Recruitment of *Picea mariana*, *Pinus banksiana*, and *Populus tremuloides* across a burn severity gradient following wildfire in the southern boreal forest of Quebec

D.F. Greene, J. Noël, Y. Bergeron, M. Rousseau, and S. Gauthier

Abstract: Most studies of postfire tree recruitment have occurred in severely burned portions, despite the fact that partial burning is common. In this study we examined regeneration following a 1997 fire in the boreal forest of Quebec. A model of postfire recruitment was elaborated using parameters such as the proportion of trees killed (severity), the proportions of postfire seedbed types and their associated juvenile survivorship, the available seed supply, the available bud supply (for *Populus tremuloides* Michx.), and the granivory rate. All three species had peak recruitment in the first or second summer, and the recruitment episode was essentially finished after the third year. Mineral soil and surviving *Sphagnum* were the best seedbeds for both conifer species. Seedbed frequency was essentially independent of crown fire severity except for surviving *Sphagnum*, which was concentrated primarily where severity was light. Conifer fecundity was much lower in the lightly burned stands, a result we attribute to a higher granivory rate. The fecundity (seedlings/basal area for the conifers or suckers/basal area for *Populus*) in the severe sites was typical of the few other North American studies of postfire recruitment, where the published data permit us to make the comparison.

Résumé : La plupart des études sur le recrutement après feu ont été réalisées dans des zones sévèrement brûlées, malgré le fait qu'il y ait fréquemment des zones légèrement brûlées. Dans cette étude, nous avons examiné la régénération qui s'est établie après un feu survenu en 1997 dans la forêt boréale québécoise. Nous avons élaboré un modèle de recrutement après feu à l'aide de paramètres tels que la proportion d'arbres tués (sévérité), la proportion de types de lits de germination après feu et la survie des jeunes tiges associées à ces lits de germination, le stock de graines disponibles, le stock de bourgeons disponibles (pour le *Populus tremuloides* Michx.) et le taux de prédation des graines. Les trois espèces ont connu un pic de recrutement durant le premier et le second été, et l'épisode de recrutement était à toute fin pratique terminé après la troisième année. Le sol minéral et la sphaigne qui avait survécu étaient les meilleurs lits de germination pour les deux espèces de conifères. La fréquence des lits de germination était essentiellement indépendante de la sévérité du feu de cime, à l'exception de la sphaigne qui avait survécu, laquelle était principalement concentrée aux endroits où la sévérité du feu était légère. La fécondité des conifères était beaucoup plus faible dans les peuplements légèrement brûlés; un résultat que nous attribuons à un plus haut taux de prédation des graines. La fécondité (nombre de semis/surface terrière pour les conifères ou nombre de drageons/surface terrière pour les peupliers) dans les sites sévèrement brûlés était typique de celle observée dans les quelques autres études nord-américaines sur le recrutement après feu dont la publication des résultats nous permet d'établir une comparaison.

Introduction

In most of the boreal forest, the most likely way for a canopy tree to die is via a large crown fire. Recruitment following a fire consists of two broadly defined cohorts (Johnson 1992). Typically, for almost all species, the subsequent canopy and subcanopy is composed of stems that arrived almost immediately following the fire, and within a severely burned area this initial regeneration episode is brief because (1) aerial seedbanks (*Pinus banksiana* Lamb. and *Picea mariana*

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(Mill.) BSP) are soon exhausted (Charron and Greene 2002); (2) suppression of dormant buds is rapidly reattained by auxins produced from the asexually established hardwoods (Lavertu et al. 1994); (3) the best seedbeds (mineral soil, thin humus) are quickly covered by the leaf litter of the developing stand and thus become much poorer substrates (Chrosciewicz 1974; Charron and Greene 2002); and more speculatively, (4) quick reinvasion of the more severely burned parts of the fire by granivores (Ahlgren 1966) may lead to a strong reduction in the initial survivorship of later cohorts.

But what would happen after fire in a less severe burn? The question is of interest, because the great variation in the severity (defined here as proportional canopy mortality) within individual crown fires has been emphasized recently by Turner and Romme (1994), Kafka et al. (2001), and Bergeron et al. (2002). In western Quebec, for example, the severely burned fraction in fires greater than 10 000 ha ranged from 17% to 95% (Bergeron et al. 2002). Nonetheless, there have been no studies of recruitment across a burn severity gradient in the boreal forest. One surmises that four factors involved in regeneration would be affected: (1) the frequency distribution of seedbed types; (2) preabscission seed mortality and the abscission schedule of the species with aerial seedbanks; (3) the initial density of granivores; and (4) ramet production in response to loss of hormonal control by burnt trees.

Seedbeds

Given the tremendous importance of seedbeds for small-seeded boreal species (Chrosciewicz 1974; Schimmel 1993), clearly it is important to understand how seedbed frequency might change across the gradient. It is well known that the worst seedbeds for small-seeded species are thick organic layers (for clearcuts, Chrosciewicz 1974; Greene and Johnson 1998; for wildfires, Charron and Greene 2002; Thomas and Wein 1985), with *Sphagnum* on hydric sites constituting an exception. Simplistically then, we might assume that postfire organic layer depth decreases with severity and thus conifer regeneration density would be directly proportional to severity.

Preabscission seed mortality and the subsequent abscission schedules

While it is known that no boreal tree species have long-lived soil seedbanks (Johnson 1992), there has been very little work on preabscission seed losses from the aerial seedbank during a fire. Reviewing the thin literature, Greene and Johnson (1999) concluded that black spruce seeds were seriously depleted, while pine was undamaged.

With regard to the abscission schedule, pine should show a more dramatic response across the severity gradient than spruce. This is because, while the abscission schedule of the semi-serotinous *Picea mariana* is accelerated by fire (Zasada 1979), we expect virtually all prefire cones to have been opened by the fourth year following fire (wildfire: Charron and Greene 2002; clearcutting: Fleming and Mossa 1996) regardless of whether the tree burned or not. By contrast, unburned serotinous *Pinus banksiana* trees are expected to abscise only a small fraction of their seeds over 4 years.

Granivory rates

The tremendous loss of seeds and seedlings to rodents in intact vegetation and their effect on plant community composition has been frequently documented (e.g., Schnurr et al. 2002; Manson et al. 2001). While we know of no studies of granivory or herbivory across a burn severity gradient, there has been a great deal of work by zoologists on small mammal mortality and subsequent postfire reinvasion. The primary cause of mortality appears to be asphyxiation, with the mortality rate approaching 100% in the severe parts of wildfires (Erwin and Stasiak 1979; Tevis 1956; Chew et al. 1958; Motobu 1978; Lawrence 1966) and prescribed burns (Ahlgren 1966; unpublished data of J. Zasada for the Alaska boreal forest). Surviving rodents find refugia in unburned residual stands, in lightly burned areas, and at the nominal burn perimeter (Gashwiler 1970; Motobu 1978; Howard et al. 1959). Rodent populations appear to suffer much less mortality in areas of patchy burning (Motobu 1978). Subsequently, as the developing vegetation provides ever more cover from predators, recovery of rodent populations is rapid during the first 4 years (Ahlgren 1966; Sims and Buckner 1973; Tevis 1956).

In short, within the severe parts of burns, we expect essentially no granivory (Charron and Greene 2002) except by birds. By contrast, at the edges in lightly burned areas, rapid reinvasion within a few weeks of the fire (Tevis 1956), adequate cover to offer protection from carnivores (Lawrence 1966), and low initial rodent mortality (Motobu 1978) should combine to produce a granivory rate that will be as high as in the intact forest.

