

Structural changes in coniferous stands along a chronosequence and a productivity gradient in the northeastern boreal forest of Québec¹

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Abstract: The influence of stand age and site conditions on the structure of coniferous stands was studied in the boreal forest of Québec's Côte-Nord, a region with low fire recurrence. Stand diameter diversity was measured in 2202 forest inventory plots in black spruce (*Picea mariana*), balsam fir (*Abies balsamea*), and mixed stands using the Shannon-Wiener diversity index. A relative productivity index was developed based on the relationship between height and age of dominant trees. A stepwise regression analysis indicated that this productivity index best explains stand structure variation in all composition types, while stand age seems to influence structure more at the beginning of stand development. The results suggest that productive stands become uneven-sized earlier than unproductive stands and also maintain a greater diameter diversity. These contrasting structural dynamics may be explained by (i) a higher growth rate in richer stands that likely induces earlier senescence and thus an earlier passage to an uneven-sized structure and (ii) a restricted maximum tree diameter in poor stands caused by a scarcity of resources, which in turn reduces the diameter diversity of these stands, even after their break-up time.

Keywords: *Abies balsamea*, balsam fir stands, black spruce stands, *Picea mariana*, site productivity, stand diameter distribution, stand dynamics, stand structure.

Résumé : L'influence de l'âge et des conditions de site sur la structure des peuplements résineux a été étudiée dans la forêt boréale de la Côte-Nord du Québec, une région à faible récurrence des feux. La diversité diamétrale des peuplements a été mesurée à l'aide de l'indice de diversité de Shannon-Wiener dans 2202 placettes d'inventaire forestier incluant des pessières (*Picea mariana*), des sapinières (*Abies balsamea*) et des peuplements mixtes. Un indice de productivité relative a été développé à partir de la relation âge-hauteur des arbres dominants. Une analyse de régression pas-à-pas a révélé que cet indice de productivité expliquait le mieux la variation de la structure des peuplements, et ce, pour tous les types de composition, alors que l'âge du peuplement semblait influencer la structure davantage au début du développement. Nos résultats suggèrent que les peuplements productifs deviennent irréguliers plus hâtivement que les peuplements peu productifs et maintiennent une diversité diamétrale plus élevée. Ces dynamiques contrastées peuvent être expliquées (i) par un taux de croissance supérieur chez les peuplements les plus riches, entraînant vraisemblablement une sénescence plus hâtive et donc un passage plus hâtif à une structure irrégulière et (ii) par un diamètre maximum des arbres qui est restreint par la rareté des ressources chez les peuplements pauvres, restreignant leur diversité diamétrale, même après l'âge de bris.

Mots-clés : *Abies balsamea*, distribution diamétrale des peuplements, dynamique des peuplements, peuplements d'épinette noire, peuplements de sapin baumier, *Picea mariana*, productivité du site, structure des peuplements.

Nomenclature: Marie-Victorin, 1964; Poole & Gentili, 1996-97.

Introduction

It is now recognized that some boreal regions of eastern Canada are subject to long fire intervals (Kneeshaw & Gauthier, 2003). In these regions, fire interval often exceeds the longevity of tree species. Stands are thus shaped by small-scale mortality and recruitment processes (Kneeshaw & Gauthier, 2003), and stand dynamics will involve changes in composition (Carleton & Maycock, 1978; Bergeron & Dubuc, 1989; Frelich & Reich, 1995; Bergeron, 2000) and/or structure (De Grandpré, Morissette & Gauthier, 2000;

Harper *et al.*, 2002). One of these structural changes is the shift from an even-sized diameter distribution towards an uneven-sized one (Smith *et al.*, 1997).

Forest structure has been acknowledged as a key element in preserving forest biodiversity and it is now widely recognized that structural attributes of old-growth forests such as snags, logs, and big live trees must be maintained in managed forest (Hunter, 1990; Kimmins, 1997; Spies, 1998; Kuuluvainen, 2002). Uneven-sized structure provides a great variety of habitats for numerous animal and plant species (Hansen *et al.*, 1991; McComb, Spies & Emmingham, 1993). However, we know little about the dynamics of stand structure in the boreal forest, *i.e.*, how uneven-sized

¹Rec. 2004-11-15; acc. 2005-11-16.

Guest Editor: Yves Bergeron.

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structure develops, when tree senescence starts, and whether these developments differ according to site characteristics. Site conditions could have significant effects on stand structure dynamics. It has been shown, for example, that site productivity can increase the successional rate (Prach, 1993; Donnegan & Rebertus, 1999). Thus, richer sites will tend to develop an uneven-sized structure more rapidly than poorer ones.

The necessity of forest management inspired by natural disturbance regime is now generally agreed upon. A better understanding of forest structure dynamics is essential for developing silvicultural strategies that can maintain the integrity of forest structural components. Since size structure is the attribute most often manipulated to achieve management objectives (Franklin *et al.*, 2002), it provides a common ground on which both foresters and ecologists can work to develop new silvicultural strategies aimed at both production and conservation objectives.

