emulate natural disturbances to mitigate the landscape-level impact of forest management. This study compares the impact of clear-cuts followed by a prescribed burn (CCPB) with clear-cuts alone (CC) and current careful logging practices (CLAAG: "careful logging around advanced growth") on understory composition within black spruce (*Picea mariana* Miller (BSP)) paludified forest stands at the plot, site, and treatment levels using a functional-type approach. Vascular and nonvascular taxa showed significant differences in composition at the plot level among treatments. We found that pioneer taxa occurred mainly in CCPB sites, while late-successional taxa characterized CC sites. CLAAG sites had higher taxa richness than CCPB and CC sites, and we found that CCPB treatments were most likely to promote vascular taxa compositions that are more similar to those observed after natural disturbances. Additionally, the relative abundance of *Sphagnum* spp., responsible for paludification, was significantly reduced in sites treated by prescribed burning. This study therefore presents results suggesting that prescribed burning might represent a sustainable alternative to current harvesting techniques in the Clay Belt of eastern Canada that could help in preserving biodiversity (in terms of understory species assemblage) while maintaining or even enhancing forest productivity.

Key words: boreal forest ecosystem, black spruce forest stands, prescribed fire, clear-cut, biodiversity, understory composition, conservation management, paludification.

Résumé : Les stratégies d'aménagement forestier écosystémique préconisent d'imiter les effets des perturbations naturelles pour atténuer l'impact de traitements sylvicoles à l'échelle du paysage. Cette étude compare les effets de coupe totale suivie de brûlage dirigé (CCPB) avec ceux de coupe totale (CC) et de pratique sylvicole appliquée limitant la perturbation du sol (CLAAG : « careful logging around advanced growth ») sur la composition des espèces de sous-bois, au sein de peuplements d'épinette noire (*Picea mariana* Miller (BSP)) touchés par la paludification. Les analyses, effectuées à l'échelle de la placette, du site et du traitement ont permis via l'analyse des taxons et des types fonctionnels d'examiner les effets respectifs de chaque traitement. Des différences de composition significatives parmi les espèces vasculaires et non-vasculaires ont été observées à l'échelle de la placette selon le type de traitement considéré. Nous avons constaté que les espèces pionnières étaient associées aux sites CCPB tandis que les espèces de fin de succession étaient caractéristiques des sites CC. Une richesse spécifique plus élevée a été observée parmi les sites CLAAG que dans les sites CCPB et CC. Nous avons par ailleurs trouvé que les traitements CCPB étaient davantage enclin à promouvoir des patrons de composition d'espèces vasculaires similaires à ceux observés après des perturbations naturelles comme les feux de forêt. Nous avons également constaté une abondance relative plus faible des espèces de sphaigne, responsable du phénomène de paludification, au sein des sites traités par brûlage dirigé. Les résultats de cette étude suggèrent ainsi que le brûlage dirigé représente une alternative durable aux pratiques sylvicoles actuelles en permettant de conserver la biodiversité (en termes d'assemblages d'espèces) et de maintenir voire d'augmenter la productivité des peuplements exploités.

Mots-clés : écosystème forestier boréal, peuplements d'épinette noire, brûlage dirigé, coupe totale, biodiversité, composition des espèces de sous-bois, gestion de la conservation, paludification.

Introduction

In boreal forests, stand-replacing wildfires are considered to be the primary disturbances that drive natural forest dynamics (Bergeron et al. 2001; Harvey et al. 2002, Bouchard et al. 2008; Johnstone et al. 2010*a*). Forest attributes, including stand composition and structure, and understory composition are strongly influenced by fire characteristics and postfire succession (Lecomte et al. 2006; Johnstone and Chapin 2006). Natural dynamics in boreal forests are also the result of secondary disturbance agents between fire events, particularly spruce budworm (e.g., *Choristoneura*

Received 4 November 2015. Accepted 9 April 2016.

N. Faivre. Cemagref, UR EMAX, 3275 Route Cézanne CS 40061, 13182 Aix-en-Provence, France.
C. Boudreault. Centre d'Étude de la Forêt and the Natural Sciences and Engineering Research Council of Canada, UQAM-UQAT Industrial Chair in Sustainable Forest Management, Université du Québec à Montréal, C.P. 8888, Succursale Centre-Ville, Montréal, QC H3C 3P8, Canada.
S. Renard. Parks Canada, 1340 Rue de la Digue, Havre-St-Pierre, QC G0G 1P0, Canada; Forest Research Institute and Natural Sciences and Engineering Research Council of Canada, UQAT-UQAM Industrial Chair in Sustainable Forest Management, Université du Québec en Abitibi-Témiscamingue, 445 boul. de l'Université, Rouyn-Noranda, QC J9X 1C5, Canada.
N.J. Fenton and Y. Bergeron. Forest Research Institute and Natural Sciences and Engineering Research Council of Canada, UQAT-UQAM Industrial Chair in Sustainable Forest Management, Université du Québec en Abitibi-Témiscamingue, 445 boul. de l'Université, Rouyn-Noranda, QC J9X 1C5, Canada.
S. Gauthier. Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre, 1055 du PEPS, P.O. Box 10380, Stn. Sainte-Foy, Québec, QC G1V 4C7, Canada.
Corresponding author: Nicole Fenton (email: Nicole.fenton@uqat.ca).

fumiferana Clemens) outbreaks in eastern Canada and windthrow. Although insects and other nonfire disturbances can impact larger areas than wildfires, their effects on vegetation communities are selective (i.e., species-specific) and will mostly result in diversified age-class distributions of forest stands and patchier landscape habitats than following fires (Bergeron and Fenton 2012).

In recent decades, forest harvest has become a dominant disturbance across the boreal forests, even more important than fire in some areas (Cyr et al. 2009; Stinson et al. 2011). This has led to a call for management techniques that mimic fire disturbances to preserve the ecosystem functions and biodiversity of the forest landscape (e.g., Gauthier et al. 2009). One important difference identified between forest harvest and wildfire is the impact on understory succession (Brumelis and Carleton 1989; Nguyen-Xuan et al. 2000; Haeussler and Bergeron 2004), which in turn can have a strong impact on the nature and future productivity of the regenerating forest (Reich et al. 2001). Initial postdisturbance microhabitat characteristics (and therefore understory composition) and subsequent temporal changes in microhabitat availability are expected to differ following fire or harvesting. In very general terms, fire is expected to remove the organic layer, thus creating a greater quantity of exposed mineral microhabitats and a more drastic departure from preharvest communities compared with clear-cutting (Nguyen-Xuan et al. 2000). In contrast, postharvest understory communities are generally more similar to the preharvest communities compared with those resulting from wildfire (Noble et al. 1977; Rees and Juday 2002) and are dominated by tolerant bryophytes and residual vascular plants (Haeussler and Bergeron 2004; Hart and Chen 2006). Pioneer species that favour postfire conditions of exposed mineral soil, charcoal substrates, and seedbed recruitment are virtually absent from the postharvest communities (Nguyen-Xuan et al. 2000; Hart and Chen 2006).

Prescribed burning is used worldwide as a management tool with various objectives such as wildfire hazard reduction, ecosystem restoration, site preparation for tree planting, or species conservation. In Fennoscandia, the use of prescribed burning has been recommended since the 1920s to stop the progressive accumulation of raw humus from causing a decline in the productivity of secondary succession stands (Sirén 1955). Although it is currently less frequently used than before, it is still considered a practice that could diversify the types of vegetation assemblages, maintain boreal forest species composition (Vanha-Majamaa et al. 2007), and reduce the differences between natural and managed forest stands (Scheller et al. 2005, although see Pidgen and Mallik 2013).

