Chapter 13
Old-Growth Forests in the Canadian Boreal: the Exception Rather than the Rule?

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13.1 Introduction

Fire is one of the most important ecological processes in North American boreal forests (Johnson 1992; Payette 1992). Forest fire regimes, defined by fire frequency, size, intensity, seasonality, fire type and severity (Weber and Flannigan 1997) have a significant influence on many boreal forest attributes. Fire regimes affect the distribution of species (Asselin et al. 2003; Le Goff and Sirois 2004), age-class distribution of stands (Bergeron et al. 2001), characteristics of wildlife habitats (Thompson et al. 1998), vulnerability of forests to insect epidemics (Bergeron and Leduc 1998), and net primary productivity and carbon balance (Peng and Apps 2000; Wirth et al. 2002).

Our understanding of the fire regimes that burn forests throughout the Canadian boreal zone is still fragmentary, making it inappropriate to generalise about fire frequency for the entire region. For example, it has often been assumed that large-scale fires that produce even-aged stands are not only omnipresent but frequent in boreal forests. However, it has become increasingly evident that short fire cycles apply only to parts of the boreal forest, and that the regional situation is considerably more complex (Bergeron et al. 2004). Nonetheless, the assumption of frequent large-scale fires has been used to justify the use of clear-cut harvesting with short rotations in most boreal forests, resulting in a reduction in the proportion of older forest stands.

One important consequence of the variability in fire frequency in the boreal zone is the amount of forests that can reach the status of old-growth forests between fire events. As the time needed to reach old-growth is difficult to define (see Chap. 2 by Wirth et al., this volume), we adopt a pragmatic definition and consider forests over 100 years after disturbance as old-growth. The post-fire cohort of trees is usually no longer dominant after 100 years and normal harvesting rotations are less than 100 years in most boreal forests. In this chapter, we discuss (1) the relative abundance of old-growth in the Canadian boreal forest, (2) the prevalence of old-growth attributes in older forests compared to younger post-fire stands, and (3) the

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implications of the importance and uniqueness of old-growth boreal forest in the context of current forest management.

13.2 Abundance of Old-Growth Forests

We calculated the proportion of forests of different ages in different boreal forest regions using historical fire frequencies (or fire cycles, i.e. the inverse). We assumed a constant fire frequency and a fire hazard independent of stand age (as commonly reported for boreal ecosystems controlled by stand-replacing fires; Johnson 1992) to predict the proportion of forest that can reach a defined age class (Fig. 13.1). Historical burn rates were determined from a literature review using available forest fire history studies in North American boreal forest (Bergeron et al. 2004; Fig. 13.2). Most of these studies used dendrochronology to estimate time since fire, and represent the average fire frequency over the last 300 years. Current fire frequency (last 50 years) from a Canada-wide database (Stocks et al. 2002) was used for the Boreal cordillera, Taiga cordillera, Taiga plain and Hudson plains ecozones (Ecological Stratification Working Group 1996) since no studies on historical fire frequency were available for these areas. Average age of the forest (time since fire) or, if not available, fire cycle before large clear-cutting activities began were used to estimate historic burn rates. The average age of the forest was preferred to the historic fire cycle because it integrates climatically induced changes in fire frequency over a long period, and because it is easier to evaluate than a specific fire cycle (Bergeron et al. 2001). The inverse of average age (or fire cycle) was used as an estimator of the annual historic burn rate.

The average fire cycle for different ecozones (Table 13.1) is highly variable, ranging from 52 years in the western boreal shield to 813 years in the Hudson plain ecozone. Differences are due mainly to a drier climate in the west since the dominant tree cover is relatively similar across the Canadian boreal biome (conifers; except for aspen, which dominates the boreal plain).

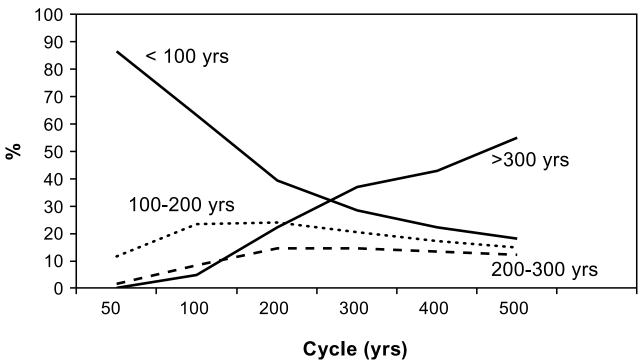

Fig. 13.1 Proportion of forests older than 100, 200 and 300 years for increasing fire cycles

Fig. 13.2 Location of the 18 studies (see Bergeron et al. 2004 for specific references) used to estimate fire frequency throughout ecozones of the Canadian boreal forests. Current fire frequency (last 50 years) was used for ecozones where no long-term studies were available

Table 13.1 Historical fire frequency (% of the area burnt per year) and – in parentheses – its inverse the fire cycle) together with the proportion of forests older than 100, 200 and 300 years for the Canadian boreal ecozones

Ecozones	Historical (% year^{-1})	Area (km^2)	% Area > 100 years	% Area > 200 years	% Area > 300 years
Montane Cordillera	0.99 (101)	490,184	37	14	5
Boreal cordillera[a]	0.39 (255)	470,502	68	46	31
Taiga cordillera[a]	0.20 (495)	267,029	82	67	55
Taiga plain[a]	0.70 (142)	645,014	49	24	12
Boreal plain	1.48 (68)	733,170	23	5	1
Hudson plains[a]	0.12 (813)	374,482	88	78	69
Taiga shield west	0.85 (118)	631,679	43	18	8
Boreal shield west	1.92 (52)	946,260	15	2	<1
Boreal shield east	0.77 (131)	931,062	47	22	10
Taiga shield east	0.6 (166)	758,763	55	30	16
Total		6,148,148	45	24	15

[a]Current fire frequency (last 50 years) was used for these ecozones as no long-term studies were available

Using relationships between fire cycle and age-classes (Fig. 13.1), we then compiled the expected proportion of forests over 100, 200 and 300 years old that would be present in different parts of the Canadian boreal forests given no additional or anthropogenic disturbances (Table 13.1). The results show that, despite a large variation from east to west, a large proportion of the boreal landscape is composed of forests over 100 years old. Assuming these studies are representative of the different ecozones, and taking into account the size of the ecozones, forests over 100, 200 and 300 years since fire should cover 45%, 24%, and 15%, respectively, of the boreal landscape in Canada. Since most dominant tree species in boreal forests are short-lived, we can conclude that a significant proportion of Canadian boreal forests is composed of stands dominated by the late-successional species typical of old-growth forests. Although significant everywhere, these proportions are distributed unevenly in Canada. As fire cycles are longer in eastern Canada, old-growth forests are more abundant.

