Structure, composition, and diversity of old-growth black spruce boreal forest of the Clay Belt region in Quebec and Ontario[1]

Karen Harper, Catherine Boudreault, Louis DeGrandpré, Pierre Drapeau, Sylvie Gauthier, and Yves Bergeron

Abstract: Old-growth black spruce (*Picea mariana*) boreal forest in the Clay Belt region of Ontario and Quebec is an open forest with a low canopy, quite different from what many consider to be "old growth". Here, we provide an overview of the characteristics of old-growth black spruce forest for three different site types on organic, clay, and coarse deposits. Our objectives were (1) to identify the extent of older forests; (2) to describe the structure, composition, and diversity in different age classes; and (3) to identify key processes in old-growth black spruce forest. We sampled canopy composition, deadwood abundance, understorey composition, and nonvascular plant species in 91 forest stands along a chronosequence that extended from 20 to more than 250 years after fire. We used a peak in tree basal area, which occurred at 100 years on clay and coarse sites and at 200 years on organic sites, as a process-based means of defining the start of old-growth forest. Old-growth forests are extensive in the Clay Belt, covering 30–50% of the forested landscape. Black spruce was dominant on all organic sites, and in all older stands. Although there were fewer understorey species and none exclusive to old-growth, these forests were structurally diverse and had greater abundance of *Sphagnum*, epiphytic lichens, and ericaceous species. Paludification, a process characteristic of old-growth forest stands on clay deposits in this region, causes decreases in tree and deadwood abundance. Old-growth black spruce forests, therefore, lack the large trees and snags that are characteristic of other old-growth forests. Small-scale disturbances such as spruce budworm and windthrow are common, creating numerous gaps. Landscape and stand level management strategies could minimize structural

Received 3 February 2003. Accepted 22 July 2003. Published on the NRC Research Press Web site at http://er.nrc.ca/ on 4 September 2003.

K. Harper[2] and P. Drapeau. Groupe de recherche en écologie forestière, Université du Québec à Montréal, Montréal, QC H3C 3P8, Canada.
C. Boudreault, L. DeGrandpré, and S. Gauthier. Groupe de recherche en écologie forestière, Université du Québec à Montréal, Montréal, QC H3C 3P8, Canada; and Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre, Québec, QC G1V 4C7, Canada.
Y. Bergeron. Groupe de recherche en écologie forestière, Université du Québec à Montréal, Montréal, QC H3C 3P8, Canada; and Sustainable Forest Management Chair, Université de Québec en Abitibi-Témiscamingue, Rouyn-Noranda, QC J9X 5E4, Canada.

[1] This article is published in this Supplement as one of a selection of papers presented at the "Old-Growth Forests in Canada: A Science Perspective" Conference, Sault Ste. Marie, Ontario, 14–19 October 2001.

[2] Corresponding author (e-mail: c1444@er.uqam.ca).

Environ. Rev. **11**: S79–S98 (2003) doi: 10.1139/A03-013

changes caused by harvesting, but unmanaged forest in all stages of development must be preserved in order to conserve all the attributes of old-growth black spruce forest.

Key words: boreal forest, old growth, paludification, *Picea mariana*, structural development, succession.

Résumé : Dans la région de la ceinture d'argile de l'Ontario et du Québec, la forêt boréale ancienne d'épinette noire (*Picea mariana*) est une forêt ouverte, où la canopée est basse, ce qui diffère considérablement de la perception que le public a d'une "forêt ancienne". Nous présentons ici un aperçu des caractéristiques de la pessière noire ancienne poussant sur dépôts organiques, argileux et grossiers. Nos objectifs étaient: (1) déterminer l'étendue des forêts plus vieilles; (2) décrire la structure, la composition et la diversité en fonction des classes d'âge; (3) mettre en lumière les processus clés dans la pessière noire ancienne. Nous avons échantillonné la composition de l'étage supérieur, l'abondance de bois mort, la composition du sous-bois et les plantes invasculaires de 91 peuplements forestiers, le long d'une chronoséquence de 20 à plus de 250 ans après feu. Nous avons utilizé le maximum de la surface terrière des arbres, observé à 100 ans sur les dépôts argileux et grossiers et à 200 ans sur les dépôts organiques, pour définir le début de la forêt ancienne. Dans la ceinture d'argile, les forêts anciennes sont abondantes, couvrant de 30 à 50 % du paysage forestier. L'épinette noire domine sur tous les sols organiques, ainsi que dans tous les peuplements plus âgés. Bien que les espèces du sous-bois soient moins nombreuses et qu'aucune d'elles ne leur soit exclusivement liée, les forêts anciennes présentent une structure variée et renferment davantage de *Sphagnum*, de lichens épiphytes et d'éricacées. La paludification, processus caractéristique des peuplements forestiers anciens sur dépôts argileux dans cette région, entraîne une diminution de l'abondance des arbres et du bois mort. Par conséquent, on ne trouve pas dans les forêts anciennes d'épinette noire, les quantités élevées de gros arbres et de chicots qui caractérisent d'autres forêts anciennes. Des perturbations à petite échelle, comme les épidémies de la tordeuse des bourgeons de l'épinette et les chablis, sont fréquentes et créent de nombreuses trouées. Des stratégies d'aménagement à l'échelle du paysage et du peuplement pourraient réduire les changements structuraux causés par la récolte; cependant, il est essentiel de préserver des peuplements non aménagés à tous les stades de développement pour conserver toutes les caractéristiques d'une pessière noire ancienne.

Mots clés : forêt boréale, forêt ancienne, paludification, *Picea mariana*, développement structurale, succession.

Introduction

Old-growth forests are commonly perceived as heterogeneous, structurally complex forests with large trees, large snags, and large logs, as well as many canopy gaps and a diverse tree community; indeed, these characteristics are often used to define "old growth" (Kneeshaw and Burton 1998; Kneeshaw and Gauthier 2003). Many of these features are noticeably lacking in old-growth black spruce (*Picea mariana* Mill. B.S.P.) boreal forest in the Clay Belt region of northeastern Ontario and northwestern Quebec. Although black spruce forest does not match the standard image of old growth, these forests may provide unique compositional or structural features to a landscape dominated by fire disturbance that should be considered in forest management.

Because of the uncharacteristic appearance of old-growth black spruce forests, we prefer to use functional attributes for defining old growth, notably as a stage of stand development when single-tree replacement has a greater influence than past stand-level disturbance events (Oliver 1981; Kneeshaw and Burton 1998; Kneeshaw and Gauthier 2003). We use this process based definition to explore changes in structure, composition, and diversity with time since fire, and we use these trends to determine the start of the old-growth stage of development in black spruce boreal forest.

This paper provides an overview of the characteristics of old-growth black spruce boreal forest in the Clay Belt region of Ontario and Quebec. Our objectives were (1) to identify the extent of older forests; (2) to describe the structure, composition, and diversity of forest stands in different age classes; and (3) to identify key processes in old-growth black spruce forest. Because stand development differs depending on surficial deposits and site characteristics (Harper et al. 2002; Gauthier et al. 2000, 2002), we address each of these objectives for three different site types: organic, clay, and coarse deposits (described below).

Methods

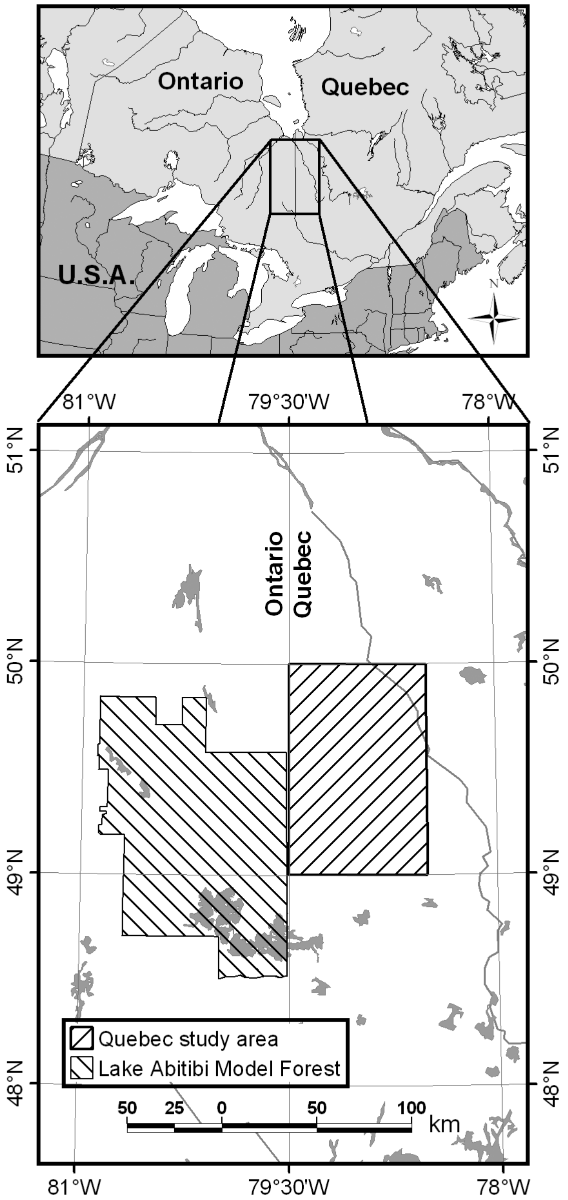
Sixty-six sites were located in black spruce boreal forest in the northwestern part of the Abitibi region in Quebec (Quebec study area) and 25 sites were in the Lake Abitibi Model Forest in northeastern Ontario (48.92°N to 49.93°N; 78.64°W to 80.64°W) (Fig. 1). The study area is part of the *Picea mariana*-moss bioclimatic domain in the Lake Matagami Lowland ecoregion of the northern Clay Belt (Saucier et al. 1998), and is characterized by lacustrine deposits and flat topography (Vincent and Hardy 1977). 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, and annual precipitation is 856/792 mm (La Sarre, Quebec, and Iroquois Falls, Ontario, weather stations, respectively, Environment Canada 1993). Although black spruce dominates most stands, jack pine (*Pinus banksiana*) is dominant on drier sites.