The Clay Belt area in eastern Canada supports a major forest industry, and most harvested black spruce (*Picea mariana* Miller (BSP)) forest stands are situated within areas prone to paludification (the accumulation of a thick *Sphagnum* layer) due to its cold climate and poorly drained landscapes (Riley 1994; Fenton et al. 2005; Lecomte et al. 2005; Simard et al. 2007). Different variants of the clear-cutting system were implemented in recent decades. Traditional clear-cut (CC) harvesting was widely used in Canadian boreal forests until the 1990s, and this treatment mixed the soil organic layers and the underlying mineral soil because of low bearing capacity soil, especially when applied during summer (Marshall 2000; Lafleur et al. 2010). In doing so, it increased organic matter decomposition rates and soil pH and induced nutrient release (Duchesne and Wetzel 1999; Scheuner et al. 2004). Concerns about soil protection and tree regeneration led to a change in harvesting methods to careful logging techniques such as "careful logging around advanced growth" (CLAAG), which is currently the recommended harvest practice in the boreal part of the province of Ontario, Canada (Groot and Adams 2005; Ontario Ministry of Natural Resources (OMNR) 1997). This harvesting practice has resulted in little impact on soil organic layer depth and physicochemical properties, as well as on understory vegetation composition and cover (Lafleur et al. 2010). Prescribed fires of moderate intensity applied shortly after harvesting have also been used in Ontario (1970–1990) as a site preparation technique mostly to reduce slash and to prepare sites for planting after clear-cutting (McRae 1985), hereafter referred to as "clear-cutting followed by prescribed burns" (CCPB). In the last two decades, the use of prescribed burning in eastern boreal Canada has significantly decreased due to financial, security, and smoke issues.

CCPB has been identified as a suitable restoration practice in ecosystem-based management, especially for its potential to limit the accumulation of raw humus in a similar way to unplanned fires (Bergeron et al. 1999; Simard et al. 2009; Renard et al. 2016). However, few studies have examined whether this practice results in understory communities more similar to wildfire than other forest regeneration strategies in Canada (although see Pidgen and Mallik (2013) in jack pine (*Pinus banksiana* Lamb.)). The existence of CCPB treatments in the Clay Belt provided an ideal experimental setting to assess the effect of such a treatment on the understory community in the context of ecosystem management. The objectives of this study were therefore (*i*) to compare the effects of CC, CLAAG, and CCPB on understory plant communities using a functional-group approach and (*ii*) to investigate the ability of each silvicultural treatment to emulate the effects of natural disturbances by comparing their respective effects on community composition by functional group with those of wildfires. We believe that CCPB will likely promote more diverse understory assemblages than other treatments by removing an important part of the organic layer and that the understory composition of CCPB sites will be more similar to those of sites affected by wildfires. We also believe that CLAAG treatments will exhibit higher community dominance by *Sphagnum* spp. and other bog mosses due to increased soil protection.

Materials and methods

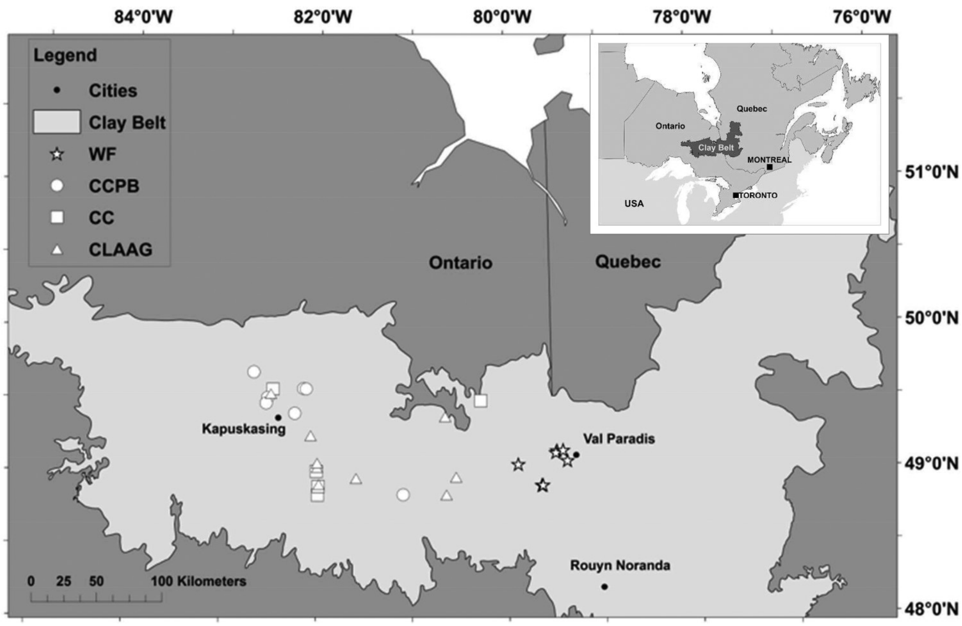
Study area

This study was undertaken in the boreal forest of the Clay Belt of eastern Canada (Fig. 1), which covers 125 000 km^2 and is characterized by a cold and humid climate. During 1981–2010, the daily average temperature recorded at Kapuskasing CDA station was 1.1 °C, the average cumulative precipitation was 838.6 mm, with 570.3 mm as rain and 274.1 cm as snow (Environment Canada 2013, http://climate.weather.gc.ca). The study sites were located in northeastern Ontario (49°25′N, 82°26′W) in the black spruce – feathermoss vegetation association (Rowe 1972; Grondin et al. 1996), where forest sites are typically dominated by black spruce and the forest floor is covered by *Sphagnum* spp. and *Pleurozium schreberi* (Brid.) Mitt. or other feathermosses. Primary disturbances in this area are large crown fires, and there has been a gradual increase in the fire-free interval since 1850 from 75–100 to 350–425 years (Gauthier et al. 2002; Bergeron et al. 2001). This increase is a result of less frequent droughts since the mid-19th century due to the impacts of climate change and more effective fire suppression over the last 50 years (Bergeron et al. 2004; Gauthier et al. 2002).

Site selection

Retrospective studies rely on a thorough site selection process to ensure the similarity of initial conditions of the study sites. We used two approaches to evaluate the similarity of the initial conditions before treatments. First, we examined archival data from the Ontario Ministry of Natural Resources (OMNR), with additional information from the forestry company Tembec, which manages the area. Secondly, we identified permanent site features in the field that could not be affected by the type of harvest treatment, i.e., mineral soil texture and drainage (following Taylor et al. 2000) and preharvest stand density (number of stumps in each site).

Fig. 1. Location of the study sites in the Clay Belt of eastern Canada. Sites are depicted according to experienced perturbation or treatment i.e., wildfire (WF), clear-cut followed by prescribed burning (CCPB), clear-cut (CC), and careful logging around advanced growth (CLAAG). The top-right inset shows the location of the Clay Belt in relation to the Great Lakes and major Canadian cities. The extent of the Clay Belt reflects the extent of glacial Lakes Barlow and Ojibway.



A total of 21 sites (seven CCPB, six CC, and eight CLAAG) were selected according to the following biophysical criteria: (*i*) mature black spruce stands > 120 years old at the time of harvest, (*ii*) preharvest canopy cover composed of at least 80% black spruce, and (*iii*) soil conditions ranging from moist mineral soil to deep fibric organic soil, with abundant *Sphagnum* spp., feathermosses, and ericaceous shrubs (Taylor et al. 2000). All retained sites were also characterized by (*iv*) slope < 3° and (*v*) soil organic layer depth > 20 cm (on average) over clay mineral soil. Such selection criteria were deemed a compromise between homogeneous preharvest understory composition for comparing treatments and maintaining inter- and intra-site variability using selection criteria that are not highly correlated. The time since treatment of the sites varied from 12 to 32 years for CLAAG treatment, from 14 to 26 years for CCPB treatment, and from 19 to 42 years for CC treatment (Table 1). In the case of CCPB, prescribed burning was used as a site preparation technique and was usually applied in the summer following clearcutting, i.e., within 12 to 24 months. Time since disturbance for these sites is considered as the time since the prescribed burn and it was treated as a single disturbance.

To compare the effects of the three treatments (CC, CCPB, and CLAAG) with those of wildfires (WF) on understory composition patterns, we also used data from previous studies in WF that occurred in the Clay Belt of Ontario and Quebec, where understory vegetation was sampled. We carefully checked that each site fulfilled the selection criteria stated above for the CC, CLAAG, and CCPB sites. The vegetation of three sites with postfire ages of 38, 39, and 46 years was sampled during the summer of 1996 in northeastern Ontario (Harper et al. 2003). Six additional sites from the Val-Paradis wildfire (Bordeleau 1998) were also selected: three of these sites were sampled in 2005 (8 years after the fire) and three other sites were sampled in 2012 (15 years after the fire).

