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# Structural development following fire in black spruce boreal forest

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## Abstract

We investigated stand development along a chronosequence on organic, clay and sand sites in black spruce boreal forest in northwestern Quebec, Canada. Our objectives were: (1) to describe trends and stages of structural development following fire; (2) to compare trends and stages of development both in isolation from and in conjunction with species replacement. We tested the hypothesis that although trends in structural development are similar among site types, productivity and composition affect the timing of developmental stages. Data on live trees, snags and logs were collected at 91 sites. Trends with time since fire were analyzed using segmented piecewise linear regression. On organic sites, tree basal area and density increased continuously with time since fire, while deadwood abundance decreased and then increased. Live tree basal area, tree density and deadwood abundance generally followed expected S-, N- and U-shaped trends, respectively, on clay sites, but often with decreases in later stages due to paludification. Fewer trends were significant on sand sites, although tree basal area decreased likely due to a change in species composition. Older forests on all site types were more structurally diverse. To estimate the timing of the stages of structural development, we introduce a new analysis technique which uses the breakpoints of the piecewise regressions. On organic sites, only three stages of stand development were evident, whereas a four-stage stand development model was appropriate for both clay and sand sites. We found that local conditions affected not only the timing of developmental stages, but also the number of stages and the trends themselves. We attributed these differences to changes in species composition and productivity. We refine the theory of structural development by representing patterns in both live and deadwood as two-stage trends with two possible outcomes for each stage. Our new method of determining the timing of the developmental stages using empirical data can be used to develop management practices that emulate structural development in order to conserve biodiversity on a landscape scale.

*Keywords:* Boreal forest; Chronosequence; Coarse woody material; Forest structure; Old growth; Piecewise linear regression; Structural development

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## 1. Introduction

Structural development is the dominant process following disturbance in forest ecosystems where there is no succession in the traditional sense of species replacement. In such ecosystems, forest structure is important for biodiversity since it provides habitat for many organisms, and is directly manipulated through forest management (Morrison et al., 1992; Jonsell et al., 1998; Franklin et al., 2002). It is thus not surprising that coarse-filter approaches aimed at the conservation of a representative array of stand structures have been proposed as a means for maintaining biodiversity in forest ecosystems (Hunter et al., 1988; Bergeron et al., 1999). Despite numerous studies on forest succession and several studies on particular structural components such as coarse woody material (e.g., Cline et al., 1980; Sturtevant et al., 1997; Clark et al., 1998), few empirical studies have specifically addressed the concurrent structural development of trees, snags and logs (but see Tyrrell and Crow (1993, 1994)). The boreal forest, which is relatively untouched by human activity, provides an ideal situation for investigating fundamental trends in structural development independent of succession since the lack of species replacement following disturbance is common in many forest stands (Carleton and Maycock, 1978).

Stages of stand development have been linked to species replacement (e.g. Palik and Pregitzer, 1993; Clark et al., 1998), but they can also apply to the development of different cohorts of the same species (fire origin and understory cohorts; Johnson, 1992). Although some authors have proposed up to nine developmental stages (e.g. Franklin et al., 2002), the four-stage model proposed by Oliver (1981) is the most familiar, and the most appropriate for the boreal forest (Chen and Popadiouk, 2002). The four stages (Oliver, 1981) are: (1) stand initiation dominated by tree establishment and abundant deadwood; (2) stem exclusion with the processes of decomposition and self-thinning (Chen and Popadiouk, 2002; Lee et al., 1997; Oliver, 1981); (3) understory reinitiation during which canopy break-up (Chen and Popadiouk, 2002; Lee et al., 1997) leads to the initiation of a new cohort (Chen and Popadiouk, 2002; Goebel and Hix, 1997; Oliver, 1981); (4) old growth characterized by high structural diversity (Cline et al., 1980; Goebel and Hix, 1997; Spies and Franklin, 1988; Sturtevant et al., 1997).

The abundance of forest structural elements appears to follow distinctive trends throughout stand development: (1) live tree density increases initially, then decreases to a plateau (e.g., Crowell and Freedman, 1994), hereafter referred to as an “N-shaped” pattern; (2) tree growth (basal area and canopy height) usually increases after a short delay, and then levels off in older forests (e.g., Spies and Franklin, 1988; Crowell and Freedman, 1994) in an “S-shaped” pattern; (3) deadwood abundance typically follows a well-defined “U-shaped” pattern of a decline followed by an increase then a plateau (e.g., Harmon et al., 1986; Spies and Franklin, 1988; Tyrrell and Crow, 1994; Sturtevant et al., 1997; Clark et al., 1998). Although the rate or timing may change, the patterns of these trends may be universal (Sturtevant et al., 1997). Attempts to determine the timing and lengths of stages of development based on these patterns have been theoretical (Bormann and Likens, 1979; Oliver, 1981), although a few studies use empirical data to estimate the timing of the transitions between two stages (e.g., Palik and Pregitzer, 1993; Harper et al., 2003). Such information would be useful to compare the timing and lengths of stages among different site types and forested ecosystems.

In this paper, we assess structural development on three different site types (organic, clay and sand, c.f. Gauthier et al., 1996) within black spruce boreal forest in northwestern Quebec, Canada. In this ecosystem, canopy structural development coincides with changes in dominant species composition towards black spruce (*Picea mariana*) on clay and sand sites, but is independent of species replacement in stands on organic sites which are always dominated almost exclusively by black spruce (Harper et al., 2002, 2003). Our specific objectives were: (1) to describe different trends and stages of structural development on three site types (organic, clay and sand) in black spruce boreal forest; (2) to compare trends and stages of development both in isolation from (organic sites) and in conjunction with species replacement (clay and sand sites). Using segmented piecewise linear regression, we identify stages of structural development and compare trends with time since disturbance on different site types in the black spruce boreal forest. We use our new approach to test the following hypothesis: although trends in structural development are similar among site types, different local conditions (e.g., productivity, composition) affect the timing of the developmental stages. We discuss how our results can refine the theory on structural development to better acknowledge the dynamics of boreal forest ecosystems.

## 2. Methods

### 2.1. Study area

We sampled sites in the black spruce boreal forest, in the northwestern part of the Abitibi region in Quebec and in the Lake Abitibi Model Forest in Ontario (48°92′–49°93′N; 78°64′–80°64′W; Fig. 1). The study area is part of the Lake Matagami Lowland ecoregion (Saucier et al., 1998) in the northern Clay Belt, a broad physiographic unit characterized by lacustrine deposits from the proglacial lakes Barlow and Objibway (Vincent and Hardy, 1977). The topography is relatively flat at an elevation of approx. 300 m asl. Soils are predominantly organic, with clay deposits and some till (Gauthier et al., 2000). According to nearby weather stations, mean annual temperature is 0.8/0.9 °C, annual precipitation is 856/792 mm, and there are 64/90 frost-free days (La Sarre, Quebec, and Iroquois Falls, Ontario weather stations, respectively, Environment Canada, 1993).

