Forestry 2014; **87**, 11–28, doi:10.1093/forestry/cpt047 Advance Access publication 29 November 2013

Constraints to partial cutting in the boreal forest of Canada in the context of natural disturbance-based management: a review

Arun K. Bose^{1*}, Brian D. Harvey¹, Suzanne Brais¹, Marilou Beaudet² and Alain Leduc³

¹Centre d'étude sur la forêt (CEF), Institut de recherche sur les forêts, Université du Québec en Abitibi-Témiscamingue, 445 boulevard de l'Université, Rouyn-Noranda, QC, Canada J9X 5E4

²Ministère des Ressources naturelles, Direction de la recherche forestière, 2700, rue Einstein, Québec, QC, Canada G1P 3W8 ³Centre d'étude sur la forêt (CEF), Département des sciences biologiques, Université du Québec à Montréal, C.P. 8888, Succursale Centre-ville, Montréal, QC, Canada H3C 3P8

*Corresponding author. E-mail: arun.bose@uqat.ca

Received 3 May 2013

Over the last 25 years, greater understanding of natural dynamics in the boreal forest has led to the integration of forest ecosystem management principles into forest policy of several Canadian provinces and, in turn, to greater interest in developing silvicultural treatments that are grounded in natural stand-level dynamics – often referred to as natural disturbance-based silviculture. As a result, alternative silvicultural practices including variants of partial cutting are increasingly being applied in the boreal forest as an approach to balancing economic and ecological management objectives. While the numerous benefits of partial cutting reported in the literature are acknowledged, the objective of this paper is to provide an overview of factors or constraints that potentially limit the application of these practices in boreal Canada in the context of forest ecosystem management and natural disturbance-based silviculture. Among constraining factors, numerous studies have reported elevated mortality rates of residual stems following partial cutting, initial growth stagnation of residual trees, problems related to recruitment of desirable species and, on certain flat or lowland sites, risks of long-term decline in site and stand productivity. A number of operational challenges to partial cutting in the boreal forest are also presented and several avenues of research are proposed.

Introduction

Management and silviculture in the boreal forests of Canada have been evolving over the last few decades and, particularly in the new millennium, motivated largely by a general movement to adopt ecosystem management practices (Burton *et al.*, 2006; Gauthier *et al.*, 2009; Puettmann *et al.*, 2009). This movement has in part been driven by the apprehension that continued generalized application of traditional management practices in the boreal forest, characterized by short rotations (60–100 years) and even-aged regimes, will eliminate much of the remaining old, often structurally complex natural forest on the managed landscape. Moreover, it is anticipated that a general rejuvenation of the forest and simplification of forest and stand structure and composition resulting from these regimes will impact on indigenous biodiversity and ecosystem resilience (Kuuluvainen, 2009).

Recognition of these ecological and social issues related to boreal forestry has coincided with the developing interest in incorporating natural disturbance dynamics into forest-level planning and stand-level silviculture and lead to the development of 'natural disturbance-based' (NDB) 'silviculture' approaches in the boreal forest (Bergeron *et al.*, 1999; Harvey *et al.*, 2002) and

elsewhere (Palik et al., 2002; Seymour et al., 2002). While even-aged harvesting (clear cutting and its variants) has been a universal practice across the Canadian boreal forest (currently >80 per cent of area harvested) (MRNQ, 2012; NFDP, 2013), numerous 'alternative silvicultural' trials - that is, alternative to clearcutting - have been established to test the operational and biological feasibility of partial cutting in the boreal forest (Thorpe and Thomas, 2007). Documented experiences in alternative cutting practices, ranging from retention silviculture to more selection-oriented treatments adapted to boreal forest conditions are, however, generally recent (<20 years) and few long-term experiments (40+ years) exist. This absence of a tradition of partial cutting in the Canadian boreal forest presents both challenges and opportunities for foresters interested in developing new NDB silvicultural practices (or adapting old ones), and our current situation could be considered as more of a learning phase than an application phase of practices with long, proven histories. Nonetheless, the idea of applying silvicultural approaches that integrate natural stand dynamics and create or maintain multifunctional forests has progressively gained interest, here and elsewhere (Gustafsson et al., 2012; Lindenmayer et al., 2012), and the concept of ecosystem management, which integrates the notion

© Institute of Chartered Foresters, 2013. All rights reserved. For Permissions, please e-mail: journals.permissions@oup.com This is an Open Access article distributed under the terms of the Creative Commons Attribution License (http://creativecommons.org/licenses/by/ 3.0/), which permits unrestricted reuse, distribution, and reproduction in any medium, provided the original work is properly cited.



of maintaining forest- and stand-level structural diversity on the managed landscape, has made its way into forest legislation in a number of provinces.

Given the relatively recent but collectively rich body of research on partial cutting in the Canadian boreal forest, as well as indications that refinements are still needed in applying these new practices, we believe that a review of current knowledge concerning biophysical and ecophysiological constraints associated with partial cutting in the boreal forest is timely. Moreover, in the context of forest ecosystem management, we were interested in assessing the degree to which tested partial cutting treatments could be associated with dominant disturbance and mortality processes occurring in the boreal forest. This review contains three parts and focuses primarily on the North American boreal forest, with a certain emphasis on the eastern Canadian boreal forest and some reference to Fennoscandian studies. We first provide an overview of the particularities of the boreal forest that are relevant to partial cutting and a working definition and classification of the most common current partial cutting practices in the Canadian boreal forest. This is followed by a brief section that presents some of the documented benefits of partial cutting in the boreal forest, followed by the principal review that addresses five important silvicultural concerns: residual tree mortality, growth responses of trees and saplings, problems related to regeneration recruitment, lowland site productivity and wood properties. We also identify a number of operational limitations associated with partial cutting in the Canadian boreal forest. The paper concludes with the principal 'take-homes' for forest management and suggests directions for future research.

The boreal forest

Total forest area in Canada covers 417.6 million hectares and nearly 90 per cent of the productive forest area is situated in the boreal forest. The Canadian boreal forest accounts for 10 per cent of the world's forest cover and 30 per cent of the world's boreal forest (Brassard and Chen, 2006; Brandt, 2009). Despite many climatic and floristic commonalities, the vast boreal forest of North America varies considerably throughout its range, largely as a result of different climatic and biophysical conditions such as natural disturbance regimes, site and soil factors, as well as management histories (Burton et al., 2003, 2010). For the purposes of this paper, we are concerned with the commercial boreal forest situated within two bioclimatic subdivisions of the North American boreal biome (Brandt, 2009), the 'Thermoboreal' and 'Mesoboreal' zones (Figure 1, Baldwin et al., 2012), referred to here as the boreal mixedwood and continuous coniferous boreal forests, respectively.

An obvious distinction of the boreal forest is the rigour of the climate, but more than this, both daily and annual temperature extremes are arguably greater in the boreal zone than any other productive forest biome. Depending on the location, summer temperatures can reach well into the $+30^{\circ}$ C range whereas winter temperatures can drop below -40° C in the same area and daily fluctuations of $>25^{\circ}$ C are not uncommon, particularly during late winter (Table 1).

Fire is the most important stand-replacing disturbance agent in the boreal forest (Johnson, 1996), and stands that originate from fire are often dense, even-aged and generally composed of

fire-adapted species that are short-lived compared with longerlived species of other biomes. Fire frequency and average annual area burned vary considerably across the boreal forest (Bergeron et al., 2004). In the eastern boreal forest where fire cycles are generally longer than in the west, much of the forest matrix has historically been older than age of tree maturity (Kneeshaw and Gauthier, 2003). As a result, time and successional processes mortality due to senescence, pathogens and secondary disturbances, canopy replacement and tree recruitment - are important drivers of forest- and stand-level dynamics and contribute to developing structural complexity in forests in these regions. In contrast, fire cycles are generally shorter in the western boreal mixedwood and, as a result, the forest matrix tends to be dominated by a younger post-fire forest with patches of older forest dispersed throughout (Johnson, 1996); this likely explains why variable retention approaches (see section Partial cutting in the Canadian boreal forest) have been favoured in this region.

Along with fire, insect outbreaks play an important role in shaping boreal forest structure and composition, and two insect defoliators in particular affect areas larger than those affected by fire and forest harvesting combined (Cooke et al., 2007). These are the eastern spruce budworm (Choristoneura fumiferana). which feeds on balsam fir (Abies balsamea spp.) and spruces (Picea spp.) and affects large areas of the coniferous and mixedwood boreal forests (Blais, 1983), and the forest tent caterpillar (Malacosoma disstria), which attacks poplars (Populus spp.) and birches (Betula spp.) primarily in the boreal mixedwood. Depending on their severity and the relative presence of host species, insect outbreaks may either be considered as a secondary (partial) disturbance, creating mortality in patches and multi-cohort stand structures or as a primary, stand-replacing disturbance. (Bergeron et al., 1998: Kneeshaw and Bergeron, 1998: Cvr et al., 2005). Other secondary disturbances such as windthrow and senescence of individual trees or groups of trees (McCarthy, 2001; Pham et al., 2004; Rich et al., 2007) influence dynamics of stand structure and composition through stand development (Bergeron, 2000), particularly in older aged stands (Aakala et al., 2008). An overview of the particularities of boreal forest is presented in Table 1.

Species composition and relative abundance in the overstorey and understorey are largely controlled by the disturbance regime, succession dynamics, the time elapsed since disturbance, site factors and differences in species' autoecological traits. These include shade tolerance, reproductive modes, initial growth rates, maximum size, longevity, site preferences and particular vulnerabilities, for example as host to specific insects or diseases (Lieffers et al., 2003). In the mixedwood forest of western Canada, trembling aspen (P. tremuloides) and white spruce (P. glauca) are the dominant early- and mid-to-late-successional species, respectively (Lieffers et al., 1996). Aspen is well adapted to short fire cycles and, in the absence of more shade-tolerant conifers (fir and spruces in particular), can maintain its presence on sites and develop a multi-cohort structure by suckering into gaps (Cumming et al., 2000). However, as a relatively short-lived, clonal and very shade-intolerant species, aspen clearly does not lend itself well to continuous cover forestry practices.

In the southeastern Canadian boreal forest, aspen, white birch (*B. papyrifera*), jack pine (*Pinus banksiana*) and black spruce (*P. mariana*), when present in fire-disturbed stands, are generally the dominant early successional species (Bergeron, 2000; Chen and Popadiouk, 2002). Slower growing, mid- to late-successional

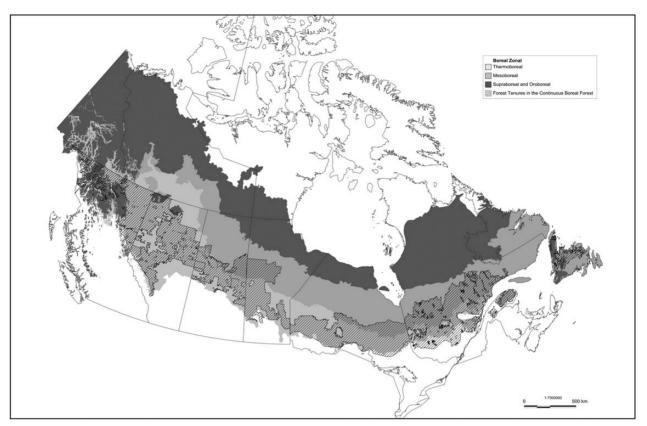


Figure 1 Map of the Canadian boreal biome with limits of the Thermoboreal, Mesoboreal and combined Supraboreal–Oroboreal bioclimatic subdivisions (Baldwin *et al.*, 2012) and area within the Thermoboreal ('boreal mixedwood') and Mesoboreal ('continuous conifer') zones currently under forest management tenure. Boreal extents are from Brandt (2009), and Baldwin *et al.* (2012) is version 1 of the Canadian component of the Circumboreal Vegetation Map (Talbot and Meades, 2011).

species, such as balsam fir (A. balsamea), white spruce and Eastern white cedar (Thuja occidentalis), tend to establish more gradually in the understorey (Bergeron and Dubue, 1989). Black spruce, while shade tolerant and slower growing than aspen, has the particularity of producing semi-serotinous cones, a fire adaptation which, like jack pine, allows it to release seeds and establish immediately following fire. In this sense, black spruce is unique in behaving both as a pioneer and later successional species. Combined with its adaptation to fire disturbance, black spruce's tolerance to extreme cold and capacity to grow in a broad range of edaphic conditions explain its dominance over much of the continuous coniferous (mesoboreal) forest. Although the range of balsam fir extends west through the Prairie provinces, it and Eastern white cedar are more common in central and eastern Canada where annual precipitation levels are considerably higher and natural fire cycles are longer than those in the western boreal forest (De Grandpré et al., 2000).

Partial cutting in the Canadian boreal forest

The Canadian Forest Service defines partial cutting as 'any cutting in which only part of the stand is harvested' (CFS, 1999). In this sense, partial cutting is a generic term, which refers to a whole range of treatments from clear-cutting with sparse, dispersed retention in which a few merchantable stems are left on site, to single-tree selection systems where the very evidence of a harvesting treatment might be too subtle to be noticed by an untrained eye.

