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ABSTRACT

Forest management has shifted from a relatively narrow focus on commercial wood supply to greater consideration of the natural dynamics and multiple ecological services provided by forest ecosystems. This recognition has generated interest in ecosystem management approaches based on diversifying and adapting silvicultural practices such as partial harvesting. The SAFE (*sylviculture et aménagement forestier écosystémiques*) project is a series of stand-level experiments undertaken in the Lake Duparquet Research and Teaching Forest (LDRTF) in the south-eastern Canadian boreal forest. The project was initiated in 1998 and tests the potential of partial harvesting as a tool for ecosystem-based silviculture in trembling aspen (*Populus tremuloides* Michx.) dominated stands. Previous studies conducted across the Canadian boreal mixedwood forest have indicated that, over the short term, partial harvesting of aspen or mixed-aspen stands can initiate a second cohort of aspen, increase the growth rate of advanced conifer regeneration and maintain most of the structural attributes of mature stands. Over the longer term (12 years), I expected that, following partial harvesting of 50% or more of basal area or through the use of gap harvesting, residual stems would be more susceptible to mortality due to windthrow compared to lighter harvesting prescriptions. This in turn would favor a progressive opening of the canopy, increase canopy gap size and change the dynamics between commercial and competitive species, thus potentially generating a shrub-dominated community. I also expected that more intense partial harvesting prescriptions would accelerate the growth of residual trees by decreasing competition and increasing resource availability as well as accelerating the development of old growth stand attributes by creating growing space for new tree cohorts.

This thesis is structured around four individual studies conducted in the SAFE project. The first and second studies were conducted in pure aspen stands (93% aspen basal area) while the third and fourth studies also used data from mixed aspen stands (81% aspen basal area). In the first study, we evaluated the effects of partial harvesting on sapling recruitment and residual tree mortality over a twelve year period. Stem analysis and neighborhood competition indices were used in the second study to assess tree-level growth responses over the same period. For the third study, we first identified and characterised, based on the literature, the structural attributes of old-growth trembling aspen (*Populus tremuloides* Michx.) - dominated stands for boreal mixedwoods. Using inventories conducted in pure aspen and mixed aspen stands, we then assessed the potential of partial harvesting in even-aged aspen-dominated stands to accelerate stand development towards these old-growth attributes. Finally in the fourth study, SORTIE-ND - a spatially-explicit stand dynamics model - was adapted and validated for the region and stand development under a range of partial harvesting scenarios was simulated over a 100-year period.

The effects of partial harvesting on stand dynamics over a twelve-year period were compared among four treatments: clearcuts (100% basal area (BA) removal); 1/3 partial cut (1/3 PC, 33% BA removal using low thinning); 2/3 partial cut (2/3 PC, 61% BA removal using high thinning) and controls (0% removal). Aspen sapling recruitment increases continuously following clearcut and partial cut treatments and no significant mortality occurred in the sapling layer over the 12-year period. Aspen sapling recruitment was disproportionally greater in the 2/3 partial cuts (56% of aspen sapling density in clearcuts) compared to the 1/3 partial cuts (5% of clearcut densities). Recruitment of conifer saplings increased with time and was significantly higher in the two partial cut treatments than in the clearcut treatment. Mortality of residual merchantable aspen was strongly associated with small stems (10-19.9 cm DBH), regardless of treatment but was initially (1-3 years after treatment) higher in the 2/3 partial cut. Both partial harvesting treatments had the effect of maintaining mountain maple (*Acer spicatum* Lamb.), a shade-tolerant, high woody shrub, at densities similar to those in control stands, whereas recruitment of mountain maple saplings was negligible in clearcuts. Annual volume increment (AVI) of individual aspen stems was analyzed as a function of treatment, tree social status, pre-treatment growth, time since treatment application (1–12 years) and neighborhood competition. There was no evidence of initial growth lag after partial harvesting. Only the most severe treatment of partial harvesting (2/3 PC) resulted in an increase in volume increment relative to trees in control stands. Annual increase in volume in the 2/3 partial cut was 25.6% higher than controls over 12 years. Annual volume increment of dominant trees was higher by 16.2 dm^3yr^{-1} than that of co-dominants and was proportional to pre-treatment volume growth.

Based on a literature review, it was determined that compared to mature, even-aged stands, old-growth aspen stands have lower merchantable stem densities and basal area, more large aspen stems and higher stem size variability, more than one cohort of trees, greater percentage area occupied by gaps and more and larger snags and downed wood. Inventories conducted over a 12-year post-treatment period indicate that while the partial harvesting treatments applied in this study successfully retained most of the structural attributes of mature aspen stands (untreated controls), they did not generally “accelerate succession” toward old-growth in the 12-year time interval. Nonetheless, overall results do suggest that by promoting irregularities in both horizontal and vertical structures, high-intensity partial harvesting will accelerate stand development towards what could be characterised as old-growth aspen-dominated mixedwoods.

The results of simulations with SORTIE-ND indicate that following the mortality of the first cohort of aspen, white spruce (*Picea glauca* [Moench] Voss) maintained dominance in un-harvested controls of pure aspen stands whereas balsam fir (*Abies* *balsamea* (L.) Mill.) dominated in mixed aspen stands. All gap cuts and 80% dispersed cuts favoured recruitment of aspen over conifers. At year 100 of simulation runs, the 1,600 m^2 gap cut resulted in highest stand basal areas in both pure aspen and mixed aspen stands with 38.0 and 34.1 $m^2.ha^{-1}$, respectively, of which 18% and 28%, again respectively, was composed of tolerant conifers.

The overall results of the thesis indicate that partial harvesting is a viable silvicultural option for trembling aspen-dominated boreal mixedwoods of Eastern Canada. This practice can be used to improve the growth of large aspen trees and to promote old-growth attributes. However, residual tree mortality immediately after treatments applied in this study and limited conifer recruitment bring into question the general potential of partial harvesting in these stand types. I argue that adapting partial harvesting treatments (intensity and spatial configuration of tree removal) based on pre-harvest stand conditions (e.g. stand age, stem size distribution, presence of conifer seed trees and advanced regeneration, and presence of woody shrubs) is the key to ensuring success of partial harvesting treatment. There has been some debate surrounding absolute retention levels to be applied in partial harvesting; however, modelling results suggest that both stand structure and timber production rates are strongly influenced not only by retention levels but also by spatial configuration of residual trees.

Keywords: Boreal mixedwood, partial harvesting, variable retention, Trembling aspen, sapling recruitment, residual tree mortality, tree-level volume increment, tree social status, neighborhood competition, pre-treatment size, old-growth, stand structural attributes, modeling stand dynamics and SORTIE-ND.

RÉSUMÉ

La gestion des forêts est passée d'une dynamique productiviste visant principalement l'approvisionnement en bois commercial à une meilleure intégration de la dynamique forestière naturelle et des multiples services écologiques des forêts. Cette évolution s'est traduite par des approches d'aménagement écosystémiques qui préconisent la diversification et l'adaptation des pratiques sylvicoles incluant le recours à des coupes partielles. Le projet SAFE (*sylviculture et aménagement forestier écosystémiques*) comprend une série d'expériences sylvicoles conduites l'échelle du peuplement en forêt boréale mixte de l'Est canadien. Le projet, initié en 1998 dans la forêt d'enseignement et de recherche du lac Duparquet, vise à valider le potentiel sylvicole des coupes partielles appliquées à peuplements équiennes matures dominés par le Peuplier faux-tremble (*Populus tremuloides* Michx.). Des études antérieures menées en forêt boréale mixte canadienne indiquent qu'à court terme la coupe partielle appliquée à des peuplements purs ou mélangés dominés par le P. faux-tremble initie une deuxième cohorte de P. faux-tremble, augmente la croissance de la régénération résineuse préétablie et maintient la plupart des attributs structurels de peuplements matures. J'ai émis l'hypothèse que, sur le plus long terme (12 ans), la mortalité les tiges résiduelles due à la chablis serait plus élevée après un prélèvement de 50% ou plus de la surface terrière (ST) ou suite à une coupe par trouées comparativement à un prélèvement moins fort. Cette mortalité favoriserait l'ouverture progressive de la canopée, augmenterait la dimension des trouées et altérerait la dynamique entre les espèces commerciales et concurrentes, favorisant ainsi la strate arbustive. J'ai aussi émis l'hypothèse qu'un prélèvement plus élevé permettrait d'accélérer la croissance des arbres résiduels en diminuant la compétition et en accroissant la disponibilité des ressources et permettrait aussi d'accélérer le développement des attributs structurels caractéristiques des peuplements plus âgés ou anciens en créant l'espace nécessaire à l'établissement de nouvelles cohortes d'arbres.

La thèse est structurée autour de quatre études individuelles menées dans le projet SAFE. Les première et deuxième études ont été réalisées dans des tremblaies pures (93% de la surface terrière en P. faux-tremble) tandis que les troisième et quatrième études ont également utilisé les données de peuplements mixtes dominés par le P. faux-tremble (81% de la surface terrière). Dans la première étude, nous avons évalué les effets de la coupe partielle sur le recrutement des gaules et la mortalité des arbres résiduels sur une période de douze ans. Des analyses de tige et des indices de compétition à l'échelle de l'arbre ont été utilisés dans la deuxième étude afin d'évaluer, pour la même période la croissance en volume des tiges résiduelles en réponse au prélèvement. Pour la troisième étude, nous avons identifié et caractérisé, à partir de la littérature, les attributs structurels caractéristiques des vieux peuplements de P. faux-tremble de la forêt boréale mixte. À l'aide d'inventaires nous avons évalué la capacité de la coupe partielle appliquée à des peuplements équiennes matures d'accélérer le développement de ces attributs. Enfin, dans la quatrième étude, SORTIE-ND - un modèle spatialement explicite de la dynamique des peuplements - a été adapté et validé pour la région. Par la suite, nous avons modélisé la dynamique des peuplements en simulant une gamme de coupes partielles de différentes intensités et selon différents patrons spatiaux. La dynamique des peuplements a été caractérisée pendant 12 années suivant l'application d'une coupe totale, d'une éclaircie par le bas de 33 % (CP1/3) de la surface terrière (ST), d'une éclaircie par le haut de 61 % (CP2/3) de la ST et dans des peuplements témoins non coupés. Au cours des 12 années suivant la coupe, le recrutement des gaules de P. faux-tremble a augmenté progressivement et de manière proportionnelle à la ST prélevée, sans mortalité significative des gaules. Douze ans après la coupe, les CP1/3 et CP2/3 généraient respectivement 5% et 56% des densités de gaules retrouvées suite à la coupe totale. Le recrutement des conifères augmentait aussi dans le temps et était significativement supérieur dans les coupes partielles que dans la coupe totale. Initialement (1–3 ans après coupe), la mortalité du P. faux-tremble reflétait principalement celle des petites tiges marchandes (10–19.9 cm DHP) et la mortalité relative la plus importante était associée à la CP2/3. L'accroissement du volume annuel (AVA) des tiges individuelles a été analysé en fonction du traitement, du statut social de l'arbre, de la croissance prétraitement, du temps écoulé depuis l'application du traitement (1-12 ans) et de la compétition par les arbres voisins. Il n'y avait aucune évidence de la stagnation de la croissance initiale après l'application des CP. Seule la CP2/3 a entrainé une augmentation de l'accroissement en volume comparativement aux arbres des peuplements témoins. Sur une période de 12 ans après coupe, l'AVA des tiges individuelles dans les CP2/3 était 25.6% plus élevé que celui des arbres des témoins. L'AVA des arbres dominants était plus élevé de 16.2 $dm^3.an^{-1}$ que celui des co-dominants, et était proportionnel à la croissance prétraitement.

Suite à une revue de la littérature, il a été établi que comparativement à des peuplements équiennes matures, les peuplements anciens de P. faux-tremble ou mixtes sont caractérisés par une densité et une surface terrière en tiges marchandes inférieures, plus de trembles de forte dimension et une plus grande variation de la taille des tiges, plus d'une cohorte d'arbres, une plus grande surface occupée par les trouées d'arbres et des touées élargies plus grandes et des chicots et débris ligneux au sol plus abondants. Les résultats indiquent que les coupes partielles spécifiques à cette étude aient réussi à conserver la plupart des caractéristiques structurelles des peuplements de trembles matures (contrôles non traités). Cependant au cours des 12 premières années après coupe, elles n'ont pas "accéléré la succession" vers des peuplements anciens. Cependant, les résultats suggèrent qu'en créant plus d'irrégularités dans la structure horizontale et verticale des peuplements, une coupe partielle de haute intensité permettra d'accélérer à plus long terme le passage des peuplements matures équiennes vers un stade plus avancé caractéristique des peupliers faux-tremble âgés de la forêt mélangée.

Les simulations réalisées à l'aide de SORTIE-ND projettent qu'après la mortalité de la première cohorte de P. faux-tremble, l'épinette blanche (*Picea glauca* [Moench] Voss) dans les peuplements non exploités de P. faux-tremble, et le Sapin baumier (*Abies balsamea* (L.) Mill.) dans les peuplements mixtes, deviennent dominants. L'ensemble des traitements par trouées et le prélèvement de 80% de la ST favorisent le recrutement du P. faux-tremble aux dépens des conifères. Après des simulations avec des pas de temps de 100 ans, la ST des peuplements est maximale à la suite d'un prélèvement par trouées de 1600 m² soit 38.0 $m^2.ha^{-1}$ dans les peuplements de P. faux-thermale et 34.1 $m^2.ha^{-1}$ dans les peuplements mixtes, avec respectivement, 18% et 28% en conifères tolérants à l'ombre.

Globalement, les résultats indiquent que le coupe partielle appliquée à des peuplements équiennes matures dominés par le P. faux-tremble est une option viable en forêt boréale mélangée de l'Est canadien. Cette pratique peut être utilisée afin d'améliorer la croissance des gros trembles et aussi pour promouvoir certains attributs des peuplements plus âgés. Cependant, la mortalité des arbres résiduels immédiatement après les traitements et le recrutement limité en conifères remettraient en question le potentiel de la coupe partielle. Je soutiens que l'adaptation des prescriptions de coupe partielle (intensité et la configuration spatiale) aux conditions des peuplements avant récolte (par exemple : l'âge et la distribution diamétrale du peuplement, la présence d'arbres-semenciers et de régénération préétablie d'espèces conifères, l'abondance des arbustes ligneux) est la clé la réussite du traitement. Les enjeux relatifs aux coupes partielles ont longtemps touché aux taux et temps de rétention des arbres résiduels. Cependant, nos résultats démontrent que la structure des peuplements et la production de matière ligneuse sont influencées non seulement par les taux de rétention, mais aussi par la configuration spatiale des arbres résiduels.

Mot-clés: Forêt boréale mixte, Aménagement écosystémique, Coupe partielle, Rétention variable, Recrutement, Mortalité des arbres résiduels, Peuplier faux-tremble, Accroissement du volume annuel des arbres, Indices de compétition à l'échelle de l'arbre, Statut social de l'arbre, Peuplements anciens, Attributs structurels du peuplement, Modélisation des dynamique de peuplements et SORTIE-ND

CHAPTER I

GENERAL INTRODUCTION

1.1. Problem statement

Over the last quarter century, ecosystem-based forest management (or forest ecosystem management - FEM) has emerged as a dominant management model for public forests in Canada – and elsewhere - and as a result, has been incorporated into forest legislation and regulations of several provinces (Perera *et al.*, 2007; Gauthier *et al.*, 2009). This approach ostensibly aims to ensure forest resilience and productivity by maintaining natural ecosystem processes and biodiversity (Grumbine, 1994). Forest ecosystem management therefore considers forests holistically and at broad spatial and temporal scales, and while many of the "ecosystem issues" surrounding forest management are focussed on cumulative, forest-level impacts of management, a good understanding of stand-level development and dynamics is also very important. This is arguably most relevant in the case of forests that are managed under extensive management regimes or are still largely modulated by natural disturbances (Christensen *et al.*, 1996; Bergeron and Harvey, 1997; Franklin *et al.*, 2002).

Boreal mixedwood forests are generally considered among the most productive forests in the boreal zone (Chen and Popadiouk, 2002), and an important source of timber for the forest industry (Penner, 2008). Although mixed species stands may occur through a broad range of age classes, boreal mixedwoods represent a transitional, post-fire stand development phase between break-up of an initial cohort of intolerant hardwoods and dominance by late-successional species (Bergeron, 2000; Chen and Popadiouk, 2002). Moreover, mixedwood stands may also develop as a result of natural partial disturbances such as insect outbreaks or diseases (Ghent, 1958; Bergeron and Leduc, 1998), following harvesting or through succession as a result of different regeneration and mortality dynamics of component species (MacDonald, 1995; Penner, 2008). This said, our understanding of the spatial and temporal variations of second growth mixedwood stands following these disturbances in the southern clay belt region of Quebec and Ontario is still fragmentary (D'Aoust *et al.*, 2004; Brassard and Chen, 2006).

Management of mixedwood forests owes much of its complexity to the numerous variants of stand structure and composition, autoecological differences (shade tolerance, reproductive capacity, growth rates, maximum size, longevity and particular vulnerabilities) among species, site characteristics and diverse disturbances (MacDonald, 1995; Lieffers *et al.*, 1996b). Additionally, the emerging paradigm of managing forests for complexity (Puettmann *et al.*, 2009) would suggest that the heterogeneity of mixedwood stand composition, structure and dynamics presents a veritable palette of management options to silviculturists working in these forests. In this respect, the development of silvicultural approaches adapted to mixedwood stands should include an improved organization of knowledge of the diversity of existing stand conditions and of their underlying forest dynamics.

On mesic sites in the boreal mixedwood region, particularly where fine-textured soils predominate, trembling aspen (*Populus tremuloides* Michx.) frequently dominates following stand-replacing fires (Bergeron, 2000). The transition from aspen-dominated stands to mixedwood is dependent on the rate at which aspen stands are invaded by shade-tolerant conifer species (Galipeau *et al.*, 1997), while succession toward conifer dominance can be set back by eastern spruce budworm (*Choristoneura fumiferana*) outbreaks (Bergeron, 2000). A defoliator of deciduous species, the forest tent caterpillar (FTC; *Malacosoma disstria* Hübner) also plays a significant role in maintaining mixedwood compositions (Moulinier *et al.*, 2011). Considerable work has been undertaken to improve understanding of aspen-shade tolerant conifer dynamics and develop adaptive silvicultural treatments in the boreal plain (Comeau *et al.*, 2005; Grover and Fast, 2007). Despite reporting of a number of studies (e.g., Prévost and Pothier, 2003; Brais *et al.*, 2004; Man *et al.*, 2008b), development of a truly adaptive silvicultural framework for eastern boreal mixedwoods is still in its infancy.

It is expected that partial harvesting will be increasingly applied in mixedwood stands, particularly where the intolerant hardwood component reaches commercial maturity before more shade-tolerant conifers. In this context, in the course of my doctorate, my aim was to explore the role of partial harvesting as a secondary disturbance influencing stand structure and key tree- and stand-level processes, such as recruitment, growth and mortality. The underlying premise of this study is that such treatments can emulate natural successional processes such as gap formation and accelerate stand development towards greater structural and compositional resemblance of over-mature, old-growth or late successional forests. This contribution to the knowledge and understanding of stand development following partial harvesting should 1) provide insights into how harvesting intensity and gap size affect stand structure and composition and influence the development of old-growth attributes, 2) help in forecasting short- to long-term outcomes of different partial harvesting treatments in boreal mixedwoods, and 3) improve the ecological basis for orienting mixedwood silviculture and ecosystem management.

1.2. Theoretical framework

1.2.1. Canadian boreal mixedwood forest region

Canada possesses 10% of global forested landmass, a figure which underscores the importance of this forest for biogeochemical cycling and biodiversity on a planetary scale (Chen and Popadiouk, 2002; Thompson and Pitt, 2003). Of the 417.6 million hectares of Canadian forest, 18% are dominated by boreal mixedwoods (Thompson and Pitt, 2003; Brassard and Chen, 2006), the most productive and diverse forest ecosystems in the North American boreal forest (De Grandpré and Bergeron, 1997; Chen and Popadiouk, 2002). Among three categories or zones (Figure 1.1) of the Canadian boreal forest, the southern-most "Thermoboreal’ zone (Baldwin *et al.*, 2012) incorporates what has traditionally been referred to the eastern and western boreal mixedwoods regions or the “boreal shield” and the “boreal plain”, respectively (Bergeron *et al.*, 2014). Forest composition (relative abundance of hardwoods and conifers) of boreal mixedwoods varies largely throughout its distribution range. This variability of forest composition is due to a range of climatic and biophysical conditions such as natural disturbance regimes, site and soil factors, as well as management histories (Burton *et al.,* 2003, 2010).

1.2.2. Structure and composition of boreal mixedwood stands

Boreal mixedwoods generally present greater resource availability and higher biodiversity than single species stands (Bergeron, 2000). As well, mixedwoods are purported to be more resilient to partial stand disturbances (e.g., insect outbreaks, blowdown) than single-species stands in the boreal region (De Grandpré and Bergeron, 1997; Chen and Popadiouk, 2002) and potentially more resistant to the invasion of pioneer species (Bergeron and Harvey, 1997).

On productive mesic sites, mixedwood stands are characterized by a mixed composition of boreal conifers and shade-intolerant deciduous species. Among these, trembling aspen, white birch (*Betula papyrifera* March), and jack pine (*Pinus banksiana* Lamb.) are common early successional species. In the eastern thermoboreal zone, balsam fir (*Abies balsamea* (L.) Mill.) is the dominant species in late-successional forests on mesic sites, and is associated with white spruce (*Picea glauca* [Moench] Voss), black spruce (*P. mariana* [Mill.] B.S.P.), and eastern white cedar (*Thuja occidentalis* L.) (Bergeron, 2000).

Trembling aspen is the dominant early successional species of the boreal mixedwoods, particularly on fine-textured soils (Bergeron, 2000; Chen and

Popadiouk, 2002). As aspen is very shade-intolerant, can regenerate abundantly locally by root suckering, has fast initial and juvenile growth and is relatively short-lived, it is adapted to a disturbance regime of short fire cycles (Frey *et al.*, 2003). Therefore, if it is present prior to severe disturbances such as fire or clearcut harvesting, an initial cohort of aspen will generally dominate affected sites following these disturbances (Frey *et al.*, 2003; LeBlanc, 2014). It can also be maintained in stands by recruiting, primarily by suckering, into gaps (Cumming *et al.*, 2000) and gap size has a direct effect on sucker density and vigour (Moulinier *et al.*, 2011). Aspen growth decline occurs around the age of 60 years (Pothier *et al.*, 2004) but is influenced by site characteristics, genetic and other predisposing factors (Frey *et al.*, 2004).

Late successional and slower growing species, such as balsam fir, white and black spruce, generally either establish almost immediately following disturbance (with the aspen) but lag in height growth or establish more gradually under aspen-dominated stands. In either case, the stand dynamics are similar in that these species attain the canopy as mid- to late-successional components (Bergeron and Dubue, 1989). White spruce and aspen are the main constituents of the western boreal mixedwood forest (Lieffers *et al.*, 1996a), whereas balsam fir is much more common than white spruce in the east (Kneeshaw and Bergeron, 1998). The biological traits of tree species of the eastern Canadian boreal mixedwood forest are presented in Table (1.1).

Stand development of the boreal mixedwood can be characterized by four different stages: 1) *stand initiation* after disturbance, where pioneer tree species colonize the growing space; 2) *stem exclusion* in which intense resource competition results in self-thinning and fosters vertical tree growth; 3) *canopy transition* in which shade-tolerant conifers grow from the understory and occupy the canopy with shade-intolerant species; and 4) *gap dynamics* in which tree recruitment occurs mostly in small openings created by the death of individuals or groups of old trees (Chen and Popadiouk, 2002). MacDonald (1995) defined stand development of boreal mixedwoods in terms of three stages: *early successional* stages dominated by trembling aspen or white birch; black or white spruce in *mid-successional* stages, and balsam fir in *late successional* stages. However, the length of these successional phases largely depends on disturbance cycle (Bergeron, 2000), species' life history traits, site characteristics and proximity of seed sources (Table 1.1; Bergeron, 2000; Brassard and Chen, 2006). In the eastern boreal mixedwood forest, long fire cycles (>200 years) favour landscape-level dominance of older stands composed largely of late-successional species such as balsam fir, spruces and white cedar (Kneeshaw and Bergeron, 1998). However, periodic insect outbreaks or other partial disturbances contributes to the maintenance of mixedwood stands on a portion of landscapes under long fire cycles, and short fire cycles positively influence the presence of intolerant hardwoods (Lieffers *et al.*, 2003).

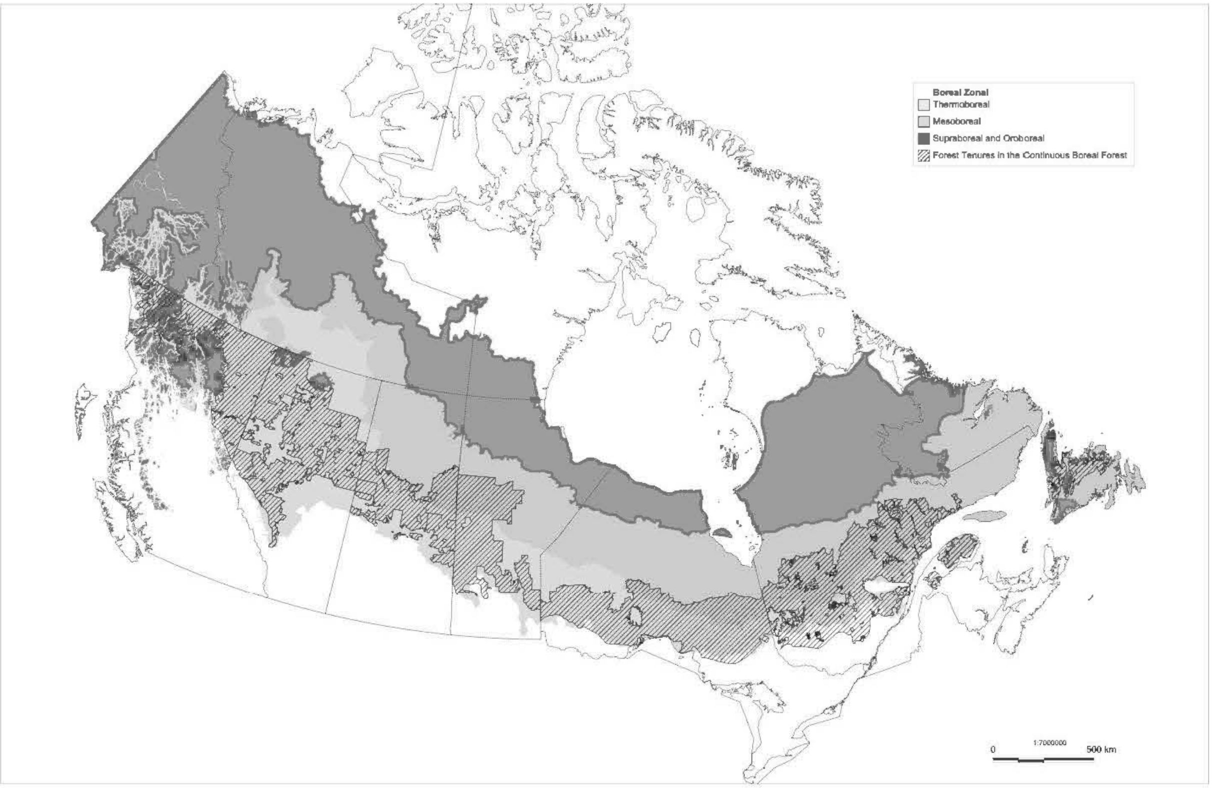

Figure 1.1. Map of the Canadian boreal biome with limits of the Thermoboreal, Mesoboreal and combined Supraboreal–Oroboreal bioclimatic subdivisions (Baldwin *et al.*, 2012) and area within the Thermoboreal ('boreal mixedwood') and Mesoboreal ('continuous conifer') zones currently under forest management 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).