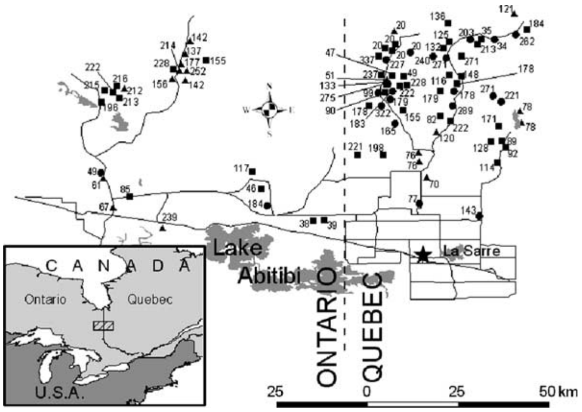

Fig. 1. Map of all the sites. Symbols represent the site type: organic (circles); clay (squares); sand (triangles). Sites are labelled with the time since the most recent fire. The inset map shows the location of the study area within Canada.

The forest mosaic in our study area is part of the *P. mariana*-moss bioclimatic domain (Saucier et al., 1998). *P. mariana* (black spruce) is dominant in stands of all ages on clay and organic sites, and in older stands on sand sites (Harper et al., 2003). Thus, succession converges to black spruce on all site types. Jack pine (*Pinus banksiana*) can be abundant on early–intermediate aged drier sites such as outwash deposits, old beaches and eskers, and some clay sites (Harper et al., 2003). Early successional species (*Populus tremuloides* and *Salix* spp.) are sometimes prominent in the youngest stands (Gauthier et al., 2000; Harper et al., 2003). Other common tree species include *Abies balsamea*, *Betula papyrifera* and *Larix laricina* (Harper et al., 2003). The disturbance regime in this region is characterized by large crown fires that kills most of the trees and aboveground vegetation; however, old-growth forests are still extensive, covering 30–50 % of the landscape (Harper et al., 2003). Moreover, the fire cycle has increased from 101 years before 1850 to 398 years since 1920 (Bergeron et al., 2004), which can result in an increase in the importance of older forest stands.

### 2.2. Sampling design

To determine changes in forest structure and composition with time since fire, we used the chronosequence approach in which stands of different ages are compared to provide insight into changes over time (e.g. Carleton and Maycock, 1978; Crowell and Freedman, 1994; Harper et al., 2002). We minimized potential shortcomings of the chronosequence approach by sampling 91 sites, and dividing the sites into 3 different site types. Using the reconstructed fire history for the region to determine time since the most recent fire (Bergeron et al., 2004), we selected site locations to span a variety of ages along a chronosequence. Accessibility and the lack of harvesting were also pre-requisites for site locations. Sites were classified as organic-hydric, mesic to subhydric-clay and xeric-sand (c.f. Gauthier et al., 1996) based on a combination of surficial deposit and hydric regime which were sampled at each site. Organic sites (25 sites) had an organic layer more than 60 cm thick and poor drainage; clay sites (46 sites) were clay deposits with moderate drainage; and well-drained sandy sites (20 sites) were designated as sand. At each site, a 200 m transect was established except for 21 sites in small stands, where 100–190 m transects were necessary to avoid logged areas or abrupt changes in environmental conditions.

### 2.3. Response variables

Data were collected on the abundance and characteristics of trees, snags and logs at all sites in 1996 and 1997. All trees and snags within a 4 m wide plot centered on each transect were inventoried, measured for height (classes: 1–5, 5–10, 10–15, 15–20, 20–25, 25–30, 30–35 m) and diameter at breast height (classes: 1–5, 5–10, 10–15, 15–20, 20–25, 25–30, 30–35, 35–40 cm). The decay stage of all snags was also determined (classes 1–4, similar to stages 3–6 in Thomas et al. (1979)). For each log (downed coarse woody material) intersecting the transect, the diameter at the point of intersection (classes: 1–5, 5–10, 10–15, 15–20, 20–25, 25–30, 30–35, 35–40 cm) and the decay stage (classes 1–5, Maser et al., 1979) were noted. We calculated log volume (Harmon et al., 1986), and total live tree and snag basal area for each site.

We define structural diversity as the number and abundance of types and sizes of different structural components such as trees, snags and logs (c.f. Spies and Franklin, 1988). Structural diversity for each site was calculated for trees, snags and logs using the Shannon index ($H$):

$$H = -\sum p_i \ln p_i$$

where $p_i$ is the relative importance of ’species’ $i$; the ’species’ were considered to be different combinations of height, dbh and decay classes (c.f. Kuuluvainen et al., 1998).

### 2.4. Data analysis

To quantify significant trends in individual structural components with time since fire, piecewise linear regressions were fitted to the data using SAS (Version 6.12, SAS Institute, 1996). Regression analysis provided information on increasing or decreasing trends with time since fire for different time periods following disturbance for each variable. Separate analyses were conducted for each site type. Response variables included: live tree basal area and density; average and maximum tree height; snag basal area and density; log volume and density; and diversity variables described above. There were missing data for a couple of the clay sites due to logistics; sample sizes are indicated in Appendix B. Regressions were not performed if there were fewer than five non-zero values.

One or more of the following equations were fit to the data:

- Linear regression

$$y = b_0 + b_1 x$$

- Two-piece linear regression

$$\text{If } x < t_1 \text{ then } y = b_0 + b_1 x,$$
$$\text{if } x \geq t_1 \text{ then } y = b_0 + (b_1 - b_2)t_1 + b_2 x$$

- Three-piece linear regression

$$\text{If } x < t_1 \text{ then } y = b_0 + b_1 x,$$
$$\text{if } t_1 \leq x < t_2 \text{ then } y = b_0 + (b_1 - b_2)t_1 + b_2 x,$$
$$\text{if } x \geq t_2 \text{ then } y = b_0 + (b_1 - b_2)t_1 + (b_2 - b_3)t_2 + b_3 x$$

where $x$ is time since fire, $t_1$ and $t_2$ are the breakpoints, $b_0$ is the $y$-intercept and $b_1$, $b_2$ and $b_3$ are the slopes for the first, second and third segments. Two and three-piece regressions were non-linear and involved parameter estimation (nlin procedure, Version 6.12, SAS Institute, 1996). Since the final parameter values were dependent on initial parameters, the data were first assessed visually to determine whether two or three-piece segmented linear regressions would be appropriate, to estimate parameters and determine whether any data could be considered outliers. Regressions were considered significant if the 95% confidence intervals of one or more consecutive slopes did not contain zero ($P < 0.05$). If two or more regressions were significant, the additional significance of the regression with the most pieces was tested using:

