Old growth in the boreal forest: A dynamic perspective at the stand and landscape level[1]

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Abstract: Old-growth forests have been identified as a potentially important stage of stand development for maintaining biodiversity in the landscape, yet they have also been targeted by the forest industry in their drive to regulate the forest. We will attempt to propose a definition of old growth, applicable throughout the North American boreal forest, that takes into account the dynamic nature of forest development and that could be useful for management and conservation purposes. We define the start of the old-growth stage as occurring when the initial post-disturbance cohort begins dying off, concurrent with understorey stem recruitment into the canopy. We propose that species longevity and the regional fire cycle can be used to assess the extent of this phase in different regions. Using published data on fire history, we show that the amount of old growth expected to occur in western and central Canada is less than in eastern Canada, where most stands (in area) escape fire for periods longer than that necessary to incur substantial mortality of the initial cohort. At the stand level, we show that the old-growth stage is characterized by small-scale disturbances that engender gap dynamics. Until recently, this process had not been studied in the boreal forest. The old-growth index we present suggests that the relationship between time since the last major disturbance and old-growth status varies most in areas that have not been disturbed for long periods. Both management and conservation strategies have to take into account that old-growth forests are dynamic. To be effective, reserves should contain all stages of development and should be sufficiently large to encompass rare but large disturbances. The abundance of old growth in many boreal regions of North America also suggests that forest management strategies other than even-aged, fully regulated systems have to be developed.

Key words: old growth, old-growth index, boreal forest, conservation, forest management, stand development.

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Résumé : Les vieilles forêts ont été identifiées comme un stade potentiellement important de développement des peuplements pour le maintien de la biodiversité dans le paysage; elles ont cependant également été ciblées par l'industrie forestière dans ses activités d'aménagement. Les auteurs tentent de proposer une définition des vieilles forêts qui serait applicable à l'ensemble de la forêt boréale de l'Amérique du Nord et qui prendrait en compte la nature dynamique du développement du peuplement forestier tout en étant utile aux fins de l'aménagement et de la conservation. Les auteurs définissent le début du stade de vieille forêt comme le moment où la cohorte initiale post-perturbation commence à mourir, concurremment avec le recrutement de tiges du sous-étage dans la canopée. Pour évaluer l'importance de cette phase dans différentes régions, ils proposent d'utiliser la longévité des espèces et le cycle régional du feu. Avec l'historique des feux, ils démontrent que la quantité de vieilles forêts espérée dans le Canada central et de l'ouest est plus faible que dans l'est du Canada, où la plupart des peuplements (en superficie) échappent au feu pendant des périodes plus longues que celles qui sont nécessaires pour apporter une mortalité substantielle à la cohorte initiale. Au niveau du peuplement, les auteurs montrent que le stade de vieille forêt se caractérise par des perturbations à petite échelle qui engendrent une dynamique d'ouverture. Jusqu'à récemment, ce processus n'a pas été étudié en forêt boréale. L'index de vieille forêt présenté par les auteurs suggère que la relation entre le temps depuis la dernière perturbation majeure et le statut de vieille forêt varie le plus dans les régions qui n'ont pas été perturbées pendant de longues périodes. Les stratégies d'aménagement aussi bien que de conservation doivent prendre en compte le statut dynamique des vieilles forêts. Pour être efficaces, les réserves devraient contenir tous les stades de développement et devraient être suffisamment grandes pour inclure de rares mais vastes perturbations. L'abondance des vieilles forêts dans plusieurs régions boréales de l'Amérique du Nord suggère que des stratégies d'aménagement autre que les systèmes èquiennes visant la normalisation de la forêt doivent être développées.

Mots clés : index de vieille forêt, vieille forêt, forêt boréale, conservation, aménagement forestier, stade de développement.

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Introduction

Conservation, restoration, and management of old-growth forests require an understanding of the defining characteristics of old-growth forests and of their development, at both the stand and landscape scales. At the stand scale, information is needed on what constitutes old growth and how stand development changes through time. Such information is needed to conserve or manage this resource. Similarly, at the landscape level, determining the "natural" proportion of old growth in the landscape will help ascertain whether it is a rare or common entity. This knowledge will be useful in planning reserve areas and for landscape-level forest management (e.g., what proportion of the landscape could be clearcut versus partial cuts, uneven-aged management versus even-aged management, forest regulation, etc.).

