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A model of the post-fire recruitment of *Picea mariana* and *Pinus* banksiana as a function of salvage timing and intensity

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ABSTRACT

In this paper, we model the post-fire recruitment dynamics of two aerial seedbank species, *Picea mariana* and *Pinus banksiana*, in response to salvage logging. The model incorporates: (1) initial seed availability as a function of source tree basal area and proportion of stand salvaged; (2) seed abscission as a function of time; (3) seedling survivorship as a function of seed mass, seedbed proportion, and granivory; and (4) seedling and seed mortality as a function of salvage operations. We also elaborate a simulation of the effect of direct seeding via cone-bearing branches fed into a moving chipper. The model performed adequately when tested against data sets from two fires in Quebec and one in Saskatchewan. In particular, it showed that *P. mariana* was more adversely affected by early salvage than *P. banksiana* because of its far slower seed abscission rate. The model predicted that a delay in salvage or a decrease in salvage proportion would enhance tree regeneration densities, especially for *P. mariana*. Finally, model projections indicate that the use of a chipper to disseminate seeds during the harvesting would permit either species to be adequately regenerated cheaply even with low pre-fire basal area per area or very early salvage.

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1. Introduction

Fire is the dominant disturbance in most of the boreal forest (Stocks et al., 2002; Schmiegelow et al., 2006), driving the structure, composition, and function of boreal forest stands, and causing significant losses in viable timber. In Canada, the fire return time ranges from 100 years in much of the southern boreal to 250 years in the taiga, and this has resulted in the dominance of pyrophilic tree species adapted to this disturbance regime (Greene and Johnson, 1999). Forestry companies and governments have responded to fire by increasingly using salvage to avoid a reduction in the annual allowable cut (Lindenmayer and Noss, 2006; St-Germain and Greene, 2009). However, largescale post-fire salvage is such a new silvicultural practice that it is presently poorly regulated, and its effects on plants, animals, and soil properties have barely been broached by researchers (St-Germain and Greene, 2009). In addition, in Canada, companies are spurred to salvage burns by provincial rules that both require and

boring insects, stain fungi, wood-decay fungi, and checking (wood splitting due to drying of the boles) (St-Germain and Greene, 2009). A more minor reason for celerity is that the standing dead trees continue to fall with time since fire (Angers et al., 2011). These degradation agents vary in their effect on wood value; in particular, wood affected by checking, stain fungi, and insect damage can still be used for pulp.

subsidize the practice. Indeed, subsidies are almost always necessary because most of the affected stands will not be at the optimal

size (age) for profitable harvesting (St-Germain and Greene, 2009).

ber in a burn, and can therefore be both more extensive and

intensive than conventional harvest techniques where the empha-

sis is on the more marketable and larger stems, and where clear-cut

size is often limited by statute (Lindenmayer and Noss, 2006).

Salvage usually occurs as rapidly as the initial road network can

be constructed, typically within a few months of the fire, and is

normally completed within 6-10 months. Companies salvage so

quickly because of the expected degradation of xylem due to wood-

Current salvage procedures generally remove all accessible tim-

Salvage negatively impacts the natural regeneration of *Pinus* mariana and *Pinus banksiana*, two common boreal forest tree species that rely on aerial seedbanks to re-establish after fire (Charron and Greene, 2002; Greene et al., 2006; St-Germain and







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Greene, 2009), as early salvage removes the aerial seedbank before many of the seeds have abscised (Greene et al., 2013). Further, up to 30% of the first-summer cohort of seedlings will be crushed by the machinery as the skid paths created by the harvesters disturb about a third of the substrate (Greene et al., 2006). Additionally, Greene et al. (2006) speculated that the drier conditions resulting from removal of the shade-casting burnt stems were a contributing factor to the reduced recruitment in salvaged sites. While a seedling density of $\sim 1/m^2$ or greater is considered adequate to fully re-stock a stand (Greene et al., 2002), post-salvage natural regeneration densities of *P. mariana* and, to a lesser extent *P. banksiana*, are typically well below this density, and therefore forest companies are required to plant trees at an average cost of USD 750/ha (St-Germain and Greene, 2009). In addition to delaying salvage to benefit natural regeneration, an unexplored alternative is partial cutting; e.g. parallel strips of burned trees might be left behind. This ought to benefit the conifer species that are so negatively affected

by salvage-related seed removal. Suitable seedbeds, which are crucial for the successful establishment of small-seeded species such as *P. mariana* and *P. banksiana* are affected by both the fire and subsequent salvage (Miyanshi and Johnson 2002; Greene et al., 2007). Fire increases the frequency of the better seedbeds by reducing organic layers (Miyanishi and Johnson, 2002). Ironically, salvage can further increase the frequency of suitable seedbeds in an area now denuded of seed sources; Greene et al. (2006) observed five times more mineral soil and humus (both are very favorable seedbeds for small-seeded species) in salvaged stands than non-salvaged (but burned) because so much organic material had been pushed to the sides of the skid path by the harvesting equipment. In other cases, of course, the harvesters might merely produce water-filled ruts.

