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Age and Size Structure of Gap-Dynamic, Old-Growth Boreal Forest Stands in Newfoundland

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The age and size structure of trees in old *Abies-Picea-Betula* forests on Newfoundland's Great Northern Peninsula were examined. It was hypothesized that the size and age structure of both the tree and regeneration "strata" of these stands display the complex structural heterogeneity characteristic of classic, self-regenerating, uneven-aged old-growth stands, and that the development and dynamics of such structures occur over long periods of time. With all tree species combined, dbh (diameter at breast height) and height distributions exhibited a strong reverse-J character, with well-defined, semi-logarithmic rotated sigmoid height and size frequencies. Seedling height and basal diameter frequency distributions were reverse-J in character. Live tree ages for all species, except white birch (*Betula papyrifera* Marsh), ranged from 25 to 269 years, and were characterized by all-age frequency distributions. Tree age and size were poorly correlated. On average, balsam fir (*Abies balsamea* (L.) Mill.) required 62 years to reach breast height (1.3 m), with black spruce (*Picea mariana* (Mill.) B.S.P.) and white spruce (*Picea glauca* (Moench) Voss) requiring 40 and 48 years, respectively. Total age of dead standing trees ranged from 45 to 232 years. Reverse-J age frequencies characterized the seedling bank, with balsam fir seedlings present in nearly all age classes up to 110, 120 and 85 years in three sample stands. Seedling size (height and basal diameter)-age relationships were characteristic of decades-long suppression. The combination of tree and seedling bank size and age structure provide strong evidence of quasi-equilibrium, small-scale, gap dynamic old-growth boreal forest stands.

Keywords boreal forests, old-growth forests, gap dynamics, age and size structure, rotated sigmoid, Newfoundland

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1 Introduction

Within any forest landscape, the relative proportion of the various stages of stand structural and/or stand successional development depends to a large extent on the periodicity, magnitude and spatial and temporal stochasticity of any particular disturbance event. Forests dominated by relatively major disturbances (fire, insects, wind) are often viewed as a mosaic of relatively discrete seral or development patches of varying age and size structure. Non-equilibrium patch dynamics have become the dominant ecological paradigm by which to understand the relationship between forest- and stand-level structure and disturbance (Pickett and White 1985, Wu and Loucks 1995). Until quite recently, this heuristic model has dominated our understanding of boreal forests.

For forests dominated by small-scale gap dynamics, however, the patch model is less applicable. Rather than a patchy mosaic, the forest may be viewed as a relatively homogeneous, old-growth forest with continuous forest cover, considered more as a fine-grain matrix, the complex vertical and horizontal structure of which is maintained by gap disturbance at the single tree or small group level (Kuuluvainen 1994, McCarthy 2001). This stage of forest development is generally termed "old-growth" (Franklin and Spies 1991, Oliver and Larson 1996). Other designations include the traditional term "climax" (Whittaker 1953), "shifting mosaic steady state" (Bormann and Likens 1981), "steady state phase" (Peet and Christensen 1980), and "shifting gap phase" (Spies and Franklin 1996).

From a structural perspective, old-growth forests generally have the following "classic" characteristics: 1) reverse-J (rotated sigmoid) tree diameter distributions, 2) uneven-aged structure with trees approaching maximal known ages, 3) standing dead trees (snags) in various stages of decomposition, 4) accumulation of coarse woody debris in all stages of decomposition, 5) relatively continuous vertical distribution of foliage (complex, "multi-storied" tree canopies), 6) small canopy gaps created by fungal-mediated individual tree mortality 7) quasi-equilibrium standing tree biomass, and 8) spatially heterogeneous, clumped regeneration in response to canopy gaps (Franklin and Spies 1991, Oliver et al. 1996, Wells et al. 1998).

The discovery of limited areas of very old boreal forest in Newfoundland raises the question of how they may be sustainably managed. They have very slow gap dynamics and have high biodiversity, conservation and wilderness attributes. Presently, such forests are clear cut with no foreseeable recovery of the cutover stands into the old growth condition for centuries to come. If classical selection cutting is to be used, then the dynamics of reverse-J stand structures including the ages and release of advanced growth need to be understood.

The purpose of this retrospective study was the characterization of the size and age structure of both the tree and regeneration "strata" of selected old-growth boreal forest stands that have most likely developed in the absence of exogenous, stand-level disturbance events. It was hypothesized that both the size and age structure of these stands display the complex structural heterogeneity characteristic of classic, self-regenerating, uneven-aged old-growth stands. Insights gained from an analysis of stand age and size structure are used as proxy evidence to infer the importance of small-scale gap dynamics in these old boreal stands.

This study forms part of a larger study that examined the relationship between type of forest disturbance and the associated stand- and landscape-level structure of two primary forest areas that have no history of forest harvesting. One study area has a long, recorded history of insect herbivory with the forest landscape dominated by a well-defined chronosequence of naturally regenerated stands. The other study area, the subject of this paper, has no recorded fire or insect history and is dominated by a homogeneous, fine-grained forest landscape of old stands (121+ years) with no evidence of regenerating, even-aged stands.

2 Material and Methods

2.1 Study Area

The 225 km^2 study area lies within the 1048 km^2 Main River watershed located at the southern end of Newfoundland's Great Northern Peninsula (Fig. 1). Regional geology is dominated by the 9000 km^2 Long Range Inlier (bounded by

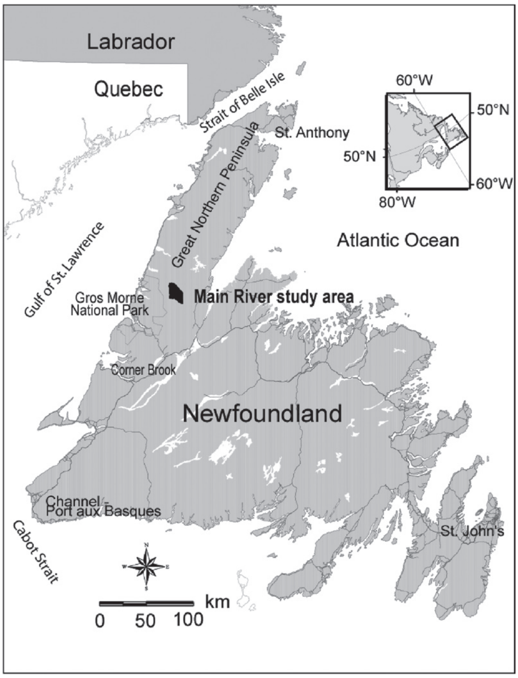

Fig. 1. Map of Newfoundland, Canada, showing the location of the Main River study site.

latitudes 49°20´N and 50°50´N), a massive of Proterozoic (1550 Ma) crystalline rocks forming the core of the northern Long Range Mountains (Owen 1991).

The location of the study site at moderately high elevations (300–600 m) on the eastern flank of the Long Range Mountains exposes it to the cold, ocean environment of the northeast Atlantic Ocean, and therefore determines a meso-climate distinctive from that of the western or Gulf of St. Lawrence side of the Long Range Mountains (C. Banfield, personal communication, 2001). Two climatic zones exist in the watershed: 1) the "east coast hinterlands" climatic zone located throughout the lower elevations of the watershed; and 2) the "western hills and mountains" zone covering the higher elevations of the watershed (Banfield 1983). The lower reaches of the watershed are less wet (900 to 1000 mm per year), with warmer and sunnier summers than the higher elevations of the watershed, where annual precipitation levels may range from 1300 to 1500 mm. Winters are cold throughout the watershed. Higher elevation snow accumulations generally exceed 350 to 400 cm per year. Snow generally falls from October to May, with small accumulations (~2 cm) in both June and September. Persistent snowbanks into the month of June are not uncommon. Average July and August temperatures are around 14 °C. Winters are cold with average January and February temperatures of –11 °C and –13 °C degrees, respectively (K. Rollings, Newfoundland and Labrador Department of the Environment, personal communication, 2002). Cool, late springs with sea ice persisting into mid-May characterize the coastal regions.