Sampling

Fieldwork for the CC, CLAAG, and CCPB sites was conducted during the summers of 2006, 2007, and 2008. In each site, we randomly established three 400 m^2 circular plots (11.28 m radius) in areas that were representative of the overall stand composition and vertical structure. Plots were located 50 m or more from the road and at least 30 m from each other. Within each plot, we conducted assessments of the soil profile. We measured the depth of the soil layer by digging three pits per plot until we reached the mineral soil; if the mineral soil was not reached, a maximum depth of 130 cm was recorded. We also measured the height and the diameter at breast height (DBH) of the highest tree and calculated the density of black spruce trees > 2 m.

We further established four circular subplots of 4 m^2 (1.13 m radius) every 2 m along the north–south axis in each plot. Within these subplots, percent cover of vascular plants, including tree saplings (<2 m), and large easily identifiable nonvascular plants in the understory were visually recorded, and their relative cover was estimated using the following ordinal scale: 1 = 0%–1%, 2 = 1%–5%, 3 = 5%–25%, 4 = 25%–50%, 5 = 50%–75%, 6 = 75%–100%, and 7 = 100%.

For the WF, the understory vegetation of the sites of the Val-Paradis fire (8 years and 15 years after the fire) was estimated in ten 4 m^2 subplots. The cover of each species was visually estimated by cover class (from 1 to 7 as above). Similarly, the cover of the understory vegetation for the three sites sampled in 1996 was also visually estimated by cover class (from 1 to 7) but in forty 1 m^2 subplots. To compare species composition among WF sites with other treatments, we calculated an average cover value per site for each species.

Statistical analyses

To preserve accuracy and consistency in data among the different surveys, we restricted our analyses to the genus level for most bryophyte and lichen species, with the exception of a few easily identified species (e.g., *P. schreberi*; for details, see Supplementary Table S1[1]). Due to the multiple data sets analyzed in this study and the inevitable differences in taxonomic precision, we refer to taxa rather than species. In addition to examining patterns in taxa, we

[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2015-0439.

Table 1. Mean ± SD of site characteristics for each treatment.

	CLAAG (N = 8)		CC (N = 6)		CCPB (N = 7)	
	Mean	SD	Mean	SD	Mean	SD
Time since disturbance (years)	23.63	6.35	22.83	3.42	19.17	4.83
Soil organic layer depth (cm)	77.64	29.94	57.83	20.23	62.08	37.03
Soil pH	4.1	0.64	3.97	0.95	4.55	0.91
Black spruce height (cm)	208.56	149.24	198.52	130.4	215.08	144.91
Stand density (stems·ha^{-1})	15 854.72	6071.06	10 754.76	6014.48	9807.54	8027.22

Note: CLAAG, careful logging around advanced growth sites; CC, clear-cut only plots; CCPB, clear-cut prescribed burn plots.

also adopted a plant functional-type approach, grouping species by characteristics that impact their function in the ecosystem (see Supplementary Table S1[1]; adapted from Hekkala et al. 2014). These types are as follows: forb, fern, evergreen dwarf shrub including Lycopodiaceaea, deciduous dwarf shrub, shrub, graminoid, lichen, forest moss, bog moss, and pioneer moss.

Comparative analysis of silvicultural treatments

Understory richness and abundance

We compared taxa richness and cover of plant functional types among treatments using mixed models (PROC MIXED; SAS Institute 2013). Taxa richness and plant functional type abundance were calculated at the subplot level. Taxa abundance corresponded to the sum of the cover of all species in each type. We considered treatment as a fixed factor and plot nested within site as a random factor, and we further estimated the denominator degrees-of-freedom (df) using Satterthwaite's approximation. Plant functional-type cover values were log transformed (log x) to satisfy the normality and homoscedasticity assumptions of ANOVA. Significant differences ($p \leq 0.05$) between classes in all ANOVAs were detected with LSmeans Tukey's HSD tests.

Understory composition patterns

We sought to evaluate the compositional differences between treatments by performing a permutational MANOVA (McArdle and Anderson 2001) using the function adonis in the vegan package (Oksanen et al. 2008) in R (R Core Team 2013). Taxa cover was averaged at the site level (n = 21), and multiple pairwise comparisons were performed to compare composition between treatments (CC vs. CCPB, CC vs. CLAAG, CCPB vs. CLAAG). We used the Bray–Curtis dissimilarity measure and tested the results for statistical significance using the Monte Carlo technique (N = 999 permutations).

We identified indicator taxa for each treatment with the method developed by Dufresne and Legendre (1997) with the labdsv function of the vegan package (Oksanen et al. 2008) in R (version 2.15.3). The analysis was conducted on taxa cover per plot (average of the four subplots). The indicator values (IVs) were calculated using the relative abundance and percent cover of taxa for each plot. IVs range from 0 to 100, where 100 indicates taxa found exclusively in all plots of a single treatment. The threshold level for the IV was set at 25% (Dufresne and Legendre 1997). The significance of these IVs was assessed by Monte Carlo tests (1000 permutations). Only taxa with a frequency greater than 10% were included in the analyses.

We investigated the influence of environmental factors on composition using partial redundancy analysis (pRDA; rda function of the vegan package in R, version 2.15.3). Taxa cover was averaged at the plot level (n = 63). Time since treatment was considered as a covariable, and environmental variables considered in this analysis were treatment, plantation, density of black spruce trees > 2 m, organic layer depth, average height of the dominant trees, average DBH of the dominant trees, black spruce sapling cover, trembling aspen (*Populus tremuloides* Michx.) sapling cover, and balsam fir (*Abies balsamea* (L.) Mill.) sapling cover. Treatment (CC, CCPB, or CLAAG) and plantation (planted or not planted) were categorical variables and were represented on the graph as centroids, while other variables were continuous. Hellinger distance was used, and only taxa with greater than 5% frequency were included in the analyses (for a total of 60 taxa).

Comparative analysis between wildfires and silvicultural treatments

Permutational MANOVA was also performed including WF sites (for a total of 30 sites), and multiple pairwise comparisons were performed to test compositional differences between treatments and WF (CC vs. WF, CLAAG vs. WF, CCPB vs. WF).

We used correspondence analysis (CA) to visually assess the composition resulting from the different treatments (CC, CCPB, CLAAG) and from wildfires (WF). The analysis was performed with the cca function of the vegan package (Oksanen et al. 2008) in R (vers. 2.15.3). Data were averaged at the plot scale, and only taxa present in more than four plots were included in the ordination (for a total of 60 taxa and 72 plots).

Results

Overall understory richness and abundance among silvicultural treatments

During our assessment, we recorded a total of 87 taxa: 64 in CC, 62 in CCPB, and 62 in CLAAG (Supplementary Table S1[1]). Overall, we found significant differences in taxa richness and mean cover of several functional types among treatments (Table 2). Taxa richness was significantly higher in CLAAG sites (p = 0.011) than in CC and CCPB sites. In terms of composition, CLAAG sites differed from CCPB and CC sites with a significantly greater cover of evergreen dwarf shrubs, forest mosses, bog mosses, and graminoid functional types. CCPB had a significantly higher cover of deciduous dwarf shrubs, lichens, and pioneer mosses than CLAAG and CC sites. CC sites were not significantly different than CLAAG sites in terms of plant functional-type cover.

Differences in understory composition among silvicultural treatments

Taxa composition varied significantly among treatments (CC, CCPB, and CLAAG) according to permutational MANOVAs (F = 2.01, p = 0.013, df = 2,18, R^2 = 0.183); however, when pairwise comparisons were made between silvicultural treatments, we found a significant difference only between CLAAG and CCPB treatments (Table 3).

