# Seed abundance versus substrate limitation of seedling recruitment in northern temperate forests of British Columbia

**Philip T. LePage, Charles D. Canham, K. Dave Coates, and Paula Bartemucci**

**Abstract**: We examine the influence of (*i*) the spatial distribution and abundance of parent trees (as seed sources) and (*ii*) the abundance and favourability of seedbed substrates, on seedling recruitment for the major tree species in northwestern interior cedar–hemlock forests of British Columbia, under four levels of canopy openness (full canopy, partial canopy, large gap, and clearcut). Substrate distribution varied with canopy openness, and substrate favourability was a function of both canopy openness and seedling species. Lack of suitable substrates was the predominant factor limiting seedling density under full canopies. Partial canopy and gap sites provided a broad range of favourable substrates in close proximity to parent trees, resulting in the highest observed seedling densities. There was much higher effective dispersion of seedlings away from parent trees in gaps than in the partially cut stands. Seedling dispersion to clearcut sites was poor with seedlings being tightly restricted to a narrow band along the forest edge. Thus, seedling recruitment in these forests was a reflection of the interaction between the abundance of seed and substrate favourability, and the relative importance of these factors varied significantly with canopy structure.

**Résumé** : Les auteurs ont examiné l'influence (*i*) de la répartition spatiale et de l'abondance d'arbres parentaux considérés comme sources de semences et (*ii*) de l'abondance et de la convenance du substrat des lits de germination, sur le recrutement des semis des principales espèces d'arbres dans les forêts de thuya et de pruche de la partie nord-ouest de l'intérieur de la Colombie-Britannique, en fonction de quatre niveaux d'ouverture du couvert (couvert complet, couvert partiel, grande ouverture et coupe à blanc). La répartition du substrat variait avec le degré d'ouverture du couvert et la convenance du substrat était fonction à la fois de l'ouverture du couvert et de l'espèce du semis. Le manque de substrats appropriés était le principal facteur qui limitait la densité des semis sous un couvert complet. Les plus hautes densités de semis ont été observées sous couvert partiel et dans les ouvertures qui procuraient un large éventail de substrats appropriés dans l'environnement immédiat des arbres parentaux. La dispersion des semis loin des arbres parentaux était beaucoup plus efficace dans les ouvertures que dans les peuplements partiellement coupés. La dispersion des semis dans les sites coupés à blanc était faible, les semis étant limités à une bande étroite située le long de la lisière de la forêt. Ainsi, le recrutement des semis dans ces forêts était le résultat de l'interaction entre l'abondance des semences et la convenance du substrat, et l'importance relative de ces facteurs variait de façon significative selon la structure de la canopée.

[Traduit par la Rédaction]

## Introduction

Tree seedling recruitment in forests is often characterized by dramatic spatial and temporal variation as a result of a broad suite of processes. These include synchronous temporal variation in seed production within populations (e.g., masting) (Godman and Mattson 1976; Graber and Leak 1992; Sork et al. 1993), highly localized seed dispersal in many tree species (Augspurger 1983, 1986; Hughes and Fahey 1988; Houle and Payette 1990), spatial and temporal variation in the abundance and foraging patterns of animal seed dispersers and consumers (Schupp 1988, Schupp et al. 1989), variation in climatic and microclimatic conditions that affect seed germination and early seedling survival, and spatial variation in substrate (seedbed) favourability and safe-site abundance (Bernsten 1955; Smith and Clark 1960; Eis 1967; Arnott et al. 1971; Minore 1972; Geier-Hayes 1987; Harmon and Franklin 1989; Anderson and Winterton 1996). Both theoretical and empirical models of forest dynamics demonstrate that interspecific variation in patterns of seedling recruitment can have important, long-term effects on forest dynamics (Ribbens et al. 1994; Clark and Ji 1995; Pacala et al. 1996). While many early models of forest dynamics assumed that seedling establishment was ubiquitous and independent of the local abundance of parent trees (e.g., the JABOWA–FORET class of models), Ribbens et al. (1994) have shown that for a suite of tree species in forests of eastern North America, spatial variation in seedling recruitment is a predictable function of the spatial distribution of parent trees in a stand. Eight of the nine species studied by Ribbens et al. (1994) had highly localized patterns of

**P.T. LePage,[1] K.D. Coates, and P. Bartemucci.** British Columbia Forest Service, Research Section, Bag 5000, Smithers, BC V0J 2N0, Canada.
**C.D. Canham.** Institute of Ecosystem Studies, P.O. Box AB, Millbrook, NY 12545, U.S.A.

[1]Corresponding author. e-mail: Phil.LePage@gems8.gov.bc.ca

seedling dispersion around parent trees. A spatially explicit model of forest dynamics (SORTIE) that incorporates these results demonstrates that localized patterns of seedling dispersion contribute to the maintenance of tree species diversity in these forests, particularly among late-successional species (Pacala et al. 1996).

Tree seedling recruitment is also a critical stage in forest regeneration following logging. Rates of natural seedling establishment can be low following intensive harvesting because of inadequate local seed sources, harsh microenvironmental conditions, and abundant populations of seed and seedling consumers (Steen et al. 1990; West 1992). As a result, in many parts of North America, tree-planting programs are required to achieve adequate rates of regeneration following clear-cutting. In British Columbia, Canada, recent changes in forest management practices have placed renewed emphasis on partial cutting and increased the focus on the use of natural regeneration.

We characterize seedling abundance of the nine major conifer and deciduous tree species of the interior cedar–hemlock (ICH) forests of northwestern British Columbia under a range of canopy conditions from full canopy, to partial canopy, to large canopy gaps, to clearcut. The nine tree species represent the dominant species of early to late-successional stands throughout the region and have a wide range of seed sizes, dispersal abilities, and substrate preferences (Burns and Honkala 1990). This study was designed to answer four main questions regarding natural regeneration in these forests: (*i*) what is the relationship between parent (seed source) abundance and proximity and seedling dispersion; (*ii*) how is seedling dispersion affected by different substrate (seedbed) types; (*iii*) do different species exhibit marked preferences for different substrate types; and (*iv*) does harvesting intensity affect substrate availability and seedling dispersion? We use methods similar to those of Ribbens et al. (1994) to characterize the relationships between seedling density and the spatial distribution and sizes of neighbouring parent trees. We have also modified the method to incorporate variation in the distribution and abundance of different seedbed substrates. Our analysis allows us to simultaneously quantify for the nine species, the effects of both seed source, and substrate favourability in determining the spatial distribution and overall abundance of seedling recruitment in forests subject to different management regimes.

## Methods

### Study area and species

Our research was conducted in sites used for the Date Creek Silvicultural Systems Study (Coates et al. 1997), located near Hazelton, B.C. (55°22′N, 127°50′W; 370–665 m elevation). The study area lies within the Moist Cold subzone of the Interior Cedar–Hemlock biogeoclimatic zone (ICHmc) (Pojar et al. 1987; Banner at al. 1993). Mature forests at Date Creek (130–140 years since fire) are dominated by western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) but are intimately mixed with western redcedar (*Thuja plicata* Donn ex D. Don in Lamb), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), lodgepole pine (*Pinus contorta* var *latifolia* Engelm.), hybrid spruce (the complex of white spruce (*Picea glauca* (Moench) Voss), Sitka spruce (*Picea sitchensis* (Bong.) Carr.), and occasionally Engelmann spruce (*Picea engelmannii* Parry ex Engelm.)), paper birch (*Betula papyrifera*

Marsh.), trembling aspen (*Populus tremuloides* Michx.), and black cottonwood (*Populus balsamifera* ssp. *trichocarpa* Torr. & Gray). Subalpine fir is commonly replaced by amabilis fir (A*bies amabilis* Dougl. ex Forbes) at higher elevations. In the old-growth stands (≥350 years since fire), western hemlock dominates with minor components of western redcedar, subalpine fir, and amabilis fir.