Forests of the Main River watershed form part of the Northern Peninsula boreal forest region B.29 (Rowe 1977) and the Eastern Long Range subregion of the Northern Peninsula Ecoregion (Damman 1983). The generally open, deep-crowned, slow-growing, old-growth forests dominated by balsam fir (*Abies balsamea* (L.) Mill.), with significant occurrence of black spruce (*Picea mariana* (Mill.) B.S.P.), flank the eastern slopes of the Long Range Mountains to an elevation of 450 to 500 m. Most of the mesic, generally mid-slope forest sites are balsam fir-black spruce moss-rich forest types that include *Pleurozium*-balsam fir, *Hylocomium*-balsam fir, *Gaultheria*-balsam fir and *Sphagnum*-balsam fir (Damman 1967, Meades and Moores 1994). Both white birch (*Betula papyrifera* Marsh) and white spruce (*Picea glauca* (Moench) Voss) occur throughout the area, tending for the most part to occur on the better sites. Peatlands cover 4.7% of the study area and consist mostly of slope bogs (Wells and Pollett 1983).

Soils are typically imperfectly to moderately well drained, Gleyed Humo-Ferric, Ferro-Humic Podzols (Silver Mountain Association, dominant association >50%) developing on exceedingly to excessively stony, moderately coarse-textured shallow glacial till derived from granite, granitic gneiss and schist (Kirby et al. 1992). Landforms are characterized by morainal veneer over hummocky and rolling bedrock.

2.2 Plot Selection, Layout and Sampling

An extensive aerial and ground reconnaissance combined with a review of aerial photography, provincial forest inventory cover type maps, and data from both temporary and permanent sample plots established by the Newfoundland Forest Service, confirmed a remarkably homogeneous, fine-grained forest landscape. Ninety-eight percent of the study area was covered by old-growth stands of age class 7 (121+ years) with no evidence of regenerating stands (stands with mean height ≤6.5 m).

The range in forest types was determined by an analysis of Geographic Information Systems (GIS)-based forest cover types produced by the Newfoundland Forest Service (1978 photography, 1980 fieldwork) for the 1:50 000 Main River topographic sheet (12 H/14) (Energy Mines and Resources Canada 1990). Stand types of poor, medium and good site quality occupied 35, 64 and 1% of the productive forest covered by the Main River map. Sampling was confined to the three stand types of medium site quality that occupied 84% of all medium stand types; bF542M, bFbS542M and bF552M (11 583 ha or 54% of the total productive forest area; bF = balsam fir, bS = black spruce). Tree species comprise ≥25% of the total stand basal area. One species indicates that 75–100% of the total stand basal area is comprised of that species. Two species indicate that 50–75% of the total stand basal area is comprised of the first species, with the remainder made up of the second species. The first number indicates stand age class; 5 = 81+ years at time of inventory. Under the current age classification 5 = 81–100 years. Note that the vast majority of stands formerly classified as age class 5 have been reclassified as age class 7 (121+ years). The second number indicates stand height (m); 4 = 9.6–12.5 m and 5 = 12.6–15.5 m. The third number indicates crown density (%); 2 = 51–75%. M = medium site quality (Newfoundland Forest Service 1993). Using these criteria, only balsam fir-dominated stands of medium site quality growing on mid-slope zonal sites were sampled.

Prospective study sites were located in the field using 1:12 500 colour aerial photographs and Newfoundland and Labrador Forest Service forest cover type maps. Random sampling from a pre-surveyed population of stands would have been preferred. However, given the general inaccessibility of the Main River study area, and the desire to sample stands within a specific range of site variability, sample plots were chosen arbitrarily without preconceived bias (McCune and Grace 2002). After preliminary reconnaissance, 13 stands (designated as M1–M13) were selected across the widest possible extent of the accessible watershed (Fig. 2). Criteria for plot selection included the following: 1) structurally homogeneous zonal sites (sensu Poore 1962) with no history of logging or extensive windthrow, 2) absence of stream channels or interior forest fens, and 3) sufficient distance from roads such that no effect of road opening was evident (i.e. windthrow). Once a suitable stand was located, the first corner of a 50 m × 50 m plot was randomly located. Each plot was laid out using a hand-held compass and a 50 m measuring tape (Newfoundland Forest Service 1993). To facilitate tree measurements, each plot was divided into approximate 5 m × 5 m

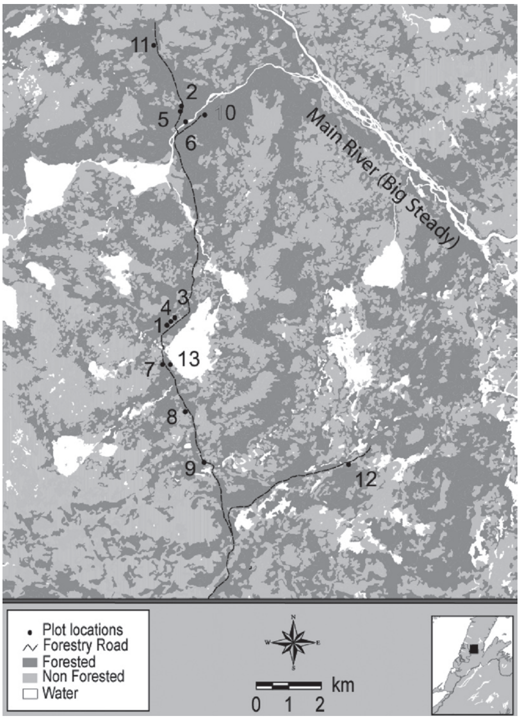

Fig. 2. Map of Main River study area showing location of sample plots. Non-forested areas include peatlands and heathlands, as well as scrub forests not capable of producing 30 m^3 gross merchantable volume ha^{-1} at rotation age.

sections. All 13 plots were located in the upper reaches of the watershed at elevations ranging from 350 to 490 m.

In the 13 plots, all live and dead trees >1.3 m in height were flagged, numbered, identified to species and measured for mortality status (dead/alive), caliper diameter outside bark at breast height (dbh; 1.3 m above ground) (0.1 cm), and other distinguishing features such as extent of moose (*Alces alces* Americana) browse, presence of layering and stem forking. For heavily browsed and twisted trees, dbh was recorded just below the extensive forking and deformation. In three plots arbitrarily designated for stand reconstruction, all live and dead trees >1.3 m in height were felled at a point as close to the ground as possible. Layered trees were cut as far as possible along the length of the lower bole. Tree length (height) (0.1 m) was measured with a 30 m measuring tape. Basal area (cross-sectional area) at 1.3 m for each tree was calculated using the formula

$$\text{Basal area } (\text{m}^2\text{ha}^{-1}) = \pi d^2/4(10000) = 0.00007854d^2 \tag{1}$$

where $d = $ dbh (cm) (Husch et al. 2003).

In the three stand reconstruction plots, the structure of the seedling/sapling layer (≤ 1.3m) was intensively sampled. After a random start beginning from a plot corner, 100 1 m^2 subplots were systematically arranged every 5 m throughout each of the three plots. Within each subplot, all sampled seedlings and saplings were identified by species, harvested, transported to the lab and placed in cool storage. Seedling height (0.1 cm) was measured from the root collar. Basal diameter was measured by calipers at the point where the seedlings were cut. The species, height (0.1 m) and basal diameter (0.1 mm) of each seedling were recorded. The number and species of all emergents were recorded in the field. Emergents were then discarded.

Detailed tree age, height and dendrochronological measurements were made in the three stand reconstruction plots. Tree age was determined from cross-sectional disks sampled from trees felled as close to the ground as possible. For layered trees, the layer was followed along the ground as far as possible and then cut. The presence of butt rot was estimated to the nearest 5%. In trees with advanced butt rot, full disks were removed further up the stem beyond the influence of the fungal decay. In cases where the incidence of rot was relatively low, disks were extracted from the lower portion of the bole. In both cases, disks that were judged to contain the longer ring series were sampled. Selected trees of larger diameter with good form and absence of butt rot were sampled at breast height as well. No effort was made to obtain breast height disks from trees of all dbh size classes. All disks were transported to the lab and stored in cool dry conditions. All tagged trees were felled in one plot. In the other two plots chosen for age analysis, only trees in approximately one-half of the plot area were felled.

