GAP DYNAMICS IN BOREAL ASPEN STANDS:
IS THE FOREST OLDER THAN WE THINK?

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Abstract. Trembling aspen (*Populus tremuloides*) in western Canadian boreal forests
is generally believed to occur as young, even-aged stands, as part of a fire-dominated
landscape. However, the available quantitative estimates of the rate of disturbance by fire
in this region differ markedly. One estimate is consistent with forests much older than are
currently thought to exist. The theory of gap dynamics may partly reconcile the discrepancy,
by suggesting a mechanism whereby old, uneven-aged aspen stands could develop and
persist.

We surveyed for canopy gaps in 44–67 yr old aspen stands in northeastern Alberta,
Canada, and found that expanded gaps occupy 3.6–16.6% of stand area, increasing linearly
with stand age over the sampled range. Gaps begin to form ~40 yr after stand initiation,
through the accumulated mortality of adjacent canopy trees. The densities of aspen (*P.
tremuloides*), balsam poplar (*P. balsamifera*), and paper birch (*Betula papyrifera*) saplings
were 2–3 times higher in gaps than in paired control areas under a closed canopy. Sample
plots in older aspen stands in the vicinity had spatially heterogeneous, uneven age structures,
consistent with gap dynamics. More extensive samples of stem-size-structure data and
forest-inventory data sets indicate that this phenomenon is widespread. We conclude that
gap dynamics can maintain near-pure deciduous stands in this region, in the absence of
shade-tolerant competitors. A cellular-automata model of aspen-stand dynamics, with spa-
tially random mortality, yields predictions consistent with our other results. It follows from
the model that stable age structures develop within 250–300 yr, that mean canopy age is
a biased estimator of stand age in stands older than 100 yr, and that small-sample maxima
have unfavorable sampling distributions. Comparable biases may be present in ages esti-
mated from aerial photography: significant areas of ''young'' aspen have age structures
characteristic of simulated old stands. We present less direct arguments that other com-
ponents of the Alberta boreal forest are also older than is generally thought, and we outline
a new model of the regional forest dynamics. We conclude that vast tracts of boreal forest
are now being managed on the basis of an incorrectly estimated age structure and a mis-
conception of their landscape dynamics.

*Key words: boreal-forest disturbance regimes; boreal mixed-wood; CO_2 emissions; canopy gaps;
cellular-automata models; forest inventory data; gap makers and gap fillers; management models
based on natural disturbance; stand age estimation; stand dynamics; trembling aspen; white spruce.*

INTRODUCTION

Natural disturbance regimes have been proposed as
models for the management of the circumpolar boreal
forest (Hunter 1993, Haila et al. 1994). Aspen-domi-
nated (*Populus tremuloides* Michx.) boreal forests, the
focus of the present study, ''may represent an ideal
candidate for management practices that use natural
disturbance as a template'' (Lee et al. 1997:69). The
natural-disturbance model offers a solution to a prob-
lem posed by Franklin (1993), namely, how to maintain
biodiversity at regional scales, without watching over
every sparrow that falls. The approach assumes that
boreal ecosystems as such (Haila 1994) or, more prop-

erly, their constituent biota (Hunter 1993) are adapted
to natural disturbances that can be emulated by man-
agement. The available supporting evidence (Bunnell
1995, Gauthier et al. 1996) draws attention to the dis-
turbance *rate,* of which wildfire is the largest compo-
nent (Johnson 1992). If harvesting and fire are to be
compensatory rather than additive, then the natural-
disturbance model implies that the rate of harvest
should be governed by the effectiveness of fire sup-
pression: the total rate of harvest plus burning should
approximate the ''natural'' rate of burning.

Mathematical models (Van Wagner 1978, Johnson
and Van Wagner 1984) relate forest age structure to
fire frequency (the probability of a unit of forest burn-
ing per unit of time [Johnson 1992:86]) or to its inverse,
the fire cycle (the time required to burn an area equal
in size to the area of study). Estimated fire cycles for
coniferous-dominated boreal forests in Canada range
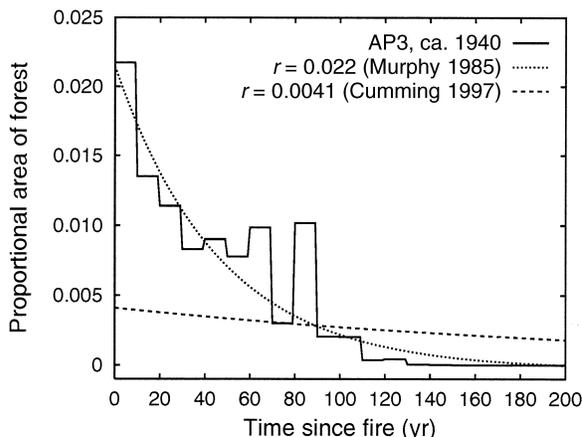
FIG. 1. Estimated age structures for boreal mixed-wood forests in Alberta, Canada. The figure illustrates the age structure for the study area, from forest inventory data back-aged to ca. 1940 (AP3), and two alternative negative exponential age structures with their rate constants r, one fitted to the inventory data (Murphy 1985) and the other estimated from analysis of 54 yr of mapped fires (Cumming 1997).

from <100 to ~500 yr (reviewed by Payette [1992]). For the boreal mixed-wood region (Rowe 1972) in northern Alberta, two different estimates exist (Fig. 1). Murphy (1985) applied Van Wagner's (1978) methods to an age-class structure derived from forest inventory data, and estimated a pre-suppression fire cycle (ca. 1940) of 46 yr, corresponding to a mean annual disturbance rate $r = 0.022$. In contrast, Cumming (1997) studied a 54-yr record (1940–1993) of reported and/or mapped fires, correcting for the effect of fire suppression by nonparametric analysis of recent changes in the fire size distribution. The resulting estimate of $r = 0.0041$, or a fire cycle of 244 yr, implies a forest much older than the inventory data suggest. Under some interpretations of the natural-disturbance model, sustainable timber yields consistent with these two rates differ by a factor of 4 (Armstrong et al. 1999).

At least 150 000 km^2 of northern Alberta's boreal forest are now being managed at harvest rates consistent with Murphy's (1985) estimated fire cycle. However, should Cumming's (1997) estimate be the more nearly correct, planned rates of harvest are incompatible with at least some aspects of a natural-disturbance model. The main objective of this paper is to present evidence for an old mixed-wood forest that shows both how old stands can develop and how their true ages may systematically be underestimated in forest inventories. We then discuss the implications of our findings in light of the regional land-use decisions that have been or are being made.

Aspen stand dynamics

Aspen is clonal. Therefore, by stand age, we mean the time since the last fire to cause substantial canopy mortality. This is not the same as the ages of aspen clones within the stand, as clonal root systems usually survive fire. The terms "uneven" and "even-aged" refer to the age structure of stems within a stand. The following outline of mixed-wood stand dynamics was abstracted from Kabzems et al. (1986) and Peterson and Peterson (1992). Trembling aspen is generally believed to occur as even-aged, pyrogenic stands, which eventually either develop into white spruce (*Picea glauca* (Moench) Voss) stands, are consumed by fire, or degenerate to brush land or meadow as the canopy of old stands collapses. Fire promotes aspen root suckering, the species' predominant form of regeneration—establishment from seed is infrequent. Most sites that support aspen can also support white spruce, whose post-fire development is characterized as following one of two paths. After a hot fire, if white spruce seed is available, high densities of both species may establish at the same time. Because of its higher initial growth rate, aspen will dominate the site for the first several decades, but after 50 yr white spruce becomes progressively more conspicuous in the understory and may dominate the canopy by 100 yr, as the aspen senesces. On the second pathway, associated with lighter fires that do not expose much mineral soil, white spruce recruitment is incremental. An "extended mixed-wood stage" (Kabzems et al. 1986:84) may develop, where the density of canopy white spruce is persistently low. In this paper, we focus on the latter pathway. However, we note that these two developmental paths are part of a continuum of stand trajectories, defined largely by the temporal pattern of white spruce recruitment and growth. The frequency distribution of these trajectories is unknown.

Uneven-aged aspen stands are well documented in the Intermountain Region of the western United States (Harniss and Harper 1982, Mueggler 1985, Perala 1990, Mueggler 1994). However, published evidence for the existence of such stands in western Canada is speculative or anecdotal. Moss (1932) suggested that mature aspen stands in central Alberta, though apparently collapsing, might develop into uneven-aged stands. Navratil et al. (1990:49) remark that "aspen stands that have escaped fire for 90 or more years may have an advanced understory of aspen, often in the range of 40 to 50 years [old]" and that still younger stems may exist in the shrub layer. This implies aspen recruitment in stands aged about 40 yr.