These estimates of the amount of older forests are conservative since they include only those areas that were spared from fire by chance; they do not include patches of old-growth forest that can be found inside fire perimeters or associated with fire breaks (Cyr et al. 2005). The proportion of fire skips inside burnt perimeters can range between 5% and 10% of the burnt areas (Eberhart and Woodard 1987; Kafka et al. 2001), and some skips, mainly those associated with wet areas, can be spared for several fires. Moreover, our study does not include differences due to topography or vegetation that could locally influence the presence of old-growth forests. These should be taken into account in any regional assessment of the abundance of old-growth forests.

13.3 Characteristics of Old-Growth Boreal Forests

It is clear from the proportions of forests in different age classes that all stages of development are present in boreal forests. This diversity of stands of different ages most likely contributes to regional biodiversity by providing stands with different habitat features (Harper et al. 2002). In order to identify the unique features of old-growth forests, it is important to understand stand development, and the changes in structure and composition of forest stands following a disturbance. Here we focus on the old-growth stage, although we assess trends throughout stand development to determine when typical old-growth attributes may be prominent.

The final old-growth stage is thought to be characterised by distinctive composition, structure and processes compared to younger stages of development. To summarise the main features reviewed in this volume (see Chap. 2 by Wirth et al., this volume), old-growth forests are considered to be compositionally complex with a high diversity of long-lived shade-tolerant tree species (Spies and Franklin 1988; Kneeshaw and Burton 1998; Wells et al. 1998; Moessler et al. 2003). Typical old-growth structural attributes consist of abundant large or old structural elements including trees, snags and logs (Spies and Franklin 1988; Kneeshaw and Burton 1998; Wells et al. 1998), high structural diversity, particularly of tree ages or sizes and of decay stages of snags and logs (Kneeshaw and Burton 1998; Wells et al. 1998; Moessler et al. 2003), a complex, heterogeneous spatial pattern with abundant canopy gaps, and a wide range of tree spacing and patchiness (Kneeshaw and Burton 1998; Wells et al. 1998). Old-growth is often described as steady state or climax forest with a stable accumulation of biomass and a net growth close to zero (Kneeshaw and Burton 1998; Wells et al. 1998; Moessler et al. 2003), dominated by small-scale disturbances with tree regeneration in gaps (Kneeshaw and Burton 1998; Moessler et al. 2003). Other processes associated with old-growth characteristics include slow tree growth and high understorey productivity (Kneeshaw and Burton 1998; Wells et al. 1998).

Old-growth forests, particularly old-growth boreal forests, may not share all these characteristics. Rather than judging the 'old-growthness' of the final stage of development of boreal forests using definitions (Wells et al. 1998) or an old-growth index (Spies and Franklin 1988; Kneeshaw and Burton 1998), we assess the uniqueness of old-growth forests in the Canadian boreal for the ensemble of old-growth characteristics listed above and described in the literature for vegetation structure and composition. Here we define old-growth forests as the final stage of development along a chronosequence rather than by a lack of human disturbance, stand age relative to forest management or aesthetic attributes. We focus on types of boreal forest in Canada for which there have been studies of stand development. By examining trends in forest structure and composition with time since fire in different types of Canadian boreal forests, we ask the question: are these old-growth attributes characteristic of the oldest stage of development in boreal forests?

13.3.1 Old-Growth Black Spruce Boreal Forest

Old black spruce forest in the Clay Belt region of northeastern Ontario or in northwestern Quebec appears to be an exception to what we commonly perceive as old-growth even at first glance. The aesthetic vision of a tall majestic forest with large trees, large broken stumps and large logs that serve as substrate for regenerating seedlings does not apply here. But how many of the old-growth attributes apply when we examine trends in forest structure and tree species composition through different stages of stand development?

In black spruce forests in the Clay Belt region, there can be a transition in tree species composition from shade-intolerant deciduous species such as *Populus tremuloides, Betula papyrifera* and *Pinus banksiana* to shade-intolerant *Picea mariana* with some *Abies balsamea* (Harper et al. 2002, 2003). However, in sites dominated by *Picea mariana* immediately after fire, structural development is not accompanied by a change in species composition. Other old-growth attributes related to species composition do not apply to this ecosystem. Tree species diversity is much lower in older black spruce forests compared to young and intermediate-aged forests (Fig. 13.3a). Indeed, most forest stands in this region contain over 75% *Picea mariana* (Harper et al. 2002, 2003). There were also fewer understorey

