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Effect of fire severity on regeneration success in the boreal forest of northwest Québec, Canada[1]

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Abstract: Fire regimes in the boreal forest are dominated by crown fires that burn over large areas. However, these fires rarely burn forest stands entirely and with the same intensity throughout, resulting in a mosaic of vegetation burnt to varying degrees of severity. The objectives of this study were to: (1) assess regeneration of tree species six or seven years after fire in relation to crown fire severity in non-salvaged jack pine and black spruce stands, and (2) assess establishment preferences of seedlings on the different types of germination beds created by fire. Logistic regressions indicated that seed trees abundance influenced regeneration success. The relationship between fire severity at the crown level and regeneration success was not significant, although seedling recruitment appeared limited in areas where severity was light to moderate. Poisson regressions showed that seedlings preferentially establish on mineral soil, and that woody debris seem to be a good substrate for germination and survival. Seedlings establish more frequently and grow better where thickness of residual organic matter is lowest. Crown fire severity, combined with severity at ground level may therefore be a good indicator of regeneration success in coniferous stands.
Keywords: germination seedbeds, *Picea mariana, Pinus banksiana, Populus tremuloides*, residual organic matter, seedling recruitment.

Résumé : En forêt boréale, bien que les régimes de feux soient dominés par des feux de cime couvrant de grandes superficies, ceux-ci brûlent rarement la forêt entièrement et uniformément. Par conséquent, il en résulte une mosaïque de végétation brûlée à divers degrés de sévérité. Cette étude avait pour objectifs de caractériser : (1) la régénération arborescente dans des peuplements non récupérés et composés principalement de pins gris et d'épinettes noires dans quatre feux de six et sept ans selon le degré de sévérité du feu au niveau de la couronne des arbres et (2) les préférences d'établissement des semis sur les différents types de litière mis en place à la suite du passage du feu. Des régressions logistiques ont indiqué que l'abondance des semenciers influençait le succès de la régénération. La relation entre la sévérité du feu au niveau de la couronne et le succès de la régénération n'était pas significative, mais le recrutement des semis semblait être limité dans les zones où la sévérité au niveau de la couronne était de légère à modérée. Des régressions de Poisson ont montré que les semis se sont établis préférentiellement sur le sol minéral et que les débris ligneux semblent être un bon substrat de germination et de survie. Une analyse de variance a montré que les semis semblent mieux s'établir et mieux croître là où l'épaisseur de matière organique résiduelle est la moins importante. La sévérité au niveau de la couronne combinée à la sévérité au sol peuvent donc être de bons indicateurs de la régénération dans les peuplements conifériens.
Mots clés : lits de germination, matière organique résiduelle, *Picea mariana*, *Pinus banksiana*, *Populus tremuloides*, recrutement des semis.

Nomenclature: Marie-Victorin, 1995.

Introduction

In many forest ecosystems, fires rarely burn forests in their entirety or in a uniform way, producing instead a mosaic of vegetation burnt to varying degrees of severity (Turner & Romme, 1994). Fire severity can be defined as the total effect of the fire on the ecosystem (Brown & DeByle, 1987) and includes tree damage and mortality as well as the quantity of burnt organic matter. Vegetation response to fire strongly depends on fire severity (Rowe, 1983; Johnston & Woodard, 1985; Thomas & Wein, 1985a; Morgan & Neuenschwander, 1988; Anderson & Romme, 1991; Chappel & Agee, 1996; Schimmel & Granström, 1996; Greene *et al.,* 2004). Furthermore, the availability of germination beds created by variation in fire severity can result in heterogeneity or spatial variability in regeneration success.

Jack pine (*Pinus banksiana*), black spruce (*Picea mariana*), and trembling aspen (*Populus tremuloides*) are fire-adapted tree species commonly present in the coniferous boreal forest. Jack pine and black spruce generally re-colonize a site after fire by seed dispersal through their serotinous and semi-serotinous cones, respectively. Trembling aspen usually regenerates after fire through suckering (Ahlgren, 1959; Bartos & Muegler, 1981; Brown & DeByle, 1987; Bartos, Brown & Booth, 1994; Romme *et al.,* 1995; Wang, 2003), although regeneration through seed dispersal is also reported (Kay, 1993; Romme *et al.,* 1997; Lavoie, 2001; Turner *et al.,* 2003; Johnstone *et al.,* 2004). In stands dominated by these species, little change in stand composition occurs after fire (Greene & Johnson,

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1999). Moreover, all three species re-colonize burns within three years after fire (St-Pierre, Gagnon & Bellefleur, 1992; Lavoie & Sirois, 1998; Greene *et al.,* 1999; Greene & Johnson, 1999; Charron & Greene, 2002). Seedling mortality is typically high at the end of the first year following establishment (Fleming & Mossa, 1994; Charron & Greene, 2002) and declines thereafter.