Proper management requires a definition of old growth that is appropriate to the dynamics of this ecosystem, as well as identification and characterization. To be useful, such a definition should also be compatible with our understanding of what constitutes an old-growth forest in other forest types. It should capture the inherent variability in species dominance, structure, and disturbance dynamics that occurs across the range of the boreal forest. The dynamic nature of forests must also be recognized. Too often, the old-growth stage has been identified as an end point of stand development. This suggests that it is a static stage that can be easily evaluated using structural or static attributes. It is crucial that this myth be dispelled so that decision-makers do not make short-sighted decisions regarding the preservation of unique stands or attributes that are dynamic and that will thus disappear over the next few decades because of natural processes. Therefore, it is necessary to develop a definition that (1) is appropriate to the boreal forest and that covers the variability across its range, (2) addresses the dynamic nature of

Table 1. Structural and functional attributes that have been used to define old-growth forest.

Static (or structural)	Dynamic (or functional)
Large, old trees	Climax forest
Structurally complex	Undisturbed by humans
Multi-layered canopy	Zero net annual growth
Wide tree spacing	Older than disturbance cycle
Large snags	Final stage of development
Minimum area	Secondary recruitment
Large logs	Steady-state conditions
Pit and mounds	Nutrient retention
Diverse tree community	All-aged structure
Patchiness	Past commercial maturity
Minimum tree age	Various states of decay

Note: For more information see Kneeshaw and Burton (1998).

forest development through time, and (3) will have direct applicability or usefulness in discussions on the conservation and management of old-growth boreal forests. A characterization of the proportion of old-growth forest in the landscape and an understanding of stand dynamics of this stage are needed to design appropriate management and conservation strategies throughout the boreal forest.

Definitions

Definitions of old growth have been developed for many forests based on the precise quantification of structural conditions (Franklin et al. 1981; Spies and Franklin 1988; Kneeshaw and Burton 1998). Such definitions are often based on expert opinion or detailed sampling of forests that were assumed to be (or pre-identified as) old growth. Some of the simpler definitions are based on a minimum age for the forest (see Braumandl and Holt 2000 and Uhlig et al. 2001). Others are based on the characterization of static attributes, including the number of trees, logs, or snags greater than some arbitrarily defined size (Table 1). Problems with such definitions occur if static characteristics change once the old-growth stage has been achieved. Therefore, what may be an old-growth forest today may not be in 50–100 years, if only static attributes are assessed. For example, an old boreal forest may contain some large aspen stems. However, these will die and may be replaced by smaller balsam fir or black spruce. If the old-growth characteristic being evaluated is the presence of large trees, then the stand will have lost its old-growth character because the replacement trees are smaller than the large aspen. Other processes such as paludification, which reduce productivity, may also pose problems for static-attribute definitions, as subsequent cohorts of species such as black spruce may contain smaller individuals than earlier cohorts. Therefore, a distinction must be made between attributes that are deemed desirable from a social or spiritual context and those that will be useful for understanding and managing this resource.

Other definitions have also been proposed that describe functional or dynamic attributes of old-growth forests (Table 1). One is that old-growth forests occur when the net annual increment or growth of a stand reaches zero (Davis and Johnson 1987). Although this is often considered a forestry definition related primarily to productivity, it also represents dynamic processes in which new growth and recruitment are balanced by mortality. Definitions of old growth as a phase of stand development (in which stands proceed through young, mature, and old-growth phases) have also been proposed by a number of authors (Bormann and Likens 1979; Oliver 1981; Oliver and Larson 1990; Hayward 1991; Moir 1992). In the boreal forest, the following stages occur after a fire: stem establishment, stem exclusion (associated with self thinning), and understorey re-initiation (Oliver and Larson 1990). The onset of old growth is defined as the stage at which the original cohort begins to die and these understorey stems are recruited to the canopy. This implies the importance of mortality and regeneration processes in the old-growth stage and, thus, the importance of gap dynamics in defining old growth (Hunter and Parker 1993), yet takes into account the fact that the old-growth phase is not static and that stands will continue to change. This definition does not preclude the development of static-attribute definitions specific to given regions. For example, the death of overstorey trees will also lead to relatively large coarse woody debris (CWD) and a multi-layered canopy due to mortality and ongoing recruitment (Kneeshaw and Burton 1998). However, definitions based on forest stand development are more likely to maintain ecosystem processes than those based solely on static attributes. Defining old growth in this way is appropriate in ecosystems that are frequently re-initiated by large-scale disturbance regimes; therefore, we propose adopting such a process-based definition for the boreal forest.