Tree disks were cut with a band saw into rectangular cross-sections and sanded with a hand-held belt sander using 80-120 grit sandpaper. The ages of most trees were determined as part of ring-width measurements conducted on a Windendro™ (Régent Instruments Inc) tree-ring analysis system (version 6.3b) of 0.01 mm resolution (Guay et al. 1992). In situations of intense juvenile suppression, ring measurements were facilitated by hand-sanding of the sample using fine-grain sandpaper and the counting of rings using a dissecting microscope (maximum magnification 40×). For the vast majority of disks, age of each of the two radii was determined, except for disks with fungal decay in which case the greater minimum age was recorded. Discontinuous, partial rings and extremely off-centre piths were not uncommon in small, suppressed trees. In these cases, ring count was taken from the radius of maximum width. All ages must be accepted as minimum ages. Despite effort to fell all trees as close to the ground as possible, the growth of adventitious roots above the root collar, and the "presence" of missing rings under suppressed conditions precluded the determination of actual germination ages (DesRochers and Gagnon 1997, Gutsell and Johnson 2002).

Due to ubiquitous adventitious rooting of balsam fir and spruce (*Picea*) in cold feathermoss and *Sphagnum* forests (LeBarron 1945, Jablanczy and Baskerville 1969), age determination of seedlings at soil level is inappropriate (Parent et al. 2000). All seedlings were therefore carefully uprooted to include as much of the root as possible. Care was taken to cut each seedling as close to the root collar as possible. This was accomplished by cutting the seedling above the generally smooth hypocotyl region devoid of bud scars and primary roots (Parent et al. 2000). This was especially important for creeping or J-shaped balsam fir seedlings that formed extensive adventitious rooting. All seedlings identified as layers were cut from the parent stem and considered equivalent to seedlings of non-layer origin for the purposes of measurement.

Ages of suppressed seedlings were estimated by counting above- and below-ground bud scars (Parent et al. 2001), as well as ring counts (Kneeshaw and Claveau 2001). Correct aging of highly suppressed seedlings with adventitious rooting can be difficult due to the common occurrence of missing rings and practical difficulties in locating the actual root/shoot interface (Niklasson 2002). For younger, faster-growing seedlings, bud scar counts under a dissecting microscope proved successful. For older and larger seedlings the use of bud scars was problematic because of the "roughening" of the bark. Ages were therefore determined from ring counts on appropriately sanded disks under a 40× dissecting microscope. In several test cases, the ages determined from ring counts were greater by 10 to 15 years than those determined from bud scales. All ages, therefore, are considered to be minimum ages. For both layered balsam fir and black spruce, the "seedlings" were cut as far back as possible. The ages of the white birch seedlings were not determined.

2.3 Data Analysis

The reverse-J tree diameter distributions were fitted using the negative exponential function

$$\hat{Y} = ae^{(-bx)} \tag{2}$$

where $\hat{Y}$ = tree density (trees ha^{-1}), x = tree dbh class (cm), and a and b are variables.

Unbiased ordinary least squares parameters were estimated using the nonlinear PROC NLIN procedure (SAS Institute Inc. 1999a). Because of the non-additivity of the sum of squares in non-linear regression, a pseudo-R^2 (1 – sum squares residual/sum squares total) was used as a goodness of fit measure for the non-linear models (Schabenberger and Pierce 2002).

The 3-parameter Weibull shape parameter (Bailey and Dell 1973) and an index of symmetry (Lorimer and Krug 1983) were used as indices of the reverse-J character of the diameter distributions. The distribution function of a 3-parameter Weibull function is given by

$$f(x) = \left(\frac{c}{b}\right)\left(\frac{x-a}{b}\right)^{c-1} e^{-\left(\frac{x-a}{b}\right)^{c}} \tag{3}$$

where $\infty > x \geq a$, $b > 0$, $c > 0$ and a = location parameter, b = scale parameter, and c = shape parameter.

The shape of the distribution is dependent on the shape parameter c. If $c < 1$, the curve is reverse-J. With $c = 1$, the Weibull reduces to the negative exponential distribution. For $1 < c < 3.6$, the density function is modal and positively skewed. A Weibull shape parameter within the range 3.25 to 3.61 approximates a normal distribution. For $c > 3.6$, the Weibull is increasingly negatively skewed (Bailey et al. 1973). Shape parameter values were calculated as maximum likelihood estimates (SAS Institute Inc. 1999a).

Lorimer et al. (1983) used an index of symmetry to successfully distinguish among descending monotonic, skewed unimodal, and symmetric unimodal tree diameter distributions in northern hardwood–upland oak forests. The symmetry index (I_s) is given by

$$I_s = \frac{(M - X_L)}{(X_{0.95} - X_L)} \tag{4}$$

where I_s = symmetry index, M = the mode, X_L = lower threshold diameter, and $X_{0.95}$ = 95th percentile of the diameter distribution. In this study, the lower diameter class was 0–2 cm; therefore, the index of symmetry was effectively reduced to the ratio of the mode and the 95th percentile of the observed diameter distribution. Negative exponential distributions have symmetry values close to 0, while normal distributions have values close to 0.5. Positively skewed distributions have values >0 and <0.5, with negatively skewed distributions showing values >0.5 and ≤ 1.0.

The relationship between live and dead tree dbh-total age, and live and dead tree height-total age were examined by Spearman rank correlation and non-parametric loess smoothing techniques (Cleveland 1994). Adjustment of the probability levels downward to correct for the risk of increasing the probability of Type I error was carried out by using more powerful adjustments to the traditional Bonferroni correction ($a' = \alpha/k$) (Hochberg 1988). Loess curves applied to residual plots confirmed that a span value of 0.5 best captured the bivariate patterns. Loess smoothing was carried out using Sigmaplot 8 (SPSS Inc. 2002). All correlation analysis were performed with PROC CORR (SAS Institute Inc. 1999b).

Tests of differences among frequency distributions of age to breast height were carried out using the Kolmogorov-Smirnov (K-S) test (Conover 1999). Bonferroni adjustments of 0.05/number of comparisons were applied to keep the Type I error rate within conservative bounds. The lognormally distributed data was log transformed to meet both normality and homoscedasticity assumptions of analysis of variance. Unbalanced analysis of variance was performed with PROC GLM (SAS Institute Inc. 1999a). Post hoc pairwise comparisons among main effects were carried out using the Tukey-Kramer test. Homogeneity of variance was tested using both standard residual analysis and Levene's test.

Both the power function

$$\hat{Y} = ax^b \tag{5}$$

and the 3-parameter sigmoidal Chapman-Richards function (Richards 1959)

$$\hat{Y} = a(1-e^{-bx})^c \tag{6}$$

were used to successfully model the seedling basal diameter-age relationships. All seedling height-age relationships were modeled using the Chapman-Richards equation. $\hat{Y}$= seedling basal diameter (mm) or height (cm), x = seedling age (years), and a, b, and c are parameters.

3 Results

3.1 Tree Species Composition, Density and Basal Area

Balsam fir dominated all plots comprising 73% of the mean total live tree density of 4165 stems ha^{-1}. Black spruce, white spruce and white birch made up 15, 10, and 2%, respectively, of the total tree density. Average tree densities (standard error of the mean = SEM) for balsam fir, black spruce, white spruce and white birch were 3054 (203.9), 618 (140.5), 428 (101.3), and 64 (15.7) stems ha^{-1}, respectively. It should be noted that these relative frequencies are a function of site variability and simply describe the average trends in the sampled "zonal" plots.