There is at present no model of the effect of salvage timing on regeneration. While Greene and Johnson (1999) modeled post-fire tree regeneration and Greene et al. (2006) modeled the regeneration of trees after the salvage of burnt stands, neither could take into account the effect of the timing of the salvage operation because they did not know the seed abscission schedules of the species. Our primary objective is to simulate the impact of both salvage timing and the proportion of stand area salvaged on natural recruitment densities of two common aerial seedbank species, P. mariana and P. banksiana. We will first validate the model using data from three fires in the boreal forest of North America. Then, we will use the model to explore how the timing and proportion of salvage affects the subsequent recruitment density of each species. At one of these fires, we have experimentally used partial cutting to leave residual trees in parallel strips, and thus our second objective is to verify that partial cutting will increase the regeneration by leaving a fraction of the aerial seed-bank available. This silvicultural alternative has never been tested before. Lastly, we will use the model to examine the potential effect of redistributing seeds (by feeding cone-bearing branches into a chipper that follows the harvester) rather than either hauling them off-site along with the boles or simply leaving the branches on-site. Dispersal of seeds from branches left on-site on the ground is not effective because they tend to be spatially concentrated and there is little seed dispersal once the cones are at or very near the ground (Greene et al., 2004).

2. The model

2.1. General approach

This model simulates the establishment (density) of *P. mariana* and *P. banksiana* seedlings from aerial seedbanks following fire and salvage using the modeling software STELLA (Costanza et al., 1998). It models seed availability, the delay of germination until the spring,

and age-specific juvenile survivorship as a function of seedbed type and proportion, seed mass, tree basal area per area, and granivory. Finally, the model includes the effect of salvage timing and proportion of stand area salvaged. This model ignores exogenous factors such as differences in weather from 1 year to the next, and competition with other plant species. It does not include cone-bearing branches (and thus seeds) that fall onto the ground as a direct result of salvage operations; indeed, it is assumed that all branches are hauled away along with the boles. A simulation period of 72 months (6 years) is used, which is expected to permit abscission of all post-fire seeds in the absence of salvage (Greene et al., 2013). The following sections address the assumptions and functions of the model, all of which are empirically documented and used solely for model calibration, and not in the model validation process.

2.2. Seed availability before and during the fire

As argued empirically by Greene and Johnson (1999) for these two species in Saskatchewan, seed production per m^2 (Q_D) is directly proportional to tree basal area per area (m^2/m^2):

(1) $Q_D = 163,400 \ (0.53) B_D^{0.95}$ (*P. mariana*)

(2)
$$Q_D = 35,097 B_D^{0.86}$$
 (*P. banksiana*)

While it is understood that *individual* basal area typically explains only about 20–50% of the variation in seed production among local conspecifics in any 1 year, it has been repeatedly emphasized that it is the only simple measure of seed production available (Calogeropoulos et al., 2003; Viglas et al., 2013). However, at the stand scale, as in our approach here, much of this individual variation is averaged out, and basal area/area is a very good predictor of seeds/area (Greene and Johnson, 1999). In Eq. (1) we follow Greene and Johnson (1999) and De Groot et al. (2004) in assuming that only 53% of the seeds of *P. mariana* survive passage of the flaming front while the *P. banksiana* seeds are not harmed by the fire. It is further assumed that the overlapping dispersal curves of individual trees result in a spatially random distribution of deposited seeds.

2.3. Seed abscission

The seed abscission schedules of *P. mariana* and *P. banksiana* following fire have been empirically documented (Greene et al., 2013). Expressing the cumulative proportion, F_t , of seeds abscised by time *t* since fire as a two-parameter Weibull distribution, we have:

$$F_t = 1 - \exp\left(-\left[\frac{t}{a}\right]^b\right) \tag{1}$$

where *a* is the scale parameter, and *b*, the shape parameter, indicates whether the probability of abscission is increasing or decreasing with *t*. With *t* expressed in months, Greene et al. (2013) found that the coefficients *a* and *b* in Eq. (1) were 17.84 and 0.633, respectively, for *P. mariana*, and 2.05 and 0.472, respectively, for *P. banksiana*. These values lead *P. mariana* to abscise seeds far more slowly than *P. banksiana*.

2.4. Seasonal availability of seeds for germination

While seed abscission occurs year-round, germination occurs only in late spring and summer. This model assumes that seeds abscised from June to August are able to germinate during this period while those abscised between September and May must wait until the following summer to germinate (Greene et al., 1999).

2.5. Granivory and cumulative juvenile survivorship

Substrates such as exposed rocks, firm logs, charred logs, and standing puddles are considered lethal for seeds. As for non-lethal seedbeds, we estimate the cumulative survivorship (S) of a cohort over its first three summers from deposited seed to seedling, following the approach of Greene and Johnson (1998), where they collated the results of numerous empirical studies (albeit the great majority were in clear-cuts rather than burns). They divided seedbeds into good (with proportion, w) and poor (1 - w), with the difference in the survivorship created by either type increasing rapidly and inversely with seed size. These two proportions sum to the total non-lethal proportion of the ground. For this study of a fire, the good seedbeds were similar to those of Greene et al. (2006): exposed mineral soil and living (surviving) mosses. The poor seedbeds had residual duff or a thick layer of leaves or dead mosses, or, more rarely, were lichens. We assumed that the survivorship on either type was dependent on germinant size, with the latter, in turn, dependent upon seed mass (m) in g. Their equation is:

$$S = gw[1 - \exp(-f_{\rm L}m^b)] + g(1 - w)[1 - \exp(-f_{\rm H}m^d)]$$
(2)

Seed mass was 0.0012 g for *P. mariana* and 0.0045 g for *P. banksiana* (Greene and Johnson, 1999). As in Greene and Johnson (1998), *b* and *d* in Eq. (2) were set at 0.43 and 0.76, respectively; f_L and f_{H} are set at 1.83 and 0.33, respectively. Finally, *g*, the survivorship through the granivory stage, is set at 0.95 for the summer of the fire itself, following the observation of Charron and Greene (2002) that granivory is extremely rare initially in the boreal fire they studied when the site is far from the fire edge or from a residual stand. We know of no other study of first-summer granivory rates after wildfire in forests that makes clear the distance to a source of small mammal dispersants. Subsequent to that first summer, *g* is reduced to 0.43 (as in Greene and Johnson, 1998) for the remainder of the simulation. Finally, it is assumed that after the third summer, the age-specific survivorship for any cohort is essentially 1.0 (Charron and Greene, 2002).