According to the theory of gap-phase dynamics (Shugart 1984, Platt and Strong 1989), recruitment into the understory may occur when the removal of one or more canopy trees creates a sufficiently large opening. Johnson et al. (1994) found no evidence for gap dynamics in montane coniferous forests of the southern Canadian Rockies. However, Kuuluvainen (1994) reviews a body of evidence for gap dynamics in the boreal coniferous forests of Fennoscandia, and Betters and Woods (1981) describe, without explicitly naming, gap dynamics in aspen stands in the Colorado Rocky Moun-
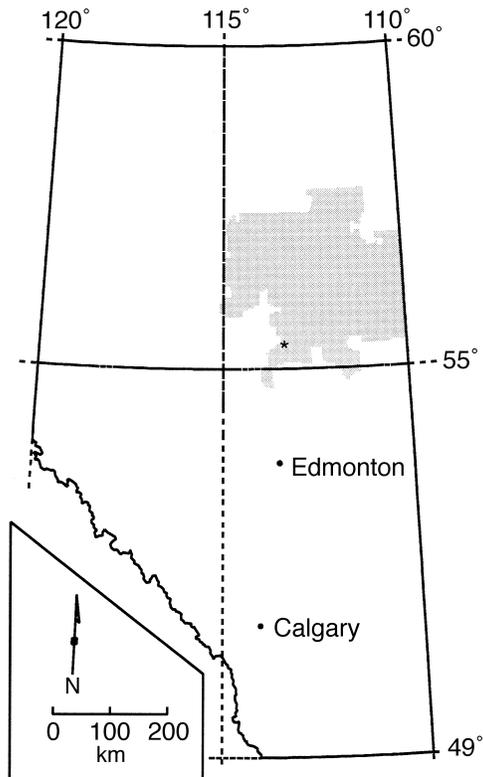
FIG. 2. Location of the 72 000 km² greater study area within the Province of Alberta (Canada) and of the Calling Lake field site, marked with an asterisk (*).

tains. Most recently, Kneeshaw and Bergeron (1998) have demonstrated gap dynamics in Québec boreal forests: in 78-yr-old aspen stands, it is associated with shifting dominance to white spruce and balsam fir (*Abies balsamea* (L.) Mill), but not with aspen self-replacement.

Aspen is regarded as a shade-intolerant species (Perala 1990), and, in boreal aspen stands in Alberta, mean irradiance at ground level is lowest at age 50–60 yr (Chesterman and Stelfox 1995), i.e., in the decades immediately following our postulated initiation of gap-phase recruitment. Considerable canopy thinning or large gaps would normally be required to regenerate an intolerant species under these conditions. However, most aspen regeneration is clonal, via root suckers that can be subsidized by canopy trees (Zahner and DeByle 1965, Perala 1990, Peterson and Peterson 1992). The ability of parental ramets to support the growth of daughter ramets in a shaded environment has been demonstrated in herbaceous clonal species (Hartnett and Bazzaz 1983), but apparently has not been investigated in aspen. While the density of aspen suckers is known to be constrained by hormonal suppression from parental ramets, by low soil temperature, and by stand age (Perala 1990, Peterson and Peterson 1992), there are always a few suckers even in the cool shady understory of mature aspen stands (P. J. Burton, *personal*

observation). Hence, when even a small gap is created, there is usually sufficient advance aspen regeneration to potentially restock the gap.

We postulated that gap dynamics explain the discrepancies and observations reported above. Because aspen is a relatively short-lived tree, self-maintaining, old-growth aspen stands would not be characterized by the presence of conspicuously large and ancient individual trees. Since stand ages in Alberta's forest inventory are mostly inferred from photo-interpreted canopy height (Anonymous 1985), the ages of old stands could be systematically underestimated, which would explain some of the difference between the estimated forest age structures of Fig. 1. We predicted that gap formation in aspen stands begins about 40 yr after stand initiation, and that gaps exhibit elevated recruitment, height growth, or survivorship of aspen saplings relative to areas beneath the closed canopy. As such stands age, an uneven, spatially heterogeneous age structure should develop.

To test this line of reasoning, we surveyed for canopy gaps and associated vegetation response in several young aspen stands on field sites in northeastern Alberta. In nearby aspen stands apparently about 130 yr old, we tested for fine-scale spatial heterogeneity in age structure, using both intensive age sampling conducted at a small number of plots, and much more extensive size-structure data. To evaluate the generality of our findings, we analyzed several forest inventory data sets, consisting of numerous stem-age samples, each of small size, but distributed over a ∼72 000 km² region. Using a simple cellular-automata model of aspen stand dynamics, we simulated changes in aspen stand age structures through time. The model output was used to test our analysis of the inventory data sets, and to evaluate the stand-aging methods on which Alberta's forest inventory data relies.

STUDY AREA

Our greater study area comprises ∼72 000 km² of the boreal mixed-wood ecological region (Rowe 1972) in northeastern Alberta (Fig. 2). The mixed-wood region, of total extent ∼485 000 km², is transitional between colder, conifer-dominated forests to the north and warmer, dryer aspen parklands to the south, which are now mostly farmland. In Alberta ∼270 000 km² of the mixed wood is still forest land (Strong 1992), most of which has never been logged. The regional ecology is described by Moss (1932), Dix and Swan (1971), Kabzems et al. (1986), and Strong (1992).

The most abundant tree species are trembling aspen (*Populus tremuloides*), black spruce (*Picea mariana*), jack pine (*Pinus banksiana*), white spruce (*Picea glauca*) and balsam poplar (*Populus balsamifera*). Paper birch (*Betula papyrifera*), tamarack (*Larix laricina*), and balsam fir (*Abies balsamea*) are widely distributed, but rarely form pure stands. Mature mixed stands with high densities of both aspen and white spruce (''mixed

stands,'' henceforth) are characteristic of the region. Peatlands and sparsely treed muskeg cover ~49% of the greater study area. The mesic, aspen-dominated stands investigated here cover ~17% of the area, or 35% of the forested land. In these stands, the most common tall shrubs are two alder species (*Alnus crispa* and *A. tenuifolia*), and several species of willow (*Salix* spp.) Shrub species common in the lower strata include bracted honeysuckle (*Sheperdia canadensis*), low-bush cranberry (*Viburnum edule*), raspberry (*Rubus ideaus*), several species of currant and gooseberry (*Ribes* spp.) and rose (*Rosa* spp.)

Our field sites are located in a ~100-km² area to the immediate west of Calling Lake, Alberta (55°15′ N, 113°30′ W), near the southwest corner of the greater study area. The area is dominated by mature aspen mixed-wood, and white spruce stands mostly over 100 yr old—the proportion of wetlands is only 5.8%. Soils are predominantly clay-loam Luvisols developed from glacial till (Wynnyk et al. 1963).

DATA SOURCES AND METHODS

Our analyses relate six different data sets, each sampled at a different spatial scale, resolution, and intensity, and collected for different purposes, at different times. They are described here in decreasing order of spatial extent, from broad-scale forest inventory data covering the entire greater study area, down to a small number of 100-m² sample plots.

Forest inventory data

The Alberta Phase 3 forest inventory (Anonymous 1985) is a set of photo-interpreted 1 : 15 000 stand maps, covering the entire forested area of the province. Each map, and the associated stand list, covers one *township,* a rectangular land-survey unit usually ~9.66 km a side. Stands are areas of approximately uniform canopy-species composition, canopy closure, and height. Other recorded attributes include the estimated decade of stand origin, and the composition, density, and apparent age of any visible understory. In the greater study area, this inventory (data set ''AP3,'' henceforth) was interpreted from leaf-on aerial photography flown between 1970 and 1984. AP3 stand origins are estimated using mapped disturbances (since ca. 1940), species-specific height–age curves, and limited field checking. In this paper, references to stand age by decade of origin (e.g., 1880s), mean ''as estimated by AP3.'' Stand ages are given in years only for those we aged ourselves. We used AP3 attributes to stratify the various data sets described below, and to guide selection of our field sites. AP3 canopy and understory species descriptions do not always distinguish between aspen, balsam poplar, or birch, often lumping them into an ''undifferentiated deciduous'' category. We refer to all such stands as ''aspen stands.''

Aspen age data

Two spatially extensive (Fig. 3) sets of tree ages were provided by Pearson-Timberline Forestry Consultants, of Edmonton, Alberta. The first data set (AAD1) was collected during pre-harvest inventories in 1993–1994, along transects intersecting 400 widely distributed AP3 stands. Trees were aged from increment cores taken at breast height (~1.3 m) from canopy codominant trees (sensu Oliver and Larson 1990). Reportedly, sampling was restricted to codominants so as to avoid biasing estimated stand ages by including the tallest trees, which were presumed to be veterans of the most recent disturbance.