Total live tree basal area ranged from 30.2 to 42.7 m^{2}ha^{-1} with an average of 35.8 m^{2}ha^{-1} (SEM = 1.0 m^{2}ha^{-1}). Balsam fir dominated the basal area in all plots. On average, balsam fir made up 76% of the live basal area with black spruce, white spruce and white birch comprising 9, 10 and 5% of the total basal area, respectively. Average basal areas (SEM) for balsam fir, black spruce, white spruce and white birch were 27.1 (3.3), 3.0 (2.9), 3.8 (3.2), and 1.9 (1.1) m^{3}ha^{-1}, respectively.

All stands exhibited similar frequency distributions of basal area by 2 cm tree diameter classes and were pooled for analysis. All three conifers had basal area accumulations across the full range of tree diameters (Fig. 3, A, B, and C). White birch basal area was noticeably concentrated on trees in the 20 to 30 cm dbh range (Fig. 3D). Almost half of the total stand basal area (48.6%, SEM = 1.7%) was concentrated on trees of approximately mid-diameter range (18 to 32 cm dbh). Trees $\leq$25 cm dbh (approximate mid-diameter range) accounted for an average of 57.1% (SEM = 3.2%) of the standing basal area in each stand. Of note is the 11.1% (SEM = 0.6%) of the total basal area attributable to the small trees $\leq$10 cm dbh.

3.2 Tree Diameter and Height Distributions

A 3-parameter Weibull shape parameter approximately equal to 1 (1.0073, SEM = 0.0073) (Bailey

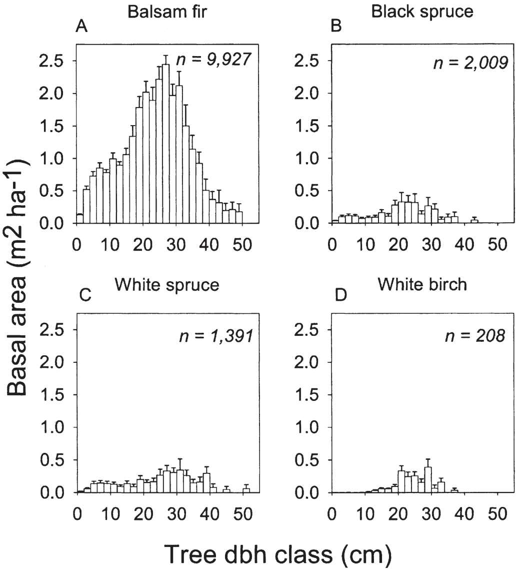

Fig. 3. Basal area for balsam fir, black spruce, white spruce, and white birch by 2 cm dbh classes. Data are means ± standard error of the mean (SEM).

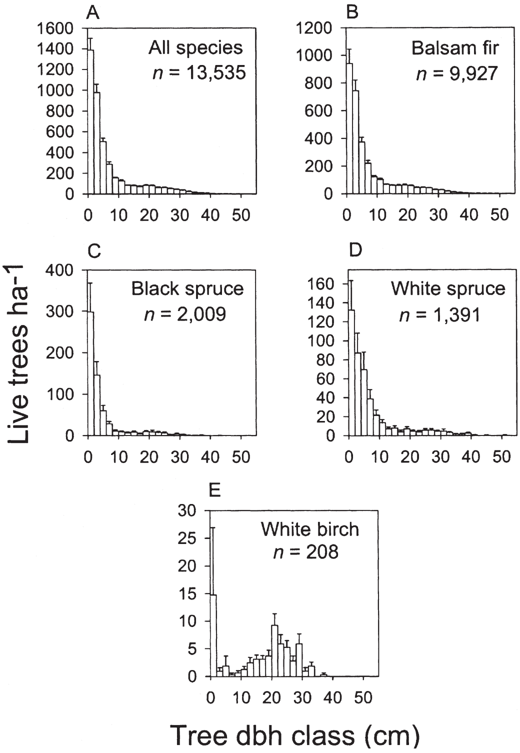

Fig. 4. Live tree dbh distribution for all pooled species and for each individual species. Data are means ± SEM.

et al. 1973) and an index of symmetry approximately equal to 0 (0.0404, SEM = 0.0045) (Lorimer et al. 1983) confirmed the exponential, reverse-J character of the all-species diameter distribution for each sample stand. Given the clear similarity among diameter distributions of each stand and for the sake of brevity, all diameter distributions were pooled for analysis. The pooled tree diameters from each plot followed a classic reverse-J distribution (Fig. 4A). Diameters ranged from 0.1 to 51.0 cm. Seventy to 86% of the total number of trees in all plots were ≤ 10 cm dbh. By contrast, trees ≤ 10 cm dbh accounted for only 8 to 15% of the total basal area.

Similar reverse-J diameter distributions occurred for balsam fir, black spruce and white spruce (Fig. 4B, C and D). The exception was white birch (Fig. 4E). Except for a spike of small trees in the 0 to 2 cm dbh class (approximately 15 trees ha^{-1}), white birch had a modal dbh distribution centred on the mid-sized and large diameter trees.

The fitted model of the mean diameter distribution (trees $\text{ha}^{-1} = 1797.82 \exp(0.2386\ (\text{dbh class}))$, pseudo-$R^2 = 0.9841$ and residual analysis for the modeled diameter distribution of each individual plot confirmed the absence of a systematic monotonic decline normally associated with negative exponential functions. Of particular interest was a “bulging” or “flattening out” of the composite curve at diameters between 14 and 26 cm (Fig. 4A). A greater proportion of trees occurred in the mid-diameter range than were theoretically described by the negative exponential model. Such a physiognomy was characteristic for all the individual conifer distributions as well. Therefore, the mid-diameter bulge in the composite curve was not an artifact caused by the addition of the modal distribution of large white birch stems to the conifer diameter distributions.

A semi-logarithmic presentation of the diameter data for all species produced a well-defined rotated sigmoidal curve (Fig. 5A). A monotonic or regular decline in the frequency of trees of the

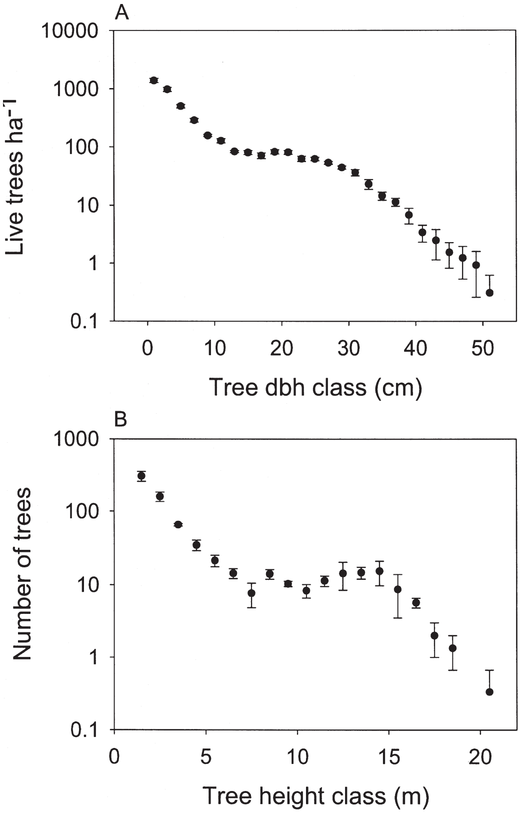

Fig. 5. Semi-logarithmic representation of A) tree dbh frequency distribution (n = 13535) and B) tree height frequency distribution (n = 2147). Data are means ± SEM.

smallest and largest dbh classes contrasted with the flattening out of the curve for trees of mid-sized diameter range.

A semi-logarithmic representation of the tree height frequency produced a rotated sigmoid relationship not unlike that seen for the diameter distributions (Fig. 5B). Between tree heights of 8 to 14 m, the observed distributions showed a plateau with a small positive slope among the taller trees. After tree heights of approximately 15 m, tree frequency declined at a rate similar to that of the shortest trees. Maximum tree height was exceptional at 20 m. Among the three plots, between 86 to 92% of all trees were less ≤10 in height. Between 77 and 81% of all trees were <5 m in height.