Six taxa had an importance value that was significantly higher in CCPB plots than in CLAAG and CC plots (IV > 25% and $p \leq 0.05$; Table 4): *Aster* spp., *Fragaria* spp., *Rosa acicularis* Lindley, *Cladonia* spp., *Polytrichum* spp., and *Hieracium* spp. Four taxa were indicators of CC: *Rubus* spp., *Carex* spp., *P. schreberi*, and *Sphagnum* spp. In the CLAAG treatment, there were seven taxa: *Maianthemum trifolium* (L.) Sloboda, *Rubus chamaemorus* L., *Ptilium crista-castrensis* (Hedw.) De Not., *Sphagnum magellanicum* Brid., Poaceae spp., *Lycopodium* spp., and *Scirpus* spp. (Table 4).

These individual taxa differences translated into community-level differences (pRDA; Fig. 2). The pRDA model explained 40.9%

Table 2. Total taxa richness (means ± SD) and cover (% ± SD) of the different plant functional types per 4 m² plot. ANOVAs were used to compare means between different treatments.

	CLAAG (*N* = 96)	CC (*N* = 72)	CCPB (*N* = 84)	dfn, dfd	*F*	*p*
Total taxa richness	23.8±4.3a	19.2±7.4b	19.7±6.7b	2, 60	4.82	**0.011**
Forb cover	21.7±19.3	22.7±16.8	24.9±21.9	2, 60	0.26	0.771
Evergreen dwarf shrub cover	33.7±20.8a	30.0±23.6ab	26.2±26.5b	2, 60	3.29	**0.044**
Deciduous dwarf shrub cover	20.3±14.4b	23.2±17.3ab	32.7±22.0a	2, 60	5.36	**0.007**
Shrub cover	20.6±20.6	18.6±23	12.0±18.1	2, 60	2.36	0.103
Forest moss cover	21.7±20.5a	24.9±26.7a	9.3±11.3b	2, 60	7.82	**0.001**
Graminoid cover	15.4±15.3ab	18.5±18.6a	9.6±15.4b	2, 60	3.64	**0.032**
Lichen cover	3.1±4.8ab	3.3±7.1b	7.8±11.3a	2, 60	4.29	**0.018**
Fern cover	0.4±1.3	0.4±1.3	0.6±2.1	2, 60	0.05	0.950
Bog moss cover	13.3±14.7a	18.8±24a	7.5±15.9b	2, 60	5.48	**0.007**
Pioneer moss cover	3.1±6.1b	2.7±5.8bc	13.4±17.6a	2, 60	11.07	**<0.001**

Note: Means followed by different letters differed significantly ($p \leq 0.05$); *p* values in bold indicate significant ($p < 0.05$) differences among treatment types. CLAAG, careful logging around advanced growth plots; CC, clear-cut only plots; CCPB, clear-cut prescribed burn plots; dfn, degrees of freedom numerator; dfd, degrees of freedom denominator.

Table 3. Permutational MANOVAs (pairwise comparisons) testing for compositional differences between treatments.

	CLAAG (*N* = 8)			CCPB (*N* = 7)			WF (*N* = 9)		
Treatment	*F*	*R*²	*p*	*F*	*R*²	*p*	*F*	*R*²	*p*
CC (*N* = 6)	1.94	0.139	0.064	1.47	0.118	0.158	2.99	0.187	**0.002**
CLAAG				2.58	0.166	**0.006**	5.18	0.257	**0.001**
CCPB							2.31	0.141	**0.009**

Note: Values in bold type are significant at $p \leq 0.05$. CLAAG, careful logging around advanced growth plots; CCPB, clear-cut prescribed burn plots; WF, wildfire sites; CC, clear-cut only plots.

Table 4. Indicator taxa based on analyses of treatments.

Indicator taxa	Functional group	IV	*p*
CLAAG			
Maianthemum trifolium	Forb	44.2	0.03
Rubus chamaemorus	Deciduous dwarf shrub	31.7	0.031
Ptilium crista-castrensis	Forest moss	42.2	0.025
Sphagnum magellanicum	Bog moss	71.5	0.001
Poaceae spp.	Graminoid	52.9	0.011
Lycopodium spp.	Evergreen dwarf shrub	38.2	0.001
Scirpus spp.	Graminoid	27.7	0.018
CC			
Rubus spp.	Deciduous dwarf shrub	26.1	0.041
Carex spp.	Graminoid	46.4	0.046
Pleurozium schreberi	Forest moss	44.2	0.042
Sphagnum spp.	Bog moss	54.9	0.001
CCPB			
Aster spp.	Forb	28.6	0.002
Fragaria sp.	Forb	40.5	0.038
Rosa acicularis	Deciduous dwarf shrub	40.0	0.002
Cladonia spp.	Lichen	64.0	0.007
Polytrichum spp.	Pioneer moss	66.3	0.001
Hieracium spp.	Forb	32.2	0.006

Note: Only species with an occurrence frequency greater than 10% were included in the analyses. The table displays only species with an indicator value (IV) > 25%. CLAAG, careful logging around advanced growth plots; CC, clear-cut only plots; CCPB, clear-cut prescribed burn plots.

of the variation in composition ($F = 2.705$, $p = 0.005$), and the first two axes explained 21.6% of this variation (axis 1 = 0.140, axis 2 = 0.075). Black spruce density, black spruce cover, and organic layer depth played an important role in the distribution of sites along the first axis, whereas trembling aspen cover, balsam fir cover, and DBH were the most important variables explaining plot positions along the second axis. CC plots were characterized by higher black spruce cover and trembling aspen cover, as well as smaller DBH, and were mostly located in the lower left-hand part of the ordination; their indicator taxa (e.g., *Carex* spp., *Rubus* spp., *Sphagnum* spp.) and the centroids of the graminoid and bog moss functional types were also found in this part of the ordination. Indicator taxa associated with CLAAG plots included *S. magellanicum*, Gramineae, Poaceae spp., and *M. trifolium* and were mostly located in the lower left-hand part of the ordination, together with forest moss functional type. In addition, CLAAG plots featured a higher black spruce density and a higher organic layer depth. In the upper part of the ordination, the presence of pioneer moss functional type and their indicator taxa, e.g., *Polytrichum* spp., *R. acicularis*, *Cladonia* spp., and *Fragaria* sp. were typical of CCPB plots. Such plots were also characterized by relatively low balsam fir cover and trembling aspen cover and relatively high DBH.

Differences in understory composition between wildfire and silvicultural treatments

Composition varied significantly among treatments according to permutational MANOVAs ($F = 2.92$, $p = 0.001$, df = 3,26, R^2 = 0.252). We found significant differences between WF and other treatments (Table 2), with the highest R^2 found for comparisons between CLAAG and WF followed, in decreasing order of R^2, by CC-WF and CCPB-WF.

Correspondence analysis (total inertia = 2.262; axis 1, $\lambda = 0.286$; axis 2, $\lambda = 0.275$) also indicated that composition varied among treatments. CLAAG plots were located in the upper right-hand part of the ordination, associated with the centroids of evergreen dwarf shrubs and forest moss functional types (Fig. 3). Plots from young WF (≤15 years) were located in the lower right-hand part of the ordination next to CCPB plots. Young WF plots were associated with a pool of taxa that generally occur at the early stages of forest succession such as *Cladonia* spp., *Cladonia* subgroup *Cladina*, *Polytrichum* spp., *R. acicularis*, *Hieracium* spp., *Vaccinium angustifolium* Aiton, and *Vaccinium myrtilloides* Michx. Older WF plots (~40 years) were located in the left-hand part, where they shared taxa with a cluster of CCPB and relatively young CC plots (around 20 years) (Fig. 3). Those assemblages were associated with soil disturbance and included *Fragaria* sp., *Aster* spp., and *Rubus* spp.