Silvicultural practices that find their origins in natural disturbance emulation emerged conceptually in the 1990s (Attiwill, 1994; Bergeron and Harvey, 1997; Angelstam, 1998). Although NDB treatments can take on the forms of other partial cutting practices, including those described in this section, certain adaptations may be required to ensure maintenance or retention of specific ecosystem attributes, such as large live, dying and dead trees. NDB silviculture is distinguished by the underlying premise that, by integrating elements of natural dynamics and disturbance outcomes into silvicultural practices, ecosystem processes and characteristics that favour biodiversity, productivity and ecosystem resilience will also be maintained (Kuuluvainen and Grenfell, 2012). The dynamics of secondary disturbances and successional dynamics in particular provide a natural reference for harvesting a portion of mature trees in anticipation of imminent mortality from non-stand-replacing events. Moreover, the concept encompasses the notion of integrating stand-level interventions to attain forest-level (ecosystem-scale) biodiversity objectives (Bergeron et al., 2002). While conceptually and operationally less mainstream than variable retention, NDB silviculture has received considerable attention in the literature and is being tested operationally in a number of provinces and boreal ecosystems (Brais et al., 2004; Man et al., 2008a,b; Kuuluvainen and Grenfell, 2012).

Table 1 Particularities of North American boreal forests

Attributes	Characteristics	References	
Climate	Very cold winters with short, mild-to-hot summers. Annual air temperatures range between –50°C and 30°C+. Generally moderate-to-low annual precipitation (400–900 mm year ⁻¹ in western and central Canada; up to 1500 mm in the eastern coastal sections)	Baldocchi <i>et al.</i> (2000)	
Recent historical fire cycles	111–500 years in eastern boreal and 71–97 years in western boreal forest	Bergeron et al. (2004)	
Species	Few tree species. Dominated by conifers: lodgepole and jack pine, white and black spruce, balsam fir, eastern larch, eastern white cedar; broadleaved species: trembling aspen, balsam poplar, white birch	Burton <i>et al</i> . (2003)	
Growing season	Less than 120 days in most areas; some possibility of frost throughout summer in many regions	Baldocchi et al. (2000)	
Natural disturbances	Large, high-severity crown fires have greatest influence on landscape mosaic and forest age; periodic insect outbreaks affect vast areas; windthrow and other secondary disturbances are more local or regional in scale	Bergeron (2000); Burton <i>et al</i> . (2003)	
Soils	Poorly drained organic sites and upland sites ranging from fine-textured to coarse-grained and sandy. Soils in the continuous conifer (Mesoboreal) zone in particular tend to have acidic, organic surface horizons and nutrient-poor mineral horizons. Slow decomposition leads to formation of a thick organic layer on poorly drained sites and lowlands that have not burned for \approx 150+ years	Landsberg and Gower (1997); Baldocchi et al. (2000); Simard et al. (2007)	

Table 2 A simple classification of partial cutting treatments operationally applied in the Canadian boreal forest

Partial cutting system	Description
Commercial thinning	Largely applied in even-aged, post-fire stands of black spruce and jack pine and second growth stands of balsam fir. Generally precedes final cut by 15–20 years (Barbour <i>et al.</i> 1994)
Regular shelterwoods	Two- or three-pass harvests to establish a continuous regeneration layer, followed by final cut once regeneration is established (Bouchard 2009)
Diameter-limit cutting	Applied largely in old, uneven-sized or irregular black spruce-dominated stands with well-stocked sapling layer; called CPPTM in Quebec; HARP in Ontario (Thorpe <i>et al.</i> 2007; Riopel <i>et al.</i> 2010)
Variable retention	Increasingly imposed by new forest regulations. Primarily biodiversity-, habitat- and other forest-services-related objectives. Retention of mature trees in dispersed or aggregated patterns, inspired by natural disturbance patterns (Bladon <i>et al.</i> 2008)

CPPTM = 'Coupe avec protection des petites tiges marchandes' (cutting with protection of small merchantable stems); HARP = harvesting with advance regeneration protection.

Because partial cutting includes a broad range of treatments, we provide an overview of those operational treatments that are most commonly used in the Canadian boreal forest (Table 2). This overview covers four forms or categories of partial cutting and therefore is not exhaustive; nor does it present partial cutting treatments in terms of specific silvicultural systems or even-, uneven- or multi-cohort management. The review that follows this section does include mention of other experimental treatments such as selection systems adapted to boreal conditions.

The use of 'commercial thinning', in the eastern boreal forest in particular, has increased over the last 25 years with the arrival of smaller, more agile and adapted multifunctional (short-wood) harvesting equipment that works well in dense, premature or mature stands with relatively small stems. Commercial thinning is generally applied in regular-structured, post-fire stands of jack pine and black spruce or post-spruce budworm/second growth stands of balsam fir with the objective of reducing density and competition and promoting diameter and volume growth of residual stems (Barbour *et al.*, 1994; Laflèche *et al.*, 2013). From an NDB silviculture viewpoint, thinning from below, which focuses removal on smaller diameter stems, often of low vigour, could be considered an analogue to density-dependent self-thinning in the stem-exclusion stage of stand development (Harvey and Brais, 2007). In contrast and depending on intensity of removal, thinning from above may resemble stand break-up or disturbances such as windthrow, ice storms or insect outbreaks (O'Hara and Ramage, 2013). First-entry thinning intensities in eastern boreal forests range from ~25 to 40 per cent of basal area (BA) and minimum harvest volume for commercial thinning in Quebec is \sim 50 m³ ha⁻¹. Because general use of the practice is relatively recent, most treated stands have not undergone more than one initial intervention (Tremblay and Laflèche, 2012). Moreover, because commercial thinning generally precedes final removal of residual stems by 10–20 years, beneficial habitat effects of this type of partial cut are of short duration and may, in some cases, be deficient in terms of maintaining habitat conditions suitable for some forest-dwelling species (i.e. Lycke *et al.*, 2011).

As elsewhere, protection and establishment of a regeneration layer is the primary objective of 'regular shelterwood systems' (Raymond et al., 2013). In general, an initial regeneration cut that removes \sim 40-50 per cent of volume is followed 10-20 years later with a final cut (or a second partial removal before final cut) once a well-stocked regeneration layer has been established. To a certain extent, with some permanent retention, this regime could be considered to mimic waves of mortality following a fire of variable intensity in which initial mortality affects forest patches that are severely burned and subsequent mortality occurs over a longer period in less-severely burned or untouched residual patches. In western Canada, two- and three-pass shelterwood harvesting in aspen-dominated stands has generally been aimed at gradual removal of canopy aspen stems while protecting and favouring recruitment and growth response of understorey to co-dominant white spruce stems (Lieffers et al., 2003).

A form of 'diameter limit partial harvesting' treatment called HARP (harvesting with advance regeneration protection) in Ontario (Thorpe et al., 2007) and CPPTM ('Coupe avec protection des petites tiges marchandes'/cutting with protection of small merchantable stems) in Quebec (Riopel et al., 2010) has been developed in response to concerns related to the poor adaptation of clear-cutting in irregular and uneven-structured black spruce (and other) stands in the central and eastern boreal forest (Bergeron et al., 1999; Groot, 2002; Cimon-Morin et al., 2010). The HARP/CPPTM system has been tested and is now operationally practised in irregularly structured stands that present dense sapling and small merchantable stem (10–14 dbh classes) layers that are targeted for protection (Riopel et al., 2010). By focussing harvesting on the larger diameter classes in irregularly structured stands, the treatment results in removals of 60-90 per cent of merchantable stand volume while leaving dense regeneration and sapling layers, some small-diameter merchantable stems and considerably more vertical structure and horizontal cover than conventional clear-cutting or careful logging systems that remove all merchantable stems. Moreover, because most of the harvested volume is concentrated in a relatively small number of larger diameter stems, this partial harvesting treatment has proven to have advantages in terms of unit processing costs both in the forest and mill.

Diameter-limit harvesting in temperate forests has long been considered an inappropriate forest practice because of its detrimental effects on medium- to long-term wood yields and value (particularly if practiced as selective high-grading) and on natural stand structure, through the elimination large-diameter stems (Angers *et al.*, 2005; Nyland, 2005). While no long-term studies of its use exist for the boreal forest, the fact that only the largest trees are harvested could make the practice subject to the same criticisms. This said, results of short-term studies tend to indicate that, compared with clear-cutting, HARP/CPPTM provides greater residual forest structure and superior habitat for some forest-dwelling taxa (Ruel *et al.*, 2013). In the context of NDB silviculture, HARP/CPPTM may be most closely associated with insect outbreaks if highest mortality occurs in dominant canopy stems or to severe wind disturbance if the tallest, most exposed trees in old, irregular-structured forests are most susceptible to snapping and blowdown.

'Variable retention' harvesting is in itself considered an element of NDB management. It can take on a variety of forms but generally involves retention of commercial-sized trees in dispersed or aggregated patterns to augment (compared with clear-cuts without retention) post-harvest structural heterogeneity in harvest blocks and at broader spatial scales (Gustafsson et al., 2012; Lindenmayer et al., 2012). Variable retention was introduced in the late-1980s as a key element of the then-emerging paradigm of new forestry and concerns related to biodiversity, wildlife conservation and maintenance of an array of ecosystem functions (Franklin, 1989). To some extent, partial harvesting and variable retention may actually be considered as synonymous although partial cutting is certainly an older notion (for example, see Lorimer, 1983) and might be considered more of an extension of historical treatments applied with specific (and more conventional) silvicultural objectives in mind. The other major distinction is that the two terms may be considered as inverse images of the same treatment in that, while partial cutting generally refers to what is removed in harvesting, variable retention focuses on what is left - hence the notion of biological legacies.

Partial cutting in the boreal forest: some documented benefits

While this paper focuses on constraints of partial harvesting in the boreal forest, we feel it is important to provide at least a brief treatment of some of the benefits that have been documented in the literature. Much of the research undertaken in recent experimental trials established in different parts of the Canadian boreal forest has focussed on the impacts of partial cutting on biodiversity (Thorpe and Thomas, 2007). To this end, there is clear evidence both from integrated and species-specific studies that by leaving more residual stand structure compared with clear-cuts, partial cutting maintains more favourable habitat attributes for a variety of organisms (Fenton et al., 2013; Ruel et al., 2013). Specific studies have shown positive effects of partial cutting on birds (Norton and Hannon, 1997; Lance and Phinney, 2001; Harrison et al., 2005; Vanderwel et al., 2007), vertebrates (Fisher and Bradbury, 2006; Vanderwel et al., 2009; Fauteux et al., 2012), invertebrates (Work et al., 2004), vascular plants and mosses (Bradbury, 2004; Fenton and Bergeron, 2007; Haeussler et al., 2007) and lichens (Boudreault et al., 2002). Numerous studies have documented similar benefits in Fennoscandian boreal forests (see reviews of Kuuluvainen, 2009; Gustafsson et al., 2010; Kuuluvainen et al., 2012).

Partial cutting has also been shown to increase residual tree growth in a variety of boreal forest types and following various treatments; for example, following diameter-limit (HARP/CPPTM) harvesting in black spruce stands (Thorpe *et al.*, 2007), following low commercial thinning in black spruce and jack pine stands (Goudiaby *et al.*, 2012), and in eastern mixedwood stands (Man *et al.*, 2008a,b; Gendreau-Berthiaume *et al.*, 2012). As well, in mature aspen-dominated stands of the eastern boreal mixedwood, both light low thinning and heavy crown thinning have been shown to increase residual growth of dominant aspen (A.K. Bose, B.D. Harvey and S. Brais, in preparation). Partial cutting can also maintain mixedwood compositions while favouring advance regeneration of softwood species in both eastern (Prévost and Pothier, 2003; Man *et al.*, 2008a,b; Brais *et al.*, 2013) and western boreal mixedwoods (Lennie *et al.*, 2009; Gradowski *et al.*, 2010). In black spruce forests of Ontario, strip and patch cut treatments were shown by Groot and Carlson (1996) to decrease frost damage of understorey white spruce regeneration compared with a clearcut treatment. Finally, in at least one study in aspen-dominated mixedwoods (Brais *et al.*, 2004), partial cutting has also been shown to increase forest floor nutrient concentrations, although this is apparently not the case in all situations (Frey *et al.*, 2003).

Besides these direct organism-, stand-, site- and habitat-level benefits of partial cutting, at a broader scale, the role of NBD silviculture in maintaining natural ecosystem-level diversity in the Canadian boreal forest has found substantial resonance in the scientific community (Gauthier *et al.*, 2009). Essentially, it is argued that, deployed as an integral part of a landscape- or forestlevel management regime, partial harvesting can contribute to maintaining much of the natural character of forest landscapes that have been generated under natural disturbance regimes (e.g. Kneeshaw *et al.*, 2011). An important component of this natural character is the presence of structurally complex forests of mid- to late- successional species. The anticipated benefits of such an approach include the increased likelihood of maintaining indigenous biodiversity and increasing ecosystem resilience to environmental stresses, including those related to climate change.