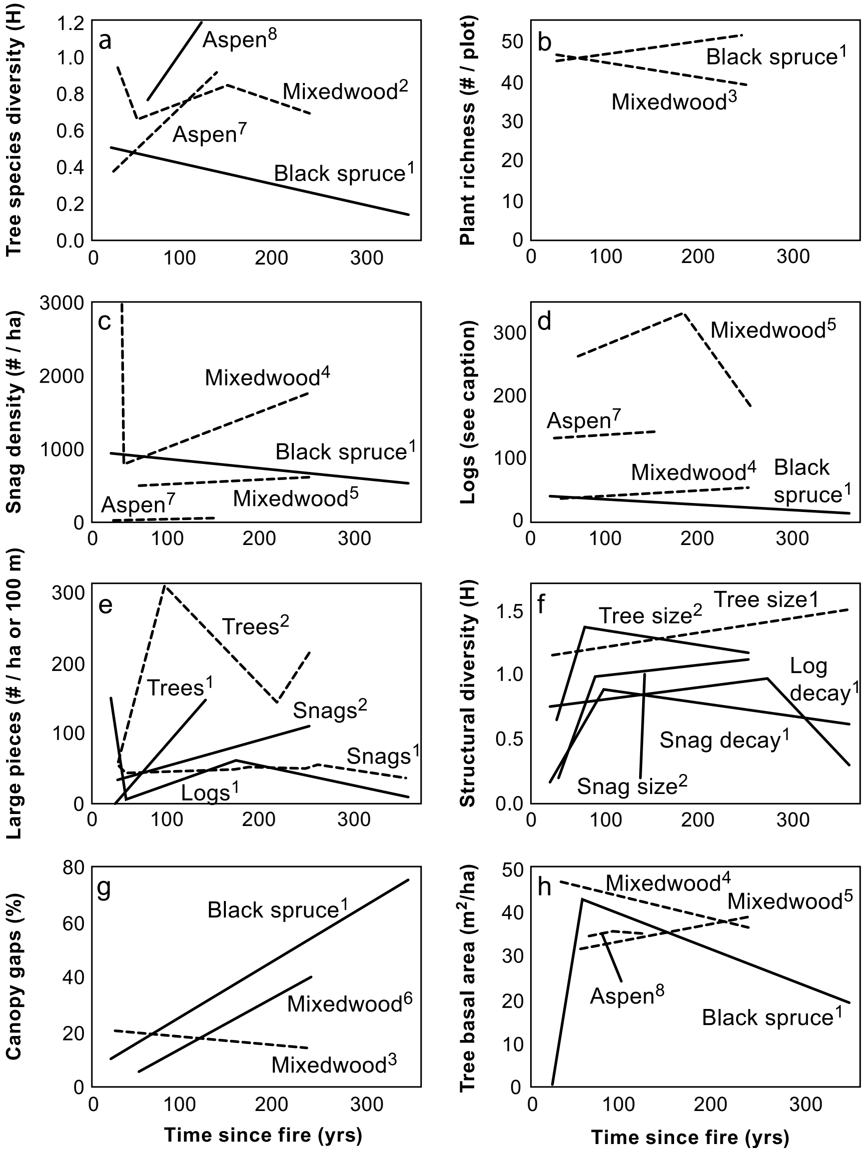

Fig. 13.3a–h Trends in typical old-growth attributes with time since fire for different types of boreal forest. **a** Tree species diversity calculated using the Shannon index based on live tree basal area except for aspen[7], which was based on the density of trees ≥10 cm diameter at breast height (dbh). **b** Understorey species richness calculated as the total number of vascular species in a plot. **c** Density of snags of unspecified size for black spruce[1] and mixedwood[4], ≥5 cm dbh for mixedwood[5] and ≥10 cm dbh for aspen[7]. **d** Abundance of logs calculated as the number per 100 m for black spruce[1], log load in tons ha^{-1} for mixedwood[4], the number ≥5 cm diameter ha^{-1} for mixedwood[5], and the number ≥11 cm diameter ha^{-1} for aspen[7]. **e** Density of large components (≥20 cm dbh or diameter) for black spruce[1] and mixedwood[2] **f** Structural diversity

species in the oldest age class and none exclusive to old-growth (Harper et al. 2003); the overall non-significant trend of increasing vascular plant richness (Fig. 13.3b) masks a peak in the intermediate age classes (Harper et al. 2003). The development of a thick *Sphagnum* moss layer in old-growth black spruce forest can hinder establishment of some vascular plants while favouring reproduction of *Picea mariana* through layering (Boudreault et al. 2002; Harper et al. 2003).

Older black spruce forests lack some of the key structural old-growth attributes of abundant deadwood and large structural components. The density of both snags and logs decreases during stand development (Fig. 13.3c, d). Likewise, the abundances of large trees, snags and logs decrease towards old-growth and were highest in intermediate stages (Fig. 13.3e). Paludification – the process in which the development of thick moss and organic layers lowers soil temperature, increases soil moisture and decreases nutrient availability (Van Cleve et al. 1983; Paré and Bergeron 1995; Gower et al. 1996; Fenton et al. 2005) – likely contributes to the different structure of old-growth black spruce forest. Due to the decrease in site productivity (Simard et al. 2007), *Picea mariana* trees that establish in later stages tend to be smaller and less numerous, leading to overall lower abundance of deadwood and large trees (Harper et al. 2003, 2005). Structural diversity for tree sizes (also for Quebec's Côte Nord, Boucher et al. 2006), snag decay classes and log decay classes also decrease in the later stages of development, resulting in less diverse old-growth (Fig. 13.3f).

Old-growth black spruce forest is more spatially heterogeneous compared to younger forests. Old-growth attributes of more abundant canopy gaps (Fig. 13.3g), a wide range of tree spacing as indicated by greater gap size diversity, more fine-scale heterogeneous tree cover and understorey patchiness were all present in older black spruce forests relative to younger forests (Harper et al. 2006). During stand development, gaps of different sizes formed by tree mortality and common small-scale disturbances such as spruce budworm and windthrow are filled in slowly due to poor regeneration and growth, leading to greater gap abundance and clumping of trees at fine scales (Harper et al. 2003, 2006).