Québec's Côte-Nord region, where the study was conducted, is characterized by a maritime climate. The fire cycle has yet to be described, but a study by Foster (1983) in an adjacent region (Labrador) estimated a recurrence of 500 y. Recent studies indicate that in the prolonged absence of fire, although composition change may occur, a large proportion of stands are uneven-sized, and that they may become more uneven-sized with time since last disturbance (De Grandpré, Morissette & Gauthier, 2000; Boucher, De Grandpré & Gauthier, 2003). This study aims at documenting stand structure dynamics using a chronosequence approach in the Québec's Côte-Nord boreal forest. Specifically, we will assess the influence of stand age and site conditions on the size structure of coniferous stands as measured by diameter diversity. The forest inventory data sampled by the Québec government were used to assess the general trends in stand structure. The availability of environmental data makes it possible to evaluate the relationship between stand age, site conditions, and forest structure. In addition to the environmental variables, a site productivity index developed from the stand dominant height–age relationship was included to evaluate its effect on stand structure dynamics.

Methods

STUDY AREA

The study was conducted in the boreal forest of the Québec's Côte-Nord region (49° 30'–53° 00' N, 62° 00'–73° 00' W) (Figure 1), which is part of the eastern *Picea mariana*–feathermoss bioclimatic sub-domain (Saucier *et al.*, 1998). Black spruce dominates this region, but balsam fir is also frequently observed. This area is characterized by a cold maritime climate with a total annual precipitation of 1000 to 1400 mm and a mean annual temperature ranging between –2.5 and 0.0 °C (Grondin, 1996). Hilly topography dominates the landscape, exceeding 800 m above sea level at some points. Undifferentiated glacial tills are the dominant surficial deposits (Grondin, 1996).

DATABASE DESCRIPTION

We used data from temporary ($n = 1691$) and permanent ($n = 511$) plots of forest inventory samples gathered

by the ministère des Ressources naturelles et de la Faune du Québec (MRNFQ). Note that only the last measurement of permanent plots was used, as re-measurements covered no more than 24 y. The sampling method is briefly described here; details on the sampling design and procedure can be found in MRNQ (2001a,b). In each 400-m² plot, the diameter at breast height (DBH) of all trees > 9 cm in DBH is measured in 2-cm classes. Trees with a DBH ≤ 9 cm, which are measured in 40-m² plots, were not used in the study since the spatial distribution of saplings is generally highly variable in uneven-sized forests. Only plots composed mainly of black spruce and/or balsam fir (more than 75% of the basal area) were used. Plots were classified into four composition groups (spruce, spruce–fir, fir–spruce, and fir) according to the proportion of canopy spruce and fir within the plot (Table I). In each plot, age determination at 1 m from the ground was estimated from increment cores (3–9 in temporary plots and 7–19 in permanent plots) on trees representative of the dominant or co-dominant canopy layers. Stand age was estimated using the age of the oldest tree cored in the plot. In some stands, the oldest tree did not belong to a post-fire cohort, and our estimate was therefore a minimal stand age. Any traces of recent disturbances that significantly affected the stand (at least 25% of the basal area) were noted (windthrow, spruce budworm outbreak, or fire). Tree dominant height (to the nearest metre) was estimated in the field as the average height of the four tallest trees in the plot (excluding exceptionally tall trees that seem to have escaped the last major disturbance).

The following abiotic variables were also recorded: elevation, slope angle and shape, aspect, location on slope, stoniness, organic layer depth, hydric regime, soil texture, humus type, and surficial deposit (Table II). Dominant understorey species were also noted and classified as indicators of medium or poor sites according to the MRNQ (1998) classification.

STAND STRUCTURE MEASUREMENT

In a previous study (Boucher, De Grandpré & Gauthier, 2003) using a similar dataset, we developed a method to discriminate among three different stand structure types using a

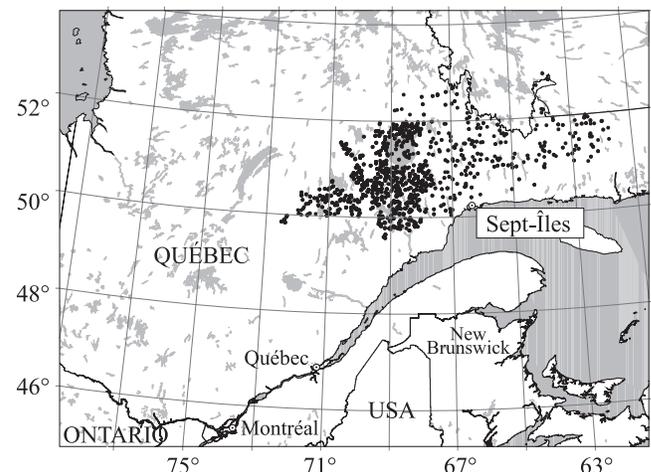


FIGURE 1. Location of sampling plots in Québec's Côte-Nord region.