The understories of both mature and old-growth interior cedar–hemlock forests are typified by sparse shrub and herb development with a thick layer of moss, dominated by red-stemmed feather moss (*Pleurozium schreberi* (Brid.) Mitt.), step moss (*Hylocomium splendens* (Hedw.) Schimp. in BSG), knight's plume (*Ptilium crista-castrensis* (Hedw.) De Not.) and electrified cat's tail moss (*Rhytidiadelphus triquetrus* (Hedw.) Warnst.) (Banner et al. 1993). Preliminary examinations of these forests indicated that understory regeneration of all tree species appears to be severely limited on the undisturbed moss layer.

The replicated treatments applied in the Date Creek silvicultural systems study created a range of forest floor disturbance and overstory canopy structure that included undisturbed forest, two levels of partial cutting (light and heavy), and clearcut forests. In the light partial cutting treatment, approximately 30% of the stand volume was removed by cutting either single stems or small groups (3–10 trees). In the heavy partial cutting treatment, approximately 60% of stand volume was removed via large gaps (0.1–0.5 ha in size) evenly distributed across the treatment units and either single tree or small gaps in the forest matrix between the large gaps. The treatment units were approximately 20 ha in size, and the logging was conducted in the fall and winter of 1992–1993. A detailed description of stand composition and structure can be found in Coates et al. (1997).

### Transect and quadrat establishment

Within the experimental framework at Date Creek, seedling data were collected from line transects established in four types of sites: (*i*) full canopy sites; (*ii*) partial canopy sites (no distinct gaps); (*iii*) large, logging-created gaps (0.1–0.5 ha.); and (*iv*) a 20-ha clearcut. Full-canopy and partial-canopy sites were distributed in both old-growth and mature forests. Transects through these stands were composed of adjacent, 1-m$^2$ quadrats distributed along a randomly oriented transect in each site ($n = 2$ sites for full canopy, $n = 6$ sites for partial canopy). From one to three transects (oriented north–south and east–west) were used in each of five large gaps. Transects were established at two sites (north and south edges) in the clearcut. On each edge, quadrats were laid out in three parallel transects spaced 5 m apart and extending into the clearcut from the forest edge. Quadrats were adjacent to one another for the first 20 m from the clearcut edge, and then spaced every 4 m out to a distance of 100 m. Across all sites, we sampled 1730 quadrats distributed as follows: 200 quadrats in the two full-canopy sites; 800 in the six partial-canopy sites; 495 in the five gaps; and 235 in the clearcut (five plots landed on compacted skid roads and were removed from the data set). The spatial position of each quadrat was mapped using a Criterion™ Laser 400 survey transit.

### Substrate sampling

The area of each quadrat was classified by seedbed substrate type (described below). The percent cover of each substrate was visually estimated (with a 1% grid used for reference) in each quadrat to the nearest 5% for substrates present with >5% cover and to the nearest 1% for substrates occupying less than 5% of the quadrat. The substrate types were as follows.
(1) Mineral soil (MS): exposed mineral soil (created by logging disturbance or windthrow), or with a sparse layer of recently colonizing mosses (e.g., *Polytrichum* sp.).
(2) Fresh logs (FL): a solid, intact log or stump from logging (slash) or windthrow.

(3) Moss-covered logs (ML): partially decomposed logs on the forest floor covered by undisturbed moss.

(4) Rotten wood (RW): logs or wood considerably decomposed and incorporated into the forest floor but recently exposed as a result of logging disturbance.

(5) Organic material (OR): moss layer has been removed, and the humus layer exposed as a result of physical disturbance.

(6) Canopy moss (CM): a well-developed, undisturbed, thick feathermoss carpet (*Pleurozium schreberi*, *Hylocomium splendens*, *Ptilium crista-castrensis*, *Rhytidiadelphus triquestrus*).

(7) Gap moss (GM): same species composition as canopy moss but diminished from exposure to higher light levels in gaps; moss layer is thin and brownish-yellow but still relatively intact.

(8) Animal disturbance (AD): small patches of mixed organic material and mineral soil associated with squirrel middens and vole dens.

(9) Tree (TR): live tree stems.

(10) Rock (RK): exposed stones and rocks (individual or groups must be ≥1% of quadrat); may be caused by logging disturbance or windthrow.

Trees and rocks were not considered receptive seedbeds but did occupy space in quadrats and thereby decreased the area available for recruitment. In practice, a combination of canopy moss, gap moss, and (or) organic materials (depending on the site type) formed a matrix within which the other substrate types were distributed. The percent cover of the 10 substrates summed to 100% for each quadrat.

## Recruit sampling

Seedlings were censused in the spring of 1996 prior to that year's seedling germination and prior to leaf-out of the herb and shrub communities. To be considered a recruit in our study, a seedling must have survived one full year since germination (i.e. one growing season and over winter). Exact age determination on young conifer seedlings can be difficult, but the upper age limit of the seedlings included in the census (i.e., considered to be recruits) was effectively 3 years old, corresponding to the time since the treatment units were logged. To distinguish older seedlings from recruits, the morphological characteristics of advance regeneration were compared with those of known recruits. Differences in size (basal caliper), foliage appearance (color and alignment), bark appearance, and growth characteristics (lateral vs. leader extension) allowed us to readily differentiate between the two. The number of recruits (1–3 years old), by species and substrate type, were recorded in each quadrat. Individual sprouts from stumps of cut paper birch were counted as recruits. Aspen suckers were also counted as recruits, as were cottonwood seedlings that grew from rooted branch fragments. Not all nine species were present in all four site types (full canopy, partial canopy, gap, and clearcut). Approximately 26 000 recruits were censused (Table 1).

## Parent tree selection and stem mapping

We mapped the distribution of all parent trees with a diameter at breast height (DBH) of ≥15 cm that were within a specified distance of either a transect line or a discrete gap edge. The specified distance varied with species, being 30 m for amabilis fir, subalpine fir, hybrid spruce, lodgepole pine, trembling aspen, black cottonwood, and paper birch, and 20 m for western hemlock and western redcedar. The shorter distance for hemlock and redcedar was used because of their high stem densities (Table 1). Although seeds from these species are known to disseminate much greater distances than our stem-mapped area (e.g., Burns and Honkala 1990), these distances were deemed appropriate because (*i*) the majority of seed falls relatively close to the parent tree and (*ii*) in our study

the primary intent was to examine seedling recruitment (dispersion) in partially cut forests, not seed dispersal into large openings (e.g., Greene and Johnson 1995, 1996). In undisturbed stands and under partially logged canopies, all parent trees within the specified distance on either side and both ends of the seedling transect were recorded. At the gap sites, all parent trees within a 20 or 30 m wide band (depending on species, as above) around the gap edge were mapped. For the two clearcut sites, parent trees were mapped within a 70 m wide and 30 m deep section of adjacent forest (centered on the three parallel transect lines) (hemlock and redcedar 20 m × 50 m section). We recorded species, DBH, and location of each parent tree. The location of each parent tree was mapped using a Criterion™ Laser 400 survey transit. Approximately 4100 parent trees were stem mapped and measured (Table 1). Detailed descriptions of our study sites, including density, species composition, and basal area, can be found in Coates et al. (1997).