AAD1 contained 557 aspen or balsam poplar stem ages sampled from 166 aspen-dominated stands. We stratified the samples into four AP3 age classes (1900s, 1880s, 1860s, and older) to qualitatively evaluate changes in stand age structure over time. Using the same stratification, a one-way ANOVA compared the relative magnitude of within-stand effects (uneven stand age structures) and between-stand effects (stands of different true ages assigned to the same AP3 age class). The ANOVA was restricted to stands with a sample size ≥4.

The second data set (AAD2) contains age, diameter, and height measurements for a further 2968 aspen stems, sampled from 897 AP3 stands. Almost all were either pure aspen or mixed stands. Unlike AAD1, AAD2 stems were sampled from all canopy strata. With AAD2 we established an empirical relation between the within-stand variances of stem age and diameter. For a few stands of 1880s origin or earlier, sample sizes were large enough to examine age structures at the
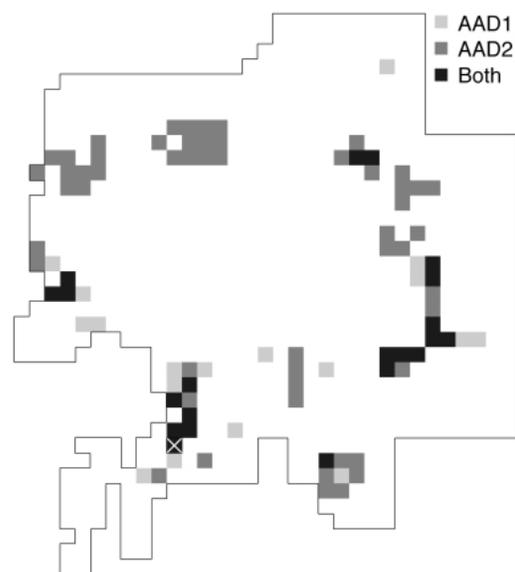
FIG. 3. Townships represented in data sets AAD1 and AAD2. The location of the Calling Lake field sites is marked by the white cross. The spatial distribution of sampled townships is partly determined by road access ca. 1995.
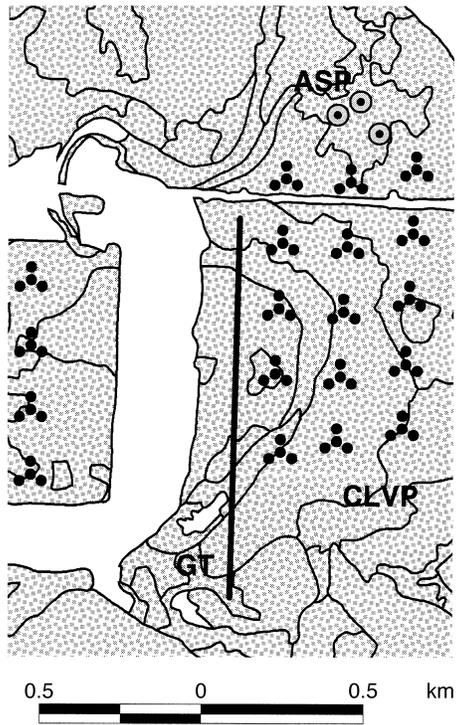
FIG. 4. Schematic sampling design for the three data sets collected at the Calling Lake field sites: an example grid of 0.04-ha vegetation plots (CLVP); a gap transect through several young stands, 100 m into the forest east of a large clearing (GT); and three age-structure plots, randomly placed within an old aspen stand (ASP).

stand level, which was not possible with data set AAD1. Additional uses of AAD2 are described in *Simulation*, below.

Calling Lake vegetation plots

In 1993–1995, vegetation data were collected in conjunction with the Calling Lake Forest Fragmentation Experiment (Schmiegelow et al. 1997). Permanent sampling points were placed on 200-m grids in each of 24 relatively homogeneous forested areas of either 1, 10, 40, or 100 ha, for a total of 186 points. Vegetation was sampled at four 0.04-ha plots at each point, one centered on the point, and three centered at 40 m distance at 0°, 120°, and 240° (Fig. 4). In each plot, trees and tall shrubs were tallied by species and diameter class (8–15, 15–23, 23–38, and >38 cm dbh [in diameter at breast height]). Saplings (<2.5 cm dbh) and poles (2.5–8 cm dbh) were tallied in 0.008-ha nested subplots. To relate the plot data to AP3 stand attributes, most of the points were linked to a digitized forest inventory map of the study area. For the present study, we selected plots situated in aspen-dominated stands of AP3 ages 1860, 1880, and 1910–1930—the latter class is abbreviated as "1920." There were 280 plots in 11 1860s stands, 67 plots in four 1880s stands, and

51 plots in three 1920s stands. We refer to this data set as "CLVP" (Calling Lake Vegetation Plots).

Gap dynamics should cause heterogeneity in age-class structure to increase over time. To test this prediction, we exploited the relation between within-stand variances in stem size and age, obtained from AAD2. CLVP stem size-class counts were compared pairwise within stands, using Magurran's (1988) version of the Morista-Horn similarity measure (Wolda 1981). This statistic takes values between 0 and 1, with values close to 1 indicating a high degree of similarity between pairs. The procedure yielded samples of similarity measures of size n_i $(n_i - 1)/2$, where n_i is the number of plots in the ith stand. These samples were pooled by AP3 stand age class, and the pooled means compared by pairwise t tests. Large sample sizes compensate for the non-normality of the distributions (Zar 1984).

Gap survey

To test for gap formation and recruitment response in young aspen stands, we conducted a gap survey (Runkle 1992) in the Calling Lake study area, during July of 1995. We ran line transects through portions of five aspen stands with an AP3 origin of 1910 or 1920, which were thus expected to be pyrogenic, even-aged stands 75–85 yr old. Transects were at least 75 m from mapped stand boundaries or recently cleared areas. The total transect length was 2.45 km, excluding encounters with seismic cut lines, meadows, or unmapped inclusions of other stand types. Canopy gaps were defined by areas of open sky formed by the death of one or more trees. The expanded gap is that polygon whose vertices are the stems of the canopy trees surrounding the canopy gap. For each canopy gap encountered, the area of the expanded gap was estimated by an elliptical approximation from measured axes. The total stand area in gaps was estimated by a line-intercept method (Runkle 1992). To estimate stand ages, the nearest canopy codominant aspen was cored and sized at breast height (1.37 m), every 50 m along each transect, and at the termini. In pyrogenic stands in western Canada, aspen saplings generally reach breast height within 2 yr (Peterson and Peterson 1992:51), so no age-to-dbh correction was applied when aging the cores.

Within each expanded gap, all individual trees and tall shrubs were tallied by species and height class (Class 1: 0.3–1.0 m, Class 2: >1.0–3.0 m, Class 3: >3.0–5.0 m, and Class 4: >5.0 m). For stump-sprouting species such as alder and willow, the height class was taken from the tallest living stem. The species, dbh, and condition of each apparent "gap maker" larger than 10 cm dbh was recorded, including standing dead trees, snags, and recently downed logs. Where discernible, the "gap winner," or stem considered most likely to reach the canopy, was noted. Vegetation sampling within the expanded gap partly takes into account the enlarged, displaced microclimatic effects of canopy openings at high latitudes (Lertzman et al. 1996).

For each expanded gap, we established a size-matched circular control plot under the closed canopy. Controls were located as close to due south of the gap as possible, at least three gap radii from the gap's edge. We tested for differences in stem density and height class structure, by species, between canopy gaps and controls using χ^2 tests. We compared species' responses to canopy gaps using paired-sample t tests on distributions of contrasts C_{ij}, defined as

$$C_{ij} = g_{ij}/g_i - c_{ij}/c_i$$

where g_{ij} is the stem count of the jth species on the ith gap and g_i is the total stem count in the ith gap; c_{ij} and c_i are the analogous counts for the ith control plot.

Age-structure plots (ASP)

As a direct test for whether older aspen stands have locally uneven, spatially heterogeneous age structures, we established three randomly placed 0.01-ha circular plots in each of three 1860s aspen stands in the Calling Lake area. The stands had <15% spruce in the canopy, and between 40 and 70% crown closure. In each plot, the species and dbh of each tree or tall shrub was recorded. All stems of 2.5–30 cm dbh were aged, using basal disks for stems <5, and increment cores at breast height otherwise. Stems ≥30 cm dbh were assumed to belong to the original cohort, and assigned a nominal age of ≥120 yr. We refer to this data set as ''ASP.'' Within- and between-stand age-class variability was assessed graphically.

Results for the gap survey and ASP data refer to specific AP3 stands by a three-digit code, unique within the study township. The arrangement of CLVP plots, the gap transects, and the age-structure plots is represented schematically in Fig. 4.