Finally, while there appears to be consensus concerning the short-term economic advantages of clear-cut harvesting compared with any system that leaves merchantable stems on site, two recent studies have introduced noteworthy caveats to this long-held paradigm: Ruel *et al.* (2013) suggest that partial harvesting – even 33 per cent selection harvesting – in uneven-aged conifer stands is profitable when economic analysis is considered over a long time frame and, based on modelling of different management scenarios, Etheridge and Kayahara (2013) conclude that partial harvesting can potentially increase allowable cut compared with a clear-cut-only regime if certain forest-level ecosystem constraints are imposed.

Responses to partial cutting: the need for nuance

The above-mentioned and other studies provide clear evidence of the utility of incorporating partial cutting practices into boreal ecosystem management regimes that include objectives beyond maximum sustained wood yield. However, it has become increasingly apparent that (1) tree- and stand-level responses both to natural and anthropogenic disturbances can vary considerably between regions, and among species, site conditions and disturbance intensities and (2) outcomes are not universally positive. Therefore, interpretations concerning short- to long-term effects of partial cutting must be made cautiously and generalizations avoided.

A major challenge for forest managers and ecologists is therefore to understand how stand structure and composition develop over time following disturbance (Coates, 2002). Success of partial cutting treatments depends on three factors or ecosystem processes: recruitment of desirable species, growth of residual and recruited stems and mortality. The literature review in the following sections treats questions related to specific indicators of boreal partial cutting outcomes and, ultimately, success of treatments: residual mortality (or inversely, survival), growth response of trees and saplings, dynamics related to recruitment, site and stand productivity and effects on wood properties.

Partial cutting and residual tree mortality

This section reviews a number of cases and causes of residual tree mortality in specific stand and treatment conditions of the Canadian boreal forest and complements studies by Thorpe and Thomas (2007), Bladon *et al.* (2008) and Lavoie *et al.* (2012). In an early partial harvesting trial at Date Creek, British Columbia, Coates (1997) observed windthrow levels of >10 per cent of those in controls 2 years after treatments. He argued that, from a silvicultural viewpoint, a post-harvest mortality rate of 10 per cent of residual trees (compared with controls) constituted an upper limit beyond which a partial cutting treatment may necessitate management intervention or be considered a failure. Although this threshold is not necessarily universal and could be time-adjusted, it serves as a useful reference for the following review.

Reduced stem density in stands treated by partial cutting combined with increased wind penetration into residual stands affect tree stability and can induce mechanical damage to individual trees and result in uprooting or stem breakage and, ultimately, tree death (Ruel *et al.*, 2003). Moreover, increased tree sway and evapotranspiration as a result of higher wind speeds and exposure can impair stem conductivity by restricting water supply to leaves (Liu *et al.*, 2003) and produce die-back symptoms including loss of foliage and tree vigour. Indeed, death of standing stems in the first decade following partial cutting can account for as much mortality as windthrown stems. While low-intensity partial cuts presumably influence water table levels less than high intensity partial harvesting or clear-cuts (Pothier *et al.*, 2003), it is possible that higher soil water levels following treatments also influence tree vigour and survival.

Even before considering the influence of the intensity and configuration of a partial cut treatment, the degree of damage incurred on residual trees will depend at least partly on a combination of pre-existing conditions that act at different scales. These include (1) individual tree characteristics such as species, age, health, wood density, total height, taper, crown dimensions, social status and rooting characteristics, (2) preharvest stand characteristics including stem density and crowdedness, vertical and horizontal structure and site characteristics and (3) supra-stand-level factors including regional climatic particularities such as predominant wind conditions and punctual extreme events, topographic position, stand exposure and wind fetch, which can be influenced by proximate roads, adjacent harvesting, etc. (Wang *et al.*, 1998; Ruel, 2000).

Working in predominately coniferous stands treated by diameter-limit partial cutting (HARP/CPPTM) in Quebec, Riopel *et al.* (2010) showed that the probability of stem loss by windthrow following this treatment is largely dependent on pre-harvest stand characteristics. Specifically, merchantable BA, and stem density, and the relative proportions of wind-susceptible and

wind-resistant species all influence vulnerability to windthrow. For example, Riopel et al. (2010) observed a positive relationship between pre-treatment BA of stands and the extent of windthrow following diameter-limit harvesting. In conifer-dominated stands of the eastern boreal, high BAs are generally associated with (1) high stem density (and not necessarily high individual stem volumes) and (2) younger, more regularly structured stands. High merchantable BA tends to correspond with low stem densities in the sapling and regeneration layers. High residual mortality rates (>25 per cent) were observed by Riopel et al. (2010) in stands with lower pre-harvest sapling densities (<1500 stems ha⁻¹), and this was especially true in spruce-fir stands with higher merchantable BAs and a high component of jack pine in the overstorey. According to Elie and Ruel (2005), because of differences in jack pine and black spruce rooting systems, the presence of jack pine negatively affects the mechanical resistance of black spruce to windthrow, whereas in pure stands, black spruce tends to develop greater mechanical support as a result of interlocking root systems among trees.

In dense stands, stems in the understorey are dependent on the protection and support of neighbouring trees for their mechanical strength against wind. In contrast, in open stands with uneven-size distributions, stems that are continuously subjected to wind exposure and snow burden develop their stability (or do not and succumb) prior to harvest and will therefore present less risk of windthrow following diameter-limit cutting. Riopel *et al.* (2010) also found that dominant stems were more susceptible to wind-throw after diameter-limit partial cutting than co-dominant or suppressed trees because of their greater exposure to the wind.

Harvest intensity - or retention level - has been shown to influence post-treatment mortality in both coniferous and mixedwood boreal forests in Canada (MacIsaac and Kryaier, 2009; Solarik et al., 2012). In one of the earliest documented partial cutting experiments in fir-dominated mixed stands in the eastern boreal forest, Hatcher (1961) noted a clear threshold at ~40 per cent BA removal, above which residual tree mortality increased steadily from \sim 10 to 60 per cent at 60 per cent BA removal, 5 years following treatments. More recently, working in black spruce - balsam fir stands in Quebec, Cimon-Morin et al. (2010) compared mortality following clear-cutting, diameter limit (HARP/CPPTM) and two variants of selection cutting (ca. removal of 94, 85, 44 and 43 per cent of merchantable BA, respectively). Three years after treatments, while absolute mortality was generally higher following selection cutting, largely due to higher residual BAs, relative mortality was highest (39 per cent) in the diameter-limit treatments, whereas values in selection cuts (22 and 28 per cent) were not significantly different from uncut controls (14 per cent). In another study comparing dispersed and group retention in two regions of boreal Quebec, Lavoie et al. (2012) noted little difference in mortality rates between dispersed and group retention in the northeastern region and suggested that higher windthrow rates after dispersed retention in the northwestern region may have been caused by several factors including flatter topography, finer-textured soils and more regular-structured stands composed mostly of shade-intolerant pioneer species.

Similarly, in aspen-dominated boreal mixedwoods, generally characterized by a fairly regular structure, the level of retention has been shown to influence survival of residual trees. For example, 4 years after similar, relatively high retention (50 per cent) cutting treatments in mixedwood stands in Ontario, residual mortality varied between 6 per cent of stems (Rice and Man, 2011) and 17 per cent of BA (MacDonald and Thompson, 2003). In contrast, working in mixedwood forests with very low structural retention (10 per cent) in Alberta, Bladon et al. (2008) observed 28 per cent annual mortality of residual trees in the first 5 years following harvesting. In another study in Alberta, MacIsaac and Krygier (2009) reported on a variety of one- and two-pass strip shelterwood regimes aimed at reducing windthrow of residual white spruce in aspen-dominated stands with understorey spruce. While results of the study need to be interpreted with nuance, maintaining permanent retention bands of at least 5-m width between cut strips that were under $2.5 \times$ tree height appeared to successfully limit windthrow. Maximum tree height of white spruce – reported as 7 m, post-harvest stem inclination (threshold of 15°) and distance from aspen shelter were also reported as determinants of windthrow mortality. Other examples of residual tree mortality after partial cutting are presented in Table 3.

Differences in species' physiological and mechanical characteristics also influence susceptibility to windthrow following partial cutting (King, 1986; Elie and Ruel, 2005). Higher allocation to height rather than diameter growth is partly responsible, along with generally lower wood densities, for the relative vulnerability of shade-intolerant species to windthrow (Givnish, 1995). For example, shade-intolerant species such as jack pine, red pine (*P. resinosa*) and trembling aspen have been found to be particularly susceptible to wind damage in the boreal forest of Minnesota (Rich *et al.*, 2007).

Windthrow rates are also likely affected by tree and stand health and McLaughlin and Dumas (1996) outlined four principal pathological risks associated with partial cutting in boreal mixedwood stands. These include pre-existing stem decay resulting from infection of false tinder fungus (Phellinus tremulae) in aspen stems, blowdown of residuals with root decay, build-up of inoculum of Armillaria root rot as a result of its colonization in stumps and roots of harvested trees and rot and decay in trunks resulting from wounding during harvesting or subsequent mechanical treatments. Among more shade-tolerant boreal conifers, balsam fir is particularly susceptible to windthrow and snapping (Meunier et al., 2002). Balsam fir is prone to a variety of heart, root and butt rots whose infection rates and effects on wood structure, quality and resistance tend to increase with age (Whitney and MacDonald, 1985; Peterson, 2004). This trait of balsam fir and the generally short lifespan of the species present specific limitations to considering continuous cover silvicultural regimes in which long-term tree stability and species longevity are key to treatment success.

Growth response of residual trees and saplings following partial cutting

Residual trees

Individual tree growth response following partial cutting will depend to some degree on its social status at time of treatment as well as its immediate neighbourhood environment following treatment. Assuming that the relative proportion of non-photosynthetic biomass influences maintenance cost and resource allocation to root growth for mechanical support, Kneeshaw *et al.* (2002) suggested that larger residual trees were more prone to growth stagnation because of their higher non-photosynthetic biomass. Depending on the intensity and the nature of tree removal – Table 3 Summary of documented cases of residual tree mortality following partial cutting in the Canadian boreal forest

Forest type, province/territory	Causal factors	Partial cutting systems	Mortality	References
Mixedwood, Ontario	Windthrow	50% structural retention	17% decrease in residual BA in first 4 years after harvest	MacDonald and Thompson (2003)
Balsam fir, Quebec	Windthrow	Shelterwood	5.6–18.6% stems damaged 6 years after harvest	Ruel et al. (2003)
Black spruce, northeastern Ontario	Logging damage and windthrow	Diameter limit	Residual-tree mortality increased 12.6 times compared with pre-harvest level 1 year after harvest	Thorpe <i>et al</i> . (2008)
85 yr old Aspen-dominated mixedwood, northwestern Quebec	Senescence	Low thinning, 33% removal	Residual mortality of 17% over 6 years compared with 18% in controls	Harvey and Brais (2007)
85 yr old Aspen-dominated mixedwood, northwestern Quebec	Senescence and post- harvest environmental stresses ¹	High thinning, 61% removal	Residual mortality of 32% over 6 years compared with 18% in controls	Harvey and Brais (2007)
Aspen-dominated mixedwood, Alberta	Moisture stress and windthrow	10% structural retention	Annual mortality of residual balsam poplar (10.2%), birch (8.7%), aspen (6.1%) and spruce (2.9%) first 5 years after harvest	Bladon et al. (2008)
Mixedwood, southeastern Yukon	Windthrow	Structural retention	At least 17.3% retained stems lost in first 5 years after harvest	Smith (2010)
Black spruce, northeastern Quebec	Windthrow	Diameter-limit (>14 cm dbh) and selection cuts	Relative mortality of 39% in diameter-limit; 22– 28% in selection cuts and 14% in controls	Cimon-Morin et al. (2010)
Mixedwood, northeastern Ontario	Windthrow	50% structural retention cut in alternating 10-m-wide strips	6% of residual stems dead after 4 years; (1.2% in controls)	Rice and Man (2011)
Black spruce and mixedwood, northwestern Quebec and North Shore, eastern Quebec	Windthrow	aggregated and dispersed structural retention	41 and 36% stems wind thrown in group and dispersed retention, respectively, in northwestern Quebec and 17.3 and 28.0% in North shore region.	Lavoie <i>et al</i> . (2012)
90 yr old Aspen-dominated mixedwood, northwestern Quebec	Possibly windthrow, senescence	Low thinning 33% removal	Net aspen and birch mortality 16 and 45% over 9 years and 18 and 49% over 12 years, respectively	Bose (unpublished data)
90 yr old Aspen-dominated mixedwood, northwestern Quebec	Possibly windthrow and post-harvest environmental stresses ¹	High thinning 61% removal	Net aspen and birch mortality 30 and 56% over 9 years and 39 and 58% over 12 years, respectively	Bose (unpublished data)

See Table 2 for treatment explanations. ¹Environmental stresses refer to sudden increases in temperature, wind speed and evapotranspiration demand after partial cutting.

crown thinning, low thinning, diameter-limit cut, gap cut, etc. – partial overstorey removal can be expected to initially reduce competition for growing space, light, soil nutrients and moisture (Smith *et al.*, 1997; Schneider *et al.*, 2008). Despite the increase in resource availability, the lack of a post-harvest release effect on residual trees has been documented by several authors (Urban *et al.*, 1994; Bladon *et al.*, 2008; Vincent *et al.*, 2009; Goudiaby *et al.*, 2012).