## Likelihood estimation of seedling dispersion functions and substrate favourability indices

We used the methods of Ribbens et al. (1994) to fit functions that predict the density (number/m$^2$) of seedlings ($R_i$) in quadrat $i$ using an equation of the form:

$$[1] \qquad R_i = \text{STR} \sum_{j=1}^{S} c_j f_j \sum_{k=1}^{T} \left( \frac{\text{DBH}_k}{30} \right)^2 \frac{1}{n} \, e^{-Dm_{ik}^3}$$

where STR (standardized total recruits) is the potential number of seedling recruits produced by a 30 cm DBH parent tree; $c_j$ and $f_j$ are the cover and favourability, respectively, of the $j = 1, 2, ..., S$ substrate types, where $S$ is the total number of substrate types; $\text{DBH}_k$ is the DBH (in centimetres) of the $k = 1, 2, ..., T$ parent trees, where $T$ is the total number of trees, within the specified radius of quadrat $i$; $n$ is a normalizer (described below); $D$ is a species-specific dispersion parameter and $m_{ik}$ is the distance (in metres) from the $i$th quadrat to the $k$th parent tree. The normalizer ($n$) (eq. 3 of Ribbens et al. (1994)) serves two functions. It reduces parameter correlation between STR and $D$ and scales the distance-dependent dispersion term so that STR is in meaningful units, i.e., the total number of seedlings produced in the entire seedling shadow of a 30 cm DBH parent tree.

The exponent (= 3) on the distance ($m_{ij}$) term allows the dispersion curve to have a distinct, convex "shoulder" at locations near the parent tree (see Fig. 2). Clark et al. (1998) set the exponent to a value of 2 for their analysis of seed dispersal in an eastern U.S. forest. Values of the exponent ≤1 would produce curves that are concave across all distances away from the parent tree. In a series of tests with our data from partial-canopy sites, we allowed the exponent to vary continuously across the range from 0 to 5. For eight of the nine species (all except hybrid spruce), the maximum likelihood values of the exponent were significantly greater than 1 (i.e., 95% lower support limits were greater than 1), and for four of the nine species, the exponents were significantly greater than 3. Our tests lead us to conclude that there was good empirical support for the presence of "shoulders" in the seedling dispersion curves, but allowing the exponent to vary did not produce a significant enough improvement in the goodness of fit of the models to convince us to add this level of complexity to the model.

Equation 1 is identical to eq. 6 of Ribbens et al. (1994) except for the addition of the summation term to incorporate the effects of $S$ different substrate types. The substrate summation term produces an effective substrate favourability index for a quadrat that is weighted by the cover and favourability of each substrate type in the quadrat (note that both $c_j$ and $f_j$ range from 0 to 1). This index then acts to reduce seedling density below the potential level set by STR. Our method calculates substrate favourability indices (that range from 0 for completely unfavourable to 1 for optimal

**Table 1.** Samples sizes of seedlings and parent trees (DBH ≥ 15 cm) in the four canopy types.

| Species | Full canopy | | Partial canopy | | Gaps | | Clearcut | |
|---|---|---|---|---|---|---|---|---|
| | Seedlings | Parents | Seedlings | Parents | Seedlings | Parents | Seedlings | Parents |
| Western hemlock | 313 | 543 | 13 664 | 1328 | 3252 | 463 | 97 | 61 |
| Western redcedar | 2 | 81 | 2012 | 581 | 1034 | 193 | 9 | 34 |
| Hybrid spruce | 0 | 45 | 599 | 120 | 1028 | 15 | 60 | 22 |
| Lodgepole pine | 0 | 18 | 7 | 12 | 36 | 17 | 1 | 0 |
| Subalpine fir | 0 | 0 | 7 | 14 | 14 | 68 | 0 | 1 |
| Amabilis fir | 1 | 7 | 967 | 113 | 0 | 0 | 0 | 0 |
| Black cottonwood | 0 | 2 | 61 | 36 | 64 | 49 | 0 | 0 |
| Trembling aspen | 0 | 5 | 386 | 25 | 241 | 5 | 106 | 1 |
| Paper birch | 0 | 12 | 564 | 172 | 1300 | 62 | 103 | 0 |
| Total | 316 | 713 | 18 267 | 2401 | 6969 | 872 | 376 | 119 |

**Note:** Seedlings were sampled in 200 quadrats in full canopy sites, 800 quadrats in partial canopy sites, 495 quadrats in gaps, and 235 quadrats in clearcut sizes.

substrates) by fitting models that predict the overall density of seedlings in a quadrat as a function of the area of each of the substrate types present in a quadrat and the distribution of parent trees. One of the benefits of this method is that it estimates substrate favourability independently of both the potential input of seeds to the quadrat (i.e. it takes the distribution of parent trees into account) and the abundance of specific substrate types.

As in Ribbens et al. (1994), we assume that the mean density of seedlings in a quadrat follows a Poisson distribution, in which the mean of the distribution is given by eq. 1. Clark et al. (1998) have recommended the use of a negative binomial distribution to fit similar functions for tree seed dispersal. In contrast to the Poisson distribution (for which the mean and variance are identical), the negative binomial distribution requires estimation of an additional parameter that allows the variance to vary as a function of the mean. Clark et al. (1998) found that this distribution provided a better fit to seed input data, particularly for heavier, animal dispersed seeds for which there was very high degree of clumping in the spatial distribution of seed rain. For better dispersed species, however, (i.e., those with lighter, wind dispersed seeds), their data closely approximated a Poisson distribution, and our species and data indicate even better dispersed patterns than their eastern hardwood species. We had independently considered the use of a negative binomial distribution and tested models based on this distribution but did not find significant improvements in model fits and, thus, have followed Ribbens et al. (1994) use of the simpler Poisson distribution.

We used likelihood estimation to fit the model (eq. 1) to our data. The models were fit independently for each species and in each of the site types (full canopy, partial canopy, gaps, and clearcuts) for which we had sufficient data. As in Ribbens et al. (1994), the likelihood ($L_i$) of observing $O_i$ seedlings given a density ($E_i$) expected under a Poisson distribution is

[2] $$L_i = \frac{e^{-E_i} E_i^{O_i}}{O_i!}$$

The log likelihood for a set of quadrats is the sum of the log of the likelihoods given by eq. 2. We solved for the parameters STR, $f_j$, and $D$(eq. 1) that maximized the log likelihood of the data set using simulated annealing with the Metropolis algorithm (Szymura and Barton 1986). We computed 95% support limits on the parameter estimates using the fact that $-2 \times$ log-likelihood is approximately $\chi^2$ distributed for large sample sizes. Because of the large number of parameters (10), we computed asymptotic confidence limits for individual parameters while holding all other parameters constant (at their best-fit values). The support limits were then computed by systematically varying the value of a given parameter

above and below its best-fit value until the log-likelihood of the model exceeded the critical $\chi^2$ value (with 1 degree of freedom). The goodness-of-fit of the models was assessed with product–moment correlations between the observed and expected seedling densities (SAS Institute Inc. 1987).

## Results

### Seedling dispersion and seed source limitation

*Full canopy sites*

Seedling density under a full canopy was extremely low (averaging 1.58 seedlings/m²), and was essentially restricted to western hemlock (313 of the 316 seedlings encountered in the 200 quadrats; Table 1). The seedling dispersion model for western hemlock failed to converge. The optimization procedure did not find a single, clear maximum likelihood solution, apparently because of the overwhelming number of hemlock parents around all of the quadrats. Given the very low estimated favourability of canopy moss substrate in the other site types (see below), and the dominance of this substrate type under full canopies (Fig. 1), substrate limitation appears to be a major factor in the very low rates of seedling establishment. Although there were parents of many other species present, especially western redcedar (Table 1), there were not sufficient numbers of seedlings in the full canopy sites to attempt model fitting.