Cohort basal area evaluation of old-growth stage

Because we have defined the beginning of the old-growth stage as the phase in which the original cohort begins dying off and is replaced by the recruitment of understorey stems, we can now identify a practical way to measure it. Our proposal, the cohort basal area ratio (CBAR), is applicable to the disturbance-dominated boreal forest. This tool and definition were originally proposed by Kneeshaw and Burton (1998), based on the ratio of the basal area of the understorey cohort (trees established in the understorey) to the basal area of the post-disturbance cohort.[3] Defining old growth in this way addresses the dynamic nature of forests, in that it reflects changes in the stages of old growth. This ratio increases as overstorey mortality increases (i.e., as the denominator decreases) or as understorey trees grow and are recruited to the overstorey. It is thus compatible with our landscape-level evaluation in which we identify potential old growth by evaluating whether time elapsed since fire has been sufficiently long to permit stand breakup to occur. To permit easy comparisons among regions, we propose a modification to the original CBAR (the Cohort Basal Area Proportion, CBAP) in which there is an upper limit of 1 and a lower limit that approaches 0. The CBAP is a ratio of the basal area of the replacement cohort to the total basal area of both replacement and initial post-disturbance cohorts:

$$[1] \qquad \mathrm{CBAP} = \frac{\mathrm{BA}_{\text{replacement cohort}} + 0.1}{\mathrm{BA}_{\text{replacement cohort}} + 0.1 + \mathrm{BA}_{\text{initial cohort}}}$$

where BA is the basal area.

The CBAP is thus sensitive to both mortality and recruitment processes and reflects the change from a forest stand in which dynamics have been controlled by large-scale disturbances to a stand in which small-scale disturbances influence dynamics. The CBAP is relatively insensitive to the total basal area of the stand. Stands can also be ranked along an old-growth gradient. A relationship between structural elements and CBAR has also been shown (Kneeshaw and Burton 1998). However, structural definitions will be local in nature and may change with time elapsed since fire. In contrast to old-growth definitions based on structural attributes (e.g., the number of large trees), the CBAR and CBAP, because of their functional base, can increase only once the old-growth stage has been reached. The old-growth cohort basal area proportion provides a method for comparing regions and forest types that, because of different species compositions, would not have the same structural attributes. This will be further illustrated in the stand-level section.

[3] To avoid a ratio which would occur if the entire post-disturbance cohort no longer existed, we propose a slight modification in that 0.1 be added to the denominator (the basal area of the post-disturbance cohort).

Table 2. Pathological rotation age (average canopy tree longevity) of important boreal tree species as derived from Burns and Honkala (1990) and old-growth onset age from Uhlig et al. (2001).

Species	Tree longevity (from Burns and Honkala 1990)	Old-growth onset age (from Uhlig et al. 2001)
Trembling aspen	50–100	90–100
Balsam fir	60–100	70–80
Jack pine	70–100	90–110
White birch	70–140	90–110
Black spruce	100–200	110–160
White spruce	200–300	110–130

Note: Averages will change (and may exceed values presented here), depending on site conditions; some individuals may live longer than these averages.

Identifying the regional extent of old growth

It has been suggested that, because of the pervasive nature of fire, old-growth forests would occupy only a small portion of the landscape in the boreal forest (Johnson 1992; Johnson et al. 1995). If old-growth forests are defined as beginning when overstorey mortality leads to the recruitment of understorey individuals, then two factors are needed to determine the extent of old growth in the landscape. The first is the timing of overstorey breakup or, in other words, an understanding of the average longevity of the dominant tree species. The second is an understanding of the return interval of major disturbances in different areas. For example, if trees are long-lived and fire return intervals are short, then old-growth forests would be rare; however, if trees are short-lived and fire return intervals are long, then a greater proportion of the forest would achieve old-growth status. It is thus imperative to compare the lifespans of the dominant tree species with fire cycles to determine the possible extent of old-growth forests.

Longevity of boreal tree species

In the North American boreal forest, the dominant tree species are black spruce (*Picea mariana* (Mill.) B.S.P.), white spruce (*Picea glauca* (Moench) Voss), balsam fir (*Abies balsamea* (L.) Mill.), jack pine (*Pinus banksiana* Lamb.), trembling aspen (*Populus tremuloides* Michx.), and white birch (*Betula papyrifera* Marsh.). Although other species occur, they are usually only a minor component of boreal stands. Longevity for any given species varies from one region to another, depending in part on genetics, soil moisture and fertility, temperature, and other biotic and abiotic factors. A range of ages for mesic and modal sites is presented in Table 2. Two different groups of species can be identified: one with average longevities that are usually reported as less than 100 years (balsam fir and poplars (*Populus* ssp.)) and another that approaches or exceeds 200 years (i.e., spruces (*Picea* ssp.)). Some individuals may live beyond the ages represented here, but the success of one or two individuals will have a small impact on the overall character of the stand. On the other hand, if stands begin breaking up at an earlier age than suggested by the numbers in Table 2, then such stands may begin changing to an old-growth stage at an earlier age. This will be important across the distribution range of a species. For example, it may be expected that trees will have different longevities in optimal parts of their range compared with the limits of their distributions.

