Seed mass and early survivorship of tree species in upland clearings and shelterwoods

D.F. Greene and E.A. Johnson

Abstract: We examined recommended sowing densities of 25 North American tree species (26 observations) to measure the relationship between juvenile survivorship and seed mass in large clearings and shelterwoods. Two models for expressing the relationship (simple power law or a cumulative negative exponential adjusted to account for rodent-repellent application and seedbed type) all showed that survivorship is highly dependent on seed mass. For a small seed, mineral soil and thin humus confer roughly equally high survivorship. Leaf litter is very poor, and undisturbed thick moss appears to be the worst possible organic seedbed on upland sites. An examination of 30 records of *Picea glauca* (Moench) Voss survivorship (3- to 6-year-old cohorts) on mineral soil revealed substantial intraspecific variation with only 50% of the values within twofold of the predicted value.

Résumé : Nous avons examiné les densités d’ensemencement recommandées pour 25 espèces d’arbres d’Amérique du Nord (26 observations) dans le but de mesurer la relation entre la survie juvénile et la masse des graines dans de grandes ouvertures et sous couvert. Deux modèles qui expriment cette relation, un modèle exponentiel simple et un modèle exponentiel négatif et cumulatif ajusté pour tenir compte de l’application d’un répulsif pour les rongeurs et du type de lit de germination, montrent que la survie est fortement dépendante de la masse des graines. Pour une petite graine, le sol minéral ou un humus mince confèrent un taux de survie élevée sensiblement égal. Une litière de feuille est très peu adéquate et un lit de mousse épaisse et non perturbée constitue le pire lit de germination organique sur les plateaux. L’examen de 30 rapports de survie de *Picea glauca* (Moench) Voss (cohorte de 3 à 6 ans) sur sol minéral a révélé l’existence d’une importante variation intraspécifique. Seulement 50% des valeurs sont comprises dans un intervalle égal à deux fois la valeur attendue.

Introduction

Plant ecologists have discussed the relationship between seed size and juvenile survivorship for at least six decades (reviewed in Harper 1977), although the bulk of this literature consists of ordinal-scale inferences from observed patterns (e.g., “climax” species tend to have larger seeds than “seral” species, and xeric herbs tend to have larger seeds than mesic herbaceous species, etc.). However, a recent series of greenhouse experiments (e.g., Leishman and Westoby 1994), each covering many orders of magnitude in seed size, has shown that, in deep shade (>90%), both survivorship and shoot length are positively correlated with seed mass. It is difficult to extrapolate these results to field expectations because the substrates were litter free and well watered. However, sowing experiments in clearings and intact forests by Zasada et al. (1983), Walker et al. (1985), and Tappeiner and Zasada (1993) indicate that seed size is indeed proportional to juvenile survivorship.

During these same six decades, foresters have been conducting a series of direct seeding experiments in openings in the forest created by cutting (Waldron 1974). In this paper we will use this direct seeding literature to analyse the relationship between seed size and juvenile survivorship for different seedbed types.

The technique of direct seeding consists of aerial broadcasting of the smaller seeded species or hand sowing of the larger seeded species (e.g., *Quercus* or, occasionally, *Pinus* in the southern United States). As seed is expensive, and overstocking of stands is as much a problem as understocking, series of field trials have led to recommended sowing densities designed to give a desired seedling density (measured usually 1–3 years after application). Thus, the ratio of the desired seedling density a few years after sowing to the recommended sowing density provides an estimate of the expected survivorship up to the advent of thinning. The prethinning survivorship of sexually produced stems with high light levels is determined primarily by the mortality in the first (especially) and second years, with very little loss after about the third summer (e.g., Zasada et al. 1992; Griffin and Carr 1974; Harris 1967; Johnson and Krinard 1985; Arnott 1974; Cayford 1964; Fleming and Mossa 1995; Lees 1970; Crossley 1955; Ackerman 1957).

The structure of the paper is as follows. First, we develop simple models for the relationship between seed mass and early survivorship based on a dichotomization of upland seedbeds as high- or low-porosity seedbeds. The low-porosity seedbeds (mineral soil, humus, well-decomposed logs) are expected to engender high first-year survivorship because...
soil water can rise via capillary action for many weeks following a thorough wetting of the soil. By contrast, the high-porosity seedbeds (litter, deep moss) are expected to have much lower initial survivorship because they will dry out quickly following rain. We then test the models using the results from the direct seeding literature. The argument is further tested using a data set on *Tsuga canadensis* (L.) Carr. (shelterwood) and *Pinus banksiana* Lamb. (fire). Finally, as the direct seeding recommendations can only provide estimates of central tendency for the juvenile survivorship of a species, we have used the literature on *Picea* (Moench) Voss survivorship on mineral soil in clearings and shelterwoods to characterize the intraspecific variation.

**Models**

Ignoring for the moment seedbed quality, total (all seedbeds lumped) seedling survivorship ($S_T$) could be modelled as a function of seed mass ($m$) by

$$S_T = am^b$$

where $b$ is the result of a dimensional assumption, and $a$ is an empirical coefficient. If survivorship is directly proportional to available carbohydrates, then $b = 1.0$. If survivorship is dependent on an area (e.g., total leaf area or total root hair area), then we expect $b = 0.67$ since geometric similarity is given by the ratio $L^b/L^b$ (where $L$ is a length). Finally, if survivorship is related to a length (e.g., hypocotyl or radicle length), then $b = 0.33$ because geometric similarity is given by $L^b/L^b$.