3.3 Species Composition and Structure of Seedling Bank

Balsam fir dominated the seedling bank with a mean of 85 143 seedlings ha^{-1} (standard deviation = SD = 96 196 seedlings ha^{-1}), accounting for an average of 88% of the total number of seedlings. The densities (SD) of black spruce, white spruce and white birch regeneration were an order of magnitude less with respective mean densities of 5016 (17 492), 1460 (4831), and 4317 (19 673) seedlings ha^{-1}.

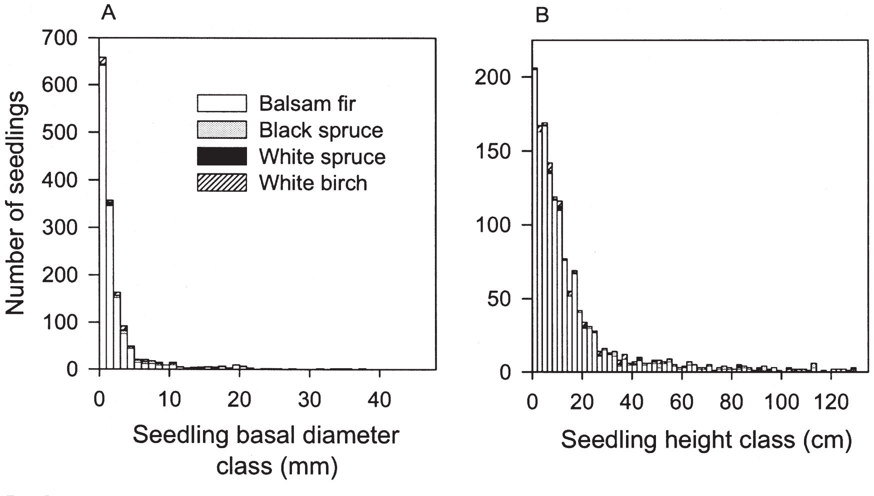

Fig. 6. Seedling A) basal diameter (n = 1500) and B) height frequency (n = 1500) distribution. Basal diameter classes = 1 mm. Height classes = 2 cm.

The basal diameter frequency distribution for all seedlings was characterized by a reverse-J distribution that showed a somewhat regular monotonic decrease in seedling frequency across the range of seedling basal diameters (Fig. 6A). About 93% of balsam fir seedlings were < 10 mm in basal diameter and seedlings rarely attained basal diameters >40 mm. A similar reverse-J frequency distribution was obtained for seedling heights (Fig. 6B). Among the three plots, about 90% (range = 89 to 92%) of all balsam fir seedlings were ≤40 cm in height. Both black spruce and white spruce seedlings generally occurred across the full range of heights. All white birch seedlings were ≤70 cm in height.

3.4 Live Tree Age Distribution and Minimum Age Structure

Tree ages for all species ranged from 25 to 269 years for plot M1, 32 to 286 years for plot M2, and 33 to 222 years for plot M7 (Table 1). Except for black spruce in plot M7, all species in each plot reached maximal ages exceeding 200 years. The oldest ages recorded for balsam fir, black spruce, white spruce and white birch were 264, 264, 247, and 286 years, respectively. Given the slow radial growth, decades of suppression, and unknown number of missing rings in these trees, all ages are best considered as minimum ages.

A well-developed all-age structure characterized each stand (Fig. 7). Note that the abrupt decline in the number of trees in the younger age classes is an artifact of including only trees > 1.3m in height. A combination of the reverse-J seedling age class distribution (Fig. 11) with the age class distribution of the trees (Fig. 7) would have produced a well-defined reverse-J age class distribution. When present in the stand, balsam fir, white spruce and black spruce were generally found in most age classes. A notable exception was white birch which, except for the unique occurrence in the youngest occupied age class in stand M1 (20 to 25 years), was found only in the older age classes; > 170 years for plot M1, > 155 years for plot M2, and > 130 years for plot M7. Except for age class 185 to 190 years in stand M7, all age classes were occupied up to age class 210 to 215 years after which empty age classes were more frequent, no doubt due to the higher mortality rate of the largest trees.

About 30% of the sampled, butt rot-balsam fir had minimum ages > 150 years. For black spruce, white spruce and white birch, the percentage of trees having a minimum age > 150 years was 75, 75 and 100%, respectively. On average, minimum ages were determined at approximately 1 m height. Given the long periods of juvenile suppression found in the majority of the shade-tolerant conifers, these trees of minimum age were certainly much older. For example, balsam

Table 1. Live tree age statistics for three stand reconstruction plots.

Plot	Species	n[a)]	Minimum	Maximum	Mean	Median	s[b)]
M1	Balsam fir	568	30	238	94.2	84	38.4
	Black spruce	144	25	212	71.7	65	33.4
	White spruce	54	31	247	84.7	73	48.8
	White birch[c)]	3	177	269	214	196	48.6
M2	Balsam fir	298	36	264	113.7	110	42.1
	Black spruce	222	32	264	76.4	68	34.0
	White birch	5	160	286	210.2	211	47.9
M7	Balsam fir	357	33	222	87.3	75	35.2
	Black spruce	66	37	138	65.2	63	18.8
	White spruce	57	46	208	86.4	78	37.0
	White birch	10	135	210	174.3	182	28.8

[a)] n = number of trees.
[b)] s = standard deviation.
[c)] One white birch tree of 25 years of age (dbh = 1.0 cm) was excluded.

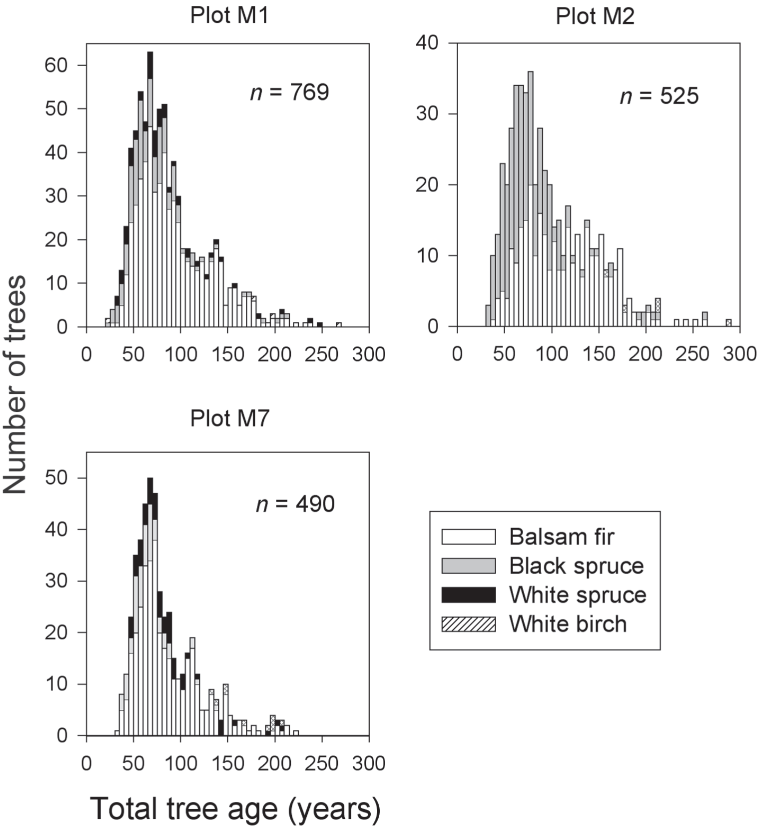

Fig. 7. Total age frequency distribution for balsam fir, black spruce, white spruce, and white birch trees in three Main River stands.

fir sampled at heights of 2.4, 2.5, and 2.5 m had minimum ages of 175, 173 and 189 years, respectively. Similarly, black spruce sampled at 0.7, 1, and 1.2 m had minimum ages of 211, 191, and 205 years, respectively. Obviously, these particular trees were much older, with total ages certainly exceeding 200 years and approaching or even exceeding 250 years. Therefore, the age structures provided in Fig. 7 clearly underestimated the actual proportion of old trees (> 150 years) in the live canopy.

