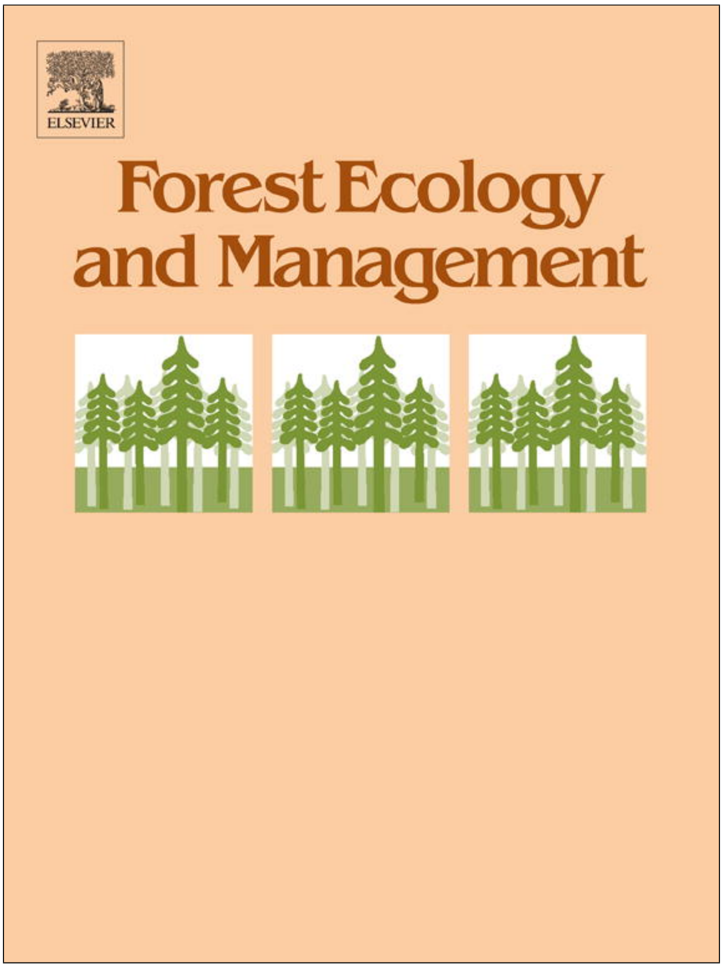
ELSEVIER
Forest Ecology
and Management

Forest Ecology and Management 303 (2013) 20–24

Contents lists available at SciVerse ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Seed abscission schedules and the timing of post-fire salvage of *Picea mariana* and *Pinus banksiana*

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ARTICLE INFO

Article history:
Received 21 September 2012
Received in revised form 26 March 2013
Accepted 29 March 2013

Keywords:
Fire
Abscission
Salvage
Seed
Regeneration
Recruitment

ABSTRACT

For aerial seedbank species, the seed abscission schedule following fire is of practical interest as it affects the optimal timing of post-fire salvage operations designed to maximize natural regeneration. It is also of theoretical interest as we would expect that the rapid deterioration of the better (very thin duff or exposed mineral soil) post-fire seedbeds due to leaf-fall from regenerating plants ought to select for rapid dissemination of seeds following burning. Nonetheless, there are no published reports of the abscission schedule of an aerial seedbank species that include the full temporal range from the fire date to several years after. In northwestern Quebec, we used eight burnt, non-salvaged stands, four dominated by black spruce (*Picea mariana*) and four dominated by jack pine (*Pinus banksiana*), in three different fires to examine the seed abscission schedule of these aerial seedbank species for the first 3 years after fire. We found that (1) the abscission schedules of populations of each species differed between fires and (2) black spruce dispersed seeds from the cones at a significantly slower rate than jack pine at all fires. Extrapolating from the regressions (all fires lumped), we conclude that approximately 90% of jack pine and black spruce seeds will have been dispersed by 1 and 5 years, respectively, after a fire. Further, we argue that due to its protracted abscission schedule, early post-fire salvage will invariably require that black spruce be planted. The approach adopted here should be useful for optimizing post-fire salvage timing for all commercially valuable species with aerial seedbanks.