The coefficient ($a$) is less clear, but forestry sources (e.g., Arnott 1974) indicate that the three major causes of first-year (age-specific) losses are granivores, fungi, and abiotic losses. The abiotic loss is primarily due to low amounts of available soil moisture. For the moment, let us assume that other factors (e.g., herbivores, thermal-induced death, frost heaving, etc.) are relatively unimportant. Further, let us assume that losses to fungi are important primarily in the high relative humidity environments of intact forests. In short, we will assume that granivory is the main biotic mortality source in clearcuts, burns, and shelterwoods. As for seedbed type, we will dichotomize it into low-porosity (e.g., mineral soil, humus, well-decomposed logs) or high-porosity (e.g., leaf litter less than 1 year old, deep moss, thick burnt moss) seedbeds. We expect the fraction ($w$) of the area occupied by low-porosity seedbeds to engender much higher survivorship than the fraction ($1 - w$) of high-porosity seedbeds because of differences in moisture availability.

Equation 1 permits a survivorship greater than 1.0 at sufficiently high seed masses. Therefore, one prefers a function which constrains survivorship so that $0 \leq S \leq 1.0$. Of course, any cumulative distribution will do this. We adopt a negative exponential function for our second model:

$$S_L = g[1 - \exp (-f_la^{mb})]$$

and

$$S_H = g[1 - \exp (-f_Ia^{mb})]$$

where $g$ is the survivorhip through the granivory stage, $f$ is an empirical coefficient, and the subscripts $H$ and $L$ denote high-porosity or low-porosity seedbeds, respectively.

Equation 2, at least, proposes a possible mortality mechanism. For example, imagine that $b = 0.33$ because the important characteristic of seed size is initial radicle length, and the wetted horizon of the soil retreats downward through the soil column following rain or spring snowmelt. If the mean maximum depth of the wetted horizon at some crucial stage (e.g., late spring following germina-

**Methods**

**Estimating survivorship**

We express the juvenile survivorship ($S$) as

$$S = R_2/R_1$$

where $R_1$ is the recommended sowing density and $R_2$ is the recommended initial seedling density desired 1 or 2 years after application (when the stocking evaluation is recommended to take place). The recommended sowing densities for 25 North American species are given in Table 1. Twenty-one are for site preparation; five are for an absence of site preparation. Pooling these sources, we find recommended stocking densities vary from about 1000 to 2000 seedlings/ha at 1–3 years following seeding. We will use the value $R_2 = 1500$ for all species. (We note there is some ambiguity in translating a minimal seedling density to a minimal stocking standard percentage. A typical minimal stocking standard is at least one seedling of the desired species per 4 m$^2$ plot ($= 0.25$m$^2$) in at least 40% of the sampling plots giving us the product (0.4) (0.25) = 0.1, or 1000 stems/ha. The fact that broadcast seeding does not result in a uniform distribution of seeds, and that age-specific mortality after the first few years (but before the onset of thinning) is low but not zero, requires that the recommended density be somewhat higher than 1000 stems/ha.)

For the five *Quercus* species (hand sowing) and the five species sown on nonscarified seedbeds in Table 1, there is only one type of seedbed involved (mineral soil or high-porosity undisturbed soil, respectively). For the remaining 17 species (partially scarified ground), we must deal with a mix of exposed mineral soil – humus, as well as undisturbed seedbeds. We will use the five undisturbed seedbed observations to estimate the parameters $f_I$ and $d$ (eq. 3). Then for the 16 species on mixed seedbeds (scarification), we can subtract the estimated contribution (seedlings/ha) on the undisturbed seedbeds from $R_2$ (= 1500 stems/ha), and then calculate $S_L$ for the low porosity (mineral soil, humus) fraction.

**Estimating the losses to granivores**

In this analysis, we will ignore losses to fungi as it is generally agreed, at least in North America, that granivores (especially rodents) are a larger problem (e.g., Arnott 1974; Radvani 1974) in large recent clearings.

Fourteen of our studies use broadcast seeds coated with rodent repellents (Table 1). Although studies of radiotagged seed losses...
for nontreated seeds indicate large variation within and between sites as well as among years, we will nonetheless, use an average consumed value of 57% as determined by Lawrence and Rediske (1962), Black (1969), Radvani (1974), and Alexander and Edminster (1983). Comparisons of repellent-coated and untreated seeds indicate that the repellents were not particularly effective: an average of 40% of the treated seeds was nevertheless consumed (Black 1969; Radvani 1974).

Thus, in eqs. 2 and 3 we will set the proportion of low porosity seedbeds (given the regression results for eq. 3) where \( w = 0 \).

### The low-porosity seedbed fraction

Twenty-two of the 27 recommendations in Table 1 call for scarification or prescribed burning to create mineral soil or humus seedbeds. The percentage of area converted to these low-porosity seedbeds varies with the efficacy of the burning operation or the expenditure on scarification. As a general rule, 15% mineral soil or humus exposure is typical for scarification (Fleming et al. 1987) and somewhat less for prescribed burning (Chrosiewicz 1983). As a general rule, 15% mineral soil or humus exposure is typical for scarification (Fleming et al. 1987) and somewhat less for prescribed burning (Chrosiewicz 1983).