Processes in the final stage of development of black spruce forests are unique to the boreal rather than typical of old-growth. Tree basal area, an indication of productivity, is lower in older forests (Fig. 13.3h). Low tree basal area is likely

Fig. 13.3 (Continued) calculated using the Shannon index on trees of different sizes and on snags and logs in different decay stages for black spruce[1] and on trees and snags of different sizes for mixedwood[2]. **g** Proportion of canopy gaps. **h** Tree basal area. *Lines* Best-fit linear or piecewise linear regression curves to data from different studies as indicated by superscripts: *1* Harper et al. (2003, 2005 or 2006); *2* Bergeron (2000); *3* DeGrandpré et al. (1993); *4* Hély et al. (2000); *5* Park et al. (2005); *6* Kneeshaw and Bergeron (1998); *7* Lee et al. (1997); *8* Hill et al. (2005). Data were from tables or values reported in the text except for *1* and *2* where data were available from the authors. *Solid* and *dashed lines* indicate regressions that are significant and non-significant (P=0.05), respectively. The number of pieces for the linear regressions was decided subjectively based on visual inspection of the data. The number of sites is as follows: n = 91 for *1*, n = 8 for *2*, n = 8 for *3*, n = 48 for *4*, n = 6 for *5*, n = 7 for *6*, n = 3 for *7*, n = 10 for *8* due to slower growth since increased mortality would have resulted in greater deadwood abundance, which was not observed. Although low productivity is considered uncharacteristic of old-growth forest (e.g. Wells et al. 1998), it may be globally widespread in the long term (after thousands of years, Wardle et al. 2004). The decrease in tree basal area and changes in other structural attributes in the final stage of development (Harper et al. 2005; Lecomte et al. 2006a) indicate that older black spruce forests are not in a typical steady state but continue to undergo structural changes. Aboveground biomass accumulation and net annual growth are not stable but are negative due to the decline in productivity brought about by paludification (Harper et al. 2003; Lecomte et al. 2006b). Instead, biomass accumulates in the forest floor with time (Lecomte et al. 2006b). As in other forests, small-scale disturbances such as windthrow and spruce budworm outbreaks increase throughout stand development but there is an exceptional decline in the oldest forests (Harper et al. 2002, 2003). In these oldest stands, trees grown in more open conditions are less prone to windthrow (Harper et al. 2002). Regeneration of *Picea mariana* in gaps was more common in older black spruce forest (Harper et al. 2005), as described for other old-growth forests.

13.3.2 Old-Growth Mixedwood Boreal Forest

Stand development in mixedwood boreal forest throughout Canada is characterised by the succession from shade-intolerant tree species such as aspen, birch and willow to shade-tolerant species such as balsam fir, white spruce and white cedar (Bergeron 2000; Awada et al. 2004). Tree species diversity is greatest in the intermediate stages of development during which the transition occurs (Fig. 13.3a, Park et al. 2005). There is evidence of more understorey plant species in older mixedwood forests compared to younger forests in Alberta (Timoney and Robinson 1996) but not in Quebec (Fig. 13.3b, De Grandpré et al. 1993; Bartemucci et al. 2006; see also Chap. 6 by Messier et al. this volume).

Trends in deadwood abundance with time are not very conclusive. More snags were found in either intermediate stages (Timoney and Robinson 1996) or in later stages (Awada et al. 2004; Hély et al. 2000; Park et al. 2005); however, trends for which we were able to obtain data are not significant (Fig. 13.3c). Trends that show greater log abundance in younger or intermediate stages are also not significant (Fig. 13.3d, Hély et al. 2000; Park et al. 2005); although Timoney and Robinson (1996) found more abundant logs in later stages of stand development. Data from Bergeron (2000) show more large trees in intermediate-aged stands but more large snags in older stands (Fig. 13.3e). Similar trends were found for structural diversity, with greater tree structural diversity in the intermediate stages and greater snag diversity in older stands (Fig. 13.3f). Tree structural diversity based on crown width was also greatest in intermediate age classes (Paré and Bergeron 1995). However, old-growth balsam fir forests in Newfoundland are uneven-aged with a multi-layered canopy (McCarthy and Weetman 2006). Fir stands in Quebec's Côte Nord also exhibited increasing tree structural diversity with age (Boucher et al. 2006).

A greater proportion of canopy gaps was found with time since disturbance in Quebec's boreal mixedwood by Kneeshaw and Bergeron (1998) and Park et al. (2005) but not by DeGrandpré et al. (1993; Fig. 13.3g). Bartemucci et al. (2006) found greater canopy light transmission levels in older forests than in younger forests, again indicating more open canopy cover. In terms of other aspects of spatial pattern, understorey patchiness – a typical old-growth attribute – was found in intermediate stages rather than in the oldest forests in boreal mixedwood (De Grandpré et al. 1993). However, Awada et al. (2004) found greater patchiness of white spruce seedlings in older (>100 years) as compared to younger mixedwood forests in Saskatchewan.

Results on processes in old-growth mixedwood forests are varied. Bergeron (2000) found regeneration of dominant trees was greatest in intermediate stands, while Awada et al. (2004) found no trend. Trends of increasing and decreasing tree productivity with time since disturbance in mixedwood forests were not significant (Fig. 13.3h; Hély et al. 2000; Park et al. 2005). Greater deadwood abundance in intermediate or later stages as described above likely indicates increasing mortality in these forests. Understorey productivity decreased steadily during stand development (measured as cover; De Grandpré et al. 1993). Stable tree basal area in later stages of development, indicating a steady-state old-growth forest, was found in the mixedwood by Hély et al. (2000) and Park et al. (2005) but not by Awada et al. (2004) or Paré and Bergeron (1995), who found a decrease in later stages of development similar to that found in black spruce boreal forest. It is also interesting to note that tree basal area decreased even over a relatively short chronosequence from 80 to 110 years in unharvested balsam fir stands in eastern Canada (Sturtevant et al. 1997).

In mixedwood boreal forest, many old-growth attributes were found in the intermediate stage of development that accompanies the change in species composition from mostly deciduous to mostly conifer tree species; these attributes include: greater tree species diversity, understorey plant species richness, more abundant deadwood, more large trees, structural diversity, heterogeneous spatial pattern, regeneration of dominant species and tree basal area. The oldest mixedwood forests were characterised by a few typical old-growth attributes such as more abundant deadwood including large snags, more gaps, patchiness of white spruce seedlings, and tree basal area. Other typical attributes, such as understorey species richness and understorey productivity, were lacking.

