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A review of the regeneration dynamics of North American boreal forest tree species[1]

D.F. Greene, J.C. Zasada, L. Sirois, D. Kneeshaw, H. Morin, I. Charron, and M.-J. Simard

Abstract: In this review, we focus on the biotic parameters that are crucial to an understanding of the recruitment dynamics of North American boreal tree species following natural (fire, budworm infestation, windthrow) or human-induced (clearcut, partial cut) disturbances. The parameters we emphasize are (*i*) the production of seeds and asexual stems (both of which, we argue, are a function of basal area density), (*ii*) the dispersal of seeds by wind (or the dispersion of asexual stems) as a function of distance from source, (*iii*) dormant seed bank capacity, (*iv*) organic layer depth as a determinant of germinant mortality and asexual bud response, and (*v*) shade tolerance as a partial arbiter of the density of advanced regeneration. Having identified the gaps in our knowledge, we conclude by suggesting a short-term research agenda whose completion would lead to the parameterized functions that would constitute the recruitment subroutine in a landscape-scale forest dynamics simulator.

Résumé : Dans cette revue de littérature, nous nous concentrons sur les praramètres biotiques qui sont cruciaux pour comprendre la dynamique du recrutement des espèces d'arbres de la forêt boréale de l'Amérique du Nord, suite à des perturbations d'origine naturelle (feu, épidémie de tordeuse, chablis) ou anthropique (coupe à blanc, coupe partielle). Les paramètres sur lesquels nous mettons l'accent sont (*i*) la production de graines et de tiges végétatives qui sont, nous le maintenons, fonctions de la densité en surface terrière, (*ii*) la dispersion des graines par le vent (ou la dispersion des tiges végétatives) en fonction de la distance de la source, (*iii*) le potentiel de la banque de semences dormantes, (*iv*) la profondeur de la couche organique en tant que facteur déterminant de la mortalité après germination et de la réponse des bourgeons asexués et (*v*) la tolérance à l'ombre, laquelle contrôle en partie la densité de la régénération préétablie. Ayant identifié les lacunes dans nos connaissances, nous concluons en suggérant un programme de recherche à court terme dont la réalisation se traduirait par des fonctions de prédiction du recrutement qui pourraient servir de sous-routine dans un modèle de simulation de la dynamique de la forêt à l'échelle du paysage.

[Traduit par la Rédaction]

Introduction

In this review, we will identify and discuss those parameters that we feel are crucial to an eventual model of recruitment. In short, our ultimate goal is to lay the framework for a subsequent general model intended to be used anywhere in the North American boreal forest in the prediction of regeneration density following both natural and human-induced disturbance. Thus, we must predict the density of the predisturbance dormant seed bank, asexual buds, and advanced regeneration, as well as their survival through the disturbance, and the additional input of postdisturbance seeds and asexual stems. We list below five biotic parameters that we feel are fundamental to understanding recruitment and four disturbance-related parameters.

Recruitment parameters

(*i*) Basal area. We argue that this crucial parameter is proportional to (at least prior to senescence) seed production and asexual bud production. Further, as basal area is proportional to height, it affects the dispersal capacity of the wind-dispersed boreal trees.

(*ii*) Seed mass. The mass of the seed is inversely proportional to annual seed production and thus affects source

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D.F. Greene.[2] Departments of Geography and Biology, Concordia University, Montréal, QC H3G 1M8, Canada.
J.C. Zasada. Forestry Science Laboratory, USDA Forest Service, 5985 Highway K, Rhinelander, WI 54501, U.S.A.
L. Sirois. Département de sciences biologiques, Université du Québec à Rimouski, 300, allée des Ursulines, P.O. Box 3300, Rimouski, QC G5L 3A1, Canada.
D. Kneeshaw and M.-J. Simard. Groupe de recherche en écologie forestière, Université du Québec à Montréal, P.O. Box 8888, Centre-ville Branch, Montréal, QC H3C 3P8, Canada.
H. Morin. Consortium de recherche sur la forêt boréale commerciale, Université du Québec à Chicoutimi, Chicoutimi, QC G7H 2B1, Canada.
I. Charron. Department of Biology, Concordia University, 1455 de Maisonneuve Boulevard, Montréal, QC H3G 4M8, Canada.

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[2] Author to whom all correspondence should be addressed. e-mail: greene@alcor.concordia.ca

strength. Further, seed mass is proportional to terminal velocity (within aerodynamic categories) and thus inversely proportional to dispersal capacity. Finally, germinant size is proportional to seed mass, and thus, the abiotic component of first-summer survivorship should be directly related to the initial seed mass.

(*iii*) Asexual reproduction capacity. Only three species in the North American boreal forest (trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus balsamifera* L.), and paper birch (*Betula papyrifera* Marsh.)) have the capacity to sprout from buds near the root collar or, for the two poplar species, from roots as well. Additionally, black spruce (*Picea mariana* (Mill) BSP) and cedar will frequently layer in older stands. This ability to regenerate in situ in large disturbances confers a remarkable advantage on these species.

(*iv*) Dormant seed bank capacity. No boreal tree species has a seed dormancy within the soil extending beyond 1 year (except perhaps paper birch (cf. Zasada et al. 1992)), but two species (jack pine (*Pinus banksiana* Lamb.) and black spruce) possess long-lived aerial seed banks. Again, the capacity to regenerate in situ within large disturbances offers a considerable advantage to these species following natural disturbance or harvesting where branches are deliberately scattered across a cut.

(*v*) Shade tolerance. The ability to persist as slow-growing stems in deep shade offers, like asexual reproduction and aerial seed banks, the advantage of in situ recruitment (at least for low-severity disturbances).

In addition to these five biotic parameters, we have identified four disturbance-related parameters that need to be explicitly dealt with in an eventual model (although not in this review). In the boreal forest of North America the primary cause of canopy tree mortality is fire in the west and a mix of fire and budworm-induced mortality in the more humid east. In addition, harvesting has, for the last few decades, been roughly equal to fire and budworm in the annual area disturbed. The four defining characteristics of disturbance are as follows.

(1) Colonization distance (mean and variance). This characteristic interacts with dispersal capacity as the distance seeds must travel from living sources and is determined by disturbance size and shape and by the pattern of residual (surviving) stands. The disturbance size is relatively unimportant for in situ regeneration.

(2) Return time (mean and variance). The return time is a crucial determinant of seed production (via basal area) and dormant bud production. Insofar as return time is sufficiently long to permit classical successional dynamics (slow replacement of shade-intolerant species by tolerant species), then it will affect the composition of both pre- and post-disturbance recruitment by seeds or asexual buds.

(3) Severity. We define the severity of a disturbance by the number of forest strata (canopy trees, advanced regeneration, organic layer) removed. Thus, a high-severity disturbance (e.g., crown fire in late May or a harvest/scarification operation) will lead to a very different species composition in the new stand than a light disturbance (such as a budworm outbreak or shelterwood) which leaves intact much of the advanced regeneration and forest floor. Organic layer removal not only acts as a mortality agent (for buried seeds) but also strongly enhances subsequent germinant survivorship.

(4) Specificity. Budworm damage is typically limited to balsam fir (*Abies balsamea* (L.) Mill.) and white spruce (*Picea glauca* (Moensch) Voss). By contrast, the 5% of the largest forest fires account for about 95% of the area burned in the boreal forest annually, and we know of no compelling evidence that the probability of surviving these high-intensity events is importantly dependent on species identity or tree size.

The review is organized as follows. In the first section, we discuss the production of seeds and asexual buds. In the second section, we link this source strength term to a dispersal term for sources of varying geometry. The third section focuses on germination of seeds and dormant buds and initial survivorship on intact or highly disturbed seedbeds. The final section treats advanced regeneration under intact canopies. We conclude with a summary of those issues that are too poorly understood as yet to permit modeling. This summary, then, will represent our recommended short-term research program.