*Partial canopy sites*

Seedling density in the partial canopy sites was the highest of the three site types where we were able to fit the model (Figs. 2–4), averaging 22.8 seedlings/m² for all species combined. Mean dispersion distances (MDD) were generally low for all species (11.3–23.8 m, Table 2). There was a slight but nonsignificant positive correlation ($r = 0.56$, df = 8, $p = 0.118$) between MDD and STR. Lodgepole pine, cottonwood and subalpine fir all had low mean dispersion distances (<15 m) and very low STR (<305 seedlings per 30 cm DBH parent tree) (Table 2). Aspen and hybrid spruce both had high mean dispersion distances (22 and 24 m, respectively) and high STR (2977 and 1721 seedlings per 30 cm DBH tree, respectively). The remaining four species had relatively low mean dispersion distances (12–16 m) but

**Fig. 1.** Percent cover of substrate types in (*a*) full canopy sites, (*b*) partial canopy sites, (*c*) gaps, and (*d*) clearcuts.
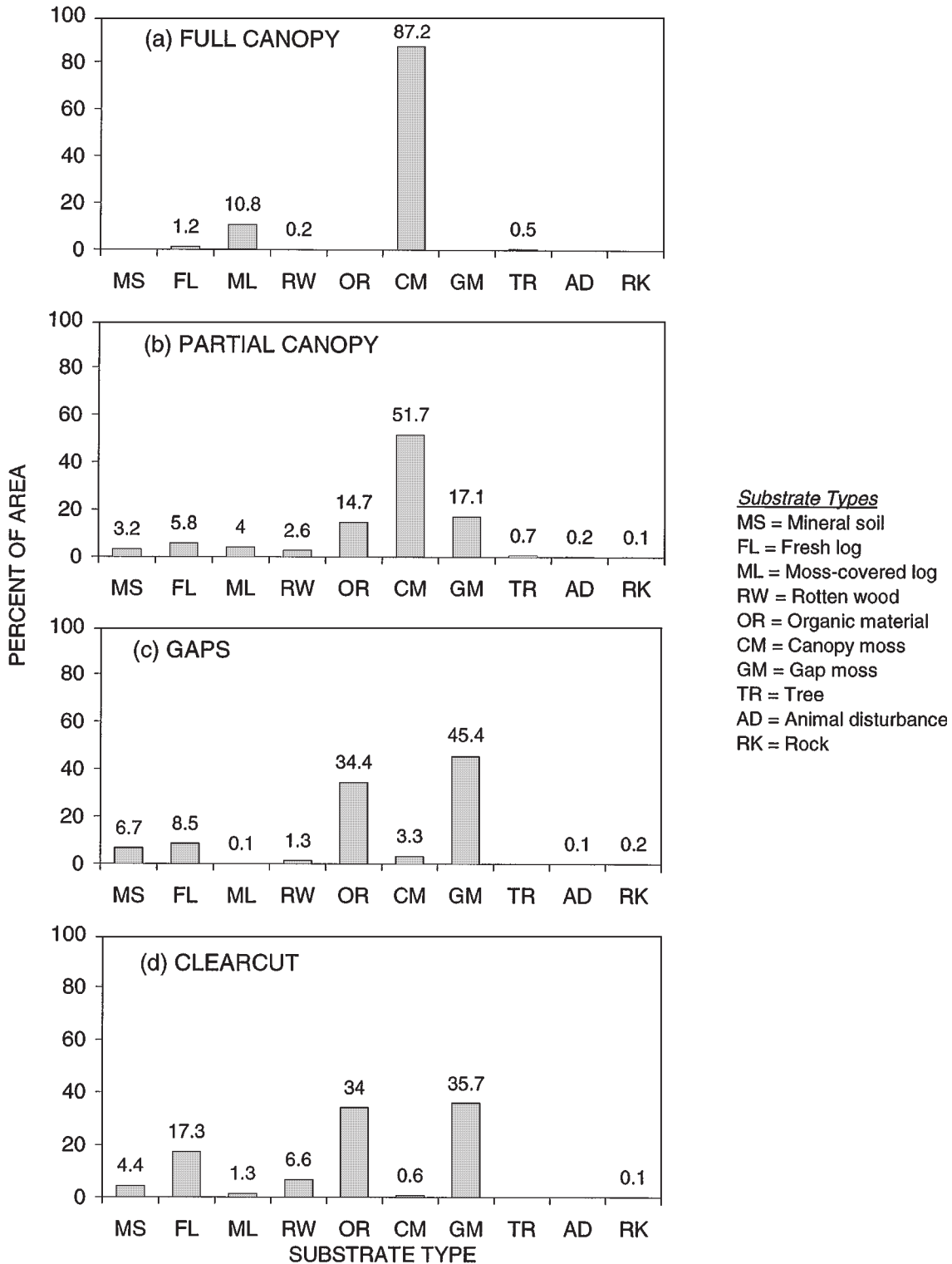


a wide range of seedling production per parent tree (STR 663–1932 seedlings per 30 cm DBH parent tree) (Table 2).

The maximum likelihood model produced good to excellent fits for five of the nine species ($r > 0.6$) and fair to poor fits for the remaining four ($0.2 < r < 0.36$) (Table 2). Hemlock had the best fit ($r = 0.87$), as a result of the wide range

of abundance of both parents and seedlings (Table 1). The poorer fits for lodgepole pine and subalpine fir ($r = 0.36$ and 0.27, respectively) were expected given the very small numbers of seedlings of those species in the data set (Table 1). We expect that the models would have produced better fits with more reasonable sample sizes. The fit of the model for

**Fig. 2.** Predicted seedling densities (m$^{-2}$, per 30 cm DBH parent), as a function of distance from parent tree (m) for partial canopy sites.
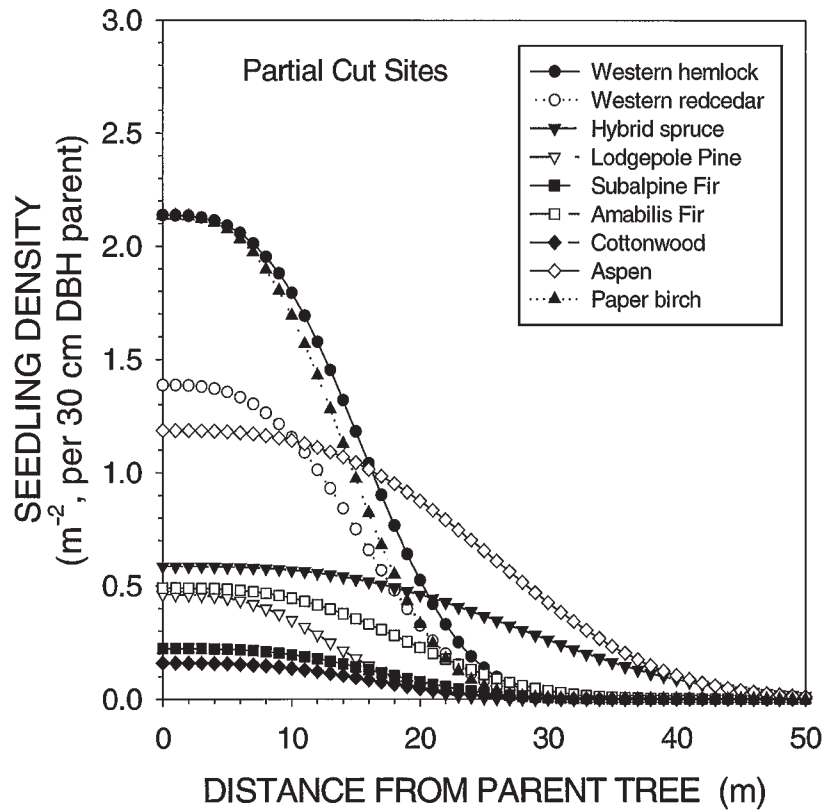