$$F = \frac{SS_{\text{res2}} - SS_{\text{res1}}}{(\text{d.f.}_{\text{res2}} - \text{d.f.}_{\text{res1}}) \times MS_{\text{res2}}}$$

where $SS_{\text{res1}}$ and $SS_{\text{res2}}$ are the residual sums of squares for the regressions with the lower and greater number of pieces respectively, $\mathrm{d.f.}_{\mathrm{res1}}$ and $\mathrm{d.f.}_{\mathrm{res2}}$ are the degrees of freedom associated with the residual terms for the regressions with the lower and greater number of pieces, respectively, and $\mathrm{MS}_{\mathrm{res2}}$ is the residual mean square for the regressions with the greater number of pieces. This was tested against $F_{(\mathrm{d.f.}_{\mathrm{res2}}-\mathrm{d.f.}_{\mathrm{res1}}),\mathrm{d.f.}_{\mathrm{res2}}}$. We modified this test of significance from the standard test for adding a variable to a regression; this was necessary to avoid problems due to parameter estimation in nonlinear regressions. This procedure allowed us to identify the piecewise regression that best fit the data, with the maximum number of pieces that were still significant. For piecewise regressions with two or more pieces, $F$ and $R^2$ statistics were not available; therefore estimates were calculated:

$$R^2 = \frac{1 - \mathrm{SS}_{\mathrm{res}}}{\mathrm{SS}_{\mathrm{y}}} \qquad F = \frac{\mathrm{MS}_{\mathrm{reg}}}{\mathrm{MS}_{\mathrm{res}}}$$

where $\mathrm{SS}_{\mathrm{res}}$ and $\mathrm{SS}_{\mathrm{y}}$ are the residual and corrected total sum of squares, and $\mathrm{MS}_{\mathrm{reg}}$ and $\mathrm{MS}_{\mathrm{res}}$ the regression and residual mean squares, respectively.

## 3. Results

Total live tree basal area increased continuously with time since fire on organic sites (Fig. 2A). On clay sites, tree basal area reached a peak at around 50 years and then decreased to values that were similar to those on organic sites. Tree basal area significantly decreased with time since fire on sand sites except for a low outlier value in the 20-year-old site. Tree density increased continuously with time since fire on organic sites except for an outlier at 49 years (Fig. 2B). Tree density followed the expected N-curve for clay sites with a plateau starting at almost 100 years, but the initial increase in density was not significant. There was no significant trend for tree density on sand sites. For maximum and average height, trends were linear increases for organic sites and two-piece regression curves for clay sites (Fig. 2C and D, respectively). On sand sites, maximum height increased to a plateau at approx. 60 years, while average height decreased continuously with time since fire.

Snag basal area followed the first part of the typical 'U-shaped curve' on organic sites by decreasing until about 40 years, and then increasing (Fig. 2E). There was no significant trend in snag basal area on clay or sand sites, despite a high value in the youngest 20-year-old sand site. There were no significant trends in snag density for organic or sand sites (Fig. 2F). On clay sites, total snag density seemed to follow the initial part of the U-curve due a high outlier value at 20 years followed by an initial increase until about 90 years; however, snag density decreased in later stages. Log volume on clay sites was the only example we observed of the complete typical U-shaped curve with a plateau in older sites (Fig. 2G). There was a decrease until about 40 years then an increase in log volume on organic sites. On sand sites, only an increase in log volume with time since fire was significant; an initial decrease following high log volume in the 20-year-old stand was not significant, most likely due to inadequate sampling in young stands (only one site younger than 50 years). Trends in log density resembled U-shaped curves but without the plateau on organic sites, and without the initial decrease on clay sites; there was no significant trend on sand sites (Fig. 2H).

In general, older forests had greater structural diversity than younger forests (Fig. 3). Structural diversity for trees, snags and logs increased with time on organic sites (Fig. 3A–C, respectively). On clay sites, there was a progression in the trends of structural diversity with decay from trees to snags to logs along the chronosequence; a peak in diversity occurred at a later time since fire for snags than for trees, and structural diversity had not yet stabilized for logs. Decreases in tree and snag structural diversity in later stages of development were apparent on clay sites, but only the decrease in tree structural diversity was significant. On sand sites, log and snag structure became more diverse, whereas live tree structure became less diverse (except for an outlier at 20 years). Structural diversity was generally lower on organic sites compared to other site types, particularly for younger sites.

## 4. Discussion

### *4.1. Processes of structural development in black spruce boreal forest*

Structural development is a prominent process in the black spruce boreal forest where there is often little