1. Introduction

The species composition of boreal forest communities is highly dependent upon the initial recruitment dynamics following very large fires (Greene et al., 1999; Johnstone et al., 2004; Amiro et al., 2001; Stocks et al., 2003). The short fire return interval in the North American boreal forest has resulted in the regional dominance of fire-adapted tree species, especially in the western half of the continent where the return time is only 50–150 years (Enright et al., 1998; Lindenmayer and Noss, 2006; Gauthier et al., 1993b; De Groot et al., 2004; Scherer-Lorenzen et al., 2005).

The three most common tree species in the North American boreal forest are aspen (*Populus tremuloides*), black spruce (*Picea mariana* (Mill.) BSP) and jack pine (*Pinus banksiana* Lamb.), the two latter species possessing aerial seedbanks (Greene et al., 1999; De Groot et al., 2004; Gauthier et al., 1993a). For these two species, the density of their regeneration is positively correlated with their pre-fire tree density, and consequently there is seldom any dramatic post-fire change in species composition, at least in the absence of salvage (Greene and Johnson, 1999; Ilisson and Chen, 2009).

These two species have small (spruce: 1 mg; pine: 3.5 mg), wind-dispersed seeds, with relatively constant seed production from year to year (Messaoud et al., 2007; Rudolf, 1965). Black spruce usually has 3–6 seed cohorts on its branches while jack pine can have 10 or more (Enright et al., 1998; Greene and Johnson, 1999; Greene et al., 1999). With increasing time, however, seed viability declines (Greene et al., 1999; Rudolf, 1965).

Although in the absence of fire old cones of jack pine will slowly open when exposed to intense solar radiation, the great majority of cones are opened by the heat of flaming combustion as the resin beneath the scales is volatilized (Enright et al., 1998; Lamont et al., 1991). By contrast, black spruce will release all the seeds of a cohort within a few years of attaining maturity regardless of fire occurrence (Enright et al., 1998; Greene et al., 1999), although Zasada (1979) showed that cone opening in black spruce in Alaska was modestly accelerated by fire.

Methods for studying seed abscission have been indirect. Charron and Greene (2002) measured the residual viable seeds

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http://dx.doi.org/10.1016/j.foreco.2013.03.049

per cone on branches along a chronosequence of stands with different times since fire. Others have tried to extrapolate seed abscission rates from seedling ages, although the difficulty of obtaining accurate seedling ages for slow-growing species can, along with temporal changes in seedbed-mediated mortality rates, obscure the relationship (St-Pierre et al., 1992; Sirois and Payette, 1989; Cayford, 1963; Charron and Greene, 2002).

We know of only three direct studies of abscission on these two species, each severely limited in the time span they record. Johnstone et al. (2009) used seed traps to examine black spruce seed rain and viability over a 2-year period following a late summer fire (August 2004) in Alaska, but the crucial first 10 months after fire were missing from the data. De Groot et al. (2004) used traps to follow the abscission of jack pine seeds only for the first 2–3 months following an experimental fire. Likewise, for black spruce Wilton (1963) monitored abscission in Newfoundland for only the first 2 months after fire, stopping because of a salvage operation. The only other serotinous tree species where the post-fire abscission rate has been closely followed was sand pine (*Pinus clausa* (Chapm. ex Engelm.) Vasey ex Sarg.); but again the study is problematic as observations were discontinued 3 weeks after the fire because of salvage (Cooper, 1951).