Abrupt and particularly large changes in canopy opening expose residual trees to environmental stresses resulting from increased temperature extremes, radiation (Carlson and Groot, 1997; Comeau et al., 2003), increased evapotranspiration rates (Bladon et al., 2006) and, as mentioned, increased wind speed and penetration into residual stands (Ruel et al., 2003; Vincent et al., 2009), all stresses that can cause initial growth stagnation. Here we interpret initial growth stagnation as an apparent, and usually temporary, decrease or absence of release effect in radial and/or height growth rate during the post-harvest period. To our knowledge, this phenomenon has not been reported for jack pine (Tarroux et al., 2010) or trembling aspen (Man et al., 2008a,b), possibly due to the presence of extensive grafted and clonal root systems in these species. Residual trees invest in root arowth partly to balance the increased evaporative demand associated with abrupt increased exposure of foliage, and it could be speculated that species with connected root networks need to invest less in root growth for mechanical support and soil moisture uptake.

Besides effects induced by direct physical injury to residual tree boles or root systems (Thorpe et al., 2008), growth stagnation is generally associated with high intensity partial cutting. For example, balsam fir, white birch (Bladon et al., 2006) and trembling aspen (Bladon et al., 2007) all experienced water stress after partial cutting with 10 per cent structural retention in mixedwood stands of Alberta. Exposed to increased evaporative demand after heavy partial canopy removal, residual trees must reduce stomatal opening to prevent excessive xylem cavitations. Because species like balsam fir and white birch do not have strong stomatal control, they are more susceptible to moisture stress and residual tree dieback after low-retention harvesting (Bladon et al., 2006). Goudiaby et al. (2012) observed a lower diameter growth rate in black spruce immediately following heavy commercial thinning compared with untreated controls in northwestern Quebec, and growth stagnation in black spruce following 36-42 per cent stem removal has also been observed by Vincent et al. (2009). However, negative effects of partial cutting on growth are often likely to be short-lived (Goudiaby et al., 2012). For example, Soucy et al. (2012) reported a 33 per cent increase in merchantable volume growth (compared with controls) 15 years after heavy thinning (50 per cent removal) in black spruce stands in Quebec.

Winter insolation might be a uniquely boreal injury associated with partial cutting (Riopel, 2012). This phenomenon occurs as a result of repeated and abrupt decreases in trunk surface temperatures following the opening up of a stand by partial cutting. During sunny winter days, solar radiation warms the exposed trunk surface through the day. If air temperatures are very cold, sudden interception of direct solar radiation, either by passing clouds or the setting sun, can cause a rapid drop in trunk surface and sub-surface temperatures. This abrupt cooling, repeated over many cycles, causes progressive vertical bark fissuring (length ca. 0.4-4 m), usually on the southwest face of the exposed lower trunk, and eventually death of the phloem, cambial and sub-cambial cells. Ten years after diameter-limit harvesting, Riopel (2012) found \sim 12 per cent of residual stems incurred winter insolation and that balsam fir was the most susceptible species. While no short-term tree mortality was linked directly to this process, wood rot was generally associated with the vertical scarring and insect galleries were also observed indicating that winter insolation affects growth and wood quality of part of the stem and, in the longer term, reduces stem resistance to wind breakage and creates points of entry for fungal infection and other parasites.

Saplings

Messier et al. (1999) summarized a host of factors that influence a seedling or sapling's potential to acclimatize to a new environment. These include its capacity to adjust photosynthetic and respiratory rates, leaf area indices, hydraulic architecture, shoot and crown architecture and balance between above- and belowground resource allocation. Tree density and understorey light interception following partial cutting are important factors in controlling the growth of seedlings and saplings (Oliver and Larson, 1990; Groot et al., 2009; Beaudet et al., 2011) and an growth response of advanced regeneration following harvesting will depend in part on configuration and sizes of the created gaps as well as species' functional traits (Ruel et al., 2000; Beaudet et al., 2011). Characteristically, species that can survive and grow in lowlight conditions (prior to harvest) do so by maintaining low respiration rates and individuals may not always be able to modify respiration rates rapidly following harvesting. Moreover, increased radiation, evaporative demand, temperatures and wind speeds are sources of stress in surviving shade-tolerant saplings and can create a negative carbon balance by increasing respiration rates (Kneeshaw et al., 2002).

Following canopy opening, saplings, like canopy trees, initially tend to allocate more resources to root growth to counterbalance heightened evaporative demand of exposed foliage and increase mechanical support against wind (Urban et al., 1994; Kneeshaw et al., 2002). Sapling growth stagnation following release has been reported in several boreal silvicultural trials; for example, growth stagnation in balsam fir was observed by Bourgeois et al. (2004) 1 year after heavy partial cutting (61 per cent BA removal) in mixedwood stands in western Quebec, but not after lighter partial cutting (33 per cent BA removal). A 2- to 3-year growth stagnation in residual saplings was also observed by Kneeshaw et al. (2002) in a conifer forest of central British Columbia. Groot and Hökkä (2000) also observed initial growth suppression of black spruce regeneration following overstorey removal in peatland black spruce forests in Ontario. Similar results have been documented with conifer saplings/seedlings by Ruel et al. (2000) and Parent and Ruel (2002) in coniferous forests in Quebec.

In the eastern Canadian boreal forest, regeneration densities of aspen (primarily of sucker origin) have shown negative responses to higher canopy retention (>50 per cent BA or volume) (Prévost and Pothier, 2003; Man *et al.*, 2010; A.K. Bose, B.D. Harvey and S. Brais, in preparation), although positive responses in height growth were observed at similar retention levels (Man *et al.*, 2008a,b; Pothier and Prévost, 2008). At the same time, several authors have suggested that lower canopy retention (<30 per cent BA or volume) might limit recruitment of shade-tolerant conifer saplings by favouring shade-intolerant aspen and shrub

species (Prévost and Pothier, 2003; Solarik *et al.*, 2010; A.K. Bose, B.D. Harvey and S. Brais, in preparation). Beaudet *et al.* (2011) further emphasized this light level – growth response relation by modelling different intensities and configurations of partial cutting in eastern boreal mixedwoods and showing that, for the same harvest level, configuration of canopy opening can be manipulated to attain light thresholds that favour shade-tolerant species and disfavour shade intolerants.

Effects of partial cutting on regeneration recruitment

Understorey competition

Whatever the forest type, the quantity and configuration of canopy stems left following partial cutting affects understorey light levels. If natural regeneration establishment and growth were simply a question of shade tolerance of canopy species, residual cover could be manipulated to generate optimal understorey light levels for recruiting desired species (Beaudet *et al.*, 2011). However, forest stands on many site types contain characteristic species – woody or ericaceous shrubs and grasses in particular – that can survive under low-light levels in the understorey, often in low densities, but respond aggressively to openings in the canopy (Mallik, 2003; MacDonald *et al.*, 2004; A.K. Bose, B.D. Harvey and S. Brais, in preparation). Species that regenerate from seed banks such as raspberry (*Rubus idaeus*) and cherries (*Prunus* spp.) present similar challenges.

The presence and response to canopy opening of these problematic species constitute a potential constraint to regeneration establishment and to growth and survival of pre-established seedlings and saplings following partial cutting on some sites. Natural canopy gaps can induce vigorous sprouting in woody shrubs such as mountain maple (Acer spicatum) and beaked hazelnut (Corylus cornuta) and generate thick multi-layered subcanopies that inhibit growth of shade-tolerant conifers (Kneeshaw and Bergeron, 1998). Hobson and Schieck (1999) observed higher shrub sprouting after forest harvesting than after forest fire in Alberta, and several studies have reported continuous shrub growth and reduced growth of conifer regeneration following partial cutting in eastern boreal mixedwoods (e.g. Bourgeois et al., 2004; MacDonald et al., 2004; Man et al., 2008a,b). MacDonald et al. (2004) found that advanced conifer regeneration was overtopped by woody shrubs within 5 years after partial cutting. In the western mixedwood, bluejoint grass (Calamagrostis canadensis) presents serious forest renewal challenges for regeneration and growth of both white spruce and aspen (Lieffers et al., 1993; Lieffers and Stadt, 1994; Landhäusser et al., 2007), and heavy presence of beaked hazelnut has been shown to reduce density of aspen suckers (Mundell et al. (2007).

In black spruce stands situated on poor-to-medium quality sites, ericaceous shrubs such as *Kalmia* and *Rhododendron* spp., when present in the understorey, typically respond aggressively following clear-cutting and can reduce growth of black spruce regeneration by competing for nutrients or changing soil biochemical conditions (Inderjit and Mallik, 1996). Depending on the degree of forest opening, these dynamics may occur following partial cutting as well, as suggested by Hébert *et al.* (2010).

Seedling recruitment

Because harvesting intensity and configuration determine residual tree density and proximity of trees within cut blocks (individual stems and patches) and in surrounding unharvested areas, they influence availability of seed sources, seed dispersal distance and the distribution and quality of seedbeds (Greene et al., 1999; Asselin et al., 2001). While Sims et al. (1990) stated that conifer seeds disperse up to 160 m and Zasada (1971) suggested white spruce seeds travel between 100 and 300 m from parent trees in open environments, Solarik et al. (2010) found that regeneration of white spruce was greatest within 60 m of seed sources. In partially cut stands - particularly those with high retention levels - this range is likely even lower, compared with clear-cuts, because of reduced wind speeds below crown heights and the physical barrier presented by residual tree crowns. In this regard, the guantity and distribution of residual patches of potential seed sources, notably for non-serotinous conifers, in both clear-cuts with retention and variants of partial cutting are key to post-harvest natural regeneration of cutover areas.

This concern should be interpreted differently for aspen for a number of reasons. First, because of their extreme light weight, aspen seeds may travel tens of kilometres in favourable wind conditions and therefore play less of a role in local regeneration (Laguerre et al., 2011). Aspen seed viability is also very short and seedbed quality, and microclimate conditions are critical to germination and germinant survival. Second, suckering from existing live root systems is the primary source of local aspen regeneration. Initial densities of aspen suckers have been attributed to a number of factors, most importantly pre-disturbance BA of mature aspen stems and the loss of apical dominance in individual trees as a result of disturbance (Frey et al., 2003). Therefore, if post-harvest recruitment of aspen is desired in stands where it is already present, less than more and aggregated rather than dispersed retention should be favoured (Prévost and Pothier, 2003; Gradowski et al., 2010). If, on the other hand, the objective is to minimize aspen recruitment, high dispersed retention (or low-intensity dispersed partial cutting) will have the effect of hormonally suppressing suckering and allowing less radiation to reach the shrub layer, a condition less conducive to sucker survival.

Once on the ground, seed viability for all boreal tree species is very short (<1 year for all species, possibly with the exception of white birch; D.F. Greene, personal communication, 2013). Partial cutting can be designed to provide seed sources and microclimatic conditions that are potentially favourable to establishment and growth of shade-tolerant species (Man et al., 2008a,b). However, if the surface organic layer is not sufficiently disturbed during or following harvest, suitable, well-distributed seedbed may be a limiting factor to successful natural regeneration (Greene et al., 1999). For example, partial harvesting in winter conditions frozen soils and thick snow - tends to produce poor seedbed, and this condition is exacerbated when low-ground-pressure multifunctional harvesters are used and trees are de-limbed in trails. Not only is this layer of fine- to medium- woody debris an extremely poor germination bed, but it constitutes a major physical barrier for any seed and seedling penetration.

Well-decomposed deadwood is also a favourable germination bed for a number of boreal species including white spruce, cedar and white birch (Simard *et al.*, 1998; Robert *et al.*, 2012). Moreover, moist, well-decomposed logs present on the forest floor can temporarily lose their quality as a germination substrate under microclimatic conditions of heightened radiation and wind exposure if partial cuts are too severe. This said, small canopy openings associated with small scale soil disturbances tend to favour establishment and growth of shade-tolerant conifer species over aspen (Lieffers *et al.*, 2003).

Influence of partial cutting on site productivity of lowland sites

Bottom slope and lowland sites in much of the boreal forest tend to be dominated by black spruce. In the absence of fire, these sites are characterized by accumulations of organic matter as a result of cold soil temperatures, low soil biological activity and favourable (wet) growing conditions for *Sphagnum* mosses and ericaceous shrubs such as *Kalmia* and *Rododendron*, all of which contribute to organic layer accumulations (Fenton and Bergeron, 2007).

Severe (and smouldering) wildfires on these sites reduce the thickness of organic layers and improve nutrient availability and growing conditions for regenerating stands (Simard *et al.*, 2007). In the absence of fire, site and forest productivity on lowland sites tend to decline in parallel with changes to stand structure from regular to irregular and uneven diameter distributions. Thus, on the same topographic situation, productive, regular-structured black spruce stands, often with feather moss species dominating the forest floor, can be found growing after severe fires, and old, low-productive, complex-structured black spruce stands, with a thick *Sphagnum* layer, generally occupy the same sites that have not burned for 150 or more years (Fenton *et al.*, 2009).