We sampled forest stands along a chronosequence in 1996 and 1997 to study changes in canopy composition and forest structure. The chronosequence approach, in which stands of different ages are compared to provide insight into changes over time, is subject to criticism that differences could be due to site characteristics rather than stand age (Johnson 1992; Linder 1998; Bergeron 2000), particularly when the sample size is small. We minimized these shortcomings by sampling 91 sites and grouping them into three different site types. Variation within each site type inevitably remained, but was probably not correlated with time since fire because of the large sample sizes. In addition, site locations were selected based on a time-since-fire map (Bergeron et al. 2001) and deposit types in order to obtain a range of stand ages and site types. There was no prior knowledge of species composition; therefore, no major stand types found in the region were excluded. We also selected sites that were accessible but were never harvested. Time since the most recent fire was determined using the reconstructed fire history for the region (Bergeron et al. 2001). Sites were classified according to surficial deposit and hydric regime: organic (organic layer >60 cm, poor drainage), clay (clay deposits, moderate drainage), and coarse (sand, rock or till; well drained). The number of sites differed among site types (Table 1). For the analysis, we grouped sites into 50-year age classes; this age range was selected to match the age classes used in Harper et al. (2002). For some of the age classes within the site types, there were either one or two sites (Table 1); therefore, our interpretations were usually based on broad trends using more than one age class.

At each site, all trees and snags within a 4 m × 200 m plot (plot lengths were shorter in 21 sites) were inventoried, identified to species, and measured for height and diameter at breast height (DBH) (in 5-m and 5-cm classes, respectively). The decay stage of all snags was also determined (classes 1–4, similar to stages 3–6 in Thomas et al. 1979). For pieces of downed coarse woody material (logs) that intersected the transect, we noted the diameter at the point of intersection (in 5-cm classes) and the decay stage (classes 1–5, Maser et al. 1979). Gaps were measured as the distance along the transect between the first living branches on either side of a gap with evidence of a treefall. We calculated total live tree and snag basal area, and log volume (Harmon et al. 1986) for each site. Relative importance (RI) for the basal area of different species of live trees was calculated as a proportion of total live tree basal area. Species diversity of trees for each site was determined using the Shannon index

$$[1] \qquad H = -\sum p_i \ln p_i$$

Fig. 1. Map of the study area showing the locations of the Lake Abitibi Model Forest (25 sites) and the Quebec study area (66 sites). The Quebec study area is the same study area as in Harper et al. (2002).



where H is the Shannon index and p_i is the relative importance of species i. Structural diversity was calculated in a similar manner using trees, snags, and (or) logs in different size and decay classes. In this case, "species" were considered to be the different combinations of height and DBH classes for tree structure; height, DBH, and decay classes for snag structure; and diameter and decay classes for log structure. For example, i could be trees <5 m tall and <5 cm DBH, or logs >20 cm and <25 cm diameter and in decay class 3. All possible combinations of classes were used.

Understorey composition was sampled in 40 1-m^2 evenly-spaced quadrats along each 200-m transect in the clay sites (45 sites). We estimated the cover of all vascular plant species in six cover classes. Nonvascular plant communities were sampled in a subset of 22 of the clay sites (all >80 years old).

Table 1. The number of sites sampled in different age classes (years) for clay, coarse, and organic sites.

	Age classes (years)					
	0–50	50–100	100–150	150–200	200–250	250+
Clay	9	5	10	8	11	2
Coarse	1	8	5	2	3	1
Organic	6	3	1	5	4	6

Cover of nonvascular terricolous species was estimated in 21 0.25-m^2 evenly-spaced quadrats along half (100 m) of the transect. Next to each of these quadrats, we collected two branches from the nearest black spruce tree. We determined the age of these trees using a Pressler increment borer. Cover of epiphytic nonvascular species was estimated on a 50-cm segment of the main section of each branch. We also conducted a thorough search of bryophyte and lichen species, including epiphytes, within a 400-m^2 plot (centred on a 100-m portion of the transect), with an emphasis on microhabitats. Nomenclature follows Marie-Victorin (1995) for vascular plants, and the United States Department of Agriculture website (http://plants.usda.gov) for mosses, hepatics, and lichens. The composition of vascular and nonvascular communities was described using three separate non-metric, multidimensional scaling ordinations (NMS) on the abundance of terricolous nonvascular species, epiphytic nonvascular species, and vascular species. Spearman correlations were performed between ordination axes and site characteristics, as well as between the axes and abundance and diversity estimates. The latter included the number of nonvascular and vascular species per transect (richness or mean richness), the average cover for nonvascular and vascular species per quadrat, and the number of species observed in the 400-m^2 plot (TNS) for nonvascular species. In addition, the total number of species in each 50-year age class was determined (total richness), and Beta diversity was calculated as 1 – (mean richness / total richness).

To complement the results from this chronosequence study, we also present results on landscape-level structural characteristics in the same region (Quebec study area, Fig. 1) using data from Harper et al. (2002). Data in this study consisted of area, surficial deposit, moisture regime, canopy composition, canopy height, canopy cover, and incidence of windthrow and spruce budworm (*Choristoneura fumiferana*) outbreaks for all forested stands in the Ministry of Natural Resources ecoforestry database (Ministère des Ressources Naturelles du Québec 1994), combined with time-since-fire dates from a fire reconstruction map in a 10 000-km^2 area in northwestern Quebec (see Harper et al. 2002 for details). The methodology used by the Ministry of Natural Resources was based on aerial photo interpretation. Surficial deposit and moisture regime was used to classify each stand into one of the three site types: clay (fine), coarse (coarse and thin soil), and organic (organic); names in brackets were those used in Harper et al. (2002), which contains detailed descriptions. These stands were also categorized into time-since-fire classes of 50-year intervals. To determine the extent of older forests on the landscape, we examined the age class distribution. We summarized canopy structural characteristics for each age class by determining the proportion of stands within different canopy cover and canopy height classes. We also report the proportion of stands with $>$75% black spruce in the canopy, stands codominated by jack pine, as well as stands affected by spruce budworm outbreaks or windthrow ($>$25% mortality of canopy trees). Diversity for canopy composition and structure was calculated using Shannon's index separately on the proportion of stands with different classes of canopy composition, and stands with different combinations of cover and height classes.

Extent of old-growth forest in the Clay Belt

We suggest that the start of the old-growth stage could be estimated as the peak in tree basal area, which would indicate the start of overstorey mortality and the subsequent recruitment of the understorey into the canopy (cf. Kneeshaw and Burton 1998; Kneeshaw and Gauthier 2003), or simply the start of overstorey mortality for stands with continuous recruitment. Although the cohort basal area ratio may be a more accurate measure, tree basal area is much less time consuming to sample and, therefore, more appropriate for larger sample sizes. This transition corresponds to the irregular second structural cohort described by Bergeron et al. (1999). Tree basal area increased to a peak at approximately 200–250 years on organic sites, and approximately 50–100 years on clay and coarse sites (Fig. 2*a*). The timing of these stages corresponds roughly to the longevity of the dominant tree species: black spruce, 100–200 years on organic and clay sites; and black spruce and jack pine, 70–100 years on coarse sites (Kneeshaw and Gauthier 2003). Combined with these estimates of tree species longevity, we expect that the peak in basal area may represent an overestimate on organic sites and an underestimate on clay and coarse sites. Therefore, we suggest that the old-growth stage of development in black spruce boreal forest starts at approximately 200 years on organic sites and approximately 100 years on clay and coarse sites. However, this stage is dynamic, as evidenced by decreases in tree abundance, followed by declines in deadwood abundance (see below).

The extent of old-growth boreal forest depends on the minimum age at which it is defined. Over half (52.4%) the area of forested stands in the black spruce boreal forest in northwestern Quebec was older than the rotation age of 100 years; 42.7 and 21.7% were older than 150 and 200 years, respectively (results not shown). These older forests are often found in large contiguous areas (Lefort 1998; Gauthier et al. 2002; Bergeron et al. 2002). Estimates of stand age of 200 years or older represent minimum ages, as the oldest trees may not represent stand age. Therefore, estimates of the relative area of stands older than 250 and 300 years (6.3 and 0.3%) are likely underestimates. Stand ages estimated using radiocarbon dating of charcoal layers reach as high as 1111 years in black spruce forests in our study region (Cyr et al. 2003).

The amount of older forests on the landscape depends on the surficial deposits; few old forests were found on well-drained coarse deposits, whereas the largest proportion of older forests occurred on organic sites (Fig. 3). For example, forests older than 150 years were over three times more abundant on organic than on coarse sites, likely due to higher soil moisture. Using 100, 100, and 200 years as we defined earlier as the start of the old-growth stage; 50, 31, and 33% of black spruce boreal forest on clay, coarse and organic sites, respectively, would be considered old growth (Fig. 3).