3.5 Live Tree Size-Age Relationships

Except for that of white birch, tree dbh-total age relationships for each species were smoothed using loess curves (Fig. 8A). For balsam fir and the two spruces, two relatively distinct age-size relationships characteristic of release of suppressed trees were recognized: 1) tree aging with relatively low rates of dbh growth, and 2) tree aging with relatively rapid increase in diameter. For balsam fir, the juncture separating the two distinct growth rates occurred around 125 years, while for both black spruce and white spruce, a similar juncture occurred shortly after 75 years. Balsam fir trees, for example, took an average of 125 years to reach 5 cm in diameter. A further 125 years, however, enabled the trees to grow from 5 to about 28 cm in diameter.

Despite the significant monotonic, curvilinear relationship between tree age and dbh for all three conifer species (Spearman rank correlation coefficients ranging from 0.6 to 0.7; $P<0.0001$), only 37% to 51% of the variation in dbh was explained

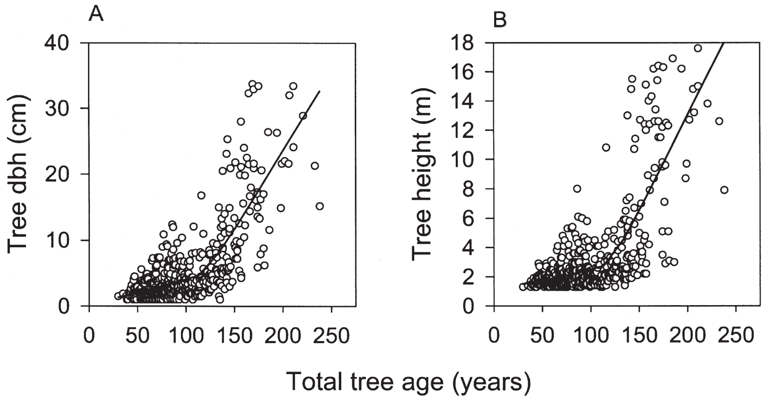

Fig. 8. A) Tree dbh-total age relationship for balsam fir. Spearman rank correlation coefficient (r_S)=0.656, P<0.0001, n=568. B) Tree height-total age relationship for balsam fir. r_S=0.604, P<0.0001, n=568. Loess smoothing with span=0.5.

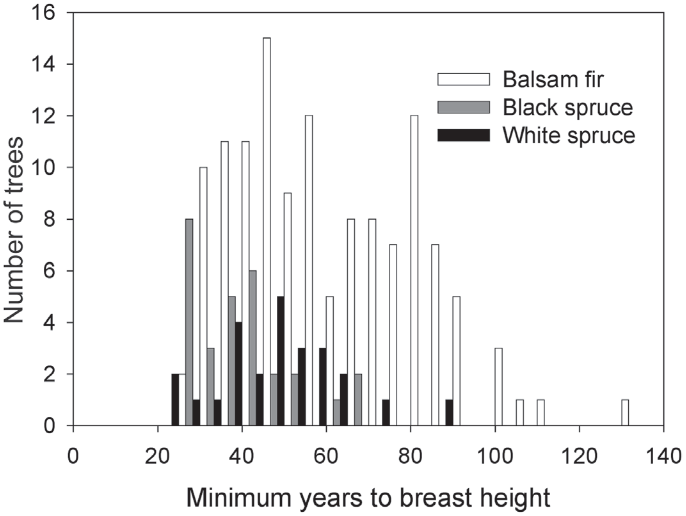

Fig. 9. Frequency distribution of minimum number of years required to reach breast height for balsam fir, black spruce, and white spruce trees. n=182.

by tree age. Balsam fir trees of 5 cm dbh, for example, had ages ranging from 50 to 175 years. Similarly, 150 year-old trees exhibited diameters ranging from 2 to 25 cm. For both black spruce and white spruce, 2 cm dbh trees had ages ranging from 30 to over 100 years.

Tree height-total age relationships paralleled tree diameter relationships (Fig. 8B). Evident were the two contrasting height growth rates. As with diameter growth, height growth of balsam fir increased noticeably after about 125 years total age.

A similar increase in height growth for both black spruce and white spruce occurred around 75 to 100 years. Except for those of white birch, Spearman rank correlations indicated significant monotonic height growth, with rank coefficient values ranging from 0.59 to 0.80. White birch data were clustered in the oldest trees.

Large height-age variability was evident for all conifers, especially for the highly shade-tolerant balsam fir. Consideration of trees ≤3 m in height exemplified this variability. Trees of any particular height may have had quite different ages. For example, a 150-year-old balsam fir displayed heights ranging from 1.5 m to 15 m. Similarly, a balsam fir tree of 1.5 m in height had ages ranging from 30 to 150 years.

3.6 Years to Breast Height

The frequency distribution of years to breast height was generally right skewed for balsam fir and black spruce, with white spruce defined more by a modal distribution (Fig. 9). A comparison of the three frequency distributions for the three study stands showed plot M2 to be marginally different than plot M1 (Kolmogorov-Smirnov, P = 0.013, Bonferroni P = 0.017). Despite this small difference, the number of years to reach breast height was pooled for each species and the resulting frequency distributions were compared. The observed distribution for balsam fir differed significantly from the distributions for both black spruce and white spruce, both of which showed no significant difference. For all multi-way comparisons, a Bonferroni adjustment (α/number of comparisons) set a critical level of P = 0.0167. Balsam fir took longer to reach breast height than either black spruce or white spruce (Tukey-Kramer, P ≤ 0.05). Average years to breast height for balsam fir was 61.8 years (s = 21.2), compared to 40.4 years (s = 11.5) for black spruce and 48.0 years (s = 15.0) for white spruce. No significant differences in number of years to breast height were detected for the two spruces.

3.7 Dead Tree Age Structure, Size-Age Relationships

Total age of dead trees ranged from 45 to 232 years (Fig 10). Balsam fir trees were present across the entire age range, with white spruce relegated to the youngest age classes (not greater than 101 years) and white birch occurring solely in the oldest age classes (176–220 years). Of the trees sampled, minimum ages of dead trees were well represented in age classes > 150 years.

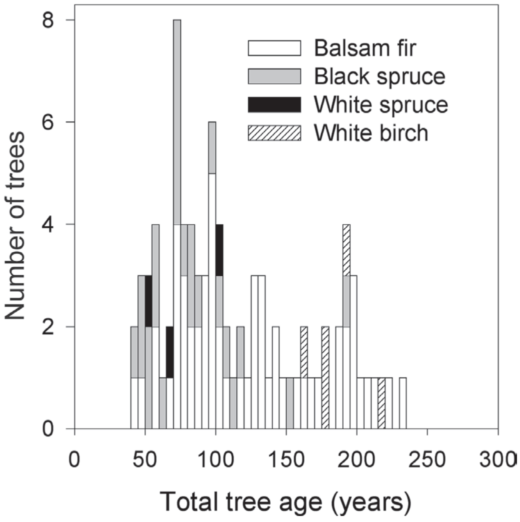

Fig. 10. Total age of dead balsam fir, black spruce, white spruce, and white birch trees. (n = 81).

The dbh-age and height-age relationships of dead trees were similar to those of live trees, exhibiting a significant curvilinear monotonic relationship. For tree dbh-age at death relationship, $r_s = 0.8099$, $P < 0.0001$, $n = 86$ and for tree height-age at death relationship $r_s = 0.6603$, $P < 0.0001$, $n = 86$. As with the live balsam fir dbh-age curve, loess smoothing of both scatterplots for the dead trees showed a noticeable upward shift in the relationship at around 125 years.