The thickness of consumed organic matter is often used as an index of fire severity at ground level (van Wagner, 1983). Burning of the organic matter layer may be essential for regeneration of jack pine and black spruce (Chrosciewicz, 1974; Abrams & Dickman, 1982; St-Pierre, Gagnon & Bellefleur, 1991), and the quality of their seed beds improves with a decrease in thickness of residual organic matter (Chrosciewicz, 1990; Payette, 1992; Zasada, Sharik & Nygren, 1992; Duchesne & Sirois, 1995). Jack pine has better establishment success with increasing fire severity at ground level, while black spruce has similar establishment success on both exposed mineral soil and on a relatively thick organic matter layer (Thomas & Wein, 1985a). However, complete exposure of the mineral soil is rarely required. A combination of mineral soil with a thin layer of humus provides optimal establishment conditions because of the presence of nutrients in the organic matter (Chrosciewicz, 1974).

It has also been shown that hair-cap moss (*Polytrichum* spp.) and *Sphagnum* moss are preferred germination beds for black spruce (Greene *et al.,* 2004) and that jack pine seedlings preferentially establish on hair-cap moss (Charron & Greene, 2002). In fact, spruce and jack pine seedlings and hair-cap moss often establish on the same micro-sites (*i.e.,* mineral soil) because of similar micro-environmental requirements (Fleming & Mossa, 1994; Lavoie, 2001).

Fire severity at crown level influences seed availability because severity is directly related to fire intensity and thus to the heat produced by the fire (van Wagner, 1983; Johnson, 1992), which will in turn influence cone opening (Waldrop & Brose, 1999). Moreover, the viability of seeds can be affected by the heat produced by the fire (Baufait, 1960; Turner *et al.,* 1997; Arseneault, 2001). The abundance of post-fire regeneration will thus depend on seed availability, the thickness of residual organic matter, and the types of germination beds created by the fire.

The role of fire severity on tree regeneration has been well studied (Thomas & Wein, 1985a; Anderson & Romme, 1991; Chappel & Agee, 1996; Turner, Romme & Gardner, 1999; Diaz-Delgado, Lloret & Pons, 2003; Pausas *et al.,* 2003; Turner *et al.,* 2003). However, few studies have been done in the eastern boreal region, and they focused on initial regeneration after fire (Lavoie, 2001; Greene *et al.,* 2004). Moreover, these studies were usually limited to only one fire, making their results not easy to generalize. Here, the study objectives were (1) to describe tree regeneration in relation to fire severity in boreal forest stands dominated by black spruce and/or jack pine within four different fires and (2) to determine establishment preferences for each species on various types of germination beds left after fire. We expected that seedlings of jack pine and black spruce would preferentially establish on a thin layer of residual organic matter or mineral soil. Second, we expected a positive relationship between the composition of regeneration and that of the stand prior to fire (Greene & Johnson, 1999; Greene *et al.,* 1999).

Methods

Study area

Four forest fires were studied in northwestern Québec (Figure 1). The Cuvillier fire occurred between August 16 and October 20, 1995 in the Abitibi region, southeast of Lebel-sur-Quévillon, extending between 48° 50' and 49° 10' N and between 75° 58' and 76° 10' W and affecting 49,070 ha. The Capichigamau fire occurred between June 11 and November 6, 1996 in the James Bay region, west of Chibougamau, extending between 50° 15' and 50° 32' N and between 75° 40' and 75° 50' W, covering an area of 23,353 ha. The Belleplage fire occurred between August and October 1995 in the Upper-Mauricie region, northeast of the Gouin Reservoir, extending between 48° 45' and 48° 60' N and between 73° 30' and 74° 05' W, covering 39,122 ha. The Parent fire occurred between August and November 1995 in the Upper-Mauricie region, south of the Gouin Reservoir and northwest of the village of Parent, extending between 46° 56' and 48° 14' N and between 74° 50' and 75° 15' W, covering an area of 62,317 ha.

The Cuvillier, Capichigamau, and Belleplage fires were located in the western black spruce–moss bioclimatic sub-domain of the upper boreal vegetation sub-zone. The Parent fire was located in the western balsam fir–white birch bioclimatic sub-domain of the lower boreal vegetation sub-zone (Grondin, 1996), but the fire burned almost exclusively in jack pine and black spruce stands. All study sites were located in the Lake Superior tectonic province of the Canadian Shield. Bedrock materials were primarily volcanic and sedimentary, although some large areas of granitic and gneissic rocks were present (Robitaille & Saucier, 1998). Surface materials were primarily glacial and fluvial-glacial, with occasional organic, rocky, fluvial, or lacustrine deposits (Robitaille & Saucier, 1998).