Salvage affects the seedbed proportions. Greene et al. (2006) observed a 30% increase in mineral soil and thin humus in a 100% salvaged site due to organic layer removal by harvesters. All of this increase was on the skid paths; i.e. the skid paths occupied about 30% of the burn. In the model we reduce both pre-salvage seedbed proportions (multiplying w and (1 - w) by 0.70) and then add 0.3 to the category w. This is far too simple as in some cases the machinery is merely baring rocks (a lethal substrate) or creating depressions (ruts) that are filled with water part of the time. That is, the assumption that 30% is added to the "good substrate" category is optimistic, however it was chosen as this is the standard amount of area expected to constitute skid paths in Quebec if salvage operations are properly executed. Spacing of skid trails during the course of operations will undoubtedly vary from site to site; therefore, given the lack of empirical data, we use this estimate.

2.6. Seed removal by salvage

Seeds not yet abscised at the time of salvage are removed during the harvest. Thus, if for example, 50% of the stand area is salvaged, it is assumed that 50% of the remaining seeds have been removed. This approach does not take into account that some cone-bearing branches will be knocked off the boles during the operation, but as there are no data available on the number of seeds per area inside cones remaining on-site immediately after salvage, we can only acknowledge that this aspect of our model will underestimate the recruitment density.

2.7. Seedling and seed mortality from salvage

Seedling and seed mortality results from the passing of machinery along skid paths. It is set at 30%, the percentage of the burn covered by the parallel skid paths (Greene et al., 2006). If for example there were 10 germinants/m² after the first summer and 100% salvage occurred between September and May, then the first summer cohort is reduced by 30% to 7.0 seedlings per m^2 . As for seeds that fell onto the ground between September and the salvage date (and had therefore not yet germinated), these likewise were reduced by 30% because the machinery heaps the organic material into "windrows" along the two sides of the skid path, and thus the vast majority of these seeds will be irremediably buried. When the salvage proportion is less than 1, then the mortality rates endured by first-summer seedlings and ungerminated seeds are reduced accordingly. Thus, for example, if 50% of the area is salvaged, then the deposited (but not yet germinated) seeds and post-germination recruits will be multiplied by 0.15 (i.e. 0.5×0.3).

2.8. Model validation

Simulated seedling densities were compared to observed densities obtained from (1) the present study conducted in the 2005 Lebel-sur-Quevillon (Quebec) wildfire, (2) the 1997 Val Paradis (Quebec) wildfire (Greene et al., 2004, 2006), and (3) the 1989 Muskeg (Saskatchewan) wildfire (Greene and Johnson, 1999; Fig. 1).

2.9. Sensitivity analysis

A sensitivity analysis was performed for four parameters under two scenarios (burned intact and 100% salvaged). First, basal area per area for the species of interest was analyzed using a minimum value of $0.001 \text{ m}^2/\text{m}^2$ and maximum value of $0.003 \text{ m}^2/\text{m}^2$, reflecting the fact that below 0.001, the species is an increasingly minor component of a stand while values >0.003 are very unlikely to be encountered. Second, the seedbed-mediated survival from seed to germinant and granivory rate were analyzed using values of 0, 25, 50, 75, and 100% of the default value (as discussed above) as there are far too few studies to permit us to estimate the 95% confidence interval as a guide to the sensitivity analysis; and finally, seed mass was varied using the 95% confidence interval based on our original samples.

3. Field observations

The Lebel-sur-Quevillon fire was located in northwestern Quebec (48°49.52' N, 77°00.07' W) approximately 80 km from the town of Lebel-sur-Quevillon. Ignited by lightning in the early summer of 2005, it burned 4113 ha of forest until it was extinguished by rain. Salvage by the company Tembec began in October 2005 within the burn and continued until February 2006 with each month accounting for a specific area harvested. Prior to fire and salvage, selected stands within this fire were dominated by mature P. mariana or, more rarely, P. banksiana. Stands dominated by the former exhibited a large variation in organic layer depth depending on proximity to the water table; many had a ground cover dominated by Sphagnum while others were mantled with feathermosses (Ptilium crista-castrensis, Hylocomium splendens, Pleurozium schreberi) and Dicranum spp. The single P. banksiana stand had thinner and dryer seedbeds dominated by feathermosses and, in a few patches, lichens (mainly Cladina spp.). Ericaceous species were common understory components in almost all the stands, and consisted mainly of Vaccinium spp., Kalmia angustifolia, Ledum groenlandicum, and Gaultheria procumbens.



Fig. 1. The location of the Lebel-sur-Quevillon, Val Paradis, and Muskeg fires.

All stands sampled within the burn had 100% tree mortality. Seven sites were selected within the burn, five of these within the salvaged portion, and each representing a different month of salvage (October to February). The stand representing October salvage was dominated by *P. banksiana*. At Lebel-sur-Quevillon for the simulations, we used the salvage date that corresponded to the particular stand sampled after fire.