Table 1.1. Biological traits of main forest species of the eastern Canadian boreal mixedwood forest

Species Name	Botanic Name	Plant traits	References
Trembling aspen	*Populus tremuloides* Michx.	Favours medium to deep loamy soils and clays; prolific local reproduction through root suckers following fire; very shade intolerant; early successional deciduous species	Perala, 1990; Bergeron, 2000; Chen and Popadiouk, 2002; Frey et al., 2003; Frey et al., 2004; Pothier et al., 2004
White birch	*Betula papyrifera* Marsh,	Favours coarse-textured soils; reproduction through stem sprouts and seed; shade intolerant and early successional species; colonize successfully after fire	Bergeron, 2000; Chen and Popadiouk, 2002; Harvey et al., 2002
Jack pine	*Pinus banksiana* Lamb.	Favours rocky, sandy and coarse-textured soils; reproduction by seeds released from serotinous cones following fire; shade intolerant and early successional species; generally not considered a typical mixedwood species	Gauthier et al., 1993; Harvey et al., 2002
Black spruce	*Picea mariana* [Mill.] B.S.P.	Large edaphic range; dominates on poor xeric and wet organic soils; post-fire reproduction by seeds from semi-serotinous cones following fire; layering and seeding in the absence of fire; shade tolerant, early to late successional species; slow growing	Bergeron, 2000; Chen and Popadiouk, 2002; Lavoie et al., 2005
White spruce	*P. glauca* [Moench]	Favours mesic sandy loams to clay soils; reproduction through seeds; slow growing, intermediate shade tolerant, mid to late successional species; no fire adaptations, seeds in from fire edges	Chen and Popadiouk, 2002; Solarik et al., 2010; Cortini et al., 2012
Balsam fir	*Abies balsamea* (L.) Mill.	Generally favours mesic sites; reproduction through seed; very shade tolerant; short lived, mid to late successional; no fire adaptations, seeds in from fire edges	Chen and Popadiouk, 2002; Bourgeois et al., 2004;
Eastern white cedar	*Thuja occidentalis* L.	Favours rich hydric sites but found on mesic and xeric sites; shade tolerant, late successional species; no fire adaptations; well-decomposed logs important for seedling establishment	Bergeron and Dubuc, 1989; Bergeron 2000; Ruel et al., 2014
Mountain maple	*Acer spicatum* Lamb.	Clonal woody shrub; favours mesic sites, regenerates by seed and stump sprouts; shade tolerant; can vigorously occupy open areas created by insect outbreaks and impede conifer recruitment by establishing dense understory canopy	Vincent 1965; Batzer and Popp, 1985; Bourgeois et al., 2004

Acer rubrum, Larix laricina, Alnus incana and *Corylus cornuta* are minor tree and shrub species of boreal mixedwoods

1.2.3. Ecosystem-based forest management

Definitions of ecosystem-based forest management may vary slightly, but one common element is the incorporation of a thorough knowledge of natural forests and their dynamics as a reference and guide to forest management planning and interventions (Grumbine, 1994; Christensen *et al.*, 1996; Gauthier *et al.*, 2009). As elsewhere, the scientific basis for forest ecosystem management in Canada largely originated out of academic research and FEM, as a management model or objective, has since progressively gained support in government and industrial sectors. In many respects, it has also gained a high degree of social acceptability, although aspects related to spatial organisation of management areas remains a contentious issue (Gauthier *et al.*, 2009).

Understanding natural forest dynamics at different spatial scales is essential to developing and implementing FEM strategies (Bergeron and Harvey, 1997; Franklin *et al.*, 2007). At the stand-scale, forest dynamics are driven by natural disturbances and other ecological processes associated with stand development; therefore, FEM silvicultural practices are underpinned by an understanding of how natural disturbance and these processes affect stand dynamics. Natural disturbance *emulation* is a better term than *mimicry* but even it should not be interpreted literally; natural disturbance dynamics *inspiration* may more accurately describe the concept (Spence *et al.*, 1999; Franklin *et al.*, 2002; Harvey *et al.*, 2002).

Even-aged silvicultural systems such as clear cutting or careful logging (*coupe avec protection de la régénération et des sols* or CPRS, in Québec) tend to simplify vegetation composition and produce structural homogeneity, especially when followed by artificial forest renewal practices. According to Franklin *et al.* (1997), these types of interventions, if applied at broad scales, can have a homogenizing effect on forests and consequently reduce ecosystem resilience. Using a variety of silvicultural practices, applied at the stand level, can cumulatively result in an increase in forest heterogeneity at the landscape level (Bergeron and Harvey, 1997; Franklin *et al.*, 2007). For example, large, irregular-shaped clearcuts with retention can mimic wildfire spatial patterns while different intensities of partial harvesting can emulate partial disturbances (gaps) resulting from insect outbreaks and windthrow or simply reflect mortality that occurs during different stages of stand development.

1.2.4. Natural disturbance regime in the eastern boreal forest

Fire is the major stand-replacing disturbance in Canadian boreal forests (Johnson, 1996) and fire cycles tend to be longer in eastern Canada than in the west (Bergeron *et al.*, 2004). Species composition following a fire usually depends on species composition before fire as well as fire severity and return intervals (Johnstone and Chapin, 2006). Short fire cycles generally maintain the dominance of fire-adapted deciduous species whereas longer fire cycles provide establishment opportunities for conifers species, such as balsam fir, white spruce and eastern white cedar, that lack regeneration mechanisms adapted to fire (Bergeron *et al.*, 2014).

When the time interval between two fires is longer than the life-span of pioneer or early-successional tree species, non-stand replacing (secondary) disturbances such as insect outbreaks, windthrow and gap dynamics associated with senescence mortality of individuals or small groups of trees modulate successional dynamics (McCarthy, 2001). In boreal mixedwoods, two insect species in particular, the forest tent caterpillar (*Malacosoma disstria* - FTC) and spruce budworm (*Choristoneura fumiferana* - SBW), play an important role in influencing tree mortality and other processes affecting stand dynamics (Bergeron, 2000; Chen and Popadiouk, 2002). Tent caterpillar effects on boreal mixedwoods dominated by trembling aspen have been well documented (e.g., Roland, 1993; Roland *et al.*, 1998; Cooke and Lorenzetti, 2006; Man *et al.*, 2008b; Cooke *et al.*, 2009; Moulinier *et al.*, 2011, 2013). It feeds on foliage of broadleaf species and can potentially accelerate the stand transition from hardwood to mixed species dominance when a conifer understory is present (Cooke and Lorenzetti, 2006). However, severe FTC defoliation in relatively pure forests of intolerant hardwoods may delay this transition by favouring hardwood recruitment in large canopy gaps (Cooke *et al.*, 2009; Moulinier *et al.*, 2011).

Spruce budworm dynamics in Canadian boreal mixedwoods have also been well documented (e.g., Blais, 1981, 1983; Morin *et al.*, 1993; Boulanger and Arseneault, 2004; Johnstone and Chapin, 2006; Kneeshaw *et al.*, 2011). Budworm can also cause severe stand- to forest-level mortality as a result of repeated defoliation of conifers, particularly balsam fir, but also white and black spruce (Blais, 1981, 1983; Morin *et al.*, 1993). Depending on the proportion of host species in the canopy layer, SBW can create a high percentage of canopy gaps and may either promote recruitment of early successional species like trembling aspen or broadleaf shrubs or maintain conifer dominance in succession (Kneeshaw and Bergeron, 1998). Although SBW outbreaks occur less frequently than those of the tent caterpillar, budworm outbreaks are generally longer and have more severe impacts in terms of tree mortality than those of the tent caterpillar (Table 1.2). In addition to mortality due to insect outbreaks, mixedwood stands may become vulnerable to windthrow as they age, particularly after insect outbreaks or after heavy partial harvesting treatments (Bladon *et al.*, 2008).

1.2.5. Partial harvesting as an alternative to even-aged management

The Canadian Forest Service (CFS, 1999) defines partial harvesting as “any cutting in which only part of the stand is harvested” (Thorpe and Thomas, 2007). Partial harvesting is therefore a generic term that encompasses a range of harvesting treatments that remove a portion of trees in a stand but retain others.

Table 1.2. Characteristics of outbreaks of two insect defoliators in Canadian boreal forests. Note. references are given in parentheses

Characteristics	Forest Tent Caterpillar	Spruce Budworm
Host tree species	Trembling aspen, White birch, Balsam poplar (4, 12, 16)	Balsam fir, White spruce, Black spruce (2, 11, 18)
Duration of outbreaks	1 - 6 years (1, 10, 16, 17)	7 - 24 years (5, 11)
Return interval	9 - 13 years (14, 16)	14 - 32 years (5, 11)
Gap formation (%)	Canopy gaps, range: 11.3 to 46.8% (19, 20)	Mean canopy gaps: 40.9 %, mean expanded canopy gaps 54% with a range 39-82% (9, 13)
Stand mortality	Heavy and persistent defoliation can cause an average mortality of 59% live stems (15, 19)	Heavy and persistent defoliation can cause an average mortality of 71% of live stems. In case of pure balsam fir forests, the average mortality can reach 87% with a range: 60-100% (3, 7)
Contributing factors	i) Stand structure and composition: dominance of deciduous trees (especially trembling aspen); larger stems are more vulnerable than smaller ones; ii) poor site quality: drought and high temperatures; iii) fragmented landscapes limit dispersal of pathogens and can result in an increase in the severity of outbreaks (6, 10, 12).	(i) Stand structure and composition: dominance of balsam fir, presence of large (≥ 10 cm DBH) conifers stems, (ii) poor site quality: low precipitation high temperatures and drought (iii) landscape spatial structure: severity is higher in continuous balsam fir-dominated landscapes than in fragmented balsam fir stands surrounded by mixed and deciduous forest (2, 7, 8, 18)

References: [1]Sippell, 1962, [2]Blais 1981, [3]MacLean and Ostaff, 1989, [4]Peterson and Peterson, 1992, [5]Morin et al., 1993, [6]Roland, 1993, [7]Bergeron et al., 1995, [8]Cappuccino et al., 1998, [9]Kneeshaw and Bergeron, 1998, [10]Roland et al. 1998, [11]Boulanger and Arseneault 2004, [12]Frey et al., 2004, [13]Pham et al., 2004, [14]Cooke and Lorenzetti, 2006, [15]Man et al., 2008b, [16]Cooke and Roland, 2007, [17]Cooke et al., 2009, [18]Bouchard and Pothier, 2010, [19]Moulinier et al., 2011, [20]Moulinier et al., 2013

Additionally, in the context of forest ecosystem management, emulating or considering silvicultural analogues to mortality processes associated with natural succession or non-stand replacing disturbances is an important aspect (Lieffers *et al.*, 1996b; Bose *et al.*, 2014c).

At the stand level, partial harvesting has been proposed and tested as a means to move stands more rapidly through succession from intolerant hardwoods to mixedwoods containing higher proportions of shade-tolerant conifer stems and greater stand structural complexity (MacDonald, 1995; Bergeron *et al.*, 1999). These are characteristics generally attributable to over-mature or late-successional stands which have become increasingly rare in managed boreal landscapes. Therefore, partial harvesting may be applied as a stand-level practice to attain forest-level objectives of maintaining a portion of managed landscapes in old forests or in forests with structural and compositional attributes approaching those of natural old-growth and over-mature stands (Lieffers *et al.*, 1996b; Bergeron and Harvey, 1997; Franklin *et al.*, 1997). Nyland (2003) suggested that 1) partial harvesting could be used to convert even-aged stands to uneven-aged structures or to maintain uneven-aged stand structure and 2) uneven-aged stand structure was important for maintaining stand diversity, supporting understory growth and increasing regeneration potential.

In Canada, many jurisdictions have adopted regulations that require live tree retention in harvest blocks. However, retention levels across Canada are generally very low (< 10%) (Thorpe and Thomas, 2007), often limited to maintaining a few trees of any commercial size and species per hectare. A number of experimental partial harvesting trials aimed at exploring alternative silvicultural systems to clearcut harvesting have been established in different parts of the North America, including the Canadian boreal mixedwood forest (Table 1.3.).

Table 1.3. Partial harvesting experimental trials in Canadian boreal forests

Establishment year	Name and Location	Silvicultural treatments	References
1993	Black Sturgeon Boreal Research Site, North-western Ontario	clearcut; uncut; patch cut; shelterwood cuts	Scarratt, 1996
1993	Alcott Creek Forest Management Demonstration Area, Central Saskatchewan	two-stage aspen harvesting (protecting of small white spruce)	adapted from Thorpe and Thomas 2007
1993	Hotchkiss River Mixedwood Timber Harvesting Study, Northwestern Alberta	eleven harvesting systems that includes un-cut, one-pass, two-pass, three-pass and four-pass shelterwood cuts and 50, 100 and 150 m strip cuts	MacIsaac *et al.,* 1999
1994	Muskeg River Silvicultural Study, southwestern Northwest Territories	clearcut; strip cut; patch cut	adapted from Thorpe and Thomas 2007
1994	Calling Lake, Alberta	clearcut and two partial cuts (high thin and low thin)	Norton and Hannon, 1997
1995	Ontario Mixedwood Silviculture Project, Cochrane, Ontario	clearcut; uncut; partial cuts with 36 and 68% BA removal	MacDonald *et al.,* 2004
1995	Bellechasse County, Quebec	clearcut; uncut; partial cuts with 35, 50, and 65% BA removal	Prévost and Pothier 2003
1998	Ecosystem management by emulating natural disturbance (EMEND), Peace River, Alberta	clearcut; uncut; partial cut with 10, 20, 50, and 75% retention	Solarik *et al.,* 2010
1998	Sylviculture et aménagement forestiers écosystémique (SAFE-1), Abitibi, Quebec	clearcut; uncut; partial cut with 33 and 61% BA removal	Brais *et al.,* 2004
2000	Sylviculture et aménagement forestiers écosystémique (SAFE-3), Abitibi,Quebec	clearcut; uncut; 45% BA removal in dispersed cut and 54% BA removal with 400 m^2 gap cuts	Brais *et al.,* 2013
2003-2004	Temiskaming region in western Quebec, Canada	Succession cut (2/3 of all intolerant hardwoods stems ≥ 10 cm DBH) and diameter limit cutting (all intolerant hardwood stems stems ≥ 10 cm DBH)	Gendreau-Berthiaume et al., 2012

1.2.6. Stand-level responses to partial harvesting

Differential responses of stands to partial harvesting can be explained by pre-treatment stand's characteristics and the characteristics of residual stands (Solarik *et al.*, 2010; Bose *et al.*, 2014c). For example, regeneration recruitment of shade-tolerant conifers varies considerably when the pre-harvest stand condition is different in terms of advanced conifer regeneration (Prévost and Pothier, 2003), seed tree density (Solarik *et al.*, 2010), availability of proper seed beds (Groot *et al.*, 1996; Calogeropoulos *et al.*, 2004; Robert *et al.*, 2012), density of understory woody shrubs (Bourgeois *et al.*, 2004; MacDonald *et al.*, 2004) and percentage of canopy gaps (Cumming *et al.*, 2000; Moulinier *et al.*, 2011, 2013). Moreover, light availability at the forest floor and regeneration layer may vary considerably among mixedwood stand types depending on the relative abundance of deciduous and conifer species in the overstory layer and presence of understory vegetation (Messier *et al.*, 1998). It should be noted as well, that establishment of conifer regeneration may vary considerably as a result of forest floor conditions including the thickness of leaf litter (Simard *et al.*, 2003; Wang and Kemball, 2005), abundance of feathermoss and quantity and state of decomposition of downed logs (Nienstaedt and Zasada, 1990).

Adequate natural regeneration and establishment of commercially desired conifer species are major silvicultural issues in mixedwood boreal forests of both eastern and western Canada (Prévost and Pothier, 2003; Peters *et al.*, 2005). Short-term (≤ 11 years) empirical studies show that partial harvesting has the potential to maintain growth and favour recruitment of shade-tolerant conifer regeneration (Prévost and Pothier, 2003; Brais *et al.*, 2004; Man *et al.*, 2008a) as well as recruitment of intolerant hardwood regeneration (Brais *et al.*, 2004; Gradowski *et al.*, 2010; Prévost *et al.*, 2010).

Mortality of residual trees is another major concern of partial harvesting in the Canadian boreal mixedwood and other forest regions of Canada. Based on a silvicultural experiment in Cedar-Hemlock forests of Northern British Columbia, Coates (1997) suggested that partial harvesting should be considered a failure if residual tree mortality exceeded 10% of that in un-treated control stands. During partial harvesting treatment application, residual trees can be physically damaged by logging operations (Moore *et al.*, 2002; Thorpe *et al.*, 2008) and after treatment, increased wind penetration into residual stands may generate greater evaporative demand in residual stems (Bladon *et al.*, 2008; Lavoie *et al.*, 2012), and impair stem conductivity by restricting water supply to leaves (Liu *et al.*, 2003). Limited information exists on medium- to long-term (>10 years) responses of trembling aspen- dominated mixedwood stands to partial harvesting in the eastern boreal mixedwood forest (Man *et al.*, 2008a; Prévost *et al.*, 2010). Current questions concerning post-treatment dynamics in these forests range across a variety of themes: mortality of residual stems, dynamics of aspen suckers, recruitment of shade-tolerant species and influence of high shrubs on growth of desired species, gap dynamics, abundance of deadwood and other potential wildlife substrates (Man *et al.*, 2008a).

1.2.7. Tree-level growth responses to partial harvesting

Post-harvest growth response of an individual tree depends on, among other factors, the neighborhood conditions created by the harvesting operation (Hartmann *et al.*, 2009). Along with neighborhood condition, age, tree size and growth rate immediately prior to harvest have been shown to influence post-harvest growth responses (Thorpe *et al.*, 2007; Jones *et al.*, 2009). These variables determine the ability of an individual to respond to competition and to new availability of resources. The position of the tree (dominant, co-dominant, intermediate or suppressed) in the canopy prior to and after harvest is also crucial to understand the mechanisms of competition. In the aspen-dominated boreal mixedwood of eastern Canada, most research has focused on stand-level growth responses to partial harvestings (Man *et* *al.*, 2008a; Prévost *et al.*, 2010), but no study has examined volume responses of mature residual trembling aspen.

Following release from competition, trees generally display an increased growth rate; however, responses may vary between intolerant and tolerant species (Jones *et al.*, 2009), and depend on crown position. Suppressed growth prior to cutting may also affect a species' ability to respond to harvest, and slow pre-harvest growth rates have been associated with relatively modest growth increases (Thorpe *et al.*, 2007). Moreover, tree size and age influence a tree's capacity to compete for resources. For example size inequality in tree populations tends to make competition asymmetric (Metsaranta and Lieffers, 2008). Larger individuals obtain a disproportionate share of resources and suppress the growth of smaller individuals (Berntson and Wayne, 2000). Additionally, tree morphology and architecture determine the way plants capture and deprive their neighbours of resources (Messier *et al.*, 1999).

The mode of competition may be determined by the nature of the resource being contested. Light favours trees in the dominant class, leading to asymmetric competition, whereas more symmetric competition may occur for water and soil nutrients (Connolly and Wayne, 1996). In uniform even-aged stands, a relatively simple distance-independent approach may be sufficient to predict tree-level growth responses to neighbourhood competition (Weiskittel *et al.*, 2011). Partial harvesting promotes a certain level of structural complexity (Zenner, 2000; Witté *et al.*, 2013) and influences the competition dynamics among tree individuals (Hartmann *et al.*, 2009). In stands with more complex structure, incorporating both distance-dependent and distance-independent approaches while integrating crowding, shading and species effects on neighbourhood competition provides insights into tree-level growth responses (Canham *et al.*, 2004; Canham *et al.*, 2006; Coates *et al.*, 2009).

1.2.8. Emulation or acceleration of stand development towards old-growth attributes through partial harvesting

Like ecosystem-based forest management itself, emulation of natural disturbance dynamics using partial harvesting is a relatively new concept. In this perspective, a major objective of partial harvesting is to emulate secondary disturbances and natural gap dynamics and to accelerate stand development towards old-growth/late successional stages of stand development (Bergeron and Harvey, 1997; Franklin *et al.*, 2002). It is expected that by retaining biological legacies and by emulating natural gap formation, partial harvesting could reduce differences between managed and natural forest ecosystems and promote a certain level of structural complexity comparable to old-growth or over-mature stands (Franklin *et al.*, 2002; Franklin *et al.*, 2007). Old-growth or late successional forest stands generally have a number of characteristic features: large canopy trees, large standing snags and important downed woody debris loads, high percentage of canopy gaps, multi-layer canopies, high structural variability in terms of tree sizes (DBH and height) and high species diversity. (see details in Franklin and Van Pelt, 2004; Zenner, 2004; Bauhus *et al.*, 2009). However, Canadian boreal forests do not contain large, towering trees like the forests of coastal British Columbia or the Pacific Northwest, and are not species-rich like tropical forests (Burton *et al.*, 2013). Therefore, they are best characterised by the presence of variable canopy gaps, multi-layered canopies, high tree size variability and the presence of late-successional species (see details in Harper *et al.*, 2003; Kneeshaw and Gauthier, 2003).

In the boreal mixedwoods, partial harvesting has been shown to accelerate stand development by facilitating recruitment of shade-tolerant conifers (Prévost and Pothier, 2003; Man *et al.*, 2008a) and increasing the variability in understory structure (Haeussler *et al.*, 2007). The benefit of partial harvesting in increasing structural complexity has also been reported for mixed conifer forests of Quebec (Witté *et al.*, 2013) and the Pacific Northwest, USA (Zenner, 2000). However, such effects often depend on the specifics of the partial harvesting treatments themselves and some studies have reported that partial harvesting decreased large tree density and standing deadwood basal area and could not replicate natural canopy gap formation (Harvey and Brais, 2007; Jacobs *et al.*, 2007). The reduction of large trees and deadwood after partial harvesting has also been cited for other forest types of North America (McGee *et al.*, 1999; Angers *et al.*, 2005; Keeton, 2006).

1.2.9. Modeling stand development after partial harvesting

Forest management has concentrated on growth and yield since its inception (Assmann, 1970) and an accurate growth and yield prediction is a prerequisite for sustainable forest management (or at least for sustained yield). Modelling approaches used to understand and project stand and tree growth reduce the time required and operational costs associated with long-term monitoring and, in fact, provide a complementary analysis tool to field trials for investigating and comparing different silvicultural options and outcomes. Foresters and silviculturists are generally familiar with empirical yield tables and recognize their utility for predicting volume yields for fairly homogenous (even-aged, mono-specific) stand conditions (Penner, 2008; Weiskittel *et al.*, 2011). Boreal mixedwood management that includes partial harvesting introduces greater complexity into stand development (e.g., multiple species, greater range of tree ages), which is not easily treated using existing yield tables. Individual-based stand dynamics models are generally more flexible than yield tables (Coates *et al.*, 2003; Groot *et al.*, 2004), allow greater exploration of silvicultural options and may provide more detailed prediction of tree sizes (Thorpe *et al.*, 2010; Weiskittel *et al.*, 2011).

SORTIE-ND is a spatially-explicit, individual-based stand dynamics model (Murphy, 2011). It originated from the small-scale disturbance model SORTIE developed and tested in the early 1990's for transitional oak-northern hardwood forests in the northeastern U.S. (Pacala *et al.*, 1996) and was re-parameterized for the Interior

Cedar-Hemlock forest of British Columbia (Coates *et al.*, 2003). Since then, it has been used to explore forest dynamics in a number of forest ecosystems, including eastern boreal mixedwoods (Beaudet *et al.*, 2011; Vanderwel *et al.*, 2011), western boreal mixedwoods (Stadt *et al.*, 2007), black spruce forests in Ontario (Thorpe *et al.*, 2010), northern hardwood forests of eastern Canada (Beaudet *et al.*, 2002), mixed temperate forests in British Columbia (Astrup *et al.*, 2008; Haeussler *et al.*, 2013) and elsewhere in the world (Canham *et al.*, 2010; Ameztegui *et al.*, 2012; Yasuda *et al.*, 2013). It is particularly suitable for applications involving mixed species stands and partial disturbances (Coates *et al.*, 2003) and has been used to explore and forecast outcomes under alternative silvicultural systems over longer time scales than those covered by existing empirical studies (Vanderwel *et al.*, 2011).

1.3. Thesis objectives and structure

This thesis was undertaken to enhance knowledge on the potential of using partial harvesting silviculture in the context of natural disturbance-based forest management in trembling aspen-dominated boreal mixedwood forests of eastern Canada. The general objective of this research was to evaluate and explore the effects of partial harvesting on dynamics of these stand types. Specifically, the thesis addresses stand-level recruitment and residual tree mortality (chapter-2) and growth of residual overstory trees (chapter-3) following partial harvesting, and the notion of emulating or accelerating natural succession (chapter-4) and, finally, explores long-term stand dynamics (chapter-5) of eastern Canadian boreal mixedwoods following and in the absence of partial harvesting.

The thesis was conducted in a series of silvicultural experiments known as the SAFE (*sylviculture et aménagement forestier écosystémiques*) project, located in the Lake Duparquet Research and Teaching Forest (Fig. 1.2 and 1.3) in the Western balsam fir-white birch bioclimatic subdomain (Saucier *et al.*, 1998). During the winters of 1998 and 2000 two stand types were respectively subjected to different cutting treatments (core treatments) including controls, complete harvesting, and two variants of partial harvesting. Treatments were adapted to stand type characteristics (structure and composition, presence or absence of natural regeneration) and replicated three times within each stand types. Experiments were monitored on a regular basis for a period of 12 years after harvesting. This study used experimental approaches (chapter 2, 3 and 4) and a stand dynamics modelling approach (chapter 5) to answer specific research questions.