Five of the 25 species in Table 1 (all of them Quercus) have seeds that are sown individually into the soil. This operation ensures that the seed is only placed in mineral soil. For the Quercus species then, low-porosity seedbed exposure is effectively 100% (\( w = 1.0 \)).

Five species in Table 1 have recommended sowing densities based on intact seedbeds. Note that the percentage of mineral soil or humus exposed following a logging operation is remarkably small, about 1% (e.g., Chrosiewicz 1983), since careful logging concentrates the dragged logs on skid trails. The proportion of seedbeds composed of well-rotted logs is dependent upon the age of the stand and its previous logging history. For the moment, we will assume that rotted logs comprise an insignificant proportion of the seedbeds.

In summary, therefore, we set the proportion of low porosity seedbeds (\( w \)) for eqs. 2 and 3 at \( w = 1.0 \) for individually sown seeds on scarified terrain, \( w = 0.15 \) for scarification or burning followed by aerial broadcasting, and \( w = 0 \) for no site preparation.

### Determination of seed mass

In the interest of standardization, we used the mean seed mass values in Schopmeyer (1974) for all species. These seed mass values represent the total mass of seed coat, endosperm, and embryo for all but two species. Instead, for Fraxinus americana L. and Acer saccharum Marsh, where the listed mass in Schopmeyer (1974) includes the wing, we have used measurements on Quebec seed samples of F. americana and Acer saccharum to reduced those masses by 42% and 25%, respectively.

### Statistical analyses

Both models (eqs. 1–3) can be reformulated as linear regressions of survivorship on seed mass (following a logarithmic transformation). For eq. 2, we must first recalculate the survivorship on the low porosity fraction of seedbeds (given the regression results for eq. 3) where \( w = 0 \).

### The Tsuga data set

Peter Hynard (Ontario Ministry of Natural Resources, Minden) generously supplied us with a data set on Tsuga canadensis (L.) Carr. regeneration following a shelterwood cut. The site, within

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Table 1. The 25 species used in the study.

<table>
<thead>
<tr>
<th>Species</th>
<th>Source</th>
<th>( R^a )</th>
<th>( m^b )</th>
<th>Comments^c</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pinus palustris Mill.</td>
<td>Barnett and Baker 1991</td>
<td>27 744</td>
<td>0.093</td>
<td>Re, W</td>
</tr>
<tr>
<td>Pinus elliottii Engelm.</td>
<td>Barnett and Baker 1991</td>
<td>26 550</td>
<td>0.038</td>
<td>Re, W</td>
</tr>
<tr>
<td>Pinus echinata Mill.</td>
<td>Barnett and Baker 1991</td>
<td>36 720</td>
<td>0.0097</td>
<td>Re, W</td>
</tr>
<tr>
<td>Pinus strobus L.</td>
<td>Barnett and Baker 1991</td>
<td>44 910</td>
<td>0.017</td>
<td>Re, W</td>
</tr>
<tr>
<td>Pinus virginiana Mill.</td>
<td>Barnett and Baker 1991</td>
<td>36 720</td>
<td>0.0082</td>
<td>Re, W</td>
</tr>
<tr>
<td>Pinus taeda L.</td>
<td>Barnett and Baker 1991</td>
<td>37 800</td>
<td>0.025</td>
<td>Re, W</td>
</tr>
<tr>
<td>Pinus banksiana Lamb.</td>
<td>Waldron 1974</td>
<td>74 100</td>
<td>0.0035</td>
<td>Re, W</td>
</tr>
<tr>
<td>Pinus contorta Dougl. ex Loud.</td>
<td>Mitchell et al. 1990</td>
<td>75 000</td>
<td>0.0048</td>
<td>Re, W</td>
</tr>
<tr>
<td>Pinus ponderosa Dougl. ex Laws.</td>
<td>Mitchell et al. 1990</td>
<td>18 000</td>
<td>0.038</td>
<td>Re, W</td>
</tr>
<tr>
<td>Picea glauca (Moench) Voss</td>
<td>Richardson 1974</td>
<td>123 500</td>
<td>0.002</td>
<td>Re, W</td>
</tr>
<tr>
<td>Picea mariana (Mill.) BSP</td>
<td>Richardson 1974</td>
<td>123 500</td>
<td>0.0011</td>
<td>Re, W</td>
</tr>
<tr>
<td>Pseudotsuga menziesii (Mirb.) Franco</td>
<td>Mitchell et al. 1990</td>
<td>60 000</td>
<td>0.111</td>
<td>Re, W</td>
</tr>
<tr>
<td>Larix occidentalis Nutt.</td>
<td>Mitchell et al. 1990</td>
<td>115 000</td>
<td>0.0033</td>
<td>Re, W</td>
</tr>
<tr>
<td>Tsuga canadensis (L.) Carr.</td>
<td>Godman and Mattson no date</td>
<td>234 000</td>
<td>0.0024</td>
<td>W</td>
</tr>
<tr>
<td>Betula papyrifera Marsh.</td>
<td>Godman and Mattson no date</td>
<td>777 338</td>
<td>0.00033</td>
<td>W</td>
</tr>
<tr>
<td>Betula alleghaniensis Britt.</td>
<td>Godman and Mattson no date</td>
<td>257 300</td>
<td>0.001</td>
<td>W</td>
</tr>
<tr>
<td>Fraxinus americana L.</td>
<td>Godman and Mattson no date</td>
<td>146 443</td>
<td>0.020</td>
<td></td>
</tr>
<tr>
<td>Acer saccharum Marsh.</td>
<td>Godman and Mattson no date</td>
<td>105 000</td>
<td>0.048</td>
<td></td>
</tr>
<tr>
<td>Tilia americana L.</td>
<td>Godman and Mattson no date</td>
<td>68 783</td>
<td>0.114</td>
<td></td>
</tr>
<tr>
<td>Picea engelmannii Parry</td>
<td>Alexander and Edminster 1983</td>
<td>1 250 000</td>
<td>0.0033</td>
<td></td>
</tr>
<tr>
<td>Picea glauca</td>
<td>Zasada 1971</td>
<td>1 363 636</td>
<td>0.002</td>
<td></td>
</tr>
<tr>
<td>Quercus nuttalli</td>
<td>Johnson and Krinard 1985</td>
<td>3 700</td>
<td>4.78</td>
<td>I</td>
</tr>
<tr>
<td>Quercus nigra L.</td>
<td>Johnson and Krinard 1985</td>
<td>3 700</td>
<td>1.24</td>
<td>I</td>
</tr>
<tr>
<td>Quercus rubra L.</td>
<td>Godman and Mattson no date</td>
<td>2 500</td>
<td>3.64</td>
<td>I</td>
</tr>
<tr>
<td>Quercus shumardii Buckl.</td>
<td>Klawitter 1959</td>
<td>3 700</td>
<td>4.55</td>
<td>I</td>
</tr>
<tr>
<td>Quercus falcata Michx.</td>
<td>Klawitter 1959</td>
<td>4 900</td>
<td>0.842</td>
<td></td>
</tr>
</tbody>
</table>