Tembec conducted a partial harvest in an area dominated by *P. mariana*. Salvage occurred in parallel strips: a 10 m wide portion of forest was salvaged leaving to the side a 10 m wide residual band. Thus, approximately 50% of the burned trees remained. One site was selected within this linear residual salvage zone for study (December salvage). Tembec also established some areas where they did not salvage. The seventh site was located in one of these intact burned areas.

At each of the seven sites, ten randomly oriented transects were established at the end of the summer of 2008. Each transect was 25 m long and 2 m wide. Along the transects we recorded seedling frequency, seedbed type (based on a point every 0.5 m along the centerline of the transect; n = 51 per transect), and basal area for any bole more than 50% within the transect. Basal area was recorded at breast height in the burned intact stand whereas in the 100% salvaged stands it was recorded using tree stumps. In the linear residual stand basal area was recorded using the standing burned trees in the residual bands. Stump diameters were converted to the slightly smaller breast height diameters using the regression in Greene et al. (2006).

Seedbed proportions (lethal; w; and 1 - w for the non-lethal proportion) were determined using field data from the Lebelsur-Quevillon wildfire. These seedbed data were obtained from a burned intact black spruce site using transects. Seedbed data were unavailable for the salvaged stands (both *P. mariana* and *P. banksiana*); therefore, we substituted the values from the burned intact *P. mariana* site.

Details on study area and sampling design for the early summer Val Paradis fire are available in Greene et al. (2004, 2006). The original studies and subsequent results included deciduous, coniferous and mixed stands subjected to low, moderate, and severe fire. For the purpose of this study we were only interested in mixed (i.e. >25% coniferous component) and pure coniferous stands subjected to moderate or severe fire. This gave us 16 intact and 19 salvaged P. mariana stands, and 10 intact and 17 salvaged P. banksiana stands. Data on species-specific pre-fire basal area/area, recruit densities, seedbed proportions, and salvage and fire date were available. Seedling densities from the 3-year study were corrected following the age-specific argument presented by Charron and Greene (2002); i.e. we included subsequent age-specific mortality for the germinant and 1-year-old cohorts; the expected cumulative survivorship (from the end of the first summer to the end of the third winter) on good seedbeds was 73.34% for P. mariana and 60.82% for P. banksiana, and 37.88% and 16.44%, respectively, on poor seedbeds. Average intact seedbed proportions for P. mariana and P. banksiana stands were used for the sites that would subsequently be salvaged. Salvage month for the Val Paradis wildfire for use in the simulations was set at 9. In reality, salvage began in August and lasted until December; we chose October (the median month), since specific dates were not available.

The 5-year-old early summer Muskeg fire of Greene and Johnson (1999) occurred on much drier sites than the two Quebec fires. None of the 18 *P. mariana* and 19 *P. banksiana* stands they examined had been salvaged; and they developed regressions for the two conifer species relating seedling density (recruits/m²) to

Table 1

Observed seedling densities, treatments, and basal area/area at the stands sampled at the Lebel-sur-Quevillion wildfire.

Site	Treatment	Salvage month	Basal area/area (m ² /m ²)	Observed seedling density/m ²
P. mariana	Burned intact	N/A	0.0015	1.02
P. mariana	50% salvaged	December	0.001	0.23
P. mariana	100% salvaged	November	0.001	0.1
P. mariana	100% salvaged	December	0.001	0.07
P. mariana	100% salvaged	January	0.001	0.11
P. mariana	100% salvaged	February	0.001	0.06
P. banksiana	100% salvaged	October	0.002	1.16

pre-fire basal area per area. Their observed seedbed proportions were quite different from the two Quebec fires: mineral soil and humus 17%, living *Sphagnum* and feathermoss 0%, thick duff 74%, lethal substrates 9%, nonetheless if we regard these proportions merely as being good, poor, and lethal seedbeds, then they are similar to the Quebec fires. Complete methods for the Muskeg fire study are available in Greene and Johnson (1999).

Data were collected at the Lebel-sur-Quevillion fire specifically for use in this study. The data from both the Val Paradis and Muskeg fires were obtained from previous unrelated studies.

3.1. Statistical analysis

Linear regressions were used to compare simulated versus observed seedling densities, by fire and by species. This was done to test the accuracy of simulated densities by determining whether slopes were significantly different from 1 and intercepts significantly different from 0. At the Lebel-sur-Quevillion fire only one *P. banksiana* stand was sampled; for that stand we examined whether the simulated seedling density fell within the 95% confidence interval of the observed density.

4. Prescriptive simulations

Exploring the model, we conducted three additional sets of simulations. First, we ascertained for each species the effect of delaying salvage. We ask: what is the pre-fire basal area per area that will provide adequate stocking (>1 seedling/ m^2) given a 100% salvage operation in the winter (December) within the first 6 years after fire. The second set of simulations was like the first except we additionally asked what would be the effect of reducing salvage intensity to values less than 100%. It is assumed for this second scenario that, with less than 100% salvage, residual stands will be in parallel rows and seed dispersal need not be explicitly examined. Third, we asked what would happen if cone-bearing branches were fed into a chipper that followed the harvester along the skid path and sprayed the mix of seeds and chips across the surrounding area behind the advancing harvester. In particular, for this third scenario we imagine that (1) the seeds are redistributed randomly across the site (including the good seedbeds created by the harvester) and (2) 75% of the residual seeds were available for redistribution, the remaining 25% being accounted for by seed mortality inside the chipper or by small branches that were not thrown into the machine.