Field sampling

Sampling was done during summer 2002, six or seven years after fire, in stands whose original composition was mainly jack pine and black spruce between 61 and 89 y of age. Sampling locations were selected in non-salvaged areas easily accessible by road. The selected fires were mapped and digitized by the Ministry of Natural Resources immediately after fire to plan salvage logging. Fire maps were produced by performing an aerial survey of the fires. Stand polygons affected by fire were delineated on 1:50,000 topographic maps. The minimum mapping unit is 1 ha and the resolution limit is 30 m. These maps reflect the variation in tree damage caused by fire and do not record damage at ground level or tree mortality several years after fire (*i.e.,* fire severity). As tree mortality increases rapidly in the few months after fire (Turner *et al.,* 1994; Kafka, Gauthier & Bergeron, 2001), maps produced immediately after fire cannot be used as fire severity maps but must be considered as fire impact maps. However, as some correlation exists between fire impact and fire severity (Jayen, 2004), we used

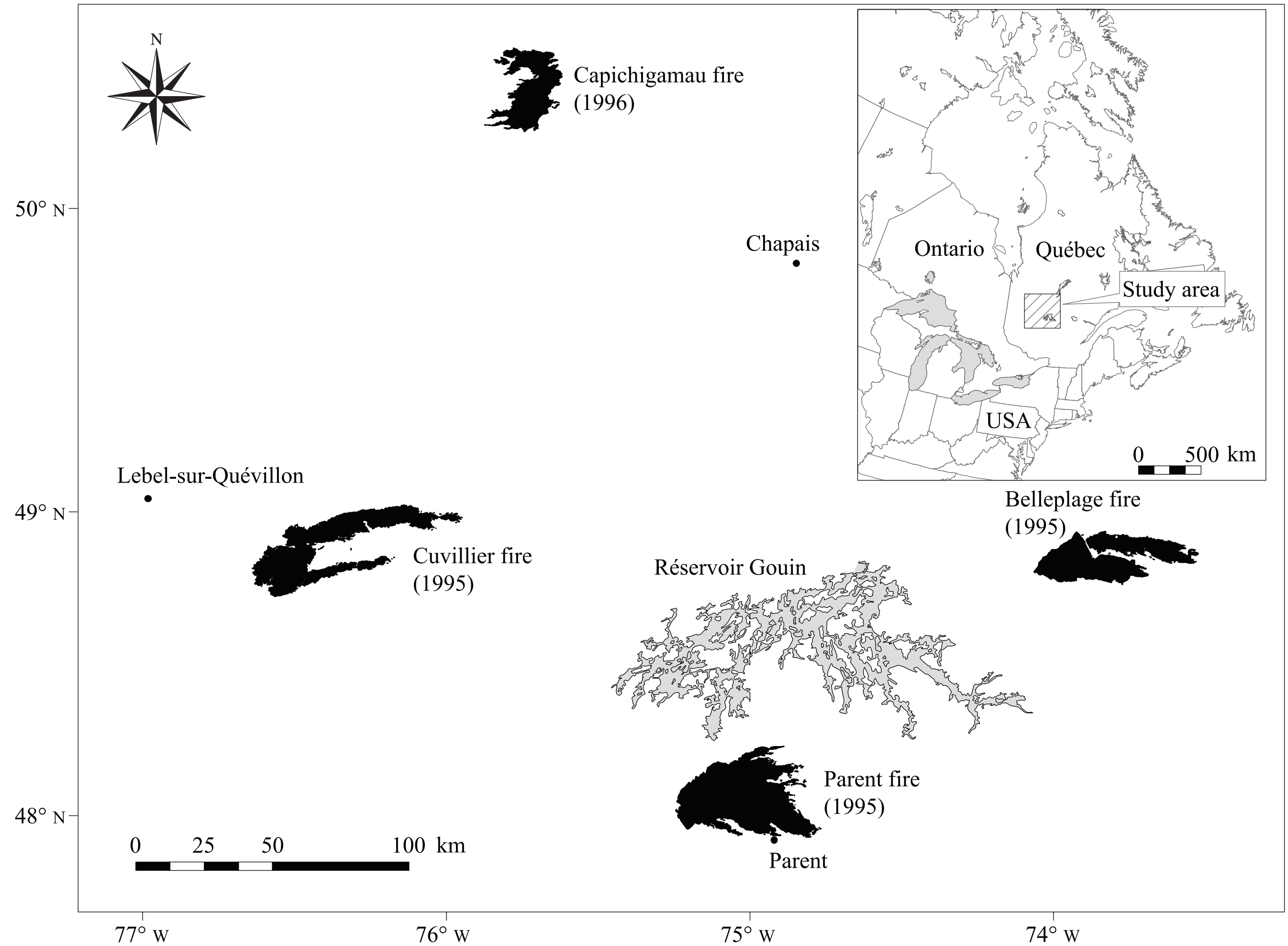

FIGURE 1. Location map of studied fires in Québec, Canada. Year of fire is indicated between parentheses.

the fire impact maps to determine the location of our sample sites in order to cover a maximum of the variability.