variety of variables. It was shown that the Shannon-Wiener diversity index applied to the DBH class data was a very good index for discriminating stand diameter structure ($R^2 = 0.73$ in discriminating between three structural types). Furthermore, this index has been widely used to evaluate stand structure (Buongiorno *et al.*, 1994; Kuuluvainen *et al.*, 1996; Ung *et al.*, 2001; Sarkkola *et al.*, 2003). In this study, to obtain a

continuous index, the size structure of the stand was evaluated using the Shannon-Wiener diversity index:

$$H' = -\sum (p_{cl} * \ln[p_{cl}]) \quad [1]$$

where H' is the Shannon-Wiener diversity index and p_{cl} is the proportion of trees (in number) in each 2-cm DBH class. As the diversity value increases, stands tend to be more uneven-sized, whereas a low diversity value would correspond to a more even-sized stand (Boucher, De Grandpré & Gauthier, 2003).

TABLE I. Description of the four composition groups in conifer-species-dominated (> 75% of basal area) stands. Percentages are relative to the coniferous component of the stands in terms of basal area. The coniferous part occupied more than 75% of the total basal area in all composition groups.

| Composition group | <i>Picea mariana</i> | <i>Abies balsamea</i> |
|-------------------|---------------------------------------|---------------------------------------|
| Spruce | ≥ 75% | < 25% |
| Spruce-fir | 50 to 75% | 2 nd most numerous species |
| Fir-spruce | 2 nd most numerous species | 50 to 75% |
| Fir | < 25% | ≥ 75% |

DATA ANALYSIS

Site productivity was estimated from the relationship between age and height of dominant trees. This relationship is widely used to estimate site productivity, as is done for site quality index (Carmean, 1975; Alemdag, 1991). Although site indices were developed for even-aged, mono-specific stands, it is possible to use the height-age relationships to estimate the stand productivity of other stands by first, determining the age at 1 m (to exclude most of the

TABLE II. Description of environmental variables sampled in permanent and temporary plots according to MRNQ (2001a,b).

| Variable | Description |
|-----------------------------|---|
| Elevation | In metres |
| Slope | In % |
| Organic matter depth | In centimetres |
| Stoniness | In % |
| Drainage | Classes 1 to 5 (rapid to poor drainage) |
| Aspect | Values from -1 to 1, where -1 corresponds to an aspect of 22.5° and 1 to an aspect of 202.5° |
| Slope-aspect | Tan [(slope (°) x aspect (as described above) x pi / 180] |
| Humus type | Mor, moder, peat, organic soil |
| Surficial deposit group | 1- Undifferentiated till 2- Rock substrate (deposit depth < 25 cm or < 50 cm with frequent rock outcrops) 3- Fluvio-glacial outwash, fluvial and shallow water glaciolacustrine deposits 4- Dead-ice moraine, drumlin, faded till, and juxtaglacial fluvio-glacial deposits 5- Organic deposits |
| B horizon texture | Coarse (sand) Medium (sandy loam) Fine (loam, silt or clay) |
| C horizon texture | <i>Idem</i> |
| Site location on slope | 1- Flat land 2- Escarpment, rounded summit or upper slope 3- Middle slope 4- Lower slope, bench, or open depression 5- Closed depression |
| Slope shape | Concave, convex, regular, irregular |
| Understory vegetation group | 1- Poor 2- Medium Dominance of <i>Kalmia angustifolia</i> , <i>Vaccinium</i> spp., <i>Pleurozium schreberi</i> , <i>Dicranum</i> spp., <i>Ptilium crista-castrensis</i> or <i>Cladina</i> spp. Dominance of <i>Alnus rugosa</i> , <i>Alnus crispa</i> , <i>Equisetum</i> spp., <i>Amelanchier</i> spp., <i>Nemopanthus mucronatus</i> , <i>Viburnum cassinoides</i> , <i>Cornus canadensis</i> , <i>Aralia nudicaulis</i> , <i>Clintonia borealis</i> , <i>Coptis groenlandica</i> , <i>Linnaea borealis</i> , <i>Maianthemum canadensis</i> , <i>Pyrola</i> spp., <i>Trientalis borealis</i> , <i>Sphagnum</i> spp. |
| Drainage-texture group | 1- Organic-hydric 2- Rock substrate 3- Xeric 4- Mesic-coarse texture 5- Mesic-medium texture 6- Mesic-fine texture 7- Subhydric Organic surficial deposit and/or drainage 5 or 6 Surficial deposit < 25 cm or < 50 cm in depth with frequent rock outcrops Deposit other than rock or organic and drainage 1 or 2 Deposit other than rock or organic, drainage 3, and coarse B horizon texture Deposit other than rock or organic, drainage 3, and medium B horizon texture Deposit other than rock or organic, drainage 3, and fine B horizon texture Deposit other than rock or organic and drainage 4 |

suppression period and thus avoid underestimation of productivity) and second, using a very large number of plots so that general trends in site productivity may be assessed. To develop a productivity index, we performed a stepwise regression analysis (REG procedure; SAS Institute, 1999) for each composition group, with dominant height as the dependent variable and stand age, logarithm of stand age, and the square of stand age as the independent variables. This allowed the best fit between dominant height and stand age. The age transformations were used to take into account the fact that stand height reaches a maximum at some age, and that it can even decrease (Harper *et al.*, 2005). The use of the residuals of the predicted regression curves allowed us to remove the age effect on tree height, thus reflecting site productivity. The residuals will hereafter be called “relative productivity index”. Plots that show a dominant tree height higher than the predicted values have a positive relative productivity index value, whereas plots with a dominant height lower than predicted have a negative productivity index value.