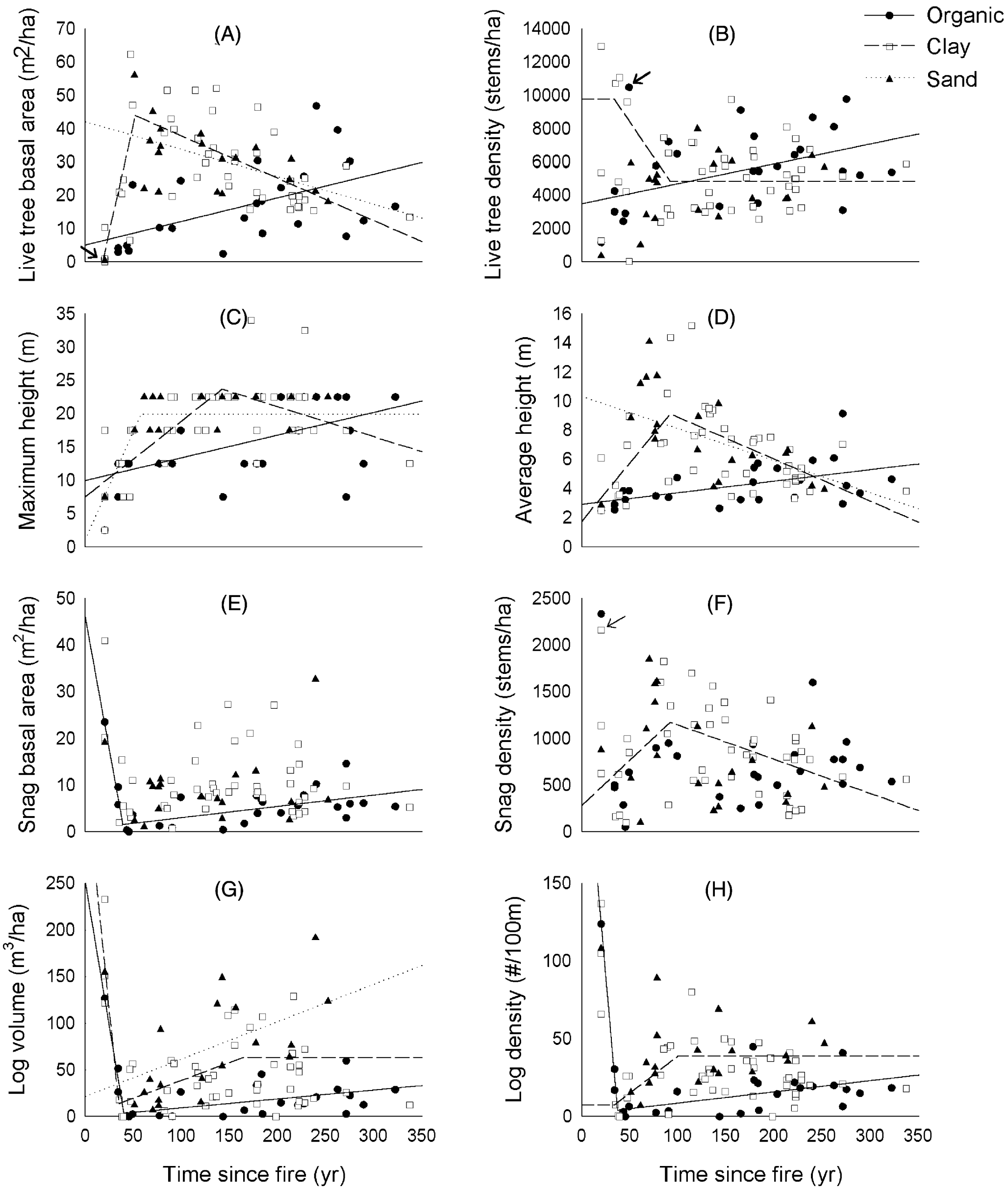

Fig. 2. Structural characteristics in relation to time since fire on organic (circles), clay (squares) and sand (triangles) sites: (A) live tree basal area; (B) live tree density; (C) canopy (maximum) tree height; (D) average tree height; (E) snag basal area; (F) snag density; (G) log volume; (H) log density. Solid, dashed and dotted piecewise regression lines were added for organic, clay and sand sites, respectively, where significant; flat pieces of the regression curves indicate that the slope was not significant. Arrows indicate outliers that were removed for the regressions for sand sites in (A), organic sites in (B) and clay sites in (F). Average diameter (not shown) had similar results as average height except that the trend with time since fire was not significant for sand sites. Statistics on the regressions are in Appendix B.

change in tree species composition. In our study, changes in forest structure with time since fire occurred on all surficial deposits throughout part or all of the approx. 300-year chronosequence. However, there were differences in the timing and the nature of structural development among site types. Other studies suggest that species composition, soil conditions, moisture regime and stand dynamics (stem

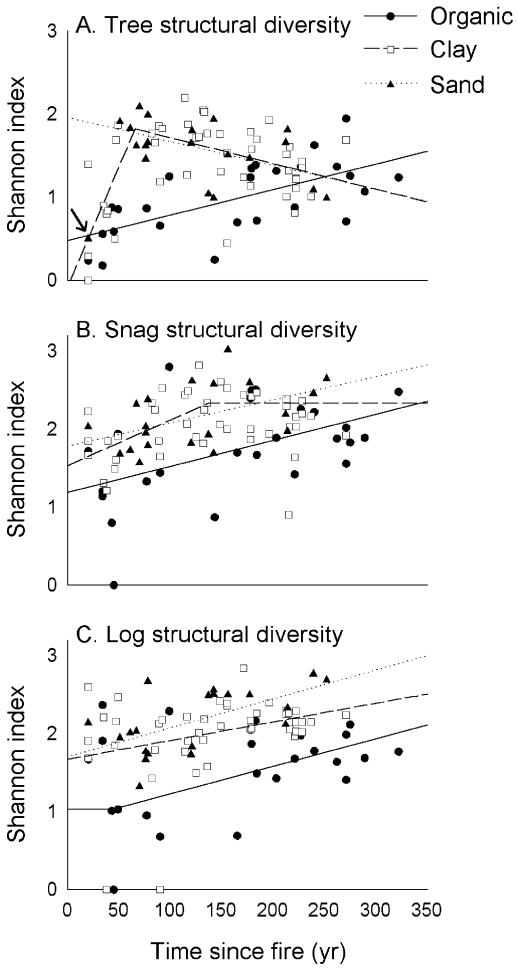

Fig. 3. Structural diversity in relation to time since fire on organic (circles), clay (squares) and sand (triangles) sites: (A) tree structural diversity; (B) snag structural diversity; (C) log structural diversity. Solid, dashed and dotted piecewise regression lines were added for organic, clay and sand sites, respectively, where significant; flat pieces of the regression curves indicate that the slope was not significant. An arrow indicates an outlier that was removed for the regression for sand sites in (A). Statistics on the regressions are in Appendix B.

growth and mortality) are among the many factors that affect forest structure, particularly deadwood accumulation (e.g., Harmon et al., 1986; Sturtevant et al., 1997; Hély et al., 2000). We examine possible factors of species replacement, productivity, paludification and secondary disturbance with regard to their contribution to structural development for the three site types in black spruce forest.

### 4.1.1. Species composition

Species replacement and structural development are independent processes that may or may not interact. On clay and sand sites, canopy structural development coincided with a change in tree composition (Harper et al., 2003). A change in dominance from *P. banksiana* to *P. mariana* on sand sites (Harper et al., 2002, 2003) probably accounts for at least part of the decline in average tree height and tree basal area in later stages of succession. Mortality of the taller, dominant tree species can change the canopy profile from a bimodal distribution to a single canopy layer (Paré and Bergeron, 1995). Faster-growing early successional species such as *P. tremuloides* and *P. banksiana* in young clay and sand sites (Gauthier et al., 2000; Harper et al., 2003) could have resulted in greater tree basal area on the younger sites. In later stages, the convergence of tree basal area on organic and clay sites may be partly due to the almost complete dominance of the smaller-stemmed *P. mariana* on both site types (Harper et al., 2002, 2003). However, changes in structure need not be species specific. Transitions between some stages of development were distinct for organic sites, despite virtually no change in canopy species composition (Harper et al., 2002, 2003).

Species replacement can also alter trends in deadwood accumulation due to differences in species productivity and decomposition rates (Hély et al., 2000). We might expect slower decomposition and therefore persistent deadwood in intermediate-aged sand sites since *P. banksiana* decomposes at a slower rate than *P. mariana*. Unfortunately, because of the lack of sites between 21 and 50 years, it is difficult to draw inferences around this time period with our data. There was an accumulation of snags in intermediate–aged sand sites and logs in older sand sites, a large proportion of which are likely *P. banksiana*, although not all trends were significant. On sand sites, the more varied tree species composition may also have masked trends in structural development, making developmental stages less pronounced or more difficult to determine using the chronosequence approach.