Based on the description of tree damage used by the Ministry of Natural Resources during aerial evaluation of the fires (Table I), three classes of impact were used (light, moderate, and high) for each of the four fires. Three transects were established in each of the Cuvillier, Capichigamau, and Belleplage fires, while two transects were established in the Parent fire. Along each transect, 10 × 10 m quadrats were established, the first located 100 m from the starting point and subsequent quadrats located at 100 m intervals. In total, 74 quadrats were sampled in the four fires and across the three impact classes (21 quadrats in light, 25 quadrats in moderate, and 28 quadrats in high impact areas).

In each quadrat, species, diameter at breast height (DBH; cm), and status (dead or alive) was determined for each tree with a DBH greater than 5 cm. These data were used to calculate the density (number·ha^{-1}) and basal area (m^{2}·ha^{-1}) for each tree species by status class. Severity (tree mortality several years after fire) was also evaluated in the field by estimating the percentage of dead trees in each quadrat. Below 35% mortality, quadrats were classified in the light severity category; between 36 and 65% mortality, as light–moderate severity; between 66 and 85% mortality, as moderate severity; and above 86% mortality, as high severity. Based on these criteria, one quadrat was classified as light severity, two were classified as light–moderate severity, six were classified as moderate severity, and 65 were classified as high severity.

Within each quadrat, nine 2 × 2 m microquadrats were established systematically to characterize regeneration. Each microquadrat was separated from its neighbours by a distance of 2 m. Seedlings (height < 60 cm, or above 60 cm but DBH < 1 cm) were recorded and used to estimate seedling density (number·m^{-2}) as well as stocking (number of microquadrats containing at least one seedling over the total number of microquadrats) for each tree species: jack pine, black spruce, and trembling aspen. We determined that aspen regeneration was not due to suckering because aspen was rarely found throughout the studied stands and the occurrence of aspen suckers is typically limited to short distances from parent trees (Greene *et al.,* 1999). The dominant litter type (mineral soil, thick organic horizon [> 10 cm], thin organic horizon [< 10 cm], moss [*Pleurozium schreberi*], hair-cap moss [*Polytricum* spp.], *Sphagnum* moss [*Sphagnum* spp.], woody debris) was recorded for each microquadrat. In addition, the thickness of residual organic matter (cm) was measured at three locations per micro-

TABLE I. Evaluation scale of forest fire impact classes (Source: Ministry of Natural Resources of Québec).

Description of the status of trees affected by fire used during aerial survey by Ministry of Natural Resources of Québec	Associated impact class
Green trees (not affected by fire)	No impact
Mixture of green trees and trees with reddish crowns; green trees more numerous	Light impact
Mixture of trees with reddish crowns and green trees; trees with reddish crowns more numerous	Moderate impact
Trees with reddish crowns and generally less than 25% blown down trees	High impact
Blackened trees with burnt crowns, often with detached bark; generally less than 40% blown down trees	High impact
Blackened trees with burnt crowns, bark is detached, and generally more than 40% blown down trees	High impact

quadrat: at the centre, underneath the seedling closest to the centre, and under the tallest seedling (on the assumption that this seedling has the highest probability of survival).

STATISTICAL ANALYSES

VARIATIONS IN STOCKING

At the stand level, stepwise logistic regressions were calculated using the LOGISTIC procedure in SAS (Allison, 1999) to determine how fire severity (mortality as measured in the field) and stand-level characteristics (tree species density and basal area) influenced regeneration stocking in each 100-m^2 quadrat. Stocking was considered as a binary variable: well stocked (1) or deficient (0) following a species-specific threshold. Black spruce and jack pine stands were considered well stocked if seedlings of these species were present in five of nine microquadrats. For trembling aspen, we considered a microquadrat well stocked if seedlings were present in three of nine microquadrats. Given the sampling area used (4 m^2), these stocking thresholds were generally considered sufficient for regenerating the stand by foresters' standards (Perron, 1996). Severity classes (high, moderate, light–moderate, and light) were treated as dummy variables in the model. This approach is the most explicit when we wish to discriminate between the positive and negative influences of each class of a categorical variable (Allison, 1999).

VARIATION IN SEEDLING DENSITY

At the microquadrat scale, Poisson regressions (Allison, 1999) were used to determine how fire severity, stand characteristics, mean thickness of residual organic matter by quadrat and by location, and litter type (thick organic, thin organic, burnt organic matter, mineral soil, moss, hair-cap moss, *Sphagnum* moss, woody debris) influenced seedling density. Poisson regression is appropriate for counted data. Moreover, it can be adjusted for clustered data to account for the pseudo-replication resulting from microquadrats nested within a quadrat (Allison, 1999). The Generalization Estimating Model method was used on clustered data to improve standard error and the coefficient values.