Production of seeds and asexual buds

Along with advanced regeneration, seeds and asexual buds are the only methods for recolonization of a disturbed site. Clearly, one of our main problems in developing an adequate theory of regeneration is the difficulty of predicting the density of buds and seeds following disturbance. The density will depend on predisturbance species composition, the interval since the last disturbance (and thus the age and size of the trees), and the intensity of the disturbance (e.g., a fire will kill any seeds in the forest floor).

Initial age/size for seed production

It has often been argued that species have characteristic juvenile intervals (Fowells 1965). In the classic dichotomy, fast-growing "pioneers" such as poplar or pine become reproductively mature (i.e., produce their first seeds) at less than 10 years, while slow-growing "climax" species such as fir might take twice as long to initiate sexual reproduction. We think it more likely that, as with herbaceous plants, a minimum stem size is required (Sedgley and Griffin 1989). Thus, characteristically fast-growing species reach reproductive status earlier, especially on more productive sites. As a rough indication of this initial size, we suggest a basal area of about 0.001 m^2 inside the bark at the base of the bole (Greene and Johnson 1994).

In addition, reproductive status also depends on canopy position. Even with same-aged cohorts, the canopy trees virtually monopolize seed production (e.g., Fowells and Schubert 1956). Thus, the time to initial reproduction depends not merely on the size of a stem but on the sizes of its nearest neighbors. It seems likely, then, that the proper measure of the capacity for sexual reproduction is not stem size but rather the size of the carbohydrate pool available to sponsor the heavy investment in reproduction. Nonetheless, in what follows, we will use the easily measured basal area as our surrogate predictor of this carbohydrate pool, and it should be understood that we will be referring only to canopy stems.

Annual seed production

Large-seeded species produce fewer seeds than small-seeded species, and large trees produce more seeds than small trees. Greene and Johnson (1994) expressed this as

$$\overline{Q} = 3067m^{-0.58}B^{0.92}$$

where $\overline{Q}$ is the mean annual crop size (and includes preabscission losses to granivores) of a single tree, m is seed mass (grams), and B is basal area (square metres). We can switch this to a density form (Q_D, seeds per square metre) courtesy of conspecific synchrony in masting behavior at the landscape scale as

$$\overline{Q} = 3067m^{-0.58}N_D\sum B^{0.92}$$

where N_D is the density of conspecific source trees. There are three limitations to the use of these equations. First, they are based on long-term forestry studies that are invariably conducted on productive sites in the interior of a species range. We may expect poorer production on less clement sites or near latitudinal/altitudinal range limits (Elliot 1979; Sirois 1996). A second problem is that the equations explicitly argue that production increases with basal area. Nonetheless, for the few species where we have a wide range of basal areas, most show that a curvilinear function would be more appropriate, given that the largest (senescing?) trees tend to produce fewer seeds than expected. At present, this more realistic function remains to be written and tested. The third problem with the equations is that they ignore the tremendous temporal variation in seed production. Coefficients of variation in seed production typically range as 1–2 for North American tree species (these are enormous values for a biological trait). Maximum values ($Q_{\max}$) in long-term studies are typically $4 \leq (Q_{\max}/\overline{Q}) \leq 55$. The probability distribution is strongly right skewed ("masting") and has not yet been successfully fitted to a function.

There has been some success (e.g., Mathews 1955) in predicting mast years as a function of weather variables (typically the weather in the year of bud differentiation), but in any case, these retrospective analyses do us little good if we cannot predict future weather. Some authors (e.g., Sork et al. 1993) have argued that species have endogenously driven cycles and thus have predictable mast years. It would greatly enhance the reliability of natural regeneration as a forestry option if this were true, but we know of no studies with the appropriate statistical analysis that demonstrate this. Statistical analysis of the long-term records of Koski and Tallquist (1978) in Finland using lagged intervals and the Spearman rank correlation revealed no evidence for a significant periodicity in seed production at the scale of one to two decades (D.F. Greene and E.A. Johnson, unpublished manuscript). At present, we leave open the possibility that there is a vague periodicity (e.g., every 4–7 years) for a species, but we doubt that it will be useful in the eventual modeling effort.

In summary, we cannot at present realistically model seed production. Two things are required. First, we require a better function that permits seed production to decline as trees begin to senesce. Second, we require a function that adequately expresses the right-skewed distribution of seed production years. A subroutine would then randomly draw values from this distribution.

Potential limiting role of pollen rain in tree seed production

Most common boreal tree species are primarily wind pollinated with either a monoecious (conifers) or dioceous (poplars) habit (Farmer 1997). Self-pollination generally results in ovule abortion due to degeneration of the embryo, mostly during early development (reviewed by Dogra 1967). The few seedlings that arise from selfing typically have poor vigor, e.g., black spruce (Park and Fowler 1984).

The production of an abundant crop of filled seeds requires that large quantities of conspecific pollen are present in the air during the period of female flower or strobili receptivity. The peak period of maturity in male and female strobili overlapped during a 5- to 6-day interval in a black spruce seed orchard (O'Reilley et al. 1982). A low synchrony between the period of pollen dispersal and female receptivity has rarely been invoked as a source of a poor seed crop.

Nevertheless, unsuccessful pollination has frequently been cited as one of the major sources of nonviable seeds in Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) (Singh and Owens 1981) and Sitka spruce (*Picea sitchensis* (Bong.) Carr.) (Owens and Molders 1980). It is likely that most of the flat, nonviable seeds frequently reported in conifers are due to a lack of pollination associated with low pollen density (Smith et al. 1990), low pollen viability (Elliot 1979), or ovule accessibility at the proximal and distal part of the female strobili (Owens and Molders 1980). Climatic factors may also interfere with pollination. Damage to pollen mother cells resulting from late frost has been documented in several coniferous species (Jonsson 1974). In addition, although occasional light precipitation may assist the pollination drop in pollen scavenging of spruce (Runions and Owens 1996), a long rainy period at the time of ovule receptivity may impede pollination.

It has been repeatedly demonstrated with both hardwoods and conifers (e.g., Alexander et al. 1982) that the proportion of filled seeds increases with crop size, and this is because pollen production is tightly synchronized with ovule production (Koski and Tallquist 1978). Ultimately, the probability of fertilization must be a Poisson process dependent only on pollen density (number per square metre) and the size of the "target" (micropyle or stigma) and independent of ovule number (Smith et al. 1990). Thus, it follows that years of poor ovule and pollen production have very low proportions of filled seeds and, further, that low densities of conspecific sources should have chronically poor seed production (as shown empirically by Nilsson and Wästljung (1987) for European beech (*Fagus sylvatica* L.) in Sweden or by Sirois (1996) along a latitudinal transect for black spruce in eastern Canada). Consequently, those species, which are often found at low densities at the scale of a kilometre (e.g., white spruce or paper birch in the southern boreal forest), will tend to have low seed production. Unfortunately, no model (either an empirical model or a pollen dispersal argument) relating fertilized ovule proportion to pollen source density has yet been advanced.

Aerial seed banks

It is probably no coincidence that the two most common conifer species in the fire-prone boreal forest (black spruce and jack pine) both possess aerial seed banks. It is an effective means of colonizing large burns in situ and permits more effective dispersal than asexual reproduction. However, the degree of serotiny varies among populations (Zasada et al. 1992).

Black spruce normally has three to four cohorts of cones on its branches in Alaska (Zasada et al. 1992), or occasionally as many as six cohorts in central Saskatchewan (Johnson and Greene 1997). In the older cohorts, however, the cones are generally empty of seeds or contain inviable seeds. For well-stocked 50- to 100-year-old stands, Johnson and Greene (1997) estimated about 4.5 million filled seeds/ha; LeBarron (1948) gave a value of 1.0–2.0 million filled seeds/ha in northern Minnesota. Black and Bliss (1980) reported even lower values for seeds per hectare in the Canadian subarctic. Sirois (1996) has shown that filled seed production declines with latitude in eastern Canada for this species.

Jack pine often has more than 10 cohorts on its branches (Smith et al. 1990). Nonetheless, most of the seed in the older cones is inviable (E.A. Johnson, unpublished data). For well-stocked stands in central Saskatchewan, Johnson and Greene (1997) reported about 1 million filled seeds/ha. Likewise, M. Beland and Y. Bergeron (unpublished data) reported around 1 million filled seeds/ha in western Quebec.