### 4.1.2. Productivity

Productivity is related to both site type and time since fire, and is reflected in forest structure. Stem exclusion is apparent as a peak in stem density on the productive clay sites, where there is adequate regeneration and growth. Canopy closure may never be reached in sites with low productivity (Franklin et al., 2002). Self-thinning appears to be absent on organic sites where establishment and growth of *P. mariana* is slow because of a deep peat layer, low productivity, high moisture and a lack of mineral seedbeds (Foster, 1985). However, Carleton and Wannamaker (1987) report that density dependent mortality still occurs in low density stands. Some thinning could have taken place on our sites, but might have been too small to be detectable using a chronosequence approach. In addition to low productivity, slower decomposition on organic sites was apparent as our results suggest that some logs and snags had not yet decomposed after 20 years.

### 4.1.3. Paludification

Paludification, the process in which the development of thick moss and organic layers lowers soil temperature and decreases nutrient availability (Van Cleve et al., 1983; Paré and Bergeron, 1995; Gower et al., 1996), likely contributes to changes in structure in the later stages of development on clay sites in black spruce forest. Paludification was evident on the clay sites as a significant linear increase in humus depth with time since fire ($P < 0.01$, $R^2 = 0.362$, De Grandpré et al., unpublished data). Due to the decrease in site productivity, *P. mariana* trees that establish in later stages tend to be smaller and less numerous, leading to overall lower tree basal area and deadwood abundance. Our results differ from those in other ecosystems, where tree basal area generally increases with age (Tyrrell and Crow, 1993, 1994; Crowell and Freedman, 1994), although a decline after 300 years has been recorded in the more productive hemlock forests (Tyrrell and Crow, 1994). Paludification may be the cause of a convergence in forest structure, notably tree basal area, among the three site types as the effect of environmental conditions decreases with time since fire (Bergeron and Dubuc, 1989; De Grandpré et al., 2000).

### 4.1.4. Partial disturbance

In the absence of stand-replacing disturbance, structural dynamics of boreal forests are affected by partial canopy disturbance. In black spruce stands, spruce budworm outbreaks and windthrow are common in stands of intermediate to late age (100–300 years old) (Harper et al., 2002), and may contribute to increases in deadwood abundance in later stages.

## 4.2. Empirical patterns and theory of structural development

Empirical patterns of structure following fire in black spruce boreal forest on different site types that are both independent of and concurrent with species replacement provide an opportunity to revisit the theory of stand development. Structural development can be depicted using trends in the changes of abundance of different structural components. These trends can then be used to define and describe stages of development. In this section, we expand and refine the theory of structural development to account for different possible trends and stages of development.

### 4.2.1. Trends with time since fire

Overall, live tree abundance increases throughout stand development, following either a N- or S-shaped pattern. A peak in overall tree density followed by self-thinning, which typifies the N-curve, was only apparent for clay sites. The plateau at the end of N- and S-curves, indicating no change during the later stages of stand development, did not always occur for tree abundance in our study area. On organic sites, tree basal area continued to increase, suggesting that forest stands had not yet reached a steady-state old-growth stage during the time period sampled. On clay and sand sites, we suggest that decreases in basal area, canopy height and large trees (Appendix A) in later stages of development were due to paludification (clay sites) or changes in tree canopy composition (sand sites) in the final old-growth stage (also see Harper et al. (2003)). Structural changes in the old-growth stage have also been detected by Tyrrell and Crow (1993). To accommodate these different patterns, we propose a slight modification of the trends in structural development. Trends in live tree abundance can be summarized in two steps (Fig. 4A): (1) to reach the understory reinitiation phase, there is either a peak or steady increase; (2) during the old-growth phase, there is either no change or a steady decrease.

Other studies have described a U-shaped pattern for the abundance of deadwood, with a decline due to

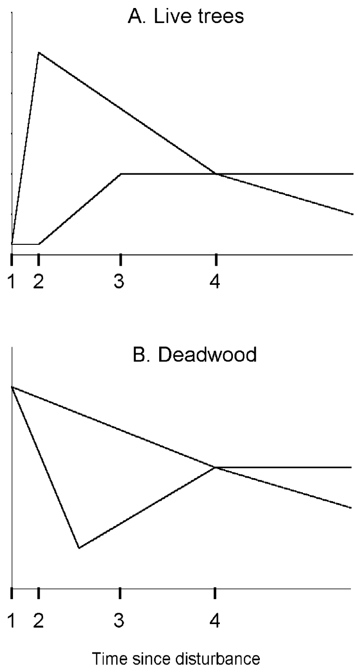

Fig. 4. Proposed segmented linear trends during structural development for (A) abundance of live trees and (B) abundance of deadwood. The $y$-axis represents abundance of live trees or deadwood. The $x$-axis represents time since disturbance; numbers on this axis refer to the four phases of structural development. Lines represent alternative trends that depend on site productivity or characteristics of structural variables.

decay from high values after disturbance, followed by an increase with material from the regenerating forest, and increasing to moderately high values in old-growth forest (e.g., Harmon et al., 1986; Spies and Franklin, 1988; Tyrrell and Crow, 1994; Sturtevant et al., 1997; Clark et al., 1998). The only example we found of this typical U-curve was for log volume on clay sites. Otherwise, the trough part of the U-curve was only evident for organic sites where logs and snags still remaining from the last fire had not yet decomposed after 20 years. On sand sites, the lack of significance for initial decreases in deadwood abundance was most likely due to inadequate sampling in young stands. The trends in deadwood abundance in the later stages of structural development mirrored those of live tree abundance; a plateau was lacking for organic and sand sites, and deadwood abundance decreased on clay sites. Decreases in snag abundance in later stages was also found in other studies (e.g., Goebel and Hix, 1996; Clark et al., 1998) due to the decline in mortality rates following self-thinning (Cline et al., 1980; Johnson, 1992). Although trends in deadwood abundance on our sites generally fit the curves described by Harmon et al. (1986), a modified set of curves that includes a possible decrease in the abundance in the later stages of structural development (Fig. 4B) should provide a more refined model. The type of trend for deadwood can be related to decay stage and size of deadwood (Appendix A).

It is important to recognize several factors that could contribute to the lack of fit of observed to hypothesized trends. First, there may have been few or no data points within a specific time span; particularly for all older (>300 years) and very young (<20 years) sites, and young–intermediate (>20 and <50 years) sand sites. For example, different trends observed for deadwood abundance can be due to inadequate time intervals for detecting the entire trend (Cline et al., 1980; Hély et al., 2000). Second, trends may have been obscured by variability in the data within site types (Gauthier et al., 2000). A weak fire severity which leaves much of the organic layer intact can cause irregular recruitment and regrowth (Johnson, 1992; Turner et al., 1997). In young stands, deadwood generated by the disturbance depends on the structure of the previous stand and the fire intensity (Lee et al., 1997; Clark et al., 1998), which may explain the presence of outliers for some of the trends. Finally, there may not be a trend for some structural components.