^aRecommended sowing density (seeds/ha).
^bSeed mass (g).
^cRe, Rodent repellents were used; W, scarification/burning was recommended; I, seed is individually sown rather than broadcast.
Cavendish Township in southeastern Ontario, was a 170-year-old (mean age) Tsuga-dominated forest with a precut inventory of about 0.0037 (basal area per area). About half of the basal area was removed by the harvest. The cut occurred in February 1988, and the survey of regeneration was conducted in late summer 1992. Eighty randomly selected plots, with four 4-m$^2$ quadrats per plot (for a total of 320 quadrats), were used to evaluate the relationship between seedling density and seedbed type. The seedbed categories were rotted logs, exposed mineral soil, exposed humus, living mosses, hardwood litter, conifer litter, and “other” (rocks and puddles). Each quadrat was assigned percentages for the seven seedbed categories (summing to 100), and the number of Tsuga seedlings in each seedbed type was tallied. Additionally, a randomly selected seedling at each plot was aged.

Two problems arose in our analysis of the data set. At four quadrats on skid trails, the forest floor was churned so well that the recorders made no attempt to assign seedlings to seedbed categories. We have deleted those quadrats (about 1% of the area examined) from our analysis. This is unfortunate because two of these quadrats had the highest seedling densities in the entire data set.

A second problem was that recorders never assigned less than 5% to any seedbed category, yet the seedling data show that over half the examples of seedlings on mineral soil or humus have no corresponding entry for the seedbed categorization. As suggested by Peter Hynard, we have assigned a value of 2.5% in such cases.

Survivorship of Pinus banksiana in a burn

We examined seedling density of Pinus banksiana in the Bittern fire (which occurred in early June 1996). This fire is located within 20 km of the eastern entrance of Prince Albert National Park in the mixedwood (southern boreal forest) of central Saskatchewan. At this fire, we subjectively chose four stands (within about 400 m of one another) that were dominated by Pinus banksiana (>75% of the stand basal area) and were on fluvioglacial stands in flat terrain. We used one transect (31 × 1 m) in each stand, and characterized the seedbed (at the transect midpoint) every m as being either exposed mineral soil, humus, or duff (invariably high porosity burned bryophytes exceeding 5 cm in depth). Additionally, for every Pinus banksiana seedling encountered on the transect, we assigned it to one of these three seedbed categories. All seedlings had germinated approximately 1 month after the June fire and were examined in mid-August (1996). We examined (filled) seed input in early July 1996 using six 0.04-m$^2$ plots along each transect.

**Results**

First-year survivorship

Figure 1 depicts the relationship between first-year survivorship ($S_T$) and seed mass using eq. 1 for the 21 species where site preparation is recommended. (Note that in all the following regressions, seed mass is in grams.) In Fig. 1, we have ignored any differences in rodent-repellent application or low-porosity seedbed exposure. Survivorship is calculated as the quotient of desired stocking (1500 stems/ha) and sowing rate (seeds/ha). The regression is highly significant.

For the five observations (three studies, five species) where neither site preparation nor rodent repellents are recommended, the regression (Table 2) has a mass exponent significantly higher than that of the site preparation regression, while the “intercept” (exponential of the regression intercept) is two times lower than that of the site preparation regression. For a seed mass of 0.1 or 0.001 g, survivorship would be 3 or 10 times greater, respectively, on low-porosity than on higher porosity seedbeds. Thus, as expected for equivalent seed mass, survivorship is higher with site preparation.