Fire frequency in North American boreal forests

It has generally been assumed that the North American boreal forest is characterized by relatively short fire cycles and by a forest mosaic composed mainly of even-aged, postfire stands (Heinselman

Table 3. Mean time since fire and observed landscape proportion (in area) of stands that have not burned for more than 100 and 200 years.*

Regions	Forest region (Rowe)†	Reference	Area (km^2)	Mean time since fire (year)	% over 100 years	% over 200 years
Labrador, Newfoundland	B	Foster 1983	48 000	NA	81	NA
Central Quebec, Quebec	B	Bergeron et al. 2001	3 844	127	54.8	15.9
Abitibi-East, Quebec	B	Bergeron et al. 2001	3 294	111	53.3	15.4
Abitibi-West, Quebec	B	Bergeron et al. 2001	15 793	139	57.4	20.4
Lake Abitibi Model Forest, Ontario	B	Bergeron et al. 2001	8 245	172	77.5	31.5
BWCA, Minnesota	B–L	Heinselman 1973	4 170	106	40	6.6
Lake St. Joseph,‡ Ontario	B	Suffling et al. 1982		47	5	
Prince Albert National Park, northern section only, Saskatchewan	B	Weir et al. 2000	1 563	97	52	1
Wood Buffalo National Park, Alberta and Northwest Territories	B	Larsen 1997	44 870	71	20	2
Rutledge Lake,‡ Ontario	B	Johnson 1979	NA	117	45	6
Porcupine River, Alaska	B	Yarie 1981	36 000	75	18	2
Kananaskis, Alberta	SA	Johnson and Larsen 1991	495	132	42	24
Kootenay National Park, British Columbia	SA	Masters 1990	1 400	172	75	32

*The information presented in this table was derived from published data. The mean time since fire, the proportion of forest older than 100 years, and the proportion of forest older than 200 years are all computed from the observed age distribution presented in the related papers. The regions are listed from east to west.

†Rowe's regions are the following: B, boreal; SA, subalpine; L, Great Lakes – St. Lawrence.

‡The data were derived from the age structure presented in Johnson et al. 1995.

1981; Johnson 1992). This generalization has led to the assumption that old forests are relatively rare in this type of system. On the other hand, long fire intervals, allowing for changes in canopy dominance and development of uneven-aged forests, have also been reported, particularly in eastern boreal forests (Foster 1983; Cogbill 1985; Frelich and Reich 1995; Bergeron 2000; Bergeron et al. 2001). The observed mean time since fire (which is an equivalent of the overall fire cycle) varies considerably across regions (Table 3). In the boreal domain itself, mean time since fire is less in the drier western and central Canada than in eastern Canada. The amount of forest older than 200 years follows the same trend. It is interesting to note that in eastern Canada, most stands (in area) have escaped fires for more than 100 years. Therefore, the old-growth phase should have started by that time for most stand types (Table 2). The occurrence of stands in the old-growth phase in the west will be smaller than in the east. Generally, there appears to be an overestimation of the importance of catastrophic stand-replacing fires and an underestimation of the importance of the effects of gaps, storms, and insects. The view of the boreal forest as an even-aged monoculture is thus an oversimplification.

Another interesting difference among boreal regions across the country concerns the size of forest areas that have escaped fire and that are old enough to encompass tree mortality and canopy replacement. In Saskatchewan, where the fire cycle is relatively short, only 5% of the stands are older than 125 years (Johnson et al. 1998), and those stands are but small remnant islands of old forest (Johnson et al. 1998; Weir et al. 2000). These remnant islands are sometimes located in sites with conditions protecting them from burning (Gandhi et al. 2001). At the landscape scale, patterns may, at least in part, be mediated by landform and result in variable persistence of old growth. On the other hand, in eastern Canada, both the extent and the size of these forests are larger. For instance, in the Lake Abitibi Model Forest, a very large area (≈800 km^2) of forest that last burned in 1760 is still present in the landscape today (Gauthier et al. 2002). In terms of management, these landscape differences have to be distinguished, because old-growth management will differ according to whether there is a large extent of old forest, such as is observed in eastern Canada, or small protected islands (biodiversity hot spots), as are observed in western Canada (Gandhi et al. 2001).