Post-fire salvage of burned stands is increasingly used to offset the economic loss resulting from otherwise foregone future harvests (Lindenmayer and Noss, 2006; Greene et al., 2004). Salvage occurs as rapidly as possible because foresters wish to (1) prevent damage to the timber from wood-boring beetles; (2) reduce checks (wood splitting) that typically develop as the standing dead trees dry; and (3) given windthrow, enhance the number of burnt trees that will still be standing when the harvesting machinery passes by Saint-Germain and Greene (2009). As a result of quick salvage, large numbers of seed-bearing cones are either deposited in slash piles at the edges of roads or end up on the ground where they cannot disperse their seeds more than a few cm (Greene et al., 2004; Lindenmayer and Noss, 2006). The studies alluded to earlier, both direct and indirect, make clear that jack pine releases seeds more rapidly than does black spruce, and thus it is not surprising that early salvage reduces the natural regeneration of black spruce far more than that of jack pine (Greene et al., 2004). In any case, a delay in salvage would benefit the regeneration potential of either species, as it would lead to a greater percentage of seeds abscising prior to the harvest. In turn, this would reduce the amount of post-fire planting required. But our ability to quantify the trade-off in the salvage timing—planting cost vs. reduced wood value—is hampered by our lack of detailed knowledge of the abscission schedule of these two common boreal species. Examining seed release of black spruce and jack pine in the first 3 years following three stand-replacing fires in northwestern Quebec, our first goal is therefore to understand at a fine temporal scale the abscission schedules, and therefore be able to suggest changes in the present approach to salvage that would minimize some of the negative effects of removing burnt trees too rapidly.

Our second objective is to examine the functional form of the abscission schedule for these two species. To our knowledge, this issue has never been broached for any plant species; instead the few abscission studies we have are simply empirical descriptions or, at best, regressions of number of seeds abscised vs time. A simple null hypothesis is that the probability of seed abscission is random with respect to time; this would result in a negative exponential loss rate. A more likely scenario however, especially for conifers, is that the abscission probability declines with time. This is because with most conifers (but not *Abies* or some Cupressaceae), scales must flex open to permit release of viable seeds, and the more distal the scale, the most resistant it is to opening widely (Dawson et al., 1997). A second reason is that the scales flex open in response to relative humidity, and this will be lowest in the first few months after the fire before regeneration can modify the initially low albedo of the charred organics (Lyons et al., 2008). We will fit the empirical data on abscission schedules to a two-parameter Weibull distribution; one of its two parameters expresses temporal changes in the loss rate.

2. Methods

We examined the abscission schedule of both species in three fires: Nemaska (2002), Mistissini (2006), and Senneterre (2007). All three are in the central boreal forest of Quebec, and were lightning-ignited, stand-replacing fires extinguished by rain. Within each fire all the stands we used to sample the post-fire seed rain had 100% tree mortality and were at least 100 m from a fire edge with surviving trees.

The Nemaska fire burned 60,000 ha from July 2 to July 12. Four 4 m^2 seed traps were installed in each of four stands (two dominated by pine; two dominated by black spruce) approximately 3 weeks after those parts of the area had been burned. The Senneterre fire (the joining of two burns: fire #193 and fire #254) started on 14 May 2007 and burned 64,000 ha in about 3 weeks. Two stands, one dominated by black spruce before the fire and the other by jack pine, were used. The Mistissini fire was ignited in the first week of June 2006, and burned 920 ha of forest before being extinguished on the 24th of June. Two stands, one dominated by black spruce before the fire and the other by jack pine, were chosen. At both Senneterre and Mistissini, seed traps were installed about 1 week after the fire was extinguished.

In order to estimate how many seeds had abscised in the brief period *before* seed trap installation, we used a coring tube to sample the organic layer next to the traps at Senneterre and Mistissini. The tube contents were dried in a lab; after sieving, the number of spruce and pine seeds per core was determined. One hundred samples were taken from each site (core aperture area = 12.6 cm^2), for a total area of 0.126 m^2 per stand. On a per area basis, for pine the seedfall in the first week was, averaging across those two fires, about 40% of all available seeds. For spruce, the average seedfall in the first week was only 10% of the total seeds available. For Nemaska, for the missing initial 3 weeks from fire to trap installation, we used estimates of the cumulative seed proportion lost by each species at the two other fires as of their third post-fire week.