Note that these seed densities for the two species will result in substantial densities of first-year seedlings. If we take 3 million seeds/ha as typical for both species, then even with a first-year survivorship (including viable seeds that fail to germinate) as low as 0.01, a well-stocked stand could give rise to a density of 3 seedlings/m^2 (cf. Cayford 1963; St. Pierre et al. 1992).

What fraction of the seed bank survives a disturbance? Zasada et al. (1979) reported a decrease in percent germination and percent filled seed for black spruce between a burned and two unburned stands, suggesting that fire affected seed viability. Beaufait (1960) found that viability of jack pine seeds was only affected when cones were heated to their ignition temperature. In both cases, temperature to which cones are heated and length of heating period are critical factors.

For nonserotinous species, this type of fire and duration of fire are critical. Obviously, all crown fires will probably destroy seeds. Timing of the fire in relation to stage of seed development is important. For conifers, ground fires that occur after morphological maturation of the embryo may kill the trees but have little effect on seed viability. J.C. Zasada (personal observation) observed this in white spruce in Alaska where an intense ground fire in August killed all trees and exposed large areas of mineral soil. But cones were apparently not affected, as germination was abundant from seeds in cones of killed trees the following summer. Rowe (1956) made a similar case for white spruce in Saskatchewan.

An interesting example of effect of season of burning on viability was observed for a fire that burned a white spruce stand on an upland site in interior Alaska (Zasada 1985). The fire occurred at about the time of pollination. Female flowers were not affected by an intense ground fire that killed trees (dead by the end of the growing season in which fire occurred), and germinability of seeds was 80% and not different from that of trees in an unburned stand (Zasada 1973). Seed yield per cone was not evaluated. Clearly, the effect of fire on seed development is complex, and simply knowing the time of year that a fire occurs is not enough information. For budworm infestations, Schooley (1978) reported that the larvae consumed a large fraction of the flower buds of balsam fir.

The effect of harvesting on seed availability is easier to predict than the effect of fire, but there are some problems here also. Obviously, if trees are harvested after embryos are morphologically mature (e.g., Zasada 1988), seeds should be viable and capable of germination. However, how much before the time of morphological maturity trees can be harvested is an open question. Zasada (1973) and Winston and Haddon (1981) have both described some degree of ripening of seeds when green cones are collected and stored under conditions that delay cone drying and opening. The opportunity to harvest trees at the appropriate time of year to maximize seeds on trees is great and should be considered when designing harvesting schedules.

Forest floor seed banks

With the possible exception of paper birch (Granstrom and Fries 1985), none of the boreal tree species have a postabscission dormancy extending beyond about 9 months (or, with the two poplar species, a few weeks). The importance of the forest floor seed bank depends therefore on the timing of the cut and the size of the previous crop. Certainly, a late autumn or winter cut will permit the forest floor seed bank to play a potential role in natural regeneration. But the low annual probability of a sizeable crop coupled with the very poor survivorship of boreal germinants on intact seedbeds makes the soil seed bank an unlikely source of new recruits in large cuts. Disking will worsen the problem by burying so much of the forest floor seed bank that the exposed mineral soil or humus would unlikely contain an appreciable fraction of the previous crop. As for natural or prescribed fire, the heat will consume, or render inviable, the entire forest floor seed bank (Johnson 1975).

Bud banks

Predicting the potential for vegetative reproduction can be generally related to the age, density, and spatial distribution of the parent stand. However, vegetative reproduction is strictly a function of the bud bank of the main stem, branches, and roots. Realization of the bud bank potential of a tree, stand, or landscape is modified by tree or meristem condition, microenvironment, associated plants, soil conditions, herbivory, and type and intensity of disturbance. In all cases, the bud bank is dynamic over a range of temporal and spatial scales as buds are added and deleted through normal developmental processes and released periodically in large numbers by disturbance. In this sense, it can be likened to the aerial seed bank. Bud banks for trees vary substantially by species. Among the boreal tree species, there is an example of all types of bud banks present in north-temperate forests, and one species, balsam poplar, provides examples of virtually all types of vegetative reproduction that occur naturally in boreal and north-temperate trees.

The basal stem and root collar buds provide the potential for exact replacement in both the spatial and genetic sense. Aspen, balsam poplar, and paper birch are capable of rapid sprouting and tree replacement at some point in their lives; however, they differ significantly in the types of bud banks and the relationship between sprouting potential and age. Aspen is most limited and the ability to basal sprout does not appear to be significant beyond an age of 15–20 years (Perala 1977; Zasada et al. 1992) in trees of root sucker origin. Trees of seed origin may behave differently, but this does not seem to have been studied. The origin of basal sprouts in aspen is assumed to be from preformed buds.

Balsam poplar and birches have the potential to sprout from preformed and adventitious buds (Stone and Cornwall 1968; Kauppi et al. 1987; Rinne et al. 1987; Zasada et al. 1992). Differentiation of these bud types is best done by location of the bud trace to the pith that is present in preformed but not adventitious buds (Romberger 1963; Kormanik and Brown 1967; Halle et al. 1978). However, shoots from adventitious buds originating from the inner bark on stumps are easily distinguished. Development from adventitious buds appears to be most common or restricted to seedlings in birch, while mature balsam poplar retains this potential. Preformed buds seem to be the main source of basal sprouts. The work of Stone and Cornwall (1968), Kauppi et al. (1987), and Rinne et al. (1987) on development and longevity of buds for birch species in Finland provides an excellent introduction to the dynamics of the bud bank.

Although the exact age at which the potential for sprouting begins to decline is not well established for these species, it seems that after approximately age 40–50 years, some trees lose the capacity (Safford et al. 1990; Zasada et al. 1992). Thus, up to that time, predisturbance tree distribution can be a good indicator of the postdisturbance stand. But as trees age, sprouting potential declines and tree distribution after disturbance is more difficult to predict. As with seed production, it would appear that a unimodal function relating sprouting capacity to age and size is required.

Reductions in sprouting potential occur when fires are severe or when harvesting activities badly damage the stumps (as can happen when harvesting occurs during the period of active cambial growth and bark layers are easily damaged) (Lust and Mohammady 1973; Zasada 1986). The timing of disturbance affects the vigor of the sprouting response, but does not prevent it (Lust and Mohammady 1973).

The buds that determine the potential for layering occur on the branches and the main stem of the tree. Successful layering depends on the ability of the branch or stem to develop roots and eventually function independently of the parent tree. Among the conifers, black spruce and cedar readily layer, while balsam fir, tamarack (*Larix laricina* (Du Roi) K. Koch), and white spruce do so on a more limited basis; layering in pines is rare. Balsam poplar is the only one of the three broad-leaved species that layers and it has the greatest potential to do so of the species considered in this paper (Bannan 1942; Bakuzis and Hansen 1965; Legère and Payette 1981; Burns and Honkala 1990*a*, 1990*b*; Zasada et al. 1992; Fayle 1996). Layering occurs when lower branches or the entire stem are pinned to the ground by branch fall or buried by moss/organic layer development or soil deposition. The rate at which a new root system develops and the distribution of adventitious roots vary between species (Bannan 1942). The conifer roots are adventitious, while balsam poplar has preformed root initials and can relatively quickly initiate roots on branches of all sizes. Site and stand conditions that promote forest floor accumulation and retention of branches at the bases of conifers increase the probability of layering, and a number of studies have described site-specific differences in layering (Bakuzis and Hansen 1965; Legère and Payette 1981; Burns and Honkala 1990*a*; Zasada et al. 1992). Layerings do not survive ground fires, but they do survive insect outbreaks or careful harvesting that kill the larger trees, leaving the understory intact. In lowland black spruce stands (as well as in upland stands in the eastern North American boreal forest), they can be an important regeneration component of the next stand provided they are not seriously damaged during logging (Jeglum and Kennington 1993).