MICRO-CONDITIONS AFFECTING SEEDLING ESTABLISHMENT

To understand how micro-conditions affected seedling establishment, an analysis of variance (GLM procedure in SAS) was done on the average residual organic matter thickness (ROMT) at each position where data were gathered (at the centre of the microquadrat, under the seedling closest to the centre, and under the tallest seedling). We also included in this analysis stand type (jack pine stand where basal area of jack pine > 50%; black spruce stand where basal area of black spruce > 50%) and fire severity to control their potential influence on residual organic matter thickness. For this analysis, the light and light–moderate fire severity classes were grouped. Duncan's means comparison test (Quinn & Keough, 2002) was used on mean ROMT in relation to seedling microquadrat locations, fire severity, and stand type.

Results

FACTORS INFLUENCING SEEDLING STOCKING

Only the density of dead trees positively influenced stocking success of jack pine (Table II), while only the basal area of dead black spruce positively influenced the stocking success of black spruce regeneration. Density of dead trembling aspen positively influenced stocking success in trembling aspen.

In all cases, crown fire severity was not statistically significant for predicting regeneration success. However, to better evaluate the relative influence of crown fire severity on the relationship between stocking success and dead jack pine density (Figure 2) and between stocking success and basal area of dead black spruce (Figure 3), we drew the logistic curves produced by the analysis on raw data and illustrated the crown fire severity class for each raw data. The raw data distribution shows considerable variability around the predicted values for jack pine and black spruce. Jack pine seedlings established even when no jack pine was present in the 100-m^2 quadrat. In quadrats where severity was high, jack pine regeneration was abundant, whereas in quadrats where severity was light, light–moderate, or moderate, few jack pine seedlings were observed, even when there was a high density of dead jack pine. For black spruce, the raw data distribution suggests a minimum threshold of basal area of dead black spruce under which regeneration success becomes compromised. We also observed lower stocking of black spruce in stands where crown fire severity was light–moderate or moderate, despite high values of basal areas for dead black spruce in the quadrats. Overall, when crown fire severity was high and basal area was higher than 15 $m^2 \cdot ha^{-1}$, black spruce regeneration was relatively well stocked.

FACTORS INFLUENCING SEEDLING DENSITY

At the microquadrat scale, the abundance of jack pine seedlings increased with the presence of hair-cap moss, with high crown fire severity, with the presence of woody debris, and with higher densities of dead jack pine; in contrast, their abundance decreased when residual organic matter layers were thick (Table III). The abundance of black spruce seedlings increased with the presence of hair-cap moss, with higher basal areas of dead black spruce, and with the pres-

TABLE II. Stocking success of jack pine, black spruce, and trembling aspen regeneration in relation to stand variables, as predicted by stepwise logistic regressions. Only jack pine density was retained in the jack pine model because no other variable was significant at the second selection step. Only black spruce basal area was retained in the black spruce model because no other variable was significant at the second selection step.

Species	Steps	Significant variables	R^2	Effect	χ^2	$P < \chi^2$
Jack pine	Step 1	Dead jack pine density	0.2404	+	18.2646	< 0.0001
		Dead jack pine basal area	na	na	14.4546	0.0001
		High severity	na	na	9.7069	0.0018
		Moderate severity	na	na	6.1858	0.0129
Black spruce	Step 1	Dead black spruce basal area	0.2502	+	18.8085	< 0.0001
		Dead black spruce density	na	na	13.1167	0.0003
Trembling aspen	Step 1	Dead trembling aspen density	0.0964	+	9.0300	0.0027
		Dead trembling aspen basal area	na	na	6.7989	0.0091

na: not applicable.

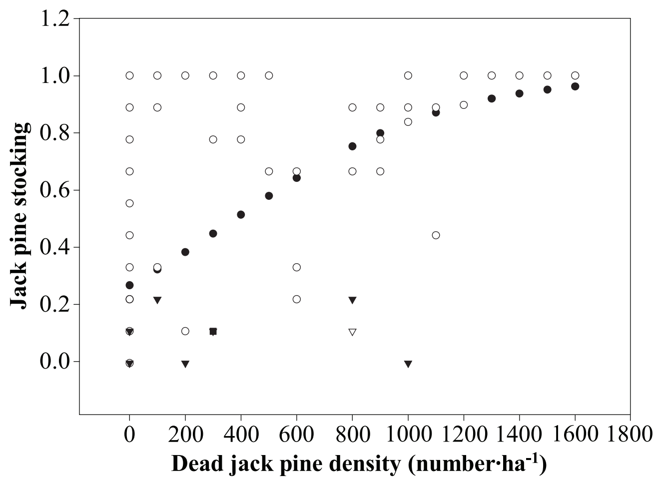

FIGURE 2. Relationship between density of dead jack pine and stocking of its regeneration. Predicted values obtained by logistic regression are represented by closed circles. Fire severity class corresponding to each sampled quadrat is shown by different symbols: open circles = high severity (n = 65); closed triangles = moderate severity (n = 6); open triangles = light–moderate severity (n = 2); closed squares = light severity (n = 1).