In many of these regions, a decrease in the area burned over the last century has been reported (Clark 1988; Bergeron 1991; Bergeron and Archambault 1993; Larsen 1996). Whether this change is the result of a climatic change (e.g., moister summers), changes in land use, or improvement in fire suppression capabilities remains unclear (Miyanishi and Johnson 2001; Ward et al. 2001), but the net result is an increase in the proportion of the forest landscape where canopy replacement is expected to occur (Flannigan et al. 1998). In central Canada, however, Flannigan et al. (1998) suggest that an increase of less than two times CO_2 in the atmosphere may lead to an increase in fire frequency because of drier and hotter summers, which will reduce the extent of old forest in these landscapes. Regional differences may therefore lead to different trends in fire cycles, and blanket statements about boreal forest dynamics may lead to erroneous interpretations of forest condition and development, as well as potential management and conservation solutions.

Old growth at the stand level

At the stand level, we have chosen (as mentioned above) to use a developmental approach to define old-growth forests. In boreal forests, short fire intervals will return the forest to earlier developmental stages. However, where fire intervals are long (Table 3), stands will continue to develop and be shaped by small-scale mortality and recruitment processes. In most forests that have escaped fire for 200 years, there has been enough time for many first cohort individuals to die (see Table 2) and for a second cohort of trees to reach the canopy. In the mixedwood region, this process results in a change in species composition (MacDonald 1995; Gauthier et al. 1996), whereas in the coniferous zone, it results in structural change (De Grandpré et al. 2000; Harper et al. 2003). In old-growth stands, other types of disturbances, such as spruce budworm outbreaks and windthrow, which are both common in the eastern Canadian boreal forest, become more important (Blais 1983; Bergeron 2000; Kneeshaw 2001, etc.). Both these disturbances become more common as forests age (Blais 1983; Bergeron et al. 1995; Harper et al. 2002) and may interact with one another (Morin 1994; McCullough et al. 1998). Forest dynamics, successional processes, and the ensuing stand structure can vary greatly following these different disturbances and combinations of disturbances (Kneeshaw and Bergeron 1998; Frelich and Reich 1995; Bergeron 2000).

The point at which understorey trees begin to replace overstorey trees can occur only through a process of gap dynamics (Runkle 1991; Hunter and Parker 1993). In boreal regions, gap dynamics have largely been ignored until quite recently (McCarthy 2001). Cumming et al. (2000), for example, suggest that parts of the boreal forest may be older than previously thought. The age of the dominant trees may not provide an accurate assessment of time elapsed since fire, as trees may represent a second or third cohort of postfire trees. What is particularly interesting about their work is that it focused on pure aspen stands and aspen has been considered a shade-intolerant pioneer species that regenerates after fire or clearcut logging. They suggest, however, that mortality occurs in groups, creating gaps that are large enough to permit the recruitment of a second cohort. We would thus suggest that these stands have achieved an old-growth stage, as mortality of the post-disturbance cohort has permitted recruitment of individuals from a second cohort. This work has been supported by research in the Abitibi region where it was also found that shade-intolerant aspen could recruit a second or third cohort of trees (Bergeron 2000). In other work in this same area, a gap size of greater than 20 m in diameter was suggested as required for the successful recruitment of aspen (Kneeshaw and Bergeron 1999).

Table 4. Species composition as a percent of total overstorey tree abundance.

Species	Current proportion in 234-year stand (%)	Traditional Markov model (%)	Model that considers tree longevity (%)
Balsam fir	63.2	53.3	25.4
White spruce	3.5	6.9	10.1
Trembling aspen	3.6	3.5	1.5
White birch	12.8	7.8	6.4
Eastern white-cedar	16.7	28.5	56.6

Note: The second column represents the proportion that was observed in an old-growth stand in Abitibi. The third column represents the changes in species abundance based on Markov transition probabilities. This traditional Markov model is based on equal ages of all species (and is explained in Kneeshaw and Bergeron 1998). The final column shows proportional species abundance when using a model that accounts for different tree species longevities.

The influence of gap dynamics has been shown to increase with the age of the forest (measured as time since fire and not tree age). For example, at the Quebec–Ontario border, it has been reported that gap size increases fairly linearly with time elapsed since fire to 200–250 years (Kneeshaw 2002). However, older stands in this region have also been greatly affected by the spruce budworm (*Choristoneura fumiferana*). In other regions, where the spruce budworm is not an active component of stand dynamics, it has been suggested that gaps may be small and that the percentage of the forest in gaps will plateau (e.g., G. Brunet, personal communication; A.T. Pham, personal communication). Harper et al. (2002) suggest that such relationships may be influenced by abiotic factors such as soil deposits. In their work in black spruce stands, a peak in gap size and the percentage of the forest in gaps occurs around 250 years on clay sites, whereas it continues to increase on sand and organic sites. Gap dynamics are thus heterogeneous across the boreal forest and do not lead to a common structural or compositional end point.