Rooting of detached branches is a variation of the layering process. This occurs only in balsam poplar and is possible because of the presence of preformed root primordia. It has been observed to occur naturally on floodplains and in harvest sites where branches are broken and buried during felling and skidding of trees (Zasada 1986).

Dispersal of seeds and asexual stems

Dispersal, along with disturbance size and predisturbance species composition, determines the regeneration composition, density, and patchiness. While there has been a great deal of empirical and theoretical work on dispersal of seeds, there has been very little study of the dispersal (perhaps dispersion is a better word) of asexual root suckers in relation to the spatial array of clonal boles.

Seed dispersal models

Important clarifications must be made at the outset. The first involves the term "dispersal curve." We will define a dispersal curve as seed density versus distance from a source. For a single tree (a point source), the distance, x, is zero at the base of the parent bole. Three other source geometries are of interest in forest ecology. We define an area source as an array of point sources measuring at least a few hundred metres in length and width. A strip source (e.g., a species tending to adhere to hillslope contours) is as long as an area source but can be much narrower. Finally, we define a patch source as a collection of point sources less than a few hundred metres in both length and width (e.g., residual stands in clearcuts, typical natural residual stands in burns).

There has been much unnecessary debate about the typical shape of dispersal curves and, worse, attempts (e.g., Johnson 1988) to statistically compare the regression parameters derived from varying source geometries. Different functions are required for each source geometry. Both empirical and theoretical work (reviewed in Greene and Johnson 1989) shows that wind dispersal point sources exhibit strongly right-skewed dispersal curves. Greene and Johnson (1989) modeled this point source curve as a lognormal expectation. The expected mode is, in some species, so close to the trunk (and is bolstered by a small fraction of the crop that abscises as single cones or catkins) that some authors have modeled the curve as a negative exponential (e.g., Hubbell 1979) or modified negative exponential (e.g., Ribbens et al. 1994). Accumulation of the deposits of the constituent point source curves within an area source will, with $x = 0$ defined as the source edge, lead to either a nearly negative exponential curve (see empirical evidence and the micrometeorological model in Greene and Johnson 1996) when the area source adjoins a clearing or a more initially gentle decline in density when the area source is located well within a forest. This difference in the shape of area source curves is due to the rapid acceleration of wind speeds at a forest–clearing edge.

By contrast, patch or strip sources should initially show a very gentle decline within about one tree height of the source edge, followed by a rapid decline. (There is almost no empirical work on seed dispersal from patch or strip sources.) Clearly, no single function can express this variety of curve shapes.

All of the boreal forest tree species are wind dispersed, and thus, we can take advantage of decades of micrometeorological research done on particulate emissions from smokestacks and on canopy flow. Greene and Johnson (1989) derived a point source model as

$$N_{\mathrm{DX}} = [Q/(2\Pi)^{1.5}\sigma_{\ln x}x^{2}]\exp\{[\ln(x/x_{0.5})]^{2}/2\sigma^{2}_{\ln x}\}$$

where Q is the crop size, N_{DX} is seed density at distance x, $\sigma_{\ln x}$ is the standard deviation of the logarithms of the distances traveled, and $x_{0.5}$ is the median distance traveled by the crop. For a single tree in a forest with a canopy of leaves, they defined $x_{0.5}$ (Greene and Johnson 1996) as

$$x_{0.5} = z_{\mathrm{h}}^{1.14}\,0.43/\bar{f}$$

where $\bar{f}$ is the mean terminal velocity (metres per second) of the seeds and z_{h} is the tree height (metres). Assuming default values for the standard deviations of the vertical wind speeds, horizontal wind speeds, and terminal velocities, Greene and Johnson (1996) defined the measure of spread in the point source curve as

$$\sigma_{\ln x} = [0.32 + (0.123/\bar{f}^{2})]^{0.5}$$

The modal distance (x_m) is given as

$$x_m = x_{0.5}[\exp(-\sigma^{2}_{\ln x})]^{2}$$

Given the typical range of boreal terminal velocities ($\bar{f}$ = 0.28 m/s for balsam poplar, $\bar{f} \cong 1.0$ m/s for cedar) and, say, a tree height of 25 m, we expect $17 < x_{0.5} < 70$ m. By contrast, the mode is expected to lie at around 5 m regardless of dispersal capacity.

The dispersal curve for sources of varying geometry can be developed on the computer simply by summing the contributions of the point sources in Cartesian space. For the special case of area sources (with distance defined perpendicular to the source edge) abutting a clearing, Greene and Johnson (1996) derived the equation

$$N_{\mathrm{DX}} = 05QM_{\mathrm{D}}\exp(-2x^{0.59}\,\bar{f}^{0.75}/z_{\mathrm{h}}^{0.69})$$

where M_{D} is the source tree density and Q should now be defined as the mean point source crop size.

The foregoing equations offer a reasonable prediction of deposited seed density, but we should point out that they can be off by as much as threefold in the prediction of density because of their heavy reliance on default values for the micrometeorological parameters. No matter what the nominal dispersal season length, the majority of abscission events seem to take place in only a few "bursts" (associated with low relative humidity and high wind speeds: Harris 1969; Greene and Johnson 1992) and these total only a few days. Thus, dispersal capacity may well vary from one year to another for the same species at the same site (Zasada et al. 1992). On the other hand, this approach has the merit of simplicity: only forest height and terminal velocity need be measured.

A final model concerns what Greene and Johnson (1995) have termed long-distance seed dispersal. A fraction of the crop will experience a positive vertical velocity (updraft) that exceeds the terminal velocity, and thus, the seed is initially rising and capable of dispersing very large distances (cf. Zasada and Lovig 1983). Greene and Johnson (1995) argued that this long-distance fraction, k, might be modeled as a uniformly distributed "bath" of seeds at the scale of several kilometres with a seed density (N_{DL}) of

$$N_{\mathrm{DL}} = gpQM_{\mathrm{D}}k$$

where g is the landscape fraction that has reproductively mature forest, p is the fraction of the forest consisting of the species of interest, and k is given as a proportion using the normally distributed "z-score":

$$(0.123 + 0.017\bar{f}^{2})^{0.5}$$

Thus, for a forest adjoining a very large clearcut or burn, we can write the full equation as the sum of N_{DL} and $N_{\mathrm{DX}}(1 - k)$. We note that this full equation exhibits a steep decline out to about 150 m; at greater distances the long-distance deposit predominates and we expect a flattening of the curve (e.g., Pickford 1929; MacArthur 1964; Galipeau et al. 1997). We note that arguments about whether empirical functions such as the negative exponential or power law (Harper 1977) better fit observed curves depend on the scale of observation. Limiting observation to 100 m from a forest edge should favor a negative exponential expression. But at greater distances, the decline becomes too gentle, and a power law function would be more appropriate.

We mention in passing that while there are published values on terminal velocities for most boreal species, it is not known how much these values vary from one population to another across a species' range. Greene (1990) documented a steep latitudinal gradient in terminal velocities for the montane lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) from Colorado to the Yukon. This resulted in almost a halving of the mean population terminal velocity.

The consequences of the constrained dispersal outlined in the above modeling exercise are well known to foresters. Sexual-origin natural regeneration after disturbance in a large clearcut or burn seldom gives adequate stocking beyond about 75 m from a forest edge even when the species of interest dominates the source (e.g., MacArthur 1964; Harris 1967; Tenhagen and Jeglum 1997). The equations developed here predict this constraint. The area source equation coupled with the production equation (preceding section) and an assumption of survivorship on the order of 0.01 for each of five consecutive cohorts predicts that a well-stocked monoculture of conifers could not achieve adequate stocking in a square clearing exceeding about 250 m on a side (and this ignores the tendency for as much as a threefold difference in azimuthal frequencies of dispersal directions).

Solutions that ameliorate the dispersal problem are likewise well known to foresters. Shelterwood and strip cuts (50–100 m in diameter) effectively eliminate the dispersal constraint. Leaving residual patches of seed trees (around 5% of the total cut area) is helpful in large cuts, but there are problems with blowdown, and there is the paradoxical problem that we should preferentially leave the trees we prefer to cut.