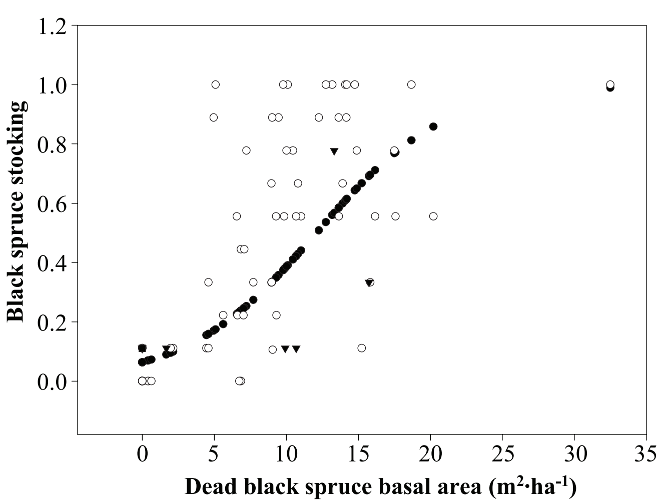

FIGURE 3. Relationship between basal area of dead black spruce and stocking of its regeneration. Predicted values obtained by logistic regression are represented by closed circles. Fire severity class corresponding to each sampled quadrat is shown by different symbols: open circles = high severity (n = 65); closed triangles = moderate severity (n = 6); open triangles = light–moderate severity (n = 2); closed squares = light severity (n = 1).

ence of woody debris (Table III). The abundance of trembling aspen seedlings was high in the presence of hair-cap moss. The density of dead trembling aspen did not influence its seedling abundance.

MICRO-CONDITIONS FAVOURABLE TO SEEDLING ESTABLISHMENT AND SURVIVAL

Comparison of residual organic matter thickness (ROMT) (Model: F = 7.59; P < 0.0001) shows that stand type explained most of the variability in ROMT (F = 13.97; P = 0.0002). Severity also influenced ROMT variation (F = 8.67; P = 0.0002); however, the relationship between crown fire severity and ROMT was not linear (Figure 4a). Finally, the relationship between measurement location and ROMT was significant (F = 3.16; P = 0.0443) even when variability generated by stand type and severity was accounted for. The interactions between the different factors were also tested in the model, but none were significant. Thus, the relationship between ROMT and measurement location was always consistent irrespective of stand type and crown fire severity. In most cases, seedlings appeared to establish and grow better on thinner organic matter (tallest seedling) (Figures 4a,b). A Duncan's test comparing only measurement locations showed that ROMT was on average higher at the microquadrat centre than under the seedling closest to the centre or under the tallest seedling. This establishment requirement is, however, more obvious in the high crown fire severity zone (Figure 4a) and in black spruce stands (Figure 4b).

Discussion

ABUNDANCE OF SEED TREES

It is known that jack pine, black spruce, and trembling aspen regeneration are directly related to their basal area prior to fire (Greene & Johnson, 1999; Greene *et al.,* 1999). For all these tree species, our results show that the most important variable in predicting the presence of well-stocked regeneration is abundance of seed trees, whether described by density or basal area.

Jack pine seedlings were present in quadrats even when mature trees were absent from the same quadrats prior to fire. Dead jack pines outside the quadrats must have disseminated their seeds inside the quadrats, allowing for successful regeneration establishment. Jack pine has a high capability for seed dispersal, as seeds can disseminate 100 m from a source tree (Ahlgren, 1960), and the quantity

TABLE III. Seedling abundance per species in relation to different variables related to stand and litter characteristics, as predicted by clustered Poisson regression models.