Disturbance, and in particular severe disturbance of the organic layer, is thus very important for maintaining or restoring the productivity of these sites and the contrast of these two conditions – young, productive, regular-structured versus old, low productive, complex-structured – frames the 'productivity-biodiversity dilemma' for partial cutting on these sites. In effect, young, productive, even-structured stands with relatively thin organic layers may be commercially thinned or treated by regular shelterwoods, probably without jeopardizing site productivity. In contrast, older, more complex-structured stands on sites with accumulated layers of *Sphagnum* present structures more conducive to diameter-limit (HARP/CPPTM) or other uneven-aged treatments but have low volumes and probably require severe site disturbance to re-establish higher site productivity levels.

High retention of canopy trees after partial cutting tends to have the effect of maintaining lower growing season soil temperatures compared with complete canopy removal by clear-cutting (Barg and Edmonds, 1999). Several studies in the claybelt region of northeastern Ontario and northwestern Quebec have shown that partial cutting of old, complex-structured black spruce stands on flat sites prone to organic matter accumulation does not disturb the organic layer enough to induce increase decomposition or favour natural regeneration (Fenton et al., 2005; Lavoie et al., 2005). These authors conclude that inadequate (low) disturbance on these sites during harvesting contributes to site paludification and longterm decline of stand productivity. Moreover, partial cutting on these poor, cold sites may not stimulate growth of residual trees if nutrients are limiting and the rooting environment remains cold and wet (Fenton and Bergeron, 2007). Heavy site preparation methods including ploughing and winter shearblading can counter these effects by either mixing organic and mineral layers or simply reducing the thickness of the organic layer (Fenton *et al.* (2009). However, these treatments are likely impractical in harvest blocks with high retention compared with conventional clear-cuts, and the relative gains in site productivity and eventual stand yields have yet to be validated.

Effects of partial cutting on wood properties of residual trees

Any factor that can change the growth pattern of a tree will likely also influence wood properties (Zobel and Buijtenen, 1989). To our knowledge, no studies exist that have looked at the effects on wood properties of a broad range of partial cutting intensities. Therefore, much of the anticipated effects of partial cutting can be cautiously inferred from commercial thinning experiments, if the specifics of treatment intensities, species, stand structure and bioclimatic factors are kept in mind. In general, by reducing competition among residual trees in even-aged stands, commercial thinning positively affects radial and volume growth rates, relative live crown length, tree taper of residual stems as well as characteristics such as branch length and knot size (Bamber and Burley, 1983; Kellomäki et al., 1999), tracheid length and width, and cell wall thickness (Mäkinen et al., 2002). These latter attributes are important for yield and quality of pulp and paper (Fuglem et al., 2003).

Wood density, a fundamental indicator of wood quality, has been shown to be compromised by commercial thinning, particularly following heavy removals (Barbour et al., 1994). In conifers, increased growth rate after thinning increases the growth of earlywood (lower density) relative to latewood (higher density) and delays the transition from juvenile to mature wood (Zahner and Oliver, 1962; Koga et al., 1997). Wood density reductions following thinning have also been reported for the Fennoscandian boreal forest; for example, Peltola et al., (2007) and Pape (1999) documented reductions of 2-8 per cent in Scots pine and Norway spruce following a range of thinning intensities. It should be noted though that these general tendencies do not occur in all cases: for example no significant influence of commercial thinning (10-52 per cent removal) was found on wood density and modulus of elasticity in black spruce forests over a 10-year period following treatments (Vincent et al., 2011).

The other, more visually evident effect of partial cutting on wood properties of residual trees is related to direct physical damage caused by logging. Particularly in partial cutting treatments other than aggregated retention, harvested trees can break branches and peel lengths of bark and sub-bark tissue of residual stems within the felling line. Machinery or felled trees can also cause severe damage to lower trunks and root systems of trees situated adjacent to hauling corridors. As discussed earlier, these injuries provide vectors for fungal infections and other pathogens that can cause decay (Bladon et al., 2008; Lavoie et al., 2012) associated with degradation of cellulose and lignin (reviewed by Ruel et al., 2010). While such injuries do not generally cause immediate mortality, they can affect the health, growth rate, wood quality and lifespan of affected trees - all important factors when most partial cutting regimes anticipate that the majority of these individuals will be alive and harvestable at some later stand entry.

Operational constraints of partial cutting in the boreal forest

The previous sections treated partial cutting in terms of potential limitations on tree- and stand-level responses. We recognize that a number of operational constraints also exist and that, for forest managers, these may constitute the most important considerations when deciding whether a specific treatment should be applied.

Stem densities of post-fire boreal forest stands are generally high through to maturity when density-dependent self-thinning gradually gives way to density-independent mortality resulting from tree senescence, disease, insect infestations or other secondary disturbance agents (McCarthy, 2001; Chen and Popadiouk, 2002). Unlike less dense, mature stands in temperate hardwood forests where harvesting machinery may be able to manoeuvre through a stand without systematically felling merchantable stems in its path, moving harvesters and forwarders or skidders in the boreal forest generally involves the use of clear, roughly parallel trails where 100 per cent of trees are systematically removed, just to provide passage for the machinery. Moreover, the smallsized merchantable stems (≥ 10 cm dbh) harvested in much of the boreal forest cost more per unit to process - in the forest, in transport and in mills - than large trees, a factor that inevitably influences the economic feasibility and application of partial cutting in the boreal forest. Note that we mentioned earlier how diameter-limit (HARP/CPPTM) cutting circumvents this constraint. However, even low-intensity (33 per cent) selection harvesting in the coniferous boreal forest is likely profitable when harvesting costs and tree dimensions of subsequent entries are taken into account (Ruel et al., 2013), or when other ecosystem services are quantified and entered into the financial equation (Anielski and Wilson, 2009).

Dense forests with small stems and a roughly even-size class diameter structure do not necessarily lend themselves well to rapid conversion to uneven-aged (or uneven-sized) structures treatable by selection systems (Kuuluvainen and Grenfell, 2012), largely because these stands often lack a dense, well-stocked reaeneration laver. Moreover, while even-aged treatments such as commercial thinning or regular shelterwoods may be appropriate partial cut systems for these types of stands, they cannot build multi-cohort vertical and horizontal structure in the short term. The presence of certain short-lived, shade-intolerant boreal species, notably trembling aspen and jack pine, also limits the use of high retention (or continuous cover) partial cutting approaches because of the regeneration constraints of low understorey light levels as well as cone serotiny in the case of jack pine (Ruel et al., 2000; Lieffers et al., 2003). Finally, because partial cutting removes less volume per hectare than clear-cutting, more forest area must be harvested if a given volume of wood is to be harvested on a regular basis. This obviously has important implications beyond the stand scale for road construction and maintenance, harvest costs and effects on wildlife and other ecosystem functions.

Management implications

Partial cutting and variable retention practices have a relatively short history of application in the Canadian boreal forest; they are

being tested and applied across Canada over a wide range of climatic, stand and site conditions and with an equally wide range of removal intensities. For these reasons, it is both difficult to suggest general recommendations and important to keep specific contexts in mind when interpreting reported findings. Posttreatment mortality is probably the greatest silvicultural concern regarding partial cutting and if we can make one generalization, it is that residual tree mortality tends to follow the degree of crown removal. Lower intensity partial cuts tend to result in lower mortality of residual stems than high intensity cuts (or low retention). In the short term, mortality of residual stems is mainly caused by windthrow but other environmental and pathogenic stresses may induce additional mortality over the longer term. Proper identification of site conditions and stand properties before harvesting is essential for tailoring treatments to specific conditions.

In silvicultural regimes that aim to maintain continuous cover or develop multi-cohort stand structures, treatment success depends on the complex interplay between treatment intensity, recruitment and growth of desired species and the response of competitive vegetation. Therefore, particular attention to understorey layers of both desirable and competitive species is important in considering long-term silvicultural scenarios. For example, adequate stem densities in the sapling and pole layers are essential for residual stand stability in diameter-limit harvesting (HARP/ CPPTM) in conifer forests and at least one source, MacDonald *et al.* (2004), recommends avoiding the use of partial cutting to promote conifer regeneration in eastern boreal mixedwoods where the understorey is dominated by tall shrub species.

Adequate retention and distribution of seed trees of target species can probably overcome seed dispersal limitations but site preparation treatments that expose and mix mineral soil with organic matter will greatly increase the probability of attaining sufficient stocking of natural regeneration. Unless adequate forest renewal funding is available or biodiversity objectives are a priority, partial cutting of low productivity, old growth black spruce forests on thick peaty phase or organic soils should probably generally be avoided in favour of conservation.

There has been some criticism that partial cutting and variable retention treatments, when applied without explicit guidelines, can and have resulted in abusive practices leading to stand conversion or degradation and inadequate legacies for biodiversity ('Take the best and leave the rest.'). For example, partial cutting practices in eastern boreal mixedwoods that favour removal of large spruce and greater residual of balsam fir and white birch stems is essentially a form of stand degradation. Moreover, from a NDB silviculture viewpoint, because spruce budworm outbreaks generally induce much higher mortality in fir than in spruce, such treatments can hardly be considered as a silvicultural analogue to budworm outbreaks. The same criticism could be made of partial cutting practices, including HARP/CPPTM, in black spruce-dominated stands with well-stocked understories of balsam fir if treatments result in stand conversion or even a significant increase in the proportion of fir. Finally, if variable retention legacies consist primarily of small stems and undesirable species such as birch that hold little value for biodiversity and are likely to die and fall in a few years, the treatment fails to achieve its purpose. This said, it is clear that regulatory measures should be imposed to ensure that best practices are adopted and applied to avoid abuse and meet explicit, desired outcomes.

Knowledge gaps and research avenues

Despite the real and anticipated potential benefits of partial cutting practices in boreal forest management, little is known about how partially harvested stands will develop over long time scales. Current knowledge is largely based on relatively recent studies and the very nature of partial cutting underscores the importance of resurrecting existing but inactive long-term silvicultural experiments and taking existing, well-designed but relatively short-term studies well into the future.

To date, commercial thinning followed by final cuts after 10–20 years has been the dominant form of partial cutting in the eastern Canadian boreal forest whereas variants of two- and three-pass shelterwoods have been applied in the western mixedwoods for at least two decades. However, little work has been done to document regimes that aim to develop uneven-sized or multi-cohort structured stands through variants of continuous cover or natural dynamics-based silviculture. It is clear that natural stand dynamics need to be well understood and documented because, in principle, they form the underlying reference for silviculture. Moreover, the pathological implications of increased use of partial harvesting in the boreal forest need greater scientific scrutiny.

Results from studies referenced in this review suggest that residual tree mortality, growth stagnation of residual stems (trees, saplings and seedlings) and recruitment limitations of desired species are the major concerns of partial cutting applications in the boreal forest.

Because residual tree mortality is probably the greatest concern, there is clearly a need to better understand response relationships among different boreal species situated in different social strata following different partial cutting intensities. Questions regarding mortality could benefit from ecophysiological approaches that aim to quantify species-specific photosynthetic responses, including saturation point, respiration, stomatal control and rooting characteristics, to increased solar radiation, evaporative demand and wind velocity. Ultimately, the development of regional and site-specific probability thresholds of tree mortality due to windthrow and other stress factors would contribute to tailoring cutting prescriptions to minimize losses due to mortality.

Regarding growth responses, including stagnation, again, applying ecophysiological approaches would help develop a better understanding of species' light requirements and crown structural plasticity at different stages of growth and provide underlying explanations to treatment responses. This too would contribute to better design of partial harvesting treatments for a variety of conditions and species mixes.

Like constraints associated with mortality and growth responses, limitations related to partial cutting and recruitment are complex and vary across stand and site types, treatment intensities and patterns and climatic conditions. Better understanding of how complex stand canopies, combined with gradients of forest floor disturbance, influence seed dispersal and sexual and vegetative reproduction of both desired and competitive species is a broad area of interest with lots of room for investigation. Ideally, this field could lead to scenarios of optimal spatial and temporal synchronicity of adequate seed input, suitable seedbed, and overstorey and understorey conditions to promote natural regeneration and growth under different stand types and climatic conditions.

While there is a need to acquire a greater understanding of the finer physiological aspects of individual tree response to partial cutting, there is also clearly a need to better comprehend how the system as a whole - that is, the forest stand and its components – functions under different conditions. Partial cutting treatments often generate complex spatial patterns of residual trees and canopy openings, as well as heterogeneous microenvironmental conditions. Although partial harvesting can offer a great deal of flexibility, anticipating how these different patterns will affect individual trees and stand-level response is not an easy task. In this regard, the real challenge for researchers and silviculturists is to bring together a huge quantity of knowledge and understand how all the parts interact and lead to various stand-level responses. Optimally tuning the various components of a harvest prescription (harvest intensity, control of DBH structure, spatial layout of trails, gaps, etc.) in specific stand conditions is a case in point for the emerging paradigm of managing for complexity. However, field experiments are intrinsically limited in the number of treatments that can be tested. The use of modelling approaches has already proven its merits as a complementary research tool to silvicultural trials for exploring stand dynamics and treatment outcomes under different conditions and scenarios. and over longer time frames than those usually covered by field trials (Coates et al., 2003). In effect, the most promising investigative approach is probably one in which valuable empirical data are obtained from field experiments and silvicultural trials - to answer questions ranging from physiological to stand - or even landscapelevels - and incorporated into conceptual and simulation models to synthesize knowledge and further explore the various implications of silvicultural scenarios involving partial cutting.