In these simulations it is assumed that the species of interest is the only component of the stand that has commercial value and figures in the stocking calculation. We also assume the following post-fire (but pre-salvage) seedbed percentages: mineral soil 17%, living *Sphagnum* and feathermoss 10%, the poor seedbeds are solely high-porosity burnt duff 60%, and lethal substrates 13%. The total fraction of good seedbeds (mineral soil plus living mosses equals 27%) is higher than seen generally in the eastern North American boreal forest but lower than in the west (Greene et al., 2007).

For pre-fire basal area per area, we only examine the range 0.001–0.003. Below 0.001, the species is an increasingly minor

component of a stand and one should not expect full stocking no matter the prescription. Meanwhile, values >0.003 are very unlikely to be encountered, especially for *P. mariana*.

5. Results

5.1. The Lebel-sur-Quevillon fire

Observed *P. mariana* and *P. banksiana* stand seedling densities, per-fire basal area per area, and salvage date can be found in Table 1. In all cases at Lebel-sur-Quevillion, there was insufficient basal area/area to warrant harvesting had these been unburned forests. All harvesting at these sites was done within 8 months of fire. In only two cases at Lebel-sur-Quevillion did recruitment exceed 1 seedling m², our normative threshold for adequate stocking.

Post-fire exposed mineral soil and thin humus did not occur at these low-lying sites. Living *Sphagnum* and feathermoss were relatively common with 11% coverage, while high-porosity burnt duff accounted for 76%. Lethal seedbeds (almost entirely charred or unburned but firm wood, the latter resulting from the splintering of wood during cutting) comprised 13% of the ground.

5.2. Model validation

The results of log-transformed regressions of the simulated versus observed seedling density for all fires and treatments are shown in Table 2. At the Lebel-sur-Quevillion fire the *P. mariana* sites were lumped due to the small sample size. Observed natural regeneration densities of *P. mariana* from non-salvaged, salvaged (100%) and partially salvaged (50%) treatments were well predicted by the simulations ($r^2 = 0.901$; p = 0.002) (Fig. 2). The intercept was not significantly different from 0 and the slope not significantly different from 1. The single predicted *P. banksiana* seedling density of $1.09/m^2$ from a 100% salvaged burn at Lebel-sur-Quevillion within the 95% confidence interval (0.80–1.52) of the observed value ($1.16/m^2$).

Observed seedling densities for *P. mariana* and *P. banksiana* from the Val Paradis wildfire (Greene et al., 2004, 2006) were compared to model predictions. The model predicted intact *P. mariana*



Fig. 2. Log-log plot of observed vs. simulated Lebel-sur-Quevillon *P. mariana* seedling densities (treatments lumped); detailed information on regression fit can be found in Table 2.

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Fire	Species	Treatment	Fire year	α	β	df	r^2	р	и
Lebel-sur-Quevillion	P. mariana	Lumped	2005	0.225 (-0.722 to 1.172)	1.308 (0.774 to 1.841)	4	0.901	0.002	9
Val Paradis	P. mariana	Intact	1997	-0.477(-1.410 to $0.456)$	0.639 (0.111 to 1.167)	14	0.277	0.021	16
		Salvaged		-2.541 (-4.786 to -0.296)	0.018(-0.806 to 0.841)	17	-0.059	0.964	19
	P. banksiana	Intact		0.060 (-1.108 to 1.228)	0.062(-0.939 to 1.062)	8	-0.122	0.891	10
		Salvaged		0.053(-0.543 to $0.649)$	1.271 (0.455 to 2.087)	15	0.385	0.005	17
Muskeg	P. mariana	Intact	1989	0.841 (0.226 to 1.456)	0.978 (0.525 to 1.431)	16	0.54	0	18
	P. banksiana	Intact		0.553 (-0.212 to 1.318)	0.735 (0.357 to 1.113)	17	0.468	0.001	19

banksiana at the 1997 fire.

Table 2

densities reasonably well ($r^2 = 0.277$; p = 0.021) (Fig. 3a), the intercept not significantly different from 0 and the slope not significantly different from 1. It failed however at predicting salvaged *P. mariana* densities ($r^2 = -0.059$; p = 0.964; Fig. 3b). The mean observed recruit density for black spruce was $0.63/m^2$ at the intact stands and $0.13/m^2$ at the salvaged stands.

For *P. banksiana* at Val Paradis the opposite trend was observed. While the model failed to predict intact seedling densities $(r^2 = -0.122; p = 0.891; Fig. 3c)$, it predicted salvaged seedling densities relatively well $(r^2 = 0.385; p = 0.005; Fig. 3d)$, with the intercept not significantly different from 0 and the slope not significantly different from 1. The mean observed recruit density for jack pine was $2.12/m^2$ at the intact stands and $1.69/m^2$ at the salvaged stands.

The model performed reasonably well predicting seedling densities for both intact *P. mariana* ($r^2 = 0.54$; p = 0.000; Fig. 4a) and *P. banksiana* ($r^2 = 0.468$; p = 0.001; Fig. 4b) stands at the Muskeg fire in Saskatchewan. In the case of *P. mariana* the intercept was significantly different from 0 while the slope was not significantly different from 1, indicating that the model tended to under-predict. By contrast, for *P. banksiana* neither the intercept nor slope was significantly different from 0 or 1.0, respectively.