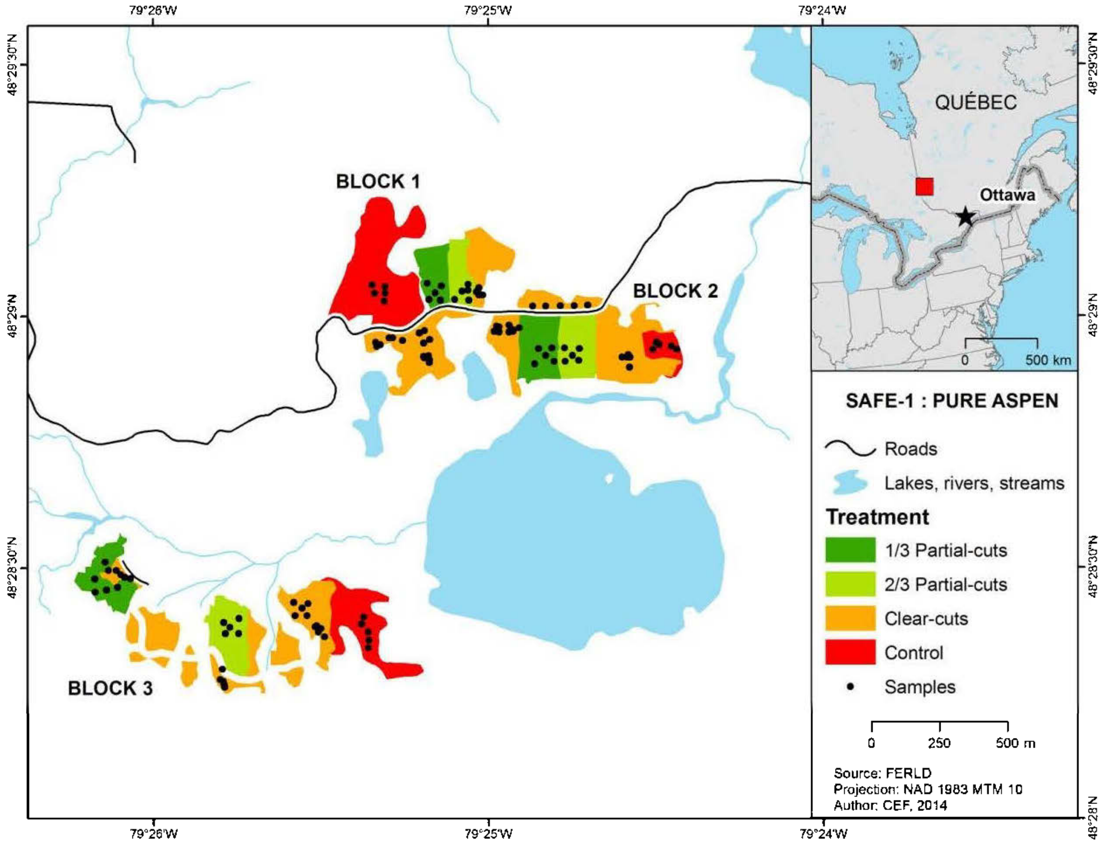

Figure 1.2. Map of pure aspen study site (SAFE1)

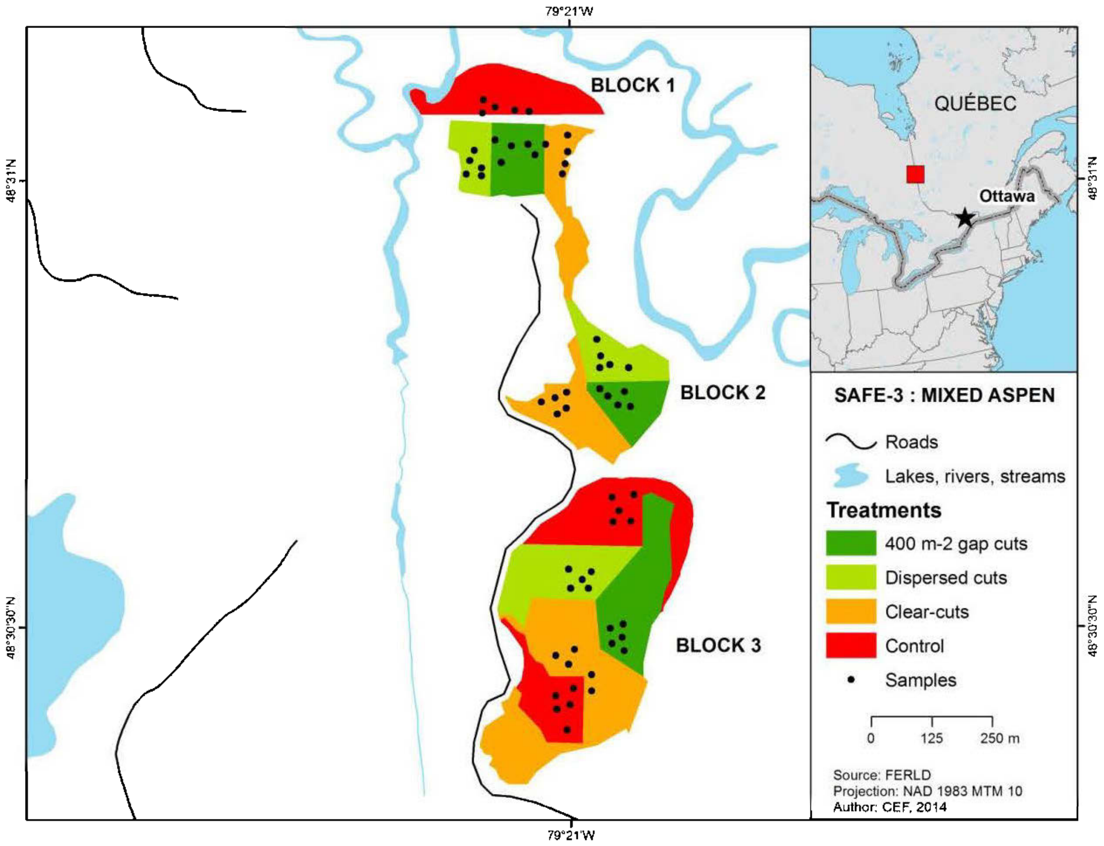

Figure 1.3. Map of mixed aspen study site (SAFE 3)

Previous studies conducted in Canadian boreal mixedwoods have indicated that, over the short-term, partial harvesting of aspen or mixed-aspen stands initiates a second cohort of aspen, increases the growth rate of advanced conifer regeneration and maintains most of the structural attributes of mature stands. Over the longer term (12 years), I expected that, following partial harvesting of ≥ 50% of basal area or gap harvesting, residual stems would be more susceptible to mortality due to windthrow compared to lighter harvesting treatments. This in turn would favour a progressive opening of the canopy, increase canopy gap size and changes in the dynamics between commercial and competitive species, potentially generating a shrub-dominated community. I also expected that the more intense harvesting prescriptions would accelerate the growth of residual trees by decreasing competition and increasing resource availability as well as accelerate the development of old growth attributes by creating growing space for new tree cohorts.

This thesis contains six chapters, four of which are written in manuscript format (chapters 2 to 5). Each of the manuscript chapters includes a separate introduction section in which its specific rationale and objectives are described. (Obviously, there is a certain level of redundancy in the introduction and study area sections of these chapters.) In Chapter 1, the background and justification of the study are presented in the context of current issues related to forest ecosystem-based management in boreal mixedwoods of eastern Canada. In addition, a theoretical framework is developed based on a thorough literature review. Chapters 2 to 5 use four different approaches to analysing the effects of partial harvesting on stand dynamics of eastern boreal mixedwoods. In Chapter 2, inventory data of permanent sample plots were used to examine post-harvest residual tree mortality and sapling recruitment relative to unharvested, naturally aging controls and clearcut treatments. Analyses were carried out separately for trembling aspen, shade-tolerant conifers (black spruce, white spruce and balsam fir) and mountain maple (a high woody shrub). In Chapter 3, a dendrometrical approach was used to examine tree-level volume growth responses of residual trembling aspen trees after two contrasting intensities of partial harvesting. This chapter investigates tree-level volume growth responses as a function of partial harvesting treatments, pre-treatment tree sizes, time since treatment application, post-treatment social status and post-treatment neighborhood competition. Based on a review of the literature, Chapter 4 provides a framework for defining and characterising old-growth or late-successional aspen mixedwoods and, using permanent sample plots and transects, evaluates the potential of partial harvesting treatments applied in the SAFE project to accelerate stand development towards the old-growth stage. In Chapter 5, the spatially-explicit stand dynamics model SORTIE-ND was used to explore short- to long-term stand development for mixedwood stands with two different starting conditions and under a variety of silviculture scenarios.

SORTIE-ND was first parameterized for the study site and model performance was evaluated using short- and long-term empirical data. We then modelled stand dynamics following a range of simulated partial harvesting treatments of different intensities (33, 61 and 80% basal area removal), and gap sizes, (400, 900 and 1600 m^2 gap size). The concluding Chapter 6 summarizes the results and their implications for partial harvesting in the boreal mixedwood, then discusses possible strategies for boreal forest management and avenues for further research.

CHAPITRE II

SAPLING RECRUITMENT AND MORTALITY DYNAMICS FOLLOWING PARTIAL HARVESTING IN ASPEN-DOMINATED MIXEDWOODS IN EASTERN CANADA

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2.1. Abstract

Boreal mixedwood management has shifted from a relatively narrow focus on commercial wood supply to greater consideration of the natural dynamics and multiple ecological services. This recognition has generated interest in ecosystem management approaches that include diversifying and adapting silvicultural practices, including partial harvesting. The effects of partial harvesting on stand dynamics was assessed over a 12-year period in trembling aspen (*Populus tremuloides* Michx.) dominated stands in northwestern Quebec, Canada. Four treatments were tested: clearcuts (100% basal area (BA) removal); 1/3 partial cut (1/3 PC, 33% BA removal using low thin); 2/3 partial cut (2/3 PC, 61% BA removal using high thin) and controls (0% removal). Aspen sapling recruitment was directly affected by harvesting intensity with 1/3 and 2/3 partial cuts generating 5% and 56%, respectively, of aspen sapling densities in clearcuts. Aspen sapling recruitment increased continuously following clearcut and partial cut treatments with no significant mortality in the sapling layer over the 12-year period. Recruitment of conifer saplings also increased with time and was significantly higher in the two partial cuts than in the clearcut treatment. Twelve years after treatments, mortality of residual aspen stems (>10 cm DBH) reached 250 stems ha^{-1} 12 yr^{-1} in controls, compared to 106, and 170 stems ha^{-1} 12 yr^{-1} in 1/3 PC, and 2/3 PC stands, respectively. Initially (1–3 years after treatments), higher overstory aspen mortality was associated with the 2/3 PC treatment. Aspen mortality was strongly associated with small-sized merchantable stems (10–19.9 cm DBH) regardless of treatment. Both partial harvesting treatments had the effect of maintaining mountain maple (*Acer spicatum* Lamb.), a shade-tolerant, high woody shrub, at densities similar to those in control stands whereas recruitment of mountain maple saplings was negligible in clearcuts due to high aspen recruitment. Our results indicate that (i) heavy-high partial harvesting promotes sapling recruitment of both aspen and conifers when advance regeneration of the latter is present, (ii) because aspen sucker response can be controlled by varying harvesting intensities and stem selection, it is possible to create a range of mixedwood conditions, depending on whether mixed, structurally complex or more regular aspen-dominated stands are desired, and (iii) on rich mixedwood sites, tall woody shrubs could hinder desirable partial harvesting outcomes.

Keywords: Boreal mixedwood, Ecosystem management, Partial harvesting, Sapling recruitment, Residual tree mortality, Variable retention

Résumé

La gestion de la forêt boréale mixte est passée d'une dynamique productiviste visant principalement l'approvisionnement en bois commercial à une meilleure intégration de la dynamique forestière naturelle et des multiples services écologiques de cet écosystème. Cette évolution s'est traduite par une approche d'aménagement écosystémique qui préconise la diversification et l'adaptation des pratiques sylvicoles incluant le recours à des coupes partielles. L'effet de coupes partielles sur la dynamique des peuplements a été étudié dans des peuplements équiennes dominés par le Peuplier faux-tremble (*Populus tremuloides* Michx.) dans le Nord-Ouest du Québec, Canada. Quatre traitements ont été appliqués : la coupe totale, une éclaircie par le bas de 33 % (CP1/3) de la surface terrière (ST), une éclaircie par le haut de 61 % (CP2/3) de la ST et un contrôle non coupé. Au cours des 12 années suivant la coupe, le recrutement des gaules de P. faux-tremble a augmenté progressivement et de manière proportionnelle à la ST prélevée, sans mortalité significative des gaules. Douze ans après la coupe, les CP1/3 et CP2/3 généraient respectivement 5% et 56% des densités de gaules retrouvées suite à la coupe totale. Le recrutement des conifères augmentait aussi dans le temps et était significativement supérieur dans les coupes partielles que dans la coupe totale. Initialement (1–3 ans après coupe), la mortalité du P. faux-tremble reflétait principalement celle des petites tiges marchandes (10–19.9 cm DHP) et la mortalité relative la plus importante était associée à la CP2/3. Douze ans après traitement, la mortalité cumulative des tiges résiduelles de P. faux-tremble (>10 cm DHP) atteignait 250 tiges ha^{-1} dans le contrôle, comparée à 106 et 170 tiges ha^{-1} sous la CP1/3 et la CP2/3 respectivement. Les coupes partielles ont maintenu à des densités similaires à celle des peuplements contrôles, d'Erable à épis (*Acer spicatum* Lamb.), une espèce arbustive tolérante à l'ombre. En revanche, le recrutement de l'E. à épis était négligeable après coupe totale. Nos résultats suggèrent que (i) la coupe partielle par éclaircie par le haut favorise le recrutement conjoint du P. faux-tremble et des conifères lorsque la régénération chez ces derniers est présente, (ii) qu'en contrôlant la ST prélevée et la structure diamétrale résiduelle, il est possible de recréer les conditions variables allant ds peuplements de P. faux-tremble purs à des peuplements mixtes, de peuplements structurellement complexes à des peuplements davantage réguliers et (iii) que sur les sites mixtes riches, la présence d'arbustes hauts pourrait entraver les effets bénéfiques des coupes partielles.

Mots clés: Forêt boréale mixte, Aménagement écosystémique, Coupe partielle, Recrutement, Mortalité des arbres résiduels et Rétention variable

2.2. Introduction

The Canadian boreal mixedwood forest is the most productive and diverse ecosystem in the North American boreal forest (Chen and Popadiouk, 2002). In recent decades, management objectives of boreal mixedwoods have shifted from a rather limited focus on commercial wood production to broader perspectives of ecological forestry (Gauthier *et al.*, 2009). Over this period, considerable interest and effort have been paid to developing and testing silvicultural systems that more closely integrate natural stand dynamics, a tenet of forest ecosystem management (Bergeron and Harvey, 1997; Gauthier *et al.*, 2009). Natural disturbance emulation (NDE), a variant of forest ecosystem management which places importance on historical disturbance regime and natural dynamics as a template for management and silvicultural strategies (Bergeron and Harvey, 1997; Perera *et al.*, 2007), is currently applied, to varying degrees, in the many parts of the boreal mixedwood.

Mixedwood stands dominated by trembling aspen (*Populus tremuloides* Michx.) are common in many parts of the eastern boreal forest of Canada where rich soils are present and average fire cycle is longer than maximum age of early successional species such as aspen and white birch (*Betula papyrifera* March) but not so long as to favor complete elimination of these species from the landscape (Girardin *et al.*, 2004; Bergeron *et al.*, 2006). In the absence of fire, partial stand disturbances (e.g., insects, windthrow) or gradual mortality of canopy trees through senescence, disease or small-scale gap formation favor the transition from intolerant hardwood dominance to mixed compositions (Kneeshaw and Bergeron, 1998). In the eastern Canadian boreal forest, balsam fir (*Abies balsamea* (L.) Mill.) is the most abundant gap filling species in aspen dominated stands (Kneeshaw and Bergeron, 1998).

It is expected that partial harvesting will be increasingly applied in mixedwood stands, partly to ensure greater structural variability on managed landscapes than produced by conventional even-aged regimes, but certainly as a complementary silvicultural approach to meeting wood production objectives. Interactions between residual tree density and pattern of retention determine residual tree influence on stand environment (Carlson and Groot, 1997; Bose *et al.*, 2014c). Success of partial harvesting ultimately depends on three factors: adequate regeneration recruitment of desired species (Messier *et al.*, 1999; Bose *et al.*, 2014c), a positive growth response of residual stems in the canopy and sub-canopy layers (Thorpe *et al.*, 2007) and limited mortality of residual and recruited trees (Coates, 1997).

One key distinction between partial harvesting and natural disturbance is the reduced potential for recruitment of deadwood, a favorable substrate for seedling establishment when in an advanced stage of decomposition (Robert *et al.*, 2012). Hence, conifer regeneration in partial harvestings may be impeded by a lack of proper seed beds (Groot *et al.*, 1996; Calogeropoulos *et al.*, 2004). In stands dominated by trembling aspen, dense sucker regeneration in gaps (Cumming *et al.*, 2000) can also hinder conifer regeneration. However, recent studies conducted in eastern aspen-dominated mixedwood stands have demonstrated that, depending on harvesting intensity, partial harvesting can initiate or inhibit adequate aspen regeneration (Prévost and Pothier, 2003; Brais *et al.*, 2004) and promote a mixedwood composition by favoring growth of advance conifer stems in the understory and recruitment of conifer regeneration (Man *et al.*, 2008a; Prévost *et al.*, 2010). This said, reduced growth of conifer trees has also been documented under heavy competition from understory shrubs (MacDonald *et al.*, 2004). For example, mountain maple (*Acer spicatum* Lamb.), a shade-tolerant woody shrub, can vigorously occupy openings such as gaps created by insect outbreaks (Batzer and Popp, 1985) and forest harvesting (Perala, 1974) and consequently limit recruitment and growth of conifer regenerations (Vincent, 1965).

Residual trees can be physically damaged by logging operations (Moore *et al.*, 2002; Thorpe *et al.*, 2008) and be affected indirectly from greater evaporative demand or wind exposure after harvesting (Bladon *et al.*, 2008; Lavoie *et al.*, 2012), effects that can ultimately induce tree mortality. In one of the rare studies that has actually made reference to a partial harvesting success/failure threshold based on post-treatment mortality, Coates (1997) suggested that partial harvesting in Cedar-Hemlock forests of Northern British Columbia should be considered a failure if residual tree mortality exceeded 10% (over mortality in control stands) in the first 2 years following treatments. In such cases, he suggested that changes to treatment applications should be imposed.

Limited information exists on medium to long term (>10 years) responses of mixedwood stands to partial harvesting in eastern boreal Canada (Man *et al.*, 2008a; Prévost *et al.*, 2010). Current questions concerning post-treatment dynamics in these forests range across a variety of themes: mortality of residual stems, dynamics of aspen suckers, recruitment of shade tolerant species and influence of high shrubs on growth of desired species (Man *et al.*, 2008a). This study addresses, at least partially, these knowledge gaps by evaluating periodical responses, over a 12 year period, of aspen-dominated mixedwood stands to partial harvesting. The objective of this study was to examine changes in aspen and conifer sapling recruitment and mortality of residual merchantable stems following partial harvesting compared to a clearcut treatment and unharvested controls. We tested the following hypotheses: (i) recruitment of trembling aspen is expected to follow a gradient of canopy opening (Frey *et al.*, 2003), (ii) sapling recruitment of shade tolerant conifer is expected to be facilitated by partial harvesting (Prévost and Pothier, 2003; Man *et al.*, 2008a), (iii) heavy-high partial harvesting is expected to result in higher aspen tree mortality due to the retention of more suppressed (low vigor) residual stems and greater changes in stand microclimate (Bladon *et al.*, 2008; Solarik *et al.*, 2012), and (iv) higher mountain maple recruitment into the sapling layer is expected in clearcuts compared to partial cuts and controls (Bourgeois *et al.*, 2004).

2.3. Methods

2.3.1. Study area

The study was conducted in the Lake Duparquet Research and Teaching forest (LDRTF) located in the Abitibi region of northwestern Quebec (48°86′N–48°32′N, 79°19′W–79°30′W). The climate is continental with mean annual precipitation (1991–2010) of 847 mm, of which 583 mm falls as rain from April to September and mean annual temperature is 1.95 °C. However, from April to September the average temperature is 11.9 °C (BioSIM, 2012). This region is characterized by the presence of extensive glaciolacustrine deposits left by proglacier Lake Ojibway (Vincent and Hardy, 1977) and rich clayey soils on upland sites (Canada Soil Survey Committee, 1987b).

The LDRTF is situated in the balsam fir (*A. balsamea* (L.) Mill.) – white birch bioclimatic domain (Saucier *et al.*, 1998). Forests of the region are characterized by a mixed composition of boreal conifers and shade-intolerant broad-leaved species. Trembling aspen, white birch, and jack pine (*Pinus banksiana* Lamb.) are common early successional species. Balsam fir is the dominant species in late-successional forests on mesic sites, and is associated with white spruce (*Picea glauca* [Moench] Voss), black spruce (*P. mariana* [Mill.] B.S.P.), and eastern white cedar (*Thuja occidentalis* L.) (Bergeron, 2000).

2.3.2. Experimental design and treatments

The SAFE project (*Sylviculture et aménagement forestier écosystémique*) (Brais *et al.*, 2004; Brais *et al.*, 2013) is a series of experiments implemented in Northwestern Quebec to assess the feasibility of ecosystem-based forest management for this region. The stands in this study originated from a stand-replacing fire in 1923 (Dansereau and Bergeron, 1993) and had not been subject to any silvicultural treatments prior to the study. At the time of harvesting treatments, stands had a mean basal area (BA) of 44 m^2 ha^{-1} composed of trembling aspen (92%), white birch (2.5%), and shade tolerant conifers (fir and spruce, 3%) (Table 2.1, Fig. 2.1A). The understory was dominated by woody shrubs, particularly mountain maple (*A. spicatum* Lamb.), but also beaked hazelnut (*Corylus cornuta* Marsh) and speckled alder (*Alnus rugosa* L.), with fairly scarce presence of conifer (mostly balsam fir) advanced regeneration (Bourgeois *et al.*, 2004).

Harvesting treatments were applied during the winter of 1998–1999 according to a complete block design with 3 blocks containing 4 experimental units ranging from 1 to 2.5 ha. Along with clearcuts and controls, 2 dispersed partial harvesting treatments were applied using manual felling and bucking and forwarded using small skidders. All trees were removed from trails that were on average 4.5 m wide and spaced at 30 meters. The first treatment (1/3 PC) was a light, low thin in which one third of the merchantable basal area, mostly intermediate and suppressed stems, were harvested. The second treatment (2/3 PC) was a heavy high thin in which two thirds of the merchantable BA, primarily dominant and co-dominant stems, were removed (Fig. 2.1B and C). Treatments were assigned randomly with minor adjustments to ensure minimum conifer understorey regeneration in partial cut treatments.

2.3.3. Field methods

Before harvesting, five 400 m^2 permanent sample plots (PSP, radius = 11.28 m) were established in each experimental unit. All stems (trees and shrubs) greater than 5 cm at breast height (1.3 m) were identified to species, tagged, and diameter (DBH) measured using a diameter tape. In a 100 m^2 quadrant of each plot, all stems between 2.0 and 4.99 cm DBH were also identified to species, tagged, and DBH measured. All stems were identified to species and tallied by height class (Brais *et al.*, 2004). Immediately following harvesting, a tally of all remaining stems was compiled and seedlings and suckers of the regeneration layer (<2 cm DBH) were inventoried in eight 1-m^2 quadrants uniformly dispersed within each PSP, for a total of 40 quadrants in each experimental unit. All PSPs were remeasured every 3 years, in 2001, 2004, 2007 and 2010. Besides DBH measurements, stems that recruited into the sapling layer were tagged and measured and stems that died in the interim period were noted and assigned to a decomposition class.

2.3.4. Data analysis

2.3.4.1. Response variables

Periodic (over each 3-year period) and cumulative sapling (2.0–9.9 cm DBH) recruitment (from time of harvesting to each periodic measurement) and mortality of residual overstory stems (≥10 cm DBH) were compiled from successive inventories of over a 12 year period. Sapling recruitment was compiled for aspen, shade tolerant conifer species (balsam fir + white and black spruce) and mountain maple. Sapling recruitment included all stems that were inventoried for the first time during a given inventory. Similarly, mortality for residual overstory trees of a given period included all dead trees that died between two consecutive inventories. Residual aspen trees were classified into three groups based on DBH size classes (small – 10–19.9 cm, medium – 20–29.9 cm, and large >29.9 cm) to estimate the effect of tree size on mortality. We also analysed periodic and cumulative mortality of mountain maple stems. Sapling recruitment between 1999 and 2001 for all species was too low to be statistically analysed. For the same reason, aspen sapling recruitment in the controls, merchantable aspen mortality in clearcuts, and mountain maple recruitment and mortality in clearcuts were not included in analyses.

2.3.4.2. Statistical analyses

Effects of treatments and time since treatment on recruitment and mortality were assessed by means of linear mixed models (Pinheiro and Bates, 2000) using the nlme package in R (Pinno and Bélanger, 2011; R-Development-Core-Team, 2011). Blocks, experimental units (EU) within blocks and permanent sample plots within EU were treated as random factors nested within each other. Treatment, time since treatment, and their interactions were treated as fixed factors. Both treatment and time since treatment were categorical variables each with four levels. In the case of aspen mortality, tree size (DBH class) was also included as a fixed factor. Differences between time periods and treatments were tested by means of contrasts. For treatments, partial cuts were compared to controls and to clearcuts and a third comparison was made between the two partial cuts. For time, consecutive 3-year periods were compared for regeneration analyses, while the first period was compared with each successive period for mortality analyses. We visually verified the assumptions of normality of residuals and homogeneity of the variances. When these assumptions were not met, a square root transformation was used.

Table 2.1. Characteristics of study stands immediately and 12 years after partial harvesting treatments. Mean values ± Standard error. LBA$_0$: live stem basal area, M$_0$: dead stem density, and DBA$_0$: dead stem basal area, immediately after treatment. LBA$_{12}$: live stem basal area, M$_{12}$: dead stems density, and DBA$_{12}$: dead stems basal area, 12 years after of treatment. CI (cutting intensity): control = no cut, 1/3PC =33% cut, 2/3 PC= 61% cut, and clearcut=100% removal. Number of independent replications (block), n=3.