Acknowledgements

We are grateful to two anonymous reviewers and the associate editor of Forestry for numerous helpful comments and suggestions for improving the original manuscript. We thank Ken Baldwin, Natural Resources Canada (Great Lakes Forestry Centre) for providing the Level 4 map (version 1) of the Canadian component of the Circumboreal Vegetation Map and Melanie Desrochers of the Centre d'étude sur la forêt for help in its production (Figure 1). Nicole Fenton, Julien Moulinier and Manuella Strukelj provided information on partial cutting trials in the eastern boreal forest.

Conflict of interest statement

None declared.

Funding

This work was supported by NSERC Collaborative Research and Development Grant CRDPJ 395368 – 09 (Eastern boreal mixedwoods: Multiscale analysis of stand structure, dynamics and silviculture, B.D. Harvey). A.K.B. acknowledges funding received through the NSERC-FQRNT-BMP Scholarship Program and contributions of Norbord Industries. Funding for Open Access charge: NSERC Collaborative Research and Development Grant CRDPJ 395368 - 09 (Eastern boreal mixedwoods: Multiscale analysis of stand structure, dynamics and silviculture, B.D. Harvey).

References

Aakala, T., Kuuluvainen, T., Gauthier, S. and De Grandpré, L. 2008 Standing dead trees and their decay-class dynamics in the northeastern boreal old-growth forests of Quebec. *For. Ecol. Manag.* **255**(3–4), 410–420.

Angelstam, P.K. 1998 Maintaining and restoring biodiversity in European boreal forests by developing natural disturbance regimes. *J. Veg. Sci.* **9**(4), 593–602.

Angers, V.A., Messier, C., Beaudet, M. and Leduc, A. 2005 Comparing composition and structure in old-growth and harvested (selection and diameter-limit cuts) northern hardwood stands in Quebec. *For. Ecol. Manag.* **217**(2-3), 275–293.

Anielski, M. and Wilson, S. 2009 *Counting Canada's Natural Capital: Assessing the Real Value of Canada's Boreal Ecosystems*. Revised edition. The Canadian Boreal Initiative and The Pembina Institute.

Asselin, H., Fortin, M.-J. and Bergeron, Y. 2001 Spatial distribution of late-successional coniferous species regeneration following disturbance in southwestern Québec boreal forest. *For. Ecol. Manag.* **140**(1), 29–37.

Attiwill, P.M. 1994 The disturbance of forest ecosystems: the ecological basis for conservative management. *For. Ecol. Manag.* **63**(2–3), 247–300.

Baldwin, K.A., MacKenzie, W.H., Pfalz, J., Meades, W.J., Meidinger, D.V. and Robitaille, A. *et al.* 2012 Level 4 map, version 1, Canadian component of the circumboreal vegetation map (CBVM). *Canadian Regional Team of the Circumboreal Vegetation Map Project*. Natural Resources Canada, Canadian Forest Service, Great Lakes Forestry Centre (Unpublished map).

Baldocchi, D., Kelliher, F.M., Black, T.A. and Jarvis, P. 2000 Climate and vegetation controls on boreal zone energy exchange. *Glob. Change Biol.* 6(S1), 69-83.

Bamber, R. and Burley, J. 1983 *The wood properties of radiata pine*. Commonwealth Agricultural Bureaux.

Barbour, R.J., Fayle, D.C., Chauret, G., Cook, J., Karsh, M.B. and Ran, S. 1994 Breast-height relative density and radial growth in mature jack pine (*Pinus banksiana*) for 38 years after thinning. *Can. J. For. Res.* **24**(12), 2439–2447.

Barg, A.K. and Edmonds, R.L. 1999 Influence of partial cutting on site microclimate, soil nitrogen dynamics, and microbial biomass in Douglas-fir stands in western Washington. *Can. J. For. Res.* **29**(6), 705–713.

Beaudet, M., Harvey, B.D., Messier, C., Coates, K.D., Poulin, J. and Kneeshaw, D.D. *et al.* 2011 Managing understory light conditions in boreal mixedwoods through variation in the intensity and spatial pattern of harvest: a modelling approach. *For. Ecol. Manag.* **261**(1), 84–94.

Bergeron, Y. 2000 Species and stand dynamics in the mixed woods of Quebec's southern boreal forest. *Ecology.* **81**(6), 1500–1516.

Bergeron, Y. and Dubue, M. 1989 Succession in the southern part of the Canadian boreal forest. *Vegetation*. 79(1-2), 51-63.

Bergeron, Y. and Harvey, B. 1997 Basing silviculture on natural ecosystem dynamics: an approach applied to the southern boreal mixedwood forest of Quebec. *For. Ecol. Manag.* 92(1-3), 235–242.

Bergeron, Y., Engelmark, O., Harvey, B., Morin, H. and Sirois, L. 1998 Key issues in disturbance dynamics in boreal forests: introduction. *J. Veg. Sci.* **9**(4), 464–468.

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**(1), 49–54.

Bergeron, Y., Leduc, A., Harvey, B.D. and Gauthier, S. 2002 Natural fire regime: a guide for sustainable management of the Canadian boreal forest. *Silva Fenn.* **36**(1), 81–95.

Bergeron, Y., Flannigan, M., Gauthier, S., Leduc, A. and Lefort, P. 2004 Past, current and future fire frequency in the Canadian boreal forest: Implications for sustainable forest management. *Ambio.* **33**(6), 356–360.

Bladon, K.D., Silins, U., Landhäusser, S.M. and Lieffers, V.J. 2006 Differential transpiration by three boreal tree species in response to increased evaporative demand after variable retention harvesting. *Agric. For. Meteorol.* **138**(1–4), 104–119.

Bladon, K.D., Silins, U., Landhäusser, S.M., Messier, C. and Lieffers, V.J. 2007 Carbon isotope discrimination and water stress in trembling aspen following variable retention harvesting. *Tree Physiol.* **27**(7), 1065–1071.

Bladon, K.D., Lieffers, V.J., Silins, U., Landhäusser, S.M. and Blenis, P.V. 2008 Elevated mortality of residual trees following structural retention harvesting in boreal mixedwoods. *Forest. Chron.* **84**(1), 70–75.

Blais, J. 1983 Trends in the frequency, extent, and severity of spruce budworm outbreaks in eastern Canada. *Can. J. For. Res.* **13**(4), 539–547.

Bouchard, M. 2009 Silviculture in a context of forest ecosystem management in boreal and southern boreal forests (Chapter 13). In Gauthier, S., Vaillancourt, M.A., Leduc, A., De Grandpré, L., Kneeshaw, D., Morin, H., Drapeau, P. and Bergeron, Y. (eds.). *Ecosystem Management in the Boreal Forest*. PUQ (319–342).

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**(6), 1080–1093.

Bourgeois, L., Messier, C. and Brais, S. 2004 Mountain maple and balsam fir early response to partial and clear-cut harvesting under aspen stands of northern Quebec. *Can. J. For. Res.* **34**(10), 2049–2059.

Bradbury, S. 2004 Understorey plant communities in boreal cutblocks with different sizes and numbers of residual tree patches. *Can. J. For. Res.* **34**(6), 1220–1227.

Brais, S., Harvey, B.D., Bergeron, Y., Messier, C., Greene, D. and Belleau, A. *et al.* 2004 Testing forest ecosystem management in boreal mixedwoods of northwestern Quebec: initial response of aspen stands to different levels of harvesting. *Can. J. For. Res.* **34**(2), 431–446.

Brais, S., Work, T.T., Robert, É., O'Connor, C.D., Strukelj, M. and Bose, A. *et al.* 2013 Ecosystem responses to partial harvesting in eastern boreal mixedwood stands. *Forests.* **4**(2), 364–385.

Brandt, J.P. 2009 The extent of the North American boreal zone. *Environ. Rev.* **17**, 101–161.

Brassard, B.W. and Chen, H.Y.H. 2006 Stand structural dynamics of North American boreal forests. *Crit. Rev. Plant Sci.* **25**(2), 115–137.

Burton, P.J., Messier, C., Smith, D.W. and Adamowicz, W.L. (eds). 2003 Towards Sustainable Management of the Boreal Forest. NRC Research Press.

Burton, P.J., Messier, C., Adamowicz, W.L. and Kuuluvainen, T. 2006 Sustainable management of Canada's boreal forests: progress and prospects. *Ecoscience*. **13**(2), 234–248.

Burton, P., Bergeron, Y., Bogdanski, B., Juday, G., Kuuluvainen, T. and McAfee, B. *et al.* 2010 Sustainability of boreal forests and forestry in a changing environment. *IUFRO World Series.* **25**, 249–282.

Carlson, D.W. and Groot, A. 1997 Microclimate of clear-cut, forest interior, and small openings in trembling aspen forest. *Agric. For. Meteorol.* **87**(4), 313–329.

CFS. 1999 *Silvicultural Terms in Canada*. 2nd edn. Canadian Forest Service, Natural Resources Canada [Online]. Available at http://nfdp.ccfm.org/ silvaterm/silvi_e/silvitermintroe.htm.

Chen, H.Y. and Popadiouk, R.V. 2002 Dynamics of North American boreal mixedwoods. *Environ. Rev.* **10**(3), 137–166.

Cimon-Morin, J., Ruel, J.-C. and Darveau, M. 2010 Short term effects of alternative silvicultural treatments on stand attributes in irregular balsam fir-black spruce stands. *For. Ecol. Manag.* **260**(5), 907–914.

Coates, K.D. 1997 Windthrow damage 2 years after partial cutting at the Date Creek silvicultural systems study in the Interior Cedar-Hemlock forests of northwestern British Columbia. *Can. J. For. Res.* **27**(10), 1695–1701.

Constraints to partial cutting in the boreal forest

Coates, K.D. 2002 Tree recruitment in gaps of various size, clearcuts and undisturbed mixed forest of interior British Columbia, Canada. *For. Ecol. Manag.* **155**(1-3), 387–398.

Coates, K.D., Canham, C.D., Beaudet, M., Sachs, D.L. and Messier, C. 2003 Use of a spatially explicit individual-tree model (SORTIE/BC) to explore the implications of patchiness in structurally complex forests. *For. Ecol. Manag.* **186**(1-3), 297–310.

Comeau, P.G., Wang, J.R. and Letchford, T. 2003 Influences of paper birch competition on growth of understory white spruce and subalpine fir following spacing. *Can. J. For. Res.* **33**(10), 1962–1973.

Cooke, B.J., Nealis, V.G. and Régnière, J. 2007 Insect defoliators as periodic disturbances in northern forest ecosystems. In *Plant Disturbance Ecology: the Process and the Response*. Johnson, E.A. and Miyanishi, K. (eds). Elsevier Academic Press, pp. 487–525.

Cumming, S.G., Schmiegelow, F.K.A. and Burton, P.J. 2000 Gap dynamics in boreal aspen stands: is the forest older than we think? *Ecol. Appl.* **10**(3), 744–759.

Cyr, D., Bergeron, Y., Gauthier, S. and Larouche, A.C. 2005 Are the old-growth forests of the Clay Belt part of a fire-regulated mosaic? *Can. J. For. Res.* **35**(1), 65–73.

De Grandpré, L., Morissette, J. and Gauthier, S. 2000 Long-term post-fire changes in the northeastern boreal forest of Quebec. *J. Veg. Sci.* **11**(6), 791–800.

Elie, J.-G. and Ruel, J.-C. 2005 Windthrow hazard modelling in boreal forests of black spruce and jack pine. *Can. J. For. Res.* **35**(11), 2655–2663.

Etheridge, D.A. and Kayahara, G.J. 2013 Challenges and implications of incorporating multi-cohort management in northeastern Ontario, Canada: a case study. *Forest. Chron.* **89**(03), 315–326.

Fauteux, D., Imbeau, L., Drapeau, P. and Mazerolle, M.J. 2012 Small mammal responses to coarse woody debris distribution at different spatial scales in managed and unmanaged boreal forests. *For. Ecol. Manag.* **266**(0), 194–205.

Fenton, N., Lecomte, N., Légaré, S. and Bergeron, Y. 2005 Paludification in black spruce (*Picea mariana*) forests of eastern Canada: Potential factors and management implications. *For. Ecol. Manag.* **213**(1–3), 151–159.

Fenton, N.J. and Bergeron, Y. 2007 Sphagnum community change after partial harvest in black spruce boreal forests. *For. Ecol. Manag.* **242**(1), 24–33.

Fenton, N.J., Simard, M. and Bergeron, Y. 2009 Emulating natural disturbances: the role of silviculture in creating even-aged and complex structures in the black spruce boreal forest of eastern North America. *J. For. Res.* **14**(5), 258–267.

Fenton, N.J., Imbeau, L., Work, T., Jacobs, J., Bescond, H. and Drapeau, P. *et al.* 2013 Lessons learned from 12 years of ecological research on partial cuts in black spruce forests of northwestern Québec. *Forest. Chron.* **89**(03), 350–359.