5.3. Prescriptive simulations

The simulations indicated that, not surprisingly, delaying salvage increased the regeneration density. For *P. mariana* to minimally achieve full stocking (>1.0 seedling/m²) with 100% salvage required a delay in harvesting until the fourth winter with basal area per area as low as 0.00125; below this basal area 100% salvage would never result in minimal stocking (Fig. 5). A delay until only the third winter permitted full stocking with a minimum basal area per area of 0.00175. First winter salvage did not provide full stocking at any reasonable (<0.003) value of basal area per area.

By contrast, *P. banksiana* required no delay to achieve adequate stocking (Fig. 5). A basal area per area of only 0.001 would fully stock the site with a December (i.e. first winter) salvage (Fig. 5).

The second set of simulations looked at the additional factor of salvage intensity. Of course, as the intensity of salvage decreased, the regeneration was augmented because fewer seeds were removed from the site and better seedbeds were available after the passage of the harvesters. For *P. mariana* only a basal area \geq 0.00175 will allow for partial salvage in the first winter following fire; anything lower will require a delay until the second or third winter (Fig. 6). For *P. banksiana*, full stocking could be achieved at any pre-fire basal area from 0.001 to 0.003 with 100% salvage.

The third and final simulations examined the effect of the redistribution of seeds (via a chipper) on final seedling density. The expected amelioration is more pronounced for *P. mariana* (Fig. 7a) than *P. banksiana* (Fig. 7b) because there were more seeds to redistribute due to its slower abscission schedule. For both species, any basal area per area value as low as 0.001 was sufficient to achieve adequate stocking, even with a first winter harvest.

5.4. Sensitivity analysis

A sensitivity analysis was performed for three parameters: basal area per area, seedbed-mediated survival from seed to germinant, and the granivory rate. In these three cases, the parameter values ranged from 0.25% of the expected mean to 4 times the expected mean. In all cases, the output (seedlings m^{-2}) was merely a linear function of the parameter value. For a fourth parameter, seed mass, we calculated the 95% confidence interval based on our original samples, and examined the range of seedling densities as mean seed mass varied from about two standard deviations to either side of the mean mass. Not surprisingly, given the relatively invariant nature



Fig. 3. Simulated versus observed seedling densities for intact (a) and salvaged (b) *P. mariana*, and intact (c) and salvaged (d) *P. banksiana* stands at the Val Paradis wildfire; detailed information on regression fit can be found in Table 2.



Fig. 4. Simulated versus observed intact *P. mariana* (a) and *P. banksiana* (b) seedling densities for the Muskeg fire; detailed information on regression fit can be found in Table 2.



Fig. 5. The year of 100% winter salvage in which minimally full stocking can be obtained given the pre-fire basal area/area.



Fig. 6. The maximum proportion of a stand that can be salvaged for *P. mariana* to achieve 1 seedling/ m^2 given a winter salvage date (first through third years) and the prefire basal area per area.



Fig. 7. (a) *P. mariana* and (b) *P. banksiana* seedling density vs. the dimensionless basal area/area following 100% salvage and 75% re-dispersal of salvaged seeds in the first 3 winters following fire (note: for *P. banksiana* year 3 has similar values to year 2 and is therefore masked).

of seed mass within a species, there was only an 8% difference in seedling density over this range.

6. Discussion

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Generally, the model performed well, for either species and for the range of 0 to 100% salvage. As expected, both observed and simulated seedling densities declined as the proportion of the forest that was salvaged increased, there was no tendency for the model to over-predict or under-predict. In two cases (both at Val Paradis; Fig. 3b and c) the regression between observed and simulated densities was not significant. In both these cases however the mean simulated density was close to the observed value; the problem was that neither pre-fire basal area per area nor seedbed quality seemed to greatly affect the observed recruit densities. What other factors were masking the effect of these two drivers?

There are five likely causes of the unexplained variation in the observed recruitment densities. The first involves seed mortality occurring during the fire. This remains a poorly explored topic, with experiments ranging from the use of a blowtorch to placing cones within a campfire to direct observations before and after an experimental burn (Beaufait, 1960; Despain et al., 1996; De Groot et al., 2004). A more systematic study than attempted to date may reveal a great deal of variation, due perhaps to differences in cone moisture as this will greatly affect the thermal connectivity, within and between stands in the seed survival during flaming front passage.

A second potential source of the unexplained variation is undoubtedly that basal area/area is a poor estimator of the prefire seeds per area. While it has the merit of being a quick measure (e.g. one could appeal to pre-fire inventory maps), nonetheless field measurements have shown that the r^2 values for seed density vs. basal area/area are typically only around 0.3 (Calogeropoulos et al., 2003; Viglas et al., 2013). A third likely source of variation in recruitment densities is that the rainfall in the first summer will undoubtedly greatly affect the first-summer age-specific survivorship of each cohort. This lack of realism in our model will be mitigated somewhat by the fact that each species at each site has more than one cohort.

A fourth and quite serious source of variation in the final seedling density is the assumption that an invariant amount of granivory occurs within each stand. In reality, even given equal distances from a source of dispersants, small mammal granivory rates can vary enormously (e.g. Côté et al., 2003; Greene and Johnson, 1998).

A final source of error in the modeling effort is that the survivorship conferred by seedbed types are on a gradient and not so easily reduced to our categories of good, bad, and lethal. Likewise, even the same seedbed type may be on a southern vs. northern aspect and thus differ greatly in moisture availability in the first summer for a cohort (Alexander, 1983). Finally, the same seedbed may differ markedly in how rapidly angiosperm leaf litter accrues (and thus changes the expected survivorship) or even if the litter has allelopathic effects (e.g. Inderjit and Mallik, 2001).