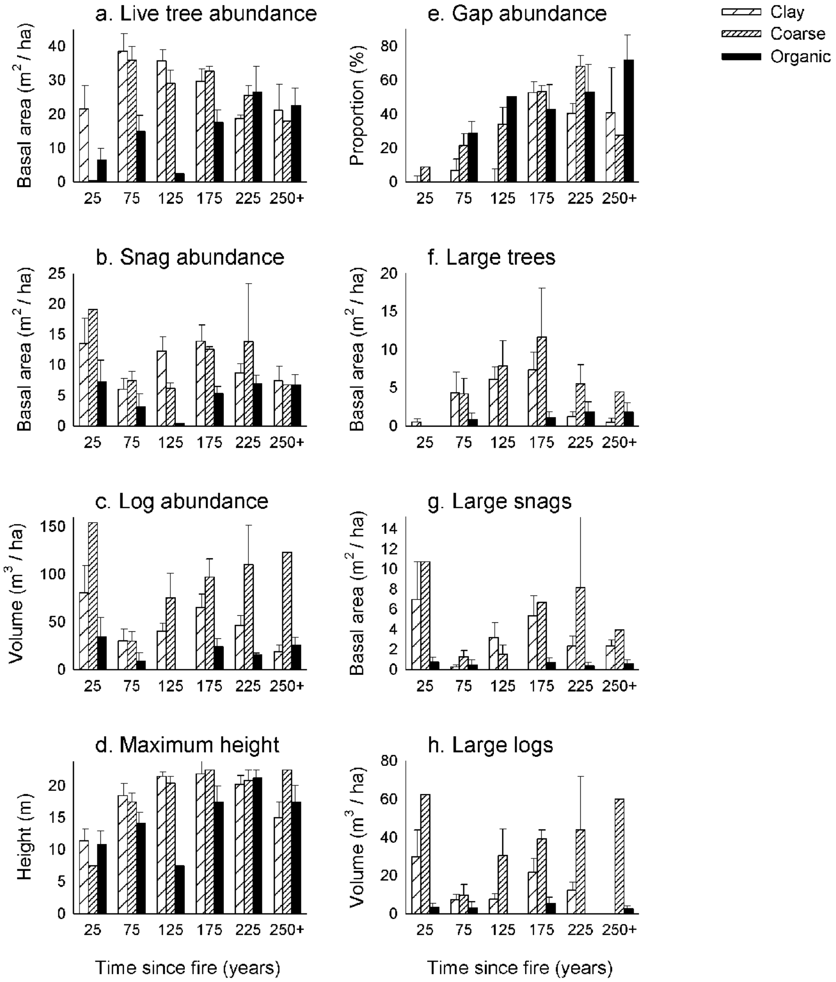
We expect that the proportion of older forests on the landscape will increase, if there is no forest harvesting. Fire frequency began to decline in the mid-19th century and decreased even further during the 20th century (Bergeron et al. 2001). Thus, forests are now less likely to burn, resulting in more old growth. Furthermore, a decrease in fire frequency has been predicted for this region as a result of global warming (Flannigan et al. 1998), which would further increase the amount of old-growth forest.

Characteristics of old-growth black spruce boreal forest

Canopy composition

Black spruce was dominant ($>$50% relative importance) in all age classes on both clay and organic sites, and in age classes $>$100 years on coarse sites (Fig. 4). Indeed, most older forests ($>$100 years old) in our study region were classified as stands with $>$75% black spruce in the canopy (Table 2; Harper et al. 2002). Our results also confirm that black spruce is dominant over the entire chronosequence on organic sites, and increases with time since fire on other site types in this region (Gauthier et al. 2000). The abundance of jack pine in young to intermediate-aged coarse sites and, to a lesser extent, clay sites (Fig. 4), resulted in its codominance in many stands up to 100 years on clay sites and up to 200 years on coarse sites (Table 2; Gauthier et al. 2000; Harper et al. 2002). Two early successional species, trembling aspen (*Populus tremuloides*) and willow (*Salix* spp.), were prominent in some of the youngest stands (Fig. 4; Gauthier et al. 2000). Balsam fir (*Abies balsamea*) on coarse sites, was the only species with greater relative importance in older sites compared to younger sites (Fig. 4; Gauthier et al. 2000). As a consequence of the increasing dominance of black spruce and the lower importance of most other tree

Fig. 2. Structural characteristics in different time-since-fire age classes for clay, coarse, and organic sites: (*a*) tree basal area, (*b*) snag basal area, (*c*) log volume, (*d*) average of the heights of the tallest tree in each stand, (*e*) proportion of area under gaps, (*f*) basal area of large (>20 cm dbh) trees, (*g*) basal area of large (>20 cm dbh) snags, (*h*) volume of large (>20 cm diameter) logs. Age classes are identified by the midpoint of 50-year time-since-fire intervals. Error bars represent ±1 SE; there is no SE for the following age classes for which $n = 1$: 0–50 years and 250+ years on coarse sites, 100–150 years on organic sites.



species, tree composition of older forest stands was less diverse at both the stand and landscape levels compared with younger stands (Fig. 5*a*, except an outlier for coarse sites in the oldest age class with only one site; Fig. 5*e*; Harper et al. 2002).

Structure

Although tree canopy composition changed little and became less diverse over time, structural development was prominent in older black spruce forests. The visual impression of old-growth black spruce boreal forest as open and sparse is evident from our results and those of Harper et al. (2002). The vast majority of older (>100 years old) stands were 7–17 m tall, with 20–60% canopy cover (Table 2; Harper et al. 2002). Younger, 50- to 100-year-old stands spanned a wider variety of canopy cover and height classes and included a greater proportion of tall and dense stands. Our results confirm lower

Fig. 3. Cumulative distribution of relative area occupied by stands of different ages (time since fire) for sites on clay, coarse, and organic sites. Data are from a fire reconstruction map and an ecoforestry database in northwestern Quebec (Harper et al. 2002).

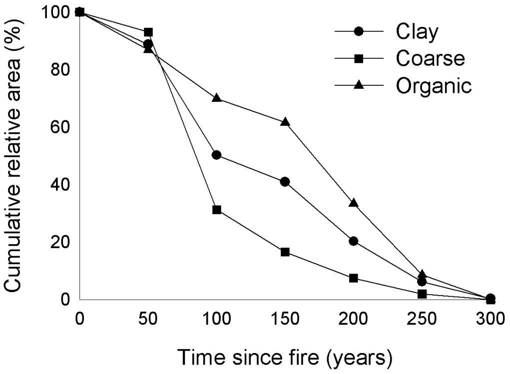


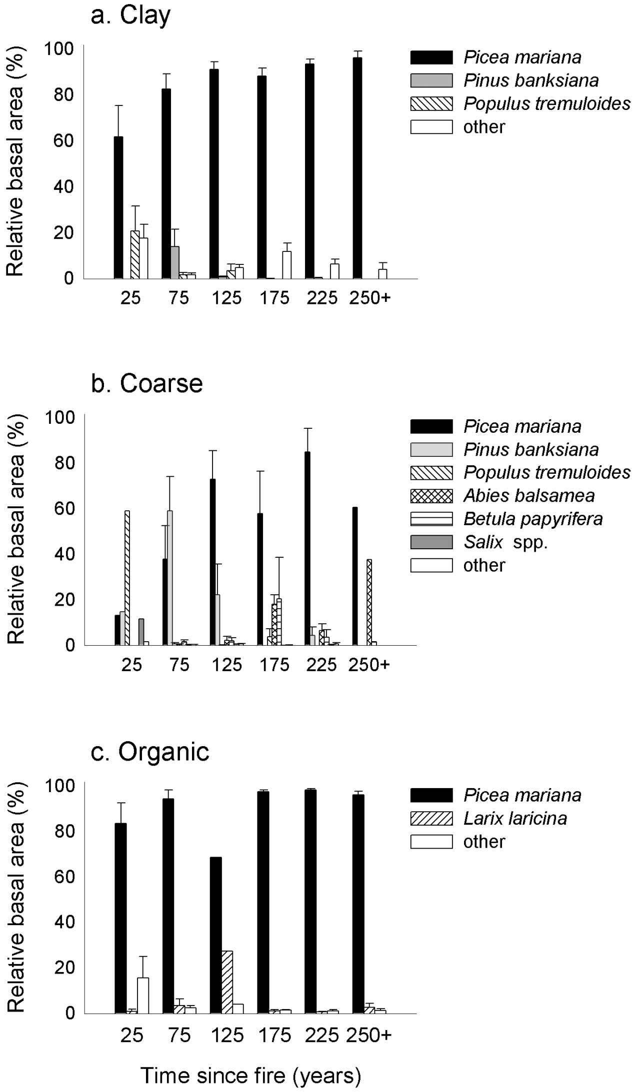
Table 2. Proportion (%) of stands with different canopy characteristics in different age classes (years) for clay, coarse, and organic sites.

