Tree recruitment from burn edges

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Abstract: We developed and tested a wind-dispersal model of tree recruitment into burns from living sources at the fire edge or from small unburned residual stands. The model was also tested on recruitment of serotinous Pinus banksiana Lamb. within a burn. The model assumed that source strength is proportional to basal area density and that an individual (point source) recruitment curve can be expressed as a lognormal distribution. The model made significant predictions of the recruitment curves of Engelmann spruce (Picea engelmannii Parry ex Engelm.), white spruce (Picea glauca (Moench) Voss), and balsam fir (Abies balsamea (L.) Mill.) to distances as great as 2.0 km, although it tended to underpredict Abies and overpredict Picea. The model gave significant prediction of recruitment for jack pine (Pinus banksiana) within burns with seeds derived from aerial seed banks, and of white spruce and tamarack (Larix laricina (Du Roi) K. Koch) up to 100 m from residual stands. By forestry standards, burns are poorly stocked by those species that must obligately recruit from edges. In large fires, adequate stocking by a species such as white spruce that had 5 m²/ha of basal area would be limited to about 70 m from the edge. Small residual stands are expected to supply about half of all the recruits of white spruce or fir at distances exceeding about 800 m from a nominal burn edge.

Introduction

Wildfires are the leading cause of catastrophic canopy mortality in the mixedwood boreal forest of western Canada. Fires exceeding 5000 ha, while few in number, account for the great majority of the area burned in the last 30 years (Johnson et al. 1998). This means that burns cover large areas in which few seed trees have survived. Consequently, species such as black spruce (Picea mariana (Mill.) BSP) and jack pine (Pinus banksiana Lamb.), which have serotinous cones, or trembling aspen (Populus tremuloides Michx.), which sprouts from underground roots, can easily colonize large burns as long as they were present in the stand before the fire (Zasada et al. 1992; Greene et al. 1999). Greene and Johnson (1999) have found that pre-burn basal area density (basal area per area) of these tree species is a good predictor of dispersal distances from the burn edge or unburned remnants in the burn.2

As reviewed in Greene and Johnson (1996, 1995), tree seed dispersal from an area source (collection of conspecific trees) into a very large clearing shows a characteristic form. There is, initially, a very steep decline in seed density with distance (roughly a negative exponential decline across the first 100–200 m). At greater distances, updrafts (Zasada and Lovig 1983; Greene and Johnson 1995) lead to a virtual

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flattening of the dispersal curve. This characteristic curve shape can be seen in recruitment curves into burns from nominal fire edges (MacArthur 1964) or residual stands (Galipeau et al. 1997; Stewart et al. 1998), as well as in large clearcuts (Timoney and Peterson 1996). This mimicry of dispersal curves by recruitment curves (e.g., Dobbs 1976) implies that juvenile survivorship is not seriously affected by density-dependent granivory nor by any distance-dependent seedbed effects. (There may of course be shade-related differences in survivorship within about 20 m of edges.)

Given this dispersal-mediated constraint to colonization, it is not clear how these three species persist through repeated fires. Any explanation for their persistence requires an understanding of (i) the coupling of seed production, dispersal, juvenile survivorship, and post-fire seedbeds for the cohorts recruited immediately after the fire; (ii) the rate of decrease in initial density due to mortality as the cohort ages; (iii) the renewal of recruitment as the initial cohorts become large enough to begin sponsoring significant local seed production; and (iv) differences in the characteristic oldest stand age. In this paper, we will only model the dispersal, source strength and densities of individuals in the initially recruited cohorts.

The objective of this paper is to derive and test a recruitment model for species invading large clearings from a living edge. The model will be sufficiently flexible that it could also be applied to large clearcuts. The first step is to develop a micrometeorological seed dispersal model from burn edges and large unburned remnants. Addition of a term for juvenile survivorship changes the dispersal model into a recruitment model. Implicitly, the equation states that survivorship is independent of distance or seed density. The second step is to test the model against empirical recruitment curves using our own data as well as some previously published curves that extend for more than a kilometer from any large area source. In addition, we will test a variant of the model for jack pine recruitment from burned trees within a fire, and for small residual stands of white spruce and larch. We have already validated the area source seed dispersal model (see Greene and Johnson 1989, 1994, 1995, 1996) and found it performed well at distances less than about 500 m. At larger distances, the model tended to underpredict seed density as the observed dispersal curve flattened more strongly than predicted.