Simulation

To simulate aspen stand dynamics, we used a simple cellular-automata model (e.g., Wissel 1992) defined by three parameters: *age* (*A*), the maximum life span of an individual stem; *gap* (*G*), the minimum gap size (in units of cells) within which successful regeneration can occur; and *fill* (*F*), the number of years required for one member of a regeneration cohort to reach the canopy, thereby filling the gap. Each model cell represents the area that would be occupied by a single mature canopy tree. The model is initialized so that every cell contains one tree of age *F*, representing an even-aged stand at the end of the stem exclusion stage (Oliver and Larson 1990). At each annual time step, trees older than *F* are subjected to independent random mortality. As with forest-gap models of the JABOWA lineage (Urban and Shugart 1992), mortality is age independent, at rates such that 1% of stems survive to the maximum age. The death of a tree forms or expands a canopy gap. Regeneration occurs within an empty cell whenever at least *G* of the cell's neighbors contain trees of age less than *F*. Thus, gap expansion leads even-

tually to regeneration. Self-thinning within regeneration cohorts is not modeled explicitly: regeneration within a cell is conceived as a pulse of recruits, exactly one of which will reach the canopy. The model was parameterized to simulate aspen, with $F = 50$ yr (see Fig. 9 and Table 1, below), $A = 200$ yr (Perala 1990) and $G = 3$. The three parameters were estimated from the literature, or through simulation experiments, prior to the field component of this work. Our simulations used a 50×50 grid of cells. The area corresponding to a cell is not fixed, but in this case our grid represents an area of ~2.2 ha (see *Results: Simulated aspen stand dynamics*, below).

We used the model to simulate trajectories of canopy stem density and age structure. From a phase plot of simulated population mean age vs. standard deviation, we developed a qualitative test for old-growth aspen stands. We applied the test to data set AAD2, to check for large errors in age estimation of old stands, which we predicted as a consequence of gap dynamics in this system. From simulated stand maps of old aspen stands, we conducted Monte Carlo experiments to evaluate the performance of small-sample maxima of stem ages as estimators of stand age.

RESULTS

Gap survey

We found 41 canopy gaps intersecting 282 m (11.5%) of the 2.45-km transect length (Table 1). The mean size of expanded gaps was 52.3 m²; the size distribution (Fig. 5) describes the scale of autogenic disturbances in these stands. The five sampled stands varied in age (Table 1), but were generally younger than their AP3 (Alberta Phase 3 forest inventory) age classes of 1910 and 1920 would suggest. Over the range of our data (44–68 yr), the proportional stand area in expanded gaps (y) increases with stand age in years (x), as $y = -0.17 + 0.0047x$ ($r^2 = 0.83$, $P = 0.031$, $n = 5$ stands.) For the parameter estimates, 1 SE = 0.068 for the y-intercept and 1 SE = 0.0012 for the slope. The age

TABLE 1. Gap-transect summary, northeastern Alberta, Canada.

Stand ident.†	Transect length (m)	Stems aged‡	Canopy age (yr)§	Gaps found	Gap area (%)‖
247	396	8	44.2 ± 2.9	3	5.9
219	388	10	48.6 ± 1.8	3	3.6
229	370	8	48.7 ± 3.0	6	8.1
303	465	9	59.6 ± 3.6	8	10.3
312	836	19	67.2 ± 4.8	21	16.6
Total	2,455	54		41	10.4

† Identification code of the mapped forest stand where the transect was run.
‡ The number of stems cored and successfully aged.
§ Canopy age (mean ± 1 SD) estimated from the sample mean stem age.
‖ The estimated percentage of stand area within expanded gaps.

FIG. 5. Size distribution of 41 expanded gaps in five boreal aspen stands, northeastern Alberta, Canada.

FIG. 6. Mean stem density in aspen canopy gaps vs. control areas, by species. PIGL = *Picea glauca*, white spruce; POBA = *Populus balsamifera*, balsam poplar; POTR = *P. tremuloides,* trembling aspen; BEPA = *Betula papyrifera*, paper birch; ALSP = *Alnus* spp., alder shrubs; SASP = *Salix* spp., willow shrubs.

when gap formation begins is given by the *x*-intercept of 36.2 yr, close to our prediction of 40 yr.

Vegetation responses.—Aspen, balsam poplar, and birch were more abundant in the expanded gaps than in controls (Fig. 6, χ^2 = 22.0, df = 5, P = 0.00053). Poplar density was greater by a factor of 3 (from 148 to 443 stems/ha) and aspen density by a factor of 2.2 (from 454 to 1002 stems/ha). By analysis of contrasts, these responses do not differ significantly (P = 0.27). However, the responses of both trembling aspen and balsam poplar exceeded that of white spruce (P = 0.024 and P = 0.0057, respectively). Excluding stand 247 (see *Gap formation* below), mean white spruce densities were also higher in gaps than in controls (74 vs. 37 stems/ha).

Species-specific height responses were not significant (Table 2), except for white spruce, which may be taller in gaps than in controls (χ^2 = 7.05, df = 3, P = 0.07). Several gaps contained white spruce stems nearing the base of the canopy (~15 m), but no such stems were found in the control plots. However, we found significant between-species differences in height-class structures: saplings of aspen were shorter than those of balsam poplar (χ^2 = 86.7, df = 3, P < 10^{-6}) and of birch (χ^2 = 65.2, df = 3, P < 10^{-6}), with proportionally more stems in the 0.3–1.0 m height class. Birch and balsam poplar height structures did not differ. We conclude that the process of gap formation in young aspen stands is accompanied by elevated recruitment of aspen and other shade-intolerant tree species, but is not associated with increased height growth.

An unambiguous gap winner was identified in 24 of 38 gaps (not counting the three gaps from stand 247, discussed below–see *Gap formation*): balsam poplar won in 9 gaps (38%), white spruce in 7 gaps (29%), aspen in 6 gaps (25%), and paper birch in 2 gaps (8%). Of the remaining 14 gaps, 5 gaps had a dense growth of alder or willow, and the rest generally had numerous stems of aspen or poplar <3 m in height, with no con-

spicuous dominant. From CLVP (Calling Lake vegetation plots), the approximate canopy composition of these stands was 77% aspen, 19% balsam poplar, 2% white spruce, and 1% birch. The species distribution of gap winners is disproportionate to the species composition of the canopy. Although white spruce exhibited the greatest proportional response, the majority of gap winners were shade-intolerant hardwoods, mostly balsam poplar. The median heights of aspen and poplar gap winners were 2.5 m and 2.8 m, respectively. Most of these saplings have escaped light competition from the shrub layer, and may be capable of reaching the canopy, especially as light levels in temperate deciduous forests increase slightly with height, up to the base of the canopy (Hutchison and Matt 1977).
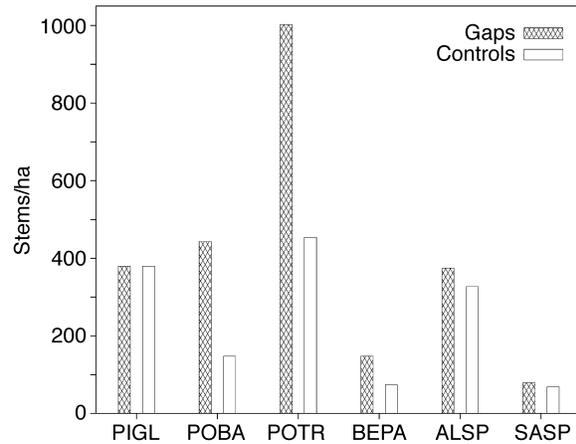
Gap formation.—We identified 111 gap makers, of which 80% were aspen and 18% balsam poplar; the remainder were *Populus* that we could not identify to species in the field because of advanced decay. This is proportionate to species composition of the canopy, as reported above. The mean number of gap makers per canopy gap was 2.7 trees. In the two older stands (303

TABLE 2. Height-class structures of understory tree species in 41 expanded canopy gaps (2143 m²) and paired control areas.

Species	Gaps				Controls			
	1	2	3	4	1	2	3	4
Populus tremuloides	71	117	1	1	31	53	1	1
P. balsamifera	7	53	17	7	2	18	4	4
Picea glauca	20	43	3	6	27	42	3	0
Betula papyrifera	3	18	4	3	3	5	2	4

Note: Table entries are total stem counts in each of four height classes (height class 1, 0.3–1 m; class 2, >1–3 m; class 3, >3–5 m; class 4, >5 m).

and 312 of Table 1) the gap makers were significantly smaller in diameter than the living canopy ($t = -5.05$, $P < 0.001$ and $t = -4.5$, $P < 0.001$, respectively). There was no significant difference between the diameters of gap makers and canopy stems in two of the younger stands. Except in stand 247, we did not observe any large downed trees that could, in falling, have created the gaps mechanically. We conclude that the usual mechanism for gap formation in aspen stands below 70 yr of age is consecutive, adjacent mortality of canopy stems. The observed mortality is consistent with self-thinning.