Aspen forests can be considered as the early-successional stage of mixedwood boreal forest. However, recent studies have found evidence of self-replacement of aspen and gap dynamics in these forests (Cumming et al. 2000), suggesting that there may be an 'old-growth' aspen forest. We do not intend to resolve this issue here, but instead assess whether the oldest aspen forests contain typical old-growth attributes as compared to younger aspen forests. Although their defining feature – the dominance of a shade-intolerant tree species – contrasts with typical old-growth forests, older aspen forests do contain many typical old-growth attributes. Tree species diversity is higher as more shade-tolerant species appear during succession (Fig. 13.3a, Lee et al. 1997; Hill et al. 2005); however, the diversity of understorey species was lower in older forests (Timoney and Robinson 1996). Although studies found more snags in either intermediate (Timoney and Robinson 1996; Lee et al. 1997) or later (Lee 1998) stages of development, logs were more abundant in older aspen forests compared to intermediate ages (Timoney and Robinson 1996; Lee et al. 1997). However, at least some of these trends were not significant (Fig. 13.3c,d). Large structural components including trees, snags and logs were all more abundant in older aspen forests (Lee et al. 1997; Lee 1998), and average tree diameter was also larger (Lee 1998). Similarly, measures of greater structural diversity and more heterogeneous spatial pattern were also found in the later stages of stand development including trees of multiple ages and sizes (Lee 1998; Cumming et al. 2000; Namroud et al. 2005), a greater diversity of snags and logs in different decay stages (Lee et al. 1997), a greater proportion of canopy gaps (Cumming et al. 2000; Hill et al. 2005) and greater heterogeneity (Cumming et al. 2000), although the latter was not found by Lee et al. (1997). There was no apparent trend for tree basal area with time since fire (Fig. 13.3h, Hill et al. 2005). Finally, Cumming et al. (2000) found evidence of the process of self-replacement or regeneration of the dominant tree species in older aspen forests. Overall, older aspen forests do seem to be typical of structurally diverse old-growth forests with gap dynamics and self-replacement of the dominant tree species. However, with time, they are likely either to develop into mixedwood stands or to succumb to fire.

13.3.3 Characterisation of Old-Growth Boreal Forests

A summary of the presence of typical old-growth attributes reveals differences among different types of boreal forest (Table 13.2). Black spruce and mixedwood forests each contain less than half of the old-growth attributes commonly listed in the literature. The attributes that do characterise these forests include the dominance of a shade-tolerant species in both forest types; greater structural diversity of deadwood; a heterogeneous spatial pattern and more abundant regeneration in black spruce forests; and more abundant deadwood including large snags and a more open canopy in mixedwood forests. The remaining old-growth attributes were often most abundant in intermediate stages and declined in the later stages of stand development, most likely due to paludification in black spruce forests or a change in species composition in mixedwood forests. The presence of typical old-growth attributes in older aspen forests, but in the intermediate stages of development of mixedwood forests, may be because these aspen forests have not yet undergone succession to shade-tolerant species.

Certain typical old-growth attributes rarely characterise old-growth boreal forests, while others are more common. Our synthesis (Table 13.2) shows that characteristics such as greater tree species diversity, understorey plant species richness and tree productivity are rarely found in older boreal forests and cannot

Table 13.2 Assessment of typical old growth attributes (as listed in the literature) for different boreal forests: the presence or absence (*Y* yes, *N* no) in each boreal forest type is indicated. The number of studies (or site types for black spruce) with evidence of a characteristic more prominent in older forests compared to younger forests sampled in each study as a proportion of the number of studies who made the comparison is indicated in brackets. The ages of the forests are relative to each study; therefore the results represent general trends. Results are based on visual inspection of the results or statements made in different studies and do not necessarily indicate significance. Aspen forests are treated separately in this table although it should be noted that they are younger than the other forest types and are often considered an earlier stage of development towards mixedwood forests

Old growth attributes[a]	Black spruce[b]	Mixedwood[b]	Aspen[b]
Composition			
Long-lived shade tolerant species[*i, iii*]	Y (7/7)	Y (3/3)	N (0/1)
Greater tree species diversity[*ii, iv*]	N (1/7)	N (0/2)	Y (2/2)
Greater richness of understorey vascular plants[*ii*]	N (0/1)	N (1/3)	N (0/1)
Abundant or large structural elements			
More snags[*ii*]	N (1/6)	Y (3/4)	N (1/3)
More logs[*ii*]	(3/6)	Y (2/3)	Y (2/2)
Greater average tree diameter[*ii*]			Y (1/1)
More large trees[*i, ii, iv*]	N (2/6)	N (0/1)	Y (2/2)
More large snags[*i, ii, iv*]	N (2/6)	Y (1/1)	Y (2/2)
More large logs[*i, ii, iv*]	N (2/6)		
High structural diversity			
Multi-aged[*ii, iii, iv*]		Y (1/1)	Y (1/1)
Greater diversity of tree sizes[ii] or multilayered canopy[*ii, iv*]	N (2/7)	(2/4)	Y (2/2)
Greater diversity of snag decay stages and sizes[*iii, iv*]	Y (4/6)	Y (1/1)	Y (1/1)
Greater diversity of log decay stages and sizes[*ii, iii, iv*]	Y (6/6)		Y (1/1)
Heterogeneous spatial pattern			
Greater proportion of canopy gaps [*ii, iv*]	(2/4)	Y (3/4)	Y (2/2)
Larger average tree spacing[*ii, iv*]		N (0/1)	
Wider range of tree spacing[*ii*]	Y (1/1)	N (0/1)	
Greater degree of patchiness or heterogeneity[*iv*]	(1/2)	N (0/1)	(1/2)
Greater understorey patchiness[*ii*]	Y (1/1)	(1/2)	
Processes			
Greater tree productivity or basal area[*ii*]	N (2/6)	N (1/4)	N (0/1)
Greater understorey productivity or cover[*ii, iv*]		(1/2)	
Steady state[ii, iii, iv] as measured by no change in tree basal area	N (1/6)	(2/4)	Y (1/1)
More small-scale disturbances[*iii*]	N (0/7)		
More regeneration of dominant tree species[*iii, iv*]	Y (2/3)	N (0/2)	Y (1/1)