To estimate how much of our productivity index was related to environmental variables, a general covariance analysis was used on each composition group (GLM procedure, SAS Institute, 1999), with the relative productivity index as the dependent variable and the environmental data as the independent variables. All double interactions (among categorical data themselves and among categorical and quantitative data) were also tested, but were excluded from the model when their effects were not significant at $\alpha = 0.05$. Slope angle and organic layer depth were log transformed, whereas latitude was square-transformed to achieve homogeneity and normality of the residuals.

A stepwise regression analysis (REG procedure; SAS Institute, 1999) was performed to determine which of the following factors contributed to the Shannon-Wiener index variation: stand age, relative productivity index, environmental variables, location (latitude and longitude), and incidence of recent disturbances. The regression analyses were done separately for the four composition groups since the productivity index cannot be used in the same analysis, as it was estimated in each composition group separately. Dummy variables were created for categorical data (aspect, disturbances, humus type, surficial deposit, texture, location on slope, shape of slope, drainage, understory vegetation group, and drainage-texture group). Stand age, slope angle, and organic layer depth were log-transformed, whereas latitude was square-transformed to achieve homogeneity and normality of the residuals. The square forms of stand age (*i.e.*, square logarithm of stand age) and relative productivity index and their interaction (stand age * productivity index) were also added to the analyses. Significance level allowing the entry of a variable into the model was set at 0.05.

Results

RELATIVE PRODUCTIVITY INDEX

The stepwise regression analysis using dominant tree height as the dependent variable and the age variables as the independent variables showed total R^2 ranging from 0.11 to 0.18 among the composition groups (Figure 2). Logarithms of age were entered into the model of all composition types.

Residuals of the regression curves thus constitute the relative productivity index from now on.

Environmental variables and geographical location explained 29 to 44% of the relative productivity index variance among the composition groups, according to the general covariance analysis (Table III). Elevation was the most significant variable associated with the relative productivity

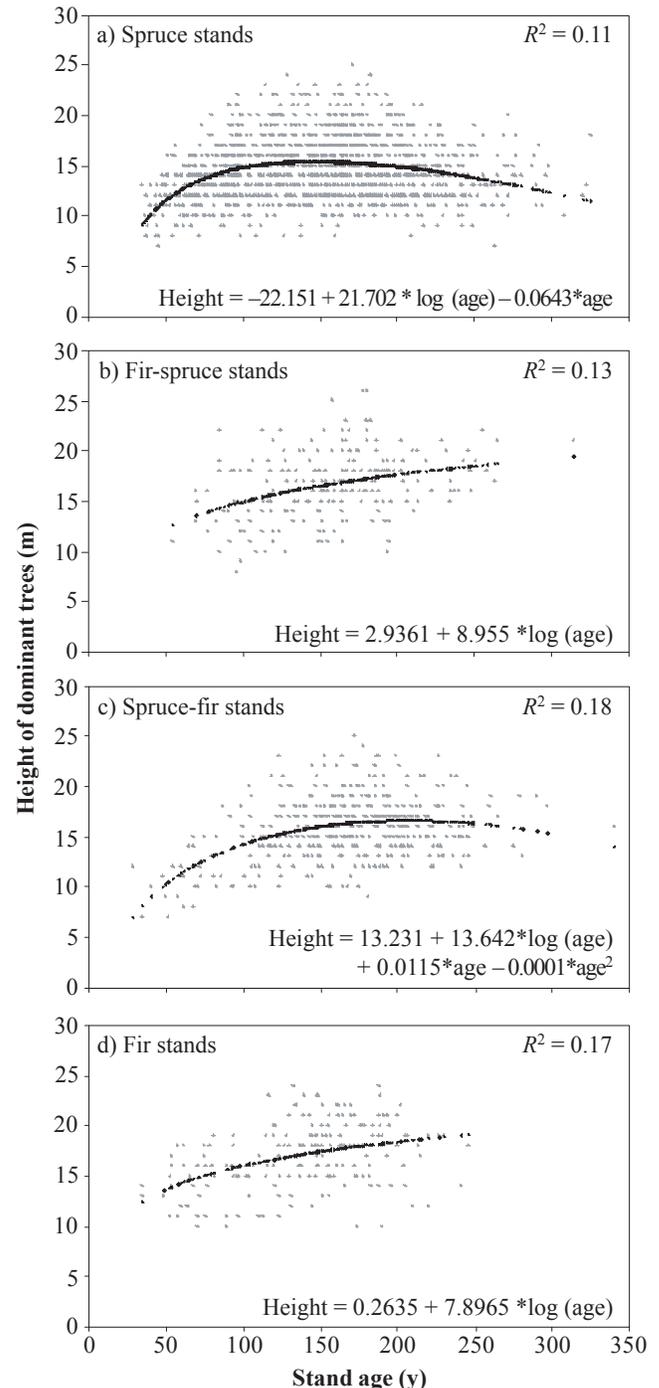


FIGURE 2. Regression curves (black dots) and equations of dominant tree height as a function of stand age for the four composition types. Each grey dot represents a sampling plot. Residuals around these regression curves constitute the relative productivity index.