As a cautionary example, Greene and Johnson (1998) showed that, even with a single species (Picea glauca, white spruce) on a single seedbed type (mineral soil) and known seed input (hand sowing), 30 separate studies of juvenile survivorship from across North America revealed a range of almost 3 orders of magnitude. Further, they found that a single study with repeated annual sowings at the same site revealed almost as much variation as their cross-continental survey. Nonetheless, while seedbed type and basal area per area are both easily measured, they also can be used simply as givens (with the former taken from regional averages of seedbed type proportions as in Greene et al. (2007) and the latter read from inventory tables). By contrast, for the additional sources of variation listed above, we have neither default values nor easy field methods. In short, whatever the shortcomings of our approach, it is clear that more research is needed before the model can be elaborated further.

Turning now to the exploratory simulations, we saw that *P. banksiana* was much less harmed by early salvage than was *P. mariana*, a conclusion that tallies with observations made by Greene et al. (2006). For example at Lebel-sur-Quevillon, for the 100% salvage stands, and with similar pre-fire basal area per area, the former had 10 times more seedlings per m² than the latter. This is to be expected because, as expressed in our abscission function, much of the aerial seedbank of *P. mariana* is still on the tree when early salvage occurs, whereas *P. banksiana* will have few seeds left in the cones by that point (Greene et al., 2013).

While there are many commercially valid reasons to salvage early (St-Germain and Greene, 2009), according to our model one cannot obtain adequate regeneration of *P. mariana* unless salvage is delayed until at least, depending on pre-fire basal area per area, the second or third winter following fire. By contrast, *P. banksiana* can be fully stocked after a first winter salvage with all but the very lowest basal area/area values. We cannot however recommend delay to foresters until there is a direct comparison of the cost of artificial regeneration vs. the cost in lost or devalued wood given that delay. There is at present no published work useful for making such a comparison.

Salvage negatively affects other species such as saproxylic beetles and woodpeckers (Lindenmayer and Noss, 2006; Morissette et al., 2002). More than 80% of saproxylic insects, and most pyrophilous ground-dwelling insects, are abundant only for 2–3 years following fire. Predators such as woodpeckers have rapid increases in population abundances in these recent burns (St-Germain and Greene, 2009). Not surprisingly, Schmiegelow et al. (2006) observed that the woodpecker species common to burned areas were absent from recently salvaged sites. As previously explained, however, the goal of forestry companies is to harvest as quickly as possible; i.e. to truncate the already-short interval in which many animal species would normally sharply increase their abundances. A delay in salvage would therefore permit more of the fire-dependent insect taxa to successfully complete their life cycles, with consequent benefits for predators such as woodpeckers.

An alternative (or addition) to the strategy of delaying would be to harvest a fraction of the area. This should be done in parallel strips so that dispersal of seeds is not a constraint. As we saw, the recruitment from our partially salvaged stand at Lebel-sur-Quevillion was intermediate between intact and 100% salvaged *P. mariana* stands. With partial stands, the good seedbeds created by the harvester would be available for a diminished but nonetheless *on-site* seed source. Ideally, the care is taken to minimize rutting: we over-predicted the recruitment at our partially salvaged stand because much of the skid path surface was reduced to water-filled ruts. For example, for *P. mariana*, a basal area per area of 0.0015 would have very low recruitment and require planting if it was 100% salvaged in the first winter, while a 59% salvage under these same circumstances would lead to full stocking.

Finally, while never tested in the field, the redistribution of seeds via a chipper is a promising method that would encourage high seedling densities of both species even when initial pre-fire basal area per area was low. Especially this technique could be useful with *P. mariana* as this species, when mature, clusters the cones at the top of the stem. Our suggested technique would require that the harvester remove the top of the tree before skidding the trunk to the landing. Subsequently an individual walking behind the chipper on the skid path would grab individual cone-laden tops and throw them into the chipper. The machine will easily scatter the material across 20 m, more than enough to insure adequate dispersion of seeds across adjacent pairs of skid path and inter-skid path areas. Note however that our guess concerning the seed loss during passage through the chipper was unsupported by any empirical evidence and thus a field experiment is called for. Further, one would need to calculate the cost of the chipping operation relative to the cost of delay, partial salvage, and artificial regeneration.

In summary, our model offers a promising method for exploring recruitment following wildfire. Introducing salvage intensity and timing permits the model to generate silvicultural prescriptions. Indeed, the most obvious and quick utilization would be to couple the model with pre-fire GIS-based inventory maps and an assumption of seedbed-type coverage from the regional values of Greene et al. (2007) so that, for example, stands requiring planting could be identified early in the salvage planning process. For example, sparse *P. mariana* stands would be salvaged after 3 years (or perhaps not at all), while denser *P. mariana* and sparse *P. banksiana* stands would be salvaged immediately. The model would further be useful for depicting how delays could be shortened as the salvage became partial rather than complete.