3.8 Seedling Age Distribution and Size-Age Relationships

A reverse-J age distribution characterized the seedling population (≤1.3 m) for each of the three sampled stands (Fig. 11). Emergents were included in the 0 to 5 year frequency class. Balsam fir seedlings, which dominated the seedling bank, were present in each age class up to age 70 years, after which the proportion of balsam fir decreased to minimum levels. Balsam fir had the widest range of ages with continuous presence

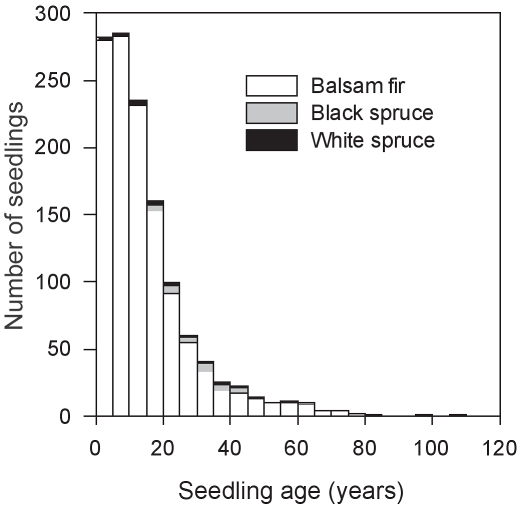

Fig. 11. Age class frequency for balsam fir, black spruce, and white spruce seedlings. n = 1457.

of seedlings in nearly all age classes up to 110, 120 and 85 years for plots M1, M2, and M7, respectively. Despite this wide age range, most seedlings were in the younger age classes, with an average 76% of all balsam fir seedlings ≤20 years of age. The age range for black spruce and white spruce seedlings was narrower with ages of black spruce ranging from 6 to 70 years, and ages for white spruce ranging from 0 to 65 years of age. The oldest recorded balsam fir, black spruce and white spruce seedlings were 116, 69, and 63 years, respectively.

All seedling basal diameter/height-age data from the three sampled stands were pooled for each species. Monotonic relationships with increasing variability characterized the seedling basal diameter-age scatterplots (Fig. 12A). The 3-parameter asymptotic Chapman-Richards function modeled the balsam fir relationship, whereas a power function best modeled both the black and white spruce relationships (not shown).

All seedling height-age scatterplots modeled by using the Chapman-Richards function displayed increased height variability with seedling age (Fig. 12B). One metre high balsam fir seedlings ranged in age from 40 to over 100 years of age. Seedlings >60 years of age were uncommon for both spruces, whereas balsam fir seedlings reached 100 years of age.

4 Discussion

Given the ubiquity of large-scale, stand-replacing fires and insect outbreaks across the boreal forests of Canada, it has generally been assumed that old-growth boreal forests are rare. This assump-

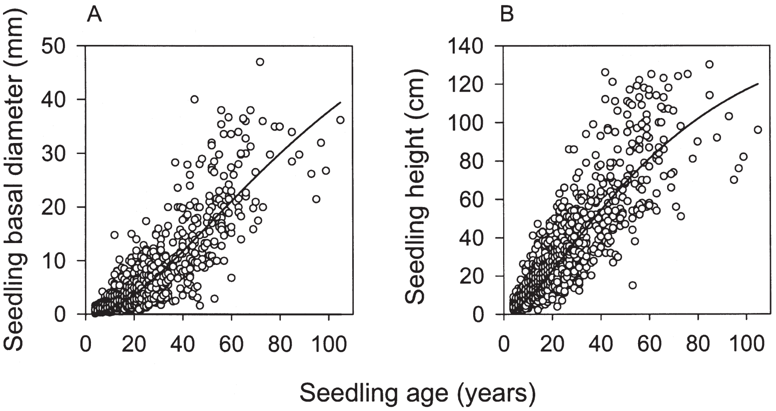

Fig. 12. A) Basal diameter-age and B) height-age relationship for balsam fir seedlings. Basal diameter = 67.295 $(1-\exp^{-0.0141\mathrm{age}})^{2.0765}$, $R^2 = 0.7679$, n = 2641; Height = 150.9 $(1-\exp^{-0.0195\mathrm{age}})^{1.671}$, $R^2 = 0.7874$, n = 2641. Emergents not included.

tion is no longer tenable. Fire cycles in the humid boreal forests of eastern Canada are longer than the 50–75 years commonly cited for the western boreal forest (Bergeron et al. 2001), reaching values of up to 500 years (Foster 1983). Under these conditions of long fire cycles, old-growth, gap-dynamic stands of irregular size structure and uneven-age may dominate a forest landscape (De Grandpré et al. 2000, McCarthy 2001, Boucher et al. 2003, Harper et al. 2003, Kneeshaw and Gauthier 2003, Pham et al. 2004).

Given the non-random sampling design, it is not possible to state univocally that old-growth stands described in this study actually dominate the entire landscape of the Main River study area. However, given the remarkably homogeneous, fine-grained structure of the forests of the entire study area as evidenced from extensive aerial and ground reconnaissance, as well as aerial photograph and permanent and temporary plot data, a claim regarding the predominance of such old-growth stand types is not unreasonable.

Old, uneven-aged stands of the Main River forests exhibited reverse-J dbh and height frequency distributions characteristic of old-growth stands. Such complex structural heterogeneity is characteristic of boreal forest stands whose disturbance regime is dominated almost exclusively by small-scale gap dynamics (McCarthy 2001).

4.1 Tree Species Composition

The dominance of balsam fir is characteristic of these generally non-pyrogenic forests of western Newfoundland. Chronosequence studies have confirmed the successional convergence of eastern Canadian boreal forests towards balsam fir following disturbance (Bergeron and Dubuc 1989, Bergeron 2000).

Large, mature white birch were dispersed throughout the stands, comprising 1.5% of the total stem density and 5% of the stem basal area. Even though white birch is traditionally considered an "early successional" species, this species can persist within old-growth boreal or subalpine coniferous stands (Taylor et al. 1996, Kuuluvainen et al. 1998). Its prolific seed-producing ability, combined with the availability of suitable microsites, especially suitably decayed coarse woody debris and tip-up mounds of tree blowdowns (Perala and Alm 1990, Carlton and Bazzaz 1998) within sufficiently large gaps, probably maintains the continued persistence of white birch.

Of note is the restricted white birch diameter distribution to the mid to large trees (20–35 cm dbh). Besides a continuous "minimum" presence of white birch, the germination and establishment of this species may be associated, as well, with episodic periods of larger gap formation that enhance microsite production and the ability of the faster-growing and more flexible white birch to successfully sequester adequate light requirements.

4.2 Rotated Sigmoid Diameter and Height Distributions

All stands expressed well-developed rotated sigmoid tree diameter and height distributions (semi-logarithmic presentation). Even though a reverse-J tree diameter distribution described by the exponential function $Y = aX^b$ has been traditionally viewed as characteristic of a stable or steady-state forest (Meyer 1952, Leak 1964), it is important to note that reverse-J diameter distributions, by themselves, are not diagnostic of small-scale gap dynamics. A wide variety of stand dynamics can lead to reverse-J tree size distributions, including even-aged, single-cohort dynamics, particularly for mixed stands composed of tree species with different growth rates (Oliver et al. 1996), or for stands that have undergone slow, long-term establishment after catastrophic stand mortality. However, interpretation of the tree size distributions in combination with stand age structure effectively minimizes the risk of such an erroneous interpretation. Therefore, the rotated sigmoid size distributions are interpreted as a function of differential mortality rates and small-scale gap dynamics rather than a function of large-scale disturbance related tree recruitment and establishment.

A semi-logarithmic representation of the exponential function normally produces a straight line of negative slope. This assumes that the natality rate is constant, and that the mortality rate is constant for all diameter classes. However, mortality rate is generally not constant throughout the life history of long-lived tree populations, but actually changes with diameter class and tree age (Hett and Loucks 1971, 1976). In fact, a semi-logarithmic presentation of diameter class frequency for old-growth forests generally produces not a straight line, but a well-defined rotated sigmoidal diameter relationship (Schmelz and Lindsey 1965, Goff and West 1975, Goodburn and Lorimer 1999, Leak 2002). A simulation study of equilibrium diameter distributions in shade-tolerant sugar maple deviated markedly from both the negative exponential and negative power functions to closely resemble rotated sigmoid curves (Lorimer and Frelich 1984). In plenter forests characterized by the presence of trees of all sizes and age classes, modeling of stand equilibrium was attained only under conditions of a rotated sigmoidal diameter distribution (Schütz 1975, 1977a, 1977b).