TABLE III. Results of general covariance analysis testing productivity index as the dependent variable and environmental variables as the independent variables, for each of the four composition types. Only significant variables are shown. “+” or “-” indicate the direction of the relationship between the variable and the productivity index.

| | df | F | P > F | Relationship |
|-----------------------------------|----|-------|----------|---------------|
| Spruce stands (n = 899) | | | | |
| <i>Model R² = 0.29</i> | 34 | 10.31 | < 0.0001 | |
| Elevation | 1 | 78.55 | < 0.0001 | - |
| Slope angle | 1 | 30.64 | < 0.0001 | + |
| Organic matter depth | 1 | 24.04 | < 0.0001 | + |
| Understorey vegetation | 1 | 15.75 | < 0.0001 | Medium > Poor |
| Latitude | 1 | 10.00 | 0.0016 | - |
| Humus type | 2 | 5.57 | 0.0040 | Mor > Peat |
| Spruce-fir stands (n = 267) | | | | |
| <i>Model R² = 0.37</i> | 30 | 4.57 | < 0.0001 | |
| Elevation | 1 | 28.12 | < 0.0001 | - |
| Slope angle | 1 | 9.37 | 0.0025 | + |
| Humus type | 1 | 7.70 | 0.0060 | Mor > Peat |
| Organic matter depth | 1 | 5.72 | 0.0176 | + |
| Slope-aspect | 1 | 5.14 | 0.0243 | - |
| Fir-spruce stands (n = 144) | | | | |
| <i>Model R² = 0.44</i> | 30 | 2.96 | < 0.0001 | |
| Elevation | 1 | 41.97 | < 0.0001 | - |
| Longitude | 1 | 5.76 | 0.0180 | + |
| Latitude | 1 | 4.13 | 0.0444 | + |
| Fir stands (n = 119) | | | | |
| <i>Model R² = 0.37</i> | 29 | 1.82 | 0.0172 | |
| Elevation | 1 | 7.51 | 0.0074 | - |
| Stoniness (%) | 1 | 4.30 | 0.0410 | + |

index. For all composition groups, a decrease in productivity was associated with an increase in elevation. Slope angle and organic matter depth in their logarithm form were positively associated with the productivity index for spruce and spruce-fir stands. Overall, it appears that the productivity index of stands dominated by black spruce was influenced both by variables at a regional level, such as elevation and latitude, and by more site-specific variables such as slope angle, organic matter depth, and humus type. On the other hand, for stands dominated by balsam fir, only regional variables were associated with the productivity index (Table III). No interactions between independent variables were significant.

FACTORS INFLUENCING STAND STRUCTURE

Stand age, environmental variables, and productivity index together explained 52 to 65% of the variation in stand structure as expressed by the Shannon-Wiener index (Table IV). Spruce-fir stands showed the highest total R^2 , whereas fir stands had the lowest one. In all composition groups, the relative productivity index was positively associated with stand structure and best explained its variation, with partial R^2 ranging from 0.25 in fir stands to 0.43 in spruce stands (Table IV). The second best explanatory variable, which is positively associated with stand structure, was stand age, with the exception of the spruce group, where stand age and the squared stand age together came third after elevation. In all composition types, as the logarithm form of stand age is significantly related to the diversity index, this relationship is semi-logarithmic. The only other variables that explained > 5% of stand structure

TABLE IV. Stepwise regression analysis testing diameter diversity (Shannon-Wiener index) against productivity index, stand age, and environmental variables. Variables in italics are dummy variables. Only variables presenting a partial- R^2 greater than 0.005 are shown. “+” or “-” indicates the direction of the relationship between the variable and the diameter diversity.

| | Partial- R^2 | |
|--|----------------|---|
| Spruce stands (<i>Model R² = 0.6168, n = 1155</i>) | | |
| Productivity index | 0.4299 | + |
| Elevation | 0.0851 | - |
| (Stand age) ² | 0.0570 | + |
| Stand age | 0.0105 | + |
| Prod. index * Stand age | 0.0096 | + |
| <i>Drainage - 4</i> | 0.0071 | - |
| (Productivity index) ² | 0.0055 | + |
| Spruce-fir stands (<i>Model R² = 0.6504, n = 282</i>) | | |
| Productivity index | 0.3271 | + |
| Stand age | 0.1905 | + |
| Elevation | 0.0624 | - |
| (Stand age) ² | 0.0334 | + |
| Prod. index * Stand age | 0.0121 | + |
| Organic matter depth | 0.0097 | - |
| <i>Humus - mor</i> | 0.0079 | + |
| (Productivity index) ² | 0.0072 | + |
| Fir-spruce stands (<i>Model R² = 0.5858, n = 188</i>) | | |
| Productivity index | 0.3908 | + |
| Stand age | 0.1283 | + |
| Elevation | 0.0477 | - |
| <i>Deposit-rock</i> | 0.0190 | - |
| Fir stands (<i>Model R² = 0.5212, n = 161</i>) | | |
| Productivity index | 0.2517 | + |
| Stand age | 0.1876 | + |
| Organic matter depth | 0.0505 | - |
| Elevation | 0.0314 | + |