	Proportion (%)					
	0–50	50–100	100–150	150–200	200–250	250+
All sites						
20–40% cover	33.5	16.2	36.6	40.3	38.7	34.1
40–60% cover	46.4	30.1	47.7	48.0	53.0	55.8
60–80% cover	19.7	41.6	13.9	11.0	7.9	9.2
80–100% cover	0.5	12.1	1.9	0.7	0.4	0.8
1.5–4 m height	34.6	1.0	0.8	0.8	0.6	0.2
4–7 m height	10.6	4.1	1.1	0.4	0.2	0.1
7–11 m height	19.7	23.5	28.5	38.9	40.0	48.2
11–17 m height	29.5	48.7	53.5	51.2	53.9	45.4
17–22 m height	5.6	18.9	14.6	8.4	5.2	6.0
>22 m height	0.0	3.9	1.5	0.3	0.1	0.0
Clay sites						
>75% *Picea mariana*	25.1	36.9	76.3	84.3	93.6	92.4
Codominated by *Pinus banksiana*	16.8	48.7	6.8	4.8	2.1	2.0
Affected by spruce budworm*	0.0	0.4	2.9	1.3	0.2	0.1
Affected by windthrow*	0.4	5.4	16.9	19.9	24.0	11.6
Coarse sites						
>75% *Picea mariana*	34.3	24.1	46.2	48.4	74.2	92.7
Codominated by *Pinus banksiana*	44.6	58.3	31.5	26.4	14.2	0.8
Affected by spruce budworm*	0.0	0.1	0.2	0.4	0.0	0.0
Affected by windthrow*	0.0	2.7	12.2	8.2	9.2	3.9
Organic sites						
>75% *Picea mariana*	98.1	79.6	92.7	96.9	98.7	98.8
Codominated by *Pinus banksiana*	0.0	15.3	0.5	0.7	0.2	0.0
Affected by spruce budworm*	0.0	0.6	4.7	8.8	6.3	1.1
Affected by windthrow*	0.0	5.7	18.3	19.3	23.5	19.8

Note: Results are synthesized from Harper et al. (2002); methods based on aerial photograph interpretation are described therein.

*>25% mortality of canopy trees.

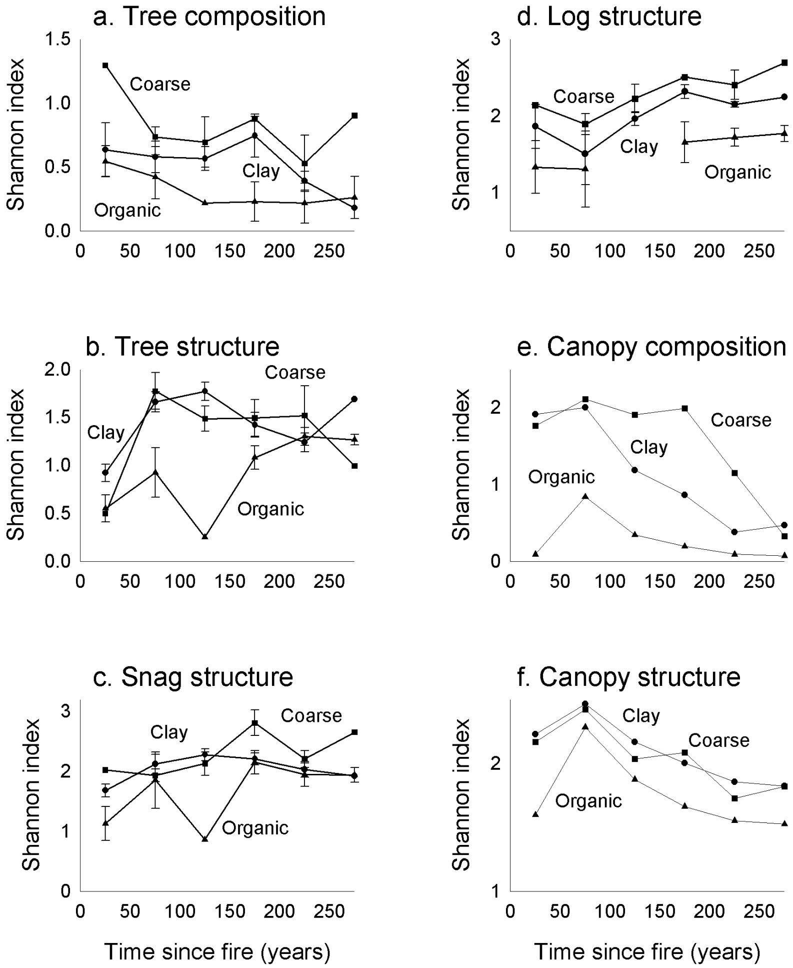
Fig. 4. Relative importance of major tree species (>10 % in at least one age class) for different time-since-fire age classes on (*a*) clay, (*b*) coarse, and (*c*) organic sites. Age classes are identified by the midpoint of 50-year time-since-fire intervals. Relative importance was calculated from basal area data. Error bars represent ±1 SE; there is no SE for the following age classes for which $n = 1$: 0–50 years and 250+ years on coarse sites, 100–150 years on organic sites.



canopy height, measured as the average height of the tallest tree in each stand, in the older stands compared with intermediate-aged stands for clay sites only (Fig. 2*d*). The minimum value of tree basal area and maximum height for 100- to 150-year-old stands on organic sites is likely an anomaly due to a sample size of one. We also found greater gap abundance, and, therefore, lower canopy cover, in older age classes (Fig. 2*e*).

Trends in stand-level structural characteristics with time since fire differed among the three site types (Fig. 2). On organic sites, older stands had greater abundance of trees, snags, and logs compared with intermediate-aged 50–150 year old stands, as would be expected for old-growth forests (Kneeshaw and Burton 1998). However, the oldest forests on clay and coarse sites had lower tree, snag, and log

Fig. 5. Trends in diversity with time since fire for clay, coarse and organic sites: stand-level diversity for (*a*) tree species composition and (*b*) structural characteristics of trees, (*c*) snags, and (*d*) logs; also landscape-level diversity for (*e*) canopy composition and (*f*) canopy structure. Stand-level diversity was calculated using the Shannon index on the relative abundance of different tree species, and of trees, snags or logs with different characteristics (see Methods for details). Error bars for stand-level diversity represent ±1 SE; there is no SE for the following age classes for which $n = 1$: 250+ years on clay, 0–50 years and 250+ years on coarse sites, 100–150 years on organic sites. Landscape-level diversity was calculated using the Shannon index based on the relative area occupied by stands with different canopy composition classes (*e*) or different canopy cover and height classes (*f*); results are synthesized from Harper et al. (2002).



(clay only) abundance than some of the younger age classes. Low sample size in the oldest age class in the clay and coarse sites may have led to anomalous results, yet these trends often extended from the 150 to 200 year age class, particularly for clay sites. Other than the youngest (<50 years old) stands, snag basal area and log volume decreased after a peak at 150–200 years on clay sites. On coarse sites, snag and log abundance increased until older age classes.

In the black spruce boreal forests, the oldest forests often do not share typical old-growth characteristics. There were fewer large trees, large snags, and large logs in the oldest two age classes on clay sites, compared with younger stands (Fig. 2). Coarse sites showed similar trends for large trees, but large snags and large logs were more abundant in the oldest age classes (150+ years) compared with

Table 3. Species richness and diversity of vascular and nonvascular understorey plants in different age classes (years) on clay sites.

	0–50	50–100	100–150	150–200	200+
Vascular species					
Mean richness	18.1±2.3	19.4±1.0	16.9±1.8	20.8±2.0	18.2±1.5
Total richness	47	38	53	58	45
Beta diversity	0.61	0.49	0.68	0.64	0.59
Nonvascular species					
Mean richness	N/A	24.5±1.7	25.3±1.7	31.6±2.3	30.2±0.9
Total richness	N/A	39	69	65	49
Beta diversity	N/A	0.37	0.35	0.51	0.38

Note: Mean richness is the total number of species per transect, averaged over all transects in each age class; total richness is the total number of species in each age class. Beta diversity is equal to 1 − (mean richness / total richness)

intermediate seral stages (50–150 years). There were few large structural components on organic sites compared with the other site types. The abundance of large snags and large logs did not increase in the oldest organic sites but large trees were most abundant in these sites. Overall, the criterion of numerous large trees, large snags, or large logs (Kneeshaw and Burton 1998) cannot always be used to identify old growth in black spruce boreal forest.