[a]References for typical old-growth attributes: *i* Spies and Franklin (1988), *ii* Wells et al. (1998), *iii* Moessler et al. (2003), *iv* Kneeshaw and Burton (1998). The following characteristics were not included: high habitat diversity (*ii*) or structural complexity (*iv*) (structural diversity measures were used instead); compositionally complex (*iv*) (tree species diversity was used instead); broken or deformed tops or boles and root decay (*ii*); pit and mound topography (*iv*); slow growth of trees (*ii*) (not usually measured or compared to other stages of development); and old trees (*i–iv*) (present in all older forests)

[b]References for forest types: *black spruce* Harper et al. (2002, 2003, 2005, 2006), Boucher et al. (2006); *mixedwood* De Grandpré et al. (1993), Paré and Bergeron (1995), Timoney and Robinson (1996), Kneeshaw and Bergeron (1998), Bergeron (2000), Hély et al. (2000), Awada et al. (2004), Park et al. (2005), Bartemucci et al. (2006), Boucher et al. (2006), McCarthy and Weetman (2006); *aspen* Lee et al. (1997), Lee (1998), Timoney and Robinson (1996), Cumming et al. (2000), Hill et al. (2005)

be used as criteria to identify old-growth in boreal forests (cf. Chap. 2 by Wirth et al., this volume). In addition, the old-growth stage of development cannot be considered a stable state, even in the absence of disturbance, since structural changes still take place, e.g. tree basal area decreases still occur over thousands of years in many ecosystems (Wardle et al. 2004). Some typical old-growth attributes that show more promise as criteria for boreal forests include a greater abundance of logs, multi-aged stands, greater structural diversity of deadwood and more open canopy with gap dynamics. However, even these characteristics might not be reliable given longer time spans with no recurrence of fire. Instead, it may be more appropriate to use indices for old-growth such as the cohort basal area proportion (a function of the basal areas of the initial and replacement cohorts, Kneeshaw and Gauthier 2003) to define the old-growth stage, especially for boreal forests. It is important to note that even though old-growth boreal forests may lack some of the typical attributes found in other old-growth forests, they still contain characteristics such as structural diversity that are unique to this stage of development and potentially important to regional biodiversity.

13.4 Implications for Forest Management

At first glance, an even-aged management approach would appear to resemble the natural disturbance regime if timber harvest rotation age approaches that of the natural fire cycle. However, a full even-aged regulation does not produce an age-class distribution similar to that of natural distribution, even for forest rotations that are as long as the fire cycle. Indeed, in an even-aged management context, a forest is referred to as fully regulated when stand age classes are uniformly distributed throughout a territory. Thus, in theory, after one complete rotation, no stands over the rotation age will exist. The same region submitted to forest fires intense enough to generate even-aged stands will, at equilibrium, present a completely different age class distribution of forest stands. Assuming that the probability of burning is independent of stand age, the forest age structure will, again theoretically, resemble a negative exponential curve, with about 37% of forests older than the fire cycle (Johnson and Van Wagner 1985). This means that, for a fire cycle and a forest rotation of similar duration, forest management will not spare any forest that exceeds rotation age whereas fire will maintain over 37% of the forest in older age classes. This difference is fundamental because it implies that full regulation in an even-aged management regime will result in the loss of mature- to old-growth forests. As discussed in the previous section, these intermediate-aged and older forests have unique characteristics that could be essential for the maintenance of biodiversity. Several studies have pointed out the importance of old growth attributes for the maintenance of diversity of many different organisms such as lichens, mosses (Boudreault et al. 2002), (Fenton and Bergeron 2008), birds (Drapeau et al. 2002), fungi (Desponts et al. 2004) and insects (Work et al. 2003; cf. also Chap. 19 by Frank et al., this volume).

Use of rotations of variable length in proportions similar to those observed in the natural fire regime is a possible alternative to fixed rotations (Seymour and Hunter 1999), in order to maintain old-growth forests. However, this approach may be applicable only in ecosystems where species are long-lived and can thus support longer rotations. In boreal forests composed of relatively short-lived species, this approach would probably lead to fibre loss and a decrease in allowable cut. Alternatively, Bergeron et al. (2002) have suggested that silvicultural practices aimed at maintaining structural and compositional characteristics of old-growth in harvested stands could, in boreal regions, guarantee maintenance of habitat diversity while only slightly affecting the allowable cut. It would be possible to treat some stands by clear-cutting followed by seeding or planting (or another even-aged silvicultural system whose outcome resembled the effect of fire), other stands with partial cuts that approach the natural development of intermediate-aged stands, and still other stands with selective harvesting in order to reflect the dynamics of old growth stands (Bergeron et al. 2002).

13.5 Conclusions

Although Canadian boreal forests are controlled by fire, long fire intervals allow for the presence of a significant proportion of old-growth forests. Some of these have been relatively undisturbed for many centuries, even millennia (Cyr et al. 2005). Long fire cycles are not unique to recent historical times but were common during most of the Holocene (Flannigan et al. 2001; Cyr et al. 2009), and old-growth forests can be considered as having been a permanent feature of the Canadian boreal forest for at least the last 10,000 years. Although not studied here, it is very likely that old-growth forests are also very abundant in Eurasian boreal forests, especially in a context where non stand-replacing fires are more common (Gromtsev 2002; Wallenius et al. 2005; Wirth 2005). However, boreal old-growth forests are not devoid of large-scale disturbances such as insects or windthrow (Kneeshaw and Gauthier 2003), and in that respect may stand apart from typical temperate or tropical old-growth forests where small gap dynamics is the typical disturbance regime.