Discussion

In this study, we found that CLAAG, CC, and CCPB had different effects on the forest floor vegetation in paludified black spruce forests of the Canadian Clay Belt region. The CLAAG treatment had the greatest taxa richness at the subplot level (4 m²), which did not support our first hypothesis that CCPB would be associated with higher species richness. We also found that the CCPB treatment generated understory compositional patterns that were most similar to those observed after wildfires. In addition, CCPB reduced *Sphagnum* spp. cover compared with other treatments, supporting the hypothesis that CCPB on paludified cut-

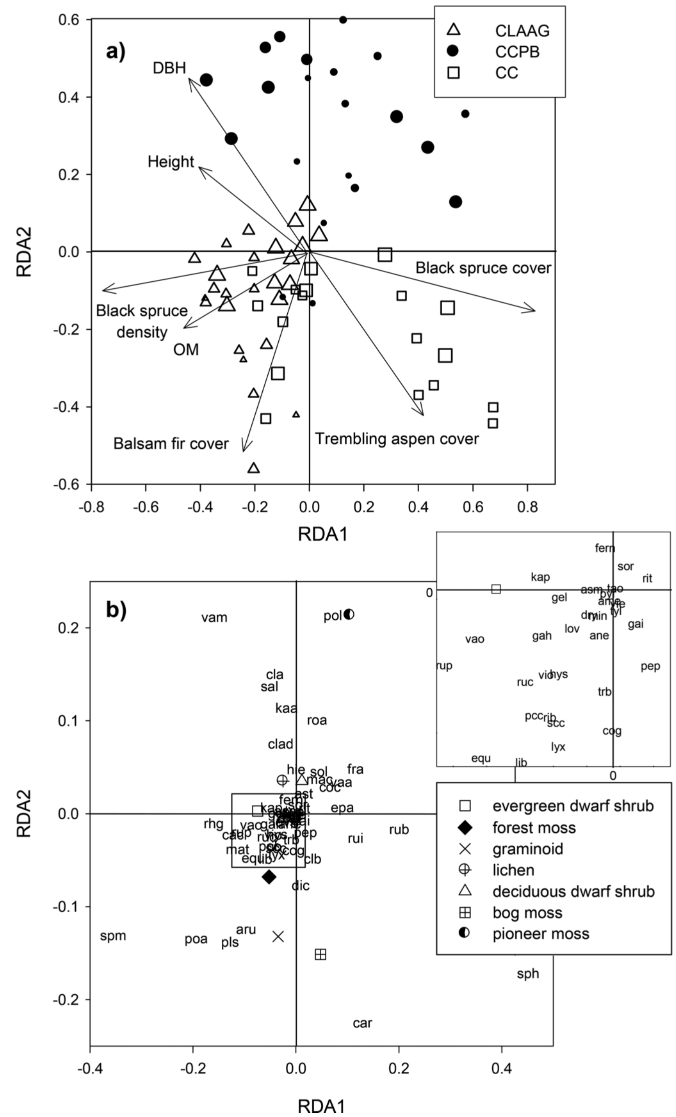


Fig. 2. Partial redundancy analysis (pRDA) diagram of the Hellinger-transformed plant abundance data constrained by the environmental variables with time since treatment as covariable showing the position of (*a*) the plots and (*b*) the taxa. Size of the symbols represents the time since treatment (TST) of the plots: small symbols are low TST and large symbols are high TST (*a*). The centroids of plant functional types that differed significantly among treatments (in Table 2) are depicted in panel *b*. The clear-cut only plots (CC) are shown as open squares; clear-cut prescribed burn plots (CCPB) are shown as solid circles; careful logging around advanced growth (CLAAG) sites are shown as open triangles; OM, organic layer depth; DBH, diameter at breast height of the highest tree; height, height of the highest tree. Taxa codes are as follows: ame, *Amelanchier* spp.; ane, *Anemone* spp.; aru, *Alnus rugose*; asm, *Aster macrophyllus*; ast, *Aster* spp.; cac, *Cassandra calyculata*; car, *Carex* spp.; cla, *Cladonia* subgroup *Cladina*; clad, *Cladonia* spp.; clb, *Clintonia borealis*; coc, *Cornus canadensis*; cog, *Coptis groenlandica*; dic, *Dicranum* spp.; dry, *Dryopteris* spp.; epa, *Epilobium angustifolium*; equ, *Equisetum* spp.; fern, other ferns than *Dryopteris* spp.; fra, *Fragaria* sp.; gah, *Gaulteria hispidula*; gai, *Gallium* spp.; gel, *Geocaulon lividum*; hie, *Hieracium* spp.; kaa, *Kalmia angustifolia*; kap, *Kalmia polifolia*; hys, *Hylocomium splendens*; lib, *Linnaea borealis*; lov, *Lonicera villosa*; lyc, *Lycopodium* spp.; mac, *Maianthemum canadense*; mat, *Maianthemum trifolium*; min, *Mitella nuda*; pep, *Petasites palmatus*; pls, *Pleurozium shreberi*; poa, *Poaceae* spp.; pol, *Polytrichum* spp.; ptc, *Ptilium crista-castrensis*; pyr, *Pyrola* spp.; rhg, *Rhododendron groenlandicum*; rib, *Ribes* spp.; rit, *Ribes triste*; roa, *Rosa acicularis*; rub, *Rubus* spp.; ruc, *Rubus chamaemorus*; rui, *Rubus idaeus*; rup, *Rubus pubescens*; sal, *Salix* spp.; sci, *Scirpus* spp.; sol, *Solidago* spp.; sor, *Sorbus* spp.; sph, *Sphagnum* spp.; spm, *Sphagnum magellanicum*; tao, *Taraxacum officinale*; trb, *Trientalis borealis*; tyl, *Typha latifolia*; vaa, *Vaccinium angustifolium*; vam, *Vaccinium myrtilloides*; vao, *Vaccinium oxycoccos*; vie, *Viburnum edule*; vio, *Viola* spp.

overs might be a suitable technique to control *Sphagnum* spp. expansion and protect site productivity.

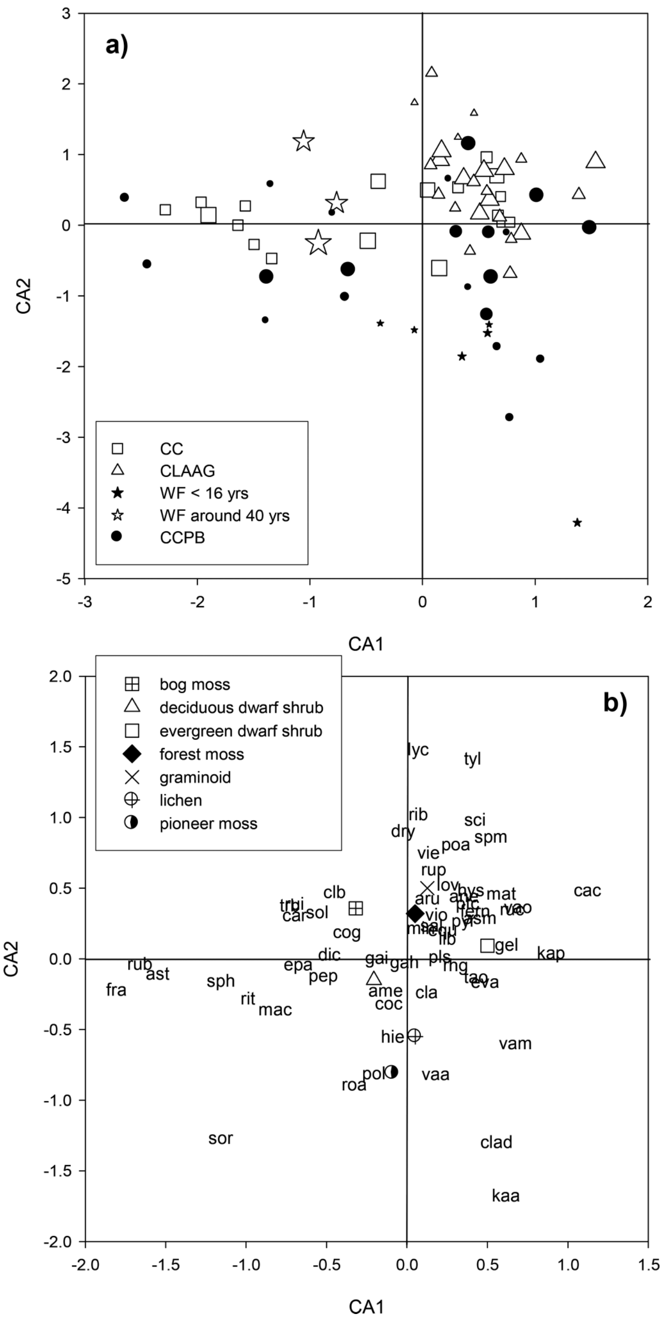
CLAAG and CCPB were the most contrasted treatments, which may be due to the contrasting levels of soil disturbance. CCPB is favourable for the establishment of pioneer taxa, as hypothesized initially. These prescribed burns created forest floor conditions that promoted the establishment of taxa that are able to re-sprout from underground rhizomes within spaces initially freed of competition (i.e., fire endurer species sensu Rowe 1983) such as *Fragaria* sp. and *R. acicularis* or to recover from fire by re-seeding from off-site sources and to rapidly colonize deforested areas (invader species sensu Rowe 1983) such as *Aster* spp., *Cladonia* spp., and *Polytrichum* spp. (Brown and DeByle 1989; Greene et al. 1999). However, taxa richness was not higher in CCPB compared with CLAAG sites. This could be partly explained by the fact that CLAAG treatments can allow the coexistence of both pioneer and late-successional taxa (Haeussler et al. 2002).