Let us return to the site preparation data but remove the expected contribution of seedlings from the high-porosity fraction of the seedbeds using the regression based on eq. 3. For the Quercus species, there is no contribution, but for the remaining 16 species (scarification with broadcasting), we expect low-porosity seedbeds to occupy 15% of the clearcut ($N = 14$) or shelterwood ($N = 3$). The regression results (eq. 2) are given in Table 2.

The regression for low porosity seedbed survivorship ($S_L$) gives a mass exponent much lower than for thick duff seedbeds. With a seed size of 0.1 g, low-porosity seedbeds encourage a survivorship nine times greater than do high-porosity seedbeds. For a seed size of 0.001 g, the increase in survivorship is about 50 times. For the remainder of this paper, we will use the exponential model for survivorship (eq. 4) with the coefficients provided in Table 2 (regressions 2 and 4).

It is worthwhile to ask what effect inclusion of the Quercus species had on the exponential model results since this genus represents our largest seed masses and is always individually sown. Averaging the Quercus seed masses ($N = 5$; $m = 3.0$) a regression on the 16 non-Quercus species yields an expectation of 3684 as the recommended sowing rate (seeds/ha). The average observed rate is 3700.

Other studies

We can seek independent verification of these results from studies of survivorship in scarified plots. Alexander and Edminster (1983) studied long-term survivorship of Picea engelmannii Parry on scarified plots on northern aspects in the Rocky Mountains of Colorado. They reported an average survivorship of 0.0066 by the fifth year following deposition. Given the seed mass of 0.0033 g (Schopmeyer 1974) and assuming $w = 0.15$ and $g = 0.43$, eq. 4 predicts an
average survivorship \( S_T \) of 0.011. The prediction is about twofold too large.

Similarly, for Pinus ponderosa Dougl. ex Laws. in Montana, Shearer and Schmidt (1970) observed survivorship based on a number of sites by the start of the second growing season, to be 0.024. This is for nontreated seeds on scarified ground. Equation 4 predicts 0.030. The prediction is about 1.2 times larger than the observed value.

McDonald (1966) examined survivorship at the end of the first growing season for three species in scarified openings following natural seed deposition in northern California. The observed survivorships were 0.018 (Pseudotsuga menziesii (Mirb.) Franco), 0.069 (Pinus ponderosa), and 0.082 (Abies concolor (Gord. & Glend.) Lindl.). The predicted survivorships from eq. 4 are 0.019, 0.030, and 0.031, respectively. Thus, the predicted/observed ratios are within 2.5-fold.

Allen and Barrett (1965) individually sowed \( w = 1.0 \) Juglans nigra L. seeds in furrows and followed survivorship only until August of the first summer. Equation 4 predicts a survivorship of 0.425 (i.e., the model assumes only losses to granivores contribute to deaths for such a large-seeded species). The observed survivorship was 0.53.

Lastly, we tested the prediction with the results of Griffin and Carr (1974) on aerial seeding of repellent-coated Picea glauca seed following a wildfire in Maine. The seeds were broadcast at a rate of 189 254/ha. Fifteen percent of the randomly located regeneration plots were unburned areas within the burn perimeter. Thus, setting \( g = 0.6 \) and \( w = 0.425 \) (i.e., about 50% of the burn consists of mineral soil or exposed humus) as in the Pinus banksiana example below in eq. 4, and given a seed mass of 0.002 g (Schopmeyer 1974) we predict a juvenile survivorship of 0.031. The regeneration survey estimated juvenile survivorship as 0.0148 by the end of the sixth growing season. We overestimate by about twofold.

We took the predicted (eq. 4) and observed survivorships from the preceding seven observations (five studies), transformed them to natural logarithms, and regressed them against one another. Neither the exponent nor the "intercept" were significantly different from an expectation of 1.0 (t test; \( p < 0.05; r^2 = 0.81 \)).

**Tsuga survivorship**

Table 3 provides the results of the Tsuga regeneration survey, which took place five growing seasons after the shelterwood cut. Post-logging-exposed mineral soil and humus accounted for less than 2% of the available seedbed types. Leaf litter comprised 80% of the seedbeds. The mean age of the seedlings was 2.02 years and the third and fifth growing seasons made up 46.8 and 50.0%, respectively, of the seedling ages (aged via terminal bud scale scars).

We can compare the relative survivorship of the seven seedbed categories as the ratio of observed density (per seedbed category) to mean density (irrespective of seedbed category). These relative survivorship values (Table 3) show that exposed humus seedbeds are as effective as mineral soil at increasing survivorship. Rotted logs have a relative survivorship about half that of mineral soil or humus. By contrast, moss, conifer leaf, and broadleaf litter have very low relative survivorships (about 70–175 times lower than mineral soil). The important variable in seedbed characterization then appears to be the distance the germinant must elongate through high-porosity material to reach the moist mineral soil or well-decomposed organic layer (humus, log).
We can attempt to predict absolute rather than relative densities if we couple eq. 4 for survivorship with an equation for seed production. Given the 50% reduction of basal area via the shelterwood harvest, the resulting “clearing” diameters are so slight (cf. Greene and Johnson 1996) we can avoid the incorporation of an explicit dispersal term. Greene and Johnson (1994) expressed the mean annual seed production (\( \overline{D} \)) of a tree as a function of individual seed mass (\( m \)) and the tree size (\( B \); basal area (m²)):

\[ \overline{D} = 3067m^{-0.58}B^{0.92} \]