Models

The point-source (single-tree) model will give recruitment (stems per square metre per distance from a single tree) using two terms: source strength (the product of seed number and survivorship) and a dispersal distance function. The area source model will consist of the summation of the point source recruitment curves from the individual trees comprising the area source with the forest edge treated as the start of the dispersal distance (x = 0).

Greene and Johnson (1996) modelled the dispersal of seeds from a forest into a clearing, taking into account the acceleration of the wind at the leeward edge of the forest. In the case of burned forests with standing dead tree boles, there are no empirical studies upon which we can model the wind acceleration. Instead, we will follow Greene and Johnson (1995) and assume that for distances greater than about 100 m, the seeds involved will be the fraction of the crop that was moving primarily within or above the canopy (before it entered the burned forest), and consequently, there is no abrupt change in wind speed near the forest border. Further, we can greatly simplify the modelling effort by assuming the source forest has the same drag coefficient as the burned forest. This assumption of a homogenous wind regime means that we will tend to overpredict seed deposition within approximately the first 40 m into the burn.

A further assumption of our model will be that the survivorship of seeds and post-germinant stems will be independent of distance into the burn. That is, the slope of the dispersal and recruitment curves will be identical.

The point source model

Following Greene and Johnson (1989) and Stewart et al. (1998), we assume a log-normal distribution of recruit density (F_Dx) as a function of distance (x) from an individual tree:

\[ F_{Dx} = \left( \frac{F}{\sigma x} \right)^{2} e^{-0.5/\left(2\pi \sigma x \ln(x/x_0)\right)^2} \]

where F is the product of terms for seed production by a single tree and seed and seedling survivorship (see below), \( \sigma \) is the standard deviation of the logarithms of the distances travelled by seeds, x is distance from the point source, and \( x_0 \) is the median distance travelled by the seed crop.

As in Greene and Johnson (1996), we assume that, at a meteorological reporting station at 10 m height (the standard reporting height), there is a median and mean horizontal wind speed of 4.3 and 5.0 m/s, respectively, with a standard deviation of the logarithms of the speeds of 0.55. The mean and median speeds are multiplied by 1.83 to account for the dependence of seed abscission on wind speed. This distribution of horizontal wind speeds is made a function of vertical position in the forest using the protocol of Greene and Johnson (1996), assuming a drag coefficient (\( \alpha \)) of \( \alpha = 2 \). This coefficient is typical of leafless forests, and thus, we are explicitly treating both the intact and burned forests as leafless stands.

Averaging the median horizontal wind speed (\( \bar{u}_{0.3} \)) from the assumed mean abscission height (\( z_a \) (where, as in Greene and Johnson (1996), \( z_a = 0.75z_b \) and \( z_b \) is forest crown height)), then there is a 0.25 probability of a late-summer fire (one month of four). Thus, at best, Zasada’s scenario might occur about 6% of the time (the joint probability becomes 0.25^2). In any case, all of the data sets that we will use in this paper show a strong decline in recruitment density with distance from living sources, and thus, we will ignore this alternative mechanism of recruitment for the moment.
height) to the ground, we obtain for a 30 m tall forest, $h_{0.5} = 2.51 \text{ m/s}$. We define the median distance travelled ($x_{0.5}$) as

$$[2] \quad x_{0.5} = \frac{z h_{0.5}}{\bar{u}}$$

where $\bar{u}$ is the mean terminal velocity (m/s). The terminal velocity is 0.66 m/s for white spruce and 0.83 m/s for balsam fir (both are estimates from Saskatchewan populations). The median distance travelled for white spruce is thus $x_{0.5} = 86$ m and for balsam fir is $x_{0.5} = 68$ m. (Note that these median distance values are three to four times higher than would be expected for dispersal within an intact forest.)

The standard deviation of the logarithms of the horizontal distances travelled ($\sigma_x$) is given as

$$[3] \quad \sigma_x = \left( \frac{\sigma_w^2}{\bar{u}^2} + \sigma_s^2 \right)^{0.5}$$

where $\sigma_w$ is the standard deviation of the terminal wind speeds and $\sigma_s$ is the standard deviation of the logarithms of the horizontal wind speeds (assumed to be 0.55). Following Greene and Johnson (1996), $\sigma_w$ is a function of the mean horizontal wind speed at a particular height in the forest. If we account for the abscission effect, and estimate $\sigma_s$ at the assumed mean abscission height ($0.75h$), then $\sigma_w = 0.78$ for a 30 m tall forest, and thus white spruce has $\sigma_x = 1.30$ and balsam fir, $\sigma_s = 1.09$.