CC and CLAAG plots differed very little in terms of composition. As some CC sites were treated during winter, when the accumulated snowpack prevents the frozen soil organic layer from the impacts of machinery, it made this treatment similar to the CLAAG. Consequently, CC and CLAAG sites did not differ much in their *Sphagnum* spp. cover. The high cover in these sites could be explained by the fact that *Sphagnum* spp. have the ability to regenerate from vegetative fragments (Rochefort and Lode 2006), suggesting that light mechanical disturbances might not prevent *Sphagnum* spp. from spreading on cutovers as prescribed burning does.

Due to their lower intensity compared with high-intensity stand-replacing WFs, prescribed fires (CCPB) are often considered as moderate-intensity fires and might be of limited usefulness for controlling some resistant late-successional species (Nguyen-Xuan et al. 2000). Prescribed fire is often performed under weather conditions that are not propitious for severe fires (Granström 1993) for security reasons and also to promote the rapid vegetative regrowth of desired species (Lewis and Ferguson 1988). Still, in this study, we found that globally, CCPB generated compositions more similar to that of WF than to CC and CLAAG. Although confirming the results from other studies (Vanha-Majamaa et al. 2007; Scheller et al. 2005), our findings contrast with the results of Pidgen and Mallik (2013), who studied jack pine sites with a more intense management regime that included scarification and herbicide treatment after prescribed burn. We believe that this disturbance sequence resulted in many compounding disturbances and therefore differs substantially from the one applied here and may explain the differences observed when comparing treatments.

In terms of the nonvascular plants, CCPB sites had less *Sphagnum* spp. cover than CC and CLAAG treatments, and this disruption of the *Sphagnum* spp. cover promoted the establishment of typical pioneer taxa (e.g., *Polytrichum* spp. and *Cladonia* spp.; Paquette et al. 2016). As time since disturbance increased, *Sphagnum* spp. competed with *P. schreberi* for available space and these patterns evolved towards a predominance of *Sphagnum* spp. over feather-mosses and reindeer lichens due to their higher growth rate in moist environments (Bisbee et al. 2001; Fenton and Bergeron 2006). For vascular plants, CCPB composition was also more similar to those observed after natural disturbances compared with CC and CLAAG. Most of the pioneer species involved in postfire

Fig. 3. Correspondence analysis (CA) of the Hellinger-transformed plant abundance data showing the position of (*a*) the plots and (*b*) the taxa. Size of the symbols represents the time since treatment (TST) of the plots: small symbols are low TST and large symbols are high TST (*a*). The centroids of plant functional types that differed significantly among treatments (in Table 2) are depicted in panel *b*. Note that for the WF, there was one plot per site. The clear-cut only plots (CC) are shown as open squares; clear-cut prescribed burn plots (CCPB) are shown as solid circles; careful logging around advanced growth (CLAAG) sites are shown as open triangles; "planted" centroids are shown as open stars; and "not planted" centroids are shown as solid stars. See Fig. 2 for taxa codes.



colonization are relatively common and do not represent a conservation issue in Canadian boreal forests. Still, the stochastic nature and high spatial heterogeneity of postfire colonization is an important feature of boreal forest fires and it explains the distinct spatial texture observed in postfire landscapes (e.g., Bergeron et al. 2002; Johnstone et al. 2010b). This variability has long-term benefits for biodiversity, as the understory is a filter for tree species establishment and subsequent forest dynamics, ultimately resulting in mature forest landscapes that contain a high diversity of habitats (Drapeau et al. 2000).

Conclusion

Our results suggest that the effects of prescribed burns following clear-cutting on understory species composition are closer to those of wildfires when compared with CLAAG. This could be partly explained by the fact that more late-successional species survive with CLAAG, whereas most of these are eliminated by CCPB, as has been shown in harvest and fire comparisons (Paquette et al. 2016). CC treatment was intermediate, permitting survival of some late-successional species, as could be predicted by studies on soil properties and tree growth (Lafleur et al. 2011; Renard et al. 2016). Prescribed fire can be considered as a valuable tool for meeting ecosystem management objectives while fulfilling timber harvest needs. Prescribed fire has previously been shown to be an effective silvicultural tool to promote tree growth by controlling species competition and to prepare a site for regeneration by favouring good tree seedbed creation (Lafleur et al. 2010; Renard et al. 2016). In a region where paludification results in a decrease in forest productivity (Crawford et al. 2003), prescribed burning might represent a sustainable alternative to current harvesting techniques that could help in preserving biodiversity (in terms of understory species assemblage) while maintaining or even enhancing forest productivity. Ideally, the specific effects of fire should be tested by comparing prescribed burning and mechanical site preparation techniques that aim to achieve similar results in terms of emulation of natural disturbance characteristics (Kpodo 2014; Henneb et al. 2015). This would permit the determination of the most appropriate technique that balances social acceptability, disturbance severity, and exotic species invasion (Haeussler et al. 2002).

Acknowledgements

This project was made possible through the UQAT-UQAM Natural Sciences and Engineering Research Council of Canada (NSERC) Industrial Chair, the Canadian Forest Service (Laurentian Forestry Centre, LFC), the Ontario Ministry of Natural Resources (OMNR), Lake Abitibi Model Forest, and Tembec Forest Industries. We thank Amar Madoui for providing the data on wildfire. The first author sincerely thanks researchers and students at UQAM-UQAT, as well as staff from the Lake Duparquet Research and Teaching Forest for support and valuable advice. K. Del Guidice from Tembec Industries and T. Tellier and K. Taylor from OMNR provided maps and forestry data reports. Sample sites were established with the help of M. Doodly, S. Rollin, and A.P. Gagnon, and fieldwork was carried out with the help of A. Saint-Denis. S. Daigle from Centre d'étude de la forêt (CEF) provided statistical assistance. Finally, we sincerely thank Pamela Cheers and Isabelle Lamarre (LFC) for editing the text.

References

Bergeron, Y., and Fenton, N.J. 2012. Boreal forests of eastern Canada revisited: old growth, nonfire disturbances, forest succession, and biodiversity. Botany, **90**(6): 509–523. doi:10.1139/b2012-034.

Bergeron, Y., Harvey, B., Leduc, A., and Gauthier, S. 1999. Forest management guidelines based on natural disturbance dynamics: stand- and forest-level considerations. For. Chron. **75**(1): 49–54. doi:10.5558/tfc75049-1.

Bergeron, Y., Gauthier, S., Kafka, V., Lefort, P., and Lesieur, D. 2001. Natural fire frequency for the eastern Canadian boreal forest: consequences for sustainable forestry. Can. J. For. Res. **31**(3): 384–391. doi:10.1139/x00-178.

Bergeron, Y., Leduc, A., Harvey, B.D., and Gauthier, S. 2002. Natural fire regime: a guide for sustainable management of the Canadian boreal forest. Silva Fenn. **36**(1): 81–95. doi:10.14214/sf.553.

Bergeron, Y., Gauthier, S., Flannigan, M., and Kafka, V. 2004. Fire regimes at the transition between mixedwood and coniferous boreal forest in northwestern Quebec. Ecology, **85**(7): 1916–1932. doi:10.1890/02-0716.