		1999 (year of treatment)					2010 (12 years after treatment)				
CI	Species	Sapling density (2-9.9 cm DBH)	Tree (≥ 10 cm DBH) density	LBA$_0$ (m^2.ha^{-1}) of (≥ 5 cm DBH)	M$_0$ (stems.ha^{-1}) of (≥ 5 cm DBH)	DBA$_0$ (m^2.ha^{-1}) of (≥ 5 cm DBH)	Sapling density (2-9.9 cm DBH)	Tree (≥ 10 cm DBH)	LBA$_{12}$ (m^2.ha^{-1}) of (≥ 5 cm DBH)	M$_{12}$ (stems.ha^{-1}) of (≥ 5 cm DBH)	DBA$_{12}$ (m^2.ha^{-1}) of (≥ 5 cm DBH)
Control	All species	1727±137	980±48	44.0±1.2	127±23	2.7±0.5	3585±285	735±45	41.5±1.8	412±31	9.7±1.5
	Trembling aspen	0	857±45	40.6±1.2	120±22	2.6±0.5	0	592±39	37.7±1.6	265±38	8.5±1.6
	White birch	125±26	48±10	1.2±0.2	0	0	55±14	30±7	0.7±0.1	87±18	0.6±0.1
	Spruce and fir	130±29	72±16	1.4±0.3	0	0	492±70	112±22	2.6±0.5	23±7	0.2±0.07
	Mountain maple	1327±169	0	-	-	-	2823±331	0	-	-	-
1/3 PC	All species	1305±114	685±40	30.9±1.6	113±19	2.2±0.4	4600±657	545±53	32.8±2.2	283±22	5.4±0.5
	Trembling aspen	0	545±40	27.3±1.9	90±17	1.8±0.2	627±311	428±38	29.1±2.2	115±11	3.8±0.5
	White birch	120±18	53±21	1.3±0.4	7±4	0.06±0.04	33±11	10±6	0.3±0.2	142±30	1.1±0.32
	Spruce and fir	117±39	53±27	1.0±0.4	8±5	0.1±0.1	978±252	87±28	2.4±0.5	8±4	0.1±0.06
	Mountain maple	1040±115	0	-	-	-	2875±399	0	-	-	-

Note: All stems (both commercial and non-commercial species) considered in calculation of density and basal area of all species. Live and dead mountain maple density and basal area (≥5 cm at DBH) were not analysed because of very low presence.

Table 2.1. continues, Characteristics of study stands immediately and 12 years after partial harvesting treatments. Mean values ± Standard error. LBA_0: live stem basal area, M_0: dead stem density, and DBA_0: dead stem basal area, immediately after treatment. LBA_{12}: live stem basal area, M_{12}: dead stems density, and DBA_{12}: dead stems basal area, 12 years after of treatment. CI (cutting intensity): control = no cut, 1/3PC =33% cut, 2/3 PC= 61% cut, and clearcut=100% removal. Number of independent replications (block), n=3.

		1999 (year of treatment)					2010 (12 years after treatment)				
CI	Species	Sapling density (2-9.9 cm DBH)	Tree (≥ 10 cm DBH) density	LBA_0 ($m^2.ha^{-1}$) of (≥ 5 cm DBH)	M_0 ($stems.ha^{-1}$) of (≥ 5 cm DBH)	DBA_0 ($m^2.ha^{-1}$) of (≥ 5 cm DBH)	Sapling density (2-9.9 cm DBH)	Tree (≥ 10 cm DBH)	LBA_{12} ($m^2.ha^{-1}$) of (≥ 5 cm DBH)	M_{12} ($stems.ha^{-1}$) of (≥ 5 cm DBH)	DBA_{12} ($m^2.ha^{-1}$) of (≥ 5 cm DBH)
2/3 PC	All species	1258±142	520±34	16.4±0.9	153±27	3.0±0.6	7807±1080	348±43	16.1±0.8	363±23	6.9±0.9
	Trembling aspen	0	397±43	13.7±1.3	108±17	2.4±0.4	3410±686	210±28	12.3±1.3	185±24	5.3±0.8
	White birch	117±21	57±14	1.3±0.3	20±7	0.1±0.06	288±74	22±7	0.5±0.1	127±19	1.1±0.2
	Spruce and fir	88±27	53±18	1.0±0.4	7±4	0.07±0.04	870±169	113±31	3.0±0.6	20±12	0.3±0.2
	Mountain maple	992±139	0	-	-	-	2667±430	0	-	-	-
Clearcut	All species	10±8	0	0	0	0	8738±1022	5±3	3.6±0.5	0	0
	Trembling aspen	0	0	0	0	0	5812±1158	0	2.4±0.5	0	0
	White birch	0	0	0	0	0	850±161	0	0.54±0.1	0	0
	Spruce and fir	10±8	0	0	0	0	392±169	5±3	0.38±0.1	0	0
	Mountain maple	Not surveyed	0	-	-	-	180±108	0	-	-	-

Note: All stems (both commercial and non-commercial species) considered in calculation of density and basal area of all species. Live and dead mountain maple density and basal area (≥5 cm at DBH) were not analysed because of very low presence.

2.4. Results

2.4.1. Stand characteristics immediately following treatments

Immediately after treatment application in the winter 1998–1999, live stem ($\geq$5 cm at DBH) basal area was 44.0, 30.9, and 16.4 $m^2.ha^{-1}$ in controls, 1/3 and 2/3 partial cut stands, respectively (Table 2.2; Brais *et al.*, 2004). Trembling aspen was the dominant canopy species (Figure 2.1A–C), occupying 92%, 88%, and 84% of live stem BA in controls, 1/3 and 2/3 partial cut stands, respectively. The sapling layer was dominated by mountain maple with a smaller proportion of white birch, balsam fir and white spruce (Table 2.1, Figure 2.1A–C). In 1999, the first year following treatments, the regeneration layer (<2 cm DBH) was dominated by mountain maple and aspen suckers in densities roughly proportional to intensity of harvesting treatments (Table 2.2). Conifer seedling density was higher in the 1/3 PC than other treatments. Standing dead stems immediately following treatments were mainly associated with smaller size classes (<20 cm DBH) of trembling aspen and white birch (Figure 2.1D–F). Trembling aspen accounted for 96%, 82%, and 80% of dead basal area in the controls, 1/3 and 2/3 partial cut treatments, respectively (Table 2.1). Some dead white birch saplings were observed in partially harvested treatments (Figure 2.1D–F).

Table 2.2. Regeneration (0-2 m height) density of different species in the year 1999 (immediately after partial harvesting treatment application). All values presented in the table is Mean values ± Standard error of n=15. Number of independent replications (block), n=3.

Treatment	Height class	Trembling aspen	White birch	Balsam fir	Spruce	Mountain maple
Control	0-100 cm	4667±3614	667±1143	1417±1285	583±579	39833±6547
	100-200 cm	250±250	0	167±114	83±83	6250±983
1/3 PC	0-100 cm	27750±17518	250±262	4833±2137	500±524	58583±13605
	100-200 cm	1000±443	0	333±192	167±167	6500±1638
2/3 PC	0-100 cm	56000±20000	1917±1771	2333±1471	167±223	70333±14938
	100-200 cm	7333±3003	0	167±167	83±83	4583±749
Clearcut	0-100 cm	91917±27684	8750±6156	1333±877	417±569	160417±54883
	100-200 cm	11000±3451	167±114	0	0	417±234

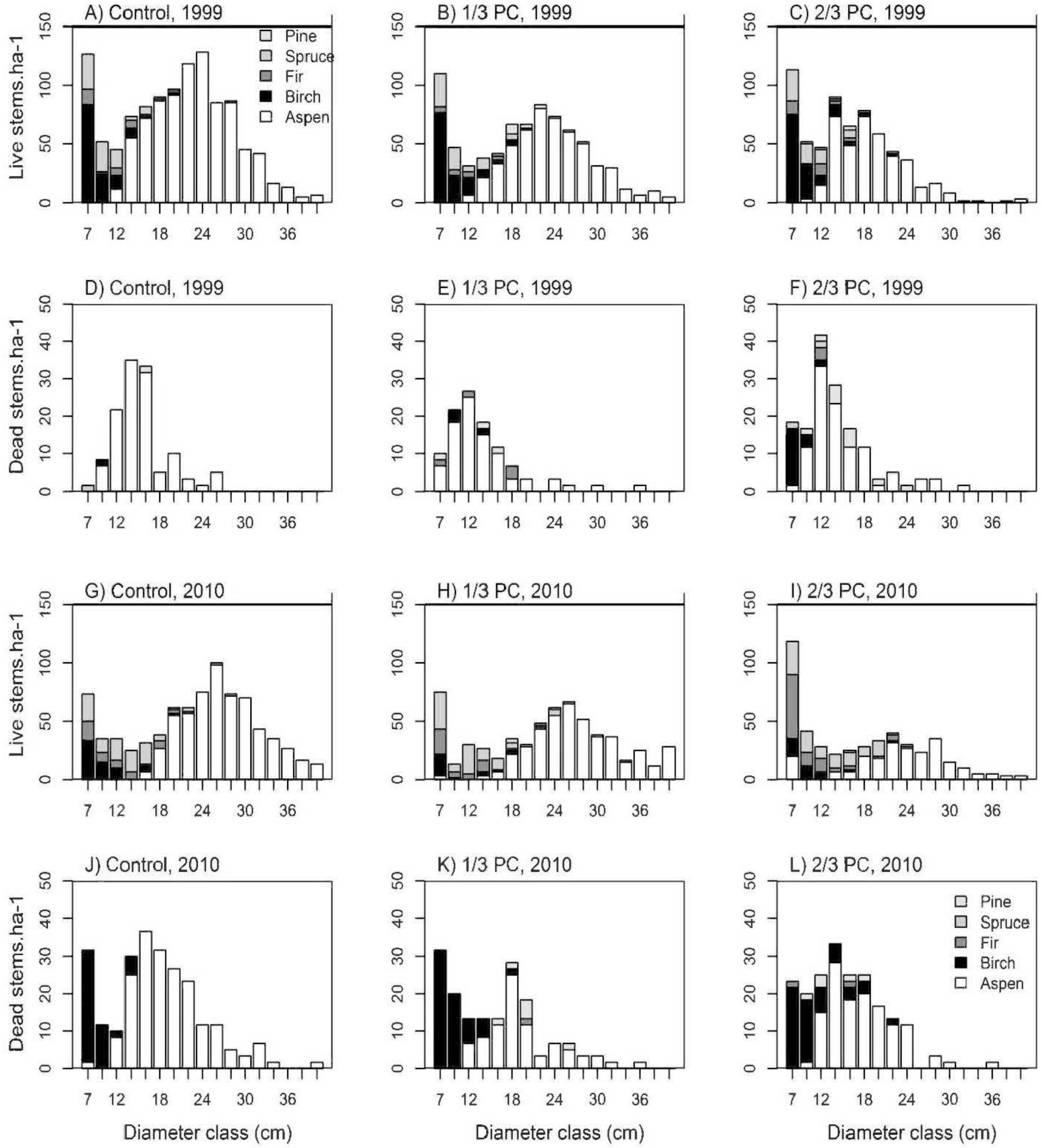

Figure 2.1. Diameter distribution of live stems and standing snags in control stands, in low-light partial cutting (1/3 PC), and in high-heavy partial cutting (2/3 PC), A-F: immediately after harvesting in 1999, and G-L: 12 years after harvesting in 2010.

2.4.2. Sapling recruitment

2.4.2.1. Trembling aspen

Recruitment of trembling aspen suckers into the sapling layer (2–9.9 cm DBH) in partial cut and clearcut treatments began 4–6 years after harvesting (Table 2.3; Figure 2.2A and B) with the highest values of periodic (3 year) increment in terms of stem density and BA observed 7–9 years following treatments. There were no significant interactions between time and treatments for sapling recruitment and no aspen sapling recruitment in controls.

Over the 4–12 year post-treatment period, periodic increment of trembling aspen saplings was significantly higher in the clearcut treatment than in partial cuts, both in term of density and BA (Table 2.3, Figure 2.2A and B). Significantly higher BA increment of saplings was found in the 2/3 partial cut compared with the 1/3 partial cut while differences in density of sapling recruitment between the two treatments was significant at the $p = 0.06$ level. A significant interaction was found between harvesting intensity and time since treatment for cumulative recruitment; the difference between the two partial cuts was significantly higher ($p = 0.004$) during the 7–9 year period than during the 10–12 year period after treatment (Table 2.3, Figure 2.2C). The cumulative recruitment of aspen saplings 12 years after treatments was 5018, 2843, and 244 stems ha^{-1} in clearcut, 2/3 and 1/3 partial cut treatments, respectively (Figure 2.2C).

2.4.2.2. Conifers

There was no conifer recruitment into the sapling layer in the first 3 years following harvesting treatments and few significant effects of either time or treatment on observed values for the three other periods. Recruitment in clearcuts also remained very low throughout the 12 year period. The peak of conifer recruitment occurred at a different period for each treatment (significant interaction between treatment and time since treatment, Table 2.3). The earliest recruitment peak occurred in the 1/3 partial cut and the latest in the clearcut treatment. Conifer recruitment in terms of BA was significantly higher in partial cuts than clearcuts. Differences in BA increment between partial and clearcut treatments decreased between the second (4–6 years) and third period (7–9 years) ($p < 0.001$) and between the third and fourth period ($p = 0.010$) (Table 2.3, Figure 2.2E). The cumulative recruitment of conifer saplings increased significantly with time since harvesting (Table 2.3, Figure 2.2F) and a significant interaction was found between harvesting intensity and time since treatment, thus indicating differences between partial and clearcut treatments increased over time (Table 2.3).

2.4.2.3. Mountain maple

While densities of mountain maple regeneration (≥2 m) were very high in partial cuts and highest in clearcuts in the year following treatments (Table 2.2), very few stems (180 stems ha^{-1}; not statistically analysed) actually recruited into the sapling layer in clearcuts. Recruitment into the sapling layer in partial cut and control treatments only began in the second period (4–6 years). Significant interactions between harvesting treatments and time since treatments were found for mountain maple periodic (3 year periods), and cumulative (12 years) recruitment (Table 2.3). For periodic recruitment, the difference between the two partial cut treatments was significantly more pronounced ($p = 0.003$) in the second period than in the third period. Similarly, the difference between controls and partial cuts in the second period was significantly higher ($p = 0.001$) than in the third period (Figure 2.2G and H). For all treatments, recruitment of mountain maple saplings was significantly higher in the fourth period than the third period in terms of both density and BA (Table 2.3, Figure 2.2G and H). Cumulative mountain maple recruitment increased over the years but did not significantly differ among partial cut and control treatments (Table 2.3; Figure 2.2I).

2.4.3. Residual overstory tree mortality

2.4.3.1. Trembling aspen and conifers

Absolute mortality (dead stems ha^{-1}) and relative mortality (% of total stems) of trembling aspen were significantly affected by intensity of partial harvesting, time since treatment and their interaction (Table 2.4). In all treatments, the highest absolute and relative mortality levels were observed 4–6 years following treatments and decreased thereafter (Table 2.4; Figure 2.3A and B). The difference in absolute mortality between the control (higher values) and both partial cuts occurred in the second period after harvesting and was significantly more pronounced than during the first period ($p = 0.010$) (Table 2.4, Figure 2.3A and B). Differences in relative mortality between the two intensities of partial cuts were significantly more pronounced in the first period than in the third ($p < 0.001$) and fourth ($p < 0.001$) periods (Table 2.4, Figure 2.3B).

Cumulative mortality of residual aspen stems occurred mostly in the smaller size class (10–19.9 cm DBH), with net relative mortality reaching more than 70% of that size class in controls over the 12-year period (Table 2.4, Figure 2.3D and E). Cumulative mortality over the 12 year period was higher in controls than partial cuts for all size classes, but did not differ between two partial cut treatments (Table 2.4, Figure 2.3D and E). The cumulative mortality of trembling aspen over the entire study period reached 250 stems ha^{-1} 12 yr^{-1} in controls, compared to 106, and 170 stems ha^{-1} 12 yr^{-1} respectively in 1/3 and 2/3 partial cut treatments (Figure 2.3C).

Although density and growth of conifer trees (≥10 cm DBH) were generally low, mortality was particularly low in the 2/3 partial cut compared to the 1/3 PC and clearcut treatments (no statistical analysis) (Figure 2.3F).

Table 2.3. Effects of complete (clearcut), partial harvesting, time since harvesting and their interaction on trembling aspen and conifer sapling (size 2-9.9 cm at DBH) and mountain maple recruitment. Significance of fixed effects is based on the Type 1 test of hypothesis. (Note: PC=Partial cutting, 1/3 PC=33% cut/low-thin, 2/3 PC= 61% cut/high-thin, CC=clearcuts, C=control/uncut, Time: treatment = interaction variable between time and treatment.

	Fixed factors					
Response variables	4-6 years Vs 7-9 years	7-9 years Vs 10-12 years	PC Vs C	1/3 PC Vs 2/3 PC	PC Vs CC	Time: treatment[1]
Periodic (3 years) recruitment						
Aspen sapling recruitment (stems.ha^{-1})	***	NS	NA[2]	NS	*	NS
Aspen sapling recruitment (cm^{2}.ha^{-1})	***	**	NA[2]	*	*	NS
Coniferous sapling recruitment (stems.ha^{-1})	NS	NS	NS	NS	NS	*
Coniferous sapling recruitment (cm^{2}.ha^{-1})	NS	NS	NS	NS	*	***
Mountain maple recruitment (stems.ha^{-1})	NS	***	NS	NS	NA[3]	**
Mountain maple recruitment (cm^{2}.ha^{-1})	NS	**	NS	NS	NA[3]	**
Cumulative recruitment						
Aspen sapling recruitment (stems.ha^{-1})	***	***	NA[2]	NS	NS	**
Coniferous sapling recruitment (stems.ha^{-1})	***	***	NS	NS	NS	*
Mountain maple recruitment (stems.ha^{-1})	***	***	NS	NS	NA[3]	NS

[1] Details of interactions provided in the text, [2] NA- not analysed because of negligible recruitment of trembling aspen in controls, [3] NA- not analysed because of negligible recruitment of mountain maple in clearcuts, ***:$p<0.001$, **:$0.001< p <0.010$, *: $0.010 < p <0.050$, NS: $p >0.051$, Response variables square-root transformed.

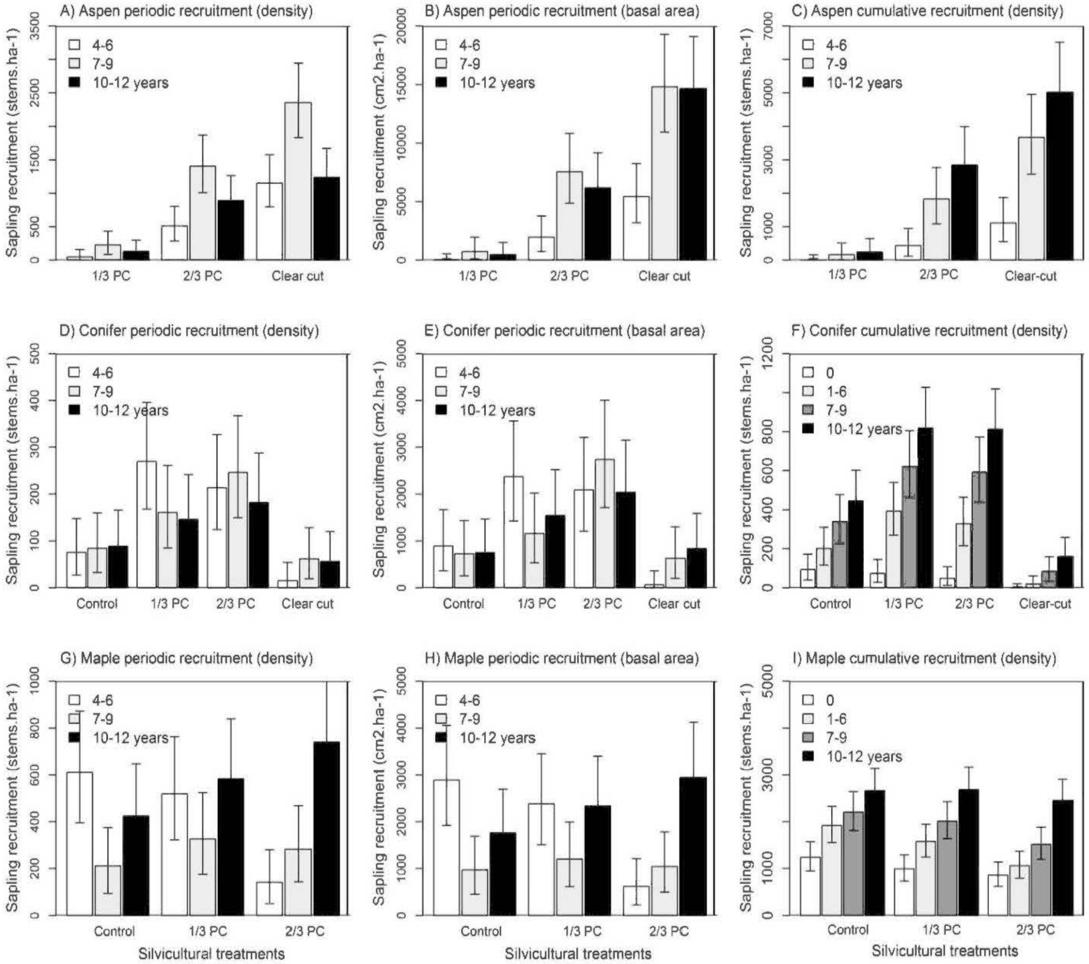

Figure 2.2. Periodic sapling recruitment in density (stems.ha^{-1}), in basal area (cm^{2}.ha^{-1}), and cumulative sapling recruitment in density (stems.ha^{-1}) after partial harvesting treatments. (A-C) Trembling aspen, (D-F) Conifer (balsam fir and spruce species), and (G-I) Mountain maple. Note: Sapling size=2-9.9 cm at dbh, Control: No harvesting, 1/3 PC: 33% BA removal, and 2/3 PC: 61% BA removal, Error bar represents Standard error.

2.4.3.2. Mountain maple mortality

A significant interaction was found between treatment and time since treatment for periodic mortality of mountain maple. The difference between controls and partial cut treatments in the first period was significantly lower ($p = 0.002$) than in the fourth period. In partial harvesting treatments, the maximum mountain maple periodic mortality occurred between 4 and 6 years after treatments (Figure 2.3G and I). Twelve years after the start of the experiment, absolute and relative mortality (relative to total stems) of mountain maple was similar in controls and the two partial cut treatments (Figure 2.3H and I).

2.4.4. Stand characteristics 12 years after treatment

Relative to 1999 values, 12 years following treatments, live stem density (saplings + trees) increased in the clearcut and 2/3 partial cut treatment as a result of recruitment of trembling aspen, but decreased in 1/3 partial cut and in controls, largely due to aspen mortality in the overstory (Table 2.1). Basal area of live stems decreased in controls and the 2/3 partial cut due to higher mortality of smaller sized residual aspen and white birch left during treatment application. Basal area increased in the 1/3 partial cut treatment (Table 2.1). Mortality (snags and tree fall) was mainly associated with smaller sized stems (<20 cm DBH) of trembling aspen and white birch, irrespective of treatment (Figure 2.1J–L). Density of snags and downed trees was 412, 283, and 340 stems ha^{-1} 12 yr_1 in control, 1/3 and 2/3 partial cut treatments, respectively (Table 2.1). Twelve years after treatments, some small shade tolerant conifers (fir and spruce) had recruited into the sapling layer and in small merchantable diameter classes of controls and partial cut treatments. These diameter classes had been largely occupied by white birch stems immediately following treatments, many of which died over the 12 year period (Figure 2.1G–I).

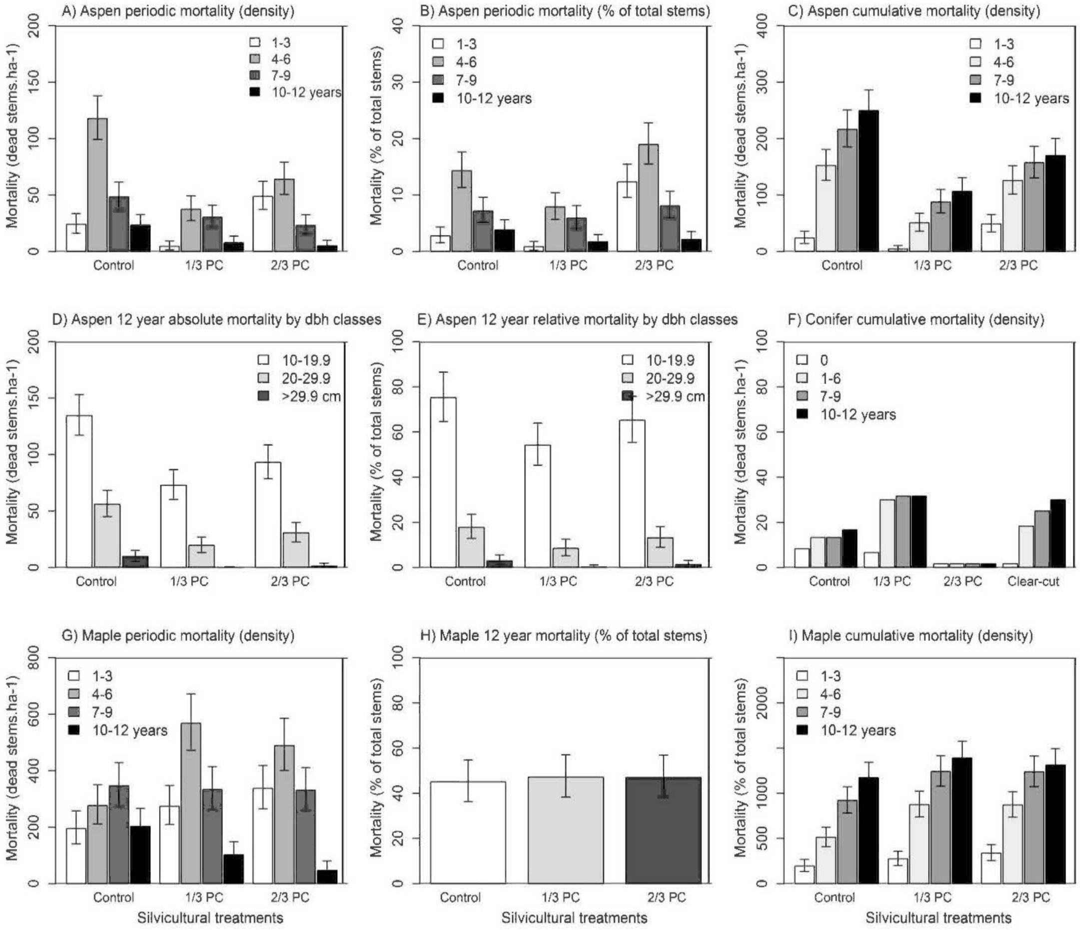

Figure 2.3. Mortality after partial harvesting treatments. (A-C) Trembling aspen periodic, and cumulative tree (≥10 cm at dbh) mortality over a 12 year period, (D-E) Trembling aspen 12 year absolute and relative mortality by dbh classes, F) Conifer cumulative mortality (no statistical analysis), G) Mountain maple periodic stem (≥2 cm at dbh) mortality over a 12 year period, H) Mountain maple 12 year relative mortality, and I) Mountain maple cumulative mortality over a 12 year period. Control: No harvesting, 1/3 PC: 33% BA removal, and 2/3 PC: 61% BA removal. Error bar represents Standard error.