Ramet production

Ignoring layering, only the hardwoods will reproduce asexually after fire. In North America *Populus tremuloides* Michx., *Populus balsamifera* L., and *Betula papyrifera* Marsh. produce basal sprouts, while only the first two species can also produce root suckers. Buds remain dormant primarily because of hormones produced by living crowns; death of the crown terminates the dormancy (Greene et al. 1999). Clearly, one expects then that the density of suckers and sprouts at the stand scale should increase with the amount of basal area per area killed by the fire (i.e., with fire severity).

However, smoldering combustion of the duff may complicate this tendency somewhat if depth of burn is correlated with severity. Reduction of overtopping organics can stimulate the production of suckers (Maini and Horton 1966; Lavertu et al. 1994) while too deep heat conduction can be lethal to roots and buds (Schimmel and Granström 1996).

In summary, we hypothesize that the net effect of these factors on the sexually recruiting stems is that regeneration density will increase with burn severity for both aerial seedbank species. The difference in seedling density ought to be greater for *Pinus banksiana* than *Picea mariana* because, with the former, abscission will be much more constrained in lightly burned areas. For the asexually recruiting hardwoods, it is expected that ramet density per basal area will, likewise, rise with severity.

The two objectives of this paper are (1) to develop a model of the initial population dynamics of *Populus tremuloides*, *Picea mariana*, and *Pinus banksiana*, the three most common species in the North American boreal forest, across a fire severity gradient using data from a recent fire in Quebec; and (2) to ascertain at this fire whether recruitment increases with severity.

Models

The aerial seedbank model

The conifer species, *Pinus banksiana* and *Picea mariana*, and the suckering *Populus tremuloides* require two separate models. We begin with the conifers. Greene and Johnson (1999) proposed a model where seedling density was a function merely of seed supply (in particular, of its proxy, basal area). Here we expand their approach to include the effects of severity-mediated (1) seedbed proportions (and thus one aspect of early survivorship); (2) granivore consumption of seeds (the other aspect of juvenile survivorship); (3) preabscission seed mortality; and (4) the subsequent abscission rate. For the sexually recruited *Pinus banksiana* and *Picea mariana*, we assume that any surviving soil seed bank is negligible (Johnson 1992) and write the model for recruitment density (F_D = seedlings/m^2) as

$$[1] \qquad F_D = Q_D S_C p_Q \overline{S}$$

The mean weighted survivorship ($\overline{S}$) is given by

$$\overline{S} = \Sigma\,(S_i p_i)$$

In eq. 1, Q_D is the germinable seeds per square metre in the aerial seed bank, S_C is the fraction of seeds in the cones surviving the passage of the flaming front, p_Q is the proportion of seeds abscised, S_i is the juvenile survivorship (from seed abscission to the end of the second summer for a cohort), and p_i is the fraction of the forest floor occupied by the ith seedbed type. We discuss these terms in turn below.

Q_D, the prefire density of germinable seeds, will be estimated by first obtaining a regression of cone number (Q_C) on basal area (B) for individual nonburned trees with the intercept forced to pass through zero.

$$[2] \qquad Q_C = bB$$

with b as an empirically determined slope. (Note: insisting that the intercept is 0 greatly facilitates the modeling. However, the fact that trees have a minimum size for sexual reproduction (Greene et al. 1999) means that eq. 2 will lead us to exaggerate the contribution of very small stems.) Next, we determine the mean number of germinable seeds per cone, N_C. We can now readily scale up to the stand level by converting germinable seeds per tree to seeds per square metre, and basal area per tree to basal area per area (B_D, the dimensionless quantity m^2/m^2).

$$[3] \qquad Q_D = bB_D N_C$$

The next term, S_C, is the survival of seeds during the passage of the flaming front through the crowns (i.e., prior to abscission). For conifers, we know that burnt *Picea mariana* seeds suffer a 42% loss in seed viability (Zasada 1979). An experiment with the better-insulated *Pinus banksiana* indicated no loss when ovulate cones were subjected to a temperature and duration similar to the passage of a flaming front (Beaufait 1960). We know of no other studies than these. We write

$$S_C = 1.0 \qquad (\textit{Pinus banksiana})$$

$$S_C = (0.58p_M) + (1 - p_M) \qquad (\textit{Picea mariana})$$

where p_M is the fraction of trees killed in a stand.

We turn next to the proportion of seeds abscised after the fire, p_Q. Although the model could be altered for nonserotinous genotypes, nonetheless in the boreal forest of western Quebec such genotypes are exceedingly rare and will be ignored here. Unencumbered by a deep empirical literature, we will assume that for *Pinus banksiana* the stand-scale abscission rate is merely the fraction of trees burning (p_M) because, as pointed out by Charron and Greene (2002), there is little abscission within intact stands, whereas fire leads to an emptying of cones from burnt pine within approximately 3 years. By contrast, for *Picea mariana*, while fire may accelerate the abscission schedule (Zasada 1979), nonetheless most seeds would still be abscised within 3 years in the absence of burning (Fleming and Mossa 1996). Thus, grossly

$$p_Q = p_M \qquad (\textit{Pinus banksiana})$$

$$p_Q = 1.0 \qquad (\textit{Picea mariana})$$

Seedbed-specific survivorship

Finally, we turn to the seedbed-mediated survivorship. We will estimate seedbed-specific and severity-specific survivorship using sowing data from a severe part of the fire and from an adjacent intact forest to ascertain S_i, the survivorship on the ith seedbed type.

Small-seeded species such as *Pinus banksiana* and *Picea mariana* necessarily have small germinants (Charron 1998; Simard 1999). Consequently, they have poor germination rates and poor first-summer age specific survivorship on porous seedbeds that can dry out quickly. By the beginning of the third summer, all cohorts have an age-specific survivorship near 1.0 regardless of the initial substrate (Charron and Greene 2002). We generalize the seedbed types as follows. Good postfire seedbeds include mineral soil (with or without a thin cover of the quickly colonizing moss *Polytrichum*) and thin humus. *Sphagnum* mosses that survive the fire are also a good seedbed when they are found in close proximity to the water table and thus tend to remain wet (Groot and Adams 1994: clearcuts).

Poor seedbeds include charred wood (essentially impervious to radical penetration) and thick burnt organic material (either humic or fibric) derived from either leaf litter or mosses. We will therefore divide seedbeds into the following four types: (1) exposed mineral soil; (2) thin burnt organics <10 cm to mineral soil; (3) thick burnt organics >10 cm to mineral soil (note: this includes dead *Sphagnum*); charred wood, and nonburnt abscised leaves (in the partially burned stands); and (4) surviving *Sphagnum*.

Severity-specific survivorship

Generalizing from the literature mentioned in the introduction, we expect that granivore density is greatest in intact forest and essentially zero in the severely burned area. Further, granivore densities should also be quite high in the lightly burned portion. Thus, we want a severity-specific survivorship function that is independent of severity up to a critical point, beyond which juvenile survivorship is positively correlated with tree mortality.