The source strength of a single tree, $F$, in eq. 1 is given by

$$[4] \quad F = Q S_j T$$

where $Q$ is mean annual filled seed production, $S_j$ is the juvenile survivorship of a regeneration cohort in a recent burn, and $T$ is the number of regeneration cohorts (years) available for colonization before the seedbeds become so poor that colonization effectively ceases. Greene and Johnson (1994) defined $Q$ as a function of seed mass ($m$) and tree basal area ($B$):

$$[5] \quad Q = 3067m^{-0.58}B^{0.92}$$

with seed mass in grams and basal area in square metres.

Greene and Johnson’s (1998) model for juvenile survivorship ($S_j$) is for the stage from abscised seed to established seedling (about the end of the second growing season), and it assumes that mortality is dependent on seed size (proportionate to germinant size) and seedbed type, with mineral soil, humus, well-decomposed logs, and certain mosses (e.g., Sphagnum) resulting in much higher survivorship than high-porosity seedbeds such as litter, feather mosses, or charred duff. For recent site-prepared clearcuts, they obtained

$$[6] \quad S_j = 0.43\left[p_1(1 - e^{-1.83m^{0.43}}) + (1 - p_1)(1 - e^{-0.33m^{0.8}h})\right]$$

with $p_1$ the proportional coverage of the optimal seedbeds and the coefficient 0.43 representing the expected survival through the granivory stage. Note that, for a small seeded species such as white spruce, it is expected from the equation above that survivorship on the better seedbeds will be about 40 times higher than on the poorer seedbeds. Note further that the equation assumes an invariant seed mass for a population. While Fleming et al. (1987) reported that the average coverage of mineral soil and humus following scarification in clearcuts was 17%, the situation with upland mesic sites that have been burned is not at all clear. Mineral soil and exposed humus are clustered around burned boles (Charron 1998) where smouldering combustion of the duff is more intense. Dymess and Norum (1983), Charron (1998), K. Miyaniishi (unpublished data for Saskatchewan fires), and M.-J. Noel, D.F. Greene, and Y. Bergeron (unpublished data for Quebec fires) report coverage of the optimal seedbeds ranging from 5 to 40% with a median of around 15%. Therefore, setting the proportion ($p_1$) in eq. 6 as 0.15, and given a seed mass of 0.0022 (white spruce) and 0.0065 g (balsam fir), we have an expected juvenile survivorship (across the entire burn) of 0.009 or 0.0148, respectively.

We idealize the recruitment process as a set of $T$ consecutive (yearly) cohorts. The number of cohorts $T$ depends on how rapidly the developing litter and feathermoss layers reduce the juvenile survivorship to, effectively, zero. An ongoing (unpublished) study by S. Gutsell (University of Calgary, Calgary, Alta.) using stand reconstructions in central Saskatchewan indicates that the great majority of canopy trees of pine, spruce, and fir recruit within the first 4 years. Experimental sowing of white spruce on mineral and humus substrates in a 1-year-old fire versus sowing on the aspen litter of an 8-year-old fire showed that the differences in survivorship are about 40-fold as expected from eq. 6 (Charron 1998). Likewise, on scarified clearcuts, Arlidge (1967) and Zasada et al. (1978) have shown that the more receptive seedbeds quickly (about 3–5 years) become poor as they agggregate with broadleaf litter. (Clearly, the duration for high receptivity depends greatly on the density and growth rates of competitors such as aspen or the grass Calamagrostis.) Tentatively, then, we set $T = 4$.

Explicitly, we will assume that the subsequent thinning mortality for spruce and fir can be ignored, because these are very young stands (except for the Galipeau et al. (1997) burn that was 68 years old) and because the conifer densities are so low that they are unlikely to strongly self-thin. We assume that the shade of overtopping Populus, Betula, or shrubs may reduce growth but not greatly affect mortality for the early arriving cohorts of conifers. Further, as the burned boles begin to fall and decompose (after say two or three decades), they provide a receptive substrate with moderate coverage (around 2–5%: e.g., Simard 1999) that can sponsor further invasion (cf. the published age structures of spruce by Youngblood (1995), Bergeron (2000), and Lieffers et al. (1996)). However, the data sets we use below will be limited to the cohorts arriving within the first few years after the burn.

Thus, we rewrite the point source strength ($F$) in eq. 4 using eqs. 5 and 6, and $T = 4$, as

$$[7a] \quad F = 3376B^{0.92} \text{ (fir)}$$

$$[7b] \quad F = 3886B^{0.92} \text{ (white spruce)}$$

Note that the seed mass terms in seed production and juvenile survivorship have essentially cancelled each other out. A smaller seeded species can produce more seeds, but this is
offset by a higher juvenile mortality (Greene and Johnson 1998).