Species	Predictive variables	Effect	χ^2	df	$P > \chi^2$
Jack pine	Hair-cap moss	+	14.32	1	0.0002
	High severity	+	6.89	1	0.0087
	Woody debris	+	6.27	1	0.0123
	Dead jack pine density	+	6.05	1	0.0139
	Thick organic matter	–	6.08	1	0.0136
Black spruce	Hair-cap moss	+	22.58	1	< 0.0001
	Dead black spruce basal area	+	11.27	1	0.0008
	Woody debris	+	5.00	1	0.0253
Trembling aspen	Hair-cap moss	+	5.89	1	0.0152

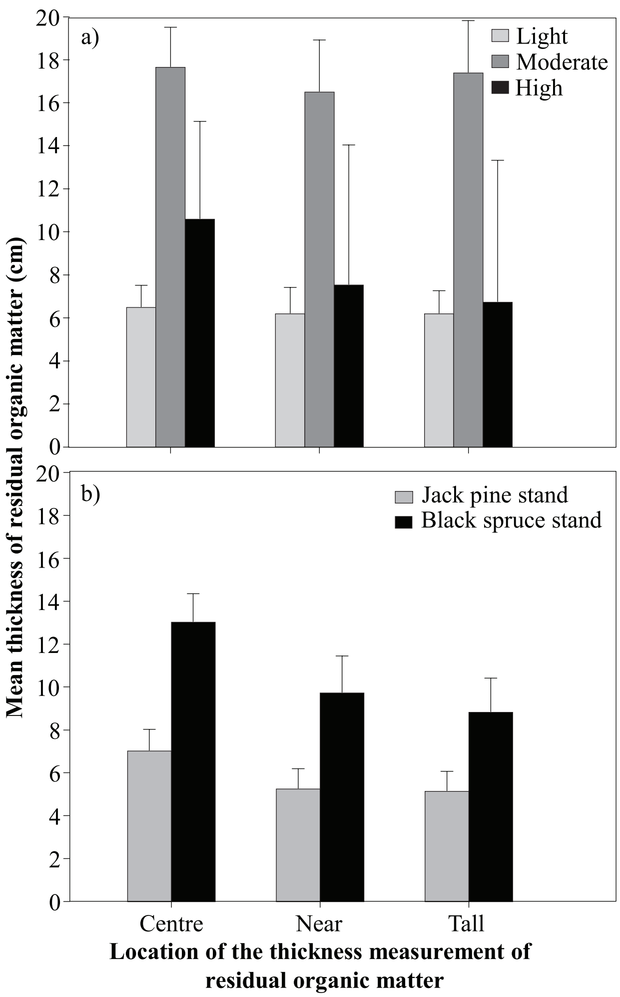

FIGURE 4. a) Mean thickness of organic matter layer, with standard error bars, in relation to fire severity, and location of thickness measurement; b) Mean thickness of organic matter layer, with standard error bars, in relation to stand type and location of thickness measurement. Centre = microquadrat centre; Near = under seedling nearest to centre; Tall = under tallest seedling.

of seeds dispersed by jack pine after fire may be considerable. The total number of seeds stored in serotinous cones can reach more than 5×10^6 seeds·ha^{-1} in the Lake States region (Eyre & LeBarron, 1944). This large seed production and the high seed-dispersal capability of jack pine allow for good regeneration, even when density of seed trees is low. Watson (1937 *in* Ahlgren & Ahlgren, 1960) suggested that jack pine regeneration stocking would be satisfactory with 185 seed trees·ha^{-1}.

In contrast to jack pine, black spruce seedlings were absent from quadrats where spruce was absent prior to fire. This finding may be explained by the weak dispersal capability of black spruce seeds. Dissemination of black spruce seeds is limited to distances equivalent to one or two times the height of the seed tree (LeBarron, 1939; Heinselman, 1957). Black spruce seedlings appear to establish more often just below black spruce trees because of the large decrease in organic matter thickness found there after fire (van Wagner, 1983; St-Pierre, Gagnon & Bellefleur, 1991). Seedlings also show a contagious distribution (St-Pierre, Gagnon & Bellefleur, 1991; Sirois, 1995; Filion & Morin, 1996). Filion and Morin (1996) observed that over 90% of black spruce seedlings were found within 2 m of the source tree.

Trembling aspen seedlings were observed despite the fact that mature trembling aspen was rarely present in the sampled stands. Aspen disperses its seeds over great distances (Burns & Honkala, 1990; Jobidon, 1995), up to 15 km (Turner *et al.,* 2003), and aspen regeneration through seed dispersal has been documented following several fires (Kay, 1993; Romme *et al.,* 1997; Lavoie, 2001; Turner *et al.,* 2003; Johnstone *et al.,* 2004). Fire creates good germination conditions for aspen seeds by burning organic matter and exposing mineral soil to supply favourable moisture conditions. Fire also eliminates competition by killing pre-existing vegetation. Aspen colonization of burnt areas by seeds will therefore occur when favourable conditions coincide, such as abundant seed production, good timing between fire occurrence and seed dispersal period, favourable moisture conditions, absence of competition, and availability of adequate substrates (Kay, 1993; Romme *et al.,* 1997; Turner *et al.,* 2003).