Lacking any literature to guide us in choosing this critical value, we will use a rate of 60% ($p_M = 0.6$) canopy tree mortality (our upper limit for the lightly burned category) as the cut-off point. Using our experimental sowing results on the seedbeds of interest (above) to obtain S_{i0} and S_{i100}, the survivorship on the ith seedbed for intact forest ($p_M = 0$) and the severely burned area ($p_M = 1$), respectively, we tentatively define survivorship (S_i) on the ith seedbed type at the stand scale for each species as

$$[4a] \qquad S_i = (S_{i100} - g) + gp_M \qquad (\text{for } p_M \geq 0.6)$$

$$[4b] \qquad S_i = S_{i0} \qquad (\text{for } p_M < 0.6)$$

and $g = (S_{i100} - S_{i0})/(1 - 0.6)$. Note that eq. 4 assumes first that the granivore density is inversely proportional to the tree mortality rate (above 60% mortality of trees), and second that there is a linear relationship between juvenile survivorship and granivore density. This second assumption is an argument for constancy in the granivory rate; that is, the proportion eaten is independent of the seed abundance. While this is undoubtedly incorrect for the tropics at a very local scale (e.g., Harms et al. 2000), density dependence at the stand scale in the mid-latitudes appears to be much more modest (e.g., Greene 2000), and thus the latter assumption is probably not as problematic as our speculative value for the cut-off point.

The *Populus tremuloides* asexual recruitment model

While *Populus tremuloides* can certainly recruit sexually (e.g., Turner et al. 1997; Greene and Johnson 1999), nonetheless in the boreal literature it is clear that the great majority of recruiting stems are derived from buds along the roots.

Let us assume that the density of buds is a function of the density of the basal area (i.e., basal area per area). Reasonably, assume that dormancy is maintained by the downward flow of auxins from living shoots. It follows then that, at the stand scale, *Populus tremuloides* sucker density (as with seedling density we will use the symbol F_D) ought to be proportional to the burnt basal area per area (the product of B_D and p_M).

$$[5] \qquad F_D = hB_Dp_M$$

where h is an empirical constant of proportionality.

A serious problem with this model is that significant mortality usually begins by the third year following disturbance (Greene and Johnson 1999), as the shade-intolerant suckers compete for light and the shared starch reserves in the communal root system. However, our estimation of sucker density will not be problematic so long as we declare that eq. 5 applies only to stands that are younger than about 4 years old.

A deep burn in the forest floor may kill many *Populus tremuloides* roots at a very local scale, and thus the local sucker density would be less than expected. However, we argue that the product B_Dp_M is of such overriding importance that substrate differences can be reasonably ignored. As we have not attempted to estimate the prefire bud density, we cannot estimate the survivorship in the transition from prefire dormant bud to inventoried sucker. Nonetheless we can estimate the relative survivorship (S_{Ri}) as

$$[6] \qquad S_{Ri} = \frac{(1/N)\sum F_D}{B_Dp_i[1 + (p_{FOTH}/p_{Fi})]}$$

where p_i is the proportion of ground occupied by the ith substrate type, p_{FOTH} is the proportion of suckers found on all other (non-i) substrates, and p_{Fi} is the proportion of suckers on the ith substrate. Note that the relative survivorship will be directly proportional to the absolute survivorship (i.e., the ratio: inventoried sucker per dormant bud) if bud density is truly proportional to basal area per area.

Methods

Site description

The fire occurred in 1997 near Val Paradis (49°10′N, 79°17′W) in the northwest of the Abitibi region of Quebec and has been described by Bordeleau (1998). From 9 to 11 June, it burned 12 540 ha. Following a cold spring, parts of the burn (especially the lowlands) still had some interstitial ice and water in the mineral and organic horizons. The fire was extinguished by rain. Hély (2000) has demonstrated that the intensity of this fire ranged from 348 to 669, 371 to 2965, and 7807 to 8126 kW/m^2, respectively, for lightly, moderately, and severely burned stands, with the intensity invariably greatest for the conifer-dominated sites.

Within the burn area, about 95% of the canopy trees were *Picea mariana*, *Pinus banksiana*, and *Populus tremuloides* (Table 1). There were very minor amounts of *Populus balsamifera* (balsam poplar), *Betula papyrifera* (paper birch), *Larix laricina* (Du Roi) Koch. (larch), *Picea glauca* (Moench) Voss (white spruce), and *Abies balsamea* (L.) Mill. (balsam fir). Lacustrine clay soils derived from the postglacial Lake Barlow (Vincent and Hardy 1977) are the primary surface deposits in the lower areas; tills and sandy fluvio-glacial soils (Tremblay 1974) dominate the higher ground. Climatic information comes from the closest meteorological station, at La Sarre (48°47′N, 79°06′W). Total precipitation is 857 mm, and the average yearly temperature is 0.8 °C, while the average frost-free period extends from 17 June to 21 August for a total of 64 days (Environment Canada 1998).

Though there had been some scattered harvesting in the area before the fire event, the vast majority of the forest had not been harvested prior to 1997. Most of the area burned in the 1997 fire dates from a much larger fire in the early 20th century (Fig. 1; Table 1; Bergeron et al. 2001). Around 5% of the stands we sampled were even older than this, and they were probably residual stands unburned by that earlier fire (Fig. 1).

Site selection process

Immediately after the fire in 1997, an agreement was reached with two forestry companies to cordon off 36 one-hectare stands that were not to be salvaged. Harvesting outside these stands began almost immediately and was concluded within about 12 months. The 36 nonsalvaged sites were selected using the following criteria. We initially chose 12 stands each for their preburn canopy composition (basal area per area):

Table 1. The 36 nonsalvaged stands at Val Paradis.

	Populus tremuloides		*Pinus banksiana*		*Picea mariana*				
Stand	F_D	B_D	F_D	B_D	F_D	B_D	% dead trees	Mean organic depth (cm)	Stand age (years)
1	1.24	23	0.04	0	0.02	0	30	5.4	77
2	1.17	29	0.01	0	0.06	4	26	5.3	84
3	1.99	23	0.29	0.4	0	0	64	9.1	75
4	1.14	20	0.01	0	0	0	20	4	—
5	2.00	29	0.06	0.2	0.01	0	59	10.7	69
6	3.43	35	13.5	11	1.78	6	85	10	86
7	0.41	29	0	0	0.11	0.1	30	9.5	70
8	1.86	25	0.16	0	0.01	0	90	10.6	75
9	8.88	28	2.24	2	0.07	1	100	6.0	86
10	4.62	49	11.0	12	0.76	5	100	9.5	86
11	0.36	0.8	0.2	0.1	0.07	0.7	100	10.7	63
12	3.71	25	0.19	0	0.08	7	100	6.0	76
13	1.72	18	0.06	0	0.04	5	89	8.1	81
14	3.22	9	0.17	17	0.05	14	63	15.0	81
15	1.74	6	0.13	16	0.69	27	46	9.1	72
16	1.79	21	0.07	0.4	0.02	15	6	1.4	81
17	1.37	10	0.23	8	0.02	8	90	6.7	72
18	1.86	17	0.08	0	0.27	21	58	14.1	72
19	1.55	25	0.08	0	0.24	15	76	8.2	85
20	2.76	22	0.42	0	0.06	7	93	6.5	76
21	5.55	34	11.9	22	1.32	17	100	9.7	86
22	1.83	19	0.11	0	0.53	13	100	7.5	85
23	1.98	18	0.04	0	0.33	6	100	8.5	69
24	3.47	19	0.77	7	0	1	100	9.2	75
25	0	0	0.01	0	0.96	25	46	25.2	150
26	0	0	0	0	0.97	29	49	12.2	—
27	0	0	0.11	14	0.31	13	40	8.3	—
28	0	0	0	0.7	0.90	5	48	22.7	136
29	0	0.2	0.97	9	1.41	33	88	16.1	—
30	0	0	0.14	18	0.53	18	91	15.9	—
31	0	0	0.3	5	0.03	5	48	5.0	—
32	0.01	0	3.36	18	1.29	18	81	13.7	—
33	0	0	1.44	9	2.72	19	100	11.5	—
34	0.22	0	1.07	1	0.68	26	100	7.0	76
35	0	0	0.76	4	0.35	27	100	13.9	85
36	0.08	0	2.31	6	0.59	15	100	9.3	—