This mean annual expectation ignores the tremendous temporal variation in seed production (coefficients of variation for long-term production studies are typically 1.0–2.5; D.F. Greene and E.A. Johnson, unpublished manuscript). Coupling eqs. 4 and 6, the individual tree’s annual fecundity (\( F_I \)) is:

\[ (F_I) = \overline{D} S_T \]

Equation 7 can be expressed as an annual density (\( F_D = \text{seeds/m}^2 \) per year) if we only enumerate the density (\( N_D \)) of dominants and codominants so that differences in \( B \) are muted (and thus, given that the exponent on \( B \) is near unity, we can use the mean value of \( B \)):

\[ F_D = 3067m^{-0.58}N_D B_m S_T \]

where \( B_m \) is a mean value. (The reader should note that with the inclusion of a spatially explicit dispersal term (e.g., Greene and Johnson 1996), eq. 8 can be applied to clearcuts and burns.)

Predicting the total density at a cut requires that we multiply the expectation in eq. 8 by the number of years since the cut occurred. Clearly, as mosses colonize and aggrade on low-porosity seedbeds, and as leaf area index increases (and thus high-porosity litter layers aggrade), the estimation of survivorship on the low-porosity fraction will become an overestimate. However, as shown by Fleming and Mossa (1995), the increase in first-year mortality on low-porosity seedbeds is relatively slight for the first few years following cutting.

For the Tsuga study, the mean basal area of the individual trees remaining after the cut was 0.1 m², and the trees were not markedly contagious in their spatial distribution. The total density of remaining basal area was 0.002 (dimensionless) with a density of 0.02 trees/m². We multiply by 5 (years) to obtain an expectation of 1217 seeds/m² over the 5-year period. We predict a density of 67 seedlings/m² on mineral soil, humus, or rotted logs (the observed averages 79), and a density of 1.7 seedlings/m² on the other seedbeds (observed = 1.0). The model errs by less than twofold. Note that in this example we have not attempted to predict the age structure of the seedlings. Almost all belong to the third and fifth cohorts following the cut. This highly variable recruitment is typical of natural regeneration because of the large temporal variation in seed production within populations.

**Pinus banksiana survivorship**

Results of the seedling density study of *Pinus banksiana* at the Bittern fire are shown in Table 4. As expected, there was little difference in density for seedlings on humus or mineral soil, but the density on thick organic seedbeds (duff) is about two orders of magnitude lower. About 99% of all seedlings were on mineral soil or humus, while these two seedbeds constitute only about 45% of the area.

We can attempt to predict the seedling densities in Table 4. Our study at the Bittern fire indicated 179 filled seeds/m² (averaging across the four transects). An ancillary study (D.F. Greene and E.A. Johnson, unpublished data) indicated that high basal area density stands of *Pinus banksiana* (aged 50–75 years old) such as these should have about 250 filled seeds/m². The predicted values are shown in Table 4. From Table 2, we predict a survivorship of 0.064 (low porosity seedbed) or 0.0019 (thick organic seedbed). For the optimal seedbeds, the predicted seedling density is within threefold. But our prediction for thick organic seedbeds is overestimating by about an order of magnitude. These high porosity seedbeds (averaging about 8 cm in thickness above humus or mineral soil) are much more inhospitable substrates than we estimated.
Spatiotemporal variation in juvenile survivorship in *Picea glauca*

To examine intraspecific variation in survivorship (which is of course lacking in Table 1), we collected 30 records from 11 studies of early survivorship in *Picea glauca* on mineral soil only (Ackerman 1957 (n = 3); Ackerman 1962 (n = 2); Arnott et al. 1971 (n = 1); Crossley 1955 (n = 4; we did not use his plots treated with unconventional scarifiers); Hughes 1967 (n = 1); Jarvis 1966 (n = 1); Lees 1970 (n = 9); Waldron 1966 (n = 1); Walker et al. 1986 (n = 1; we used only the point bar site); Youngblood and Zasada 1991 (n = 6); Zasada et al. 1992) (n = 1; only the 1970 crop with initial seed density as a personal communication from Zasada). These data are for sites ranging from Alaska to the Maritime provinces, and for the range of parent materials on which *Picea glauca* might normally be found (floodplain alluvium, till, fluvioglacial deposits, and Shield). Our desiderata in choosing studies was that they must (i) have the estimate of survivorship be based on initial viable seeds, (ii) follow survival for 3–6 years, and (iii) use mineral soil seedbeds in clearings (burn, cut) or shelterwoods.

The data are provided in Table 5. From eq. 3, we predict a mean survivorship of 0.05; the mean value for Table 5 is 0.082. While this is quite close to the prediction, nonetheless there is marked variation. The extreme values range as 0.0005 to 0.35, and only about 50% of the records are within twofold of the expectation (83% within fivefold). It is noteworthy that the distribution of the records is right skewed: the median survivorship is about half the value of the mean, and the distribution can be fairly characterized as a log-normal (Kolmogorov–Smirnov test; p < 0.05).