Old forests in the boreal zone possess unique characteristics such as greater structural diversity and gap dynamics not observed in post-fire even-aged cohorts. Other typical old-growth attributes, including higher tree species diversity, greater abundance of larger trees and snags and greater tree basal area, are often found instead in intermediate-aged stands that are still older than the current harvest rotation age. Current forest management practices that use short even-aged rotations do not reproduce the historical age structure, and a decrease in old-growth attributes may threaten biodiversity.

In this context, protecting a proportion of the remaining old-growth in boreal forest is urgently required, but probably insufficient to restore the abundance of old-growth forest in the pre-industrial landscape. Development of silvicultural techniques that maintain or restore old-growth forest compositional, structural and functional characteristics at different scales in the landscape is an important option to explore.

References

Asselin H, Payette S, Fortin MJ, Vallée S (2003) The northern limit of *Pinus banksiana* Lamb in Canada: explaining the difference between the eastern and western distributions. J Biogeogr 30:1709–1718

Awada T, Henebry GM, Redmann RE, Sulistiyowati H (2004) *Picea glauca* dynamics and spatial pattern of seedlings regeneration along a chronosequence in the mixedwood section of the boreal forest. Ann For Sci 61:789–794

Bartemucci P, Messier C, Canham CD (2006) Overstory influences on light attenuation patterns and understory plant community diversity and composition in southern boreal forests of Quebec. Can J For Res 36:2065–2079

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

Bergeron Y, Leduc A (1998) Relationships between change in fire frequency and mortality due to spruce budworm outbreak in the southeastern Canadian boreal forest. J Veg Sci 9:493–500

Bergeron Y, Gauthier S, Kafka V, Lefort P, Lesieur D (2001) Natural fire frequency for the eastern Canadian boreal forest: consequences for sustainable forestry. Can J For Res 31:394–391

Bergeron Y, Leduc A, Harvey BD, Gauthier S (2002) Natural fire regime: a guide for sustainable management of the Canadian boreal forest. Silva Fenn 36:81–95

Bergeron Y, Flannigan M, Gauthier S, Leduc A, Lefort P (2004) Past current and future fire frequency in the Canadian boreal forest: implications for sustainable forest management. Ambio 33:356–360

Boucher D, Gauthier S, De Grandpré L (2006) Structural changes in coniferous stands along a chronosequence and a productivity gradient in the northeastern boreal forest of Quebec. Ecoscience 13:172–180

Boudreault C, Bergeron Y, Gauthier S, 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

Cumming SG, Schmiegelow FKA, Burton PJ (2000) Gap dynamics in boreal aspen stands: is the forest older than we think? Ecol Appl 10:744–759

Cyr D, Bergeron Y, Gauthier S, Larouche AC (2005) Are the old-growth forests of the Clay Belt part of a fire-regulated mosaic? Can J For Res 35:65–73

Cyr D, Gauthier S, Bergeron Y, Carcaillet C (2009) Forest management is driving the eastern part of North-American boreal forest outside its natural range of variability. Front Ecol Environ 7: (in press)

De Grandpré L, Gagnon D, Bergeron Y (1993) Changes in the understory of Canadian southern boreal forest after fire. J Veg Sci 4:803–810

Desponts M, Brunet M, Bélanger L, Bouchard M (2004) The eastern boreal old-growth balsam fir forest: a distinct ecosystem. Can J Bot 82:830–849

Drapeau P, Nappi A, Giroux JF, Leduc A, Savard JPL (2002) Distribution patterns of birds associated with snags in natural and managed eastern boreal forests. In: Laudenslayer WF Jr, Shea PJ, Valentine BE, Weatherspoon CP, Lisle TE (eds) Proceedings of the symposium on the ecology and management of dead wood in western forests, Reno, NV. Gen. Tech. Rep. PSW-GTR-181. US Department of Agriculture: Pacific Southwest Research Station, Forest Service, Albany, CA, pp 193–205

Eberhart KE, Woodard PM (1987) Distribution of residual vegetation associated with large fires in Alberta. Can J For Res 17:1207–1212

Ecological Stratification Working Group (1996) A national ecological framework for Canada. Agriculture and Agri-Food Canada and Environment Canada, Ottawa

Fenton NJ, Bergeron Y (2008) Does time or habitat make old-growth forests species rich? Bryophyte richness in boreal *Picea mariana* forests. Biol Conserv 141:1389–1399

Fenton N, Lecomte N, Legare S, Bergeron Y (2005) Paludification in black spruce (*Picea mariana*) forests of eastern Canada: potential factors and management implications. For Ecol Manag 213:151–159

Flannigan M, Campbell I, Wotton M, Carcaillet C, Richard PJH, Bergeron Y (2001) Future fire in Canada's boreal forest: paleoecology, GCM and RCM results. Can J For Res 31:854–864

Gower ST, McMurtrie RE, Murty D (1996) Aboveground net primary production decline with stand age: potential causes. Trends Ecol Evol 11:378–382

Gromtsev A (2002) Natural disturbance dynamics in the boreal forests of European Russia: a review. Silva Fenn 36:41–55

Harper KA, Bergeron Y, Gauthier S, Drapeau P (2002) Post-fire development of canopy structure and composition in black spruce forests of Abitibi Quebec: a landscape scale study. Silva Fenn 36:249–263

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

Harper KA, Bergeron Y, Drapeau P, Gauthier S, De Grandpré L (2005) Structural development following fire in black spruce boreal forest. For Ecol Manag 206:293–306

Harper KA, Bergeron Y, Drapeau P, Gauthier S, De Grandpré L (2006) Changes in spatial pattern of trees and snags during structural development in *Picea mariana* boreal forests. J Veg Sci 17:625–636