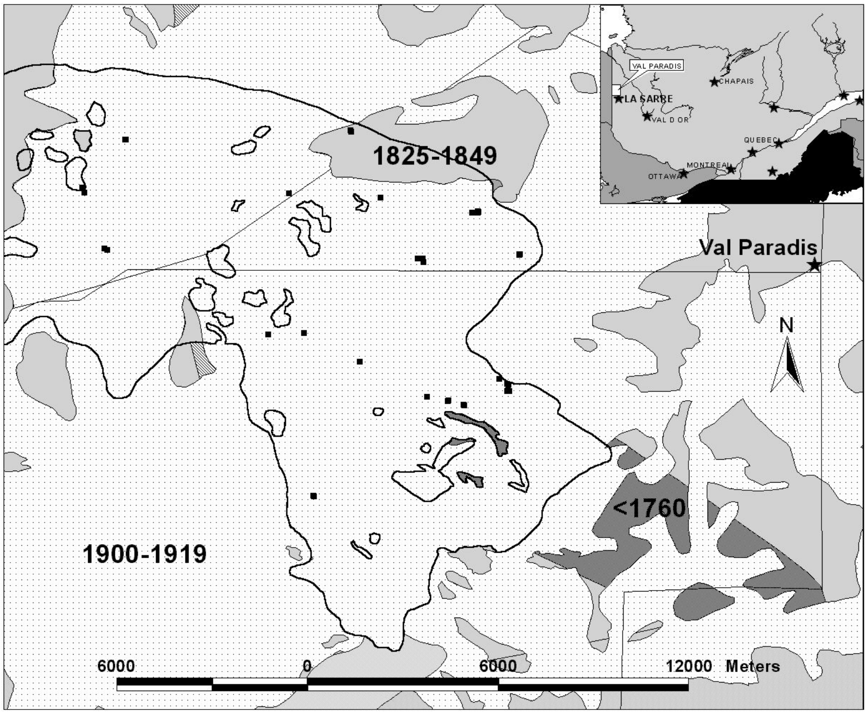
Note: F_D is seedlings or suckers per square metre and B_D is basal area per area expressed in square metres per hectare. In the equations, we use the dimensionless square metre per square metre for the latter measure.

Populus tremuloides dominated (>70% *Populus tremuloides*), mixed (10%–70%), and coniferous (<10% *Populus tremuloides*). In turn, we required that the 12 stands in each compositional class be subdivided into three severity classes: lightly burned (<25% canopy mortality), moderately burned (25%–75% mortality), and severely burned (100%). Having selected these 36 stands, they were well flagged in the midsummer of 1997 to avoid accidental salvage.

As salvage was beginning immediately, we could not delay stand selection until the final mortality levels of the canopy trees had become evident. The initial ranges for the severity classes necessarily changed as a great deal of mortality occurred during the next 2 years among those trees with partially burned crowns. Maintaining 12 stands in each class, as of 1999 (see the data in Table 1) our census of dead individuals led us to redefine the severity categories as: light (<59% dead), moderate (59%–95% dead), and severe (100% dead). This involved the transfer of two stands originally classed as light into the moderate class, and two initially moderate stands into the light category. Ultimately, these peculiar class limits do not matter greatly, as in much of the following analysis we will use the interval scale value p_M. As yet, the literature offers no consensual meaning for words like “moderate”, etc.

In the middle of each nonsalvaged 1-ha stand, a 20 m × 20 m plot (4% of 1 ha) was used for sampling. Within this 400-m^2 plot we measured diameter at breast height (DBH) for every burnt stem, ignoring trees that were clearly already dead at the time of the fire. The only exceptions to this were four stands where the 20 m × 20 m plot had a strikingly different

Fig. 1. Fire history map of the Val Paradis area. The 1999 burn is represented by the solid line, and the dots represent the sample sites.



prefire composition from the adjacent area (at the scale of 30 m). In these four stands only, we sampled a 40 m × 40 m area for tree diameters.

At each 20 m × 20 m plot (including the four stands mentioned above), we sampled seedbeds using a 30 m long (1 m wide) transect centered within the plot. Seedbeds (or perhaps we should call them substrates for the *Populus tremuloides* suckers) were sampled in two ways. First, at the edge of each 1-m^2 segment of a 30-m transect, we noted the seedbed (thus, 31 points sampled per stand). Second, for every seedling or sucker within this 30-m^2 transect, we recorded the seedbed type at the base of the stem. Thus, from these data we can calculate in eq. 4, for each stand, the p_i (proportion of ground occupied by seedbed type i) and $p_{\mathrm{F}i}$ (proportion of stems occurring on the ith seedbed type).

Finally, in twenty-five 1-m^2 randomly selected quadrats within each 20 m × 20 m stand we established permanent plots. Recruit density was enumerated each year from 1997 through 1999 in the late summer. When it became apparent that recruitment had effectively ended after 1999, we examined only 10 of the 36 stands in 2000 and 2001 to ensure that, indeed, very few recruits were being added.

Cone production and seeds per cone

In July 2000, at 10 areas just outside of the burn edge of the Val Paradis fire, we sampled three trees of both conifer species for a total of 30 trees/species. In each area, we measured DBH for a dominant, a codominant, and a subcanopy stem. These trees were then cut down at a time when the relative humidity had been low for at least 2 consecutive days. Cones that were fully opened were ignored, as were just-ripening green cones. The remaining cones for each tree were then classified as closed (=1.0) or partially opened (= 0.5). The cone count per tree, intended to be directly proportional to seed availability at the time of a June fire, was simply the summation of these values (1; 0.5).

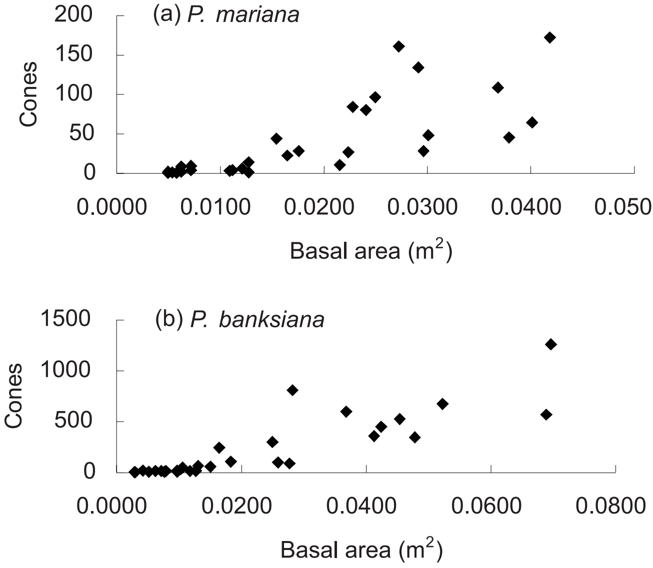
We also randomly selected 50 trees of each conifer species to cut down outside the fire perimeter. Subsampling 100 cones, we estimated the number of filled seeds per cone via a cutting test. Subsampling these filled seeds, we determined germinable seeds per cones with trials on wetted paper in the lab (70% for *Picea mariana*; 75% for *Pinus banksiana*).