variation were elevation for spruce-fir stands and organic matter depth for fir stands (Table IV).

Overall, the variability of the diversity index was greater in pure spruce stands compared with other composition groups (Figure 3), and stands dominated by fir included a smaller number of even-sized stands. To illustrate the suggested evolution of stand structure with time, we calculated the predicted structural development for stands with productivity indices of 4, 0, and -4, based on the regression equations (Figure 3). Based on diameter distribution with 2-cm classes, stands with a Shannon-Wiener index value smaller than 1.7 are even-sized and those with a value higher than 2.0 are uneven-sized (with a transition phase in between) (Boucher, De Grandpré & Gauthier, 2003); these results suggest that stands on productive sites will become uneven-sized earlier than those on less productive ones. For example, according to the regression curves, spruce-fir stands with a productivity index of 0 would reach the 1.7 diversity level approximately 30 y later than those with a productivity index of 4, and those with a productivity index of -4 would reach it 100 y later.

Discussion

PRODUCTIVITY INDEX AND ENVIRONMENTAL VARIABLES

The productivity index, based on the tree age-height relationship, reflected to some extent local and regional vari-

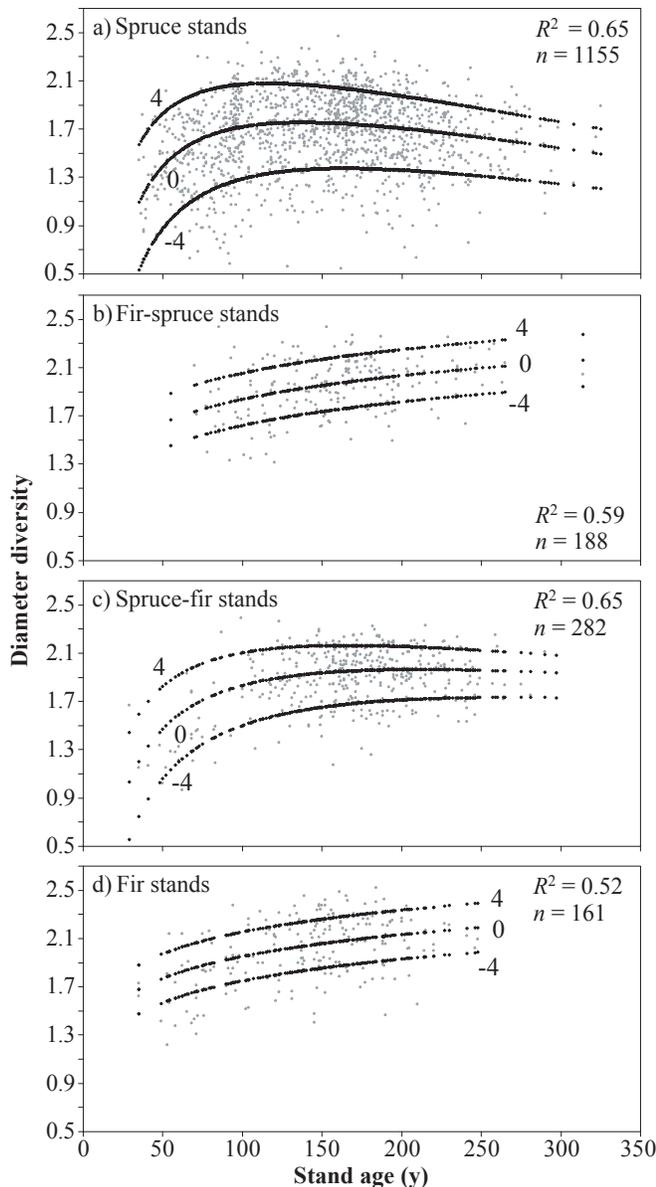


FIGURE 3. Diameter diversity of sampling plots (grey dots), measured by the Shannon-Wiener index, as a function of stand age for the four composition types. The predicted evolution of diameter diversity for stands with productivity indices of 4, 0, and -4 is shown (black dots).

ables. Regardless of the forest type, a decrease in productivity was observed with increasing elevation. The same trend has been observed in a wide variety of ecosystems (Klinka *et al.*, 1996; Raich, Russell & Vitousek, 1997; Chen, Klinka & Kabzems, 1998; Bolstad, Vose & McNulty, 2001). The productivity index of spruce-dominated stands was the only one to be significantly related to local site conditions such as slope angle, organic matter depth, and humus type. Black spruce can grow under a much wider range of environmental conditions than balsam fir (Burns & Honkala, 1990), leading probably to a greater variability in the site productivity on which spruce stands could be found. This could explain the stronger association between local site conditions and the productivity index for black spruce sites.