Fisher, J.T. and Bradbury, S.M. 2006 Understorey protection harvest expedites recolonisation of boreal forest stands by North American red squirrels. *For. Ecol. Manag.* 234(1-3), 40-47.

Franklin, J.F. 1989 Towards a new forestry. Am. For. 95, 37–44.

Frey, B.R., Lieffers, V.J., Munson, A.D. and Blenis, P.V. 2003 The influence of partial harvesting and forest floor disturbance on nutrient availability and understory vegetation in boreal mixedwoods. *Can. J. For. Res.* **33**(7), 1180–1188.

Fuglem, G., Sabourin, M. and Lundqvist, S. 2003 Influence of spruce wood properties on thermomechanical pulping–pilot scale results. *Proceedings of International Mechanical Pulping Conference, Quebec City.* 2–5.

Gauthier, S., Vaillancourt, M.-A., Leduc, A., Grandpre, L.D., Kneeshaw, D. and Morin, H. et al. 2009 Ecosystem Management in the Boreal Forest. PUQ.

Gendreau-Berthiaume, B., Kneeshaw, D.D. and Harvey, B.D. 2012 Effects of partial cutting and partial disturbance by wind and insects on stand composition, structure and growth in boreal mixedwoods. *Forestry.* **85**(4), 551–565.

Givnish, T.J. 1995 Plant stems: biomechanical adaptation for energy capture and influence on species. *Plant Stems: Physiology and Functional Morphology*.

Goudiaby, V., Brais, S., Berninger, F. and Schneider, R. 2012 Vertical patterns in specific volume increment along stems of dominant jack pine (*Pinus banksiana*) and black spruce (*Picea mariana*) after thinning. *Can. J. For. Res.* **42**(4), 733–748.

Gradowski, T., Lieffers, V.J., Landhäusser, S.M., Sidders, D., Volney, J. and Spence, J.R. 2010 Regeneration of Populus nine years after variable retention harvest in boreal mixedwood forests. *For. Ecol. Manag.* **259**(3), 383–389.

Greene, D.F., Zasada, J.C., Sirois, L., Kneeshaw, D., Morin, H. and Charron, I. *et al.* 1999 A review of the regeneration dynamics of North American boreal forest tree species. *Can. J. For. Res.* **29**(6), 824–839.

Groot, A. 2002 Is uneven-aged silviculture applicable to peatland black spruce (*Picea mariana*) in Ontario, Canada? *Forestry.* **75**(4), 437–442.

Groot, A. and Carlson, D.W. 1996 Influence of shelter on night temperatures, frost damage, and bud break of white spruce seedlings. *Can. J. For. Res.* **26**(9), 1531–1538.

Groot, A. and Hökkä, H. 2000 Persistence of suppression effects on peatland black spruce advance regeneration after overstory removal. *Can. J. For. Res.* **30**(5), 753–760.

Groot, A., Man, R. and Wood, J. 2009 Spatial and temporal patterns of *Populus tremuloides* regeneration in small forest openings in northern Ontario. *For. Chron.* **85**(4), 548–557.

Gustafsson, L., Kouki, J. and Sverdrup-Thygeson, A. 2010 Tree retention as a conservation measure in clear-cut forests of northern Europe: a review of ecological consequences. *Scand. J. For. Res.* **25**(4), 295–308.

Gustafsson, L., Baker, S.C., Bauhus, J., Beese, W.J., Brodie, A. and Kouki, J. *et al.* 2012 Retention forestry to maintain multifunctional forests: a world perspective. *Bioscience*. **62**(7), 633–645.

Haeussler, S., Bergeron, Y., Brais, S. and Harvey, B.D. 2007 Natural dynamics-based silviculture for maintaining plant biodiversity in *Populus tremuloides*-dominated boreal forests of eastern Canada. *Can. J. Bot.* **85**(12), 1158–1170.

Harrison, R.B., Schmiegelow, F.K.A. and Naidoo, R. 2005 Stand-level response of breeding forest songbirds to multiple levels of partial-cut harvest in four boreal forest types. *Can. J. For. Res.* **35**(7), 1553–1567.

Harvey, B.D. and Brais, S. 2007 Partial cutting as an analogue to stem exclusion and dieback in trembling aspen (*Populus tremuloides*) dominated boreal mixedwoods: implications for deadwood dynamics. *Can. J. For. Res.* **37**(9), 1525–1533.

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. Manag.* 155(1-3), 369-385.

Hatcher, R. 1961 Partial cutting balsam fir stands on the Epaule River watershed, Quebec. Forest Research Branch Technical Note No. 105. 29 pp.

Hébert, F., Thiffault, N., Ruel, J.-C. and Munson, A.D. 2010 Comparative physiological responses of *Rhododendron groenlandicum* and regenerating *Picea mariana* following partial canopy removal in northeastern Quebec, Canada. *Can. J. For. Res.* **40**(9), 1791–1802.

Hobson, K.A. and Schieck, J. 1999 Changes in bird communities in boreal mixedwood forest: harvest and wildfire effects over 30 years. *Ecol. Appl.* **9**(3), 849–863.

Inderjit, and Mallik, A.U. 1996 Growth and physiological responses of Black Spruce (*Picea mariana*) to sites dominated by *Ledum groenlandicum*. *J. Chem. Ecol.* **22**(3), 575–585.

Johnson, E.A. 1996 Fire and Vegetation Dynamics: Studies from the North American Boreal Forest. Cambridge University Press.

Kellomäki, S., Ikonen, V.-P., Peltola, H. and Kolström, T. 1999 Modelling the structural growth of Scots pine with implications for wood quality. *Ecol. Model.* **122**(1–2), 117–134.

King, D.A. 1986 Tree form, height growth, and susceptibility to wind damage in Acer Saccharum. Ecology. **67**(4), 980–990.

Kneeshaw, D.D. and Bergeron, Y. 1998 Canopy gap characteristics and tree replacement in the southeastern boreal forest. *Ecology*. **79**(3), 783–794.

Kneeshaw, D. and Gauthier, S. 2003 Old growth in the boreal forest: a dynamic perspective at the stand and landscape level. *Environ. Rev.* **11**(S1), S99–S114.

Kneeshaw, D.D., Williams, H., Nikinmaa, E. and Messier, C. 2002 Patterns of above- and below-ground response of understory conifer release 6 years after partial cutting. *Can. J. For. Res.* **32**(2), 255–265.

Kneeshaw, D.D., Harvey, B.D., Reyes, G.P., Caron, M.N. and Barlow, S. 2011 Spruce budworm, windthrow and partial cutting: do different partial disturbances produce different forest structures? *For. Ecol. Manag.* **262**(3), 482–490.

Koga, S., Oda, K., Tsutsumi, J. and Fujimoto, T. 1997 Effect of thinning on the wood structure in annual growth rings of Japanese larch (*Larix leptolepis*). *IAWA J.* **18**, 281–290.

Kuuluvainen, T. 2009 Forest management and biodiversity conservation based on natural ecosystem dynamics in northern Europe: the complexity challenge. *Ambio.* **38**(6), 309–315.

Kuuluvainen, T. and Grenfell, R. 2012 Natural disturbance emulation in boreal forest ecosystem management – theories, strategies, and a comparison with conventional even-aged management. *Can. J. For. Res.* **42**(7), 1185–1203.

Kuuluvainen, T., Tahvonen, O. and Aakala, T. 2012 Even-aged and uneven-aged forest management in boreal Fennoscandia: a review. *Ambio.* **41**(7), 720–737.

Laflèche, V., Larouche, C. and Guillemette, F. 2013 L'éclaircie commerciale, Chap. 15 (p. 301–327) In Ministère des Ressources naturelles, « Le guide sylvicole du Québec Tome 2 – Les concepts et l'application de la sylviculture », Les Publications du Québec.

Lance, A.N. and Phinney, M. 2001 Bird responses to partial retention timber harvesting in central interior British Columbia. *For. Ecol. Manag.* **142**(1–3), 267–280.

Landhäusser, S.M., Mulak, T.L. and Lieffers, V.J. 2007 The effect of roots and litter of *Calamagrostis canadensis* on root sucker regeneration of *Populus tremuloides*. *Forestry*. **80**(4), 481–488.

Landsberg, J.J. and Gower, S.T. 1997 Applications of physiological ecology to forest management. Elsevier.

Laquerre, S., Harvey, B.D. and Leduc, A. 2011 Spatial analysis of response of trembling aspen patches to clearcutting in black spruce-dominated stands. *For. Chron.* **87**(1), 77–85.

Lavoie, M., Paré, D., Fenton, N., Groot, A. and Taylor, K. 2005 Paludification and management of forested peatlands in Canada: a literature review. *Environ. Rev.* **13**(2), 21–50.

Lavoie, S., Ruel, J.-C., Bergeron, Y. and Harvey, B.D. 2012 Windthrow after group and dispersed tree retention in eastern Canada. *For. Ecol. Manag.* **269**(0), 158–167.

Lennie, A.D., Landhäusser, S.M., Lieffers, V.J. and Sidders, D. 2009 Regeneration of aspen following partial and strip understory protection harvest in boreal mixedwood forests. *For. Chron.* **85**(4), 631–638. Lieffers, V. and Stadt, K. 1994 Growth of understory *Picea glauca*, *Calamagrostis canadensis*, and *Epilobium angustifolium* in relation to overstory light transmission. *Can. J. For. Res.* **24**(6), 1193–1198.

Lieffers, V.J., Macdonald, S.E. and Hogg, E.H. 1993 Ecology of and control strategies for *Calamagrostis canadensis* in boreal forest sites. *Can. J. For. Res.* **23**(10), 2070–2077.

Lieffers, V.J., Stadt, K.J. and Navratil, S. 1996 Age structure and growth of understory white spruce under aspen. *Can. J. For. Res.* **26**(6), 1002–1007.

Lieffers, V.J., Messier, C., Burton, P.J., Ruel, J.C. and Grover, B.E. 2003. Naturebased silviculture for sustaining a variety of boreal forest values (Chapter 13). In Burton, P.J., Messier, C., Smith, D.W. and Adamowicz, W.L. (ed.).*Towards Sustainable Management of the Boreal Forest*. NRC Research Press. pp. 480–530.

Lindenmayer, D.B., Franklin, J.F., Löhmus, A., Baker, S.C., Bauhus, J. and Beese, W. *et al.* 2012 A major shift to the retention approach for forestry can help resolve some global forest sustainability issues. *Conserv. Lett.* **5**(6), 421–431.

Liu, X., Silins, U., Lieffers, V.J. and Man, R. 2003 Stem hydraulic properties and growth in lodgepole pine stands following thinning and sway treatment. *Can. J. For. Res.* **33**(7), 1295–1303.

Lorimer, C.G. 1983 Eighty-year development of northern red oak after partial cutting in a mixed-species Wisconsin forest. *For. Sci.* **29**(2), 371–383.

Lycke, A., Imbeau, L. and Drapeau, P. 2011 Effects of commercial thinning on site occupancy and habitat use by spruce grouse in boreal Quebec. *Can. J. For. Res.* **41**(3), 501–508.

MacDonald, G.B. and Thompson, D.J. 2003 Responses of planted conifers and natural hardwood regeneration to harvesting, scalping, and weeding on a boreal mixedwood site. *For. Ecol. Manag.* **182**(1–3), 213–230.

MacDonald, G.B., Cherry, M.L. and Thompson, D.J. 2004 Effect of harvest intensity on development of natural regeneration and shrubs in an Ontario boreal mixedwood stand. *For. Ecol. Manag.* **189**(1–3), 207–222.

MacIsaac, D.A. and Krygier, R. 2009 Development and long-term evaluation of harvesting patterns to reduce windthrow risk of understorey spruce in aspen-white spruce mixedwood stands in Alberta, Canada. *Forestry.* **82**(3), 323–342.

Mäkinen, H., Saranpää, P. and Linder, S. 2002 Wood-density variation of Norway spruce in relation to nutrient optimization and fibre dimensions. *Can. J. For. Res.* **32**(2), 185–194.

Mallik, A.U. 2003 Conifer regeneration problems in boreal and temperate forests with ericaceous understory: role of disturbance, seedbed limitation, and keystone species change. *Crit. Rev. Plant Sci.* **22**(3–4), 341–366.

Man, R., Kayahara, G.J., Rice, J.A. and MacDonald, G.B. 2008a Eleven-year responses of a boreal mixedwood stand to partial harvesting: Light, vegetation, and regeneration dynamics. *For. Ecol. Manag.* **255**(3-4), 697–706.

Man, R., Kayahara, G.J., Rice, J.A. and MacDonald, G.B. 2008b Response of trembling aspen to partial cutting and subsequent forest tent caterpillar defoliation in a boreal mixedwood stand in northeastern Ontario, Canada. *Can. J. For. Res.* **38**(6), 1349–1356.

Man, R., Rice, J.A. and MacDonald, G.B. 2010 Five-year light, vegetation, and regeneration dynamics of boreal mixedwoods following silvicultural treatments to establish productive aspen-spruce mixtures in northeastern Ontario. *Can. J. For. Res.* **40**(8), 1529–1541.