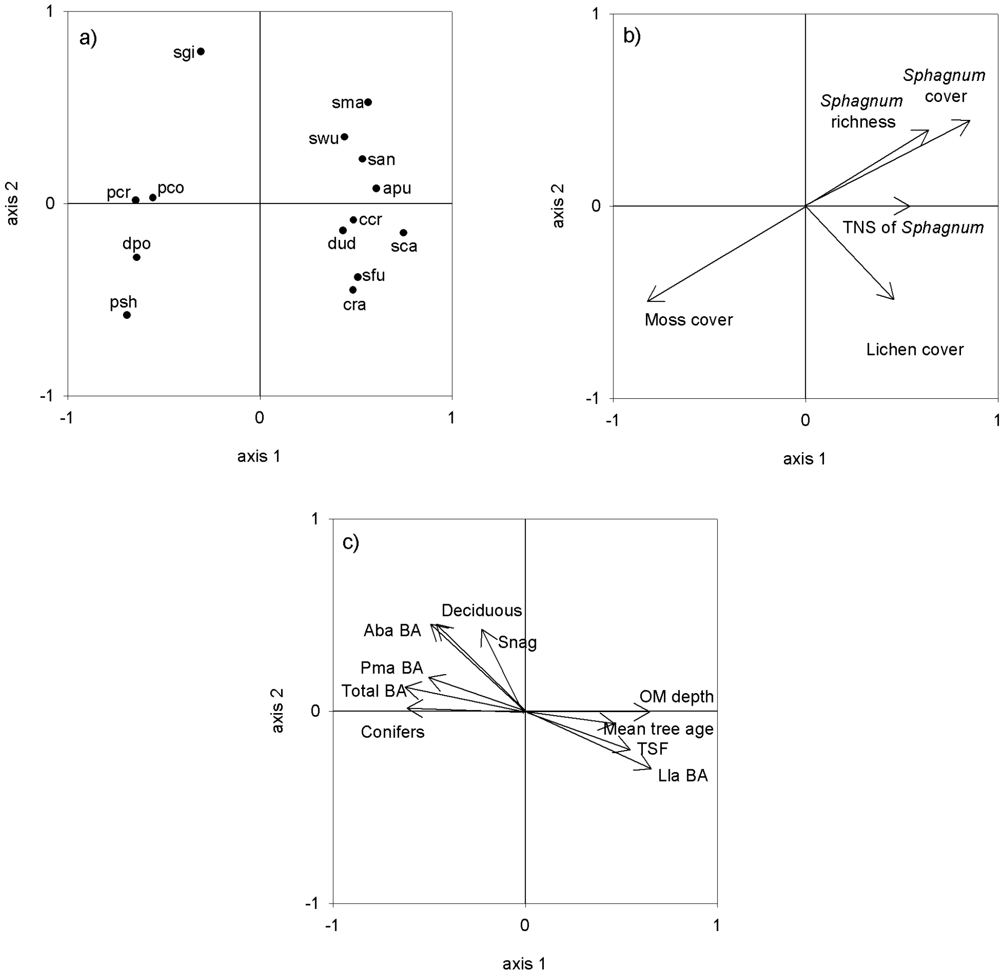
Old-growth sites generally had greater within-stand structural diversity than younger sites. Tree structural diversity was highest on the oldest organic sites, but peaked in the intermediate age class on clay and coarse sites (Fig. 5). Structural diversity of snags and logs was generally greater in older sites. However, at the landscape level, older stands were less diverse in terms of canopy structure (Fig. 5*f*). Thus, old-growth stands were uniformly short and open, but with snags and logs in a variety of sizes and decay stages.

Understorey composition

Most of the 224 taxa in the understorey on the clay sites were nonvascular, including ten species of *Sphagnum*, 40 species of other mosses, 13 taxa of liverworts, 38 species of epiphytic lichens, and 38 species of terricolous lichens (also see Boudreault et al. 2002). There were 85 vascular plant species, of which half were forest herbs and about 30% were woody species. None of the species commonly encountered in our study were found exclusively in old growth. Neither nonvascular nor vascular total species richness increased throughout old-growth development along the chronosequence (Table 3). Maximum mean richness and diversity were found in the 150- to 200-year-old stands, but generally decreased as the composition of the understorey became more uniform. The notable exception is mean nonvascular richness that was substantially higher in older (150+ years) compared with intermediate-aged stands.

In intermediate-aged forests, high tree basal area and relatively low organic matter depth created suitable conditions for the development of a carpet of mosses heavily dominated by *Pleurozium schreberi*, *Ptilium crista-castrensis*, *Polytrichum commune*, and *Dicranum polysetum* (Fig. 6; also see Boudreault et al. 2002). These mosses are typical of closed boreal forests located on fairly well-drained sites (La Roi and Stringer 1976; Heinselman 1981; Foster 1985). Along with the decline in tree basal area, the old-growth phase is also characterized by an increase in organic matter thickness (Boudreault et al. 2002) and another phase of nonvascular community development at about 150 years since fire. Old-growth sites typically have high richness and cover of *Sphagnum* spp. compared with younger sites, although their ground layer is still dominated by *Pleurozium schreberi*. Terricolous lichen cover also increased along the time-since-fire gradient.

Fig. 6. Non-metric multidimensional scaling ordination diagram showing (*a*) scores for terricolous nonvascular plant species, (*b*) vectors showing Spearman correlations of the axes with diversity and abundance estimates, and (*c*) vectors showing Spearman correlations of the axes with environmental variables. Only species, environmental variables, and diversity and abundance estimates that were significantly correlated ($p < 0.05$) with one or both of the two axes are shown. (*a*) Species codes are apa, *Aulacomnium palustre*; cra, *Cladina rangiferina/stygia*; ccr, *Cladonia crispata*; dpo, *Dicranum polysetum*; dud, *Dicranum undulatum*; pco, *Polytrichum commune*; pcr, *Ptilium crista-castrensis*; psh, *Pleurozium schreberi*; san, *Sphagnum angustifolium*; sca, *Sphagnum capillifolium*; sfu, *Sphagnum fuscum*; sgi, *Sphagnum girgensohnii*; sma, *Sphagnum magellanicum*; swu, *Sphagnum wulfianum*. (*b*) TNS refers to total number of species in the 400-m^2 plot; richness is the total number of species in the quadrats along each transect; cover is the average cover per quadrat; Moss cover refers to mosses other than *Sphagnum*. (*c*) Codes for environmental variables are: Aba BA, basal area of *Abies balsamea*; Conifers, basal area of conifers; Deciduous, basal area of deciduous trees; Lla BA, basal area of *Larix laricina*; Mean tree age, average age of sampled trees; OM depth, thickness of organic matter; Pma BA, basal area of *Picea mariana*; Snag, snag basal area; Total BA, total basal area; TSF, time since fire.



Epiphytic flora of younger forests was characterized by greater abundances of *Tuckermannopsis americana*, *Parmeliopsis ambigua*, *Hypogymnia physodes*, and *Bryoria furcellata*; whereas *Mycoblastus sanguinarius*, *Bryoria trichodes*, and *Usnea* spp. were more abundant in older forests (Fig. 7; also see Boudreault et al. 2002). The total number of epiphytic lichen species in the 400-m^2 plots was greater in young forests where trembling aspen and jack pine were present. Greater tree species diversity (Fig. 5*a*) resulted in higher epiphytic species richness by providing a greater variety of substrates for species colonization. Furthermore, the presence of deciduous trees in intermediate-aged coniferous stands has been linked to greater epiphytic species richness since they are colonized by a unique set of species (Kuusinen 1994; Boudreault et al. 2000). However, the abundance of epiphytic lichens increases with stand age (McCune 1993; Neitlich 1993; Esseen and Renhorn 1996), and is closely and positively related to mean tree age. On older trees, there has been a longer time available for colonization, vegetative expansion, and sexual reproduction, compared with younger trees.

Differences in vascular understorey composition were strongly related to live tree basal area and time since fire (Fig. 8). Herb species such as *Cornus canadensis*, *Maianthemum canadense*, and *Trientalis borealis* characterized the understorey of closed canopy forests with high tree basal area. In these forests, there was greater cover and richness of herbs and low shrubs, as well as fern richness, compared with older forests. As stands develop and tree basal area decreases in the absence of fire, the understorey community composition of old-growth forests is characterized by greater vascular plant cover, due to the increase in ericaceous species abundance. Furthermore, ericaceous species richness was highest in the understorey of older forests. *Ledum groenlandicum*, *Cassandra calyculata*, *Vaccinium myrtilloides*, and *Kalmia polyfolia* are dominant components of these forests. Because young and old forests both have more open canopies, they are more similar, in terms of understorey composition, to each other than to closed forests (results not shown).