ABUNDANCE AND QUALITY OF SEED GERMINATION BEDS

Post-fire regeneration success will depend not only on seed tree abundance but also on the abundance of appropriate seed germination beds. Post-fire seedling density was correlated with certain litter types encountered in the studied fires. The presence of hair-cap moss (*Polytrichum* spp.) was the best indicator of the abundance of jack pine, black spruce and trembling aspen seedlings. The strong association between these seedlings and hair-cap moss has also been observed by others (Filion & Morin, 1996; Lavoie, 2001; Greene *et al.,* 2004). Hair-cap moss and seedlings usually establish simultaneously after fire on the same germination substrate: bare mineral soil, or mineral soil with a thin layer of organic matter (Fleming & Mossa, 1994; Lavoie, 2001). Because of the stability of its moisture content, mineral soil offers favourable germination conditions for tree seeds and hair-cap moss spores, while the organic matter supplies required nutrients (Chrosciewicz, 1974; 1990).

Although mineral soil is recognized as a favourable germination bed, it did not seem to influence regeneration observed seven or eight years after fire. This may be explained not only by the minor presence of this substrate within the studied fires (approximately 2.5%), but also by the colonization of the substrate by hair-cap moss. Because seedlings are strongly associated with hair-cap moss, we can surmise that seedlings probably initially established on the underlying mineral soil at the same time as hair-cap moss. Mineral soil is therefore a germination bed that is probably more abundant immediately after fire and that is favourable to seedling establishment.

The presence of woody debris positively influenced density of jack pine and black spruce seedlings, as previously observed by Filion and Morin (1996). Decomposing wood retains moisture very well (LeBarron, 1944), and woody debris may also increase seedling survival by providing some shade (Gray & Spies, 1997).

The presence of thick layers of organic matter was detrimental to the establishment and/or survival of seedlings, particularly for jack pine. This finding is in agreement with Chrosciewicz (1990) and Charron and Greene (2002). Fibrous organic matter lets water filter through without retaining it and therefore tends to dry out rapidly at its surface. Furthermore, organic matter has a low thermal conductivity, so its surface temperature can increase considerably when directly exposed to solar radiation (Duchesne & Sirois, 1995). Organic matter rapidly loses moisture under these conditions (Chrosciewicz, 1990), and moisture availability is an important factor for germination success and seedling growth (Foster, 1985; Thomas & Wein, 1985b; Duchesne & Sirois, 1995). With a thin organic matter layer, seedlings can benefit from a constant water supply by being closer to the mineral soil, which is subjected to fewer variations in moisture content than organic matter (Ahlgren & Ahlgren, 1960). A reduction in organic matter thickness therefore seems necessary for the establishment and survival of seedlings (Chrosciewicz, 1974; St-Pierre, Gagnon & Bellefleur, 1991). High fire severity at ground level thus promotes regeneration success by decreasing the thickness of organic matter and exposing mineral soil, creating a suitable germination substrate for hair-cap moss as well as for seedlings of jack pine, black spruce, and trembling aspen.

Although crown fire severity was not statistically significant for predicting regeneration success, likely due to the low representation of moderate and low fire severity, it seemed to limit the regeneration success of jack pine and black spruce (Figures 2 and 3). After high severity fires, stocking of both species was dependent on the abundance of seed trees, whereas regeneration was sparse after light, light–moderate, or moderate severity fires and independent of seed tree abundance. In those cases, fire severity was probably not high enough to stimulate the opening of sufficient cones for seed release and/or not high enough to create favourable germination beds (Noël, 2001). Fire severity described in terms of dead trees is directly related to fire intensity and thus to the heat produced by the fire (van Wagner, 1983; Johnson, 1992), which in turn influences cone opening during the fire (Waldrop & Brose, 1999). Higher severity at ground level results in a reduction of organic matter and thus improves the quality of germination beds (Chrosciewicz, 1990). Although seed mortality may occur in high-intensity crown fire, regeneration success will be best where there is high fire severity at both crown level and ground level.

Conclusion

Even though our analyses did not show a direct influence of fire severity on regeneration success, we have nevertheless shown that jack pine and black spruce regeneration was more limited in areas of light to moderate fire severity than in areas of high severity. High-severity fires resulted in high densities of dispersed jack pine and black spruce seeds and a reduction in the thickness of the organic matter layer and increased exposure of mineral soil, resulting in improved quality of germination beds. Fire severity measured at crown level, combined with severity at ground level, may therefore be a good indicator of regeneration success in coniferous stands.

These results may have implications for forest management, in particular for salvage logging of burnt stands. Since regeneration seems poor in areas of light to moderate crown fire severity, and since areas of high fire severity have higher regeneration success, it seems appropriate to develop salvaging methods that limit impacts on natural regeneration in high severity sectors. Further studies on regeneration dynamics in relation to fire severity, at crown as well as ground level, would be useful to expand upon the findings of this study.

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