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

Hill SB, Mallik AU, Chen HYH (2005) Canopy gap disturbance and succession in trembling aspen dominated boreal forests in northeastern Ontario. Can J For Res 35:1942–1951

Johnson EA, Van Wagner CE (1985) The theory and use of two fire history models. Can J For Res 15:214–220

Kafka V, Gauthier S, Bergeron Y (2001) Fire impacts and crowning in the boreal forest: study of a large wildfire in western Quebec. Int J Wildland Fire 10:119–127

Johnson EA (1992) Fire and vegetation dynamics studies from the North American boreal forest. Cambridge Studies in Ecology, Cambridge University Press, Cambridge

Kneeshaw DD, Bergeron Y (1998) Canopy gap characteristics and tree replacement in the southeastern boreal forest. Ecology 79:783–794

Kneeshaw DD, Burton PJ (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 DD, Gauthier S (2003) Old-growth in the boreal forest at stand and landscape levels. Environ Rev 11:S99–S114

Lecomte N, Simard M, Bergeron Y (2006a) Effects of fire severity and initial tree composition on stand structural development in the coniferous boreal forest of Northwestern Quebec Canada. Ecoscience 13:152–163

Lecomte N, Simard M, Fenton N, Bergeron Y (2006b) Fire severity and long-term ecosystem biomass dynamics in coniferous boreal forests of eastern Canada. Ecosystems 9:1215–1230

Lee P (1998) Dynamics of snags in aspen-dominated midboreal forests. For Ecol Manag 105:263–272

Lee PC, Crites S, Nietfeld M, Van Nguyen H, Stelfox JB (1997) Characteristics and origins of deadwood material in aspen-dominated boreal forests. Ecol Appl 7:691–701

Le Goff H, Sirois L (2004) Black spruce and jack pine dynamics simulated under varying fire cycles in the northern boreal forest of Quebec Canada. Can J For Res 34:2399–2409

McCarthy JW, Weetman G (2006) Age and size structure of gap-dynamic old-growth boreal forest stands in Newfoundland. Silva Fenn 40:209–230

Moessler A, Thompson I, Pendrel BA (2003) Overview of old-growth forests in Canada from a science perspective. Environ Rev 11:S1–S7

Namroud MC, Park A, Tremblay F, Bergeron Y (2005) Clonal and spatial genetic structures of aspen (*Populus tremuloides* Michx). Mol Ecol 14:2969–2980

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

Park A, Kneeshaw D, Bergeron Y, Leduc A (2005) Spatial relationships and tree species associations across a 236-year boreal mixedwood chronosequence. Can J For Res 35:750–761

Payette S (1992) Fire as a controlling process in the North American boreal forest. In: Shugart HH, Leemans R, Bonan GB (eds) A system analysis of the global boreal forest. Cambridge University Press, New York

Peng CH, Apps MJ (2000) Simulating global soil-CO_2 flux and its response to climate change. J Environ Sci 12:257–265

Seymour R, Hunter M (1999) Principles of ecological forestry. In: Hunter ML Jr (ed) Maintaining biodiversity in forest ecosystems, Cambridge University Press, Cambridge UK, pp 22–61

Simard M, Lecomte N, Bergeron Y, Paré D, Bernier PY (2007) Forest productivity decline caused by successional paludification of boreal forests. Ecol Appl 17:1619–1637

Spies TA, Franklin JF (1988) Old growth and forest dynamics in the Douglas-fir region of western Oregon and Washington. Nat Areas J 8:190–201

Stocks BJ, Mason JA, Todd JB, Bosch EM, Wotton BM, Amiro BD, Flannigan MD, Hirsch KG, Logan KA, Martell DL, Skinner WR (2002) Large forest fires in Canada 1959–1997. J Geophys Res Atmos 107:1–12

Sturtevant BR, Bissonette JA, Long JN, Roberts DW (1997) Coarse woody detritus as a function of age, stand structure, and disturbance in boreal Newfoundland. Ecol Appl 7:702–712

Thompson ID, Flannigan MD, Wotton BM, Suffling R (1998) The effects of climate change on landscape diversity: an example in Ontario forests. Environ Monit Assess 49:213–233

Timoney KP, Robinson AL (1996) Old-growth white spruce and balsam poplar forests of the Peace River Lowlands, Wood Buffalo National Park, Canada: Development, structure, and diversity. For Ecol Manag 81:179–196

Van Cleve K, Dyrness CT, Viereck LA, Fox J, Chapin FSI, Oechel W (1983) Taiga ecosystems in interior Alaska. BioScience 33:39–44

Wallenius TH, Pitkänen A, Kuuluvainen T, Pennanen J, Karttunen H (2005) Fire history and forest age distribution of an unmanaged *Picea abies* dominated landscape. Can J For Res 35:1540–1552

Wardle DA, Walker LR, Bardgett RD (2004) Ecosystem properties and forest decline in contrasting long-term chronosequences. Science 305:509–513

Weber MG, Flannigan MD (1997) Canadian boreal forest ecosystem structure and function in a changing climate: impact on fire regime. Environ Rev 5:145–166

Wells RW, Lertzman KP, Saunders SC (1998) Old-growth definitions for the forests of British Columbia Canada. Nat Areas J 18:279–292

Wirth C (2005) Fire regime and tree diversity in boreal forests: implications for the carbon cycle. In: Scherer–Lorenzen M, Körner C, Schulze E-D (eds) Forest diversity and function: temperate and boreal systems. Ecological Studies, vol 176. Springer, Berlin, pp 309–344

Wirth C, Czimczik CI, Schulze E-D (2002) Beyond annual budgets: carbon flux at different temporal scales in fire-prone Siberian Scots pine forests. Tellus Ser B Chem Phys Meteorol 54:611–630

Work TT, Shorthouse D, Spence JR, Volney WJ, Langor D (2003) Coarse-filter conservation strategies in boreal mixedwood forests: initial invertebrate responses from the EMEND experiment. Can J For Res 34:417–430