Sowing experiments

Using seeds provided by the Quebec Ministry of Natural Resources, we sowed, in 1998, 800 seeds of each of the two conifer species on each of four seedbed types in a severe part of the Val Paradis fire far from any residual stand or edge. The seedbed types were the following: exposed mineral soil; surviving *Sphagnum*; thin burnt organics <10 cm to mineral soil; and thick burnt organics >10 cm to mineral soil (this includes dead *Sphagnum*). Granivores were not excluded. We measured the germinable fraction of the seed lots using wetted paper in the lab. In the late summer of 1999, we inventoried the seedlings to determine the juvenile survivorship. As with our own permanent plot results from the severe parts of the Val Paradis fire (see also the permanent plot results of Charron and Greene 2002), we assumed that about 20% of these first-summer seedlings from the sowing experiment would die in the next 2 years, as the age specific survivorship asymptotically approached 1.0. Our adjusted sowing results (the initial survivorship results multiplied by 0.8) become the estimation of the seedbed-mediated survivorship (S_{i100}) in eq. 4.

We also sowed seeds of the two conifer species on the same four seedbed types in an intact forest near Val Paradis in late August of 2000. As these seeds were derived from the cone study, we will use the same germination fractions as

Fig. 2. Cone availability as a function of basal area (m^2) for individual unburnt stems of *Picea mariana* (*a*) and *Pinus banksiana* (*b*).



previously mentioned in that section. We sowed 400 seeds per species per seedbed type. Survivorship was estimated via a census in August 2002. The age-specific survivorship should be approaching 1.0 (Charron and Greene 2002) after the second summer, and so we will not multiply by 0.8. These values become the survivorship estimates S_{i0} in eq. 4.

Ages of burnt stands

In 2000, at 27 of the 36 unsalvaged 1-ha stands, we sampled five living *Populus tremuloides* or *Pinus banksiana* by extracting disks from stems we cut with a chainsaw as low to the ground as possible. We ignored the slow-growing *Picea mariana* stems.

Results

Cone production

Regression results for ovulate cone production as a function of basal area are shown in Fig. 2. Both correlations were significant ($p < 0.05$; $r^2 = 0.54$ and 0.71 for *Picea mariana* and *Pinus banksiana*, respectively; $N = 30$ for both species). As mentioned in the Modeling section, for ease in the subsequent quantification, we have forced the regression line to pass through the origin, and this leads to a slight overprediction of the crop production of very small trees.

Since the intercepts are forced to equal 0 in Fig. 2, we can substitute basal area per area ($B_\mathrm{D} = \mathrm{m}^2/\mathrm{m}^2$) for basal area in the cone production equations, thus yielding cone density (cones/m^2). Our germination tests on wet paper indicated 19.6 or 16.4 germinable seeds/cone for *Picea mariana* and *Pinus banksiana*, respectively. Multiplying cone density by these seeds per cone values, we arrived at the expected number of germinable seeds per square metre (Q_D):

$$Q_\mathrm{D} = 41\,115\ B_\mathrm{D} \qquad (\textit{Picea mariana}) \tag{7a}$$

$$Q_\mathrm{D} = 146\,566\ B_\mathrm{D} \qquad (\textit{Pinus banksiana}) \tag{7b}$$

Seedbeds and juvenile survivorship for the two conifer species

Frequency distribution of seedbeds

Table 2 shows the relative frequencies of seedbed types by severity class. The three severity classes had different seedbed representation (χ^2 test; $p < 0.05$), but inspection of Table 2 indicates that the primary difference was the greater proportion of surviving *Sphagnum* (and, consequently, less of the thick burnt organics) in the lightly burned area. Quantifying this observation, the χ^2 test was no longer significant if we added the *Sphagnum*, which was quite deep, to the thick organic category. Likewise, a regression of mean organic depth on proportion of trees killed (data in Table 1) was not significant. Thus, contrary to intuition, there is no obvious gradient in exposed mineral soil, or exposed humus, as a function of the burn severity measured among the canopy trees. Likewise, mean postfire organic thickness (Table 2) was not related to burn severity. Pair-wise *t* tests for the three crown fire severity classes yielded no probability smaller than 0.37. In summary, there was a decoupling of fire effects between the canopy and the forest floor. For seedbeds, however, a fraction of the thick organic layer comprised surviving *Sphagnum*, and this seedbed was limited almost entirely to the lightly burned area.

Table 3 shows the frequency distribution of seedbeds versus prefire canopy species composition. As with canopy burn severity, the mineral soil proportion is relatively constant. The surviving *Sphagnum* was primarily in coniferous stands, especially the *Picea mariana* dominated lowland sites. For the nine stands with surviving *Sphagnum*, *Picea mariana* averaged 19.7 m^2/ha of basal area, while *Pinus banksiana* had 7.4, and *Populus tremuloides* had 0.70. Given that the surviving *Sphagnum* was quite thick, one might reappraise Table 3 as a gradient where postfire organic thickness increased with the proportion of *Picea mariana*. Pair-wise *t* tests indicated a significant difference in organic thickness for the conifer stands versus the hardwood stands ($p = 0.003$) but not for the conifer versus the intermediate stands ($p = 0.06$). Thus, our major conclusion is merely that the conifer stands had thicker organic layers and more surviving *Sphagnum*, and this difference was dictated primarily by the *Picea mariana* dominated stands that occupy the wetter portions of the landscape.

Sowing experiments

Results of the sowing experiments on the severely burned sites and in the intact forest are shown in Table 4. In both cases the results for *Sphagnum* and mineral soil were so similar that we have lumped them together. At both the severely burned and intact sites, mineral soil was a much better seedbed than thick burnt fibric material (burn) or fresh thick organics (intact forest). While the absolute difference between mineral soil and thick organics in the intact forest is unclear as no seedlings survived in our experiment there, Simard (1999) and Duchesneau and Morin (1999) reported a roughly 10-fold difference for *Picea glauca* (a species with a germinant size intermediate between our two conifers). Greened-up (i.e., surviving) *Sphagnum* was also a good seedbed as in clearcut studies such as Groot and Adams (1994). Our thinner duff layers (<10 cm) were a reasonable seedbed for *Pinus banksiana* but somewhat poor for *Picea mariana*.

Table 2. Proportional cover of seedbed by fire severity class (12 stands per class) where the severity class is determined by the proportion of canopy trees killed.

Burn class	Thick burnt organics and wood	Mineral soil	*Sphagnum*	Thin burnt organics	Mean organic thickness (cm)
Light	0.46	0.04	0.19	0.31	10.9
Moderate	0.64	0.06	0.01	0.28	10.2
Severe	0.68	0.04	0.00	0.27	9.1

Note: The severity classes, based on a third-summer canopy tree mortality census, are the following: light (<59% killed), moderate (59%–95% killed), and severe (100% killed). For seedbeds, "wood" included both charred downed wood present before the fire as well as charred wood that fell after the fire. Mineral soil included both *Polytrichum*-colonized mineral soil as well as uncolonized mineral soil. "*Sphagnum*" comprised only surviving (green) moss; dead *Sphagnum* was assigned to either of the appropriate organic classes. Thick organics was defined as >10 cm, while thin organics was <10 cm. The mean organic thickness (cm) is also given.