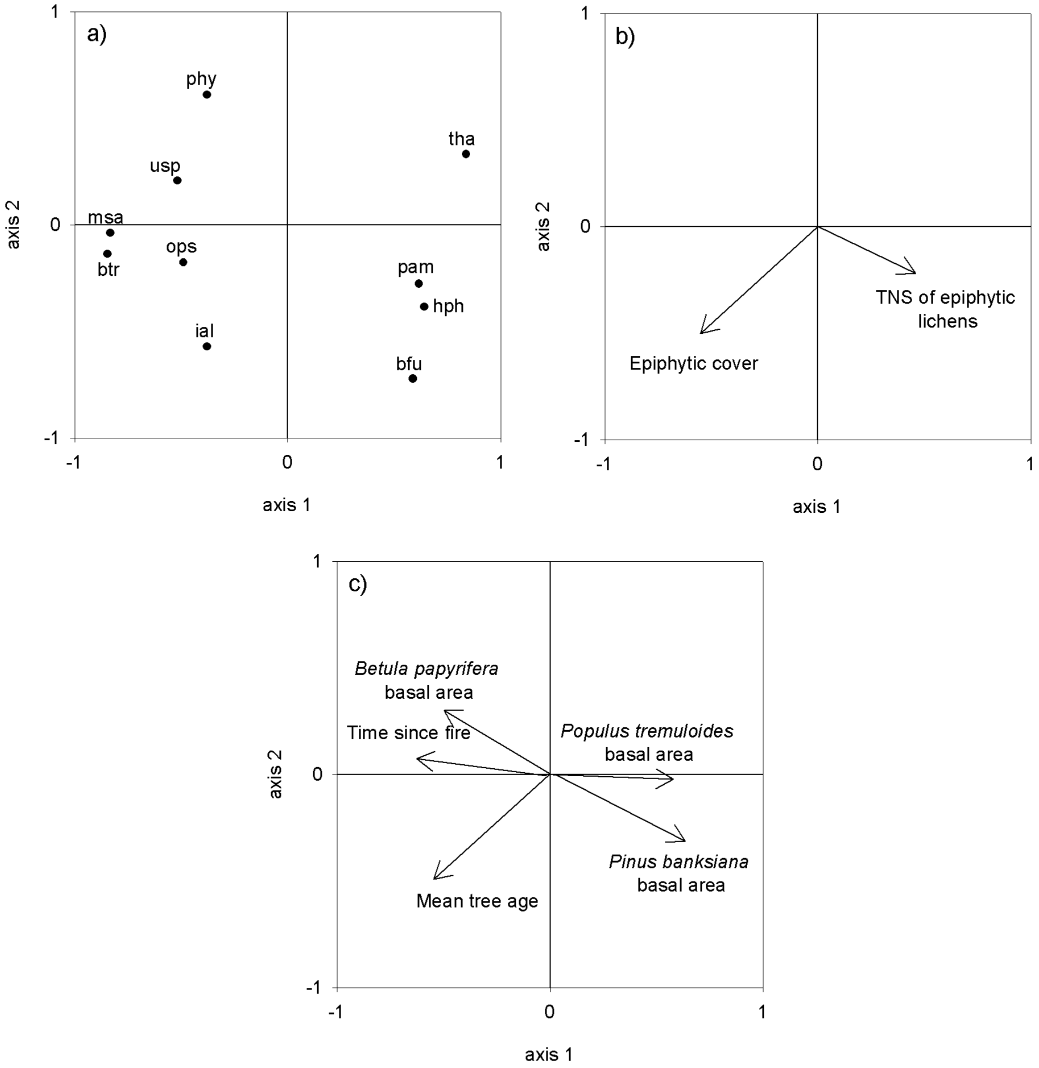
Processes in black spruce boreal forest

The old-growth stage starts when single tree replacement processes dominate and the effects of stand-level disturbance are no longer prominent, according to the definition we have used. We suggest this is evidenced as a peak in tree basal area, indicating the start of canopy breakup. In the black spruce boreal forest, this transition to old-growth forest is characterized mostly by structural changes rather than species succession. This is particularly true for clay and organic sites, which remain dominated by black spruce throughout stand development. On coarse sites, however, tree species composition changes from jack pine to black spruce during this transition (Harper et al. 2002). Succession from deciduous or *Pinus* sp. to *Picea* sp. has also been observed elsewhere in the Canadian boreal forest (Carleton and Maycock 1978; Bergeron and Dansereau 1993; Lesieur et al. 2002). Changes in structure on coarse sites such as the decrease in live tree and snag abundance, and decreases in canopy cover and height, can likely be attributed to this succession in canopy composition.

Most structural changes in old-growth black spruce boreal forest occur as a result of tree replacement processes including secondary disturbance and gap dynamics. Two types of secondary disturbance can be frequent: spruce budworm and windthrow. Mortality due to spruce budworm outbreaks was generally not very common; outbreaks mostly affected intermediate-aged stands on organic sites, and did not have much impact on stands on other site types (Table 2; Harper et al. 2002). Windthrow was prominent in older stands on clay and organic sites (Table 2; Harper et al. 2002). However, our data underestimate the total amount of secondary disturbance because partial disturbance assessed using aerial photograph interpretation was defined as >25% of trees affected, which means that with a resolution of <8 ha for stands, disturbed areas <2 ha were not included. A decrease in canopy cover from other causes may have reduced stability in these black spruce stands with poor rooting substrate (Smith et al. 1987; Ruel 1995).

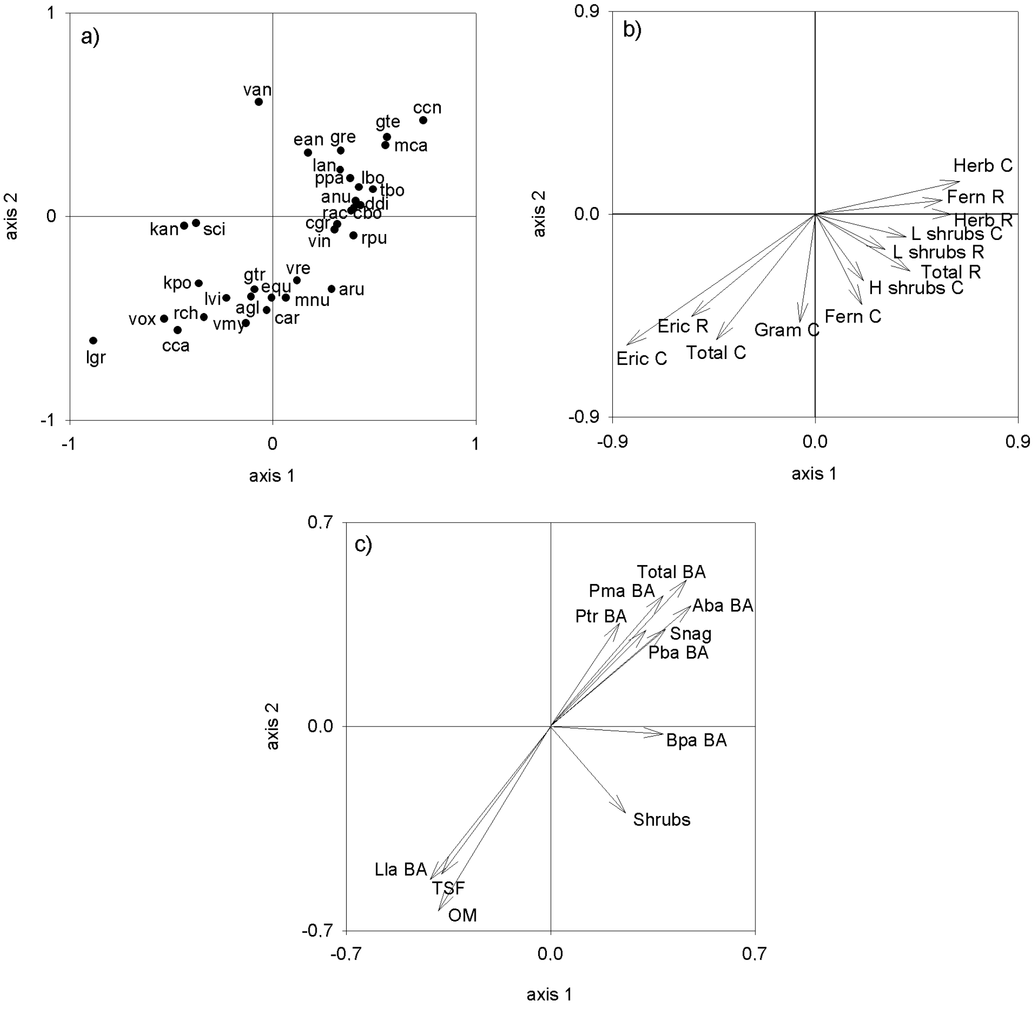
Although in other forest ecosystems, gap disturbance creates favourable microsites for other tree species (e.g., Kuuluvainen 1994; Frelich and Reich 1995), black spruce remains dominant in older black spruce stands. Mixedwood stands are not maintained through recruitment of deciduous trees in gaps as they are in boreal forests further south near Lac Duparquet (Bergeron 2000). The development of the extensive, thick moss layer prevents seedling establishment. This maintains the dominance of black spruce that reproduces mainly by layering in old-growth forests, and is tolerant of cold, wet, nutrient poor conditions (Viereck 1983).

Fig. 7. Non-metric multidimensional scaling ordination diagram showing (*a*) scores for epiphytic nonvascular plant species, (*b*) vectors showing Spearman correlations of the axes with diversity and abundance estimates, and (*c*) vectors showing Spearman correlations of the axes with environmental variables. Only species, environmental variables, and diversity and abundance estimates that were significantly correlated ($p < 0.05$) with one or both of the two axes are shown. (*a*) Species codes are bfu, *Bryoria furcellata*; btr, *Bryoria trichodes* subsp. *trichodes*; hph, *Hypogmnia physodes*; ial, *Imshaugia aleurites*; msa - *Mycoblastus sanguinarius*; ops, *Ochrolechia pseudopallescens*; pam — *Parmeliopsis ambigua*; phy, *Parmeliopsis hyperopta*; tha, *Tuckermannopsis americana*; uspp, *Usnea* spp. (*b*) TNS refers to total number of species in the 400-m^2 plot; cover is the average cover per quadrat. (*c*) Mean tree age is the average age of sampled trees.