We mention finally the boreal species that has caused the most problems for foresters: white spruce. While it is tolerably well dispersed ($\bar{f} \cong 0.60$ m/s), it often comprises less than 50% of the total basal area. In consequence, it often fails to meet stocking standards except near edges. Worse, it has one of the highest coefficients of variation of seed production of any boreal species and has, compared with cedar or balsam fir, relatively low densities of advanced regeneration. It is therefore not surprising that its natural regeneration is so unreliable. It may be small comfort to foresters, but white spruce performs no better in the immediate aftermath of fire: stocking criteria are reached only near burn edges (MacArthur 1964; Galipeau et al. 1997; Johnson and Greene 1997). Indeed, white spruce serves as a reminder that metapopulation persistence is not necessarily mediated at the regeneration stage.

Secondary dispersal

Secondary dispersal of seeds by wind on intact seedbeds is a very unlikely event (Johnson and Fryer 1992), as the rough microtopography offers too many "dead air" spaces. The small seeded poplars ought to be the most likely candidates, but personal observation indicates that plumes adhere to organic and inorganic surfaces following even a slight wetting such as dew.

Greene and Johnson (1997) argued that long-distance (>500 m) dispersal on snow by seeds of the primarily autumn-dispersing (nonpoplar) species should be relatively unimportant because too little of the crop (around 10% or less) abscises on snow (cf. Zasada et al. 1992). However, J.C. Ruel (personal communication) has documented that 30–50% of the crops of white spruce and balsam fir abscise on snow in central Quebec, and this large proportion should, given the model of Greene and Johnson (1997), considerably enhance seed deposition at distances greater than a few hundred metres. In any case, while secondary dispersal distances on snow can be considerable in clearings, it is unimportant well within forests where wind speeds at the snow level are rarely high enough to permit entrainment (Greene and Johnson 1997). Secondary dispersal of poplar seeds on water certainly occurs (cf. Zasada et al. 1992) but it has not been quantified.

"Dispersal" of asexual stems

There is no "dispersal" or clonal expansion as a result of stump sprouting. Paper birch (following fire or cutting) can merely replace itself with a large number of basal sprouts that thin to one or a few stems at 50–100 years following disturbance (Safford et al. 1990; Zasada et al. 1992).

In the forest–tundra transition zone, layering in black spruce does not result in clonal dispersal exceeding a few metres from the parent crown edge (Legère and Payette 1981), although the process is important in maintaining these treeline populations.

Dispersal of root suckers of the two poplar species can be considerable. Aspen suckers have been observed up to 21 m from the nearest bole (Graham et al. 1963; Barnes 1966; Tappeiner 1982). However, in well-stocked balsam poplar or aspen clones, expansion at the edges is typically on the order of 6–10 m (Perala 1977; Krasny et al. 1988). Greene and Johnson (manuscript) found no aspen suckers more than 11 m from the nearest isolated aspen boles in a 2-year-old Quebec burn. It would appear, then, that most poplar root suckers are located within about 5 m of the nearest bole with a far tail for the dispersal curve that declines rather abruptly for the ensuing 10 m.

How might we model this "dispersal?" Ribbens et al. (1994) modeled American beech (*Fagus grandifolia* Ehrh.) root sucker point source dispersal as

$$N_{\mathrm{DX}} = (aB/d)\exp(-bx^3)$$

where a is a production coefficient that translates the basal area (B) of a single bole into a total asexual stem production, b is a slope determining the rate of decline, and d is a rescaling parameter dependent on b. This function has the merit that it assumes that a large basal area confers a correspondingly greater reserve of carbohydrates in the local root system, and it permits an initial gentle decline in sucker density to give way to a very steep decline (the cube of distance). A problem is that it assumes that the dispersal coefficient, b, is independent of tree size (B) and, further, does not permit sprouting density to decline as trees senesce. Preliminarily, we suggest that if aspen sucker densities following disturbance (say, the third year) are on the order of 15/m^2 in a large cut or burn (Zasada et al. 1992), basal area density in the predisturbance stand is 0.0025 with a bole density of 0.07/m^2, and 95% of recruitment is within 10 m, then reasonable values would be $a = 6000$, $b = 0.002$, and $d = 179$. Testing this prediction in a clonal array of boles would require the same maximum likelihood approach as used by Ribbens et al. (1994).

Germination and early survivorship

The length of the hypocotyl is proportional to the mass of the seed, and thus, germinant size is dependent on seed size for the first few weeks until the deployed first true leaves replace the endosperm and cotyledons as the primary source of carbohydrates (Grime and Jeffrey 1965; Charron 1998). This leads to two predictions. Much of the tremendous mortality in the first summer will be due to desiccation, and thus, larger seeded species should have higher survivorship due to their greater length (penetration of high porosity, rapidly drying litter or moss layers) and lower surface to volume ratios. The second prediction is that survivorship will be highest on those seedbeds (mineral soil, humus, or well-rotted logs) where porosity is low and water can rise freely via capillary action.

Relative to tropical or midlatitude forests, there is relatively little interspecific diversity in seed size in the boreal forest. We can arbitrarily divide them into two groups. The conifers have larger seeds (2–10 mg (black spruce to balsam fir)) whereas the three hardwood species have much smaller seeds (0.1–0.5 mg (balsam poplar to paper birch)). There is more than an order of magnitude difference in hypocotyl lengths and radicle lengths between balsam poplar and balsam fir (Charron 1998).

Clearings

Most of the experimental and descriptive work on survivorship/seedbed relationships has been with the two most common boreal species: black spruce and jack pine. In both burns and clearcuts on nonhydric sites, there is broad agreement that mineral soil, humus, and well-rotted logs have the highest initial survivorship (St. Pierre et al. 1992; Fleming and Mossa 1994, 1995*a*, 1995*b*; Groot and Adams 1994; Duchesne and Sirois 1995; cf. the review of Zasada et al. 1992). Further, the great majority of the mortality for a cohort in the first few years following disturbance occurs in the first summer (e.g., Cayford 1963; Fleming and Mossa 1995*a*).

The optimal seedbeds (mineral soil, organic layers less than a few centimetres in thickness) comprise about 20% of Saskatchewan burns (Johnson and Greene 1997), which is a much larger percentage than for scarified (e.g., Fleming et al. 1987) or prescribed burn clearcuts (e.g., Chrosciewicz 1976). Typical seedling densities for jack pine and black spruce in burned stands with a prefire basal area density (summed basal area per area) exceeding 0.001 are 1–10/m^2 (St. Pierre et al. 1992; Johnson and Greene 1997). Survivorships for early arriving cohorts of these two species vary between about 0.01 and 0.1 depending on the study (e.g., Cayford 1963; Groot and Adams 1994).

There is little comparable work with the other boreal forest species (especially the hardwoods). For the montane subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) and Engelmann spruce (closely related to balsam fir and white spruce, respectively), Day (1963, 1964), and Alexander and Edminster (1983) reported similar seedbed preferences as with black spruce and jack pine. One month following a spring burn in Saskatchewan, Charron (1998) found no balsam poplar germinants on any seedbed except mineral soil that was within a few centimetres of a burnt trunk (presumably due to the enhanced moisture from stem flow and shading). Likewise, Zasada et al. (1983) found aspen and balsam poplar seedlings only on mineral soil seedbeds following burning and artificial seeding.

We argue that there is a narrow window of opportunity for invasion of clearcuts and burns. By about the fifth to seventh year following disturbance, the accrual of litter and the aggradation of mosses make the optimal seedbeds sufficiently uncommon that establishment becomes a rare event except perhaps for the very tolerant balsam fir. For white spruce and paper birch, J.C. Zasada and T. Wurtz (unpublished data) and Zasada et al. (1978) showed a decline in first-year survivorship with seedbed age. Similarly, Fleming and Mossa (1995*b*) reported a decline in first-year survivorship with black spruce. By the fifth year after a site-prepared clearcut, Fleming and Mossa (1995*b*) reported that mineral soil and thin organic seedbeds had been reduced to 20% of their original coverage. When stem ages have been carefully measured, it appears that the great majority of the sexual-origin stems of all species arrived within the first 6 years following fire or cutting (Cayford 1963; St. Pierre et al. 1992; Johnson and Greene 1997).