**Fig. 3.** Predicted seedling densities (m$^{-2}$, per 30 cm DBH parent), as a function of distance from parent tree (m) in gaps.
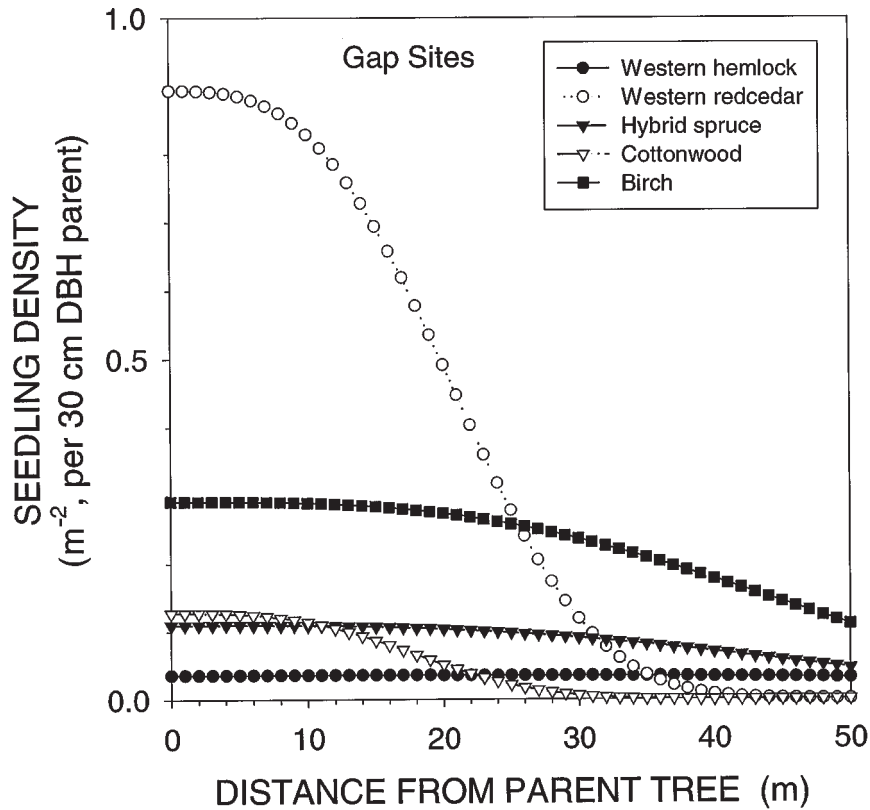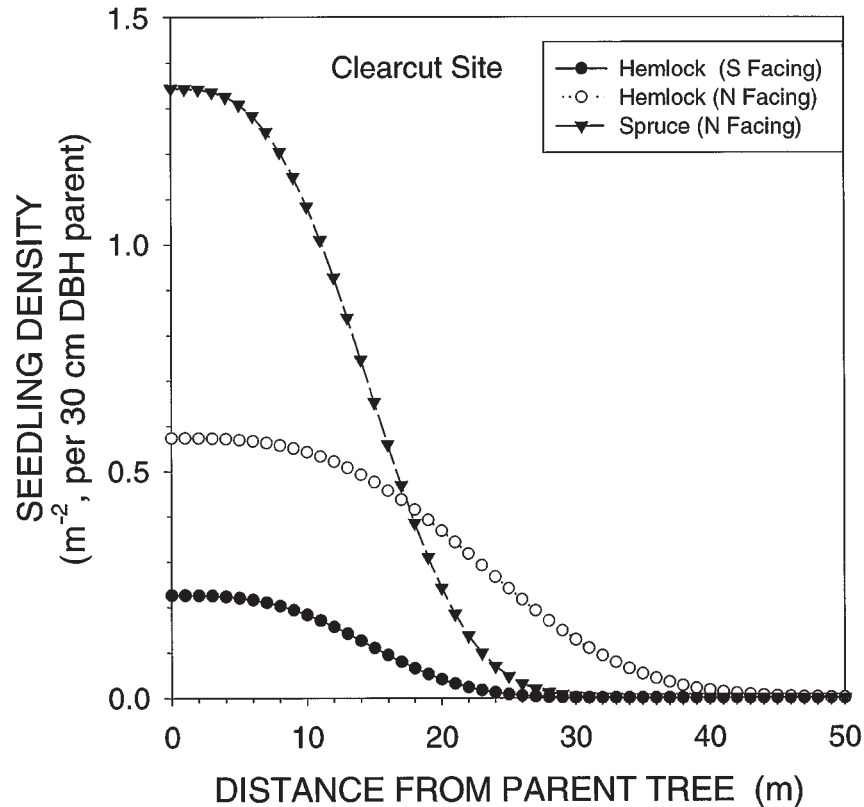
**Fig. 4.** Predicted seedling densities (m⁻², per 30 cm DBH parent), as a function of distance from parent tree (m) in clearcuts.



aspen was also only fair ($r = 0.30$), but some of the aspen recruits were root suckers that may have originated from the root systems of stems harvested prior to the census and, therefore, were not represented in the parent tree map. The model showed the poorest fit ($r = 0.21$) for cottonwood. This may be a reflection of both the low numbers of seedlings in the data set ($n = 61$) and the fact that some of the cottonwood seedlings may have originated from rooted fragments produced during logging. Once again, the parent trees were not necessarily all still present to be included in the parent tree map.

*Gap sites*

Overall, average seedling density in the gap sites (all species combined, 14.1 seedlings/m²) was 38% lower than in the partial canopy sites. Seedling dispersion models could be estimated for five species in gaps (Table 3, Fig. 3). Lodgepole pine and subalpine fir seedling densities were too low ($n = 36$ and 14 seedlings, respectively) for the models to converge. Although trembling aspen seedling densities (suckers) were reasonable, the models failed to converge. In many cases the suckers appeared to have originated from the root systems of stems that were harvested within the gap and, therefore, were not represented in the parent tree map. For the five species for which models could be fitted, MDDs were higher in the gaps than partial canopy sites (and for three of the five species, much higher), but the total numbers of recruits per parent tree (STR) were lower (Tables 2 and 3). The magnitude of the differences in seedling dispersion between partial-canopy and gap sites varied sharply among species. Western hemlock showed the largest change, with

an increase in MDD of almost 46 m (from 13 to 59 m) coupled with a 67% reduction in the number of established recruits per parent tree. Paper birch also showed a large increase in MDD (from 12 to 37 m) but only a small reduction in STR (Tables 2 and 3). The MDD of hybrid spruce in gaps was 63% higher than under partial canopies and there was a 31% decrease in STR. Western redcedar had a more modest 4.5 m increase in MDD and only a marginal increase in STR. Black cottonwood showed only a small increase in MDD (1.4 m) and a 1% decrease in STR. Again, many cottonwood recruits originated from rooted branch fragments, and the lack of difference in seedling dispersion between partially cut and gap sites was expected. Thus, in general, seedlings were more widely dispersed away from individual parent trees than in the partial-canopy sites (i.e., greater MDD), but there were fewer seedlings associated with each parent tree in gaps.