FACTORS INFLUENCING STAND STRUCTURE

Site productivity clearly appears to be the main factor influencing the diameter structure of coniferous stands in Québec's Côte-Nord region. Stand age came second for all composition types except for pure spruce stands, where it came third. Thus, stands on rich sites become uneven-sized earlier and reach their maximum diversity faster than stands on poor sites. Once a maximum has been reached, the richest sites also would maintain a higher diversity through time than poorer ones. This pattern is common to all composition types, but levels of diversity reached and the shape of the relationship with stand age do vary among composition types.

For balsam fir-dominated stands and mixed stands, levels of diversity were less variable between poor and rich sites than for the spruce stands. Level of diversity also increased slowly with stand age. On black spruce-dominated stands, after a rapid increase in diameter diversity in the first 100 y, we observed a slow decline afterwards, regardless of site productivity. A similar structural development for black spruce-dominated stands was observed in western Québec (Harper *et al.*, 2005; Lecomte & Bergeron, 2005). The structure of spruce-dominated stands was in fact the most strongly affected by site productivity. Several unproductive spruce stands older than 200 y showed a low size diversity index, indicative of an even-sized structure, while many young productive spruce stands were already showing an uneven-sized structure. Differences in structural development have also been found according to site type and moisture regime in the western boreal forest of Québec (Harper *et al.*, 2002; Harper *et al.*, 2005).

Two elements may explain the contrasting structural dynamics between poor and rich stands: 1) differences in growth rates, which induce a delay in senescence time, and 2) site resource limitations. The first element could apply to all composition types, whereas the second one would be more specific to spruce-dominated stands, which represent more than 80% of all plots.

DIFFERENCE IN GROWTH RATES

It can first be hypothesized that on rich sites, tree growth and stand development progress faster, leading to an earlier spreading of the size distribution due to different individual growth rates. This results in a rapid increase of the diameter diversity. Furthermore, higher growth rate likely induces earlier tree senescence, resulting in a faster successional rate (Romme & Knight, 1981; Prach, 1993; Donnegan & Rebertus, 1999). Also, mortality may be accelerated since trees with a higher growth rate rapidly reach a height that will make them susceptible to windthrow (Ruel *et al.*, 2000). It is recognized that tree longevity increases with a decrease in growth rate in harsh environments or unfavourable sites (Schulman, 1954; LaMarche, 1969; Robichaud & Methven, 1993; Pothier & Savard, 1998; Laberge, Payette & Bousquet, 2000). We can therefore suppose that senescence occurs much later and over a longer period of time in poor sites, which keeps the stands even-sized for longer.

However, if this delay in tree senescence were the only element responsible for the differences in structural dynamics,

we would observe that the diameter diversity of stands on poor sites would increase and eventually reach, although later, the same level as richer stands. But we did not observe such a convergence between poor and rich stands, as the regression curves were rather parallel. This suggests that there is a second element involved in this difference.

SITE RESOURCE LIMITATION

It is probable that resource limitations in an unproductive site restrict the maximum DBH that trees can attain. This is especially the case in poor sites dominated by black spruce. In fact, we observed in our old poor black spruce stands that the biggest trees were rather small, often less than 18 cm in DBH. Even though these stands are old and have gone beyond their break-up time, they cannot reach a high diversity value if the maximum DBH is only 16 or 18 cm (and the smallest DBH class is 10 cm). In other words, trees on poor sites remain small, and so does the diameter diversity. The Shannon-Wiener diversity reflects this fact as it is restricted by the range of values (Scherrer, 1984) and, in this case, by the number of possible diameter classes of the stand. Moreover, in poor sites, the low diameter diversity can reflect a forest that may remain open through time (Franklin *et al.*, 2002) with a very small structural diversity build-up (Harper *et al.*, 2005) or even a decrease with time (Lecomte & Bergeron, 2005).

Even though the diversity index also increases with time on poor sites, the size difference between trees of old unproductive stands will be too subtle to be perceived in the field and they will look even-sized. The age data of old, poor and even-sized stands, when considering only stands with more than nine cored trees, support the suggestion that stand break-up had already occurred since most of these stands showed an uneven-aged structure. The Shannon-Wiener index, however, is not sensitive to the spatial structure that might be created following gap mortality in these stands.