Over the course of the study, seed trap contents were examined six times each at Nemaska and Mistissini, and seven times at Senneterre. In order to determine the cumulative proportion of seeds abscised by any date, we need to also know the total number of seeds remaining in cones when the study was terminated. At the end of this period (3 years after the fires at Nemaska and Mistissini, and 2 years after the Senneterre fire), 10 cones of black spruce and jack pine were taken from 10 separate trees of each species for a total of 100 cones per site. The remaining filled seeds within these cones were counted after drying at room temperature for several months to determine the final number of full-sized seeds not yet abscised. Based on the size of the imprint of absent but full-sized seeds on the scales of these cones we also estimated the original number of filled seeds available at the time of fire. On a per area basis, we estimated that pine still retained about 6% of its seeds at Senneterre (end of second summer since fire) and about 7% at Mistissini and Nemaska (end of third summer since fire). For black spruce these estimated values were 39% and 24%, respectively. The estimated total complement of full-sized seeds/cone at the time of fire was about 24 seeds for pine and 31 for spruce.

Expressing the cumulative proportion, F_t, of seeds abscised by time t as a two-parameter Weibull distribution, we have:

$$F_t = 1 - \exp(-[t/a]^b) \quad (1)$$

where a is the scale parameter (time to lose 63% of seeds; an invariant property of the distribution), and b, the shape parameter, indicates whether the probability of abscission is increasing ($b > 1$) or decreasing ($b < 1$) with t. This equation can be manipulated into a linear form for least-squares regression.

To experimentally verify the rate of opening of jack pine scales we took 15 cones of jack pine from the Mont Laurier region (the transition between the boreal and eastern hardwood forest) of southern Quebec and boiled them to melt the resin. We then appended the cones upside down above a lab bench. After 30 days we checked to see how many filled (full endosperm as determined via a cutting test) seeds had fallen from the flexed scales. To determine how many seeds remained, we used pliers to open up the distal scales more fully so we could extract the remaining filled seeds.

3. Results

The parameter estimates from fitting the data to the Weibull are shown in Table 1; all correlations were significant ($p < 0.01$). Among pine at the four sites (three fires), slopes (b) ranged from 0.24 to 0.68. Three of the four slopes were significantly smaller than 1.0. A set of six pairwise comparisons showed that two of the slopes were significantly different from one another (Senneterre vs either JP2 or Mistissini; $p < 0.05$; t-test; a Kolmogorov–Smirnov test was first used to demonstrate the normality of the transformed data). The scale parameter (time to 63% seed loss), a, ranged from 0.16 to 5.13 months (time is expressed in months of 30.4 days); pairwise comparisons showed no difference among the a values ($p > 0.05$; t-test).

For spruce at the four sites, the smallest slope was 0.52 while the largest was 1.02. Two of the four slopes were significantly smaller than 1.0. Six pairwise comparisons of the four stands indicated that all three comparisons involving Senneterre were significantly different from the others, as well as the comparison of BS2 vs Mistissini ($p < 0.05$; t-test). None of the four slopes were significantly different from one another. The scale parameter, a, varied from 15.7 to 23.1 months. Pairwise comparisons indicated that no spruce a value was different from the others.

Combining all the data for each species, spruce was significantly slower at releasing seeds (i.e. had a smaller a value) than pine (Fig. 1; $p < 0.001$); 17.8 vs 2.1 months, respectively. As well, combining fires, the slope, b, of spruce was significantly larger than that of jack pine (0.63 vs 0.47, respectively). Finally, for both species with fires combined, the two slopes were significantly smaller than 1.0.

For the 15 boiled jack pine cones, after 1 month in the absence of wind or vibration 72% of all filled seeds had abscised. By contrast, the Weibull expectation for seed loss after 1 month based on the pooled (three fires) regression in Table 1 would be 51%.