The source of this considerable variation is not regional. The coefficient of variation for Lees (1970, n = 9) at a single site is about the same as for the rest of the data set (n = 21). As Lees (1970) study is the only one where seeds are sown annually on scarified seedbeds, we can infer that the bulk of the variation in Table 5 is ultimately temporal, and a likely causative agent is annual variation in drought intervals.

**Discussion**

**Seed mass and juvenile survivorship**

It has long been argued that seed mass is related to disturbance regimes (reviewed in Harper 1977). Salisbury (1942) was perhaps the first to stress that the mean seed mass of tree species tended to be larger for “climax” than for “pioneer” species. Recent experiments such as those of Leishman and Westoby (1994) have shown that extremely low light levels favour survival of species with large seed masses. Here we have expanded these results to show that species that arrive in upland clearings or shelterwoods have juvenile survivorships proportional to seed mass and that survivorship is greater on low-porosity seedbeds than on high-porosity seedbeds. The low-porosity seedbeds are humus, exposed mineral soil, and well-decomposed logs. The high-porosity seedbeds are thick living mosses, leaf litter, and thick burnt duff layers.

Our initial dichotomization of seedbeds into low- or high-porosity types is clearly inadequate. Humus and mineral soil offer approximately equivalent survivorship for a given seed mass, while leaf litter is a good deal more inimical to survival, and logs engender intermediate survivorships. Deep moss (burnt or living) appears to be the worst possible seedbed (except with *Sphagnum* species, e.g., Groot and Adams 1994).

These results for survivorship must be taken as suggestive. In particular, the regressions for nonmineral seedbeds, while significant, are based on only five observations. In addition, the 26 observations in Table 1 were based on seeds that arrived immediately after the disturbance. The rapid accrual of leaf area in a developing stand will not only affect the quality of the substrate (a gradual change toward litter- and moss-dominated seedbeds) but also the availability of light (Fleming and Mossa 1995). Light availability has not been dealt with here, but clearly, it must be taken into account. Further, we have assumed that losses to granivore or fungi are density independent (this must be incorrect) and seed size independent. Both effects, if strong enough, would have a direct bearing on the estimate of the mass exponent that was assumed to scale seed mass to the mortality due to abiotic factors. For example, if losses to granivores are strongly dependent on deposited seed density (which, as a sowing recommendation, is inversely proportional to seed mass), then the exponents in Table 2 would all become lower.

What is the explanation for the observed mass exponents? All four regressions in Table 2 had exponents significantly different from 0.33. Length seemed a promising candidate for the dimension that scaled seed mass into survivorship, as it was conceptually easy to visualize a radicle elongating downward toward a retreating wetted horizon in the absence of rain, or a hypocotyl pushing up into the much higher light environment a few centimetres above the litter or moss. Further, evidence exists that length scales with mass to the power 0.33. We have regressed the data on aboveground length and seed mass of Grime and Jeffrey (1965) and Seiwa and Kikuzawa (1991) for their experiments with lowest light levels and found exponents of 0.34 and 0.30, respectively. Likewise, I. Charron and D.F. Greene (unpublished data) have found that the total length (radicle plus hypocotyl) scales with seed mass as 0.35. Yet the effect of length must be confounded by other factors (such as density-dependent losses).

A second possibility was the areal dimension, in which case geometric similitude predicts a scaling exponent of 0.67. However, neither two of the regressions for the site preparation studies have an upper 95% confidence band that includes 0.67. Note however that length and stem diameter do not scale as 1:1. For nonwoody mature dicots, length is proportional to diameter raised to the power 1.26 (Niklas 1994). Assuming that length is proportional to $n^{0.32}$ (as noted above), then a cross-sectional area of the germinant stem would be proportional to $n^{0.52}$. However, I. Charron and D.F. Greene (unpublished data with six species) found that conifer hypocotyl diameters were proportional to seed mass raised to the power 0.27. In any case, we clearly need a thorough study of the scaling of hypocotyl length and diameter and radicle length with seed mass for a large number of species (including hardwoods). Speculatively, hypocotyl cross-sectional area may be important for several reasons, such as buckling problems as the elongating hypocotyl lifts up litter, transpiration losses in the absence of rain, or
perhaps in the probability of dying from thermal heat stress on mineral soil in clearings. All these speculations are amenable to greenhouse and field tests.

We remind the reader that our results are site specific. They are based on the direct seeding literature, which itself is based on experimental sowings on sites where the species are capable of performing well. In effect, the results in Table 2 or eqs. 8–10 must be viewed as maximal values. For example, *Picea engelmannii* in Colorado had an observed survivorship of 0.0066 on scarified northern aspects where it is an abundant canopy tree, but no seedlings survived in any trials (scarified or undisturbed) on southern aspects (unless moisture loss was reduced by artificial shading) where the species is quite rare (Alexander and Edminster 1983).

Foresters have long known that exposed mineral soil was not the only seedbed type engendering high survivorship (e.g., the review of Arnott 1974); exposed humus and rotted logs are also good. They have focused on mineral soil exposure primarily because of the ease with which it can be created via mechanical disking or prescribed burning. The seedbeds where survivorship is low (Tables 3 and 4) are characterized by high porosity (deep moss in particular), and thus dry out rapidly. Logs have a survivorship intermediate between low-porosity and high-porosity seedbeds.