In stand 247, gap makers were significantly larger than the surrounding canopy ($t = 4.7$, $P = 0.0035$). This stand is anomalous in several respects, and is apparently the relic of a mature aspen–spruce stand that was damaged by a low-intensity fire in 1968 (Alberta Environmental Protection, *unpublished archival maps*). Some of the original canopy was still standing, but large, highly decomposed downed logs were abundant; these features were not present in the other four stands. Based on pooled samples from the gaps and controls, the density of white spruce saplings in stand 247 was 2,714 stems/ha, compared with a mean of 51 stems/ha in the other four stands. The other four stands exhibited no conspicuous evidence of past fire. However, we found clear evidence of a ~50-yr-old burn in a moist area just south of stand 219. This stand probably originated in the 1040-ha ''Long Lake'' burn of 1941, mapped by Delisle and Hall (1987). Thus, at least two of the five gap-transect stands appear to be pyrogenic, as we have assumed.

Indirect evidence for gap dynamics

Age-structure plots.—In our age-structure plots within 1860s aspen stands, we found uneven age structures, at both the plot and stand scales (Fig. 7). Stand age structures were spatially heterogeneous at the 0.01-ha sampling scale, consistent with past recruitment in asynchronously formed canopy gaps. Moreover, the presence of *Populus* stems in the 60–90 yr age classes argues that some of the observed recruitment in gaps within 48–69 yr old stands can survive to reach the canopy. The sample mean density of white spruce saplings in these stands was 290 stems/ha. We conclude that these older stands represent later stages in the development of the younger stands sampled by the gap survey.

Heterogeneous size-class structures.—Within-stand heterogeneity in aspen size-class structure increases with stand age (Fig. 8). Mean Morista-Horn statistics were 0.87 in 1920s stands, 0.71 in 1880s stands, and 0.58 in 1860s stands, and these means are different ($P < 10^{-7}$). In 36 AAD2 stands where 10 or more stems were measured, sample standard deviations of age and diameter at breast height (dbh) were correlated ($r^2 = 0.74$, $P < 0.001$). We therefore conclude that within-stand spatial heterogeneity in age structure also in-
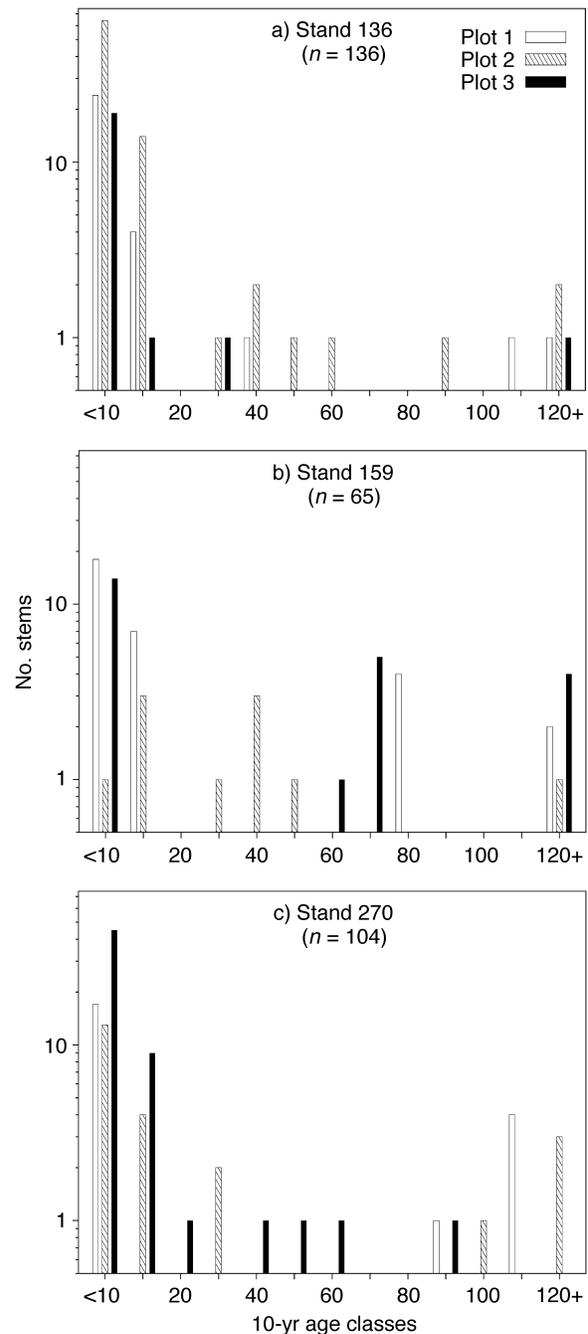
FIG. 7. *Populus* age structures in 100-m² sample plots, randomly placed within three different 1860s-origin aspen stands. Age class ≥120 yr represents 15 canopy stems >30 cm dbh that were not cored; n = no. of stems.

creases with AP3 stand age, and that the spatially heterogeneous, uneven age structures of data set ASP (Fig. 7) are typical of old aspen stands in the Calling Lake area.

Pooled stem-age data sets.—Pooled aspen age samples from AAD1 show that different AP3 age classes have distinctive stand age structures (Fig. 9). Except
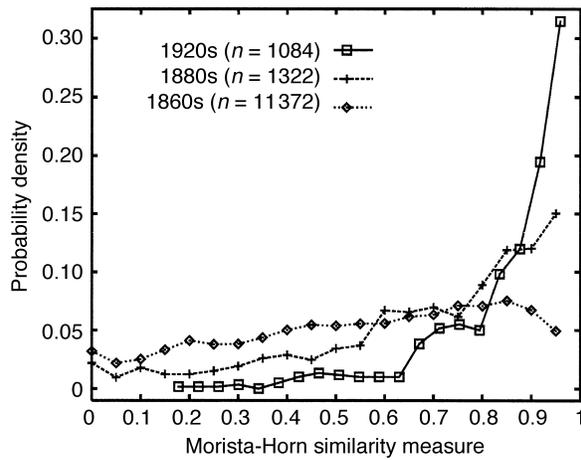
FIG. 8. The distributions of within-stand Morista-Horn similarity measures of aspen size structures from the Calling Lake vegetation plots (CLVP) data set; n = no. of pairwise comparisons used to generate the distribution of similarity measures. The distributions show that spatial heterogeneity increases with stand age.

in the oldest (1850s) age class, the distributions have peaks at about the expected ages. The 1850s stands are dominated by young stems, although a few trees of the expected age (~150 yr) are present. The canopy co-dominant sampling regime censored the age distributions, imposing a lower limit of ~50 yr. The three older age classes are all dominated by stems far too young to belong to the putative original cohort.

By one-way ANOVA, between-stand variability exceeded within-stand variability in 1900s stands ($F_{7,34}$ = 35.7, $P < 0.001$), 1880s stands ($F_{6,28}$ = 4.03, P = 0.005), and 1860s stands ($F_{3,15}$ = 3.92, P = 0.030). Samples sizes for older AP3 age classes were insufficient for the analysis. The hypothesis that these collections of stands have the same mean ages must be rejected in all cases. However, for our purpose the important result is that the proportion of sample variance due to within-stand variability increases with AP3 age. That is, canopy age structures become increasingly uneven in older stands, consistent with our field data (CLVP and ASP).