4. Discussion

The results indicate that black spruce released seeds far more slowly than jack pine; this is consistent with indirect observations made by Charron and Greene (2002). With data combined for all three fires, black spruce would take 10 months to abscise 50% of its seeds, while jack pine would require only about 1 month. Likewise, the 90th percentile of seed release for pine would occur 1 year after the fire, but for spruce would occur, because of the high slope value, after more than 5 years. These latter results are remarkably similar to what Charron and Greene (2002) observed indirectly via a chronosequence of seeds/cone observations following wildfires in Saskatchewan; e.g. after about 24 months they found that 65% of the seeds of spruce and 97% of pine had abscised, whereas our regression results indicate that 70% and 96%, respectively, of the seeds had been released after 2 years.

For the combined data (and most cases of individual fires), the regression slope was significantly smaller than 1.0, indicating that the probability of abscission declined with time. Why would seed release be initially so rapid? There are two possibilities. The first is that the central scales open far more readily than the more apical and (especially) distal scales, a characteristic easily observed after boiling the pine cones. (Note that we are ignoring the unfilled and typically tiny seeds concentrated at the extreme distal and apical ends of the cone.) Almost 25% of the pine seeds fell from the appended cones in the lab in the absence of wind by the second day. Another 50% of the seeds required 27 more days to abscise. This is because only the most central scales were very widely flexed after a few days. Another reason for the decline in release probability with time is undoubtedly the increasing albedo of a burn as re-vegetation progresses (Lyons et al., 2008). Initially the blackened surface resulting from smoldering combustion of the organic horizon would make the air at canopy height quite warm. This decrease in the relative humidity around the appended cones would hasten the process of scale flexing. As plants recruit (most vigorously by asexual reproduction), the albedo would quickly rise over the first 2 years, increasing the relative humidity and therefore slowing the rate of cone opening following each precipitation event. Note that if this latter cause of slowing abscission is important, then seed release for these two species should exhibit slopes that are steeper than observed here (i.e. closer to 1.0) if nonburned sites are studied (and of course non-serotinous species should, therefore, generally have slopes near 1.0).

Why should pine abscise faster than spruce seeds? Without fire, very young jack pine will, before the serotinous trait is expressed, abscise essentially all seeds within about 1 year following the late-summer initiation of scale opening. By contrast, in the absence of fire, each cohort of black spruce tends to persist for several years after seed maturation before scales begin to open; indeed, at tree

Table 1

Regression results for eight stands at four fires for jack pine (jp) and black spruce (bs). The fitted parameters (a and b) for the Weibull are shown, as well as the 95% confidence limits for b. The probability for the correlation is p. The expected time to abscise a percentage of the seeds is from the regression equation. The Nemaska fire has two separate stands (1,2) for each species.

Site	Fire/# months recorded	n	r^2	p	a	b	b 95% conf. interval	Time (months) to lose % seeds		
								10%	50%	90%
JP-1	Nemaska/37	6	0.7	0.024	2.459603	0.5	0.107–0.889	0.027304	1.181724	13.04057
JP-2	Nemaska/37	6	0.84	0.007	4.030697	0.66	0.307–1.013	0.133226	2.313165	14.26237
BS-1	Nemaska/37	6	0.86	0.005	19.89908	0.965	0.486–1.444	1.932253	13.61085	47.22653
BS-2	Nemaska/37	6	0.95	0.001	23.05537	1.066	0.761–1.371	2.792284	16.34755	50.41522
JP	Mistissini/35.5	6	0.91	0.002	5.126183	0.681	0.416–0.945	0.18822	2.992661	17.44544
JP	Senneterre/26.8	7	0.93	<0.0001	0.156971	0.236	0.169–0.303	1.13E−05	0.033216	5.378131
BS	Mistissini/35.5	6	0.99	<0.0001	15.65794	0.767	0.66–0.874	0.832761	9.709699	46.44986
BS	Senneterre/26.8	7	0.93	<0.0001	20.12823	0.471	0.371–0.666	0.16936	9.243902	118.2608
JP	All fires	25	0.68	<0.0001	2.05078	0.472	0.336–0.608	0.017431	0.943376	12.00398
BS	All fires	25	0.89	<0.0001	17.84131	0.633	0.54–0.726	0.509887	9.999221	66.62657