OTHER ENVIRONMENTAL VARIABLES

Environmental variables alone explain only a small fraction of stand structure variation. Since our productivity index showed a relatively good relationship with the environmental variables, its ability to explain structural variation is caused by the fact that it integrates the effects of all environmental variables, even those not measured in this study. However, even when considering the productivity index, some of the variation that remains is explained by environmental variables such as elevation, organic matter depth, and surficial deposits. Their importance for stand structural dynamics should be investigated more thoroughly with experimental studies. However, it could be hypothesized that the relationship between elevation and stand structure may reflect different disturbance regimes among sites along an elevation gradient, as climate would for example control insect development. This has been observed for spruce budworm, where stands at higher elevations sustained less defoliation than stands at lower elevations (Magnussen, Boudewyn & Alfaro, 2004). Also, it must be noted that other important factors, not measured in this study, may influence stand structure, notably initial stand composition, seed availability, structural legacies from past disturbances,

and disturbance regime (Kafka, Gauthier & Bergeron, 2001; Franklin *et al.*, 2002).

STAND COMPOSITION AND STRUCTURE

We found a large number of old pure spruce stands in the study area, the majority of which showed an uneven-sized structure. This supports the suggestion that a substantial portion of spruce stands evolved towards a multi-layered structure without compositional change in this region (De Grandpré, Morissette & Gauthier, 2000). Data also suggest that a portion of spruce stands may evolve towards fir-spruce stands (De Grandpré, Morissette & Gauthier, 2000). Therefore, we have to consider that among the pure spruce stands that were analyzed, there are both young stands that will evolve towards spruce-fir stands and others that will evolve towards uneven-sized spruce stands. Consequently, the regression curve for spruce stands could be somewhat biased, as some old stands may have become fir-spruce stands through succession. Since it has been suggested that the presence of fir preferentially increases on fertile sites (Carleton & Maycock, 1978; Bergeron & Dubuc, 1989), this could also explain in part the curve decline at an advanced age in spruce stands, as most of the old spruce could be on unfertile sites (Figure 3). However, this bias may not be that important since the majority of spruce stands seem to remain as such in this region over a 60-y period (S. Gauthier, unpubl. data).

Although fir is a late-successional species succeeding to spruce or hardwood species (Carleton & Maycock, 1978; Bergeron & Dubuc, 1989; Frelich & Reich, 1995), we found a significant proportion of even-sized fir stands that were less than 100 y old. These stands may have undergone a severe spruce budworm or hemlock looper outbreak, since it has been shown that such outbreaks can completely reinitiate fir stands by allowing the release of advanced regeneration (Baskerville, 1975; MacLean, 1984; Morin, 1994). The resulting stands frequently show an even-sized structure (Morin, 1994). Fir stands seem to rapidly achieve an uneven-sized structure, and although not tested in this study, we observed that their diameter diversity is generally higher than that of spruce stands. The great shade tolerance of fir makes this species an efficient gap-filler following tree mortality, and this contributes to increasing the diameter diversity by including small trees in the stand. Furthermore, the higher susceptibility of fir to windthrow and spruce budworm outbreaks compared to spruce (MacLean, 1980; Ruel, 2000) can favour the development of uneven-sized structures.

Conclusion

This study showed that stand structure of the Québec's Côte-Nord coniferous forest was not only related to stand age, but was also a function of site conditions. Site productivity strongly influenced stand structural changes, to such an extent that classical models of stand development (Oliver, 1981; Oliver & Larson, 1996) may not be adapted to reflect structure development under all site conditions. Spruce stands on very poor sites would escape the passage from an even- to an uneven-sized structure. These sites, as noted by Harper *et al.* (2005) and proposed by Franklin

et al. (2002), have a low tree density that may not be sufficient throughout stand development to support a closed canopy, and thus could escape the stem exclusion stage. Furthermore, our results indicate that once senescence has begun, size diversity of black spruce stands may slowly decrease, suggesting that gap formation resulting from the mortality of trees of the first cohort is a faster process than gap filling (Lecomte & Bergeron, 2005). Unless a major disturbance resets succession in these stands, size diversity should decrease until most of the trees from the first cohort have died. Beyond that point it is difficult to predict the outcome of structural development. In order to improve these predictions, the role of natural disturbances in structure dynamics has to be investigated. This is especially important for stands that are dominated by balsam fir, a species that is susceptible to a wide variety of disturbances. Over the landscape, the interactions between site conditions, disturbance types, and successional stages that create complex assemblages of structure and composition (Romme & Knight, 1981) are only starting to be described.

The results of the current study have important implications for natural-based forest management planning, where the maintenance of structural attributes is highly desirable. Although this study only considered changes in diameter diversity, it is known that these changes are accompanied by changes in other structural attributes such as coarse woody debris, snags, logs, and gaps in the canopy, all of which are recognized to be important for maintaining biodiversity (Spies, 1998). The fact that productivity influences structural changes stresses the importance of considering this factor when developing silvicultural strategies.

Acknowledgements

The authors thank M. Bernier-Cardou for statistical support, P. Cheers and I. Lamarre for editing the text, the ministère des Ressources naturelles et de la Faune du Québec for allowing us to use their forest inventory data, and P. Y. Bernier, M. Simard, C.-H. Ung, and four anonymous reviewers for their comments. Funding was provided by the Sustainable Forest Management Network and the Fonds québécois de recherche sur la nature et les technologies.

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