**The area source model**

The area source recruitment curve is the summation of the individual recruitment curves using eq. 1 for a uniformly distributed array of point sources adjacent to a burn. The intact forest edge is \( x = 0 \). The density of recruits \( F_{DS} \) as a function of distance can be reasonably expressed by a modified negative exponential function:

\[
F_{DS} = \left( \frac{F_{D}}{2} \right) e^{-ax^2}\]

(Greene and Johnson 1996) where \( F_D \) is the potential source strength (seedlings/m²) within the unburned forest, and \( a \) and \( b \) are empirical coefficients from a regression of \( x^2 \) on \( F_{DS} \). At the burn edge \( (x = 0) \), we expect the seedling density to be half of what it would be potentially deep inside the area source (i.e., if the intact forest had as high a proportion of good seedbeds as will the adjacent burn). (Note that the model is not intended to apply to seedling densities within the unburned forest; well inside the forest, it is the seed density that is double that of the edge.)

From eq. 5 remember that the exponent \( B \) (individual basal area) is so close to 1.0 that we can, with much less than twofold inaccuracy, write \( B^{0.92} \approx (2B^{0.92}/A) \), where \( A \) is the area examined (m²) and \( B_D \) is the dimensionless (m²/m²) basal area per area. Therefore, \( F_D \) (seedlings/m²) in eq. 8 becomes, by modification of eq. 7:

\[
F_D = 3376B_D^{0.92} \quad \text{fir}
\]

\[
F_D = 3866B_D^{0.92} \quad \text{white spruce}
\]

Two other factors must be accounted for in eq. 8. The first involves the proportion of the landscape that is forested. Field estimates of \( B_D \) (basal area per area) are, of course, made only in forested stands (e.g., Galipeau et al. 1997), and we cannot extrapolate to a source area at the scale of a few kilometers without an overestimate of \( B_D \) because of roads, lakes, meadows, young (not reproductively mature) stands, etc. For two burns in central Saskatchewan, E.A. Johnson and D.F. Greene (unpublished data) used forest inventory maps and calculated that only about 60% of the area had been seed sources prior to the burn for tree species. Thus, the expected source strength for each species must be multiplied by the proportion \( (g) \) of the landscape that is seed-producing forest, \( g = 0.6 \). Note that, if the basal area per area estimate were originally based on inventory data, then this factor, \( g \), could be ignored. Note further that when we deal with a small residual stand (as below), all the source trees are easily enumerated, and thus again, the factor \( g \) can be ignored.

The final consideration involves residual (unburned) stands within the nominal burn perimeter. Eberhart and Woodard (1987) reported that such stands are quite common in boreal fires. E.A. Johnson and D.F. Greene (unpublished data) found that residual stands constituted about 5% of the burn area for Saskatchewan fires exceeding 8000 ha, with the residual stands having a logarithmic size distribution such that residual areas less than 0.5 ha comprise only 0.003 (0.3%) of the total burn area (about 6% of the total residual area). (This result is similar to that of Eberhart and Woodard (1987) for Alberta fires.) As we will see, these small stands should provide a large fraction of the expected recruitment at distances hundreds of metres from the nominal burn edge. However, for the data sets we will use in our test of the recruitment model, the authors ignored the very small residual stands (roughly, those less than about 0.5 ha). MacArthur (1964) reported which sampling plots were near large residual stands, and we have removed those plots from the analysis. Galipeau et al. (1997) re-evaluated the distance \((x)\) in relation to any large source (including very large residual stands). Therefore, for both these studies, we need to account for the contribution of only the smaller residual stands. Thus, our area source eq. 8 for recruitment within a burn as a function of distance becomes

\[
F_{DS} = \left( \frac{F_{D}}{2} \right) e^{-ax^2} + R
\]

where \( R \) is the proportion of the area in small residual stands and is assumed to be, in this exercise, \( R = 0.003 \) (i.e., the small residual stands constitute 0.3% of the nominal burn area). Note that eq. 10 cannot be applied to recruitment from a single small residual stand, but below we will follow the lead of Stewart et al. (1998) and develop the recruitment curve merely as the summation of the individual point source curves.