Table 3. Proportional cover of seedbed types by prefire species composition.

Composition	Thick burnt organics and wood	Mineral soil	*Sphagnum*	Thin burnt organics	Organic layer thickness (cm)
Hardwood	0.47	0.03	0	0.50	8.5
Intermediate	0.67	0.07	0.01	0.26	8.2
Conifer	0.67	0.04	0.19	0.10	13.4

Note: The categories comprise a gradient from pure *Populus tremuloides* to pure conifers (*Picea mariana* and *Pinus banksiana*). The classes were defined as hardwood dominated (0%–29% conifers); intermediate (30%–90% conifers); and conifer dominated as >90% conifers. The organic layer thickness (cm) is also given. There were 12 stands in each category.

Table 4. Survivorship estimates (2-year-old seedlings per germinable seed sown) from the sowing experiments.

	Severe burn		Intact forest	
Substrate	*Pinus banksiana*	*Picea mariana*	*Pinus banksiana*	*Picea mariana*
Mineral and surviving *Sphagnum*	0.194	0.184	0.023	0.020
Thin organic (<10 cm)	0.080	0.011	0.010	0.011
Thick organic (>10 cm) and charred wood	0.0014	<0.0019	<0.003	<0.004

Note: Where no germinants survived, we present a maximum survivorship estimate (i.e., <1/*n*, where *n* is the number of germinable seeds sown).

The difference between the survivorship on mineral soil or *Sphagnum* in the severely burned area versus intact forest is about what we would expect given the estimate of Simard (1999), who calculated the granivory rate as 0.8 in intact stands about 100 km from Val Paradis. Multiplying the survivorship values for the best seedbeds in Table 4 by 0.2, we obtain values similar to the same seedbeds in the intact forest. Likewise, if we multiply the survivorship obtained on thin organics for *Pinus banksiana* by 0.2, we obtain approximately the same result as in the intact forest (but this would not be true for *Picea mariana*, where the survivorship on thin organics is about the same for both sites). Speculatively, then, we ascribe to granivory the difference in these sowing results for the burn versus the intact forest.

The effect of fire severity on conifer fecundity

Table 5 presents the scalar $\Sigma F_D / \Sigma B_D$ (a mean fecundity: recruits per square metre of parent basal area). The value of this scalar increases with increasing fire severity for both species, and, as we hypothesized, the difference is much more dramatic for *Pinus banksiana* than for *Picea mariana*.

Table 5 also shows the regression results for the observed F_D versus the predicted F_D (from eq. 1) by species and by severity class. All correlations were significant except for *Pinus banksiana* on lightly burned sites. For the five significant correlations, the intercept was not significantly different from 0, nor was the slope significantly different from 1.0. Lumping all 36 stands together for each species, the correlation was significant for both species, and again 0 and 1.0 fell within the confidence intervals of the observed intercepts and slopes, respectively, (Fig. 3). To see how well the model performed, consider a regression (all 36 stands for each species) of observed F_D on B_D (basal area per area) alone. While both regressions were significant (r^2 = 0.26 for *Pinus banksiana* and 0.29 for *Picea mariana*), the variance explained is only half of that explained by the full model (Table 5).

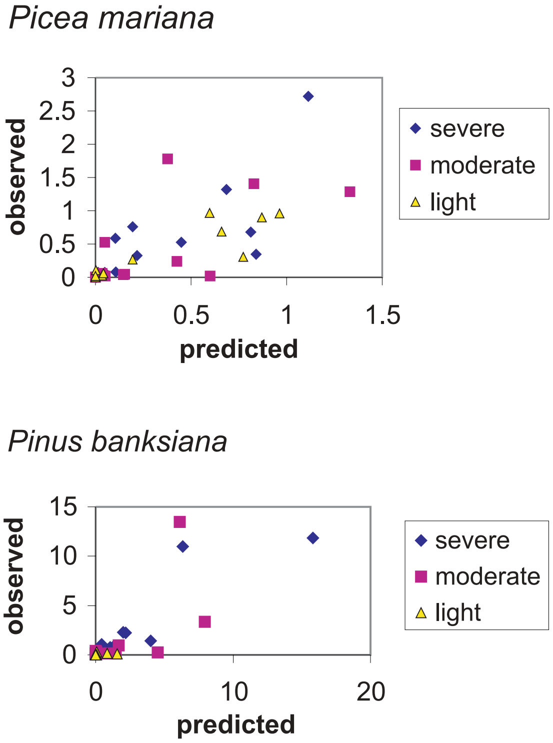
As this is the first study to include seedbeds and a gradient in severity in a model of postfire recruitment, we cannot directly compare our results with other publications. We can, however, ask whether our results are similar to other studies undertaken in severe fires, as there are a few papers that pro-

Table 5. The mean fecundity $\Sigma F_D / \Sigma B_D$ (sum of the recruits per square metre divided by the sum of the basal area per square metre) and regressions of observed F_D on predicted F_D (eq. 1) by severity class.

Burn class	*Picea mariana*	*Pinus banksiana*
Light	$\Sigma F_D/\Sigma B_D = 290$	$\Sigma F_D/\Sigma B_D = 198$
	$a = 0.05$ (–0.12, 0.21)	$a = 0.05$ (–0.01, 0.11)
	$b = 0.92$ (0.59, 1.24)	$b = 0.06$ (–0.06, 0.17)
	$r^2 = 0.80$	$r^2 = 0.10$
Moderate	$\Sigma F_D/\Sigma B_D = 393$	$\Sigma F_D/\Sigma B_D = 2415$
	$a = 0.12$ (–0.33, 0.57)	$a = -0.07$ (–2.50, 2.36)
	$b = 1.01$ (0.16, 1.88)	$b = 0.90$ (0.15, 1.65)
	$r^2 = 0.41$	$r^2 = 0.42$
Severe	$\Sigma F_D/\Sigma B_D = 540$	$\Sigma F_D/\Sigma B_D = 4961$
	$a = 0.053$ (–0.43, 0.54)	$a = 0.39$ (–1.09, 1.86)
	$b = 1.50$ (0.58, 2.4)	$b = 0.82$ (0.54, 1.11)
	$r^2 = 0.57$	$r^2 = 0.81$
Total	$a = 0.075$ (–0.13, 0.28)	$a = 0.06$ (–0.70, 0.82)
	$b = 1.15$ (0.76, 1.53)	$b = 0.86$ (0.64, 1.53)
	$r^2 = 0.51$	$r^2 = 0.66$

Note: F_D is the recruited stems per square metre, and B_D is the basal area per area (m^2/m^2). Burn severity (light, moderate, severe) is defined in relation to tree canopy mortality (see text) with 12 stands for each category. "Total" is the combination of the 36 stands from the three severity classes (N = 12 stands in each). For the regressions, "a" is the intercept, "b" is the slope (with confidence interval in parentheses), and r^2 is the variance explained. Acceptable prediction requires that the intercept is near 0 and the slope is near 1.