Definitions based solely on static attributes are only applicable in a given region to describe a short period of development and do not represent the changes that can occur within old-growth stands. An example from Abitibi, Quebec, based on data from Kneeshaw (1998), shows that composition has not yet reached what can be considered a climax state in an old-growth balsam fir forest (Table 4). In this shade-tolerant forest, the stand may therefore continue to change in composition. The proportion of a shade-tolerant species, such as eastern white-cedar (*Thuja occidentalis* L.), that is not affected by insect infestations can increase until it replaces fir as the dominant species (Table 4). Therefore, what is currently considered an old-growth forest will continue to change through time (Kenkel et al. 1998).

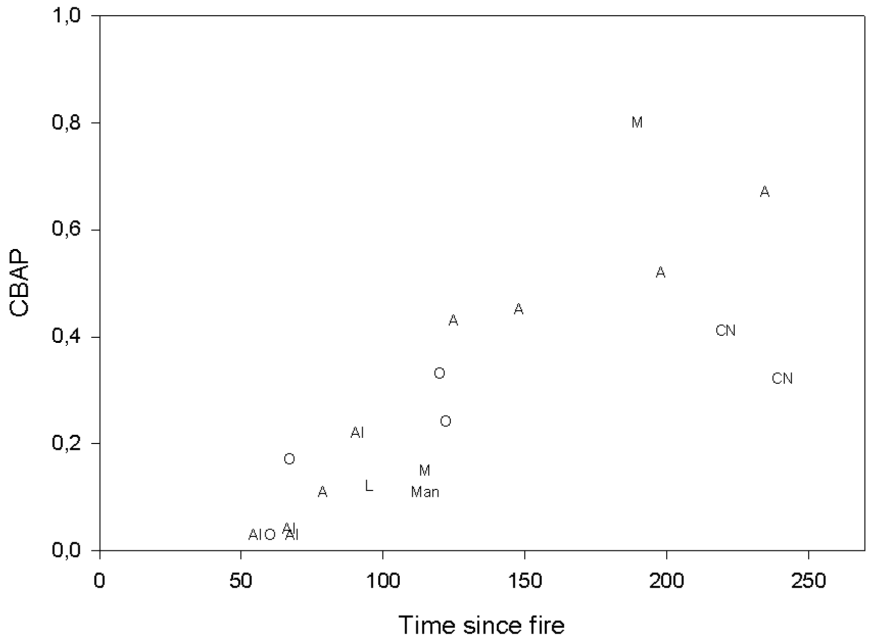
In monospecific stands, the change may not be compositional, but may instead reflect a structural change. This structural change will be important in forests dominated throughout stand development by late-successional, shade-tolerant individuals such as black spruce or balsam fir. In these stands, overstorey mortality will lead to recruitment from understorey individuals of the same species. Old-growth stands will thus be multi-layered, uneven-aged stands that may appear decrepit because of the amount of dead wood. However, these old stands will also contain regenerating stems. They will thus be structurally heterogeneous both horizontally and vertically (Fig. 1).

A comparison of the CBAP from different areas of the boreal forest shows that although the characteristics of old growth are linked to time elapsed since fire (Fig. 2), stand development can occur at different rates (Table 5). Stands that were initiated at the same time will thus not necessarily have achieved the same condition (e.g., in British Columbia, a 193-year time elapsed since fire stand has a CBAP of 0.20 whereas a 217-year time elapsed since fire stand has a CBAP of 0.07, Table 5), perhaps due to different stand histories or the legacy of pre-fire stands. For example, one stand may have experienced

Fig. 1. Photos of black spruce forests showing horizontal and vertical diversity in structure.

a severe fire followed by a long colonization period and slow growth as soil nutrients were being built up, while a neighbouring stand may have been quickly colonized by species of shorter longevity that began to break up at an earlier age. Interregional differences may also be caused by climatic and species differences. In areas with long-lived individuals, e.g., those outside of the boreal forest in western North America, stand breakup may occur at an advanced age due to the long lifespan of the dominant trees. In the boreal forest, old-growth conditions in black spruce forests should similarly begin at a greater age

Fig. 2. Relationship between the time since fire and the CBAP. CN, Côte-Nord; A, Abitibi; M, Minnesota; O, Ontario; Man, Manitoba; Al, Alberta.



than in fir- or aspen-dominated forests. Similarly, when the first cohort is dominated by extremely large individuals, the ratio may change rapidly when these individuals die off and are replaced by smaller understorey trees of different species. For practical reasons, static attribute definitions may also be more appropriate in forests dominated by long-lived species than in forests such as the boreal ones that are dominated by short-lived species, where structure may change rapidly. A ratio of 0.3–0.4 may represent a point at which postfire effects are being lost and the stand begins entering an old-growth stage.