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References

- Alexander, R.R., 1983. Seed:Seedling Ratios of Engelmann Spruce After Clearcutting in the Central Rocky Mountains. Res. Note RM-426. USDA Rocky Mt. For. Exp. Sta., Fort Collins, CO, 7 pp.
- Angers, V.A., Gauthier, S., Drapeau, P., Jayen, K., Bergeron, Y., 2011. Tree mortality and snag dynamics in North American boreal tree species after a wildfire: a long-term study. Int. J. Wildland Fire 20, 751–763.
- Beaufait, W.R., 1960. Some effects of high temperatures on the cones and seeds of jack pine. For. Sci. 6, 194–199.
- Calgeropoulos, C., Greene, D.F., Messier, C., Brais, S., 2003. Refining tree recruitment models. Can. J. For. Res. 33, 41–46.
- Charron, I., Greene, D.F., 2002. Post-wildfire seedbeds and tree establishment in the southern mixedwood boreal forest. Can. J. For. Res. 32, 1607–1615.
- Costanza, R., Duplisea, D., Kautsky, U., 1996. Ecological Modelling on modelling ecological and economic systems with STELLA. Ecol. Model. 110, 1–4.
- Côté, M., Ferron, J., Gagnon, R., 2003. Impact of seed and seedling predation by small rodents on early regeneration establishment of black spruce. Can. J. For. Res. 33, 2362–2371.
- De Groot, W.J., Bothwell, P.M., Taylor, S.W., Wotton, B.M., Stocks, B.J., Alexander, M.E., 2004. Jack pine regeneration and crown fires. Can. J. For. Res. 34, 1634–1641.
- Despain, D.G., Clark, D.L., Reardon, J.J., 1996. Simulation of crown fire effects on canopy seed bank in lodgepole pine. Int. J. Wildland Fire 6, 45–49. Greene, D.F., Johnson, E.A., 1998. Seed mass and early survivorship of tree. Species
- in upland clearings and shelterwoods. Can. J. For. Res. 28, 1307–1316.
- Greene, D.F., Johnson, E.A., 1999. Modelling recruitment of *Populus tremuloides Pinus banksiana*, and *Picea mariana* following fire in the mixedwood boreal forest of central Saskatchewan. Can. J. For. Res. 29, 462–473.
- Greene, D.F., Zasada, J.C., Sirois, L., Kneeshaw, D., Morin, H., Charron, I., Simard, M.-J., 1999. A review of the regeneration dynamics of North American boreal forest tree species. Can. J. For. Res. 29, 824–839.
- Greene, D.F., Kneeshaw, D.D., Messier, C., Lieffers, V., Cormier, D., Doucet, R., Coates, K.D., Groot, A., Grover, G., Calogeropoulos, C., 2002. Modelling silvicultural alternatives for conifer regeneration in boreal mixedwood stands (aspen/white spruce/balsam fir). For. Chron. 78, 281–295.
- Greene, D.F., Noël, J., Bergeron, Y., Rousseau, M., Gauthier, S., 2004. Recruitment of *Picea mariana, Pinus banksiana, and Populus tremuloides across a burn severity* gradient following wildfire in the southern boreal forest of Quebec. Can. J. For. Res. 34, 1845–1857.
- Greene, D.F., Gauthier, S., Noël, J., Rousseau, M., Bergeron, Y., 2006. A field experiment to determine the effect of post-fire salvage on seedbeds and tree regeneration. Front. Ecol. Environ. 4, 69–74.
- Greene, D.F., Macdonald, S.E., Haeussler, S., Domenicano, J.N., Jayen, K., Charron, I., Gauthier, S., Hunt, S., Gielau, E.T., Bergeron, Y., Swift, L., 2007. The reduction of organic-layer depth by wildfire in the North American boreal forest and its effect on tree recruitment by seed. Can. J. For. Res. 37, 1012–1023.
- Greene, D.F., Splawinski, T.B., Gauthier, S., Bergeron, Y., 2013. Seed abscission schedules and the timing of post-fire salvage of *Picea mariana* and *Pinus banksiana*. For, Ecol. Manage. 303, 20–24.
- Inderjit, Mallik, A.U., 2001. Can Kalmia angustifolia interference to black spruce (Picea mariana) be explained by allelopathy? For Ecol Manage. 5518, 1–10.
- mariana) be explained by allelopathy? For Ecol Manage. 5518, 1–10.
 Lindenmayer, D.B., Noss, R.F., 2006. Salvage logging ecosystem processes, and biodiversity conservation. Conserv. Biol. 20, 949–958.
- Miyanishi, K., Johnson, E.A., 2002. Process and patterns of duff consumption in the mixedwood boreal forest. Can. J. For. Res. 32, 1285–1295.
- Morissette, J.L., Cobb, T.P., Brigham, R.M., James, P.C., 2002. The response of boreal forest songbird communities to fire and post-fire harvesting. Can. J. For. Res. 32, 2169–2183.
- Schmiegelow, F.K.A., Stepnisky, D.P., Stambaugh, C.A., Koivula, M., 2006. Reconciling salvage logging of boreal forests with a natural-disturbance management model. Conserv. Biol. 20, 971–983.
- St-Germain, M., Greene, D.F., 2009. Salvage logging in the boreal and cordilleran forests of Canada: integrating industrial and ecological concerns in management plans. For. Chron. 85, 120–134.
- Stocks, B.J., Mason, J.A., Todd, J.B., Bosch, E.M., Wotton, B.M., Amiro, B.D., Flannigan, M.D., Hirsch, K.G., Logan, K.A., Martell, D.L., Skinner, W.R., 2002. Large forest fires in Canada, 1959–1997. J. Geophy. Res.: Atmos. (1984–2012) 107 (D1), FFR 5.1–FFR 5.12.
- Viglas, J.N., Brown, C.D., Johnstone, J.F., 2013. Age and size effects on seed productivity of northern black spruce. Can. J. For. Res. 43, 534–543.