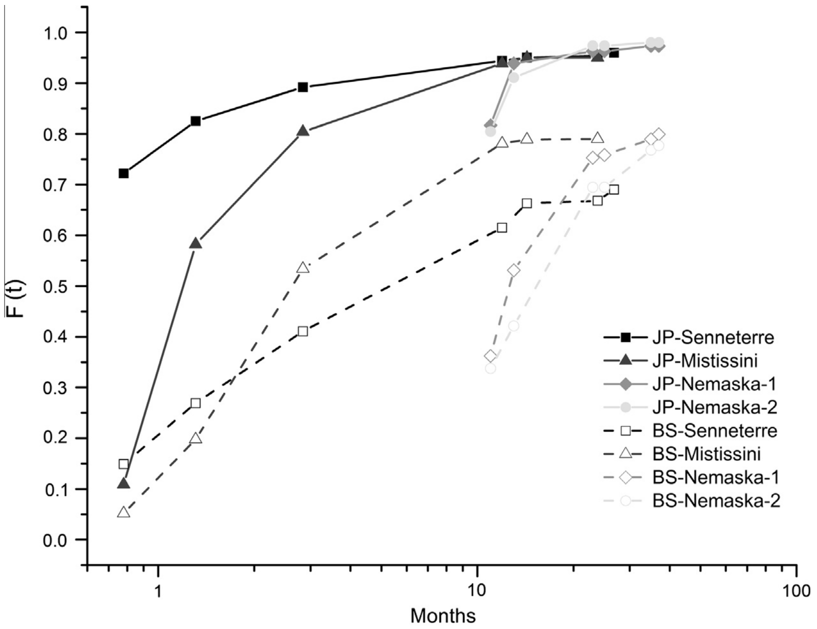

Fig. 1. Seed abscission schedule of black spruce (bs) and jack pine (jp) following three wildfires (Nemaska, Mistissini, and Senneterre). $F(t)$ is the cumulative proportion of seeds abscised by time t (months; log scale). Nemaska has two separate stands (1,2) for each species.

seed nurseries black spruce is notoriously the most reluctant of all the conifer species to abscise its full complement of seeds under any mechanical treatment (Haavisto et al., 1988). Fire melts the resin bonds in the serotinous pine cones and appears to modestly accelerate seed fall in black spruce (Zasada, 1979). It may be then that, following fire, pine behaves as if it were younger or simply non-serotinous (i.e. releasing almost all seeds within a year) while the abscission behavior of black spruce is hardly changed. Further, although there are no other studies on this, it follows then that each cone cohort of black spruce would be opening sequentially after fire over the course of several years.

Undoubtedly, the abscission process is not as temporally uniform as expressed by the Weibull. For example, rain will temporarily reverse the scale opening process. Also, the wind must play a major role in abscission. This role could be drag, proportional to the square of the speed, directly pushing a seed-wing unit from under a flexed scale, or it could be an inertial force as wind vibrates the branch to which the cone is appended. (Neither mechanism has been studied in conifers.) Differences between fires in the subsequent weather (rain and wind) would then be expected to lead to difference in, for example, the observed regression slope. Indeed, we do see significant differences among the three fires. In particular, Senneterre, where seeds were lost very rapidly, accounted for both of the comparisons where the slope for pine differed significantly between fires, and for three of the four examples of significant slope differences for spruce.