*Clearcut sites*

Seedling density in the clearcut was extremely low (1.6 seedlings/m²) and, interestingly, similar to the density observed under a full canopy. Only two of the six species (western hemlock and hybrid spruce) found in the clearcut had sufficient numbers of both parents and seedlings to attempt model fitting (Table 1). There were adequate numbers of aspen and birch seedlings, but only one potential parent (an aspen) was found standing within the 30-m search area. This is a limitation of our methodology for predicting recruitment into large clearcuts, especially for trees species whose seed is know to disseminate widely (i.e., paper birch). We fit separate models for the north- and south-facing clearcut sites

**Table 2.** Maximum likelihood estimates of dispersal parameters (STR and $D$ in eq. 1) and substrate favourability for seedling establishment in partial canopy sites.

| | Hemlock | Redcedar | Spruce | Subalpine fir |
|---|---|---|---|---|
| No. of quadrats | 800 | 620 | 402 | 216 |
| Likelihood | –11 092.96 | –1861.98 | –651.07 | –16.05 |
| $r$ | 0.871 | 0.675 | 0.649 | 0.272 |
| MDD | 13.2 | 13.1 | 23.8 | 14.5 |
| Normalizer | 903.9 | 884.1 | 2937.3 | 1092.4 |
| **Dispersal parameters** | | | | |
| STR | 1932.5 | 1225.7 | 1720.6 | 244.2 |
| | (1922.8–2338.3) | (1176.7–1293.1) | (1626.0–1952.9) | (87.9–682.6) |
| $D$ $(\times 10^4)$ | 1.757 629 | 1.817 046 | 0.300 026 | 1.323 024 |
| | (1.652–1.889) | (1.463–1.999) | (0.249–0.368) | (0.119–4.042) |
| **Substrate favourability** | | | | |
| Mineral soil | 0.995 | 0.678 | 0.946 | 0.991 |
| | (0.975–1) | (0.546–0.739) | (0.823–1) | (0.312–1) |
| Fresh log | 0.353 | 0.424 | 0.070 | 0.028 |
| | (0.297–0.383) | (0.214–0.475) | (0.006–0.175) | (0.028–0.028) |
| Mossy log | 0.058 | 0.024 | 0.054 | 0.550 |
| | (0.041–0.071) | (0–0.074) | (0–0.157) | (0.547–0.553) |
| Rotten wood | 1.000 | 1.000 | 0.994 | 0.966 |
| | (0.995–1) | (0.970–1) | (0.954–1) | (0.961–0.971) |
| Organic | 0.983 | 0.391 | 0.778 | 0.278 |
| | (0.978–1) | (0.342–0.424) | (0.774–0.782) | (0.276–0.279) |
| Canopy moss | 0.009 | 0.010 | 0.009 | 0.019 |
| | (0.009–0.012) | (0.006–0.013) | (0.009–0.009) | (0.019–0.019) |
| Gap moss | 0.129 | 0.480 | 0.391 | 0.017 |
| | (0.124–0.140) | (0.422–0.511) | (0.389–0.393) | (0.016–0.017) |
| Animal disturbance | 0.541 | 0.689 | 0.199 | 0.389 |
| | (0–0.544) | (0–0.882) | (0.198–0.200) | (0.387–0.391) |
| CV | 0.86 | 0.73 | 0.97 | 1.00 |

**Note:** Correlations between observed and expected seedling density ($r$), the mean dispersion distance (MDD) for seedlings, the normalizer in eq. 1, and coefficients of variation (CV) for substrate favourability, both across substrates and across species are also shown. The number of quadrats reported is the number for which at least one parent tree occurred within the search radius (see Methods). The 95% support limits are given in parentheses for all parameter estimates.

because of field observations that seedling distribution patterns differed significantly for the two exposures. Our results confirmed this observation (Table 4, Fig. 4). Hemlock seedling dispersion at the north-facing site was characterized by a greater mean dispersal distance (MDD 19.4 m versus 12.4 m for the south-facing site) and much greater total seedling production by individual parent trees (STR 1117 vs. 180 seedlings in the south-facing site). Hemlock and spruce seedling dispersion was much lower at the clearcut sites than in the gap sites. We would expect that conditions for seed dispersal in the clearcut sites were at least as favourable, if not more favourable, than in the gap sites (i.e., Greene and Johnson 1996). Our results indicate, however, that seedling establishment was fairly tightly limited to the edges of the clearcut site, particularly on the south-facing edge of the clearcut.

## Substrate distribution and favourability

The distribution of substrates varied significantly among the four site types ($p < 0.05$). The full-canopy sites were overwhelmingly dominated by canopy moss, with a small amount of moss-covered logs and very minor amounts of fresh logs (due to windthrow) and rotten wood (Fig. 1a).

The partial-canopy sites had a more diverse substrate mix but were again dominated by canopy moss (Fig. 1b). Gap moss and organic materials were the next most common substrates, but each occupied less than one third the area of canopy moss. Small amounts of fresh logs, moss-covered logs, mineral soil, rotten wood, and animal disturbance substrate types were recorded.

The gaps also had a diverse mix of substrates; however, they were dominated by gap moss, while canopy moss was dramatically reduced in cover (Fig. 1c) and restricted to a narrow band along the edge of the gaps. Organic materials were the second most prominent seedbed after gap moss, with lesser amounts of fresh logs and mineral soil, and negligible cover of rotten wood, animal disturbance, or moss-covered logs (Fig. 1c). The most common substrates in the clearcut sites were gap moss and organic materials (Fig. 1d). Fresh logs (logging slash) were more numerous in the clearcut than in other types and accounted for 17.3% of the area. Rotten wood, mineral soil, moss-covered logs, and canopy moss substrates were found in relatively small amounts (Fig. 1d).

In general, the rankings of substrate favourability (averaged across species within a site type) were similar in both

**Table 2** (*concluded*).

| Amabilis fir | Pine | Cottonwood | Aspen | Birch | CV |
|---|---|---|---|---|---|
| 331 | 173 | 324 | 325 | 362 | |
| –831.41 | –13.90 | –116.25 | –662.23 | –683.87 | |
| 0.642 | 0.359 | 0.211 | 0.301 | 0.620 | |
| 16.1 | 11.3 | 13.9 | 22.0 | 12.0 | |
| 1352.0 | 663.1 | 995.4 | 2510.0 | 748.9 | |
| **Dispersal parameters** | | | | | |
| 662.8 | 305.7 | 158.9 | 2977.2 | 1600.6 | |
| (616.4–702.6) | (97.8–739.9) | (110.4–220.1) | (2887.9–4555.1) | (1464.5–1736.6) | |
| 0.960 790 | 2.797 252 | 1.521 050 | 0.379 826 | 2.330 910 | |
| (0.956–0.966) | (0.196–6.406) | (1.513–1.529) | (0.289–0.467) | (1.946–2.914) | |
| **Substrate favourability** | | | | | |
| 0.789 | 0.039 | 0.013 | 0.996 | 0.899 | 0.567 |
| (0.785–0.793) | (0–1) | (0.013–0.013) | (0.961–1) | (0.894–0.903) | |
| 0.001 | 0.566 | 0.413 | 0.017 | 0.381 | 0.873 |
| (0.001–0.001) | (0–1) | (0.411–0.415) | (0–0.133) | (0.238–0.439) | |
| 0.305 | 0.008 | 0.771 | 0.180 | 0.800 | 1.053 |
| (0.303–0.307) | (0–0.687) | (0.767–0.775) | (0.078–0.861) | (0.740–1) | |
| 0.217 | 0.817 | 0.032 | 0.016 | 0.252 | 0.757 |
| (0.216–0.218) | (0–1) | (0.032–0.032) | (0–0.062) | (0–0.655) | |
| 0.274 | 0.155 | 0.310 | 0.013 | 0.001 | 0.933 |
| (0.273–0.276) | (0–0.419) | (0.308–0.311) | (0.013–0.013) | (0.001–0.001) | |
| 0.815 | 0.004 | 0.315 | 0.010 | 0.120 | 1.859 |
| (0.811–0.819) | (0–0.030) | (0.314–0.317) | (0.010–0.011) | (0.119–0.120) | |
| 0.064 | 0.462 | 0.950 | 0.781 | 0.687 | 0.744 |
| (0.064–0.065) | (0.460–0.464) | (0.945–0.954) | (0.778–0.785) | (0.683–0.690) | |
| 0.004 | 0.324 | 0.175 | 0.262 | 0.393 | 0.617 |
| (0.004–0.004) | (0.322–0.325) | (0.174–0.176) | (0–0.316) | (0.391–0.395) | |
| 1.06 | 1.01 | 0.90 | 1.37 | 0.73 | |

partial canopy and gap sites (Tables 2–4). While exposed mineral soil was rare in all site types (Fig. 1), it was the most favourable substrate (>0.6) for the majority of species. Canopy moss and fresh logs were consistently the least favourable substrates (Tables 2–4). The average favourability of all eight substrate types was higher in gaps than in partial-canopy sites (Tables 2 and 3).