Bisbee, K.E., Gower, S.T., Norman, J.M., and Nordheim, E.V. 2001. Environmental controls on ground cover species composition and productivity in a boreal black spruce forest. Oecologia, **129**: 261–270. doi:10.1007/s004420100719.

Bordeleau, P. 1998. The Val-Paradis Fire #322/97, case study presented within the framework of the Wildland Fire Behaviour Specialist course. Société de protection des forêts contre le feu (SOPFEU), Québec (Quebec).

Bouchard, M., Pothier, D., and Gauthier, S. 2008. Fire return intervals and tree species succession in the North Shore region of eastern Quebec. Can. J. For. Res. **38**(6): 1621–1633. doi:10.1139/X07-201.

Brown, J.K., and DeByle, N.V. 1989. Effects of prescribed fire on biomass and plant succession in western aspen. USDA Forest Service, Intermountain Research Station, Ogden, Utah, Res. Pap. INT-412.

Brumelis, G., and Carleton, T.J. 1989. The vegetation of post-logged black spruce lowlands in central Canada. II. Understory vegetation. J. Appl. Ecol. **26**(1): 321–339. doi:10.2307/2403670.

Crawford, R.M.M., Jeffree, C.E., and Rees, W.G. 2003. Paludification and forest retreat in northern oceanic environments. Ann. Bot. **91**: 213–226. doi:10.1093/aob/mcf185.

Cyr, D., Gauthier, S., Bergeron, Y., and Carcaillet, C. 2009. Forest management is driving the eastern North American boreal forest outside its natural range of variability. Front. Ecol. Environ. **7**: 519–524. doi:10.1890/080088.

Drapeau, P., Leduc, A., Giroux, J.-F., Savard, J.-P.L., Bergeron, Y., and Vickery, W.L. 2000. Landscape-scale disturbances and changes in bird communities of boreal mixed-wood forests. Ecol. Monogr. **70**: 423–444. doi:10.1890/0012-9615(2000)070[0423:LSDACI]2.0.CO;2.

Duchesne, L.C., and Wetzel, S. 1999. Effect of clear-cutting, prescribed burning and scarification on litter decomposition in an Eastern Ontario jack pine (*Pinus banksiana*) ecosystem. Int. J. Wildl. Fire, **9**: 195–201. doi:10.1071/WF00016.

Dufresne, M., and Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol. Monogr. **67**: 345–366. doi:10.1890/0012-9615(1997)067[0345:SAAIST]2.0.CO;2.

Environment Canada. 2013. Canadian climate normals. Available from http://www.climat.meteo.gc.ca/climate_normals/results_1981_2010_e.html?stnID=4157&lang=&dCode=1&dispBack=&StationName=&SearchType=&province=&provBut=&month1=12&month2=12&submit=View.

Fenton, N.J., and Bergeron, Y. 2006. Facilitative succession in a boreal bryophyte community driven by changes in available moisture and light. J. Veg. Sci. **17**: 65–76. doi:10.1111/j.1654-1103.2006.tb02424.x.

Fenton, N., Lecomte, N., Légaré, S., and Bergeron, Y. 2005. Paludification in black spruce (*Picea mariana*) forests of eastern Canada: potential factors and management implications. For. Ecol. Manage. **213**(1–3): 151–159. doi:10.1016/j.foreco.2005.03.017.

Gauthier, S., Lefort, P., Bergeron, Y., and Drapeau, P. 2002. Time since fire map, age-class distribution and forest dynamics in the Lake Abitibi Model Forest. Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre, Québec (Quebec), Inf. Rep. LAU-X-125.

Gauthier, S., Vaillancourt, M.-A., Leduc, A., De Grandpré, L., Kneeshaw, D., Morin, H., Drapeau, P., and Bergeron, Y. 2009. Ecosystem management in the boreal forest. Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre, Québec (Quebec).

Granström, A. 1993. Spatial and temporal variation in lightning ignitions in Sweden. J. Veg. Sci. **4**(6): 737–744. doi:10.2307/3235609.

Greene, D.F., Zasada, J.C., Sirois, L., and Kneeshaw, D. 1999. A review of the regeneration dynamics of North American boreal forest tree species. Can. J. For. Res. **29**(6): 824–839. doi:10.1139/x98-112.

Grondin, P., Ansseau, C., Bélanger, L., Bergeron, J.F., Bergeron, Y., Bouchard, A., Brisson, J., De Grandpré, L., Gagnon, G., Lavoie, C., Lessard, G., Payette, S., Richard, P.J.H., Saucier, J.-P., Sirois, L., and Vasseur, L. 1996. Écologie forestière. *In* Manuel de foresterie. *Edited by* J.A. Bérard and M. Côté. Les Presses de l'Université Laval, Sainte-Foy (Quebec). pp. 134–179.

Groot, A., and Adams, M.J. 2005. Long-term effects of peatland black spruce regeneration treatments in northeastern Ontario. For. Chron. **81**(1): 42–49. doi:10.5558/tfc81042-1.

Haeussler, S., and Bergeron, Y. 2004. Range of variability in boreal aspen plant communities after wildfire and clear-cutting. Can. J. For. Res. **34**(2): 274–288. doi:10.1139/x03-274.

Haeussler, S., Bedford, L., Leduc, A., Bergeron, Y., and Kranabetter, J.M. 2002. Silvicultural disturbance severity and plant communities of the southern Canadian boreal forest. Silva Fenn. **36**(1): 307–327. doi:10.14214/sf.565.

Harper, K.A., Boudreault, C., De Grandpré, L., Drapeau, P., Gauthier, S., and Bergeron, Y. 2003. Structure, composition, and diversity of old-growth black spruce boreal forest of the Clay Belt region in Quebec and Ontario. Environ. Rev. **11**(S1): S79–S98. doi:10.1139/a03-013..

Hart, S., and Chen, H. 2006. Understory vegetation dynamics of North American boreal forests. Crit. Rev. Plant Sci. **25**(4): 381–397. doi:10.1080/07352680600819286.

Harvey, B.D., Leduc, A., Gauthier, S., and Bergeron, Y. 2002. Stand-landscape integration in natural disturbance-based management of the southern boreal forest. For. Ecol. Manage. **155**(1–3): 369–385. doi:10.1016/S0378-1127(01)00573-4.

Hekkala, A.-M., Tarvainen, O., and Tolvanen, A. 2014. Dynamics of understory vegetation after restoration of natural characteristics in the boreal forests in Finland. For. Ecol. Manage. **330**: 55–66. doi:10.1016/j.foreco.2014.07.001.

Henneb, M., Valeria, O., Fenton, N.J., Thiffault, N., and Bergeron, Y. 2015. Mechanical site preparation: key to microsite creation success on Clay Belt paludified sites For. Chron. **91**(2): 187–196. doi:10.5558/tfc2015-030.

Johnstone, J.F., and Chapin, F.S. 2006. Effects of soil burn severity on post-fire tree recruitment in boreal forest. Ecosystems, **9**(1): 14–31. doi:10.1007/s10021-004-0042-x.

Johnstone, J.F., Hollingsworth, T.N., Chapin, F.S., III, and Mack, M.C. 2010*a*. Changes in fire regime break the legacy lock on successional trajectories in Alaskan boreal forest. Glob. Chang. Biol. **16**(4): 1281–1295. doi:10.1111/j.1365-2486.2009.02051.x.

Johnstone, J.F., McIntire, E.J.B., Pedersen, E.J., King, G., and Pisaric, M.J.F. 2010*b*. A sensitive slope: estimating landscape patterns of forest resilience in a changing climate. Ecosphere, **1**(6): 14. doi:10.1890/ES10-00102.1.

Kpodo, E. 2014. Impacts des conditions pré-récolte sur l'efficacité des traitements sylvicoles dans la pessière à mousses de la ceinture d'argile du Québec. M.Sc. thesis, Université du Québec en Abitibi-Témiscamingue, Rouyn-Noranda (Quebec).