Both species avoid potentially problematic schedules where abscission is too hurried or too delayed. It has been argued by a minority of authors that the first-summer cohort of post-fire seeds of any species frequently has poor survival because germination-inhibiting ash deposits are still thick (e.g. De Groot et al., 2004; Thomas and Wein, 1985; Wang and Kemball, 2005). But even jack pine by September 1, 4 months after a late spring fire, would have about 25% of its crop still available for the second summer (Further, some fraction of seeds abscised in the late summer will delay germination until the next summer). In consequence, even a prohibitive depth of ash would not be catastrophic for jack pine as a great deal of the seed crop would still be available to germinate under more clement conditions. A fire that occurred later in the summer would pose even fewer problems. At the other extreme, the slow deterioration of the better seedbeds as broadleaf litter accrues (reviewed in Greene et al., 1999) should not deleteriously affect the more slowly-releasing black spruce. Age-specific early survivorship on the best seedbeds (exposed mineral soil and thin humus) appears to not decline seriously until about the 4th year following fire (or even later if there are few broadleaved shrubs and trees: Charron and Greene (2002)). However, where angiosperm species grow rapidly from surviving perennating organs, this more lethargic abscission schedule of black spruce may lead to poor post-fire regeneration.

Our results indicate that the seasonal timing of both fire and salvage will impact the proportion of seeds available to germinate in the first summer. Salvage usually occurs as fast as possible, within a few months of the fire after road construction is completed. Despite our evidence that abscission occurs most rapidly in the first few months after fire, this will still not give black spruce, and to a lesser extent, jack pine, sufficient time to abscise enough seeds to adequately stock the burned stand, thus leading to poor natural conifer regeneration and, necessarily, expensive planting (Greene et al., 2004). Based on time of abscission only, our results suggest that salvage be delayed until the second winter following fire for stands dominated by black spruce, and until the first winter for jack pine stands. This would allow for a much greater proportion of seed abscission to occur (90% of the crop for pine after 1 year; 65% for spruce after 2 years) and thus greatly reduce or eliminate entirely the costs associated with planting (The situation is certainly less neat than imagined here). We are presently developing a model that includes not only these abscission schedules and the timing of both the fire and salvage operations, but complications such as (1) the expected fraction of germinants killed by harvesting after a delay, as well as (2) the fact that skid paths are often very good seedbeds because of mineral soil exposure.)

The quick removal of burnt trees affects not only conifer regeneration but also plants and animals that rely on these species for survival, and thus there are other, equally compelling, reasons to delay salvage. Many animals are attracted to burnt areas; for example, charred trees are used by woodpeckers and owls, carnivorous mammals, and saprophagous beetles (Lindenmayer and

Noss, 2006; Nappi et al., 2004; Greene et al., 2006; Saint-Germain and Greene, 2009). Pyrophilous ground-dwelling insects are present only for 2–3 years following fire. This in turn limits the concentration of fire-associated animal species to the same temporal window between fire and salvage (Saint-Germain and Greene, 2009). Presumably a 2–3-year delay in salvage would therefore be quite beneficial for these species, and not just for the sexually-recruiting plants.

More generally, almost all of the species in the world with aerial seedbanks are associated with fire-prone environments (Lamont et al., 1991). For the fraction of these species of commercial value in forestry, we face the problem that while the probability of post-fire seed abscission will be greatest initially, there will still be too few seeds on the ground by the time forestry companies are ready to begin salvage. While the value of the burnt wood will be maximized by salvaging at the earliest possible date (Saint-Germain and Greene, 2009), the cost of the replanting necessitated by inadequate regeneration, on the order of $1000 USD/ha (Greene et al., 2006), must also be considered. For any of these species, understanding the abscission schedule will permit us to calculate the salvage date that leads to the lowest cost overall by avoiding costly artificial regeneration.

Acknowledgments

We thank the Chantiers Chibougamau company for setting aside the Mistissinni plots and Tembec for setting aside the Senneterre plots. We would also like to thank the MRN and SOPFEU for providing information concerning the fires. Funding was provided by an NSERC CRD Grant with Tembec and Domtar. A. Savoie, A. Sullivan, T. Gielau, N. Tasse, D. Gervais, O. Radu, M. Atkinson, O. Proulx, and S. Brennan assisted in the field. Cory Alder helped in the lab.

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