Averaging substrate favourability across species, however, hides often dramatic variation among the species in their success at becoming established on specific substrates (Tables 2–4). For example, in contrast to the general pattern, mineral soil was unfavourable for establishment of both lodgepole pine and cottonwood in partial-canopy sites, while canopy moss appeared to be very favourable for amabilis fir establishment (Table 2). Rotten wood was a very unfavourable substrate for birch in the partial-canopy sites but a favourable substrate in gaps (Tables 2 and 3).

The two most common tree species in these forests, western hemlock and western redcedar, showed different patterns of preference for the major substrates in partial canopy and gap sites. In partial canopy sites, western hemlock had very low establishment on gap moss and a strong preference for organic substrates, while western redcedar had intermediate establishment on both substrates (Table 2). Canopy moss was an unfavourable substrate for both species. In gap sites, however, western hemlock showed a strong preference for both organic and gap moss substrates, while redcedar showed poor establishment on both (Table 3).

Using the partial canopy sites as a basis for comparison, all of the species showed a wide range of preference for different substrate types (CV of substrate favourability across substrate, by species, ranged from 0.73 to 1.37; Table 2). Among the conifers, hemlock and hybrid spruce had the least selective substrate requirements for seedling establishment, with three substrate types for which favourability indices were >0.75. Western redcedar and lodgepole pine had the most restrictive substrate requirements, with only one substrate each for which favourability was >0.75. Among the deciduous species, aspen had the highest variability in substrate preference (as measured by the coefficient of variation of favourability across substrate types; Table 2), with only two substrates (mineral soil and gap moss) for which favourability exceeded 0.3, and four substrate types on which favourability was less than 0.02. Paper birch, in contrast, was one of the least variable of all of the species in terms of substrate preference in partial canopy sites, with

**Table 3.** Maximum likelihood estimates of dispersal parameters (STR and D in eq. 1) and substrate favourability for seedling establishment in gap sites.

| | Hemlock | Redcedar | Spruce | Cottonwood | Birch |
|---|---|---|---|---|---|
| No. of quadrats | 499 | 499 | 499 | 477 | 499 |
| Likelihood | –3779.541 | –1059.222 | –957.008 | –162.658 | –1652.715 |
| $r$ | 0.507 | 0.723 | 0.687 | 0.468 | 0.541 |
| MDD | 59.4 | 17.6 | 38.7 | 15.2 | 37.3 |
| Normalizer | 21 075.7 | 1600.2 | 7801.0 | 1209.3 | 7236.0 |
| **Dispersal parameters** | | | | | |
| STR | 640.8 (634.4–807.5) | 1489.4 (1407.5–1601.1) | 1191.4 (1143.8–1328.4) | 157.1 (122.6–201.9) | 1916.0 (1887.3–2452.5) |
| $D$ (×10$^4$) | 0.011 358 (0.010–0.012) | 0.746 204 (0.631–0.847) | 0.069 281 (0.036–0.096) | 1.135 853 (0.761–1.653) | 0.077 576 (0.072–0.090) |
| **Substrate favourability** | | | | | |
| Mineral soil | 0.958 (0.953–1) | 0.916 (0.820–1) | 0.998 (0.908–1) | 0.999 (0–1) | 0.997 (0.978–1) |
| Fresh log | 0.967 (0.963–0.972) | 0.319 (0.249–0.418) | 0.042 (0–0.203) | 0.029 (0–0.565) | 0.435 (0.432–0.437) |
| Mossy log | 0.700 (0.697–0.704) | 0.048 (0–0.191) | 0.307 (0–1) | 0.867 (0–1) | 0.503 (0.501–0.506) |
| Rotten wood | 0.687 (0.683–0.690) | 0.509 (0.186–0.766) | 0.978 (0.362–1) | 0.258 (0–1) | 0.786 (0.782–0.790) |
| Organic | 0.913 (0.908–0.918) | 0.179 (0.149–0.210) | 0.574 (0.516–0.640) | 0.616 (0.412–0.822) | 0.865 (0.861–1.003) |
| Canopy moss | 0.894 (0.889–0.898) | 0.001 (0–0.012) | 0.123 (0–0.155) | 0.079 (0–0.404) | 0.410 (0.408–0.412) |
| Gap moss | 0.925 (0.920–0.929) | 0.213 (0.187–0.244) | 0.589 (0.586–0.592) | 0.666 (0.560–0.786) | 0.998 (0.993–1) |
| Animal disturbance | 0.830 (0.826–0.834) | 0.609 (0–1) | 0.986 (0.981–0.991) | 0.979 (0.974–0.984) | 0.878 (0.874–0.883) |

**Note:** Correlations between observed and expected seedling density ($r$), the mean dispersion distance (MDD) for seedlings, and the normalizer in eq. 1 are also shown. The number of quadrats reported is the number for which at least one parent tree occurred within areas mapped along gap margins (see Methods). The 95% support limits are given in parentheses for all parameter estimates.

only one substrate with a favourability index <0.10 (Table 2).

## Discussion

### Seed abundance versus substrate limitation of seedling recruitment

Our results indicate that seedling recruitment in these forests is a reflection of the interaction between seed source availability and substrate favourability and that the relative importance of these two factors varies in forests with different canopy structure and management histories. The undisturbed stands (full canopy) were dominated by a thick mossy understory (Fig. 1*a*) that appears to be highly unfavourable for seedling establishment of virtually all tree species. Recruitment in the undisturbed stands was virtually nonexistent for all species except western hemlock, which established in very low numbers despite a large number of parent trees (average of 522 stems/ha). Based on our work in these northern interior forest types, we do not believe light levels in undisturbed stands, varying from 5 to 15% full sunlight (Wright et al. 1998*b*, K.D. Coates, unpublished data; C.D. Canham, unpublished data) are low enough to significantly inhibit seedling establishment. Since areas with a diversity of substrates and similar densities of hemlock parents (on the edges of gaps) had more than 10 times the number of recruits, the lack of a suitable substrate appears to be the immediate factor limiting seedling recruitment under undisturbed canopies.

The partial-canopy sites had a more diverse mix of substrate types, and substrates that were very favourable for seedling establishment were present in most quadrats (Fig. 1*b*). As a result, overall seedling densities were higher than in the full-canopy sites. Despite the increase in the availability of suitable seedbeds, the mean dispersion distances of seedlings for all nine species were still generally low (11–24 m). Therefore, seedling densities of any individual species are predicted to be low in portions of stands where parent trees are not in the immediate neighbourhood (i.e., within 25 m). There was clearly the potential for seed source limitation of seedling establishment in the partially logged sites, particularly for the rarer species (pine, amabilis and subalpine fir, cottonwood, aspen, and birch). We conclude that substrate favourability was primarily responsible for the high overall seedling density and that seed source limitation was the primary factor responsible for the high spatial variation in seedling recruitment observed within these sites. It is recognized that different substrates may vary in their ability to capture and hold seed (e.g., Chambers et al. 1991), and this is implicitly included in our analysis of seedbed favourability.