### 4.2.2. *Stages of development*

The timing of the stages of structural development can be estimated by averaging the time since fire for breakpoints between pieces with a significant change in slope (Table 1). For the start of the second stage, a peak in tree density and a trough in deadwood abundance mark the end of initial recruitment and decomposition of disturbance-generated deadwood, respectively. At the end of self-thinning, tree density should stop decreasing, and snag and log densities should stop increasing. We also used the completion of stand growth (increases in basal area and maximum height) to estimate this transition between stages 2 and 3. The start of the old-growth stage is difficult to detect using overall live tree abundance. Therefore, we estimated this transition only using snag basal area and

Table 1
Breakpoints in the piecewise regression curves that were used to determine the timing of the stages of development

| Structural components | Transition between stages 1 and 2 | Transition between stages 2 and 3 | Transition between stages 3 and 4 |
|---|---|---|---|
| Live trees | Tree density (●╲[a]) | Tree basal area,<br>maximum height (╱●[b]);<br>tree density (╲●─[c]) | |
| Deadwood | Snag basal area,<br>snag density,<br>log volume,<br>log density (●╱[d]) | Snag density,<br>log density (╱●[b]) | Snag basal area,<br>log volume (╱●[b]);<br>log density,<br>snag density (╲●─[c]) |

The symbols indicate the breakpoints that were used to calculate the timing of the transition; they represent the breakpoints either before or after parts of the piecewise regressions with different slopes. Timing between stages was estimated using live trees and deadwood.

[a] Peak—breakpoint before decrease.

[b] Peak—breakpoint after increase.

[c] Stabilization—breakpoint between decrease and flat.

[d] Trough—breakpoint before increase.

log volume which would continue to increase throughout stage 3 as larger trees die during canopy break-up.

All four stages of stand development were clearly evident only on clay sites (Table 2). The processes of stem exclusion and subsequent understory reinitiation do not appear to apply to organic sites where there were no distinct stages of overall live tree abundance. Instead, there is a short 40-year decomposition stage based on trends in deadwood abundance, and a long tree establishment and growth stage, most likely followed by an old-growth stage after 200–300 years (Harper et al., 2003). On sand sites, inadequate sampling may have prevented the detection of transitions between stages. On clay sites, our timing estimates for transitions between stages were slightly later than suggested by Lieffers et al. (2003) (stages 2–4 starting at 10, 50 and 120 years, respectively), Harper et al. (2002) (old-growth stage starting at 100 years) and Taylor et al. (1987) (paludification during old-growth starting at 100–120 years). The transition between stages 2 and 3 on clay sites was defined by a peak in basal area at about 50 years and a peak in maximum height at approx. 140 years, suggesting that there was tree mortality even as canopy height increased. This gradual transition suggests that there can be continual changes in structural development, stages of structural development may not be distinct and, therefore, the classification can be arbitrary (Franklin et al., 2002).

Table 2
Timing of the four stages of structural development for the three site types, calculated using the breakpoints outlined in Table 1

| Method | Duration of stages of stand development (years) | | | |
|---|---|---|---|---|
| | Stand initiation | Stem exclusion | Understory reinitiation | Old-growth |
| Organic | | | | |
| Live trees | 0–? | ?–? | ?+ | |
| Deadwood | 0–39 | 39–? | ?–? | ?+ |
| Both live and dead | 0–39 | 39–? | ?–? | ?+ |
| Clay | | | | |
| Live trees | 0–34 | 34–95 | 95+ | |
| Deadwood | 0–34 | 34–96 | 96–164 | 164+ |
| Both live and dead | 0–34 | 34–96 | 96–164 | 164+ |
| Sand | | | | |
| Live trees | 0–? | ?–58 | 58+ | |
| Deadwood | 0–? | ?–? | ?–? | ?+ |
| Both live and dead | 0–? | ?–58 | 58–? | ?+ |

Timing between stages was estimated using live trees, deadwood or both. ? = no significant breakpoints to define this transition.

Surprisingly, the timing of the transitions based on trends of live tree and deadwood abundance was remarkably similar for clay sites. We also found no evidence of trends in logs following trends in snags. The time lag between increases in abundance for trees, snags and logs could be minimal compared to the variation among sites. In other ecosystems where decomposition may be slower than tree establishment, we might expect tree density to increase, followed by snag density, and then log density. Franklin et al.

(2002) suggest that deadwood abundance would reach a minimum in their maturation stage (late understory reinitiation stage) and increase in their diversification stage (old-growth stage). Clearly, the correlation between trends of live tree and deadwood abundance varies among ecosystems, and depends on factors such as tree establishment and growth rates, as well as mortality and decomposition rates.

The timing of the stages of structural development was sometimes similar between site types despite differences in species composition (also see Appendix A). Palik and Pregitzer (1993) also found similar duration and timing of developmental stages within and among landscapes. However, there were some differences. The stand initiation phase was slightly longer for organic black spruce sites than for the more productive clay sites, perhaps due to slower decomposition and lower productivity. Stem exclusion ended earlier on sand sites than clay sites, where *P. banksiana* trees likely reached canopy height sooner. In faster-growing *Populus*-dominated forests, the stem exclusion phase lasted only until 25–35 years (Palik and Pregitzer, 1993) or up to 75 years after fire (Paré and Bergeron, 1995). However, increases in height and volume from 68 to 140 and 124–196 years after fire in *Pinus sylvestris* and *Picea abies* stands in Sweden (Linder, 1998) indicate even longer timing of structural development. The longer duration in coniferous forests is probably due to slow growth rather than establishment of trees, as most *P. mariana* establishment occurs in the first years after fire (Sirois and Payette, 1989; St.-Pierre et al., 1992). Thus, we can tentatively state that site productivity and species composition appear to affect the timing of developmental stages. However, transition times were often calculated based on only one or a few piecewise regression results.

### *4.3. Structural diversity and management implications*

Overall, black spruce forest stands were structurally more diverse with time since fire, despite lower tree species diversity (Harper et al., 2003). In general, different types of both live trees and deadwood continually accumulate from tree establishment and stand growth, followed by self-thinning, secondary disturbance and subsequent regeneration. Diversity of different types of deadwood also increased with age in other studies (Cline et al., 1980; Tyrrell and Crow, 1994; Lee et al., 1997). In older forests, mortality from secondary disturbances (e.g. insects, disease, windthrow) affects a variety of tree sizes (Cline et al., 1980) and is continuous, resulting in deadwood of a variety of different decay stages at any given time; whereas self-thinning in young forests kills only smaller trees. Paludification can lead to a reduction in among stand structural diversity (Harper et al., 2002) and within stand tree structural diversity, as larger trees are replaced by smaller ones during the less productive old-growth stage. This contrasts with other forests, where tree size distributions became more even and diverse with age (e.g., Spies and Franklin, 1988; Tyrrell and Crow, 1993, 1994; Goebel and Hix, 1997; Lee et al., 1997). Paludification could eventually lead to a decrease in snag and log diversity as the range of sizes of deadwood decreases.