Examples of the expected area source recruitment curves from eq. 10 are given in Fig. 1 for spruce and fir with \( R \) (the proportion of the burn containing small residual stands) equal to 0.003 or 0 and a density of 0.5 recruits/m² at the burn edge. The regression results for the two coefficients in eq. 10 yield for white spruce \( a = 0.42, b = 0.37 \), and for balsam fir yield \( a = 0.59, b = 0.33 \).

**Problems with the model**

It is useful at this point to discuss the larger sources of error in the model and in the testing of the model with field data. A major source of error in the model validation concerns empirical measures of \( B_D \) for the species of interest. The data sets we use (including our own) rely on sampling the forest edge near the origin of a set of transects into the burn. This is acceptable for prediction of recruitment within a few hundred metres, but at distances exceeding say, 500 m, the source area in question is greatly magnified. Field sampling of basal area across such a large area is prohibitive, and one ought to rely instead on forestry inventories (although these also are problematic). In short, in this exercise we do not know if the sampled \( B_D \) is representative of a much larger area, and we cannot even estimate adequately the potential error. By contrast, our assumption that 60% of the landscape is forested with reproductively mature trees is very unlikely to be more than 1.5-fold in error.

Directionality bias at the time of abscission is ignored in the model. Conifer seeds abscise when relative humidity is low and when wind speeds are high (reviewed in Greene et al. 1999). All things equal, the prevailing westerly winds should lead to an azimuthal bias. However, in all but one (Vermilion Pass) of the post-fire data sets used below, the sampling transects either cross the burn or they are a set of transects radiating out from a small residual stand. Thus, the
seedling density at a given distance has averaged out the directional bias. In any case, directional bias for dispersed seeds is usually only one- to three-fold (Greene and Johnson 1996). The situation with seedlings is less clear because of shading effects within the first 20 m of an edge. For example, Dobbs (1976) found little difference in white spruce seed density within the first 10 m for a southwest and northeast clearcut edge, but the southwest edge had 2.5 times more germinants. (The difference in germinant densities was not noticeable at greater distances into the cut.) Stewart et al. (1998) found about fourfold greater white spruce recruit distances at all distances for a westerly than for an easterly direction from a small residual stand, while Ronco (1970) found no obvious relationship between azimuth and recruitment density of Engelmann spruce (*Picea engelmannii*) in clearcuts.

Our understanding of the mean and range of the percentage coverage of the more receptive seedbeds following fire is hampered by the paucity of empirical studies. Further, none of the studies used in this paper made an estimate of the coverage as the studies occurred too long after the fires. At small spatial scales (say, at the scale of 1–20 m) differences can be pronounced with mineral soil and humus comprising anywhere from 0 to 90% of the ground (Charron 1998). These small-scale differences in duff consumption will tend to be averaged out at the large scales we will use here (up to 2 km), but there may well be significant differences among fires. At this point, based on personal observation of recent burns in Saskatchewan and Quebec, we can only say that we doubt that the mean percentage coverage of mineral soil and humus for entire burns will ever be greater than 50% or less than about 5%. Thus, the value used in this modelling exercise (15%) should be within about threefold of the correct value.

**Methods**

We used an unpublished data set of the present authors (collected in 1985) on recruitment of Engelmann spruce in the 1968 Vermilion Pass burn in the southern Canadian Rockies near Banff, Alta. Recruitment of spruce was tallied along parallel transects extending 0.5 km into the burn at right angles from an unburned forest edge dominated by spruce and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.). The nearest other burn edge was about 2 km away and was an almost pure lodgepole pine (*Pinus contorta* Dougl. ex Loud.) stand. Bud scale scars were used to estimate spruce age, and the minority of the recruits that arrived after 1975 (about 20%) were deleted from the data set. A description of the study site can be found in Greene and Johnson (1996). As Engelmann spruce has a terminal velocity, seed mass, and seedbed requirements (Day 1964) similar to white spruce, we have lumped the results with studies of white spruce recruitment into burns from Galipeau et al. (1997) and MacArthur (1964). Galipeau et al. (1997) examined a Quebec fire that was 68 years old, and we only use the portion of their data set that represented the initial post-fire recruitment event. MacArthur’s (1964) burn in eastern Quebec was 16 years old at the time of his recruitment survey. Both MacArthur (1964) and Galipeau et al. (1997) also obtained data we will use below on balsam fir recruitment.