The consistently low seedling dispersion distances in the partial-canopy sites are presumably a reflection of low seed dispersal distances because of the presence of a forest canopy that not only alters the flow patterns and speed of the wind, but also provides abundant physical barriers to seed dispersal. Although many studies have shown seed (not seedlings) to disperse long distances, particularly into large openings (Isaac 1930; Ronco 1970; Bjorkbom 1971; Dobbs 1976; Greene and Johnson 1996), our seedling (not seed) dispersion patterns covered much shorter distances. Both the

**Table 4.** Maximum likelihood estimates of dispersal parameters (STR and *D* in eq. 1) and substrate favourability for seedling establishment in clearcut sites.

| | Hemlock, south facing | Hemlock, north facing | Spruce, north facing |
|---|---|---|---|
| No. of quadrats | 117 | 118 | 118 |
| Likelihood | –195.434 | –86.064 | –259.907 |
| *r* | 0.460 | 0.520 | 0.266 |
| MDD | 12.4 | 19.4 | 12.4 |
| Normalizer | 796.4 | 1948.0 | 791.9 |
| **Dispersal parameters** | | | |
| STR | 180.1 (123.4–188.1) | 1116.9 (899.1–1446.4) | 1063.8 (835.1–1111.7) |
| D ($\times 10^4$) | 2.125 03 (2.115–2.157) | 0.555 528 (0.553–0.558) | 2.143 364 (2.133–2.165) |
| **Substrate favourability** | | | |
| Mineral soil | 0.974 (0.263–1) | 0.689 (0.685–0.692) | 0.845 (0.516–1) |
| Fresh log | 0.328 (0–0.586) | 0.037 (0.037–0.037) | 0.842 (0–1) |
| Mossy log | 0.410 (0–1) | 0.045 (0.045–0.046) | 0.718 (0–1) |
| Rotten wood | 0.693 (0.347–1) | 0.200 (0.199–0.201) | 0.715 (0.06–1) |
| Organic | 0.718 (0.147–0.808) | 0.007 (0.007–0.007) | 0.910 (0.692–1) |
| Canopy moss | 0.435 (0–1) | 0.076 (0.075–0.076) | 0.589 (0–0.898) |
| Gap moss | 0.002 (0–0.068) | 0.100 (0.099–0.100) | 0.987 (0.750–1) |
| Animal disturbance | 0.973 (0.968–0.978) | 0.417 (0.415–0.419) | 0.695 (0–1) |

**Note:** Correlations between observed and expected seedling density (*r*), the mean dispersion distance (MDD) for seedlings, and the normalizer in eq. 1 are also shown. The number of quadrats reported is the number for which at least one parent tree occurred within the area mapped for potential parent trees (see Methods). The 95% support limits are given in parentheses for all parameter estimates.

estimated MDD and STR for the six conifers and three deciduous species included in our study are generally higher than those reported by Ribbens et al. (1994) for two conifer and seven hardwood tree species under closed canopy conditions in forests of the northeastern United States. We attribute the generally higher dispersion distances for our western species to several factors, including greater average tree heights and lower mean seed masses. The differences in STR may be a function of many factors, including inherent differences in fecundities of the species and variation in the importance of processes such as seed predation in the different forest types.

The gap sites also contained a wide diversity of substrate types that were favourable for seedling recruitment (Fig. 1*c*). In general, seedling dispersion distances in gaps were higher (and in some cases, much higher) than in the partial-canopy sites (Table 3). Our results, however, indicate that, while seedlings were able to establish at much greater distances from parents along the gap edge, the available substrate was generally less hospitable, and individual seedlings had a lower chance of becoming established (i.e. lower estimated STR). It is likely that the broader range of variation among species in dispersion distances in gaps is a better reflection of the natural variation in potential seed dispersal among species (because of factors such as seed size, wing size, and seed weight). In the gap sites, both substrate availability and seed dispersal (and perhaps microclimate) combined to regulate spatial variation in seedling recruitment. This finding is consistent with that of a companion study that observed a strong effect of substrate and microclimate on seedling germination and survival in study gaps at the Date Creek research area (Wright et al. 1998*b*).

Substrate diversity in the clearcut was similar to the gap sites; however, mean seedling dispersion distances and both the density and diversity of seedlings were dramatically lower than in partial-canopy and gap sites (Table 4). Substrates favourable for recruitment in both partial canopy and gap sites were still relatively common in the clearcut sites, yet seedling dispersion distances were quite limited. Since seeds of species such as hemlock, redcedar, and spruce have been shown to disperse far out into openings (Isaac 1930; Clark 1970; Coates et al. 1994), it is likely that a harsh microclimate was responsible for the very low overall seedling densities and the steep declines in seedling densities at distances greater than 20 m from a clearcut edge. This interpretation is supported by the fact that the dispersion distances of seedlings from the exposed (south-facing) north edge of the clearcut were lower than from the south edge (north facing) (Fig. 4).

This study is a component of a larger undertaking to develop an integrated simulation model (based on SORTIE; Pacala et al. 1996) of the dynamics of these northern temperate forests (Kobe and Coates 1997, Wright et al. 1998*a*, Canham et al. 1999). Throughout this work, we have tried to keep the model and its subcomponents simple and to use as few parameters as possible. The functional form of the seeding dispersal equation we use is simple and flexible in shape. Many other functional forms could potentially be used to predict regeneration abundance based on parent abundance and seedbed substrate. The functional forms we use to predict seedling dispersion are phenomenological (at least in clearcuts) but provide a good fit to the data. The addition of more parameters did not sufficiently improve the goodness of fit to justify the added level of complexity to the model.

### Summary and management implications

The results of this study have important implications for management of these high-latitude, mixed-species forests. If natural regeneration is to be a reliable method of reforestation

after logging, it is important to understand the effects of management practices on seed tree distribution, substrate availability, and seedling establishment. Our study has shown that some level of ground cover disturbance is required to break up the thick moss layer that severely restricts seedling establishment in undisturbed interior cedar–hemlock forests. The forest floor disturbance associated with partial cutting creates a diversity of favourable substrates for seedling establishment. Effective seedling dispersion distances, however, are still relatively limited in partially cut stands; therefore, a good distribution of seed trees will be required to ensure a mix of species in natural seedling regeneration. Cutting more trees to form distinct gaps removes physical barriers to seed dispersal from those trees bordering the gap, resulting in higher effective seedling dispersion distances but, at the same time, slightly reducing the favourability of conditions for establishment of individual seedlings. Clear-cutting appears to shift recruitment control away from seed availability and substrate favourability and brings microclimate effects into play. Our sampling in clearcuts was done relatively close to the clearcut edges (<100 m); however, despite this close proximity to a seed source and a diverse mix of substrates, seedling densities were extremely low.

The effects of management practices on seedling recruitment represent just one facet of a complex suite of factors that need to be considered to predict the effects of management on long-term forest dynamics. The greatest rates and diversity of seedling recruitment occurred in the partially logged sites, where there were abundant seed sources and favourable substrates as well as moderate seedling dispersion distances for all species (Tables 2 and 3). On the other hand, the nine species studied here differ widely in their shade tolerance (Kobe and Coates 1997), and the eventual success of canopy recruitment by seedlings will depend on the presence of a suitable range of light environments. Thus, a silvicultural system that combines partial harvesting with the creation of large (0.1–0.5 ha) gaps appears to hold the greatest promise for maintaining the diversity of both seedling and canopy recruitment in these forests.

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