Paludification is a process in which soil temperature, nutrient availability, decomposition rates, and productivity decrease with time since fire with the build-up of thick moss and organic layers (Van Cleve et al. 1983; Paré and Bergeron 1995; Boudreault et al. 2002). Although it is possible that stands with greater moss thickness might have escaped disturbance longer, we believe that this is unlikely. Since older stands are found in large contiguous areas (Lefort 1998; Gauthier et al. 2002; Bergeron et al. 2002), these forest stands were probably not fire skips that had escaped fire merely because of a

Fig. 8. Non-metric multidimensional scaling ordination diagram showing (*a*) scores for vascular plant species, (*b*) vectors showing Spearman correlations of the axes with diversity and abundance estimates, and (*c*) vectors showing Spearman correlations of the axes with environmental variables. Only species, environmental variables, and diversity and abundance estimates that were significantly correlated ($p < 0.05$) with one or both of the two axes are shown. (*a*) Species codes are agl, *Andromeda glaucophylla*; anu, *Aralia nudicaulis*; aru, *Alnus rugosa*; car, *Carex* spp.; cbo, *Clintonia borealis*; cca, *Cassandra calyculata*; ccn, *Cornus canadensis*; cgr, *Coptis groenlandica*; ddi, *Dryopteris disjuncta*; ean, *Epilobium angustifolium*; equ, *Equisetum* spp.; gre, *Goodyera repens*; gte, *Goodyera tesselata*; gtr, *Galium triflorum*; kan, *Kalmia angustifolia*; kpo, *Kalmia polifolia*; lan, *Lycopodium annotinum*; lbo, *Linnaea borealis*; lgr, *Ledum groenlandicum*; lvi, *Lonicera villosa*; mca, *Maianthemum canadense*; mnu, *Mitella nuda*; ppa, *Petasites palmatus*; rac, *Rosa acicularis*; rch, *Rubus Chamaemorus*; rpu, *Rubus pubescens*; sci -*Scirpus* spp.; tbo, *Trientalis borealis*; van, *Vaccinium angustifolium*; vin, *Viola incognita*; vmy, *Vaccinium myrtilloides*; vox, *Vaccinium oxycoccos*; vre, *Viola renifolia*. (*b*) The following codes are used: C, cover; R, richness; Eric, ericaceous; Gram, graminoids; H shrubs, high shrubs (>1 m); L shrubs, low shrubs (<1 m); richness is the total number of species in the quadrats along each transect; cover is the average cover per quadrat. (*c*) Codes for environmental variables are: Aba BA, basal area of *Abies balsamea*; Bpa BA, basal area of *Betula papyrifera*; Lla BA, basal area of *Larix laricina*; OM, thickness of organic matter; Pba BA, basal area of *Pinus banksiana*; Pma BA, basal area of *Picea mariana*; Ptr BA, basal area of *Populus tremuloides*; Shrubs, basal area of shrubs; Snag, snag basal area; Total BA — total basal area; TSF, time since fire.



thick moss layer. We expect that paludification does occur on clay sites and causes structural changes, including decreases in tree basal area, canopy height, canopy cover, and deadwood abundance. There was also some evidence of these changes on organic sites, but at a later time since fire. Because of lower productivity, black spruce trees that establish through layering are shorter and smaller, resulting in more open forests with discontinuous canopies. Taylor et al. (1987) hypothesized that paludification of stands associated with increased dominance of *Sphagnum* spp. contributes to the dominance of ericaceous species and the homogenization of understorey species composition. Site quality is poorer, and there are fewer microhabitats available for colonization by terricolous and epiphytic bryophytes and lichens; in particular, coarse woody material is quickly covered by *Sphagnum* spp. or feather mosses (Boudreault et al. 2002). As a consequence, old-growth forests in our area are not reservoirs for high richness of nonvascular and vascular plant species. We suggest that paludification is a process characteristic of old growth on clay and organic sites in the black spruce boreal forest of the Clay Belt region. Paludification has also been reported in the Hudson Bay Lowlands and in many areas of Newfoundland (Heinselman 1981; Taylor et al. 1987).

Management of old-growth black spruce forest

An important result of our study is the “atypical” nature of the older stages of the black spruce forest of the Clay Belt region. The disturbance dynamics of this ecosystem, its flat topography and the life history traits of its dominant tree species, black spruce, set the stage for old-growth forests that are much more open, less multilayered and with fewer large trees than what we intuitively consider an old-growth forest. Old-growth black spruce boreal forests also differ from old growth in other ecosystems in that they are not reservoirs of understorey diversity. Another key conclusion is that the transition to old-growth stages is a continuous process whose timing depends on edaphic conditions and site productivity, but this transition produces an array of forest structures across the landscape. Moreover, on clay and organic sites in the black spruce forest system, tree species composition remains relatively stable though time, and structural development is the key process in the transition to old-growth forests. Paludification, a process characteristic of old-growth forests on more humid sites, has important consequences for both forest structure and understorey composition in our study area. Old-growth forests also form an extensive component of this forest zone, where they represent about 40% of the land base in naturally disturbed forests (also see Bergeron et al. 2001). For the Clay Belt, this regional importance contributes to the overall open canopy structure of the landscape (Harper et al. 2002) and this, in turn, has a direct influence on its biodiversity (Drapeau et al. 2003). Old-growth forests, therefore, are extensive and important across the landscape. They provide unique structural features, and their dynamics is driven by unusual processes, such as paludification.

The structural characteristics linked to old-growth forests at the landscape level could be eliminated by current harvesting practices in the Clay Belt. The truncation of the age–class distribution of forest stands with current even-aged management raises concerns about the long-term maintenance of biological diversity and ecological processes. When considering the importance and extent of old-growth stands in the landscape, it clearly becomes difficult to justify the use of an even-aged management silvicultural system with clearcutting over large areas and short rotations as a means to emulate natural disturbances. The structure and composition might be maintained through forest harvesting practices with an increased rotation period (Harris 1984; Burton et al. 1999; Seymour and Hunter 1999). Extending the rotation age could be favourable for species, such as epiphytic lichens, that need time for colonization and growth (Esseen and Renhorn 1996; Boudreault et al. 2002), but may be difficult to justify economically because the short longevity of eastern boreal tree species would imply a decrease in allowable cut. Another option is to maintain structural attributes found in old-growth forests by simulating different stages of structural development through a diversification of silvicultural treatments on the landscape (Bergeron et al. l999, 2002). Such an approach could provide a means of maintaining structural diversity while only slightly modifying allowable cut (Bergeron et al. 1999; Harvey et al.

2002). In the black spruce forest of the Clay Belt region, this approach would include some traditional clearcutting to create an even-aged structure analogous to that observed after fire; combined with partial cutting that would simulate the transition of stands to old growth, and selective cutting that would emulate secondary disturbance and gap dynamics in the later stages of old-growth forests. Assuming an average forest age of 139 and 172 years for the Quebec and Ontario Clay Belt, respectively (Bergeron et al. 2001), and the current harvesting rotation age of 100 years, Bergeron et al. (1999) recommend the following proportions of stands treated with each of these silvicultural practices: 39–49% clearcut, about 25% partially cut and 26–37% selectively cut. However, much of the portion allocated as selectively cut would be considered non-commercial forest and thus remain unharvested. Instead, if we want to maintain forests that resemble old-growth black spruce forests, efforts should be focused on introducing partial cutting as an important silvicultural treatment because the main loss of old-growth forests occurs at the transition to the old-growth stage.

Maintaining a diversity of structural development stages at the landscape level may not be enough to preserve the diversity of all organisms. At the stand level, the development of forest management approaches based on an understanding of natural disturbance dynamics should consider key habitat attributes such as old trees, snags, and coarse woody material. Old or large trees are essential for trunk forager birds (Red-breasted Nuthatch, Brown Creeper, Drapeau et al. 2003) and the maintenance of epiphytic lichens (Boudreault et al. 2000, 2002). Such attributes are most abundant in the early stages of the transition to old-growth forests in the Clay Belt region. Hence, in intermediate-aged forest stands that are either clearcut or partially cut, clumps of large and old trees should be retained to provide adequate habitat conditions for organisms associated with such attributes. The retention of old deciduous trees is particularly important as they possess a particular epiphytic flora (Kuusinen 1994; Neitlich and McCune 1997; Dettki and Esseen 1998; Boudreault et al. 2000), and are a potential source of propagules for the inoculation of conifers for species that can live on either deciduous or conifer trees (Sillett and Goslin 1999). In addition, partial cutting and selective harvesting should be implemented in a way to limit damage to the ground cover, in order to reduce the effects on terricolous bryophyte and lichen species that can be restricted to various microhabitats (Boudreault et al. 2002).

Since there are few, if any, species that are restricted to old-growth forests, this landscape and stand-level forest management may go a long way towards conserving structural and compositional biodiversity. However, the conservation of some unmanaged old-growth forest is needed to serve as control sites to monitor the effectiveness of harvesting strategies, and as safety sites in case these strategies fail to conserve all aspects of biodiversity (Kneeshaw and Gauthier 2003). Because of the persistent, unpredictable nature of the fire regime, we must also conserve the developmental sequence that leads to the formation of old growth. This is even more important since productive intermediate-aged forests are more at risk than unproductive open old-growth black spruce forests. To ensure the future protection of all developmental stages including old growth, reserve areas must be either very large or be placed in many different areas (Kneeshaw and Gauthier 2003).

Conclusions

In the black spruce boreal forest in the Clay Belt region of Ontario and Quebec, both structure and composition change in the first few hundred years following fire, as the stand develops into old-growth forest. On clay deposits, the mostly black spruce forest canopy starts to break up after about 100 years following fire, when the forest is considered “old growth”. At this time, numerous gaps appear, from either spruce budworm outbreaks or, more likely, windthrow. In later stages, the largest trees, although characteristic of old growth in other forests, disappear. The moss layer becomes thicker, and the colder soil temperature and lower decomposition rates reduce productivity; as a result, newly regenerated trees produced from layering are not as large. A variety of sizes of deadwood in various stages of decay become more abundant. There are also more epiphytic lichens on trees, more ericaceous shrub species in the understorey, and more of the characteristic *Sphagnum* spp. on the ground. These changes occur a century later on organic sites. On coarse sites, jack pine persists as a codominant tree species in the canopy for the first century; the death of these canopy trees cause a decrease in tree basal area and in the number of large trees, marking the start of the old-growth stage at about 100 years after fire.