This interpretation of the ANOVA is supported by
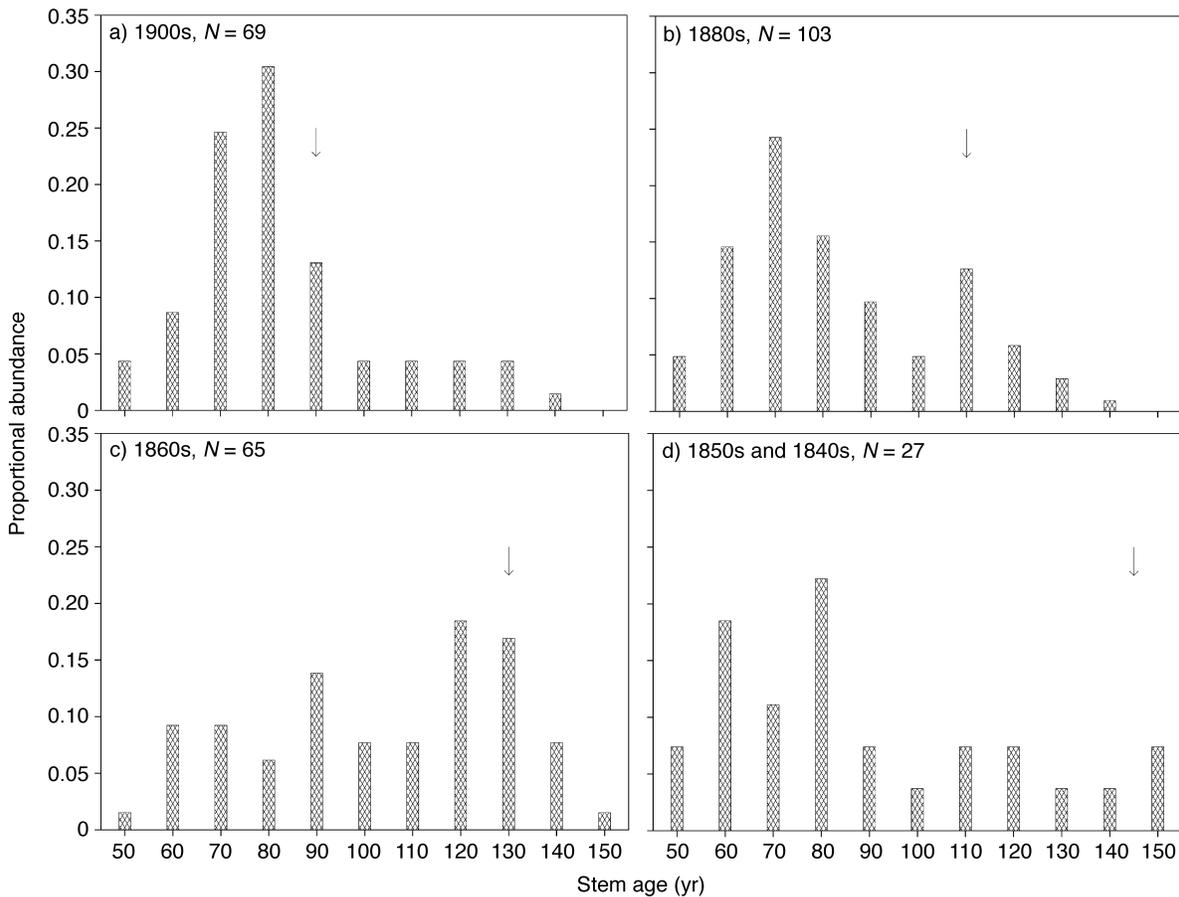
FIG. 9. Pooled age structures of canopy codominant aspen trees sampled from four age classes of aspen or mixed aspen–white spruce stands: (a) 69 stems from 26 stands with estimated decade of origin 1900s; (b) 103 stems from 54 1880s stands; (c) 65 stems from 31 1860s stands; and (d) 27 stems from 21 stands dated 1850s and 1840s. The expected age of stems is shown by an arrow in each panel.
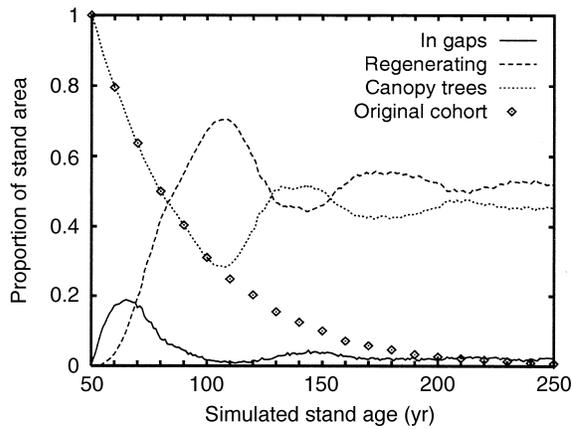
FIG. 10.   Simulated dynamics of gap and canopy stem density in an initially even-aged stand of aspen-like trees.

the larger data set AAD2. There, in stands with sample size ≥6, the mean age range was 23.7 yr in 1880s stands (*n* = 7), and 69.8 yr in 1860s stands (*n* = 6) (recall that sampling for AAD2 was not deliberately biased towards one stratum of the canopy, unlike AAD1). The few 1880s and 1860s AAD2 stands with sample size ≥10 contain some stems of roughly the expected age, and then a second group of stems about 50 yr younger, aged 60–80 yr. This is consistent with data sets AAD1 (Figs. 9b and c) and ASP (Fig. 7). The 40–50 yr lag between cohorts is consistent with the age at which gap formation begins.

The forgoing suggests that many 1880s and 1860s stands may contain stems of all age classes, as found in the ASP plots (Fig. 7). If so, stand features resembling aspen understories should be common. According to AP3, 31% of aspen-dominated stands dated 1880 or earlier have an understory with a deciduous component. This is likely an underestimate, since AP3 was interpreted from leaf-on aerial photography in which understories would be obscured. We conclude that uneven-aged aspen stands are abundant and widespread in the greater study area.

Simulated aspen-stand dynamics

We first review the model parameter values in light of our data. The "fill" (*F*) parameter value $F = 50$, the time required for a regenerating stem to reach the canopy and fill a gap, is consistent with AAD1 (Fig. 9), in that very few stems <50 yr were sampled as canopy codominants. The mean stem diameter sampled along the gap transects (20.4 cm dbh) implies a mean crown radius of ~1.5 m (Jones and DeByle 1985). Then the "gap" (*G*) value $G = 3$ corresponds to an expanded gap area of ~48 m², close to the sample mean of 52.3 m² (Fig. 5). Since we are modeling circular crown projections inscribed within square grid cells, the 50×50 simulated grid represents an area of ~2.2 ha. With the "age" (*A*) value at $A = 200$, 20.3% of the original cohort survived to 120 yr, a density of 231 stems/ha.

The observed density of the presumptive original cohort in 120-yr-old stands (data set ASP) was 156 stems/ha. Stem densities of 500–600 stems/ha have been reported for 120-yr-old aspen stands (Peterson and Peterson 1992), but no age- or size-structure data is supplied with these estimates. We conclude that the mortality component in the model is approximately correct. However, in the absence of life-table data adequate to calibrate the mortality model, the results reported here must be treated as illustrative.

In simulated stands, the area occupied by "canopy" stems (those older than 50 yr) declines exponentially between 50 and 100 yr. After 100 yr new recruits begin to enter the canopy, and canopy area stabilizes, after some damped oscillation, at about 46% (Fig. 10). The area of forest in small, non-regenerating canopy gaps rises quickly to 19% as the canopy first begins to open. In the early stage of gap dynamics, most gaps are too small to allow regeneration. However, in stands ≥100 yr old, the area of "empty" gaps stabilizes at ~2%. In the model, the short life span of aspen and the large openings required for regeneration prevent the maintenance of a uniform, closed canopy forest once the original even-aged canopy begins to break up. In comparison, simulations parameterized for a longer lived, more shade-tolerant species (e.g., *Pseudotsuga menziesii*) predict a steady-state canopy closure of ~80%.

The simulated canopy age structure at 150 yr (Fig. 11) agrees fairly closely with the empirical age structure of 140–150 yr old stands in data set AAD1 (Fig. 9d), especially in the younger age classes. However, the model predicts more survivors of the original cohort than are actually found in AAD1. We attribute this to four factors: (1) the fixed mortality rate used in the model may be incorrect, at least for older individuals; (2) high rates of decay in old stands (Hiratsuka and Loman 1984) makes aging the oldest stems difficult,
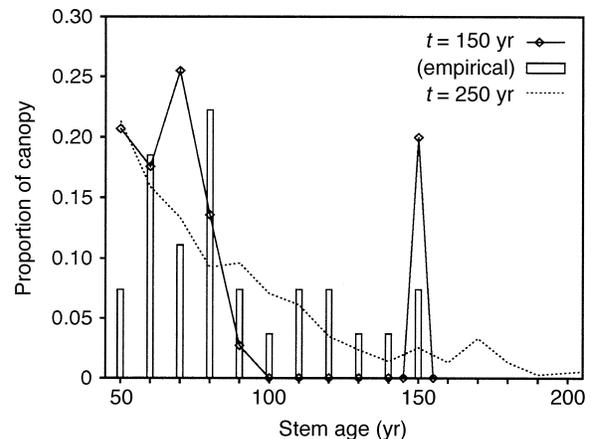
FIG. 11.   Simulated aspen canopy age structure at $t = 150$ and $t = 250$ yr from stand origin. By 300 yr (not shown), a near-stable age structure has developed. At $t \le 100$ yr, the canopy is even aged. The pooled age structure from some reportedly 150-year-old aspen stands (Fig. 9) is also shown.
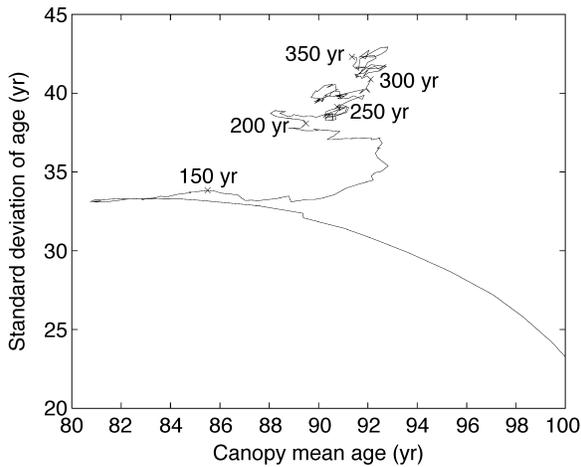
FIG. 12. Simulated trajectory of the mean and 1 SD of canopy tree ages, starting at simulation year 110.