We studied recruitment of jack pine germinants in 1997 following the June rainy season in a 1996 fire (Bittern Creek) 30 km east of Prince Albert National Park in the southern boreal forest of central Saskatchewan. We used a 50 m long transect in a burned forest that was primarily black spruce (*Picea mariana* (Mill.) BSP). The transect was deliberately chosen so it would pass through a stand of burned jack pine (about 50% of the total tree burned basal
area in the center of the transect). Jack pine trees within 50 m to either side of the transect were assigned Cartesian coordinates, and their basal areas were measured. Additionally, potential pine source trees at distances greater than 50 m beyond either end of the transect were identified. Germinants were tallied 1.0 m to either side of the 50 m transect. We sampled the germinants in 5 m long transect segments to diminish the effect of seedbed conditions (mineral soil and humus are much better seedbeds than thick burned fibric organic layers), which vary at the scale of interbole distances, 1–3 m (Charron 1998).

Recruitment of white spruce and larch was studied in 1995 at the 1989 Muskeg Fire 40 km east of the northeastern corner of Prince Albert National Park. We used three residual stands for spruce and two for larch. Stands were chosen so that they were at least 200 m from a nominal burn edge or another residual stand containing either species. At each stand, four 100 m long transects radiated out along cardinal azimuths. Along each transect, recruitment density was sampled in 3 m radius circular plots at 10, 20, 30, and 40 m, and then at 60, 80, and 100 m. Within the residual stands, the number of source trees and their basal area were measured. All residual stands were about 0.1 ha in size (the modal size for residual stands in Saskatchewan fires; E.A. Johnson and D.F. Greene unpublished data). Examination of the bud scale scars indicated that about 95% of the seedlings had recruited in the interval 1989–1993.

Results

Dispersion of jack pine recruits in a recent fire

The measured terminal velocity of the jack pine seeds was 0.73 m/s. The mean height of the canopy trees was 14 m, and thus from eqs. 2 and 3, the median distance travelled ($x_{0.5}$) and standard deviation of log distances ($\sigma_l$) were, respectively, 35 m and 1.12.

Because the trees are serotinous, we could not use eq. 5. The source-strength term for the aerial seed bank of this species has been estimated by Greene and Johnson (1999) as

$$Q = 35 \times 10^6 B^{0.86}$$

where $Q$ is the stored seed production per tree and $B$ is the maternal parent’s basal area (m$^2$). In an ongoing regeneration study at this fire, I. Charron and D.F. Greene (to be published) estimated that 80% of the total aerial seed bank ($Q$) was available for germination in the early summer of 1997 (15% in 1996, 7% in 1998, and 3% in 1999), and 98% of all the 1997 germinants had appeared by early July when the present study was undertaken. Further, sowing experiments (200 m from the present study site) indicated that the initial survival rate ($S_1$) of the seeds from late spring to the end of the June rainy season (i.e., during the transition from abscised seed to censused germinant) was 0.33 (a weighted average across seedbed types). Note that eq. 6 for juvenile survivorship will underestimate because it applies to the first two growing seasons for a cohort.

Thus, the fecundity ($F$, germinants per tree) in eq. 1 for the 1997 cohort can be estimated as

$$F = 0.76QS_0 = 8803B^{0.86}$$

and we sum the contribution of each pine tree to the transect given their Cartesian coordinates and basal area.

The results of the transect through the pine stand are shown in Fig. 2. As mentioned earlier, the transect was placed so as to bisect a stand of higher pine density (roughly equal to the black spruce density in the distance interval 20 < $x$ < 30 m) with no pine sources at $x$ > 50 m. A regression of predicted recruit density ($F_{DP}$) from eq. 12 on observed fecundity ($F_{DO}$) yielded a significant result:

$$F_{DO} = 0.58 + 0.86F_{DP}$$

$r^2 = 0.64$; $p < 0.05$; $N = 10$
where neither the intercept nor slope are significantly different from 0 and 1.0, respectively. In Fig. 2, there is a rough congruence of $B_D$ and observed recruitment density, but the ninefold range in basal area per area is reduced to a fivefold range in stems per square metre because of dispersal (i.e., the dense pine source in the center of the transect is a net exporter of seeds).

There is clearly some directionality in the recruitment as we tend to overpredict the first 25 m of the transect and underpredict in the subsequent 25 m. The prevailing westerly winds are from the direction of low $x$ to high $x$. We can remove this azimuthal bias (undoubtedly because of abscission events) by taking an average (for both observed and predicted) at $x = 25, 30; x = 20, 35; \ldots$ and then, again, regress observed on predicted. We now obtain $F_{DO} = 0.17 + 1.0 F_D$ ($r^2 = 0.992$, $p < 0.05$, $N = 5$). In short, the model well predicts the pine recruitment.