Conservation and management implications

Many examples of the need to maintain natural old-growth forests can be found in the papers in this issue of Environmental Reviews. Frelich and Reich (2003), for example, cite old-growth forests, unexplained resistance to invasion by earthworms, compared with all managed forests, whatever their age, which contain earthworms in abundance. Mosseler et al. (2003) show that old-growth forests have a larger (or better) gene pool that ensures a greater number of filled seeds, as well as bigger trees, than younger or managed stands. Gauthier et al. (1993, 1996) have shown that old-growth jack pine stands contain both non-serotinous and serotinous trees that confer on old-growth populations the ability to reproduce both with and without fire. Silviculturally, we may be able to reproduce many of the structural attributes associated with old growth, but we do not have sufficient knowledge to ensure reproduction of the dynamic processes associated with this stage of stand development. Again, this suggests that the use of static attribute definitions may lead to the erroneous belief that we can effectively manage to maintain this resource, whereas a functional approach suggests that we need to maintain old-growth reserves to act as controls against which we can compare our ongoing forest management experiments.

An inspection of old growth at different scales suggests that management and conservation strategies for maintaining it in the boreal forest have to be tailored to the disturbance dynamics and longevity of the species found in different regions throughout this ecosystem. Where fire cycles are short, the risk

Table 5. Cohort basal area ratios (CBAR) and cohort basal area proportions (CBAP) and the associated stand age for different regions across the North American boreal forest.*

Region	Stand type	Stand age (years)	CBAR	CBAP
Labrador	Birch	95	0.14	0.12
Côte-Nord, Eastern Quebec	Fir stand	221	0.69	0.41
	Black spruce	241	0.48	0.32
Abitibi, Western Quebec	Aspen	79	0.12	0.11
	Boreal mixedwood	125	0.75	0.43
	Mixedwood	148	0.81	0.45
	Conifer (fir)	198	1.08	0.52
	Conifer (fir)	235	1.99	0.67
Minnesota	Boreal mixedwood	115	0.18	0.15
		190	4.02	0.8
Ontario	Black spruce – pine	60	0.03	0.03
		60–75	0.004	0.17
		100–135	0.32	0.24
		120	0.48	0.33
Manitoba	Black spruce	115	0.1	0.11
Alberta	Mixedwood	55	0.03	0.03
	Mixedwood	64	0.04	0.04
	Mixedwood	68	0.03	0.03
	Mixedwood	91	0.28	0.22
Sub-boreal British Columbia	Subalpine fir – interior spruce	117	0.02	0.02
		154	0.04	0.04
		193	0.26	0.2
		217	0.08	0.07
		246	0.38	0.28
		337	8.11	0.89

*Data from this table are gathered from or estimated from Foster and King (1986) for Labrador, unpublished data by S. Gauthier for the North Shore of Eastern Quebec, Kneeshaw and Bergeron (1998) and unpublished data from Kneeshaw for the Abitibi region, Frelich and Reich (1995) for Minnesota, Carleton (1982) for Ontario, Ehnes (2001) for Manitoba, Lieffers et al. (1996) for Alberta, and Kneeshaw and Burton (1998) for sub-boreal British Columbia.

of any given stand burning at shorter intervals than the lifespan of the species is quite high (Johnson 1992; Johnson et al. 1995). Conservation strategies designed to protect stands on small land areas are thus doomed to failure, as the natural fire disturbance regime will eventually cause the stand to burn. At the stand level, approaches to conserve stands with certain characteristics are also inadequate as they ignore the fact that forests are not static entities but will instead continue to develop and change.

In designing reserves, we must go beyond planning for disturbances that are typical for an ecosystem; it is crucial to consider the impact of catastrophic disturbances of large size, even if they are quite rare (Pickett and Thompson 1978). Reserve areas must include all developmental stages to allow for continuous dynamic processes (Frelich 1995). Therefore, reserve areas must either be large enough to allow for natural disturbances to occur within their boundaries (Baker 1989) or be made up of multiple areas.