Intact forests

There is little work on first-year survivorship of boreal species under intact forest. Generalizing from the sparse literature, it would appear that initial survivorship is inversely proportional to organic depth (as in clearings) and that with equal depth, survivorship declines as moss-covered logs > moss > needle litter > broadleaf litter (Knapp and Smith 1982; Bonan and Shugart 1989; Harmon and Franklin 1989; Bartlett et al. 1991; Coté and Belanger 1991; Nakamura 1992; McLaren and Janke 1996; Szewczyk and Szwagrzyk 1996; M.-J. Simard, unpublished manuscript). There is some evidence that germination rates are higher on broadleaf than needle litter but that subsequent survivorship is higher on needles (McLaren and Janke 1996). Such changes in the comparative quality of organic seedbeds at different stages appear to be common (Collins 1990; Schupp 1995).

By 20 years of age, the rapid accrual of leaf area in the developing stand and the aggradation of mosses makes mineral soil and humus seedbeds increasingly rare. These latter seedbeds comprise only about 1% of the forest floor in an intact 150-year-old *Tsuga* forest on level ground in Ontario (Johnson and Greene 1997) or a 100-year-old fir forest in Saskatchewan (D.F. Greene and E.A. Johnson, unpublished data). First-year survivorship should decline with stand age (as organic layers thicken), while seed production per square metre should increase as basal area density increases. The net effect of these two opposed tendencies can be gauged from the chronosequence study of Kneeshaw and Bergeron (1998) where some boreal species tend to show a unimodal temporal distribution of advanced regeneration densities in relation to stand age.

First-year survivorship appears to be more strongly related to seed size (germinant size) than to shade tolerance (M.-J. Simard, unpublished data). One might speculate that species-specific differences in shade tolerance do not begin to affect relative seedling densities until perhaps the second year, as the effect of tolerance is masked by the extraordinarily high mortality during the germination stage.

In conclusion, early survivorship under intact canopy is possibly similar to the situation in clearings except that organic seedbeds cover the great majority of the seedbeds and, consequently, seedling densities are much lower. Although we could employ production and dispersal arguments to estimate the seed density in Cartesian space, we are presently unable to assign species-specific first-year survivorships to any of the boreal species as a function of seedbed characteristics or (as a surrogate) stand age.

One might ask: why bother with the first-year stage under intact crowns? Why not instead rely on estimates of advanced regeneration density as a function of stand age, light conditions, and source basal area? Our response is that the cohort in its first year can have appreciable densities, and, unlike the advanced regeneration, these densities are less strongly related to shade tolerance. Thus, budworm crown damage, wind-induced disturbances, or careful logging can potentially leave a substantial density of intolerant species in the initial recruitment if the disturbance was preceded by a mast year.

Influence of surface conditions on vegetative reproduction

Surface conditions influence the density, spatial distribution, and rate of development of vegetative reproduction to varying degrees depending on species and types of bud banks. Of the main types of bud banks described above, the basal stem buds are probably least influenced by surface conditions, although reduction of forest floor depth around the base of the tree might result in the release of more buds and an increased rate of early sprout development from buds originating below the forest floor (Rinne et al. 1987).

For aspen, a number of studies from different parts of the range have shown that soil temperature influences sucker production (Perala 1990). The depth of the forest floor influences the temperature in the zone where aspen roots are concentrated, thus potentially influencing sucker density. Depth and condition of the forest floor are directly influenced by disturbances like fire and forest harvesting. Bella (1986), for example, found that the amount of logging residue influenced the density of suckers, but suckering was sufficient in all cases and comparable with the range of sucker density following fire.

Compaction of the forest floor and surface soil layers can greatly reduce suckering potential. The most severely disturbed areas in harvested stands, e.g., skid trails and landings, often have low sucker density or no suckers because of damage to soil or the roots. Studies of aspen suckering response to varying levels of soil compaction and organic matter removal indicate that both variables affect sucker density and early growth, but that the magnitude of the effect is greater on clay soils and less on sandy soils (D. Stone, personal communication; J.C. Zasada, unpublished data).

In black spruce, layering is affected by forest floor accumulation. Generally, in the western boreal forest, layering is much less common on upland than on lowland sites where moss grows over lower branches (Viereck and Johnston 1990). By contrast, in Ontario, Quebec, and the Maritime Provinces, layering can play a significant role in black spruce regeneration (Hatcher 1964; Doucet 1990; Cauboue and Tremblay 1993).

Survival of asexual stems in clearings

Unlike sexual stems, cohorts of asexual stems of aspen and balsam poplar continue to have very low survivorship after the first year. Presumably, this is due to competition for shared carbohydrates in the clonal root system rather than (at least in the first years) competition for light. D.F. Greene and E.A. Johnson (unpublished manuscript) have used data sets from recent fires (2–18 years) in Alaska, Saskatchewan, and Quebec, as well as yield tables for aspen in central Saskatchewan (20–100 years old), to show that asexual stem density (F_D) is a function of prefire basal area density B_T and time since burning (t) as

$$F_D = 45\,000\,(t+1)^{-1.64} B_T$$

According to this argument, low-density postfire poplar stands will thin as rapidly as dense stands because the initial stored carbohydrate pool is correspondingly smaller, although empirically low prefire B_T stands have their subsequent stem density underpredicted by about two to threefold.

Advance regeneration

Advance regeneration consists of seedlings and vegetative reproduction present in a mature forest and potentially able to replace the overstory following natural or human disturbance. Species composition of the regeneration may be similar to the overstory or a different species and may or may not be the desired species. Although advance regeneration has been recognized as potentially important for postharvest stand replacement for many years, it was mostly ignored when forest management followed the agricultural model and planting was the preferred means of stand replacement. With escalating costs of regeneration and the desire to have forest management more closely approximate natural processes, there has been renewed interest in encouraging advance regeneration and taking advantage of it in harvested areas. In the work done to date, and cited below, it is obvious that factors regulating natural regeneration in the understory of managed and unmanaged forests are different from those in areas that have been clearcut or essentially so. The following discussion summarizes some of the important factors associated with the presence of advance regeneration across the boreal forest. The factors considered here are overstory condition, seedbed condition, and type and severity of disturbance.

The condition of the overstory in terms of composition, potential for seed production, distribution of species, canopy cover, and age is critical for understanding the potential for regeneration of desirable trees and the potential for development of plant species that interfere with establishment. These factors affect other biotic processes, for example herbivory, that may determine regeneration success. There are many ways to characterize the overstory; stand basal area is one common way and some considerations in using this variable are discussed below. Béland and Bergeron (1993) and Kneeshaw and Bergeron (1996) found that advance regeneration was positively correlated with the basal area density of parent trees; however, Morin and Laprise (1997) and others have not found this relationship. There is most likely a threshold such that the abundance of advance regeneration is correlated with the basal area of adult trees at low basal areas but that this relationship is less significant or nonexistent at higher basal areas when the overstory completely dominates the site. The presence of advance regeneration was strongest for cedar and black spruce in the Kneeshaw and Bergeron (1996) study, but for both, the majority of the variation in regeneration was not related to basal area; in both cases, the partial R^2 was about 0.2. For balsam fir and white spruce, the percentage of the variation in seedling abundance explained by parent tree basal area was about 10% whereas for the hardwood species, even less variation could be explained. In the stands studied by Kneeshaw and Bergeron (1996), balsam fir basal area density ranged from about 0.000 42 in the youngest stands to 0.001 55 in the 147-year-old stands. (Grouped by stand composition, fir basal area density ranged from 0.000 29 in hardwood stands to 0.001 31 in mixed conifer stands). In the Morin and Laprise (1997) study, the balsam fir basal density was 0.002 33 – 0.007 19, with an average of approximately 0.004 in mixed balsam fir – paper birch stands. At these basal areas, the relationship with seedling abundance is weak but significant at least in some areas at low density. The direct relationship between advance regeneration and basal area of mature overstory trees needs to be further explored before it can be used as a predictor of advance regeneration. We point out that for hardwoods and conifers in Connecticut, Ribbens et al. (1994) found that a simple recruitment model with two parameters (source basal area and distance) explained typically 50% of the variation in germinant (and for two species the 1- to 3-year-olds) densities. Their study operated at a scale of hundreds of metres, and thus the problem in the boreal studies may be related to scale (dispersal).