Table 2.4. Effects of complete (clearcut) and partial harvesting, time since harvesting, diameter class, and interaction between time since harvesting and harvesting treatment on tree (> 9.9 cm at DBH) mortality. Significance of fixed effects is based on the Type 1 test of hypothesis. (Note: Diam.1=Diameter class1 (10-19.9 cm), Diam.2=Diameter class2 (20-29.9 cm), Diam.3=Diameter class3 (>29.9 cm), PC=Partial cutting, 1/3 PC=33% cut/low-thin, 2/3 PC= 61% cut/high-thin, CC=clearcuts, C=control/uncut.

	Fixed factors								
Response variables	1-3 years vs 4-6 years	1-3 years vs 7-9 years	1-3 years vs 10-12 years	PC vs C	1/3 PC vs 2/3 PC	PC vs CC	Time: treatment^1	Diam.1 vs Diam.2	Diam.1 vs Diam.3
Periodic (3 years) mortality									
Aspen tree absolute mortality (stems.ha^{-1})	***	NS	*	NS	*	NA^2	***	-	-
Aspen tree relative mortality (% stems.ha^{-1})	***	NS	NS	NS	**	NA^2	**	-	-
Mountain maple mortality (stems.ha^{-1})	**	NS	***	NS	NS	NA^3	**	-	-
Cumulative mortality									
Aspen tree absolute mortality (stems.ha^{-1})	***	***	***	NS	*	NA^2	***	-	-
Aspen tree mortality by DBH class (stems.ha^{-1})	-	-	-	*	NS	NA^2	-	***	***
Aspen tree relative mortality by DBH class (% of total stems)	-	-	-	NS	NS	NA^2	-	***	***
Mountain maple absolute mortality (stems.ha^{-1})	***	***	***	NS	NS	NA^2	NS	-	-
Mountain maple relative mortality (% of total stems)	-	-	-	NS	NS	NA^2	-	-	-

[1] Details of interactions are provided in text., [2] NA : not analysed because of negligible mortality of trembling aspen in clearcuts, [3] NA : not analysed because of negligible mortality of mountain maple in clearcuts, - : not included in hypothesis, ***:$p<0.001$, **:$0.001< p <0.010$, *: $0.010 < p <0.050$, NS: $p >0.051$, response variables square-root transformed.

2.5. Discussion

The picture that emerges from our study is that, in these stands, high intensity partial harvesting (61% BA removal) created more favorable conditions over other treatments for sapling recruitment of both aspen and conifer species. That said, this relatively heavy and high thinning treatment generated higher residual tree mortality initially (first 6 years after treatments), probably due to higher retention of smaller, less vigorous stems.

2.5.1. Recruitment of aspen saplings

Our results support the hypothesis that aspen sapling recruitment follows a gradient of canopy opening (clearcut > 2/3 partial cut > 1/3 partial cut > control) (Table 2.3, Figure 2.2A–C). Aspen sapling recruitment was directly affected by harvesting intensity with 1/3 and 2/3 partial cuts, respectively generating 5% and 56% of aspen sapling densities in clearcuts over the 12 year period (Figure 2.2C). The lower aspen recruitment in the two partial cut treatments may be explained by at least two factors. First, the maintenance of dispersed aspen stems has the effect of maintaining auxin production in crowns over the area affected. This production may partially counterbalance cytokinin production in the interconnected root systems, thus having the effect of inhibiting sucker initiation (Frey *et al.*, 2003; Wan *et al.*, 2006). Second, residual canopies can produce understory light levels low enough to restrict sucker growth and survival (Beaudet and Messier, 2002; Pothier and Prévost, 2002). Using the SORTIE-ND light model to predict understory light levels in stands similar to those in our study, Beaudet *et al.* (2011) predicted that 30% and 60% BA removals using a dispersed partial cutting pattern would generate gap light indices (GLI) of 14% and 26%, respectively. These GLI values likely underestimate the difference between our two partial cut treatments, given that the 1/3 partial cut was a low thinning (lower light transmission through canopy than after a free thinning for equivalent BA) and the 2/3 partial cut was a high thinning (more light transmission than equivalent free thinning). This would provide some explanation for the 5% and 56% aspen sapling recruitment values above; that is, the 1/3 partial cut created unfavorable conditions for aspen suckers by maintaining low light levels in the regeneration layer (Figure 2.2C) whereas the 2/3 partial cut treatment created larger canopy openings that resulted in higher light transmission and higher recruitment of aspen saplings (Table 2.3, Figure 2.2A–C). To some extent, these results reflect natural gap dynamics in aspen stands affected by repeated defoliation by forest tent caterpillar (*Malacosoma disstria* Hübner) (Moulinier *et al.*, 2011). Moreover, in the context of natural disturbance-based silviculture and the emerging concept of managing for forest complexity (Filotas *et al.*, 2014), this provides an example of the potential of partial harvesting treatments to promote the transition of even-aged stands into more complex, multi-cohort structures.

Other studies have also confirmed relationships between aspen regeneration levels and the degree of residual cover following partial harvesting. In western Canada, Gradowski *et al.* (2010) have gone so far as to produce a 3-dimensional response surface for poplar (aspen + balsam poplar (*Populus balsamifera*)) sucker density based on pre- and post-treatment BA values of poplar. Other silvicultural experiments in North America have also shown the possibility of managing sucker response in aspen-dominated mixedwoods by varying partial harvesting intensities (or, inversely, levels of residual retention) in eastern Canada (Prévost and Pothier, 2003) and the USA (Schier and Smith, 1979; Ffolliott and Gottfried, 1991).

Our results 12 years after treatments provide a striking contrast to sucker values observed immediately after treatments in this same experiment (Brais *et al.*, 2004). For example, observed sucker densities in clearcuts in years 1 and 2 were 102,916 stems ha^{-1} and 94,917 stems ha^{-1}, respectively. By year 2, 16,000, 9000 and 2000 stems ha^{-1} had reached the 1–2 m height class in clearcuts, 2/3 and 1/3 treatments, respectively. However, by year 12, only 5018, 2843, and 244 stems ha^{-1}, respectively, had recruited into the sapling layer. Cumulative recruitment of aspen saplings in the clearcut and 2/3 partial cut treatments indicates continuous recruitment over this period (starting in period 4–6 years, Fig. 2.2C) and suggests that recruitment could continue in the following years. This said, although we have no evidence yet of aspen mortality occurring in the sapling layer, the same intense intraspecific competition that exists in the regeneration layer (<2 m) should persist if the regenerating clearcuts and 2/3 partial cut stands develop similarly to the original stands. These young, regenerating stands with ≈5000 and 2800 stems ha^{-1}, respectively, in year 12 should self-thin down to ≈850 stems ha^{-1} by year 75 (Table 2.1).

2.5.2. Recruitment of conifer saplings

Our results suggest that, in these aspen-dominated mixedwoods with a conifer regeneration layer, partial harvesting better promotes recruitment of conifer saplings than clearcuts (Table 2.3). This supports our second hypothesis and corroborates a number of other studies undertaken in similar forest types of the eastern and western boreal mixedwood (Prévost and Pothier, 2003; Man *et al.*, 2008a; Solarik *et al.*, 2010). However, we did not find significant differences in the effects between the two intensities of partial cuts on conifer sapling recruitment. This supports work by Solarik *et al.* (2010) in the case of white spruce recruitment in the western boreal mixedwood, but not that of Prévost and Pothier (2003) for balsam fir recruitment in south-central Quebec where densities of advance fir regeneration are much higher than in our sites.

Immediately after treatments, an average of 1584, 5167, 2501, and 1333 stems ha^{-1} (<2 cm DBH) of conifer regeneration was present in control, 1/3, 2/3 partial cut and clearcut treatments, respectively (Table 2.2). Twelve years after treatment, 446, 819, 792 and 160 stems ha^{-1} of conifer regeneration had successfully recruited into the sapling layer (≥2 cm DBH), which represents 28%, 15%, 31% and 12% of initial advanced regeneration (Table 2.2) of control, 1/3 partial cut, 2/3 partial cut and clearcut treatments, respectively. Therefore, the 2/3 partial cut treatment promoted higher conifer recruitment over the 12 years (Figure 2.2F) than the clearcut treatment.

Our results indicate that time did not influence conifer sapling recruitment, irrespective of treatment types. Periodic recruitment was similar among controls and the two partial cuts, although highest recruitment occurred at different periods for the three treatments (Table 2.3, Figure 2.2D and E). In the first 3 years following the treatments in this experiment, Bourgeois *et al.* (2004) observed better height growth of balsam fir regeneration following the clearcut and 2/3 partial cut treatments. However, at least for the clearcut treatment, this superior growth of seedlings did not translate into higher conifer sapling densities 12 years post-harvest, probably because of heavy competition from aspen suckers. Interestingly, Bourgeois *et al.* (2004) also observed tremendous densities of mountain maple stems in clearcuts, peaking ≈350,000 stems ha^{-1} in year 2, whereas sapling densities in clearcuts were actually too low to include in our analyses. In partial cuts and controls where it was present, mountain maple did not appear to have an effect on conifer recruitment, due in part to low values for conifer regeneration and similar levels of mountain maple in the three treatments. Heavy recruitment of mountain maple (Figure 2.2I) illustrates the dense multi-layered and multi-stemmed condition of the understory. Mountain maple has the ability to recruit vigorously in small gaps via sprouting and layering (Batzer and Popp, 1985), a condition which could inhibit germination, survival and growth of germinants and seedlings of small seeded conifer species (Greene *et al.*, 1999). Several studies have also reported continuous growth of shrub species after partial harvesting in eastern boreal mixedwoods (e.g., MacDonald *et al.*, 2004; Man *et al.*, 2008a). MacDonald *et al.* (2004) recommended avoiding the use of partial harvesting to promote conifer regeneration in stands with understories dominated by tall woody shrubs. They found that mean height growth of shrubs exceeded conifer advanced regeneration 5 years after partial harvesting.

2.5.3. Mortality of residual aspen trees (≥10 cm DBH)

Natural self thinning of trembling aspen in controls in the first 6 years of the study (1999–2004 – stand age 76–81 years) occurred primarily in the suppressed and intermediate layers (Harvey and Brais, 2007). While self thinning of aspen continued over the next 6 years (2005–2010 – stand age 82–87 years), with stem density (≥10 cm DBH) decreasing from 690 to 592 stems ha^{-1}, aspen BA only decreased 0.48 $m^2.ha^{-1}$, and this without any recruitment into the ≥10 cm DBH size class (Table 2.1). This illustrates that individual tree growth, mostly in mid- to larger-sized stems, generates almost enough stand-level increment to compensate for self-thinning mortality in small sized stems (Figure 2.3D and E). The effect of the low 1/3 partial cut treatment then was to essentially replace self thinning of suppressed stems, thus decreasing stem mortality and resulting in an increase in stand basal area from 29.8 to 32.8 $m^2.ha^{-1}$ during the last 6 years (Table 2.1). The continued growth of these stands seems surprising given that aspen is considered a short-lived species and the onset of aspen senescence has been calculated to generally occur around 60 years in Quebec (Pothier *et al.*, 2004). These authors did, however, find large variation around the mean age (64 years) of aspen senescence and, according to Frey *et al.* (2004), a number of factors, such as site and stand history including events such as defoliation, drought and other extreme weather events, can ultimately influence the senescence processes. Our study stands were variably defoliated by forest tent caterpillar (*M. disstria*) in 2001 and experienced relatively dry summers in 2001 and 2002 (Harvey and Brais, 2007). These two factors may have partially influenced the self thinning process, as highest aspen mortality in controls and partial cuts occurred during the second period (2001–2004) (Figure 2.3A and B). Between 2004 and 2010, tree mortality was still largely concentrated in small DBH classes (Figure 2.1G and J).

The study confirms our third hypothesis concerning higher mortality of residual aspen following heavy, high partial cutting (2/3 partial cut) in these stands. In effect, the 2/3 partial cut caused higher mortality of residual trees, probably due to both stand level factors such as greater exposure to wind and snow damage and tree-level factors such as higher evaporative demand as a result of greater canopy opening and the relative low vigor of (smaller) residual stems immediately following treatment (Carlson and Groot, 1997; Bladon *et al.*, 2008; Lavoie *et al.*, 2012). Twelve percent (12%) of total stems died in the 2/3 partial cuts 3 years after treatments compared to 1% in the 1/3 partial cut and 3% in controls (Figure 2.3B). This high initial mortality after heavy partial harvesting has been documented in similar stand types elsewhere. For example, MacDonald and Thompson (2003) observed a 17% residual BA reduction 4 years after partial harvesting which removed 50% BA and Solarik *et al.* (2012) observed 15% of residual aspen tree mortality 5 years after a similar intensity of partial harvesting. Moreover, these authors noted higher mortality levels with higher BA removals. Inversely, the very low mortality (1% of total stems) in the first period (1–3 years) following the 1/3 treatment supports arguments made for higher structural retention (≥70% BA retention) to reduce residual tree mortality (Thorpe and Thomas, 2007; Solarik *et al.*, 2012). But there again, lower mortality is expected under low thinning and our design precludes a meaningful comparison between low and high thinning with similar residual basal areas or between light and heavy thinning with similar distributions of removal across size classes.

Beyond immediate (short term) responses, the success of partial harvesting depends of the ability of a treatment to meet longer term goals. A number of studies have documented elevated initial mortality 5 years after harvesting treatment. Our results indicate that pre-treatment stand conditions and stem selection during harvesting affect post-harvest survival or, inversely, mortality. Mortality was clearly associated with smaller size stems, and the treatment that left more of these stems resulted in higher mortality, particularly during the first half of the study period (1–6 years). After 6 years, mortality of residual aspen was similarly very low among controls and the two partial cutting treatments (Fig. 2.3A and B). Despite their age, control stands appear to still be in the self-thinning phase, in which mortality occurs as a diffuse and continuous process, but may be transitioning into a more stochastic phase of density-independent mortality. In contrast to our study, both Prévost *et al.* (2010) and Solarik *et al.* (2012) observed continuous increases and greater mortality rates over the first 10 years following partial cutting (retention) in mixedwood stands in Quebec and Alberta, respectively. For example, Prévost *et al.* (2010) found 14% cumulative aspen mortality 5 years after, and 59.1% 10 years after a treatment of 50% BA removal in stands that were about 10 years younger than ours, compared to 31% cumulative aspen mortality 6 years after, and 41% 12 years after the 2/3 partial cuts in our study (Figure 2.3B). In their study, Prévost *et al.* (2010) attributed heavy mortality of residual aspen to senescence whereas we generally found continuous growth of vigorous aspen trees (Table 2.2, Bose *et al.*, 2014a).

2.5.3.1. Mountain maple

Immediately following harvesting treatments (first 3 years), clearcuts created the most favorable conditions for mountain maple recruitment (Bourgeois *et al.*, 2004). However, by the 12th year after clearcutting, only 180 stem ha^{-1} of mountain maple had recruited into the sapling layer ($\geq$2 cm DBH), and that recruitment occurred only in a third of permanent sample plots. Contrary to these opposing portraits of short- and medium-term mountain maple recruitment in clearcuts, cumulative mountain maple recruitment in controls and the two partial cuts were very similar, in a range of 2444–2686 stems ha^{-1} 12 yr^{-1} (Figure 2.2I) and these densities reflect the initial observations by Bourgeois *et al.* (2004). Because mountain maple is shade tolerant and can persist in the understory in low light levels where aspen cannot survive, it is favored by the low, light treatment of the 1/3 partial cut but clearly at a disadvantage relative to aspen in the clearcut treatment. Conditions in the 2/3 partial cut are such that the two species are on a more equal competitive footing and aspen saplings must pierce the mountain maple sub-canopy into the relatively open understory to survive. Like recruitment, mountain maple mortality over 12 years in controls and the two partial cuts occurred similarly to its initial response following treatments (Bourgeois *et al.*, 2004, Figure 2.3H). Thus, contrary to our fourth hypothesis and initial observations by (Bourgeois *et al.*, 2004), clearcuts did not benefit mountain maple; rather, closed-canopy (or partial canopy) forests clearly maintained the sapling layer dominance of mountain maple in the mid-term post-harvest period.

2.5.4. Management implications

The notion of natural dynamics-inspired silviculture, notably as a means for maintaining certain attributes of old and or complex structured stands, is now part of forest regulations in a number of jurisdictions in Canada, including the province Quebec (Gauthier *et al.*, 2009). Where natural disturbance regime provides a reference for forest age structure and natural fire cycles have historically been long, extended rotations and partial harvestings should be considered integral parts of a strategy to maintain old forests – or stands with old forest attributes – on the managed landscape. In managing boreal mixedwoods, partial harvesting will likely be increasingly integrated into wood supply strategies and applied to emulate patterns of anticipated natural mortality related to processes such as self-thinning, canopy succession, insect defoliation, stand dieback and low-intensity fires (Bergeron and Harvey, 1997). The silvicultural approaches to be applied, or at least tested, may not vary a great deal from existing treatments such as low thinning, group shelterwood or group selection systems that, with the exception of commercial thinning, have had very limited operational application to date in the Canadian boreal forest (Bose *et al.*, 2014c).

The 12-year outcome of the 2/3 partial cut treatment – a heavy, high thinning that could be said to emulate stand break-up (Harvey and Brais, 2007) – presents high initial mortality of smaller stems and substantial recruitment of both aspen and conifer saplings. This suggests that, if most residual aspen stems remain standing for the foreseeable future, high intensity partial cuts have the potential to promote multi-cohort mixed aspen-conifer stands. This heavy and high treatment could probably be improved upon however by a heavy free thinning in which stem removal is distributed over all merchantable size classes, thus recuperating some of the imminent mortality of smaller stems and retaining more large and vigorous stems. Moreover, it is possible to generate more within treatment structural and compositional variability by varying the layout of stem removal in such a way that smaller gaps created following removal of smaller stems favor conifer advanced regeneration and large gaps favor aspen sucker recruitment.

The 12-year outcome of the 1/3 partial cut treatment – a silvicultural analogue for natural self-thinning – presents low mortality and continued growth of vigorous aspen trees and limited aspen sucker recruitment. If management goals include extending aspen stand rotations to the biological limit of the species, for example in order to maintain forest cover, produce bigger log sizes, protect understory conifer and/or limit aspen recruitment, partial harvesting could theoretically target removal of all small-sized stems prone to self-thinning. Although technically impractical and economically less interesting in the short-term than more intensive treatments, this approach would decrease residual tree mortality by retaining vigorous stems – at least as long as other factors do not begin to affect tree health – and smaller gaps would continue to favor conifer recruitment and growth over aspen. One could anticipate that when sufficient conifer regeneration had recruited into the canopy and sub-canopy layers, a second partial cut of aspen canopy trees would release conifer stems and promote a second generation of aspen suckers in the created gaps. This said, light intensity thinning from below generally tends to simplify stand structure (O’Hara, 2001), resulting in two-cohort stands of intolerant species in the canopy layer and tolerant conifers in the understory. Moreover, unless specific standards are imposed, repeated recuperation of less vigorous stems will reduce the quantity of dead and dying stems, an attribute of concern in the context of natural disturbance-based ecosystem management.

It is possible that, by restricting conifer seedling establishment and recruitment of stems into large sapling size classes, very dense, multi-layered understories of tall woody shrubs like mountain maple at least temporarily induce successional stagnation and delay the transition from intolerant hardwood dominance to mixedwood compositions. On rich sites where tall woody shrubs are reasonably abundant in the understory, mixedwood management could include a treatment to disturb the understory shrub layer during or following partial harvesting.

2.6. Acknowledgements

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CHAPITRE III

TREMBLING ASPEN (*Populus tremuloides* MICHX) VOLUME GROWTH IN THE BOREAL MIXEDWOOD: EFFECT OF PARTIAL HARVESTING, TREE SOCIAL STATUS, AND NEIGHBORHOOD COMPETITION

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3.1. Abstract

Variable retention harvesting, with a focus on maintaining biological legacies on managed landscapes, has been practised in the trembling aspen (*Populus tremuloides* Michx.) dominated boreal mixedwood forests for about two decades. However, little attention has actually been given to the growth response of aspen to partial harvesting. This is the first study to report on tree-level volume growth response of aspen after partial or variable retention harvesting in the Canadian boreal forest. During the winter of 1998– 1999, an uncut control, and two partial harvesting treatments – 1/3 partial cut (1/3PC, 33% BA removal using low thin); 2/3 partial cut (2/3PC, 61% BA removal using high thin) – were applied in 75 year old aspen-dominated mixedwood stands in a complete randomized block design. Twelve years after treatment application, 27 dominant and 27 co-dominant trees were collected from unharvested controls and the two partial cut treatments for stem analysis. Annual volume increment (AVI) of individual stems was analyzed as a function of treatment, tree social status, pre-treatment growth, time since treatment application (1–12 years) and neighborhood competition. The latter was estimated using a variety of neighborhood competition indices (NCI). There was no evidence of initial growth lag after partial harvesting applications. Only the most severe treatment of partial harvesting (2/3 PC) resulted in an increase in volume increment relative to trees in control stands. Annual increase in volume in the 2/3 partial cut was 25.6% higher than controls over 12 years. AVI of dominant trees was higher by 16.2 dm^3yr^{-1} than that of co-dominants and was proportional to pre-treatment volume growth. No interaction between treatment and social status or pre-treatment growth was observed. The overall results indicate that competition for resources in these stands is essentially size symmetrical. These results should contribute to the development of silviculture prescriptions that aim to maintain both stand productivity and biological legacies.

Keywords: Boreal mixedwood, trembling aspen (*Populus tremuloides* Michx.), partial harvesting, annual tree volume increment, neighborhood competition indices, tree social status

Résumé

Au cours des deux dernières décennies, la coupe avec rétention variable, visant le maintien des legs biologiques dans les paysages aménagés, a été pratiquée en forêt boréale mixte dominée par le Peuplier faux-tremble (*Populus tremuloides* Michx.). Cependant, la réponse des tiges résiduelles du P. faux-tremble aux coupes partielles (CP) est encore peu documentée. Cette étude est la première à rendre compte de la croissance en volume du P. faux-tremble après coupes partielles en forêt boréale canadienne. Au cours de l'hiver 1998-1999, trois traitements ont été appliqués à des peuplements équiennes de P. faux-tremble selon un dispositif en blocs aléatoires complets, soit une éclaircie par le bas de 33 % (CP /3) de la surface terrière (ST), une éclaircie par le haut de 61 % (CP2/3) de la ST et un contrôle non coupé. Douze ans après l'application des traitements un total de 27 arbres dominants et 27 arbres co-dominants ont été récoltés dans 3 répétitions de chaque traitement afin d'effectuer des analyses de tige. L'accroissement du volume annuel (AVA) des tiges individuelles a été analysé en fonction du traitement, du statut social de l'arbre, de la croissance prétraitement, du temps écoulé depuis l'application du traitement (1-12 ans) et de la compétition par les arbres voisins. Cette dernière a été estimée en utilisant une variété d'indices de compétition à l'échelle de l'arbre. Il n'y a aucune évidence de la stagnation de la croissance initiale après l'application des CP. Seul le traitement sévère des CP (2/3 en éclaircie haute) a entrainé une augmentation de l'accroissement en volume comparativement aux arbres des peuplements témoins. Sur une période de 12 ans après coupe, l'AVA des tiges individuelles dans les CP2/3 était 25.6% plus élevé que celui des arbres des témoins. L'AVA des arbres dominants était plus élevé de 16.2 $dm^3.an^{-1}$ que celui des co-dominants, et était proportionnel à la croissance prétraitement. Aucune interaction entre le traitement et le statut social ou la croissance prétraitement n'a été observée. Les résultats indiquent que la compétition pour les ressources dans ces peuplements est essentiellement symétrique. Ces résultats devraient contribuer à l'élaboration de recommandations sylvicoles qui visent à maintenir à la fois la productivité des peuplements et les legs biologiques.

Mot-clés: Forêt boréale mixte, peuplier faux-tremble (*Populus tremuloides* Michx.), coupe partielle, accroissement du volume annuel des arbres, indices de compétition à l'échelle de l'arbre, statut social de l'arbre.

3.2. Introduction

Variable retention harvesting, with a focus on maintaining biological legacies on managed landscapes, has been practised in the aspen-dominated boreal mixedwood forest for about two decades (Lieffers *et al.*, 1996b; Bose *et al.*, 2014c). Depending on the amount and configuration of tree retention, this system ostensibly emulates primary natural disturbances such as high intensity wildfires (less retention) or secondary disturbances such as insect outbreaks or individual or group mortality (more retention) (Thorpe and Thomas, 2007). In the boreal mixedwood, the southernmost swath of forest that extends across the boreal forest biome of Canada, partial harvesting has been proposed where intolerant hardwoods, especially trembling aspen (*Populus tremuloides* Michx.), reach maturity before more shade-tolerant softwood species (Lieffers et al., 1996; Bergeron and Harvey, 1997). While attractive from an ecosystem management viewpoint, from a timber supply and economic perspective, partial harvesting practices need to be evaluated over more than the short term (Ruel *et al.*, 2013) and can be considered successful if residual trees respond well in terms of growth and survival (Coates, 1997; Thorpe *et al.*, 2007).

In the last 15 years, a number of experiments have been set up across the boreal mixedwood forest to test the ecological feasibility of forest ecosystem management (FEM) (e.g., Brais *et al.*, 2004; MacDonald *et al.*, 2004; Solarik *et al.*, 2010). While a number of studies have examined stand-level responses to partial harvesting (e.g., Man *et al.*, 2008a; Gradowski *et al.*, 2010; Brais *et al.*, 2013), fewer have focused on how residual aspen trees respond individually to partial harvesting (Bladon *et al.*, 2007; Solarik *et al.*, 2012) and these have mainly focussed on aspen mortality in response to variable retention. Some other studies have evaluated tree-level growth responses in the continuous conifer boreal region, such as black spruce (*Picea mariana* (Mill.) responses to harvesting with advanced regeneration protection

(Thorpe *et al.*, 2007) and to commercial thinning (Goudiaby *et al.*, 2012). We have found no studies quantifying the volume growth response of mature aspen trees to partial harvesting.