TABLE 3. Performance of small-sample maxima as an estimator of stand age, determined by sampling from simulated stand maps at $t = 150$, 200, and 250 yr, at sample sizes (n) of 5, 10, and 20 stems.

Stand age (yr)	Minimum stem age (yr)	5 stems		10 stems		20 stems	
		p	$\tilde{m}$	p	$\tilde{m}$	p	$\tilde{m}$
150	25	0.55	118	0.80	137	0.99	149
	50	0.70	130	0.93	145	0.99	149
200	25	0.16	119	0.35	146	0.51	165
	50	0.29	139	0.41	158	0.72	182
250	25	0.04	131	0.07	152	0.10	168
	50	0.07	149	0.09	164	0.19	185

Note: To simulate the effects of different sampling regimes, stem ages were censored at 25 and at 50 yr. The statistic p is the proportion of samples that correctly aged the stand, and $\tilde{m}$ is the sample mean of sample maxima. Each data pair is the result of 100 independent draws from the simulated stands.

which biases the samples in AAD1; (3) the AAD1 canopy codominant sampling selects against the tallest, oldest aspen trees; and (4) small errors in AP3 decades of origin—a decade either way would tend to increase the number of stems in the 100–140 year age classes. We conclude that the model is a reasonable qualitative representation of aspen stand dynamics in the absence of succession.

The model predicts that a stable (negative exponential) canopy age structure develops by about 250 yr (Fig. 11). However, the means and standard deviation of canopy tree ages are nearly stable after 120 yr, with $\mu \sim 90$, $\sigma > 35$ yr (Fig. 12). Mean canopy age is a negatively biased estimator of age in simulated stands older than 100 yr, consistent with the empirical data summarized in Figs. 7 and 9. Small-sample maxima are negatively biased estimators in stands 150 yr or older (Table 3). These estimators would be worse behaved in real stands, because the heartwood of older stems is often badly decayed.

In the model, as in reality, the original canopy will eventually decay past the detection threshold of any sampling protocol. In AP3, this threshold is defined as 5% canopy closure. Depending on the mortality rate used in the model, this threshold is passed between 120 and 160 yr. Aspen stands exceeding this age would be incorrectly aged, based on the height of the first regeneration wave. Fig. 12 implies that such errors could be detected from stem age data. We examined AAD2 in this light (Fig. 13) and found that 9–10% of stands in the 1900s, 1920s, and 1940s AP3 age classes have sample mean ages of about 80 yr with standard deviations >20.0 yr, characteristic of simulated stands 110 yr or older. These three age classes comprise 60% by area of the aspen and mixed stands in the greater study area, so at least 6% by area of the commercial forest may be significantly under aged in the inventory.

DISCUSSION

We found that canopy gaps begin to form in aspen stands about 40 yr after stand initiation, by accumulation of adjacent mortality of canopy trees. Kneeshaw and Bergeron (1998) also report multiple tree-fall gaps in young aspen stands in Quebec, which they attribute to synchronous mortality of small clones. However, by simulation, spatially independent random mortality explains our observations. Relative to matched control areas, gaps exhibit elevated recruitment of shade-intolerant hardwoods, mostly aspen and balsam poplar. White spruce is a gap winner more often than expected given its abundance in the canopy, and we found some evidence that gaps facilitate recruitment or height growth for this species. Nonetheless, in four of five stands surveyed, the current density of understory white spruce was insufficient to replace the existing aspen canopy.
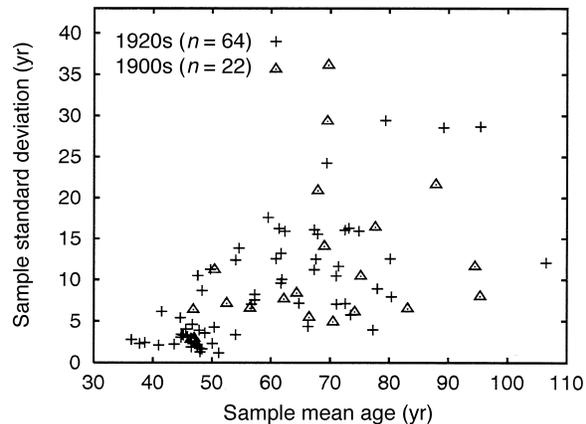
FIG. 13. Sample mean age and 1 SD for stands in the AAD2 data set having an AP3 (Alberta Phase 3 forest inventory) origin of 1900s or 1920s, and a sample size ≥6; n = no. of stands.

Elevated aspen recruitment within canopy gaps has been correlated with small increases in irradiance. Mean light levels beneath 40-yr-old aspen stands are 18–19% of above-canopy values (Lieffers and Stadt 1994, Carlson and Groot 1997). Experimental circular openings of 4.5-m radius ($\sim$60 m^2) raised light transmittance to 26% (Carlson and Groot 1997). In these openings, first-year sucker densities were 15 times greater than beneath the closed canopy (Groot et al. 1997). Soil temperature is thought to be the main exogenous factor influencing sucker development in aspen (Peterson and Peterson 1992), but openings of the sizes we found do not raise seasonal mean soil temperature at these latitudes (Carlson and Groot 1997). Therefore, we suggest that the elevated recruitment we observed in canopy gaps is due to small increases in light levels at the forest floor, which enhance initiation or survivorship of aspen and poplar suckers. However, our data cannot distinguish the relative importance of increased resource levels and the release from apical dominance resultant from overstory mortality, which would also elevate suckering.

In three aspen-dominated stands with inventory ages of 130 yr, we found spatially heterogeneous, uneven age structures, consistent with protracted gap-phase dynamics. Aspen stems old enough to have originated in early gaps were present. Spatially extensive stem-age data, and forest inventory understory attributes, show that such stands are both abundant and widely distributed in our greater study area. A simulation model shows that such stands could be maintained indefinitely, converging to a stable age structure by about 250 yr. The model predicts features of the age structure of old aspen stands that are found in $\sim$10% of stands classified as young in the forest inventory. Deciduous stand ages estimated from air-photo interpretation or from canopy mean ages are negatively biased for stands whose true age exceeds 120 or 100 yr, respectively. Current estimates of the age structure of the boreal mixed-wood forest are therefore compromised.

The aspen stands surveyed for canopy gaps and the older stands whose age structures were measured may be construed as a chronosequence, although they were not selected as such, as white spruce densities in the former category were not known in advance. This chronosequence does not reflect the only developmental pathway for pyrogenic aspen stands (see *Introduction: Aspen stand dynamics*, above). For example, near to our field sites we have observed mature aspen stands with well-developed white spruce subcanopies, indicative of the regionally classic transition from aspen to white spruce dominance. Evidently, considerable variation in the rate of white spruce recruitment is to be expected even within a relatively small, comparatively homogeneous area (see also Lieffers et al. 1996).

The existence of old-growth stands in the boreal mixed-wood forest has only recently been recognized. Stelfox (1995) and Timoney and Robinson (1996) have characterized old-growth deciduous stands in the Alberta mixed-wood, in terms of features of the canopy and forest floor and of the time required for these features to develop: $\sim$120 yr. Our results are consistent with a functional definition of the old-growth condition in boreal forests, based on the processes of individual mortality and regeneration that create and maintain uneven-aged stands, and the relative dominance of the original cohort (Kneeshaw and Burton 1997). Further, our findings emphasize that gap dynamics are not restricted to late-successional forests composed of shade-tolerant species. Assuming otherwise compromises studies of disturbance regimes, forest age structures, and landscape dynamics, through the uncritical use of inappropriate or biased data sets and sampling methods.

Our results may apply to other regions of the circumpolar boreal forest in which aspen or a functionally similar species is abundant. They may also bear on the study of any ecosystem characterized by intense, episodic disturbances such as fire, where neither the rate of disturbance nor the present patch-age structure are precisely known. To compare estimates of the disturbance rate and patch-age structure requires statistical independence. The derivation of rates from age-structure data that either assume that old stands do not exist or else depend on sampling methods biased against their detection is tautological. This may seem obvious, but the experience in western Canada, where both sorts of errors have been made, is probably not unique.