Fig. 3. Regressions of observed recruit density (F_D: recruits/m^2) on predicted recruit density for the three fire severity classes.



vide both B_D (basal area/area) and F_D (recruits/m^2) for severe parts of burns in a power-law relationship. Let us first recast our results for the severely burned stands as a regression of F_D on B_D in a power-law form (ignoring stands where F_D or B_D = 0):

$$[8a] \quad F_D = 279 B_D^{0.65} \quad (\textit{Pinus banksiana};\ r^2 = 0.63;\ N = 9;\ p < 0.05)$$

$$[8b] \quad F_D = 83 B_D^{0.75} \quad (\textit{Picea mariana};\ r^2 = 0.57;\ N = 11;\ p < 0.05)$$

Neither the exponents nor the intercepts in eq. 8 were significantly different (t test; $p < 0.05$) from the power-law results obtained at two separate recent fires for these same species by Greene and Johnson (1999) in Saskatchewan.

Figure 4 shows results from other studies, where we restricted ourselves to examples with fires 3–5 years old at the time of the census: Heinselman (1981: Minnesota) and St-Pierre et al. (1992: Quebec). Additionally, we add three stands from each of two Saskatchewan fires studied by Greene and Johnson (1999) evaluating their power-law regressions across the broad range B_D = 0.000 025, B_D = 0.000 25, and B_D = 0.0025. Likewise, for the Val Paradis fire, we draw from our regressions (eq. 8) using the same B_D values as mentioned in the previous sentence. The recruitment responses were quite similar (Fig. 4). Therefore, it follows that Val Paradis is a typical southern boreal forest fire, and it implies that the mean survivorship in an early summer fire does not vary greatly across regions, if we examine only the severely burned portions of a fire.

Age structures

Our age structures (Fig. 5), based on the fifth year since fire, show a peak in the first or second summer with little added after the third summer. The window is narrow because of exhaustion of the seed bank for both species. A cursory examination of 20 cones on standing burnt trees of each species in 2001 (the fifth growing season since the fire) indicated that only about 2%–5% of the filled seeds remained in the cones.

Aspen asexual recruitment

Table 6 shows our estimates of the substrate-specific relative survivorship (eq. 6) of *Populus tremuloides* assuming, as in the model (eq. 5), that only dead boles were sponsoring suckers. Unlike the conifers, *Populus tremuloides* recruit density was only mildly affected by substrate (compare with Table 4). Clearly, mineral soil was the worst substrate for all three severity classes. The recruitment was limited to the first 3 years (Fig. 5).

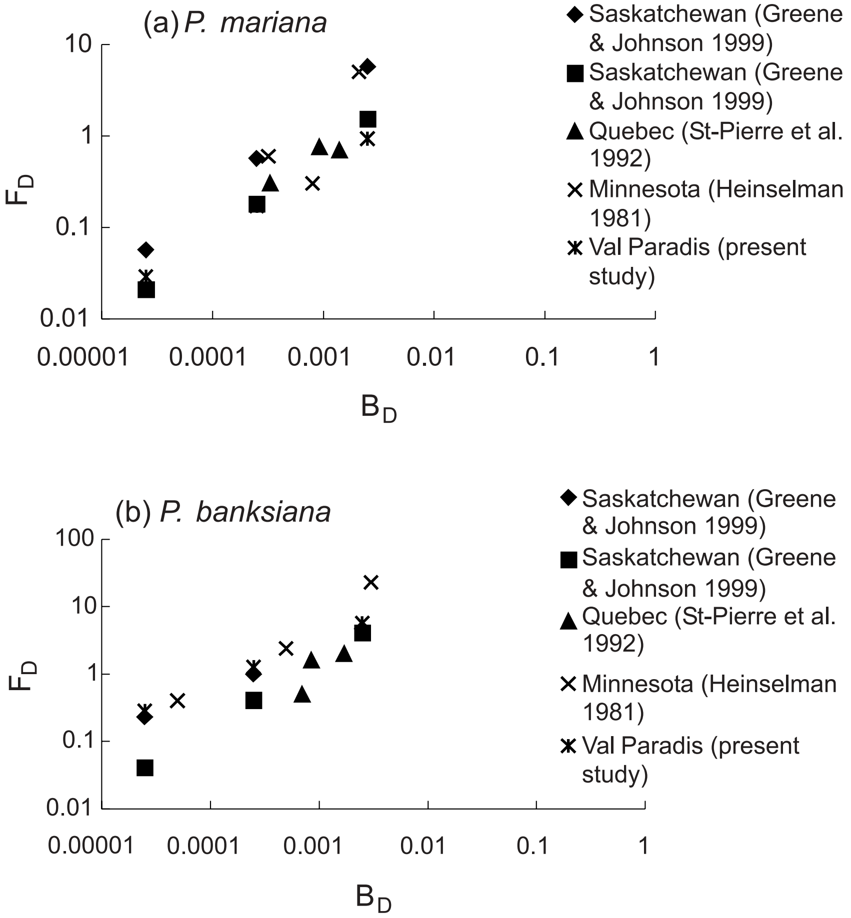
Comparing a power-law regression with only the severely burned stands (eq. 9a) or lumping stands from all three severity classes (eq. 9b) we can see that the r^2 rises significantly (t test; $p < 0.05$) if we include severity (p_m):

$$[9a] \quad F_D = 35 B_D^{0.46} \quad (r^2 = 0.27;\ p < 0.05;\ N = 24)$$

or

$$[9b] \quad F_D = 95 (B_D p_M)^{0.58} \quad (r^2 = 0.53;\ p < 0.05;\ N = 24)$$

Fig. 4. Comparison of the Val Paradis power-law regressions of recruit density (recruits/m^2) on basal area per area (m^2/m^2) at Val Paradis (severely burned sites only) for *Pinus banksiana* and *Picea mariana* with the other available results in the literature.



Discussion

Cone production

The *Picea mariana* coefficient values (eq. 7*a*) were near the low end of forestry estimates. For example, with $B_D = 0.0025$ (25 m^2/ha) we predicted 1.3×10^6 seeds/ha, whereas the reported range for fully stocked stands is 1×10^6 seeds/ha (LeBarron 1948) in Minnesota to 5×10^6 seeds/ha (Skeates and Haavisto 1987) in Ontario. Of course, much will depend on the basal area per hectare, which those authors do not provide.

By contrast, the *Pinus banksiana* results were higher than most other reports. For $B_D = 0.0025$, we predicted 2.6×10^6 seeds/ha, with the reported range being 0.6×10^6 seeds/ha (Roe 1963) to 3×10^6 seeds/ha (Bruce and Walker 1965).

Substrates

Postfire organic thickness was independent of fire severity at Val Paradis. There are two possible explanations. First, the canopy and belowground processes (flames and smoldering combustion, respectively) may not be closely related (Myanishi 2001). Note, however, that this conclusion concerning decoupling might well be modified if we had examined many stands with very few dead trees (we only had one stand with <20% mortality) where, presumably, some areas of duff would not combust at all. The second possible explanation for our result is that combustion may be more intense or prolonged where crown fire intensity is greatest, but initial prefire differences in duff thickness (due to topography-dictated moisture gradients and differing stand ages) are so great as to override this effect. Clearly with the data set in hand, we are unable to distinguish between these two arguments.

With the exception of surviving *Sphagnum*, seedbed types, like organic layer thickness, were independent of either severity or prefire tree species composition. The living *Sphagnum* was found primarily at lightly burned sites dominated by *Picea mariana*; in turn, these sites tended to be confined to the wetter parts of valley floors. We were surprised by the low amounts of mineral soil: typically about 5% of the seedbeds. This value is much lower than the typical value (35%–50%) reported by Lutz (1956) for severe fires in Alaska. It is possible that our value is this low, because ice was still present in the soil in some parts of the area during the fire.