**Spruce and fir recruitment from burn edges**

Empirical results for white spruce and balsam fir are shown in Figs. 3 and 4 and expressed using eq. 8:

\[
F_{Dr} = \left( \frac{gF_D}{2} \right) e^{-0.55(x_f)^{0.36}} \quad \text{(spruce)}
\]

\[
F_{Dr} = \left( \frac{gF_D}{2} \right) e^{-0.26(x_f)^{0.41}} \quad \text{(fir)}
\]

with $r^2 = 0.52$ ($N = 27, p < 0.05$) for spruce and $r^2 = 0.72$ ($N = 27, p < 0.05$) for fir. The 95% confidence intervals on the coefficient $a$ (0.23–1.1 for spruce; 0.1–0.65 for fir) include the model prediction (eq. 10: $a = 0.42$ or 0.59, respectively). Likewise, the confidence intervals for the exponent $b$ (0.22–0.50 for spruce; 0.26–0.57 for fir) span the model estimates ($b = 0.37$ or 0.33, respectively). Nonetheless, as can be seen in Figs. 3 and 4, there is a tendency to overpredict spruce and underpredict fir (especially with the oldest fire (Galipeau et al. 1997)).

We assume that the shape of the empirical curve (the magnitude of $a$ and $b$) is determined by dispersal rather than distance-dependent or density-dependent mortality. Using the seed dispersal data of Greene and Johnson (1996) at the Vermilion Pass burn for Engelmann spruce, we obtain $a = 0.27$ and $b = 0.47$. Neither value is significantly different from the regression results (Fig. 3) or the model (eq. 10).

It is of interest to compare these results with a recruitment curve for spruce in a clearcut (Timoney and Peterson 1996). In this case, we set $R = 0$ (no residual stands) and the model coefficients then become $a = 0.15$ and $b = 0.52$. A regression using the results of Timoney and Peterson (1996) for clearcuts in Wood Buffalo National Park yielded $a = 0.152$ and $b = 0.59$ ($r^2 = 0.65, N = 8, p < 0.05$). The data set of Timoney and Peterson (1996) extends to 400 m from any source tree. These coefficients are not significantly different from those of our model. Likewise, a study of seed dispersal of Engelmann spruce into a clearcut (Squillace 1954) yielded for $x > 100$ m, $a = 0.13$ and $b = 0.60$ ($r^2 = 0.683, N = 5, p < 0.05$), values which are almost exactly the same as those for Timoney and Peterson (1996).

**White spruce and larch recruitment from small residual stands**

Finally, we turn to the recruitment of white spruce and larch from residual stands at the 1989 Muskeg Fire in Saskatchewan. Our sampling plots (3 m diameter) were clearly too small for white spruce as we observed no recruitment in about 40% of the sampling plots. Given that the residual stands were about the same size (0.095–0.146 ha) and that the total number of white spruce canopy trees (about 30) was roughly the same, we have averaged the results for all
three stands (Fig. 5). Following Stewart et al. (1998), eq. 1 was used to model the recruitment at any distance as the sum of the individual point source contributions in a square residual stand of 0.1 ha with 30 source trees of 15 m height and mean basal area of 0.015 m$^2$ distributed in a uniform manner. The fecundity ($F$) in eq. 1 is 70 recruits/tree. The logarithmic regression of predicted on observed (Fig. 5) recruitment density was significant ($\chi^2 = 0.92$; $N = 5$; $p < 0.05$) with neither the slope nor intercept significantly different from 1.0. However, as in Fig. 3, there is a tendency to overpredict spruce recruitment. (Note that the axes used in Fig. 5 are contrived so that the model predicts that spruce and larch observations should be indistinguishable from one another.)
Turning now to the two larch stands, we will again average the results for the regeneration density (as with white spruce, there were too many zero values). Average values for the two larch residual stands were 27 trees per 0.995-ha stand with a height and basal area of 13 m and 0.011 m², respectively. Thus, we expect an average of 52 recruits/tree. A logarithmic regression of predicted on observed recruit density provided a significant result ($r^2 = 0.94$, $p < 0.05$, $N = 5$), where neither the intercept nor slope was significantly different from 1.0.