In older black spruce forests, structure rather than tree composition provides diverse habitat for local biodiversity. The capacity of a forest stand to support biodiversity can be assessed in part through its within-stand structural diversity; structural complexity is a good predictor of overall biodiversity (Kuuluvainen et al., 1996). In particular, the amount and types of deadwood are important factors for biodiversity in boreal forests (Ohlson et al., 1997), since different organisms require different decay stages or sizes of deadwood (Harmon et al., 1986; Jonsell et al., 1998). Microhabitat for understory plant species is also provided by greater tree height diversity which allows the penetration of more diagonal light (Goebel and Hix, 1997).

Black spruce forest stands older than 100 years, the current harvest rotation length in the study region, have unique and diverse structural attributes that, despite their lower productivity, may provide important habitat for biodiversity. Following the coarse-grained approach to the conservation of biodiversity, structural characteristics of these older stands should be reproduced at both the stand and landscape scales in managed forests. Within harvested stands, retaining trees and snags for deadwood could minimize structural changes caused by harvesting. At the landscape scale, a possible management strategy that could better maintain structural characteristics is ‘management by cohorts’ in which developmental stages are simulated through diverse silvicultural treatments; clear-cutting, partial cutting and selection cutting are used to establish the first, second and third cohorts (Bergeron et al., 1999). Management by cohorts could use the timing of developmental stages to determine the number of cohorts and their rotation periods for different site types. For clay sites, we would suggest three cohorts of approx. 0–90 (stages 1 and 2 combined since timber would not be marketable after only 35 years), 90–160, and 160–300 years. Management by cohorts might not be sufficient for organic sites where there are no major structural development stages between 40 and 300 years. Multicohort management will likely contribute to an overall increase in key structural features that are important for both structural and functional aspects of forest ecosystems. However, this will probably not be sufficient to conserve regional biodiversity. Unharvested representative areas of different ages should be preserved on all site types to allow structural development following fire, the dominant stand-replacing disturbance in the region (Harper et al., 2003).

## 5. Conclusions

A general theory of structural development should take into account local site characteristics, especially productivity, as well as tree species composition. In response to our hypothesis, we found that local conditions affected not only the timing of developmental stages, but also the number of stages and the trends in structural components with time since fire. The four-stage stand development model applies well to forest stands on both clay and sand sites in the black spruce forest, but it should be recognized that trends of deadwood abundance occur within these stages: (1) stand initiation, with initial recruitment and decomposition of fire-generated deadwood; (2) stem exclusion, with stand growth and self-thinning, and increasing density of deadwood; (3) understory reinitiation, with stand break-up and high tree structural diversity, further recruitment and increasing volume of deadwood as larger trees die; (4) old growth, with decreasing tree abundance due to paludification (clay sites) or changes in species composition (sand sites), and high structural diversity. However, even as few as four distinct stages of structural development may not be universal. Our results suggest that a peak in tree density and subsequent self-thinning did not occur on organic black spruce sites, where tree establishment and growth were limited by low productivity. Instead, we propose the following three stages of stand development: (1) decomposition, with initial recruitment and decomposition of fire-generated deadwood; (2) tree growth, with stand growth, further recruitment and accumulation of deadwood; (3) old growth, with relatively high tree abundance and structural diversity. Different models of stand development should be applied to different forested ecosystems, and should consider the abundance of deadwood to provide a complete picture of stand development. Timing of developmental stages determined using empirical data can be an important tool in developing management practices that emulate structural development in order to conserve biodiversity on a landscape scale.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found in the on-line version at doi: 10.1016/j.foreco.2004.11.008.

## References

Bergeron, Y., Dubuc, M., 1989. Succession in the southern part of the Canadian boreal forest. Vegetatio 79, 51–63.

Bergeron, Y., Harvey, B., Leduc, A., Gauthier, S., 1999. Forest management guidelines based on natural disturbance dynamics: stand- and forest-level considerations. For. Chron. 75, 49–54.

Bergeron, Y., Gauthier, S., Flannigan, M., Kafka, V., 2004. Fire regimes at the transition between mixedwood and coniferous boreal forest in northwestern Quebec. Ecology 85, 1926–1932.

Bormann, F.H., Likens, G.E., 1979. Catastrophic disturbance and the steady state in northern hardwood forests. Am. Sci. 67, 660–669.

Carleton, T.J., Maycock, P.F., 1978. Dynamics of the boreal forest south of James Bay. Can. J. Bot. 56, 1157–1173.

Carleton, T.J., Wannamaker, B.A., 1987. Mortality and self-thinning in postfire black spruce. Ann. Bot. 59, 621–628.

Chen, H.Y.H., Popadiouk, R.V., 2002. Dynamics of North American boreal mixedwoods. Environ. Rev. 10, 137–166.

Clark, D.F., Kneeshaw, D.D., Burton, P.J., Antos, J.A., 1998. Coarse woody debris in sub-boreal spruce forests of west-central British Columbia. Can. J. For. Res. 28, 284–290.

Cline, S.P., Berg, A.B., Wight, H.M., 1980. Snag characteristics and dynamics in Douglas-fir forests, western Oregon. J. Wild. Manage. 44, 773–786.

Crowell, M., Freedman, B., 1994. Vegetation development in a hardwood-forest chronosequence in Nova Scotia. Can. J. For. Res. 24, 260–271.

De Grandpré, L., Morissette, J., Gauthier, S., 2000. Long-term post-fire changes in the northeastern boreal forest of Quebec. J. Veg. Sci. 11, 791–800.

Environment Canada, 1993. Canadian Climate Normals 1961–1990. Canadian Climate Program. Atmospheric Environment Service, Downsview, Ontario.

Foster, D.R., 1985. Vegetation development following fire in *Picea mariana* (black spruce)—*Pleurozium* forests of south-eastern Labrador. Canada J. Ecol. 73, 517–534.

Franklin, J.F., Spies, T.A., Van Pelt, R., Carey, A.B., Thornburgh, D.A., Berg, D.R., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K., Chen, J., 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. For. Ecol. Manage. 155, 399–423.

Gauthier, S., Leduc, A., Bergeron, Y., 1996. Forest dynamics modelling under natural fire cycles: a tool to define natural mosaic diversity for forest management. Environ. Mon. Assess. 39, 417–434.

Gauthier, S., De Grandpre, L., Bergeron, Y., 2000. Differences in forest composition in two boreal forest ecoregions of Quebec. J. Veg. Sci. 11, 781–790.

Goebel, P.C., Hix, D.M., 1996. Development of mixed-oak forests in southeastern Ohio: a comparison of second-growth and old-growth forests. For. Ecol. Manage. 84, 1–21.

Goebel, P.C., Hix, D.M., 1997. Changes in the composition and structure of mixed-oak, second-growth forest ecosystems during the understory reinitiation stage of stand development. Ecoscience 4, 327–339.