The basal area of the different species in the overstory is an indirect measure of the understory microenvironment that affects seedbed conditions, light, understory composition, and other biotic and abiotic factors that directly determine the potential for the establishment of advance regeneration. A number of authors have noted that conifer tree regeneration is reduced on hardwood leaf litter when compared with conifer needle or moss seedbeds (Place 1955; Côté and Bélanger 1991; Bélanger et al. 1993). Kneeshaw and Bergeron (1996) also noted little conifer regeneration under aspen and birch stands. Doucet (1988) found that balsam fir advance regeneration was most controlled by stand type. A dense herb community will not only compete for resources, but will create a barrier to the establishment of seedlings due to its leaf litter (Coates et al. 1994). Dense herb layers are often associated with rich sites. It has been suggested that such dense herb layers may explain the lower regeneration densities found on rich sites (Harvey and Bergeron 1989; Groot 1995).

Youngblood (1995) found that white spruce was recruited in widely varying densities among different community types in mixedwood stands in Alaska. Lieffers et al. (1996) also showed that white spruce recruitment can be highly variable. Furthermore, they suggested that recruitment is limited by light levels: aspen stands transmit sufficient light to permit continual low-density recruitment whereas sites with a high conifer basal area may have little recruitment due to low light levels. White spruce recruitment may therefore occur under aspen canopies until the developing understory spruce develops sufficient leaf area to impede further recruitment.

Disturbance in the boreal forest often occurs as a result of insect defoliation or bark beetles that may or may not result in death of the overstory. Spruce budworm outbreaks have a negative impact on balsam fir regeneration density. Most studies (Ghent et al. 1957; Fye and Thomas 1963; Osawa 1994; Morin and Laprise 1997) show that fir and spruce seedlings establish before the outbreak. The budworm consumes the reproductive tissue of host trees, and thus, seed production is limited to trees not attacked by the budworm. Many studies have shown that mortality and damage of fir are less where fir basal area is low. The proportion of mortality and damage increases as the total fir basal area increases (e.g., Ghent et al. 1957; Bergeron et al. 1995; Su et al. 1996).

The number of balsam fir seedlings killed directly by the budworm (Spencer 1985; Ruel 1991) or due to falling trees and shrub competition (Ghent et al. 1957) increases with the severity of the outbreak. Direct mortality is proportional to the height of the advance regeneration, with taller seedlings experiencing greater damage then smaller seedlings (Spencer 1985; Ruel 1991). Ruel (1991) found that the abundance of stems taller than 1 m decreased with increasing defoliation, while Ruel and Huot (1993) found few fir stems greater than 50 cm in height where defoliation was severe. Vincent (1955) found that regeneration less than 25 cm in height experienced only light defoliation. In Minnesota, shrub success was found to be greatest where balsam fir mortality was greatest (Batzer and Popp 1985).

The ratio of species success was also found to vary following budworm outbreaks. Ghent et al. (1957) suggested that increases or decreases in the fir to spruce ratio are due to regional differences. Kneeshaw and Bergeron (1998) also found that compositional type had an impact on species recruitment following budworm outbreaks. In their work, balsam fir, although always the most abundant seedling, decreased in proportion in the older conifer-dominated stands whereas cedar increased. Furthermore, they found that fir was negatively correlated with gap size (and gap size increases with increasing forest age), while other species such as birch were often positively correlated. Frelich and Reich (1995) also suggested that cedar, because it is a nonhost tree, is able to increase at the expense of fir where fire does not occur for long periods.

Marchand (1990) suggested that spruce budworm outbreaks result in the forest shifting back and forth between birch and fir dominance. In forests to the east, spruce budworm outbreaks have been suggested to cause a cycling of fir forests (Baskerville 1975; MacLean 1988; Morin 1994). However, changes in seedling density following budworm outbreaks were also found to vary with stand structure in these eastern forests. In one study, hardwood regeneration increased the most in mature stands and the least in immature stands, while fir regeneration abundance had its greatest declines in the older stands (Spencer 1985).

Gaps may also be formed by individual or group tree mortality due to other insects, pathogens, or wind or ice storms. Species regeneration dynamics have long been associated with gap processes in tropical and temperate forests, and in the last decade, they have also been studied for higher latitude coniferous forests. In Appalachian forests, balsam fir seedling densities were found to be significantly higher under canopies than in gaps (Perkins et al. 1992). In boreal forests of northern Sweden, Hytteborn et al. (1987) found that the presence of gaps was necessary for the survival of birch seedlings whereas spruce established and survived in both gaps and under the canopy. Another study from the boreal forests of Sweden suggested that most gaps were too small for the favorable regeneration of intolerant species (Qinghong and Hytteborn 1991).

Most research seems to show that the response to openings is in terms of growth rather than increased regeneration abundance for conifer seedlings (e.g., Dai 1996 for Scandinavian species). Intolerant species may, however, have positive correlations with partial disturbances in terms of seedling abundance (e.g., birch seedling density was positively correlated with gap size: Kneeshaw and Bergeron 1998). Gaps are also correlated with seedling survival, with openings being necessary for the survival of intolerant species. As discussed earlier, the creation of the gap may result in the mortality of advance regeneration.

Large-scale climatic patterns will also have an impact on species regeneration densities; warmer or colder climates may favor the regeneration of one species over another (Steijlen and Zackrisson 1987). Changes in climate may also have indirect effects by influencing disturbance regimes, which in turn influence regeneration patterns. Warmer and moister summers have been linked to an increase in the fire return interval (Bergeron and Archambault 1993) which permits the establishment of a greater abundance of late successional species seedlings (Liu 1990; Richard 1993). Where species mixes are more complex, different species may replace or interact with fir following outbreaks. On rich sites (e.g., the claybelt of western Quebec), shrub competition may also be an important factor limiting seedling densities.

Two important considerations in attempting to utilize advance regeneration in forest management are assuring its presence and protecting it during harvesting of the overstory. Active promotion of regeneration usually involves removal of a portion of the overstory and, depending on the site conditions, some type of disturbance of the forest floor to create a desirable seedbed. Treatment of the overstory may be designed to create a uniform distribution of trees, as in the classic uniform shelterwood, or groups of trees with gaps of various sizes and shapes, conditions that create microclimates similar to the natural disturbances and stand conditions mentioned above. In upland, mixedwood forests in Alaska dominated by white spruce, Zasada and Grigal (1978), Wurtz and Zasada (1987), and J.C. Zasada and T. Wurtz (unpublished data) described regeneration of white spruce, paper birch, and aspen in uniform shelterwoods with a residual overstory of 10 m^2/ha. Putman and Zasada (1986) and Youngblood and Zasada (1991) reported successful regeneration of artificially sown white spruce seeds on both mineral soil and organic matter seedbeds under uniform shelterwoods. Lees (1964) found excellent white spruce regeneration under shelterwoods in Manitoba. Perala and Alm (1989) reported successful regeneration of paper birch in a uniform shelterwood in Minnesota. From these reports and from general observation, it seems obvious that all of the boreal species considered in this review can be regenerated under some level of residual overstory and that the spatial distribution of the overstory can be managed in such a way that most species will survive and grow with residual mature trees on the site.