By removing trees from different canopy layers, partial harvesting affects light availability, and thereby competition among residual trees (Hartmann *et al.*, 2009). Individual tree-level growth responses to partial harvesting have been shown to depend on tree age (Thorpe *et al.*, 2007), size (Jones and Thomas, 2004), physiological traits (Jones *et al.*, 2009; Anning and McCarthy, 2013b), and preharvest growth rate (Thorpe *et al.*, 2007). Immediately following harvesting treatments, it is also expected that tree growth response will depend on acclimation to evolving growing conditions including availability of light and soil resources, post-harvest social status, and neighborhood competition (Thorpe *et al.*, 2007; Hartmann *et al.*, 2009; Anning and McCarthy, 2013a). Several studies have documented an initial (2–5 years) growth stagnation in residual trees immediately following harvesting (Jones and Thomas, 2004; Thorpe *et al.*, 2007; Goudiaby *et al.*, 2012) probably due to the sudden change in the stand's microclimatic condition (Bose *et al.*, 2014c). Kneeshaw *et al.* (2002) suggested, that larger trees may be more prone to initial growth stagnation due to the presence of higher non-photosynthetic biomass requiring higher maintenance costs and higher allocation to root growth for mechanical support.

The SAFE project (‘‘Sylviculture et Aménagement Forestier Ecosystémique’’) (Brais *et al.*, 2004; Brais *et al.*, 2013) is a series of experiments undertaken in Northwestern Quebec, Canada to assess the feasibility of FEM silvicultural practices for this region. The first phase of the SAFE project was established in post-fire, naturally regenerated aspen-dominated stands (Brais *et al.*, 2004; Harvey and Brais, 2007) that were submitted to four levels of harvesting, including two intensities of partial harvesting, in 1998.

The objective of the study is to evaluate the effects of partial harvesting on the annual volume increment of residual trees of trembling aspen over a 12-year period following harvesting. We specifically investigated the effects of partial harvesting treatment and tree social status on volume increment of residual trees. Because stand conditions evolve in response to harvesting (Harvey and Brais, 2007; Bose *et al.*, 2014b), we also considered pre-treatment volume growth and neighborhood competition as possible explanatory factors for volume increment during last 3 year period (10–12 years following treatments). Accordingly, we tested the following hypotheses: (i) tree volume increment would increase with increasing intensities of partial harvesting (Thorpe *et al.*, 2007), but decrease with increasing neighborhood competition in the longer term (Hartmann *et al.*, 2009; Anning and McCarthy, 2013a); (ii) size-dependent competition indices are expected to better explain the annual volume increment of aspen residual trees over distance-dependent indices (Canham *et al.*, 2006); and (iii) a growth lag is expected immediately after treatment applications followed by a linear increase in annual volume increment (Jones and Thomas, 2004; Thorpe *et al.*, 2007). We also anticipated that the size of residual trees could affect their response in two different ways: (iv) dominant stems or stems with the highest pre-treatment volume increment would experience the strongest volume growth response following harvesting (Berntson and Wayne, 2000; Jones and Thomas, 2004) or, inversely, light-limited co-dominant trees (relative to dominants) could benefit the most from canopy opening (Walter and Maguire, 2004).

3.3. Methods

3.3.1. Study area

The study area is located in the Lake Duparquet Research and Teaching Forest (48°86′N–48°32′N, 79°19′W–79°30′W) in the Abitibi region of Northwestern Quebec. The region is part of the balsam fir-white birch bioclimatic domain (Saucier *et al.*, 1998), and is characterized by the presence of extensive clay deposits left by proglacial Lake Ojibway (Vincent and Hardy, 1977). Soils are gray Luvisols and soil texture is that of heavy clay (>75% clay). The forest floor is a thin mor of 2–7 cm

(Canada Soil Survey Committee, 1987b). The climate is continental with mean annual precipitation (1991–2010) of 847 mm, of which 583 mm falls as rain from April to September. Mean annual temperature is 1.95 °C with an average daily temperature of 11.9 °C from April to September (BioSIM, 2012).

The stands are even-aged (76 years old at time of treatment) and originated from a wildfire in 1923 (Dansereau and Bergeron, 1993). Before treatment application, average stand basal area was 44.0 $m^2.ha^{-1}$ of which 92.6% was trembling aspen and 3.3% conifer species. The shrub layer was dominated by mountain maple (*Acer spicatum* Lamb.) with an average density of 1327 $stems.ha^{-1}$ (Bourgeois *et al.*, 2004). Four harvesting treatments, including a no harvest control, two intensities of partial harvesting and a clearcut, were applied during the 1998–1999 winter. The two partial harvesting treatments were designed to remove 33% (1/3 partial cut) and 61% (2/3 partial cut) of the stand's merchantable basal area. Stands in the 1/3 removal were low thinned with primarily smaller, low-vigor aspen stems removed (1/3 partial-cut). This treatment was intended to emulate density dependent mortality (self-thinning) in stand development. Stands in the 2/3 removal were crown thinned with more vigorous co-dominant and dominant aspen stems preferentially selected (2/3 partial-cut), thus presenting a mortality analogue of stand senescence (Brais *et al.*, 2004). Harvesting treatments were applied according to a complete randomized block design with three replications (blocks) of each treatment. Experimental units ranged from 1 to 2.5 ha. In 2001, the stands were affected by a forest tent caterpillar (FTC, *Malacosoma disstrium* Hübner) outbreak.

3.3.2. Data collection

Trees selected for stem analyses were harvested in the fall and winter of 2011 and summer of 2012 in control and partially harvested experimental plots. Both dominant and co-dominant residual trees were selected based on their diameter, crown size and crown's relative exposure among neighbors. Average diameter at breast height (DBH, 1.3 m) was first compiled from the most recent tree inventory (2010) in permanent sample plots for each of the three experimental blocks in order to determine size ranges for each social status. DBH size was used as a first step because of its strong correlation with tree height (r = 0.77). Trees were considered dominant if their DBH was ≥2 standard deviations (SD) of the experimental block average, and co-dominants if their DBH was ≥1 SD. In addition to diameter size, visual inspection of relative crown size and exposure among neighbors was also used to select sample trees. Specifically, trees in the dominant social class (according to DBH) had to clearly have large crowns compared to others in the canopy and crowns of ''DBH co-dominants'' situated close to dominants had to be smaller than those of dominants. Harvested trees were located at least 20 m from roads to minimize edge effects, from permanent sample plots and from other sampled trees. All sampled trees were free of any visible damage, decay or infection.

Three trees of each social status were selected from each experimental unit (control, 1/3 partial cut and 2/3 partial cut) within each of the 3 blocks for a total 54 trees (Table 3.1). To develop and compare a number of competition indices, the neighborhood around each sampled tree was characterized. All live-standing neighbor trees/ high shrubs (≥5 cm at DBH) within a 10 m radius were identified and their DBH measured. Their distance to the center of the plot (to target tree) was also measured. Distance to the center was measured with a precision of 0.1 m using a Vertex clinometer (Haglöf, Sweden).

Sampled stems were cut at the base. Eleven cross-sectional disks were collected along the stem starting with a disk (D.1) at 0.15 m or stump height (SH) and a second disk (D.2) at 1.3 m (breast height, BH). The remaining nine disks (D.3–D.11) were collected at equally spaced positions between breast height and the top of the stem (Chhin *et al.*, 2010). After harvesting sample trees (at the ground), length and width of the live crown were measured.

3.3.3. Laboratory analyses

All disks were sanded with progressively finer grits of sandpaper (60–400 grain). Disks were examined under a microscope; pointer years (severe growth declines in 1954, 1980 and 2001) and false rings (Chhin *et al.*, 2010) were marked and trees were aged to the year 2010. Tree rings were measured and analyzed using WinDendro version 2009 (Regent Instruments). The measurements were carried out on three radii per disk (Lopatin *et al.*, 2008). Visual cross-dating and tree-ring measurements were further validated using pointer years and the COFECHA program (Grissino-Mayer, 2001). For each sampled stem, we corrected the number of missing or mistakenly-dated rings. The correlation coefficient with a master chronology created by COFECHA was 0.62– 0.97 using all sample stems. Annual volume increments were then estimated using WinStem software (Regent Instruments).

3.3.4. Neighborhood competition indices

The neighborhood competition surrounding each sampled tree in 2011 was quantified using the neighborhood competition index (NCI) equation used by Hartmann *et al.* (2009) for Sugar maple (*Acer saccharum* Marsh.) in Quebec.

$$NCI = \frac{\sum_{j=1}^{N} (DBH_j)^{\alpha}/(dist_{ij})^{\beta}}{1000} \qquad (1)$$

where DBH_j is the DBH (in cm) of a neighbor tree *j*, which is located at a distance $dist_{ij}$ (in m) from the target tree *i*.

The neighbor size effect on competition is defined by α, whereas β defines the slope at which the competition from neighboring trees declines with their distance to the target tree. An $\alpha = 0$ indicates that competition from neighboring trees is independent of their size, an $\alpha = 1$ indicates that competition is proportional to neighbors' diameters, and an $\alpha = 2$ indicates that neighbors' effect is proportional to their basal area (Canham *et al.*, 2006). A $\beta = 0$ indicates the competition exerted by neighbors is independent of their distance to the target tree; a $\beta = 0.5$ indicates competition is proportional to the square-root of the distance to the target tree; a $\beta = 1$ indicates that neighbors' competitive effect decreases with distance; and a $\beta = 2$ indicates that the effect increases with the power of the distance (Coates *et al.*, 2009). The R value is the radius within which neighbors have an effect on a target tree. Thirty-six different models of NCI were considered based on all possible combinations of three α values (0, 1, or 2), four β values (0, 0.5, 1, or 2) and three R values (6, 8, or 10 m) (Appendix 3.1). Because trembling aspen represented 81% of neighborhood basal area of all target trees and because neighbors within 8 m of all target trees were mostly trembling aspen, we did not account for neighbor species effect in NCI estimations.

3.3.5. Statistical analysis

3.3.5.1. Selection of the NCI that best predicts annual volume increment

A model selection approach based on Akaike's Information Criterion, corrected for small samples (Burnham and Anderson, 2002; Mazerolle, 2006), was used to identify which NCI among the 36 NCI models was the most appropriate predictor of recent volume increment. Annual volume increment ($dm^3.yr^{-1}$) of each tree was averaged over the last 3 years (2008–2010). A linear mixed model (Pinheiro and Bates, 2000) was fitted between average annual volume increment of years 2008–2010 and NCIs using the nlme package of R (Pinheiro *et al.*, 2011; R-Development-Core-Team, 2011) with NCI treated as a fixed effect, and blocks and experimental units (EU) within blocks treated as random factors. A squareroot-transformation was applied to the response variable to ensure the normality and homogeneity of the residuals of models. Model selection was implemented using the AICcmodavg package of R (Mazerolle, 2011). Along with 36 NCI models, we included a null model to test the null hypothesis of no NCI effect on annual volume increment. The best NCI model with the highest Akaike weight was retained for further analyses.

3.3.5.2. Factors affecting tree response to partial harvesting

We also used linear mixed models (Table 3.2) to assess the relationships (1) between the 1999–2010 (post-treatment) annual volume increments and harvesting treatment, tree social status and time (linear and quadratic), and (2) between the 2008–2010 average annual volume increment and harvesting treatment, NCI, tree social status and pre-treatment volume increment (average annual volume increment of last 3 years before treatment). Selected interactions were also included in models (Table 3.2). Additionally, a null model was included in both analyses to test the null hypothesis of no effect of explanatory variables on annual volume increment. Block, experimental unit and tree (each one nested in the former) were treated as random factors. We also accounted for the compound symmetry correlation structure between repeated (annual) measurements of individual trees. A square root transformation was applied to annual volume increment and to average annual volume increment to comply with the assumptions of normality and homogeneity of residuals.

We considered 13 and 15 candidate models for analysis-2 and analysis-3, respectively (Tables 3.5 and 3.6). Candidate models were compared using Akaike's Information Criterion corrected for small samples. Akaike weights were computed to assess the support in favor of each model. When the top-ranked model had an Akaike weight <0.9, we used multi-model inference to compute the model-averaged estimates of the explanatory variables and their 95% confidence intervals (Burnham and Anderson, 2002). A confidence interval excluding 0 indicated that the response variable varied with the explanatory variables of interest (Burnham and Anderson, 2002; Mazerolle, 2006). The power of the correlation (R^2) between predicted and observed values was computed as a measure of the predictive power of all candidate models.

Table 3.1. Characteristics of dominant and co-dominant trembling aspen trees sampled in boreal mixedwood stands submitted to partial harvesting 12 years prior to sampling.

Treatment	Social status	DBH range (cm)	Mean DBH (cm)	Height range (m)	Mean height (m)	Live crown length (range) (m)	Mean length of live crown (m)	Crown width (range) (m)	Mean crown width (m)	Mean height at age 50 years	DBH range in 1998 (pre-treatment) (cm)	Mean DBH in 1998 (pre-treatment) (cm)
Control	Dominant	34-45.4	39.5	25.6-31.1	28.02	6.8-13.6	9.7	11.1-16.4	13.3	24.2	30.4-39.0	34.3
	Co-dominant	24-27.6	25.9	22.8-28.9	25.07	2.9-9.3	6.6	6.7-9.8	8.4	21.5	18.3-25.4	21.8
1/3 partial-cut	Dominant	32.1-47.7	39.7	24.1-28.7	26.53	7.9-11.4	10.2	11.1-15.5	13.1	22.3	26.7-38.1	32.7
	Co-dominant	20.3-25.5	22.8	19.6-26.7	23.18	3.8-10.8	6.4	7.6-11.7	8.9	20.4	18.6-23.6	21.8
2/3 partial-cut	Dominant	31.2-48.4	37.7	23.5-28.9	25.89	5.5-12.2	7.8	10.8-14.1	12.9	22.0	22.3-40.4	29.0
	Co-dominant	21.7-27.2	24.2	20.8-27.5	24.25	4.4-10.6	6.8	8-10.3	9.4	19.5	17.6-24.6	20.0

Note: All sampled trees were 87-88 years old. Crown width was calculated by adding the length of two largest branches from two opposite sides of the tree

Table 3.2. Mixed linear model analyses of annual volume increment of trembling aspen stems, 1 to 12 years following harvesting.

Analysis	Research questions	Response variables	Explanatory variables
1.	Best probable neighborhood competition indices	Average annual volume increment (dm^3 year^{-1}) of the last three years (2008-2010) prior to destructive sampling of stems	Variants of NCI based on α (0, 1, and 2), β (0, 0.5, 1, and 2), and R (6, 8, and 10 m).
2.	Effect of harvesting treatment, social status and time since treatment application	Annual volume increment (dm^3 year^{-1})	Treatment, social status, time, time^2, treatment * social status, partial harvesting* time, and partial harvesting* time^2.
3.	Effect of harvesting treatment, social status, NCI, pre-treatment volume increment	Average annual volume increment (dm^3 year^{-1}) of the last three years (2008-2010) prior to destructive sampling of stems	Treatment, social status, NCI, pre-treatment volume increment, partial harvesting*social status, partial harvesting* NCI, partial harvesting* pre-treatment volume increment

Note: Interaction terms are specified with a * (e.g., partial harvesting* social status)

3.4. Results

3.4.1. Annual volume increment of trees over time

Annual volume increment of sampled trees over time since stand initiation (Figure 3.1) was roughly continuous from 1923 to 1980 (age 57), then remained more or less stable thereafter. Dominant trees accumulated higher volume and exhibited higher variability in annual increment than co-dominants. Strong growth anomalies (pointer years) in 1954, 1980, and in 2001 were common to all sampled trees, including those in controls. Change in annual volume increment following partial harvesting treatments in the winter 1998–1999 are visually apparent, especially in the 2/3 partial cut (Figure 3.1). Cumulative volume increment (12 years) of dominants was 268.8 ± 51.6, 309.1 ± 57.7 and 323.7 ± 74.1 dm^3 (mean ± 95% confidence intervals) in controls, 1/3 partial cut and 2/3 partial cut, respectively. Cumulative volume increment (12 years) in co-dominants was 84.1 ± 18.4, 92.0 ± 24.6 and 120.1 ± 30.7 dm^3 in controls 1/3 partial cut and 2/3 partial cut, respectively (Table 3.3).

3.4.2. Characterization of neighborhood competition 10–12 years after treatment

Of the 37 (36 + 1 null model) models of neighborhood competition indices (see Appendix 3.1), NCIs proportional to diameters of neighboring trees ($\alpha = 1$) were among the nine indices with the highest Akaike weight and the highest R^2 (Table 3.4). Among these, the three most probable NCIs were independent of the distance between neighboring and target trees ($\beta = 0$). The NCI based on neighboring trees located within 6 m of the target tree ($R = 6$ m) had the highest support (Akaike weight of 0.25) and was 1.5 times more likely to the second-ranked model (Akaike weight of 0.17) (Table 3.4). Only the most probable NCI model was retained for further analyses.

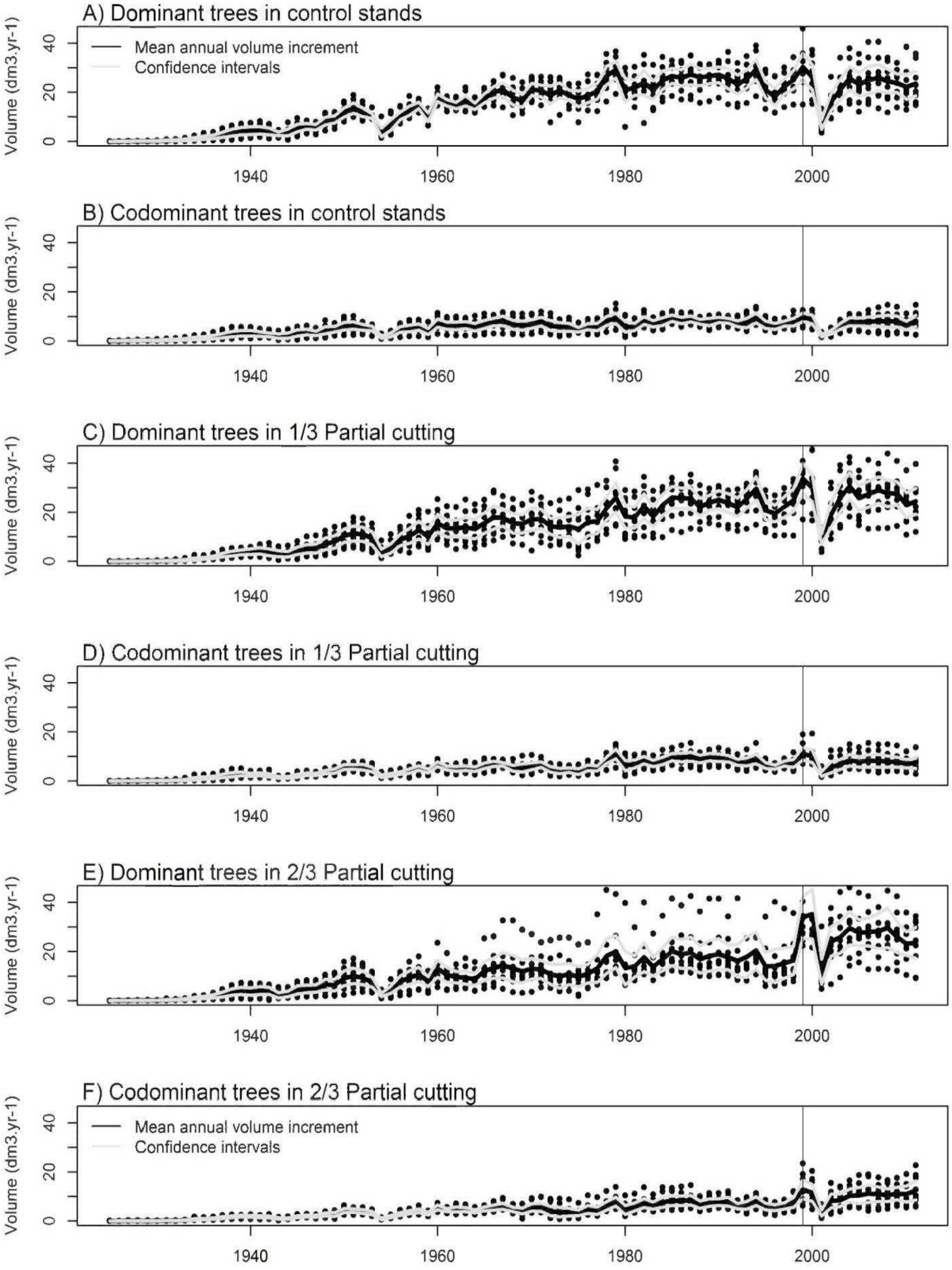

Figure 3.1. Annual volume increment of sampled trees according to social status and treatments. Note. Vertical line indicates year of harvesting treatments.

Table 3.3. Average annual and cumulative volume increment (dm^3) for the entire twelve year post partial harvesting treatment. Presented values are mean±95% confidence intervals of n=9.

Treatment	Social status	Observed cumulative volume increment1-12 years after treatment	Observed average annual volume increment 1-12 years after treatment	Predicted average annual volume increment 1-12 years after treatment	Observed average annual volume increment for 2008-2010 years	Predicted average annual volume increment for 2008-2010 years
Control	Dominant	268.8±51.6	22.4±4.3	21.6±4.0	23.3±4.6	23.9±3.7
	Co-dominant	84.1±18.4	7.0±1.5	6.4±2.2	7.4±2.1	6.9±1.9
1/3 partial-cut	Dominant	309.1±57.7	25.8±4.8	23.8±4.2	26.1±5.0	24.1±3.7
	Co-dominant	92.0±24.6	7.7±2.1	7.6±2.4	7.6±2.0	7.6±2.0
2/3 partial-cut	Dominant	323.7±74.1	27.0±6.2	26.2±4.4	26.3±6.0	31.8±5.1
	Co-dominant	120.1±30.7	10.0±2.6	9.0±2.6	10.9±2.7	10.8±2.4

Table 3.4. Model selection based on AICc criteria of the most probable neighborhood competition indices (NCI) accounting for average (2008-2010) annual volume increment 10-12 years following partial harvesting of mixedwood stands. Of the 36 tested models, only the nine with the highest AICc weight are presented. R : limit of neighborhood radius, α and β : exponents as defined in Eq. (1), K: number of parameters, AICc: Akaike's Information Criterion corrected for small samples, ΔAICc: AICc relative to the most parsimonious model, w_i: AICc model weight.

R (m)	α	β	K	AICc	ΔAICc	AICc weight (w_i)	R^2
6	1	0	5	175.96	0.00	0.25	0.24
8	1	0	5	176.68	0.72	0.17	0.21
10	1	0	5	176.74	0.78	0.17	0.20
10	1	0.5	5	177.15	1.19	0.14	0.20
8	1	0.5	5	177.67	1.71	0.10	0.21
6	1	0.5	5	178.56	2.60	0.07	0.20
10	1	1	5	180.64	4.68	0.02	0.16
8	1	1	5	181.35	5.39	0.02	0.15
6	1	1	5	181.66	5.70	0.01	0.16

Note. Top nine models based on Akaike weight (w_i) are presented. Square root transformation was applied to response variable.

3.4.3. Effect of harvesting treatment, time since harvesting and tree social status on annual volume increment

Three out of the 13 models for annual volume increment over the entire post-treatment period of 12 years had AICc weights $\geq$0.01 (Table 3.5) and all included treatment, social status and time effects. The model that included all the single factors (treatment, social status and time) and no interactions had an Akaike weight of 0.98 and was more probable than the second-ranked model (Akaike weight of 0.01) which included the same factors without the quadratic effect of time.

According to the most probable model, annual volume increment of residual trembling aspen trees increased linearly with time since partial harvesting over the 12 year period. A decrease in annual increment in 2001, resulting from defoliation by eastern tent caterpillar (*Malacosoma disstria*), accounted for the quadratic effect of time over annual volume increment. Trees in the 2/3 partial cut had a substantial increase in volume increment starting in the first growing season after treatment application (Table 3.5, Figure 3.2A and B). Considering both dominants and co-dominants, the average annual increment in the 2/3 partial cut was 25.6% higher than in untreated control stands over the 12 year period (Table 3.3). No difference was found between the 1/3 partial cut and controls. The response in volume increment following harvesting was independent of tree social status, as indicated by the low Akaike weights of models that included the interaction between harvesting and social status (Model 12, Table 3.5). However, in all treatments including controls, annual volume increment of dominant trees was higher than that of co-dominants by an average of 16.2 dm^3. $tree^{-1}$.yr^{-1} over the 12 year period (Table 3.3, Figure 3.2A and B).

3.4.4. Effect of treatment, social status, NCI, and pre-treatment growth on the 2008–2010 average annual volume increment (AAVI)

Two of the 15 models for the 2008–2010 average annual volume increment (AAVI) had AICc weights >0.01 and both contained pre-treatment volume increment, tree social status and harvesting treatment as explanatory variables (Table 3.6). The model that included the additive effects of treatment, pre-treatment volume increment and social status had the most support (Akaike weight 0.60). This model was 1.5 times more likely than the second ranked model (Akaike weight 0.40) which also included NCI. Because no single model had all the support of Akaike weights, we used the entire model set for inference (Table 3.6). Considering both dominant and co-dominants, the 2008–2010 AAVI was higher in the 2/3 partial-cut than in the controls by an average of 11.8 $dm^3.tree^{-1}.yr^{-1}$ (Table 3.3). However, no effect of harvesting was found in the 1/3 partial cut when compared with control stands. Tree social status and pre-treatment volume increment affected AAVI (Table 3.6, Figure 3.2C and D) with dominant trees and trees with highest pre-treatment annual volume increment (10–40 $dm^3.tree^{-1}.yr^{-1}$) showing the highest 2008–2010 AAVI (Figure 3.2C and D). Multi-model inference produced a parameter estimate for NCI that was not significantly different from 0 (Table 3.6).