McCarthy, J. 2001 Gap dynamics of forest trees: a review with particular attention to boreal forests. *Environ. Rev.* 9(1), 1–59.

McLaughlin, J.A. and Dumas, M.T. 1996 Pathological implications of partial cutting in boreal mixedwood stands. *Pages 167–169* In Advancing Boreal Mixedwood Management in Ontario: Proceedings of a Workshop, October

Constraints to partial cutting in the boreal forest

17–19, 1995. C.R. Smith and G.W. Crook, compilers. Natural resources Canada, Canadian Forest Service, Great Lakes Forestry Centre, 239 p.

Messier, C., Doucet, R., Ruel, J.-C., Claveau, Y., Kelly, C. and Lechowicz, M.J. 1999 Functional ecology of advance regeneration in relation to light in boreal forests. *Can. J. For. Res.* **29**(6), 812–823.

Meunier, S., Ruel, J.C., Laflamme, G. and Achim, A. 2002 Résistance comparée de l'épinette blanche et du sapin baumier au renversement. *Can. J. For. Res.* **32**(4), 642–652.

MRNQ. 2012 Ressources et industries forestières: Portrait statistique 2012 Ministère des Ressources naturelles du Québec. Consulted online 2013-03-10: http://www.mrn.gouv.qc.ca/publications/forets/portrait-statistique-2012.pdf.

Mundell, T.L., Landhäusser, S.M. and Lieffers, V.J. 2007 Effects of *Corylus cornuta* stem density on root suckering and rooting depth of *Populus tremuloides. Can. J. Bot.* **85**(11), 1041–1045.

NFDP. 2013 Silvicultural Quick Facts. National Forest Data Base. Consulted online 2013-03-10. http://nfdp.ccfm.org/silviculture/quick_facts_e.php.

Norton, M.R. and Hannon, S.J. 1997 Songbird response to partial-cut logging in the boreal mixedwood forest of Alberta. *Can. J. For. Res.* **27**(1), 44–53.

Nyland, R.D. 2005 Diameter-limit cutting and silviculture: a comparison of long-term yields and values for uneven-aged Sugar maple stands. *North. J. Appl. For.* **22**(2), 111–116.

O'Hara, K.L. and Ramage, B.S. 2013 Silviculture in an uncertain world: utilizing multi-aged management systems to integrate disturbance. *Forestry.* **86**(4), 401–410.

Oliver, C.D. and Larson, B.C. 1990 Forest Stand Dynamics. McGraw-Hill, Inc.

Palik, B.J., Mitchell, R.J. and Hiers, J.K. 2002 Modeling silviculture after natural disturbance to sustain biodiversity in the longleaf pine (*Pinus palustris*) ecosystem: balancing complexity and implementation. *For. Ecol. Manag.* **155**(1–3), 347–356.

Pape, R. 1999 Effects of thinning regime on the wood properties and stem quality of *Picea abies. Scand. J. For. Res.* **14**(1), 38–50.

Parent, S. and Ruel, J.-C. 2002 Chronologie de la croissance chez des semis de sapin baumier (*Abies balsamea* (L.) Mill.) après une coupe à blanc avec protection de la régénération. *For. Chron.* **78**(6), 876–885.

Peltola, H., Kilpelainen, A., Sauvala, K., Raisanen, T. and Ikonen, V. 2007 Effects of early thinning regime and tree status on the radial growth and wood density of Scots pine. *Silva Fenn.* **41**(3), 489.

Peterson, C.J. 2004 Within-stand variation in windthrow in southern boreal forests of Minnesota: Is it predictable? *Can. J. For. Res.* **34**(2), 365–375.

Pham, A.T., De Grandpré, L.D., Gauthier, S. and Bergeron, Y. 2004 Gap dynamics and replacement patterns in gaps of the northeastern boreal forest of Quebec. *Can. J. For. Res.* **34**(2), 353–364.

Pothier, D. and Prévost, M. 2008 Regeneration development under shelterwoods in a lowland red spruce – balsam fir stand. *Can. J. For. Res.* **38**(1), 31–39.

Pothier, D., Prévost, M. and Auger, I. 2003 Using the shelterwood method to mitigate water table rise after forest harvesting. *For. Ecol. Manag.* **179**(1–3), 573–583.

Prévost, M. and Pothier, D. 2003 Partial cuts in a trembling aspen conifer stand: effects on microenvironmental conditions and regeneration dynamics. *Can. J. For. Res.* **33**(1), 1–15.

Puettmann, K.J., Coates, K.D. and Messier, C.C. 2009 A Critique of Silviculture: Managing for Complexity. Cambridge University Press.

Raymond, P., Legault, I., Guay, L. and Godbout, C. 2013 La coupe progressive régulière, Chap. 19 (p. 411–453) In Ministère des Ressources naturelles, « Le

guide sylvicole du Québec Tome 2 – Les concepts et l'application de la sylviculture », Les Publications du Québec.

Rice, J.A. and Man, R. 2011 *Wind Damage in a Partially Harvested Boreal Mixedwood Stand in Northeastern Ontario*. Ontario Forest Research Institute. Forest Research Report No. 175. 14 p.

Rich, R.L., Frelich, L.E. and Reich, P.B. 2007 Wind-throw mortality in the southern boreal forest: effects of species, diameter and stand age. *J. Ecol.* **95**(6), 1261–1273.

Riopel, M. 2012 Étude de coupes avec protection des petites tiges marchandes (CPPTM) 5 et 10 ans après traitement: probabilités de pertes, distribution de la régénération et probabilités d'insolation hivernale. Ph.D. Thesis, Université Laval, Quebec City.

Riopel, M., Bégin, J. and Ruel, J.-C. 2010 Probabilités de pertes des tiges individuelles, cinq ans après des coupes avec protection des petites tiges marchandes, dans des forêts résineuses du Québec. *Can. J. For. Res.* **40**(7), 1458–1472.

Robert, E., Brais, S., Harvey, B.D. and Greene, D. 2012 Seedling establishment and survival on decaying logs in boreal mixedwood stands following a mast year. *Can. J. For. Res.* **42**(8), 1446–1455.

Ruel, J.-C. 2000 Factors influencing windthrow in balsam fir forests: from landscape studies to individual tree studies. *For. Ecol. Manag.* **135**(1-3), 169–178.

Ruel, J.-C., Messier, C., Claveau, Y., Doucet, R. and Comeau, P. 2000 Morphological indicators of growth response of coniferous advance regeneration to overstorey removal in the boreal forest. *For. Chron.* **76**(4), 633–642.

Ruel, J.C., Raymond, P. and Pineau, M. 2003 Windthrow after shelterwood cutting in Balsam fir stands. *North. J. Appl. For.* **20**(1), 5–13.

Ruel, J.-C., Achim, A., Herrera, R.E., Cloutier, A. and Brossier, B. 2010 Wood degradation after windthrow in a northern environment. *For. Prod. J.* **60**(2), 200–106.

Ruel, J.-C., Fortin, D. and Pothier, D. 2013 Partial cutting in old-growth boreal stands: an integrated experiment. *For. Chron.* **89**(03), 360–369.

Schneider, R., Zhang, S.Y., Swift, D.E., Bégin, J. and Lussier, J.-M. 2008 Predicting selected wood properties of jack pine following commercial thinning. *Can. J. For. Res.* **38**(7), 2030–2043.

Seymour, R.S., White, A.S. and deMaynadier, P.G. 2002 Natural disturbance regimes in northeastern North America – evaluating silvicultural systems using natural scales and frequencies. *For. Ecol. Manag.* **155**(1–3), 357–367.

Simard, M.-J., Bergeron, Y. and Sirois, L. 1998 Conifer seedling recruitment in a southeastern Canadian boreal forest: the importance of substrate. *J. Veg. Sci.* **9**(4), 575–582.

Simard, M., Lecomte, N., Bergeron, Y., Bernier, P.Y. and Paré, D. 2007 Forest productivity decline caused by successional paludification of boreal soils. *Ecol. Appl.* **17**(6), 1619–1637.

Sims, R., Kershaw, H.M. and Wickware, G. 1990 *The Autecology of Major Tree Species in the North Central Region of Ontario.* Forestry Canada, Ontario Region, Great Lakes Forest Research Centre.

Smith, D.M., Larson, B.C., Kelty, M.J. and Ashton, P.M.S. 1997 *The Practice of Silviculture: Applied Forest Ecology*. John Wiley and Sons, Inc.

Smith, F. 2010 Mortality in the Yukon: post-harvest effects on structural retention. PhD Thesis, University of Toronto.

Solarik, K.A., Lieffers, V.J., Volney, W.J.A., Pelletier, R. and Spence, J.R. 2010 Seed tree density, variable retention, and stand composition influence recruitment of white spruce in boreal mixedwood forests. *Can. J. For. Res.* **40**(9), 1821–1832.

Solarik, K.A., Volney, W.J.A., Lieffers, V.J., Spence, J.R. and Hamann, A. 2012 Factors affecting white spruce and aspen survival after partial harvest. *J. Appl. Ecol.* **49**(1), 145–154. Soucy, M., Lussier, J.-M. and Lavoie, L. 2012 Long-term effects of thinning on growth and yield of an upland black spruce stand. *Can. J. For. Res.* **42**(9), 1669–1677.

Talbot, S.S. and Meades, W.J. 2011 Circumboreal Vegetation Map (CBVM): mapping the Green Halo. Concept Paper. CAFF Strategy Series Report No. 3. CAFF Flora Group (CFG), CAFF International Secretariat. ISBN 978-9935-431-05-9. www.caff.is/flora-cfg/circumboreal-vegetation-map.

Tarroux, E., DesRochers, A. and Krause, C. 2010 Effect of natural root grafting on growth response of jack pine (*Pinus banksiana*) after commercial thinning. *For. Ecol. Manag.* **260**(4), 526–535.

Thorpe, H.C. and Thomas, S.C. 2007 Partial harvesting in the Canadian boreal: Success will depend on stand dynamic responses. *For. Chron.* **83**(3), 319–325.

Thorpe, H.C., Thomas, S.C. and Caspersen, J.P. 2007 Residual-tree growth responses to partial stand harvest in the black spruce (*Picea mariana*) boreal forest. *Can. J. For. Res.* **37**(9), 1563–1571.

Thorpe, H.C., Thomas, S.C. and Caspersen, J.P. 2008 Tree mortality following partial harvests is determined by skidding proximity. *Ecol. Appl.* **18**(7), 1652–1663.

Tremblay, S. and Laflèche, V. 2012 Résultats obtenus 5 ans après traitement dans les placettes du réseau de la mesure des effets réels de l'éclaircie commerciale en peuplements résineux. Mémoire de recherche forestière no. 166, Direction de la recherche forestière, Ministère des Ressources naturelles, Gouvernement du Québec.

Urban, S., Lieffers, V. and MacDonald, S. 1994 Release in radial growth in the trunk and structural roots of white spruce as measured by dendrochronology. *Can. J. For. Res.* **24**(8), 1550–1556.

Vanderwel, M.C., Malcolm, J.R. and Mills, S.C. 2007 A meta-analysis of bird responses to uniform partial harvesting across North America. *Conserv. Biol.* **21**(5), 1230–1240.

Vanderwel, M.C., Mills, S.C. and Malcolm, J.R. 2009 Effects of partial harvesting on vertebrate species associated with late-successional forests in Ontario's boreal region. *For. Chron.* **85**(1), 91–104.

Vincent, M., Krause, C. and Zhang, S.Y. 2009 Radial growth response of black spruce roots and stems to commercial thinning in the boreal forest. *Forestry.* **82**(5), 557–571.

Vincent, M., Krause, C. and Koubaa, A. 2011 Variation in black spruce (*Picea mariana* (Mill.) BSP) wood quality after thinning. *Ann. For. Sci.* **68**(6), 1115–1125.

Wang, Y., Titus, S.J. and LeMay, V.M. 1998 Relationships between tree slenderness coefficients and tree or stand characteristics for major species in boreal mixedwood forests. *Can. J. For. Res.* **28**(8), 1171–1183.

Whitney, R.D. and MacDonald, G.B. 1985 Effects of root rot on the growth of balsam fir. *Can. J. For. Res.* **15**(5), 890–895.

Work, T.T., Shorthouse, D.P., Spence, J.R., Volney, W.J.A. and Langor, D. 2004 Stand composition and structure of the boreal mixedwood and epigaeic arthropods of the Ecosystem Management Emulating Natural Disturbance (EMEND) landbase in northwestern Alberta. *Can. J. For. Res.* **34**(2), 417–430.

Zahner, R. and Oliver, W.W. 1962 The influence of thinning and pruning on the rate of summerwood initiation in red and jack pines. *For. Sci.* **8**, 51–63.

Zasada, J.C. 1971 Natural regeneration of interior Alaska forests-seed, seedbed, and vegetative reproduction considerations. *Fire in the Northern Environment – A symposium. USDA, For. Serv. Pacif. Northw. For. Range Exp. Sta.*, 231–246.

Zobel, B.J. and Buijtenen, J.V. 1989 Wood Variation: Its Causes and Control. Springer.