Harvesting impacts advance regeneration directly by physically disturbing the seedlings and indirectly by altering the microenvironment, which may then stress the small tree that has developed under lower light conditions. Clearcutting often has a dramatic effect on the survival and thus the abundance of advanced regeneration following the disturbance. A study of mechanical and manual whole-tree harvesting suggests a 92% reduction in softwood regeneration (Harvey and Bergeron 1989). They also suggested that black spruce was at least partially limited by the lack of seed trees. Frisque et al. (1978) reported a loss of up to 80% of the seedlings during harvesting. In both studies the decreases in stocking were much less than the decrease in seedling densities, and after harvest, stocking is more important than density in assuring an effectively regenerated stand. Reductions in stocking were 60% in the Harvey and Bergeron (1989) study, 4–26% in the Frisque et al. (1978) study, and 30% in Candy's (1951) study. Youngblood (1990) reported less damage to white spruce seedlings in areas where a uniform shelterwood was removed by a cable yarding system than where a ground-based system was used. Youngblood's (1990) work showed that damage to advance regeneration during the process of harvesting can be reduced by properly designing the harvesting system and choosing the proper season for harvesting. Hardwood stems also decreased following cutting, but their abundance relative to the conifer species was found to increase. As described elsewhere in this review, hardwoods have the advantage of being able to sprout from the basal bud bank after a disturbance and, unless the bud bank is destroyed, will maintain themselves in spite of fairly severe disturbance. On rich sites in western Quebec, Harvey and Bergeron (1989) also reported an increase in competition from shrubs after harvesting. Harvesting of areas that have been severely attacked by the spruce budworm may also lead to understocked sites (Ruel and Huot 1993).

Conclusions

Our aim was to review the literature on tree recruitment in the boreal forest with an emphasis on those biotic parameters that we deemed to be crucial in a subsequent modeling effort. In short, we hoped to arrive at the functions and parameter initializations that would constitute a recruitment subroutine within a landscape-scale simulator. We have not succeeded. However, we have identified the gaps in our knowledge that must be filled before a realistic recruitment subroutine can be constructed. In effect, then, we propose the following research program.

(*i*) Seed production. Seed production by a species rises with basal area but it is not understood what happens at the individual or stand level as trees begin to senesce. We propose that, for all the boreal tree species, a study of filled seed production be conducted in stands of varying stem density, basal area density, and age (with site held more or less "constant"). The study need not last many years (temporal variation is not the issue) but can take advantage of landscape synchronicity in masting behaviour to arrive at a function relating seed production to initial stand density and (via a stand growth simulator which predicts basal area density) to stand age.

A second requirement is a close examination of the (quite large) body of forestry studies on temporal variation in seed production. The function that could be most appropriately used in a recruitment subroutine remains unknown.

(*ii*) Asexual stem production. As with seed production, the relationship between basal area density, age, and asexual stem density is not understood in a sufficiently quantitative manner to permit us to write and initialize a function. Further, there is rapid immediate thinning in asexual stems, but the degree to which it is determined by present sucker density and predisturbance basal area density (the size of the carbohydrate pool?) is not understood. One could examine the asexual stem densities of the three hardwood species, say 5 years after fire, censusing both living and dead stems across a broad range of prefire basal area densities and ages. A similar study would be required for a set of harvested blocks.

(*iii*) Dispersal. The seed dispersal model needs to be verified for the important cases of patch and strip sources. At present, we know of no empirical data to use in such a test. There are no studies of seed dispersal of either poplar species from any type of source geometry.

Root sucker dispersal for the poplars remains to be tested. In stands where the predisturbance basal area density was high, this is not a pressing issue; a "bath term" ought to suffice. But for the special cases of low-density stands and clonal edges, a spatially explicit model will be of value.

(*iv*) Germination and advanced regeneration. Within clearings, a great deal of work has been done on commercial species (the two spruce species, fir and jack pine), and it permits us to make rough estimates of typical first-year survivorship as a function of broadly defined seedbed types. But for the other species, there are too few data at present, and experimental studies (artificial sowings) are required. In particular, repeated sowings for the first few years following a disturbance would be invaluable in allowing us to define the "window of opportunity" where initial cohort survivorship is still relatively high.

For intact forest, there are too few data at present for us to make estimates of initial or subsequent survivorship. We call for artificial sowing of all species on a range of seedbed types with cohorts followed for at least 3 years. Thus, the role of shade tolerance will be subsumed in the expected age-specific survivorships.

The relative frequencies of the seedbed types following varying disturbance agents or, in the absence of disturbance, as a function of disturbance intensity, stand age, and site type cannot yet be generalized. Yet, initial survivorships for a species often vary by more than an order of magnitude across seedbed types, and thus the relative frequency of the seedbeds becomes a crucial factor. Stand age, particularly as it affects moss thickness and the availability of well-decomposed boles, would appear to be a crucial parameter. It may also be the confounding variable in the poor relationship between advanced regeneration density and basal area density for the tolerant (cedar, balsam fir) and mildly tolerant (white spruce) boreal species.

While it is clear that careful harvesting can permit acceptable stocking levels via advanced regeneration, this option is only useful if we can predict the preharvest densities without recourse to a ground survey in each planned cut block. This, however, we cannot yet do. It would appear that the three factors of most importance are forest floor characteristics, light availability, and basal area density. What is required is a set of large data sets that relates spruce and fir advanced regeneration to these three factors and also provides the size and age structures. We then ought to be able to predict advanced regeneration density as a population process.

In conclusion, the full range of functions and species-specific coefficients required for a thorough recruitment subroutine is not yet available. It is of course possible to write a subroutine now that ignores some functions or assigns somewhat arbitrary ordinal scale values as multipliers (e.g., FORET or SORTIE). We see no reason for haste. The research program outlined here could be completed within 4 years if ecologists and foresters were sufficiently mobilized.

Silvicultural applications

The traditional criticism of natural regeneration as a forestry option has been its unreliability relative to planting. However, recent advances with certain species-site manipulations have begun to change this attitude. In particular, there has been widespread success with vegetative regeneration of aspen from its extensive bud bank, with the aerial seed banks of jack pine and black spruce, and with the seedling banks of black spruce and balsam fir. What these success stories have in common is that (*i*) the source of the colonizing stems is provided in situ, and thus, dispersal does not constrain cut size, and (*ii*) the new stems are derived from many years of accumulated banks (buds, seeds, tolerant seedlings), and thus the uncertainty of masting behavior is avoided.

We see two potential impediments to the potential increase in the utilization of natural regeneration. The first challenge involves maximizing the reproduction potential for the success stories mentioned above. Using aspen as an example, it is clear that stocking objectives can be more reliably obtained if soil compaction and damage to root systems are avoided (e.g., Sheppard 1993; Stone and Elioff 1998). Thus, to a greater extent than in the past, silvicultural prescriptions must take into account factors such as season of harvest and soil conditions.

The second challenge is to encourage natural regeneration with the presently more difficult species, and here of course in North America the outstanding problem is white spruce. This species has neither bud nor seed nor (extensive) seedling banks, it has marked (and unpredictable) masting, and it seldom comprises the majority of the source basal area at the scale of a large harvesting block (and consequently, the source strength is not great). In short, it has the suite of characteristics that almost guarantee unreliable stocking in large cuts. These problems can be reduced (but not eliminated) by silvicultural systems guided by three simple principles. First, obviate the dispersal constraint by reducing the maximum distance from source to seedbed (via strip cuts or shelterwood). Second, enhance the density of seed deposition by leaving a large amount of source trees at cut edges (i.e., somewhat counterintuitively, the cut perimeter must not deliberately enclose the highest volume per hectare of the most commercially valuable boreal species). Third, expose as much mineral soil and humus as possible. Whether this prescription is economically viable relative to large-scale planting remains to be seen. In any case, as was pointed out earlier, the reason that white spruce seldom forms near-monocultures in nature is that its reproductive traits render it intrinsically unreliable as a colonist. Thus, following wildfire, there is seldom adequate stocking beyond about 100 m from a burn edge with a dense source, and of course, there is only a sprinkling of individuals (via long-distance dispersal) near edges with few source trees. In short, it requires an optimism bordering on hubris to imagine that we can someday obtain reliable white spruce regeneration in large cuts when "nature" cannot achieve it. The prescription outlined above would at best allow foresters to obtain adequate stocking the majority of the time, but spot planting would undoubtedly be required in the majority of cases if we are bound to meet what is perhaps an "unnatural" stocking criterion.

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