Gower, S.T., McMurtrie, R.E., Murty, D., 1996. Aboveground net primary production decline with stand age: potential causes. Tr. Ecol. E vol. 11, 378–382.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K.J., Cummins, K.W., 1986. Ecology of coarse woody debris in temperate ecosystems. Adv. Ecol. Res. 15, 133–302.

Harper, K.A., Bergeron, Y., Gauthier, S., Drapeau, P., 2002. Structural development of black spruce forests following fire in Abitibi, Québec: a landscape scale investigation. Silva Fenn. 36, 249–263.

Harper, K.A., Boudreault, C., De Grandpré, L., Drapeau, P., Gauthier, S., Bergeron, Y., 2003. Structure, composition and diversity of old-growth black spruce boreal forest of the Clay Belt region in Québec and Ontario. Environ. Rev. 11, S79–S98.

Hély, C., Bergeron, Y., Flannigan, M.D., 2000. Coarse woody debris in the southeastern Canadian boreal forest: composition and load variations in relation to stand replacement. Can. J. For. Res. 30, 674–687.

Hunter, M.L., Jacobson, G.L., Thompson, W., 1988. Paleoecology and the coarse-filter approach to maintaining biodiversity. Conserv. Biol. 2, 375–385.

Johnson, E.A., 1992. Fire and Vegetation Dynamics. Cambridge University Press, Cambridge, UK.

Jonsell, M., Weslien, J., Ehnstrom, B., 1998. Substrate requirements of red-listed saproxylic invertebrates in Sweden. Biodivers. Conserv. 7, 749–764.

Kuuluvainen, T., Penttinen, A., Leinonen, K., Nygren, M., 1996. Statistical opportunities for comparing stand structural heterogeneity in managed and primeval forests: an example from boreal spruce forest in southern Finland. Silva Fenn. 30, 315–328.

Kuuluvainen, T., Jarvinen, E., Hokkanen, T.J., Rouvinen, S., Heikkinen, K., 1998. Structural heterogeneity and spatial autocorrelation in a natural mature *Pinus sylvestris* dominated forest. Ecography 21, 159–174.

Lee, P.C., Crites, S., Nietfeld, M., Van Nguyen, H., Stelfox, J.B., 1997. Characteristics and origins of deadwood material in aspen-dominated boreal forests. Ecol. Appl. 7, 691–701.

Lieffers, V.J., Messier, C., Burton, P.J., Ruel, J.C., Grover, B.E., 2003. Nature-based silviculture for sustaining a variety of boreal forest values. In: Burton, P.J., Messier, C., Smith, D.W., Adamowicz, W.L. (Eds.), Towards Sustainable Management of the Boreal Forest. N.R.C. Press, Ottawa, Canada, pp. 481–530.

Linder, P., 1998. Structural changes in two virgin boreal forest stands in central Sweden over 72 years. Scand. J. For. Res. 13, 451–461.

Maser, C., Anderson, R.G., Cromack Jr., K., Williams, J.T., Martin, R.E., 1979. Dead and down woody material. In: Thomas, J.W. (Ed.), Wildlife Habitats in Managed Forests: the Blue Mountains of Oregon. Department of Agriculture Forest Service, Washington, U.S, pp. 78–95.

Morrison, M.L., Marcot, B.G., Mannan, R.W., 1992. Wildlife–Habitat Relationships—Concepts and Applications. University of Wisconsin Press, Madison, WI.

Ohlson, M., Soderstrom, L., Hornberg, G., Zackrisson, O., Hermansson, J., 1997. Habitat qualities versus long-term continuity as determinants of biodiversity in boreal old-growth swamp forests. Biol. Conserv. 81, 221–231.

Oliver, C.D., 1981. Forest development in North America following major disturbances. For. Ecol. Manage. 3, 153–168.

Palik, B.J., Pregitzer, K.S., 1993. The repeatability of stem exclusion during even-aged development of bigtooth aspen dominated forests. Can. J. For. Res. 23, 1156–1168.

Paré, D., Bergeron, Y., 1995. Above-ground biomass accumulation along a 230-year chronosequence in the southern portion of the Canadian boreal forest. J. Ecol. 83, 1001–1007.

Saucier, J.P., Bergeron, J.F., Grondin, P., Robitaille, A., 1998. Les régions écologiques du Québec méridional (3ième version). L'Aubelle Supplément, p. 12.

Sirois, L., Payette, S., 1989. Postfire black spruce establishment in subarctic and boreal Quebec. Can. J. For. Res. 19, 1571–1580.

Spies, T.A., Franklin, J.F., 1988. Old growth and forest dynamics in the Douglas-fir region of western Oregon and Washington. Nat. Areas J. 8, 190–201.

St.-Pierre, H., Gagnon, R., Bellefleur, P., 1992. Régénération après feu de l'épinette noire (*Picea mariana*) et du pin gris (*Pinus banksiana*) dans la forêt boréale, Québec. Can. J. For. Res. 22, 474–481.

Sturtevant, B.R., Bissonette, J.A., Long, J.N., Robert, D.W., 1997. Coarse woody debris as a function of age, stand structure, and disturbance in boreal Newfoundland. Ecol. Appl. 7, 702–712.

Taylor, S.J., Carleton, T.J., Adams, P., 1987. Understorey vegetation change in a *Picea mariana* chronosequence. Vegetatio 73, 63–72.

Thomas, J.W., Anderson, R.G., Maser, C., Bull, E.L., 1979. Snags. In: Thomas, J.W. (Ed.), Wildlife Habitats in Managed Forests: the Blue Mountains of Oregon and Washington, U.S. Department of Agriculture Forest Service, pp. 60–77.

Turner, M.G., Romme, W.H., Gardner, R.H., Hargrove, W.W., 1997. Effects of fire size and pattern on early succession in Yellowstone National Park. Ecol. Monogr. 67, 411–433.

Tyrrell, L.E., Crow, T.R., 1993. Analysis of structural characteristics of old-growth hemlock-hardwood forests along a temporal gradient. In: Fralish, J.S., McIntosh, R.P., Loucks, O.L. (Eds.), John T. Curtis: Fifty Years of Wisconsin Plant Ecology. Wisconsin Academy of Sciences, Arts and Letters, Madison, WI, pp. 237–246.

Tyrrell, L.E., Crow, T.R., 1994. Structural characteristics of old-growth hemlock-hardwood forests in relation to age. Ecology 75, 370–386.

Van Cleve, K., Dyrness, C.T., Viereck, L.A., Fox, J., Chapin III, F.S., Oechel, W., 1983. Taiga ecosystems in interior Alaska. BioScience 33, 39–44.

Vincent, J.S., Hardy, L., 1977. L'Évolution et l'extension des lacs glaciaires Barlow et Ojibway en territoire québécois. Géogr. Phys. Quat. 31, 357–372.