It has been suggested that reserves should be at least three times larger than the greatest disturbance (Johnson and Gutsell 1994), or at least 50 times larger than the average disturbance size (Shugart and West 1981; Shugart 1984). Using the first definition, boreal reserves may, therefore, either be impossible or at least impractical to establish, as fires covering more than a million hectares have been reported (Shugart et al. 1992). The second method of determining reserve size may be possible because average fire sizes have been reported to cover 2500 ha in the boreal mixedwood and 4500 ha in the conifer-dominated zone in western Quebec (A. Leduc et al. 2000). These same authors also noted that the entire age-class structure of the fir-dominated boreal forest could be found in a 300 000-ha area, whereas 500 000 ha were required for the black spruce zone (A. Leduc, personal communication).

Governments have, however, been reluctant to set aside such large land bases. If old-growth conservation in the boreal zone is to be a functional reality, we suggest that reserves of at least 100 times the average fire size or equal to the largest known fire event would be needed. Although Baker (1989) suggests that it might not be the best option, another alternative to ensure that all developmental stages are maintained would be to spread out multiple replicate reserves (or perhaps to use a system of floating reserves) across the landscape so that an event that might set back one reserve to an earlier successional state would not affect all the others. A reasonable size must still be maintained and the distance between reserves must be sufficiently large to ensure that a single event will not destroy all reserves. For example, in Quebec, the largest fire that has been reported in the last 50 years (a period with reduced fire activity) covered 3800 km^2, suggesting that multiple reserves must cover an area larger than this to ensure their long-term effectiveness. A hybrid of the two strategies may be the best approach (large conservation area + multiple smaller ones). The use of multiple reserves would also be enhanced by active old-growth management (as discussed later) in the forested matrix found between reserves.

In parts of the boreal forest where the fire cycle is long, a large proportion of the landscape might be old growth. Regulation of the age-class structure will thus radically alter the natural dynamics of these forests. Clearcutting large areas, basing rotation age on maximal mean annual increment (MAI) and even-aged management should only be practised on a small portion of the forest. The development of uneven-aged treatments and systems must therefore be pursued. Partial cutting would be needed to ensure that smaller scale disturbances are imitated in the overall forest management strategy. Bergeron et al. (1999) and Burton et al. (1999) provide constructive ideas on how to develop this type of ecologically based planning for the boreal forest.

Stand-level management of old growth

An understanding of old-growth dynamics also suggests that dead wood would be an important element in these stands (Harmon et al. 1986). Managers must find creative ways of ensuring that dead wood (of all species and all size classes) is left behind on at least a portion of the landscape. More research should be devoted to the importance of this legacy to ecosystem processes in these old stands. In both Fennoscandia and the west coast of North America, CWD has been shown to be important in ecosystem processes (Harmon et al. 1986).

We must also change our perception of old growth. Images of old growth as majestic towering forests such as those found on the west coast are inappropriate for the boreal forest. We have a duty to convince decision makers and foresters of the ecological value of stands that may appear decrepit from a purely fibre-based point of view. At present, our ability to do this has been hampered by gaps in knowledge and not enough research. Nor is time on our side, because current policy results in the liquidation of these stands. It is thus imperative, while continuing research, to act now based on the best available knowledge that science can provide (Franklin 1993).

Conclusions

The boreal forest is dynamic! The use of static attributes to define old growth will not maintain old-growth functioning in these forests. However, a better understanding of forest dynamics and their relationship to the fire regimes of the various boreal forest regions of North America should help to define the key attributes that constitute the uniqueness of this stage in each region. These key attributes could be used to define targets to be maintained in management activities, as well as to establish monitoring programs aimed at evaluating the effectiveness of these attributes in maintaining the functions of the ecosystems. Old-growth forest must be seen as a dynamic entity that is increasingly influenced by small-scale mortality and recruitment. In the boreal zone, the transition between different states may be quick, because of the relatively short lifespan of the tree species compared with those in other regions (e.g., coastal temperate rainforests.)

It should also be emphasized that old-growth forests are more abundant in many regions of the boreal forest than traditionally thought. Management and conservation implications may need to be revised and they should be specific to the disturbance history of the various boreal regions. To be effective, conservation efforts must be based on reserves that contain all stages of stand development. Where old growth is currently abundant, even-aged management of large areas with the goal of developing a regulated forest will not approximate natural dynamics in these stands. If we are serious about conserving biodiversity, we must develop a management strategy that contains both even-aged and uneven-aged management systems that are defined in a regional context, and combined with a conservation strategy that ensures maintenance of all developmental stages.

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