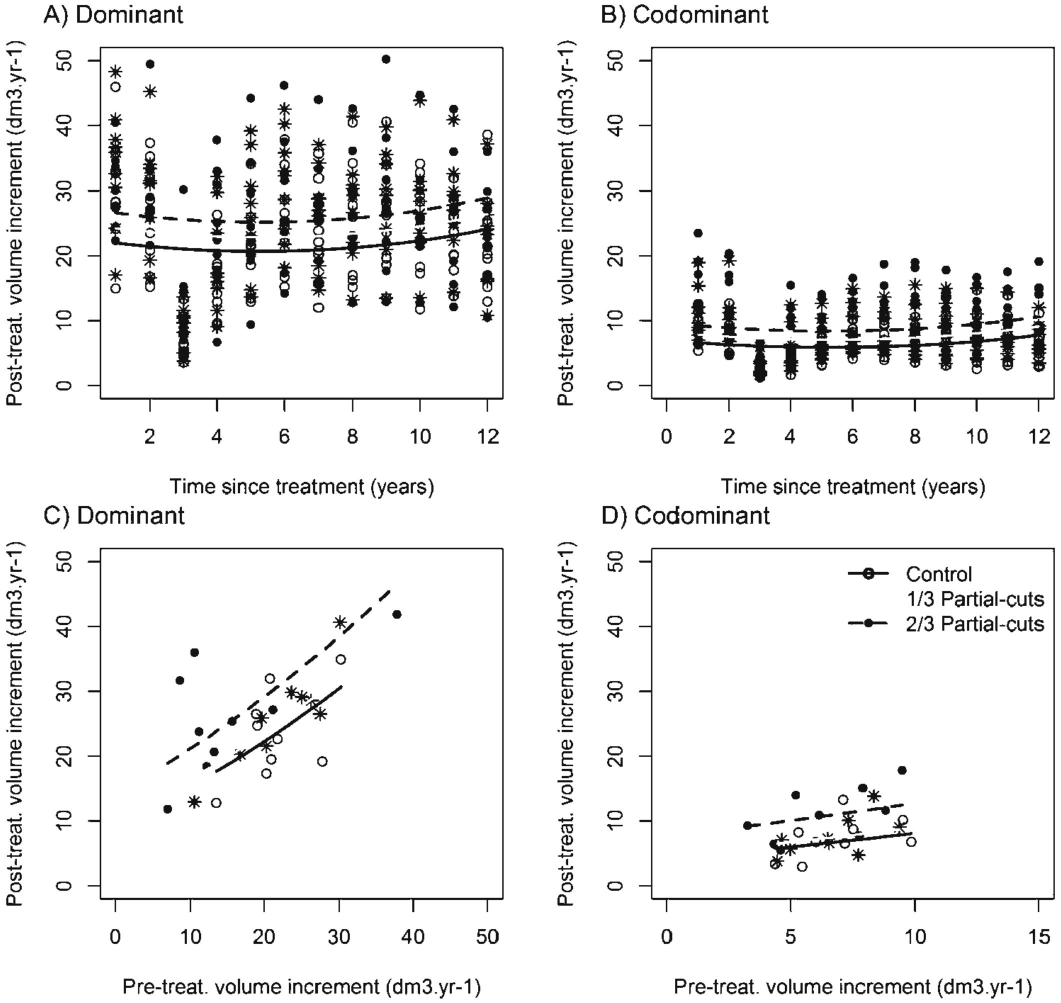

Figure 3.2. Post-treatment annual volume increment of residual trembling aspen stems following partial harvesting of boreal mixedwood stands. Annual volume increment is presented as a function of time since treatment for (A) dominant and (B) co-domimant trees. Average (2008-2010) annual volume increment10, 11 and 12 years post-treatment presented as a function of pre-treatment volume growth of (C) dominant and (D) co-dominant trees.

Table 3.5. List of models, priori hypotheses for analysis-2 (Table 3.2), results of model selection and the weights of estimates with unconditional confidence intervals. Note that interaction terms are specified with a star (e.g., TREAT*SS); annual volume increment (AVI), partial harvesting treatment (TREAT), time since harvesting (TIME (linear), and TIME^2 (quadratic)) and tree social status (SS).

Model No.	Candidate models	Biological hypothesis
1	AVI~TREAT	Positive effect of treatments
2	AVI ~SS	Positive effect of tree social status
3	AVI ~TREAT+SS	Positive effect of treatments with an additive effect of tree social status
4	AVI ~ TREAT+SS+TREAT*SS	Positive effect of treatments, but different effect for each social status
5	AVI ~ TIME	Positive effect of time
6	AVI ~TREAT+TIME	Positive effect of time with an additive effect of treatments
7	AVI ~TREAT+TIME+TIME^2	Positive effect of treatments with a quadratic effect of time
8	AVI ~TREAT+SS+TIME	Positive effect of treatments with an additive effect of tree social status and time
9	AVI~TREAT+SS+TIME+TIME^2	Positive effect of treatments with an additive effect of tree social status and quadratic effect of time
10	AVI ~TREAT+TIME+ TREAT*TIME	Positive effect of treatments with an additive effect of time but effect changes for each time period
11	AVI ~ TREAT+TIME+TIME^2+ TREAT*TIME+TREAT*TIME^2	Positive effect of treatments with a quadratic effect of time but effect changes for each time period
12	AVI~TREAT+SS+TIME+ TIME2+TREAT*SS+ TREAT*TIME+TREAT*TIME^2	Global model
13	AVI~1	Null model

Table 3.5. continues

Table 3.5. Selection of mixed linear models based on AICc for annual volume increment (AVI) of residual aspen stems 1 to 12 years after partial harvesting. K: number of parameters, AICc: Akaike's Information Criterion corrected for small sample sizes, ΔAICc: AICc relative to the most parsimonious model, w_i: AICc model weight. Only models showing AICc weights are presented below.

Model No.	Candidate models	K	AICc	ΔAICc	AICc weight(w_i)	R^2
9	AVI~TREAT+SS+TIME+TIME^2	10	1417.54	0.00	0.98	0.81
8	AVI ~TREAT+SS+TIME	9	1426.52	8.98	0.01	0.80
12	AVI~TREAT+SS+TIME+ TIME2+TREAT*SS+ TREAT*TIME+TREAT*TIME^2	16	1428.61	11.07	0.01	0.81

Estimates and precision (i.e., unconditional SE) of the effect of time, treatment and tree social status on annual volume increment based on model averaging.

Parameter	Estimate (β)	Lower 95% CI	Upper 95% CI
Time	**0.0198**	**0.0053**	**0.0242**
Time^2	**0.008**	**0.0033**	**0.0127**
TREAT1 (1/3 partial-cut vs controls)	0.2309	-0.1616	0.6234
TREAT2 (2/3 partial-cut vs controls)	**0.4696**	**0.0771**	**0.862**
SS (Co-dominant vs dominant)	**-2.1187**	**-2.4391**	**-1.7982**

Note: No significant interactions were found to affect annual volume increment for the period of 1999-2010. Elements in bold indicate a strong effect of that explanatory variable on response variable. Only top ranked model (model-9) was used to compute the model-averaged estimates of the explanatory variables and their 95% confidence intervals as the top-ranked model had an Akaike weight > 0.9.

Table 3.6. List of models, priori hypotheses for analysis-3 (Table 3.2), results of model selection and weights of estimates with unconditional confidence intervals. Note that interaction terms are specified with a star (e.g., TREAT*SS); average annual volume increment (AAVI) for the period of 2008-2010, partial harvesting treatment (TREAT), tree social status (SS), pre-treatment volume increment (PT) and neighborhood competition index (NCI).

Model No.	Candidate models	Biological hypothesis
1	AAVI~TREAT	Positive effect of treatments
2	AAVI ~SS	Positive effect of tree social status
3	AAVI ~PT	Positive effect of pre-treatment growth
4	AAVI ~ NCI	Positive effect of neighborhood competition indices
5	AAVI ~TREAT+SS	Positive effect of time with an additive effect of tree social status
6	AAVI ~TREAT+PT	Positive effect of treatments with an additive effect of pre-treatment growth
7	AAVI ~TREAT+NCI	Positive effect of treatments with an additive effect of neighborhood competition indices
8	AAVI~ TREAT+SS+PT	Positive effect of treatments with an additive effect of tree social status and pre-treatment growth
9	AAVI ~ TREAT+SS+NCI	Positive effect of treatments with an additive effect of tree social status and neighborhood competition indices
10	AAVI ~ TREAT+SS+PT+NCI	Positive effect of treatments with an additive effect of tree social status, pre-treatment growth and neighborhood competition indices
11	AAVI ~ TREAT+PT+TREAT*PT	Positive effect of treatments but the treatment effect change according to pre-treatment growth
12	AAVI ~ TREAT+SS+TREAT*SS	Positive effect of treatments but the treatment effect changes for each tree social status
13	AAVI ~ TREAT+NCI+TREAT*NCI	Positive effect of treatments but the treatment effect changes according to neighborhood competition indices
14	AAVI ~ TREAT+SS+PT+NCI+ TREAT*SS+TREAT*NCI +TREAT*PT	Global model
15	AAVI~1	Null model

Table 3.6. continues

Table 3.6. Selection of mixed linear models based on AICc for the average annual volume increment (AAVI) residual stems of trembling aspen 10 - 12 years following partial harvestings. K: number of parameters, AICc: Akaike's Information Criterion corrected for small sample sizes, ΔAICc: AICc relative to the most parsimonious model, wi: AICc model weight. Only models have AICc weights presented below.

Model No.	Candidate models	K	AICc	ΔAICc	AICc weight(w_i)	R^2
8	AAVI ~ TREAT+SS+PT	8	100.56	0.00	0.60	0.85
10	AAVI ~ TREAT+SS+PT+NCI	9	101.36	0.80	0.40	0.86

Estimates and precision (i.e., unconditional SE) of the effects of treatment, NCI, pre-treatment growth and tree social status on average annnal volume increment based on model averaging.

Parameter	Estimate (β)	Lower 95% CI	Upper 95% CI
TREAT1 (1/3 partial-cut vs controls)	0.1003	-0.2489	0.4494
TREAT2 (2.3 partial-cut vs controls)	**0.6308**	**0.2232**	**1.0383**
NCI (neighborhood competition index)	-1.7547	-4.1039	0.5945
PT (pre-treatment annual volume increment)	**0.0798**	**0.0536**	**0.1061**
SS2 (Co-dominant vs dominant)	**-1.0131**	**-1.4487**	**-0.5776**

Note. No significant interaction was found for average annnal volume increment for years 2008-2010. Elements in bold indicate a strong effect of that explanatory variable on response variable. All models were used to compute the model-averaged estimates of the explanatory variables and their 95% confidence intervals as the top-ranked model had an Akaike weight < 0.9.

3.5. Discussion

Annual volume increment of residual trees following partial harvesting of virtually pure and mature even-aged aspen stands is a function of partial harvesting prescription, tree social status and pre-treatment growth rate of residual trees. Crown thinning of 61% of basal area induced a long-lasting positive effect on tree growth that was independent of the neighborhood competition 10–12 years following treatment, as measured through NCI. Tree growth after treatment was proportional to tree growth before treatment application. Despite being over 80 years old, residual aspen trees continued to grow vigorously.

3.5.1. Effect of partial harvesting prescription on annual volume increment

We had hypothesized that annual volume increment would increase with partial harvesting intensity. However, after partial harvesting treatments, residual trembling aspen trees showed a sizeable increase in annual volume increment only in the 2/3 partial cut. Removal of up to 33% of basal area using a low thinning had little effect on residual aspen growth. This was probably due to both the low intensity of the treatment and the fact that most stems were removed from the smaller diameter classes. These stems therefore exerted less competition for light and soil resources prior to the treatment than the residual stems that were generally larger. That is, the 1/3 partial cut (light, low thin) had little effect on resource availability for larger stems.

In the first years following partial harvesting of these stands, light availability increased with decreasing residual basal area (Brais *et al.*, 2004). However very few differences in soil temperature and moisture or organic matter decomposition and mineralization were observed between partial cuts and control stands (Brais *et al.*, 2004). The strong response of understory vegetation to canopy opening in the years following harvesting was attributed to the increase in light availability (Brais *et al.*, 2004; Lapointe *et al.*, 2007). However, light availability is generally not limiting for dominant trees; rather, trees with crowns in the mid- to lower-canopy should experience greater release after partial harvesting treatments, such as crown, selection or free thinning, because of the greater change in the light environment in these layers (Walter and Maguire, 2004). Following harvesting, canopy opening (measured at 3 m height) increased by 60% in the 1/3 partial harvesting treatment and this occurred mostly close to skid trails whereas the 180% increase in the 2/3 partial harvesting treatment reflected more openings created between trails as more trees were removed from the upper canopy (Brais *et al.*, 2004). In the 2/3 partial cut, canopy opening was probably sufficient to increase light availability to the lower crown of residual trees. As trembling aspen is very shade intolerant, all trees likely benefited from this increase. Nonetheless, 12 years after harvesting, this response did not translate into any significant differences in crown dimensions within social status and between treatments (Table 3.1). Hence, volume growth response in partial harvesting treatments was not related to increased crown size. Crown dimension could change in last 12 years, but that change is equal in every treatments (results not shown).

Besides shade tolerance, other physiological traits of trembling aspen may explain the observed growth patterns. Trembling aspen is a nutrient demanding species (Paré *et al.*, 2002), and because it is also a clonal species, individual stems that have suckered from a common root section or even a common parent tree can remain connected through stand development. This potentially allows transfer of carbohydrates and soil resources through a larger root network than that of an individual to connected stems. Root grafts can also contribute to maintaining a connected root network, even after some of connected trees have died (DesRochers and Lieffers, 2001; Jelínková *et al.*, 2009). While confirming whether connections between root systems of harvested and unharvested trees improve growth response of the latter would require further testing, we could speculate that harvesting larger stems through a severe crown harvesting would provide a greater root network to exploit soil resources for residual stems. The similar, unambiguous response of dominant and co-dominant trees to partial harvesting would indicate that changes in soil resource availability were among the mechanisms underlying the increase in volume increment.

3.5.2. Effect of tree social status and pre-treatment volume growth on post-treatment volume increment

Based on stem analyses, social status of trembling aspen residual trees 12 years after treatments was consistent with their social status prior to treatment application. Dominant trees exhibited the highest increment both in absolute and relative terms (relative to pre-treatment condition) than co-dominants across time, irrespective of treatments (Tables 3.5 and 3.6). The higher volume increment by larger trees may simply reflect the greater capacity of larger crowns to capture more light for photosynthesis (Wyckoff and Clark, 2005). Metsaranta and Lieffers (2008) demonstrated that size inequality within tree populations tends to make competition asymmetric, in that larger individuals obtain a disproportionately high share of resources (Berntson and Wayne, 2000). In our study, however, response to harvesting treatments was independent of both residual stem social status and pre-treatment volume increment indicating that response to increased availability in resources was size symmetrical; that is, an individual's access to resources was proportional to its size (Schwinning and Weiner, 1998). This again raises the question regarding the role of root networks in individual tree response to changes in stand conditions.

Our results suggest that vigorous as well as less vigorous residual aspen trees will both experience increased growth following partial harvesting intensities similar to the 2/3 partial cut treatment but that the increase will be proportional to the pre-treatment growth. In even-aged aspen stands, tree social status does not tend to change following partial harvesting. That said, other studies have found size of residual stems to be a good predictor of growth following selection harvesting for a number of North American shade intolerant and tolerant species (Thorpe *et al.*, 2007; Jones *et al.*, 2009).

3.5.3. Effect of time since treatment application on annual volume increment

Our results showed an immediate increase in annual volume increment of residual trees following partial harvesting that was maintained over a 12 year period. This is in contrast with other studies (Youngblood, 1991; Thorpe *et al.*, 2007; Jones *et al.*, 2009; Goudiaby *et al.*, 2012) that have shown growth lag initially (1–5 years) after a range of partial harvesting prescriptions and in a variety of stand types. Trembling aspen is very shade intolerant and all sampled trees were healthy at the time of treatment application. Moreover, they were in the dominant and co-dominant layers of the canopy so at least upper crowns had direct exposure to light. We presume that partial harvesting did not create unfavorable conditions, such as increased wind exposure to critical levels, to the extent of damaging or inducing stress on residual aspen trees.

Annual tree volume increment of aspen did decrease sharply in the third year following treatment applications as a result of forest tent caterpillar defoliation. This affected tree volume increment in all treatments, including controls (Figure 3.1, Figure 3.2A and B). Aspen trees recovered promptly from this punctual natural disturbance and maintained the rate of annual volume increment until the last monitoring year (2010). This consistent tree-level growth occurred similarly in all treatments and reflects stand-level responses and our observation that these stands are approaching but have not yet arrived at the onset of stand decline (Bose *et al.*, 2014b). Man *et al.* (2008b) also reported near full recovery of diameter growth in surviving aspen trees following 3 years of moderate to severe tent caterpillar defoliation in similar aspen dominated forests situated just west of our study sites. However, they observed 70% aspen mortality in the 11 years following the outbreak and higher mortality in partially cut stands than in controls. In our study, aspen stem mortality 12 years after partial harvesting was 41% in the 2/3 treatment and 19% in 1/3 treatment compared to 29% in controls (Bose *et al.*, 2014b).

3.5.4. Effect of NCI on average annual volume increment 10–12 years following treatments

The NCI analyses were based on the tree neighborhood around our target trees that were destructively sampled (for stem analyses) in year 12 post-treatment. NCI analyses were done only for the growth period 10–12 years following treatments because we could not assume that the neighborhood remained relatively constant for a longer previous period, for example for the entire post treatment period (i.e. that some neighborhood trees did not die or that new stems did not recruit into the ≥5 cm DBH). In effect, compared to control treatments, cumulative aspen stem mortality over the 12 year post-treatment period was 14% higher in the 2/3 partial harvesting treatment and 10% lower in the 1/3 treatment (Bose *et al.*, 2014b).

The neighborhood competition indices (see Appendix 3.1) were based on distances of the target (sampled) tree to neighborhood trees, neighbor tree sizes, and neighborhood radius (6, 8 or 10 m). Similar to what Canham *et al.* (2006) observed for trembling aspen in New England, the most probable NCI index was dependent on the size of the closest neighbors (neighborhood radius=6 m) but independent of the actual distance between these neighbors to the target trees. However, even the most probable NCI model was a poor predictor of residual aspen volume increment 10–12 years after treatments, despite significant differences in aspen mortality observed between treatments over the 12-year period (Bose *et al.*, 2014b). This is consistent with the observed constant difference in annual volume increment between trees in the 2/3 partial cuts and controls over the 12 year period.

3.6. Management implications

While recent interest in partial harvesting in the Canadian boreal mixedwood forest has largely been driven by concerns related to maintenance of biodiversity and other ecosystem services, the importance of these most productive of boreal forest ecosystems as a sustainable source of quality timber has not been lost on forest managers (LeBlanc, 2014). Reports of high residual tree mortality and growth stagnation in some situations following partial harvesting have raised questions concerning the possible negative effects of such practices on maintenance of a continuous timber supply in mixedwood regions (Thorpe and Thomas, 2007; Bose *et al.*, 2014c). Coates (1997) and Thorpe *et al.* (2007) emphasized that partial harvesting can only be considered as a viable silvicultural treatment if residual mortality is reasonably low and growth of residual trees is enhanced. Our results have shown a substantial tree level increase of annual volume increment after severe partial harvesting (heavy crown thinning) both for dominant and co-dominant individuals. Moreover, growth response was sustained over the entire monitoring period (12 years) except for 1 year of a tent caterpillar outbreak. Although stand-level basal area decreased slightly over this same period, due largely to mortality of small merchantable stems (Bose *et al.*, 2014b), the enhanced and constant volume growth of residual trembling aspen stems following heavy partial harvesting, even in these mature stands, should provide some incentive for greater use of such practices in mixedwood management. This is particularly true if (1) treatments also promote vigorous recruitment and growth of a second cohort of desirable species (Bose *et al.*, 2014b) and (2) bigger piece sizes can be expected at a later entry. Certainly from a silvicultural viewpoint, if abundant aspen recruitment and increased stand-level complexity were important objectives, a group shelterwood regime would probably enhance both better than the dispersed thinning applied in this study (Haeussler *et al.*, 2007). Such a treatment would also have the potential effect of maintaining more large stems – key biological legacies – in the residual stand than following a severe high thinning.

That the mature (76–87 years old) aspen trees in our study responded to partial harvesting is, in itself, a somewhat surprising result. However, recent demonstration by LeBlanc (2014) of sustained growth of a portion of old, large trembling aspen trees and the development of multiple cohorts of aspen in aspen and mixed stands have important implications concerning the effects of partial harvesting and multi-cohort structure on wood supply and carbon sequestration.

3.7. Acknowledgements

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Appendix 3.1. List of models and a priori hypotheses for analysis-1 (NCI), using equation of $\boldsymbol{NCI} = \frac{\sum_{j=1}^{N} (DBH_j)^{\alpha}/(dist_{ij})^{\beta}}{1000}$, candidate models are based on three coefficients: neighbor size effect (α), distance between neighbors to target tree (β) and the limit of neighborhood radius (R). Here response variable is average annual volume increment for the period of 2008-2010 of each tree. Note, neighbor's size is its DBH.

Model-no	Coefficients of candidate models	Biological hypothesis
1	α=0, β = 0 and R=6	No size and distance effect; competition effect within 6 m radius
2	α=1, β = 0 and R=6	Effect of neighbor's size but not distance; competition effect within 6 m radius
3	α=2, β = 0 and R=6	Effect of neighbor's basal area but not distance; competition effect within 6 m radius
4	α=0, β = 0.5 and R=6	No size but square-root of the distance effect; competition effect within 6 m radius
5	α=1, β = 0.5 and R=6	Effect of neighbor size and square-root of the distance; competition effect within 6 m radius
6	α=2, β = 0.5 and R=6	Effect of neighbor basal area and square-root of the distance; competition effect within 6 m radius
7	α=0, β = 1 and R=6	No size but distance effect; competition effect within 6 m radius
8	α=1, β = 1 and R=6	Effect of neighbor size and distance; competition effect within 6 m radius
9	α=2, β = 1 and R=6	Effect of neighbor basal area and distance; competition effect within 6 m radius
10	α=0, β = 2 and R=6	No size but squared distance effect; competition exists within 6 m radius
11	α=1, β = 2 and R=6	Effect of neighbor size and squared distance; competition effect within 6 m radius
12	α=2, β = 2 and R=6	Effect of neighbor basal area and squared distance; competition effect within 6 m radius
13	α=0, β = 0 and R=8	No size and distance effect; competition effect within 8 m radius
14	α=1, β = 0 and R=8	Effect of neighbor size but not distance; competition effect within 8 m radius
15	α=2, β = 0 and R=8	Effect of neighbor basal area but not distance; competition effect within 8 m radius
16	α=0, β = 0.5 and R=8	No size but square-root of the distance effect; competition effect within 8 m radius
17	α=1, β = 0.5 and R=8	Effect of neighbor size and square-root of the distance; competition effect within 8 m radius
18	α=2, β = 0.5 and R=8	Effect of neighbor basal area and square-root of the distance; competition effect within 8 m radius
19	α=0, β = 1 and R=8	No size but distance effect; competition effect within 8 m radius
20	α=1, β = 1 and R=8	Effect of neighbor size and distance; competition effect within 8 m radius

Appendix 3.1. continues

Appendix 3.1. List of models and a priori hypotheses for analysis-1 (NCI), using equation of $\boldsymbol{NCI} = \frac{\sum_{j=1}^{N} (\boldsymbol{DBH_j})^{\alpha}/(\boldsymbol{dist_{ij}})^{\beta}}{\mathbf{1000}}$, candidate models are based on three coefficient neighbor size effect (α), distance between neighbors to target tree (β) and neighborhood radius (R). Here response variable is average annual volume increment for the period of 2008-2010 of each tree. Note, neighbor's size is its DBH.

Model no	Coefficients of candidate models	Biological hypothesis
21	α=2, β = 1 and R=8	Effect of neighbor basal area and distance; competition effect within 8 m radius
22	α=0, β = 2 and R=8	No size but squared distance effect; competition effect within 8 m radius
23	α=1, β = 2 and R=8	Effect of neighbor size and squared distance; competition effect within 8 m radius
24	α=2, β = 2 and R=8	Effect of neighbor basal area and squared distance; competition effect within 8 m radius
25	α=2, β = 2 and R=10	No size and distance effect; competition effect within 10 m radius
26	α=1, β = 0 and R=10	Effect of neighbor size but not distance; competition effect within 10 m radius
27	α=2, β = 0 and R=10	Effect of neighbor basal area but not distance; competition effect within 10m radius
28	α=0, β = 0.5 and R=10	No size but square-root of the distance effect; competition effect within 10 m radius
29	α=1, β = 0.5 and R=10	Effect of neighbor size and square-root of the distance; competition effect within 10 m radius
30	α=2, β = 0.5 and R=10	Effect of neighbor basal area and square-root of the distance; competition effect within 10 m radius
31	α=0, β = 1 and R=10	No size but distance effect; competition effect within 10 m radius
32	α=1, β = 1 and R=10	Effect of neighbor size and distance; competition effect within 10 m radius
33	α=2, β = 1 and R=10	Effect of neighbor basal area and distance; competition effect within 10 m radius
34	α=0, β = 2 and R=10	No size but squared distance effect; competition effect within 10 m radius
35	α=1, β = 2 and R=10	Effect of neighbor size and squared distance; competition effect within 10 m radius
36	α=2, β = 2 and R=10	Effect of neighbor basal area and squared distance; competition effect within 10 m radius
37	Y~1	Null model

CHAPITRE IV

DOES PARTIAL HARVESTING PROMOTE OLD-GROWTH ATTRIBUTES OF BOREAL MIXEDWOOD TREMBLING ASPEN (POPULUS TREMULOIDES MICHX) STANDS?

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4.1. Abstract

In the current context of forest ecosystem management, partial harvesting has been proposed as a silvicultural tool to augment forest variability on managed landscapes and to accelerate the development of structural and compositional attributes of old-growth/late successional stands. The aims of this paper were 1) to identify and characterise, based on the literature, the structural attributes of old-growth aspen-dominated stands in the North American boreal mixedwood forest, and 2) to examine the mid-term potential of partial harvesting in aspen-dominated stands to accelerate stand development towards these old-growth characteristics. Two stand types – pure aspen (93% aspen basal area) and mixed aspen (81% aspen basal area) - were monitored over a 12-year post-treatment period. Compared to pure, even-aged stands, old-growth aspen stands have lower merchantable stem densities and basal area, more large aspen stems and higher stem size variability, more than one cohort of trees, greater percentage area occupied by gaps and higher expanded gap area, and more and larger snags and downed wood. In addition, old-growth aspen mixedwoods characteristically have more shade-tolerant conifers in all understory and overstory layers than younger, mature stands. Results indicate that while the partial harvesting treatments applied in this study successfully retained most of the structural attributes of mature aspen stands (untreated controls), they did not generally "accelerate succession" toward old-growth in the 12-year time interval. Nonetheless, overall results do suggest that by promoting irregularities in both horizontal and vertical structure, high-intensity partial harvesting, using either regular (diffuse) or gap removal, will accelerate stand development towards what could be characterised as old-growth aspen-dominated mixedwoods over longer time periods.

Keywords: Boreal mixedwood, trembling aspen (*Populus tremuloides* Michx.), partial harvesting, old growth forests, stand structure, variable retention.