Finally, Stewart et al. (1998) applied eq. 1 to the recruitment of white spruce out to distances of 300 m from two different residual stands. Both small residual stands were about the same size as ours and contained about the same different residual stands. Both small residual stands were

\[ \text{regeneration density} \times 0.23 \text{ trees/m}^2 \]

\[ N \text{ is the quadrat area (m}^2) \text{ and } F_{D0} \text{ is, as above, seedlings/m}^2 \text{ at distance } x \text{ (m)}. \]

\[ J = 1 - e^{-AF_{D0}} \]

where $A$ is the quadrat area (m²) and $F_{D0}$ is, as above, seedlings/m² at distance $x$ (m). Let us take the Quebec stocking criterion of one seedling per plot ($A = 4$ m²) in at least 60% ($J > 0.6$) of the random plots. For an infinitely wide burn (and thus we can ignore dispersal from another side), where white spruce sources had $B_0$ = 0.0005 (20% of a forest with 25 m²/ha basal area), then $gF_{D0}/2$ in eq. 14 becomes 1.0, and the proportion of stocked plots declines to 0.6 at a distance of 30 m and when the seedling density is 0.23 stems/m². The studies by Stewart et al. (1998), MacArthur (1964), Galipeau et al. (1997), and our residual stand data do not show a density this high at any distance. Only the Vermilion Pass study provides this density but for distances less than 75 m. Dempster et al. (1999) used 6-m² plots, reporting stocking but not density for natural recruitment into a burn. If we assume adequate stocking requires about 70% stocking with a plot of this size (by extrapolation: Quebec requires 60% for 4-m² plots, while Alberta requires 80% for 10-m² plots), then stocking was adequate within about 50 m of the burn edge.

On the other hand, if we picture a second edge contributing to the recruitment, and if we average eq. 15 across this imaginary burn, then a fire that was only 255 m across would, like the recommended clearcuts of Wurtz and Zasada (1986) and Squillace (1954), be expected to have adequate stocking.
In the foregoing exercise, a Poisson expectation at any distance is overly optimistic about the stocking proportion expected from a particular stem density, because both the seed sources and the better seedbeds will be clumped in space. On the other hand, the exercise ignored the contribution of the small residual stands that would stock a minority of the plots far from the edge. In any case, this simple scenario, coupled with the empirical work presented in this paper, makes clear that nature is no better than foresters at adequately stocking a very large clearcut with modest amounts of humus and mineral soil exposure.

It is of some interest that Johnson and Greene (unpublished data) found that the average distance between edges (nominal or residual) and random points within large burns (5000 – 13 000 ha) in Saskatchewan was about 150 m. The distance is so short because small residual stands are very common and because the nominal burn perimeter is markedly invaginated. An outstanding problem in boreal ecology has been the explanation of the persistence of the three species (white spruce, balsam fir, and larch) that possess neither aerial seedbanks nor a reliable method of asexual regeneration. Appeals to classical succession are misplaced in landscapes such as the western boreal forest where fire return time is typically less than 100 years (Johnson 1996), and thus, only a small fraction of the landscape becomes old forest. We argue here that a species such as white spruce may well comprise only a small minority of the total regeneration density (typically, recruit density is greater than 3 stems/m² for aspen, jack pine, and black spruce in areas where their pre-burn basal area per area was large; Greene and Johnson 1999; Zasada et al. 1992) across the fire, but if its thinning mortality is small relative to the species with higher abundance, then it can persist at a temporal scale demarked in units of fire cycles.

Imagine that, at 69 years old, half a landscape burns (a negative exponential time-since-fire distribution with a 100-year return time). At this age, assume 0.1 canopy trees/m² (all species, of which white spruce has 0.02/m² (20%). We require that this species achieves an average recruitment density of 0.01 (there is another area source on the other side of the burn), and we assume thinning losses from years 5 to 69 are small enough to be ignored. Using eq. 14, the distance at which the recruit density will equal 0.01 is about 600 m, and thus, the mean fire diameter could be 1.3 km. Large burns commonly have residual stands sufficiently large that eq. 11 would apply, and burns >7000 ha have only a small proportion of their areas with distances to a large source (nominal or large residual edge) greater than 600 m (E.A. Johnson and D.F. Greene, unpublished data; Eberhart and Woodard 1987). We note that this argument is independent of the initial white spruce forest proportion because a doubling of source strength would merely require a doubling of the recruitment density required for self-replacement. In short, we offer here an admittedly rough argument for how white spruce could persist in a fire-prone landscape where classical successional dynamics have little opportunity to operate. On average, across the landscape, white spruce would be much less common than species with in situ mechanisms such as black spruce, jack pine, and aspen. In areas near old burn edges (and old, large residual stands) it would be found at high local densities, especially when the stands managed to avoid fire and become part of the far tail of the probability distribution of return times. But across most of the landscape, white spruce would be present at very low densities.

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