A major problem in defining the mineral soil and humus fraction is that it must change through time. In a small windthrow gap or a selection cut, the dispersal capacity of leaves is not exceeded and so one wonders how quickly the age-specific early mortality increases for a small-seeded species as litter and moss accumulate. By contrast, in larger cuts (shelterwood, clearcut) or natural disturbances (burns; windthrows exceeding 10 m diameter) there will be little leaf input from residual trees, but the developing stand can rapidly increase its leaf area index beyond 4 in as little as 10 years (Marks 1974). Increased decomposition rates in these large gaps may initially transfer part of the litter category to humus (where survivorship will be similar to mineral soil), but this effect may be overridden by the steadily increasing litter input and moss aggradation (on wetter sites). Continued annual sowing on initially scarified seedbeds shows that early age-specific mortality increases with time since disturbance, although the increase is modest (Lees 1970; Zasada et al. 1992; Fleming and Mossa 1995).

In short, our insistence on using categories (dictated by the nature of the data sets) leads to insoluble difficulties as we pose process-oriented questions. The most likely short-term solution is to continue in this empirical manner, e.g., one observes that stripcuts behave as if $w$ is a certain value for 6 years. But the ultimate goal should be to understand mechanistically the relationship between seed mass, germinant size, water availability, and the physical structure of seedbeds.

**Fecundity**

The fecundity argument (eq. 8) indicates that seed mass effects on seed production (inversely proportional) and survivorship (directly proportional) tend to cancel out. Taking the North American extremes for the seed mass values (0.0001 to 10 g; Schopmeyer 1974), this five orders of magnitude difference leads to only a 15-fold advantage for the smallest seed in a disturbance, which is 50% low-porosity seedbeds, or a 4-fold advantage for the largest seed when the seedbeds are purely high porosity types.

Note, however, that the interaction of gap size and dispersal capacity has been ignored so far. In small windthrow gaps or partial cuts, we can argue that differences in dispersal capacity are unimportant: the worst dispersing species can still adequately cover an adjacent 5–10 m diameter gap with seeds. But with large gaps, the density of seedlings in the clearing will be inversely proportional to clearing size and inversely proportional to seed mass (at least for wind-dispersed species). As shown by Greene and Johnson (1993), for aerodynamic reasons the larger seeds must have higher terminal velocities and thus be more poorly dispersed. (The scaling of dispersal capacity and seed mass for animal dispersal is not understood at present.)

**Variation in survivorship**

The coefficient of variation (standard deviation divided by the mean) was 1.1 for the *Picea glauca* records in Table 5. The source of this enormous variation cannot be shelterwoods versus clearings (they have similar mean survivals in Table 5), nor can it be regional climate differences. (The 9 records of Lees (1970) have a coefficient of variation almost equal to the remaining 19 records in Table 5.) We think that the bulk of the variation is temporal, as Lees’ (1970) repeated sowings on the same (rescarified) seedbeds indicate. The likely candidate for the source of this temporal variation is annual differences in drought intervals, especially as they affect mortality in the first year or two (when greater than 95% of the total prethinning mortality takes place).

It may be that topographic differences at the geomorphic scale (slope position and soil particle size will both affect available soil moisture) also make a considerable contribution to the total variation in Table 5, but it must be remembered that the investigators in Table 5 are deliberately trying to mute this effect. That is, they are trying to keep the site as constant as possible as they test for survivorship differences due to seedbed type and (or) scarification regime. What would be ideal for examining this question would be a sowing experiment along a transect oriented perpendicular to slope contours with light and seedbed (e.g., mineral soil) held (as much as possible) constant.

**Applications**

As we saw with the *Tsuga* and *Pinus banksiana* data sets, we can couple the expectations for survivorship and seed production and arrive at a satisfactory prediction of seedling density. But how often can we do this? The *Picea glauca* data set in Table 5 makes clear that the survivorship estimate will be within twofold of the real value about half the time but will err by more than fivefold about 15% of the time. If the majority of the variation is due to weather then of course there is little we can do to make predictions more precise.

If other species turn out to have, like *Picea glauca*, log-normal distributions of survivorship then we can of course develop confidence intervals for the expected survivorship on a given seedbed type. However, given that we have the same problem predicting seed production (i.e., we know the mean and the variance but not the value in any particular year: Greene and Johnson 1994), it seems simpler to draw
random values from the survivorship and production distributions in a computer simulation and then estimate the probability of exceeding a density criterion given, say, 5 years to invade the disturbance before the optimal seedbeds deteriorate. This approach can be extended to other situations (e.g., clearcut, stripcut, or natural burn) by the addition of a dispersal term (Greene and Johnson 1989, 1996). The only input variables required for the dispersal model are the dimensionless basal area density (basal area per area) to gauge source strength, terminal velocity (there are, now, published reports for many commercial species), and forest height. Thus, one need only measure the two variables that already are standard forestry measurements for volume calculations.

The results reported here may also serve as a rough guide to required sowing densities for noncommercial species. For example, if one wants to locally sow seeds of a rare species, then eq. 4 offers a guide to the expected relationship between sowing density and juvenile density. This, of course, assumes that paucity of seed is one of the important causes of the local rarity.

Finally, we should underscore our conclusion that seed mass plays a pivotal role in regeneration dynamics. Seed mass figures prominently in the equations for production (Greene and Johnson 1994), dispersal (Greene and Johnson 1989, 1993, 1996), and juvenile survivorship (present study). There is nothing new in this conclusion.

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