Although there are fewer species found in these old-growth forests and none that are exclusive to old growth, there are unique processes, such as paludification and small-scale gap disturbances, as well as high structural diversity. Furthermore, old-growth forests cover 30–50% of black spruce boreal forest in the Clay Belt region, and this amount is expected to increase based on past and present global warming. Thus, even in this system with relatively high fire frequency and low tree species diversity, old-growth forests are extensive and important components of the landscape. Management strategies at the landscape and stand levels could minimize structural changes caused by harvesting, but the preservation of large or multiple unmanaged forest in all stages of stand development is essential for the conservation of old-growth black spruce boreal forest.

Acknowledgements

Many thanks to Thuy Nguyen, Steve Fievet, Marie-Hélène Longpré, Yong Ban, Eric Desjardins, and Amy Barker. The map was done by Jacques Morissette. Funding was provided by Ministère de Ressources Naturelles du Québec, Sustainable Forest Management Network, Lake Abitibi Model Forest, Natural Sciences and Engineering Research Council, Fonds pour la Formation de chercheurs et l'aide à la recherche, and the Chaire Industrielle en Aménagement Forestier Durable.

References

Bergeron, Y. 2000. Species and stand dynamics in the mixed woods of Quebec's southern boreal forest. Ecology, **81**: 1500–1516.

Bergeron, Y., and Dansereau, P.-R. 1993. Predicting the composition of Canadian southern boreal forest in different fire cycles. J. Veg. Sci. **4**: 827–832.

Bergeron, Y., Harvey, B., Leduc, A., and 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., Kafka, V., Lefort, P., and Lesieur, D. 2001. Natural fire frequency for the eastern Canadian boreal forest: consequences for sustainable forestry. Can. J. For. Res. **31**: 384–391.

Bergeron, Y., Leduc, A., Harvey, B.D., and Gauthier, S. 2002. Natural fire regime: A guide for sustainable forest management of the Canadian boreal forest. Silva Fenn. **36**: 81–95.

Boudreault, C., Gauthier, S., and Bergeron, Y. 2000. Epiphytic lichens and bryophytes on *Populus tremuloides* along a chronosequence in the southwestern boreal forest of Québec, Canada. Bryologist, **103**: 725–738.

Boudreault, C., Bergeron, Y., Gauthier, S., and Drapeau, P. 2002. Bryophyte and lichen communities in mature to old-growth stands in eastern boreal forests of Canada. Can. J. For. Res. **32**: 1080–1093.

Burton, P.J., Kneeshaw, D.D., and Coates, K.D. 1999. Managing forest harvesting to maintain old-growth forest in the Sub-Boreal Spruce zone of British Columbia. For. Chron. **75**: 623–631.

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

Cyr, D., Bergeron, Y., Gauthier, S., and Larouche, A. 2003. How vulnerable to fire are the old-growth forests of the Clay Belt? To be published.

Dettki, H., and Esseen, P.-A. 1998. Epiphytic macrolichens in managed and natural forest landscapes: a comparison at two spatial scales. Ecography, **21**: 613–624.

Drapeau, P., Leduc, A., Bergeron, Y., Gauthier, S., and Savard, J.-P. 2003. Les communautés d'oiseaux des vieilles forêts de la pessière à mousses de la ceinture d'argile : Problèmes et solutions face à l'aménagement forestier For. Chron. **79**(3): 531–540.

Environment Canada. 1993. Canadian climate normals 1961–1990. Canadian climate program. Atmospheric Environment Service, Downsview, Ontario.

Esseen, P.-A., and Renhorn, K.-E. 1996. Epiphytic lichen biomass in managed and old-growth boreal forests: effect of branch quality. Ecol. Appl. **6**: 228–238.

Flannigan, M., Bergeron, Y., Engelmark, O., and Wotton, M. 1998. Future wildfire in circumboreal forests in relation to global warming. J. Veg. Sci. **9**: 469–476.

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.

Frelich, L.E., and Reich, P.B. 1995. Spatial patterns and succession in a Minnesota southern-boreal forest. Ecol. Monogr. **65**: 325–346.

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

Gauthier, S., Lefort, P., Bergeron, Y., and Drapeau, P. 2002. Time since fire map, age-class distribution and forest dynamics in the Lake Abitibi Model Forest. Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre, Information Report LAU-X-125.

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., and 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., and Drapeau, P. 2002. Structural development of black spruce forests following fire in Abitibi, Québec: a landscape scale investigation. Silva Fenn. **36**: 249–263.

Harris, L.D. 1984. The fragmented forest. *In* Island biogeography theory and the preservation of biotic diversity. University of Chicago Press. 211 p.

Harvey, B.D., Leduc, A., Gauthier, S., and Bergeron, Y. 2002. Stand-landscape integration in natural-disturbance based management of the southern boreal forest. For. Ecol. Manage. **155**: 369–385.

Heinselman, M.K. 1981. Fire and succession in the conifer forests of North America. *In* Forest succession: concepts and application. *Edited by* D.C. West, H.H. Shugart, and D.B. Botkin. Springer-Verlag, New York. pp. 374–405.

Johnson, E.A. 1992. Fire and vegetation dynamics — Studies from the North American boreal forest. *In* Cambridge studies in ecology. Cambridge University Press, Cambridge, Mass. 129 p.

Kneeshaw, D.D., and Burton, P.J. 1998. Assessment of functional old-growth status: a case study in the sub-boreal spruce zone of British Columbia, Canada. Nat. Areas J. **18**: 293–308.

Kneeshaw, D.D., and Gauthier, S. 2003. Old-growth in the boreal: a dynamic perspective. Environ. Rev. **11**(Suppl. 1): S99–S114.

Kuuluvainen, T. 1994. Gap disturbance, ground microtopography, and the regeneration dynamics of boreal coniferous forests in Finland: a review. Ann. Zool. Fenn. **31**: 35–51.

Kuusinen, M. 1994. Epiphytic lichen flora and diversity on *Populus tremula* in old-growth and managed forests of southern and middle boreal Finland. Ann. Bot. Fenn. **31**: 245–260.

La Roi, G.H., and Stringer, M.H.L. 1976. Ecological studies in the boreal spruce-fir forests of the North American taiga. II. Analysis of the bryophyte flora. Can. J. Bot. **54**: 619–643.

Lefort, P. 1998. Influence du climat et de l'occupation européenne sur le régime des feux de forêt dans la région du lac Abitibi. M.Sc. thesis, Université du Québec à Montréal, Québec, Canada. 70 p.

Lesieur, D., Gauthier, S., and Bergeron, Y. 2002. Fire frequency and vegetation dynamics for the south-central boreal forest of Quebec, Canada. Can. J. For. Res. **32**: 1996–2009.

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

Marie-Victorin, F. 1995. Flore Laurentienne. 3rd ed. Les Presses de l'Universit é de Montréal, Montréal. 1083 p.

Maser, C., Anderson, R.G., Cromack, K., Jr., Williams, J.T., and Martin, R.E. 1979. Dead and down woody material. *In* Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington. *Edited by* J.W. Thomas. U.S. Department of Agriculture Forest Service.

McCune, B. 1993. Gradients in epiphyte biomass in three *Pseudotsuga-Tsuga* forests of different ages in western Oregon and Washington. Bryologist, **96**: 405–411.

Ministère des Ressources Naturelles du Québec. 1994. Cartes écoforestière 1/20000 (32E02, 32E03, 32E06, 32E07, 32E10, 32Ell, 32E14, 32E15, 32L02, 32L03, 32L04, 32L07). Direction des inventaires forestiers.

Neitlich, P.N. 1993. Lichen abundance and biodiversity along a chronosequence from young managed stands to ancient forest. M.Sc. thesis, University of Vermont, Vt.

Neitlich, P.N., and McCune, B. 1997. Hotspots of epiphytic lichen diversity in two young managed forests. Conserv. Biol. **11**: 172–182.

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

Paré, D., and 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.

Ruel, J.-C. 1995. Understanding windthrow: silvicultural implications. For. Chron. **71**: 434–445.

Saucier, J.-P., Bergeron, J.-F., Grondin, P., and Robitaille, A. 1998. The land regions of southern Québec (3rd version): One element in the hierarchical land classification system developed by the Ministère des Ressources Naturelles du Québec. Internal report, MRNQ. 21 p.

Seymour, R., and Hunter, M. Principles of ecological forestry. 1999. *In* Maintaining biodiversity in forests ecosystems. *Edited by* M.L. Hunter. Cambridge University Press, Cambridge, U.K.

Sillett, S.C., and Goslin, M.N. 1999. Distribution of epiphytic macrolichens in relation to remnant trees in a multiple-age Douglas-fir forest. Can. J. For. Res. **29**: 1204–1215.

Smith, V.G., Watts, M., and James, D.F. 1987. Mechanical stability of black spruce in the Clay Belt region of northern Ontario. Can. J. For. Res. **17**: 1080–1091.

Taylor, S.J., Carleton, T.J., and Adams, P. 1987. Understory vegetation change in a chronosequence. Vegetatio, **73**: 63–72.

Thomas, J.W., Anderson, R.G., Maser, C., and Bull, E.L. 1979. Snags. *In* Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington. *Edited by* J.W. Thomas. U.S. Department of Agriculture Forest Service.

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

Viereck. 1983. The effects of fire in black spruce ecosystems of Alaska and northern Canada. *In* The role of fire in northern circumpolar ecosystems. *Edited by* R.W. Wein and D.A. MacLean. John Wiley and Sons Ltd., New York, N.Y.

Vincent, J.S., and Hardy, L. 1977. L’évolution et l‘extinction des lacs glaciaire Barlow et Ojibway en territoire québécois. Géogr. Phys. Quat. **31**: 357–372.