Juvenile survivorship of conifers

Mineral soil and surviving *Sphagnum* were, as expected, the best seedbeds for both species. While the relative ranking of seedbed-specific survivorship was typical of fires, clearcuts, and intact forests (Greene et al. 1999), the absolute values in our severely burned area were much higher than have been reported for the latter two site types. We speculate that this difference is due to granivory. Sowing

Fig. 5. Age structures (percentage of inventoried recruits versus year of their origin) for the three tree species at Val Paradis as of the late summer, 2001, the fifth growing season since the fire. By this point, cohorts were being inventoried in only 10 of the original 36 plots.

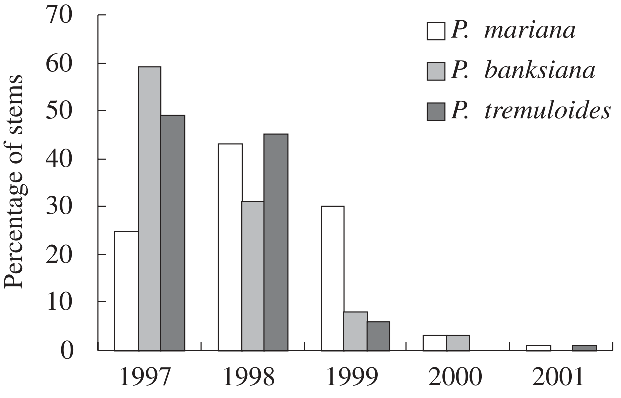


Table 6. Estimates of the "relative survivorship" (from eq. 9) for *Populus tremuloides* in relation to fire severity (see text for definition) and substrate type.

Burn class	Thick organics and charred wood	Thin organics	Mineral soil
Light	1588	2115	825
Moderate	842	1624	322
Severe	1094	2525	993

Note: *Sphagnum* is not included among the substrates, as it almost exclusively occurred in *Picea mariana* stands lacking burnt *Populus tremuloides* boles.

studies have shown repeatedly that rodent exclusion leads to sharp increases in seedling density (reviewed in Simard 1999). At a site in intact forest near Val Paradis, Simard (1999) reported a granivory rate of 80%. By contrast, Charron and Greene (2002) argued that they found no evidence of granivory in a severe part of a Saskatchewan fire. Nonetheless, while studies of rodents leave little doubt that the immediate postfire rodent density is inversely proportional to severity (Motobu 1978; Ahlgren 1966), the argument that the granivory rate is likewise proportional remains to be tested. One imagines that sowing for 3 consecutive years across a severity gradient in a recent fire would provide an adequate test of the hypothesis.

The aerial seedbank recruitment model

As expected, the density of conifer recruits was a function of burn severity and basal area per area. Similarly, for *Pinus contorta* (closely related to our *Pinus banksiana*), Turner et al. (1997) found that postfire regeneration densities were greater in severely burned than in lightly burned parts of the Yellowstone fire. (Direct comparison with their study is hampered by the fact that their severity gradient is qualitative, and their recruit densities are not corrected for basal area per area or seedbeds.)

Ignoring the lightly burned sites for *Pinus banksiana*, we showed that the recruitment model was a good predictor of regeneration density at Val Paradis. Further, we showed that our results, at least for the severely burned areas, were typical of the few other North American fire studies available in the literature (Heinselman 1981; St-Pierre et al. 1992; Greene and Johnson 1999). Why should there be this generality? At the scale of a few metres there are of course tremendous differences in seedbed type and therefore seedbed-mediated survival (Charron and Greene 2002). But at the stand scale (and all our data have been stand-level averages), these differences are largely averaged out. Meanwhile at the landscape scale, a tentative argument for similarity in results among studies is that the proportion of mineral soil and thin organics is relatively constant on upland sites among fires. On lowland sites, there may be a simple trade-off where modest combustion promotes *Sphagnum* survival, but more intense combustion provides more mineral soil or thin organics. Thus, ignoring granivory, the mean seedbed-mediated survivorship across stands may be relatively constant among burns.

In conclusion, the single most important factor in the model is basal area per area (the proxy for seed supply). Alone, it predicts about 25% of the variance in recruitment across the severity gradient and a good deal more within a severity category (Greene and Johnson (1999) using only severely burned stands). As we showed, the full model could double the explained variance compared with using basal area per area alone as a predictor. But most of that increase in explanatory power was due to our presumed gradient in granivory. Seedbeds were less important because they varied less across the landscape.

Aspen recruitment across the severity gradient

Mineral soil was the poorest of the substrates for aspen asexual recruitment, although the substrate effect was mild compared with the conifers. One surmises that some fraction of the local dormant buds was killed by deep penetration of the smoldering front. This echoes the conclusion of Schimmel and Granström (1996) for postfire shrubs in the Swedish boreal forest, although the effect here was much more muted than they found.

Prediction of *Populus tremuloides* recruitment was adequate for all the severity categories. By far the most important predictor is burnt basal area per area, as the response of this species conforms to the severity gradient.

There are only two other burns with *Populus tremuloides* sucker density examined as a function of basal area per area (Greene and Johnson 1999, both in Saskatchewan) within the age range 3–5 years. At these two fires, mortality was 100% ($p_M = 1$). Their power-law results are similar to our Val Paradis results. With a stand of aspen having 25 m^2/ha, we predict (eq. 9*b*) 2.9 recruits/m^2, whereas they predict 6.4 (Trolley fire) or 5.6 stems/m^2 (Muskeg fire). At the other extreme, if burnt aspen had only 0.25 m^2/ha, then we would expect 0.20 recruiting stems/m^2 versus 0.19 (Trolley) or 0.37 stems/m^2 (Muskeg). We conclude that aspen regeneration is largely controlled by burnt basal area per area, and that this relationship is generally the same across North American fires.

Age structures

Earlier studies (e.g., Sirois and Payette 1989) of conifer recruitment as well as some recent literature (Payette et al. 2000) derived ages from increment cores extracted long after the fire. They concluded that the immediate postfire seedbeds engendered such high mortality that the peak recruitment year, especially for *Picea mariana*, occurred well after the burn, and then continued for decades subsequently. By contrast, St-Pierre et al. (1992), using bud scale scars in a recent burn, argued that recruitment for both conifer species was immediate and brief. Likewise, but using permanent plots, Charron and Greene (2002: *Picea mariana* and *Pinus banksiana*) and Cayford (1963: *Pinus banksiana*) argued that the episode was brief with a peak in the first or second growing season. Outside the boreal forest, Turner et al. (1997) reported little additional regeneration of *P. contorta* by the third summer following fire. Clearly, our results echo these latter studies; aerial seed banks are soon depleted. Recently, it has become clear that ages based on coring have greatly underestimated the real ages of those species (e.g., *Picea*, *Abies*) that have characteristically slow height extension during the juvenile phase (e.g., Desrochers and Gagnon 1997; Parent et al. 2001).

As for *Populus tremuloides*, there has been no debate. To the best of our knowledge, this is the first postwildfire permanent plot study of *Populus tremuloides* recruitment, and our data showed that *Populus tremuloides* recruited asexually as promptly after a fire as after clearcuts (>95% of recruits within three summers: e.g., Bella 1986).

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