The extended mixed-wood stage revisited

Here, we elaborate the implications of the extended mixed-wood stage described by (Kabzems et al. (1986). Of five 44–67 yr aspen stands that we surveyed for gaps, four had low densities of understory white spruce (51 stems/ha, above 30 cm), and only $\sim$2% of spruce in the canopy. The three 1860s stands containing our age-structure plots had <15% spruce in the canopy, and $\sim$290 stems/ha of understory spruce. If most of these survive to reach heights of 20 m or more, a matter of perhaps 100 yr (Lieffers et al. 1996), the stands would appear to photo-interpreters as 100–120 yr old mixed stands (Alberta Forest Service 1985). However, their true age would exceed 200 yr. If this alternative developmental pathway, where the amount of canopy spruce increases incrementally, is common, current estimates of forest age-class structure are further compromised. We outline a new model of boreal mixed-wood dynamics, which explicitly recognizes this possibility.

Soil moisture deficits sufficient to limit white spruce recruitment are not characteristic of the mixed-wood's climate (Hogg and Schwarz 1997). Rather, on upland mesic sites, immediate post-fire recruitment is limited by the availability of mineral-soil seedbeds and by seed rain. Both factors are related to the size, intensity, and frequency of fire. Seedling establishment and growth are also limited by herbaceous competitors (Lieffers

and Stadt 1994), which rapidly colonize mineral soil. Thus, the coincidence of fire with a white spruce mast year may be a necessary condition for a high density of white spruce recruitment (Peters, Dale and Mac-Donald [University of Alberta], *unpublished data*). Large fires in the mixed-wood burn heterogeneous areas containing spruce, mixed and aspen stands of various ages and condition (Cumming 1997). These fires will not always coincide with a mast year. However, high densities of young aspen stems will initially develop by suckering on most burnt mesic sites, provided even low densities of canopy aspen were present (Lavertu et al. 1994). Large fires therefore tend to homogenize the forest.

Recruitment in the post-fire decades will be delayed pending a suitable conjunction of seed source and substrate. Autogenous substrate, in the form of downed decayed aspen logs, is important in 50–80 yr old aspen stands (Lieffers et al. 1996). This substrate is also abundant in ≥120-yr-old stands (Lee et al. 1997). Once a few white spruce trees establish and eventually reach the canopy (perhaps facilitated by gap formation, as our data suggest), local seed production will dramatically increase because seed trees are more abundant, dominant within the stand, and hence more likely to produce large crops of viable seed (Zasada and Viereck 1970). Since, in the meantime, gap dynamics will have maintained an aspen canopy and a resultant input of downed logs, recruitment into the understory will accelerate. Several successive generations of canopy trees (i.e., several centuries) could be required for white spruce to become dominant through these processes. Larsen and MacDonald (1988) report paleolimnological evidence of local dominance by *Populus* lasting for several centuries, followed by a gradual increase in white spruce. Of course, such stately dynamics are more plausible if fires are relatively infrequent.

Natural disturbance models and the boreal forest

If the rate of natural disturbance is to provide a basis for managing regions of the circumpolar boreal forest, as Hunter (1993) and Haila et al. (1994) have proposed, regional disturbance regimes must be quantified. Much of the boreal region is remote, and lengthy historical records of disturbance are unavailable. The only spatially extensive data sets available are likely to be photo-interpreted stand maps, as in Alberta and the rest of Canada. However, such inventories are designed primarily to estimate the available volumes of merchantable tree species. The "stand-origin" estimates they contain are best interpreted as the modal age of the dominant canopy layer. This cannot be assumed to equal stand age. An independent estimate of regional forest age structure is required.

There are several ways to proceed. Inventory "ages" could be validated against true stand ages, if these could be somehow determined. A landscape-scale age structure could be then estimated by applying the em-pirical error model to the inventory age classes. Another strategy is to characterize the regional natural disturbance directly, by estimating the parameter(s) of a theoretical model (Johnson and Van Wagner 1984). This can be done from a time series of maps of known fires or similar data, or by fitting a sample of known stand ages to a chosen model. A third method, which involves estimating the mean interval between fires from fire-scarred trees (Johnson and Gutsell 1994), would be difficult to apply to species such as aspen, which do not fire-scar readily. In the present case, if the 54 yr of fire-incidence data and mapped fires studied by Cumming (1997) (Fig. 1) are considered insufficient, then one must develop some way to estimate stand ages from field data. Thus, both approaches may ultimately depend on the ability to estimate the ages of forest stands.

Unbiased estimation of stand ages may prove difficult in the mixed-wood. We have shown that canopy mean age is biased. Some workers (e.g., Larsen 1997) use small-sample maxima of stem ages as an estimator. However the simulated sampling distribution of this statistic shows it to be an imprecise and negatively biased estimator in older stands. These results recapitulate previous work on disturbance-rate estimation by Fox (1989), who treated the effect of progressive loss of age indicators, such as members of an original cohort, and by Finney (1995) who also discusses the difficulty of unbiased selection of stands to be aged. Using the rate of natural disturbance as a guide to developing or evaluating forest management plans requires empirical data that are difficult to obtain in boreal forests.

A significant effort will be required to settle the issues we have raised. Direct methods of stand reconstruction have been applied to forests in coastal Alaska (Fastie 1995). These forests may be analogous to our mesic sites, in that stand development depends on a variable history of recruitment and growth of *Picea sitchensis* (Bong.) Carr., a species closely related to white spruce. These exhaustive methods could perhaps be applied to a carefully selected set of stands, in order to calibrate less direct but also less difficult and expensive methods based on structural attributes such as crown area and stem diameter distributions (Lorimer 1985). Other useful indirect measurements might include the joint sample age-class structure of aspen and white spruce, as given by simulation models such as we explored here. We hope that our results will encourage field ecologists, modelers, and statisticians to collaborate on this problem.

Regional management implications

Since the mid-1980s, essentially all of the boreal mixed-wood in western Canada has been brought under management, largely for the purpose of bleached kraft pulp production, with aspen as the most important raw material. The white spruce lumber industry has a longer

history, and has developed towards full utilization of the resource since the 1950s. The intended rotation ages are roughly 70 yr for aspen and 110 yr for white spruce. In view of these regional land-use decisions, at least three areas of concern arise from our results: (1) wildlife habitat availability; (2) sustainability of the white spruce harvest; and (3) carbon emissions from forest soils.

Older aspen and mixed stands are preferred habitat for many species of birds and mammals in the boreal mixed-wood (Stelfox 1995). We cannot say at present how common very old aspen may be, nor whether they differ significantly from the 120–130 yr old stands studied by Stelfox (1995) and colleagues, with respect to habitat quality or the community structure of any taxa. However, if old-growth stands are both older and more abundant than has been thought, the adaptationist argument that boreal communities are resilient to high rates of disturbance loses some of its force.

Problems of white spruce regeneration in the boreal mixed wood are reviewed by Lieffers and Beck (1994). White spruce and mixed stands tend to regenerate with high densities of aspen after harvesting, which at least temporarily inhibits spruce establishment or growth. Silvicultural interventions designed to prevent or ameliorate this effect are expensive and prone to failure. The present allocation of the white spruce resource is based on a long-run sustained-yield management policy, assuming an ~110-yr rotation. The feasibility of this rotation age depends on the reliability of the volume–age curves for spruce-bearing stands, which depend crucially on the estimated stand ages. If a significant portion of the stands now having merchantable volumes of white spruce followed an extended trajectory, and are ≥ 200 yr old, then the current white spruce harvest is unsustainable under present conditions.

Finally, forest management in the Canadia boreal is predicted to result in net carbon emissions (Kurz et al. 1997), mostly (68%) from soil pools of humified organic matter. In the western Canadian boreal, 63% of total stored carbon is in this form (Kurz and Apps 1999). These pools can continue to sequester carbon from litterfall and root turnover long after standing biomass equilibrates. Thus, very old aspen or mixed stands probably store larger amounts of carbon than younger stands of similar structure and composition. If so, forest management in the mixed-wood region will release more carbon than expected. Attempts to stabilize Canadian CO^2 emissions at 1990 levels, pursuant to international agreements, are predicted to have persistent negative impacts on the Alberta economy (Holling and Somerville 1998). Our results imply that stabilization or mitigation costs may be higher than expected.

Conclusion

The occurrence of gap-phase dynamics in aspen stands, the probable self-replacement of deciduous-dominated stands, and the possible abundance of old stands of mixed aspen and white spruce in an extended mixed-wood stage, seriously undermine current management strategies for large areas of western Canada, with important ecological and economic implications. Present rates of harvest are justified partly by an appeal to natural rates of disturbance by fire, which may have been overestimated. In that case, projected harvest rates combined with fire suppression are not consistent with a natural-disturbance management model, or with the model of landscape dynamics that we have outlined. We propose methods for improving estimates of the landscape age structure, and of increasing our understanding of the underlying stand and landscape dynamics. We suggest that the importance of gap formation and stand self-replacement may have been similarly underestimated in other parts of the circumpolar boreal forest. We urge that the issues raised here be considered in any planned application of natural-disturbance management models to these forests.

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