Lafleur, B., Fenton, N.J., Paré, D., and Bergeron, Y, 2010. Contrasting effects of season and method of harvest on soil properties and the growth of black spruce regeneration in the boreal forested peatlands of Eastern Canada. Silva Fenn. **44**: 799–813. doi:10.14214/sf.122.

Lafleur, B., Paré, D., Fenton, N.J., and Bergeron, Y, 2011 Growth and nutrition of black spruce seedlings in response to disruption of Pleurozium and Sphagnum moss carpets in boreal forested peatlands. Plant Soil, **345**(1–2): 141–153. doi:10.1007/s11104-011-0767-1.

Lecomte, N., Simard, M., Bergeron, Y., Larouche, A., Asnong, H., and Richard, P.J.H. 2005. Effects of fire severity and initial tree composition on understorey vegetation dynamics in a boreal landscape inferred from chronosequence and paleoecological data. J. Veg. Sci. **16**(6): 665–674. doi:10.1111/j.1654-1103.2005.tb02409.x.

Lecomte, N., Simard, M., and Bergeron, Y. 2006. Effects of fire severity and initial tree composition on stand structural development in the coniferous boreal forest of northwestern Québec, Canada. Ecoscience, **13**(2): 152–163. doi:10.2980/i1195-6860-13-2-152.1.

Lewis, H.T., and Ferguson, T.A. 1988. Yards, corridors, and mosaics: how to burn a boreal forest. Hum. Ecol. **16**(1): 57–77. doi:10.1007/BF01262026.

Marshall, V.G. 2000. Impacts of forest harvesting on biological processes in northern forest soils. For. Ecol. Manage. **133**: 43–60. doi:10.1016/S0378-1127(99)00297-2.

McArdle, B.H., and Anderson, M.J. 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. Ecology, **82**: 290–297. doi:10.1890/0012-9658(2001)082[0290:FMMTCD]2.0.CO;2.

McRae, D.J. 1985. Prescribed burning of boreal mixedwood slash in the Ontario Clay Belt region. Canadian Forest Service, Great Lakes Forestry Research Centre, Information Report O-X-367.

Nguyen-Xuan, T., Bergeron, Y., Simard, D., Fyles, J.W., and Paré, D. 2000. The importance of forest floor disturbance in the early regeneration patterns of the boreal forest of western and central Quebec: a wildfire versus logging comparison. Can. J. For. Res. **30**(9): 1353–1364. doi:10.1139/x00-067.

Noble, M.G., DeBoer, L.K., Johnson, K.L., Coffin, B.A., Fellows, L.G., and Christensen, N.A. 1977. Quantitative relationships among some *Pinus banksiana* – *Picea mariana* forests subjected to wildfire and postlogging treatments. Can. J. For. Res. **7**(2): 368–377. doi:10.1139/x77-046.

Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Simpson, G.L., Henry, M., Stevens, H.H., and Wagner, H. 2008. vegan: Community ecology package. R package version 1.13-1.

Ontario Ministry of Natural Resources (OMNR). 1997. Silvicultural guide to managing black spruce, jack pine and aspen on boreal forest ecosites in Ontario. Version 1.1. Ontario Ministry of Natural Resources, Queen's Printer for Ontario, Toronto, Ontario.

Paquette, M., Boudreault, C., Fenton, N., Pothier, D., and Bergeron, Y. 2016. Bryophyte species assemblages in fire and clear-cut origin boreal forests. For. Ecol. Manage. **359**: 99–108. doi:10.1016/j.foreco.2015.09.031.

Pidgen, K., and Mallik, A.U. 2013. Ecology of compounding disturbances: the effects of prescribed burning after clearcutting. Ecosystems, **16**(1): 170–181. doi:10.1007/s10021-012-9607-2.

R Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from http://www.R-project.org/.

Rees, D.C., and Juday, G.P. 2002. Plant species diversity on logged versus burned sites in central Alaska. For. Ecol. Manage. **155**(1–3): 291–302. doi:10.1016/S0378-1127(01)00566-7.

Reich, P.B., Bakken, P., Carlson, D., Frelich, L.E., Friedman, S.K., and Grigal, D.F. 2001. Influence of logging, fire, and forest type on biodiversity and productivity in southern boreal forests. Ecology, **82**(10): 2731–2748. doi:10.1890/0012-9658(2001)082[2731:IOLFAF]2.0.CO;2.

Renard, S.M., Gauthier, S., Fenton, N.J., Lafleur, B., and Bergeron, Y. 2016. Prescribed burning after clearcut limits paludification in black spruce boreal forest. For. Ecol. Manage. **359**: 147–155. doi:10.1016/j.foreco.2015.09.037.

Riley, J.L. 1994. Peat and peatland resources of northeastern Ontario. Ontario Geological Survey, Miscellaneous Paper 153.

Rochefort, L., and Lode, E. 2006. Restoration of degraded boreal peatlands. *In* Boreal peatland ecosystems. *Edited by* R.K. Wieder and D.H. Vitt. Vol. 188, pp. 381–423.

Rowe, J.S. 1972. Forest regions of Canada. Canadian Forest Service Publication No. 1300.

Rowe, J.S. 1983. Concepts of fire effects on plant individuals and species. *In* The role of fire in northern circumpolar ecosystems. *Edited by* R.W. Wein and D.A. MacLean. John Wiley and Sons Inc., New York. pp. 135–153.

SAS Institute. 2013. SAS for Windows, version 9.4. SAS Institute Inc., Cary, North Carolina, USA.

Scheller, R.M., Mladenoff, D.J., Crow, T.R., and Sickley, T.A. 2005. Simulating the effects of fire reintroduction versus continued fire absence on forest composition and landscape structure in the Boundary Waters Canoe Area, northern Minnesota, USA. Ecosystems, **8**: 396–411. doi:10.1007/s10021-003-0087-2.

Scheuner, E.T., Makeschin, F., Wells, E.D., and Carter, P.Q. 2004. Short-term impacts of harvesting and burning disturbances on physical and chemical characteristics of forest soils in western Newfoundland, Canada. Eur. J. For. Res. **123**: 321–330. doi:10.1007/s10342-004-0038-2.

Simard, M., Lecomte, N., Bergeron, Y., Bernier, P.Y., and Paré, D. 2007. Forest productivity decline caused by successional paludification of boreal soils. Ecol. Appl. **17**(6): 1619–1637. doi:10.1890/06-1795.1.

Simard, M., Lecomte, N., Bergeron, Y., Bernier, P.Y., and Paré, D. 2009. Ecosystem management of Québec's northern Clay Belt spruce forest: managing the forest and especially the soils. *In* Ecosystem management in the boreal forest. *Edited by* S. Gauthier, M.-A. Vaillancourt, A. Leduc, L. De Grandpré, D. Kneeshaw, H. Morin, P. Drapeau, and Y. Bergeron. Presses de l'Université du Québec, Québec (Quebec). pp. 257–286.

Sirén, G. 1955. The development of spruce forest on raw humus sites in northern Finland and its ecology. Acta For. Fenn. **62**(4): 1–408.

Stinson, G., Kurz, W.A., Smyth, C.E., Neilson, E.T., Dymond, C.C., Metsaranta, J.M., Boisvenue, C., Rampley, G.J., Li, Q., White, T.M., and Blain, D. 2011. An inventory-based analysis of Canada's managed forest carbon dynamics, 1990 to 2008. Glob. Chang. Biol. **17**: 2227–2244. doi:10.1111/j.1365-2486.2010.02369.x.

Taylor, K., Arnup, R., Merchant, B.G., Parton, W.J., and Nieppola, J. 2000. A field guide to forest ecosystems of northeastern Ontario. 2nd ed. Queen's Printer for Ontario, Sudbury, Ontario.

Vanha-Majamaa, I., Lilja, S., Ryömä, R., Kotiaho, J.S., Laaka-Lindberg, S., Lindberg, H., Puttonen, P., Tamminen, P., Toivanen, T., and Kuuluvainen, T. 2007. Rehabilitating boreal forest structure and species composition in Finland through logging, dead wood creation and fire: the EVO experiment. For. Ecol. Manage. **250**(1–2): 77–88. doi:10.1016/j.foreco.2007.03.012.