The rate of mortality is high in the understory, decreases and levels off for the dominant, vigorous overstory, and then increases again for the senescent overstory. This U-shaped mortality function is biologically consistent with rotated sigmoid size distributions. Studies have consistently reported U-shaped mortality rates for old-growth stands (Platt et al. 1988, Runkle 2000, Lorimer et al. 2001). Suppressed understory trees die from interspecific competition among the clumped regeneration common in the gaps of old-growth forests (Moeur 1997). Furthermore, long periods of seedling and sapling regeneration would only enhance mortality-inducing physiological stresses. Mortality rates would be relatively low for vigorous released trees that had attained the co-dominant or dominant canopy position. Dendrochronological data (unpublished) indicated that most (if not all) of the sampled canopy trees had experienced long periods (up to 100 to 120 years) of juvenile suppression, only to experience relatively rapid and sustained growth once they were released. Old senescent trees are common in the dominant canopy, indicating the absence of large-scale canopy disturbance. At the same time, these old, large trees have a higher mortality rate than the mid-diameter, faster growing trees because of the higher incidence of root and butt rots (unpublished data), and greater disposition to stem snap. Stem snap was the dominant cause of tree fall in these stands (unpublished data).

4.3 Longevity of Balsam Fir

Balsam fir is traditionally considered a short-lived tree species, not generally exceeding 200 years of age (Frank 1990, Hardin et al. 2001). Due to its proclivity to infection by root rots and butt rots (Lavallée 1986, Whitney 1995), balsam fir is generally prone to early mortality.

In these slow-growing, old-growth stands, the highly shade-tolerant balsam fir (and associated black spruce) may be more tolerant of extremes than normally considered, thus explaining the greater longevity. Slow-growing trees growing under "adverse" conditions can display enhanced longevity (Larson 2001, Laberge et al. 2000). The recorded ages of balsam fir from the study site exceeded maximum recorded ages by 30–40 years. Maximum ages of balsam fir have been recorded as 212 years (≥30 cm core height) (Sirois 1997), 202 years (Leak 1985) and 220 years for trees growing in Labrador (Wilton 1965).

The great age of balsam fir in the upper watershed of the Main River is reflective of a number of factors. First, is the relatively high elevation (350 to 500 m) at which the trees were sampled. Despite the long history of stand-replacing spruce budworm (*Choristoneura fumiferana* (Clem.)) and hemlock looper (*Lambdina fiscellaria fiscellaria* (Guen.)) outbreaks in Newfoundland's forests (Otvos and Moody 1978, Hudak et al. 1996), the forests of the upper Main River watershed have no recorded history of insect outbreaks (Corner Brook Pulp and Paper Limited 2001). The wet, cool climatic conditions of these high-altitude forests may prevent the development of insect populations to levels that can cause tree and stand mortality. Secondly, in this region of the Long Range Mountains, tree line occurs at approximately 500 to 550 m, so the sampled stands are relatively close to their ecological limits. Under such climatic and edaphic conditions, slow-growing trees may be less prone to fungal decay and will therefore live longer (Worrall and Harrington 1988). Thirdly, trees growing on productive sites usually have higher mortality rates, with an acceleration of stand break-up (Franklin et al. 1987, Robichaud and Methven 1993). This can be attributed to the rapid height growth on more productive sites and the attainment of critical windthrow heights earlier in the tree's life (Smith et al. 1987). Tree mortality from windthrow (tip-up mounds) was uncommon, with fungal decay-mediated tree snap being by far the dominant reason for tree mortality (unpublished data). Fourthly, it seems that the long periods of juvenile suppression experienced by most balsam fir has promoted trees of great chronological age. The seedling bank of balsam fir and other *Abies* species are known to undergo decades of juvenile suppression (Morris 1948, Antos et al. 2000). Furthermore, the physiological age of a balsam fir that has been suppressed for a century is much less than its chronological age (Morris 1948).

4.4 Size-Age Structure

Long and differential periods of suppression in individual balsam fir and spruce promoted another characteristic of old-growth forests – the generally poor relationship between tree age and size (dbh and height). Trees of equal height and diameter differed in age by as much as 120 years. Tree size, therefore, provided minimum indication of the actual chronological age of trees in these old-growth stands. Tree growth is best understood on an individual tree basis, as trees respond to the stochastic release of growing space, or by simply growing slowly upward into the canopy. This wide variability in the tree age-size relationship found in old-growth stands comprised of shade-tolerant tree species is well known (Gates and Nichols 1930, Parish et al. 1999). This general lack of relationship between tree age and size in old stands confirms the established notion that size is generally more important than actual chronological age in assessing reproductive development and stand dynamics (Harper and White 1974, White 1980).

4.5 Age Structure and Stand Stability

Under current climatic and small-scale gap disturbance regime, balsam fir, black spruce and white spruce are well adapted to maintain reverse-J age distributions and continuous canopy cover for long periods of time: 1) once established, the high shade tolerance of fir and spruce (especially balsam fir) (Logan 1969) confer the ability to persist for decades in a suppressed state under the high canopy (Antos et al. 2000); 2) morphological plasticity of *Abies* and *Picea* species permits maximum possible photosynthetic rates in reduced light conditions (Greis and Kellomäki 1981, Claveau et al. 2002); 3) vegetative reproduction of all three species, especially in continuously moist, moss-rich boreal forests (Bannan 1942, LeBarron 1945); 4) the ability of both seedlings and layers to respond vigorously in height growth in response to released growing space upon the death of a neighbouring tree or trees (Baskerville 1961, Paquin and Doucet 1992); and (5) the ability of both *Abies* and *Picea* to germinate on moss-covered and coarse woody debris microsites commonly found in humid, old-growth boreal and subalpine forests. *Picea* will often preferentially germinate on suitably decomposed coarse woody debris microsites, whereas *Abies* seedlings will germinate on a wider variety of microsites (Place 1955, Nakagawa et al. 2003, Simard et al. 2003). Similar reverse-J age distributions have been documented for old-growth Engelmann spruce-subalpine fir forests in western North America (Rebertus et al. 1992, Parish et al. 1999, Antos and Parish 2002a, 2002b).

The demographic age and size structure of these stands point to the continued, long-term maintenance of balsam fir-dominated old-growth forests. Continuous reverse-J age distributions for both the seedling bank and tree layer, and semi-logarithmic rotated sigmoid diameter distributions, are strong primae facie evidence of small-scale gap dynamics as the dominant disturbance regime in these stands. Furthermore, fungal-mediated tree snap and accumulations of coarse woody debris in all stages of decomposition (unpublished data) confirm the dominance of gap dynamics. Although not actually measured in these stands, field observations confirmed that the majority of canopy gaps were <200 m^2, a size consistently found in studies on gap dynamics in boreal forests (McCarthy 2001, Bartemucci et al. 2002, Pham et al. 2004).

The predominant restriction of white birch to the oldest age classes for total live age, total dead age and minimum live age probably indicates a historic period of sufficient canopy disturbance or climatic variation that permitted enhanced recruitment and growth of white birch.

4.6 Management Implications

Traditional even-aged based clearcutting regeneration methods are beyond the historic range of disturbance in these forests. Classic methods of selection harvesting are biologically feasible, but the slow growth rates, high logging costs, low volume stands (<100 m^3 ha^{-1}), and pulpwood or rough dimension lumber market effectively preclude the economic possibilities of such methods.

5 Conclusion

The age and size structure of trees and advance regeneration in high altitude, slow-growing old-growth boreal forest stands of western Newfoundland were examined. These stands were all-aged with complex diameter and height heterogeneity characteristic of classic, self-regenerating, old-growth stands dominated by shade-tolerant fir and spruce. The well-defined rotated sigmoidal dbh and height distributions (semi-logarithm) confirmed the quasi-equilibrium population structure under current climatic conditions. The tree age structure of these stands is consonant with the prevalence of small-scale gap dynamics as the dominant disturbance regime.

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