Résumé

Dans un contexte d'aménagement forestier écosystémique, les coupes partielles sont proposées comme une alternative permettant d'accélérer le développement des attributs structurels propres aux peuplements anciens/ou stades successionnels avancés. Les objectifs de cette étude étaient: 1) d'identifier, à partir de la littérature scientifique, les caractéristiques structurelles des vieux peuplements de la forêt boréale mixte Nord Américaine dominés par le Peuplier faux-tremble (*Populus tremuloides* Michx.) et 2) d'examiner le potentiel à court terme des coupes partielles appliquées à peuplements équiennes matures dominés par le P. faux-tremble d'accélérer le développement de ces caractéristiques. Deux types de peuplement - le premier dominé par le tremble (93% de la surface terrière en tremble) et le deuxième mixte, tremble et résineux (81% de la surface terrière en tremble) - ont été suivis sur une période de 12 ans après coupe. Comparativement à des peuplements équiennes matures, les peuplements anciens de P. faux-tremble ou mixtes sont caractérisés par 1) une densité et une surface terrière en tiges marchandes inférieures, 2) plus de trembles de fortes dimensions et une plus grande variation de la taille des tiges, 3) plus d'une cohorte d'arbres, 4) une plus grande surface occupée par les trouées d'arbres et des touées élargies plus grandes et 5) des chicots et débris ligneux au sol plus abondants. En outre, on retrouve plus de conifères tolérants à l'ombre dans les strates du sous-bois et arborescentes des peuplements anciens que dans celles des peuplements matures équiennes. Les résultats indiquent que les coupes partielles spécifiques à cette étude aient réussi à conserver la plupart des caractéristiques structurelles des peuplements de trembles matures (contrôles non traités). Cependant au cours des 12 premières années après coupe, elles n'ont pas "accéléré la succession" vers des peuplements anciens. Cependant, les résultats suggèrent qu'en créant plus d'irrégularités dans la structure horizontale et verticale des peuplements, une coupe partielle de haute intensité appliquée selon un patron régulier ou par trouées permettra d'accélérer à plus long terme le passage des peuplements matures équiennes vers un stade plus avancé caractéristique des peupliers faux-tremble âgés de la forêt mélangée.

Mots-clés: forêt boréale mixte, peuplier faux-tremble (P*opulus tremuloides* Michx.), coupe partielle, peuplements anciens, structure du peuplement, rétention variable

4.2. Introduction

The concept of forest ecosystem management (FEM) has taken hold in many parts of the World (Gustafsson *et al.*, 2012; Lindenmayer *et al.*, 2012), including Canada (Lieffers *et al.*, 1996b; Bergeron and Harvey, 1997; Harper *et al.*, 2003). FEM recognizes the importance of mitigating the differences between natural (of natural disturbance-origin and unmanaged) and managed forest systems, and as such, silvicultural practices, are underpinned by an understanding of how natural disturbance and ecosystem processes affect stand dynamics (Grumbine, 1994; Christensen *et al.*, 1996). The natural disturbance emulation approach of FEM aims, in part, to mitigate the undesirable impacts of generalized application of even-aged forest management on biodiversity (Fedrowitz *et al.*, 2014) and ecosystem processes (Likens *et al.*, 1978; Keenan and Kimmins, 1993), thus favouring long-term sustainability of ecosystem goods and services (Christensen *et al.*, 1996).

Partial harvesting has been identified as a key silvicultural tool in the implementation of FEM in the boreal forest (Lieffers *et al.*, 1996b; Bose *et al.*, 2014c). It is assumed that partial harvesting can 1) contribute to maintaining ecosystem functions within their historical variability by retaining greater residual structure in harvested forests (Drever *et al.*, 2006; Franklin *et al.*, 2007; Gauthier *et al.*, 2009), and 2) potentially accelerate stand development towards an old-growth stage - or accelerate the acquisition of compositional and structural characteristics associated with the old-growth stage - by creating growing space of variable sizes for new cohorts (Franklin *et al.*, 2002; Harvey *et al.*, 2002). Old-growth stands have been recognized as functionally and structurally diverse relative to young, intensively managed stands (Spies and Franklin 1988, Mosseler et al. 2003, Franklin and Van Pelt 2004) and stands with high structural variability are considered more likely to provide a variety of wildlife habitats and to increase ecosystem resilience to environmental stresses (Drever *et al.*, 2006; Fischer *et al.*, 2006).

In Canada, boreal mixedwoods generally occur on productive sites and have long been recognized as being among the most structurally complex stand types in the Canadian boreal forest (De Grandpré and Bergeron, 1997; Chen and Popadiouk, 2002; Haeussler *et al.*, 2007). In boreal mixedwoods, shade-intolerant hardwoods, mostly trembling aspen (*Populus tremuloides* Michx.) and white birch (*Betula papyrifera* Marsh), and shade-tolerant conifers coexist in different proportions depending of time since the last stand replacing fire, climatic factors and interactions between a range of abiotic and biotic factors (Bergeron *et al.*, 2014; Nlungu-Kweta *et al.*, 2014). Trembling aspen regeneration by suckering is favoured by severe disturbances (Perala, 1974; Frey *et al.*, 2003; Brais *et al.*, 2004) and boreal aspen stands have been traditionally managed under even-aged silvicultural system (MacDonald, 1995; Bergeron *et al.*, 2002). However, studies conducted in boreal mixedwood forests have shown that, in the absence of fire, aspen may regenerate successfully in gaps, leading to older, uneven-aged stands with distinct aspen cohorts (Bergeron, 2000; Cumming *et al.*, 2000; LeBlanc, 2014).

Regional studies have provided insights into the range of attributes that define old-growth aspen stands or mixed aspen stands in the boreal forest (Lee *et al.*, 1997; Bergeron, 2000; LeBlanc, 2014). However, a more comprehensive review of the attributes of old-growth boreal trembling aspen stands is required to assess the effectiveness of partial harvesting of even-aged aspen stands to promote the development of these attributes. The potential of partial harvesting to promote old-growth characteristics has been tested for Northern hardwood forests of the United States (McGee *et al.*, 1999; Keeton, 2006), for hardwood forests of Canada (Angers *et al.*, 2005), and in other parts of the world (Barbati *et al.*, 2012; Motta *et al.*, 2014), but not for the North American trembling aspen-dominated boreal mixedwoods. Studies conducted in boreal mixedwoods have shown that partial harvesting can create multi-layer canopies by favouring recruitment of intolerant hardwood regeneration and establishment of conifer regeneration (Prévost and Pothier, 2003;

Man *et al.*, 2008a; Bose *et al.*, 2014b). However, Haeussler *et al.* (2007) found that while partial harvesting treatments in aspen-dominated mixedwoods may retain attributes of un-harvested stands, in the short term, they do not necessarily hasten the development of older stand attributes. Moreover, by destroying well-decomposed logs, partial harvesting can also cause a loss of structural variability and species diversity (Brais *et al.*, 2004).

The objectives of this study are to (i) identify and quantify structural attributes that characterize old-growth aspen-dominated mixedwoods of the North-American boreal forest and (ii) to examine whether specific partial harvesting treatments applied 12 years previously in pure and mixed aspen stands promote structural attributes of old-growth stands in the mid-term. We tested the following hypotheses: 1) low intensity, diffuse partial harvesting has little impact on stand structure as it creates few large gaps and retains most of the structural attributes of even-aged stands (O'Hara, 1998; Haeussler *et al.*, 2007); 2) high-intensity partial harvesting treatments applied in either a regular (diffuse) or a gap pattern create a higher percentage of canopy gaps and wide tree spacing, effects that produce greater variability in tree size classes through recruitment and growth of a second cohort of aspen (Ball and Walker, 1997; McCarthy, 2001; O'Hara, 2001) and by prompting the growth of late successional species, when present (Brais *et al.*, 2013; Prévost and DeBlois, 2014). However, high-intensity partial harvesting can reduce the density of large trees, density and basal area of standing snags and volume of downed logs relative to in untreated control stands (McGee *et al.*, 1999; Angers *et al.*, 2005; Keeton, 2006).

4.3. Methods

The first objective was addressed through a search of the scientific literature 1) containing reference to old-growth aspen and stand structural attributes associated with canopy, understory vegetation and deadwood (snags and downed logs) characteristics or 2) describing changes in these characteristics along natural succession in North American boreal mixedwoods. Papers were based on studies conducted in the Canadian provinces of Alberta (e.g., Lee *et al.*, 1997; Lee *et al.*, 2000), Saskatchewan (e.g., Hobson and Bayne, 2000; Brandt *et al.*, 2003), Manitoba (e.g., Ball and Walker, 1997; LeBlanc, 2014), Ontario (e.g., Basham, 1958; Hill *et al.*, 2005) and Québec (e.g., Kneeshaw and Bergeron, 1998; Bergeron, 2000) as well as in Minnessota (USA) (e.g., Frelich and Reich, 1995; Reich *et al.*, 2001). Old-growth was defined as stands between 100 to 200 years of age (LeBlanc, 2014) corresponding to the time at which the initial post-fire cohort begins to die and understorey stems are recruited to the canopy (Kneeshaw and Gauthier, 2003). The upper limit (200 years) was defined as the period when aspen stems are no longer dominant or co-dominant in terms of relative proportion of stand basal area (Bergeron, 2000). This particular stage (old-growth aspen stands) has also been defined as intermediary stage of the succession in the boreal mixedwoods (Bergeron and Harper, 2009).

4.3.1. Study sites

The second objective was addressed using empirical data. This empirical part was conducted in the Lake Duparquet Research and Teaching Forest (LDRTF) in the Abitibi region of northwestern Quebec, 45 km northwest of the city of Rouyn-Noranda (48°86′N–48°32′N, 79°19′W–79°30′W). This region is characterized by the presence of extensive clay deposits left by proglacier Lake Ojibway (Vincent and Hardy, 1977) and rich clay soils on upland sites (Canada Soil Survey Committee, 1987a). The climate is continental and cold temperate with a mean annual temperature of 0.7 °C and mean annual precipitation of 889.8 mm (Environment Canada, 2011).

The LDRTF is located in the balsam fir-white birch bioclimatic domain (Saucier *et al.*, 1998). Forests of the region are characterized by a mixed composition of boreal conifers, and shade-intolerant broadleaved species. Trembling aspen, white birch

(*Betula papyrifera* Marsh), and jack pine (*Pinus banksiana* Lamb.) are the most frequent early successional species. Balsam fir (*Abies balsamea* (L.) Mill.) is the dominant species in late-successional forests on mesic sites, and is associated with white spruce (*Picea glauca* [Moench] Voss), black spruce (*P. mariana* [Mill.] B.S.P.), and eastern white cedar (*Thuja occidentalis* L.) (Bergeron, 2000).

The SAFE Project (*Sylviculture et aménagement forestier écosystémiques*) (Brais *et al.*, 2004; Brais *et al.*, 2013) is a series of replicated experiments set in the LDRTF. Experiments were designed to validate the ecological and operational feasibility of a FEM strategy involving partial harvesting for the eastern Canadian boreal mixedwoods (Bergeron and Harvey, 1997; Bergeron *et al.*, 2002). This study makes use of data from two experiments of the SAFE project. The first one was set in "pure aspen stands" which originated from a wildfire in 1923. Average pre-treatment stand basal area was 42.1 $m^2.ha^{-1}$ of which 92.6% was trembling aspen and 3.3% conifer species. In the winter 1998-1999, three harvesting treatments, including a no harvest control and two intensities of partial harvesting were applied according to a complete randomized block design with three replications (blocks) of each treatment. Each block contained the three harvesting treatments, each applied to an experimental unit (EU). The sizes of EUs ranged from 1.0 to 2.5 ha. Harvesting treatments were applied using manual felling and bucking and logs were forwarded using small skidders. All trees were removed from trails that were, on average, 4.5 m wide and spaced at 30 meters (Bose et al., 2014b). The two partial harvesting treatments were designed to remove 33% (1/3 partial cut) and 61% (2/3 partial cut) of merchantable basal area (primarily aspen) in an evenly dispersed spatial pattern. Stands in the 1/3 partial cut were low thinned while stands in the 2/3 partial cut were primarily crown thinned aimed to emulate natural dynamics such as self-thinning and stand senescence, respectively (Brais *et al.*, 2004). In silvicultural terms, these treatments could be referred to light, low thinning and heavy, crown thinning, respectively, but for consistency with previous publications, we maintain the 1/3 and 2/3 partial cut terminology throughout this paper.

"Mixed aspen stands" in the SAFE project originated from a wildfire fire in 1910. Average pre-treatment stand basal area was 41.0 $m^2.ha^{-1}$ of which 80.8% was trembling aspen and 17.8% conifer species. In the winter of 2000, three harvesting treatments, again including a no harvest control and two intensities of partial harvesting treatments, were applied. Similar to the design in the pure aspen stands, treatments in the mixed aspen stands were applied according to a complete randomized block design with three replications (blocks) of each treatment. Each block contained the three harvesting treatments, each applied to an EU. The sizes of EUs ranged from 2.0 to 3.0 ha (see details in Brais *et al.*, 2013). All harvesting treatments were applied using multifunctional (short-wood) harvesters and forwarders. In dispersed cuts, all trees were removed in 5 m wide hauling trails and approximately 25 % of stems were harvested to a depth of 6 to 7 m in the adjacent strips. In gap cuts, gaps were created by alternately harvesting stems in the trail only and enlarging the cutting area to a depth of 6 to 7 m on either side of trails (total width 16 – 18 m), done on lengths of 20 m. In both treatments, an unharvested band of 5 - 6 m was left between each sequence of trail – partially harvested strip. The two partial harvesting treatments were 1) an evenly dispersed treatment that removed 45% of BA aimed to emulate individual-level tree mortality and 2) 400 m^2 gap cuts (average 54% BA removal) aimed to emulate tree mortality in patches. In silvicultural terms, these two treatments could be considered an intermediate-intensity free thinning (cutting in all commercial stem sizes) and group shelterwood treatments, respectively, but again, for reasons of consistency, we refer to them as the 45% dispersed cut and gap cut treatments.

Besides differences in overstory composition, the main difference between the two stand types was in the seedling and sapling layers: balsam fir was very dense in mixed aspen stands, whereas total conifer regeneration was very low and a woody shrub, mountain maple (*Acer spicatum* Lamb.), dominated the regeneration layer in pure aspen stands.

4.3.2. Field methods

In each EU, five permanent sample plots (PSP, 400 m^2, radius=11.28 m) were established before treatment application. All stems (trees and shrubs) greater than 5 cm at breast height (1.3 m) were identified to species, tagged, and their diameter at breast height (DBH) was measured. In the northeast quadrant (100 m^2) of each PSP, all stems between 2.0 and 4.99 cm DBH was also identified to species, tagged, and their DBH measured. A similar inventory was conducted for snags (dead stems > 1.3 m in height) within PSP. Snags were identified to species, measured (DBH), and tagged. Immediately following harvesting, a tally of all residual stems was compiled. All PSP in the pure aspen and mixed aspen stands were measured again 12 years after treatment application.

Twelve years after treatment application, canopy gaps were characterized in all experimental units. Canopy gap is defined as "the vertical projection of a canopy opening and gap length is the distance between crown edges (the area with no overhead foliage). The expanded gap is delimited by the stems of trees whose crowns define the canopy gap (Runkle, 1982; Kneeshaw and Bergeron, 1998). Using transects oriented perpendicular to skid/forwarding trails (250 m total in each EU), canopy openness was assessed every 30 cm either as covered with tree crown or open due to the partial harvesting or tree mortality. For each gap, gap length (m) and expanded gap area (m^2) were measured and calculated, respectively. Expanded gap area was evaluated using the formula for an ellipse (Runkle, 1982; Kneeshaw and Bergeron, 1998). In all experimental units, the volume of downed logs was inventoried twelve years after treatment application using the line intercept method (Van Wagner, 1982).

4.3.3. Data analysis

Based on our literature review, we used 18 structural attributes describing old-growth characteristics of aspen-dominated boreal mixedwoods (Table 4.1). Tree species were divided in two classes in relation to their successional status. Intolerant hardwoods consisted of trembling aspen, balsam poplar (*Populus balsamifera* Gray) and white birch, whereas the shade-tolerant conifers included white spruce, black spruce, balsam fir and eastern white cedar. Ratio of sub-canopy to canopy basal area was calculated following Lee *et al.* (2000), where dominants and co-dominants (≥ 20 cm DBH) represents the canopy trees and intermediate and suppressed (5 - 19.9 cm DBH) represents the sub-canopy trees. Tree height was calculated using species-specific allometric equations (Beaudet *et al.*, 2011). Maximum height is the height of the tallest tree in a PSP. Standard deviations of DBH and height were used to indicate horizontal and vertical structural variability, respectively (Zenner, 2000). Differences among treatments prior to application were tested for stand density and basal area of live trees and for snag density and basal area.

4.3.4. Statistical analysis

Effects of harvesting treatments on structural attributes immediately and 12 years after harvesting were assessed by linear mixed models (Pinheiro and Bates, 2000) using the nlme package in R (Pinheiro *et al.*, 2011; R-Development-Core-Team, 2011). Blocks and experimental units (EU) nested within blocks were treated as random factors. Treatment was treated as a fixed factor. Stands and time periods (immediately after and 12 years after treatment) were analysed separately and the differences among treatments were tested by means of contrasts, 1) controls vs 1/3 partial cut and 2) controls vs 2/3 partial cut in pure aspen stands, whereas 1) controls vs dispersed cut and 2) controls vs gap cuts in mixed aspen stands. We verified the assumptions of normality of residuals and homogeneity of the variances. When these assumptions were not met, a square root transformation was used. Bar plots with mean±95% confidence intervals were used in all figures to illustrate the interval estimate of the estimated population parameter.

4.4. Results

4.4.1. Characteristics of old-growth trembling aspen-dominated boreal mixedwoods

Old-growth aspen stands are characterized by a high percentage of canopy gaps, multiple canopy layers and high structural variability both in the overstory and in the understory layers (see Table 4.1 for ranges of values and references). Old-growth stands differ from younger or earlier successional stands by their lower total tree density, and particularly that of intolerant hardwoods, and lower stand basal area. Density, basal area and volume of shade-tolerant conifers, large trees, trees with heart rot, large snags and downed logs are higher in old-growth stands relative to those values observed in younger stands (Table 4.1).

Table 4.2. Structural attributes of old-growth trembling aspen stands of the North-American boreal mixedwood forests. Attributes are quantified using the literature. For the remaining attributes (not provided quantitative range) cited references did not contain any numbers. Attributes that not measured in current study mentioned as “not measured”.

Stand structural characteristics	Attributes of old-growth aspen stands relative to younger, homogenous stands	Ref.	Attributes measured in current study
Stand age	100 to 200 years	19	Not used in this study
Horizontal structure	Lower total merchantable stem density due to mortality (≈640 - 900 stems.ha^{-1})	4, 6, 7	Stand density (≥ 10 cm DBH, stems.ha^{-1})
	Lower merchantable stem density of intolerant hardwoods due to the mortality of first cohort aspen, (≈215 - 650 stems.ha^{-1})	10, 15	Intolerant hardwood density (≥10 cm DBH, stems.ha^{-1})
	Higher stem density of shade-tolerant conifers due to the recruitment in canopy gaps (≈ 200 - 375 stems.ha^{-1})	10, 18	Shade-tolerant conifer tree density (≥10 cm DBH, stems.ha^{-1})
	Lower stand basal area due to partial mortality of first cohort aspen (≈25 - 28 m^2.ha^{-1})	10	Stand basal area (≥ 10 cm DBH, m^2.ha^{-1})
	Wider range of diameter size classes (high standard deviation of DBH)	19	Standard deviation of DBH
	Higher mean stand DBH (≈29 - 45 cm) due to presence of large, old aspen and spruce stems, or lower following dieback of large aspen trees	6, 7, 10	Quadratic mean DBH (cm)
	Wider range of tree spacing and higher horizontal structural variability	14	Not measured
Canopy gaps	Higher percentage of canopy gaps (≈19 - 35%) and expanded canopy gaps, (≈26 - 32%) of total stand area	9, 15	Percentage of canopy gaps (%)
	Higher variability in canopy gap area (≈6 – 1200 m^2) and expanded canopy gap area (≈34 – 1,450 m^2)	9, 15	Expanded canopy gap area (m^2)
Vertical structure	Greater presence of large old canopy trees (≥15% of total stand density or ≈96-115 stems.ha^{-1})	11, 12, 13	Density of large trees (≥30 cm DBH, stems.ha^{-1})
	Multi-layered tree canopy	3, 4, 19	Not measured
	Wider range of height size classes (high standard deviation of tree height)	19	Standard deviation of tree height
	Higher maximum tree height (≈ 22 - 30.0m)	6, 7, 16	Maximum height (m)
	Higher ratio of sub-canopy to canopy basal area (range 0.8-2.0)	12	Ratio of sub-canopy to canopy basal area

[1]Basham 1958, [2]Thomas et al. 1960, [3]Frelich and Reich 1995, [4]Schieck et al. 1995, [5]Ball and Walker 1997, [6]Lee et al. 1997, [7]Crites and Dale 1998, [8]Lee 1998, [9]Kneeshaw and Bergeron 1998, [10]Bergeron 2000, [11]Hobson and Bayne 2000, [12]Lee et al. 2000, [13]Schieck et al. 2000, [14]Kneeshaw and Gauthier 2003, [15]Hill et al. 2005, [16]Savignac and Machtans 2006, [17]Haeussler et al. 2007, [18]Thompson et al. 2013, [19]Leblanc 2014

Table 4.1. continues

Table 4.1. Structural attributes of old-growth trembling aspen stands of the North-American boreal mixedwood forests. Attributes are quantified using the literature. For the remaining attributes (not provided quantitative range) cited references did not contain any numbers. Attributes that not measured in current study mentioned as “not measured”.

Stand structural characteristics	Attributes of old-growth aspen stands relative to younger, homogenous stands	Ref.	Attributes measured in current study
Understory structure	Higher density of shade-tolerant conifer regeneration (balsam fir, white and black spruce, eastern white cedar)	3, 5, 9, 10, 18,	Shade-tolerant conifer sapling density (2 - 9.9 cm DBH, stems.ha^{-1})
	Lower density of intolerant hardwood regeneration in case of small gap formations and presence of shade-tolerant conifers. Large gaps and absence of conifers make a higher density of intolerant hardwood regeneration	2, 3, 5	Intolerant hardwoods sapling density (2 - 9.9 cm DBH, stems.ha^{-1})
	Higher species and structural diversity of non-tree species including shrubs, herbs and other vascular and non-vascular plants	7, 17	Density of woody shrubs (2 - 9.9 cm DBH, stems.ha^{-1})
Deadwood structure	Higher density and basal area of snags, excluding snags and logs of pre-fire origin. (snag density ≈ 338 - 675 stems.ha^{-1} with large snag (≥ 20 cm DBH) density representing 15 - 20 % of total)	4, 6, 8, 10, 18	Density of snags (≥10 cm DBH stems.ha^{-1}) Basal area of snags (≥10 cm DBH m^{2}.ha^{-1})
	Higher volume of downed logs (117-132 m^{3}.ha^{-1}) and more large logs (excluding pre-fire logs)	4, 6, 7	Volume of downed logs (m^{3}.ha^{-1})
	Greater range of decay classes present and higher percentage of well-decayed downed wood	1, 2	Not measured

[1]Basham 1958, [2]Thomas et al. 1960, [3]Frelich and Reich 1995, [4]Schieck et al. 1995, [5]Ball and Walker 1997, [6]Lee et al. 1997, [7]Crites and Dale 1998, [8]Lee 1998, [9]Kneeshaw and Bergeron 1998, [10]Bergeron 2000, [11]Hobson and Bayne 2000, [12]Lee et al. 2000, [13]Schieck et al. 2000, [14]Kneeshaw and Gauthier 2003, [15]Hill et al. 2005, [16]Savignac and Machtans 2006, [17]Haeussler et al. 2007, [18]Thompson et al. 2013, [19]Leblanc 2014

4.4.2. Structural attributes of pure aspen and mixed aspen stands in relation to partial harvesting treatments

Prior to treatment application, there were no statistical significant differences among treatments in terms of stand density of live trees, stand basal area of live trees, snag density and snag basal area (results not shown).

4.4.2.1. Horizontal structure

Twelve years after harvesting of pure aspen stands, the significant initial reductions in total stand density and intolerant hardwood tree density (stems ≥ 10cm DBH) induced by harvesting were found to be significant in the 2/3 partial cuts only (Table 4.2, Fig. 4.1A and B). In mixed aspen stands, total stand and intolerant hardwood tree densities were initially similar between controls and dispersed cuts, but 12 years after harvesting both densities were significantly lower in the dispersed cuts. Twelve years after treatment application, the 400 m^2 gap cuts had significantly lower stand and intolerant hardwood densities than the controls (Table 4.2, Fig. 4.1A and B). In both stand types, tolerant conifer density remained similar across treatments over the twelve year period. Again in both stand types, the initial significant reductions in basal area induced by harvesting remained significant 12 years after harvesting (Table 4.2, Fig. 4.1C and D). At that time, stand basal area of pure aspen stands was 40.9±3.3 (mean±95% confidence interval), 31.8±3.3 and 14.3±3.3 $m^2.ha^{-1}$ in controls, 1/3 and 2/3 partial cuts respectively. In mixed aspen stands, the average stand basal area was 38.0±3.7, 19.3±3.7 and 13.9±3.7 $m^2.ha^{-1}$ in controls, dispersed cuts and gap cuts respectively (Fig. 4.1D). In both stand types, no differences in average tree DBH were found between harvesting treatments and controls, regardless of period since harvesting (Table 4.2, Fig. 4.1E). Twelve years after harvesting, quadratic mean DBH was lower in 2/3 partial cuts than in controls of pure aspen stands and also lower in gap cuts than in controls of mixed aspen stands (Table 4.2, Fig. 4.1E). The significant initial reductions in tree DBH size variability (standard deviation of tree DBH) in 400 m^2 gap cuts were no longer significant 12 years after treatment application (Table 4.2, Fig. 4.1F).

4.4.2.2. Canopy gaps

Twelve years after harvesting of pure aspen stands, the percentage of canopy gaps and average expanded canopy gap area were larger in the 2/3 partial cuts than in controls whereas no difference was observed between controls and the 1/3 partial cuts for either attribute (Table 4.2, Fig. 4.2A, B). Twelve years after harvesting of mixed aspen stands, gap cuts had a higher percentage of canopy gaps and larger average expanded canopy gap area than controls. Only the canopy gap percentage was found to be significantly higher in the dispersed cuts than controls (Table 4.2, Fig. 4.2A, B).

4.4.2.3. Vertical structure

The sub-canopy to canopy basal area ratio was found to be significantly higher relative to controls in the 2/3 partial cuts of pure aspen stands and in the 400 m^2 gap cuts of mixed aspen stands 12 years after treatment application (Table 4.2, Fig. 4.2C). The density of large trees, relative to controls, was reduced in the 2/3 partial cuts of pure aspen stands and in the dispersed and gap cuts of mixed aspen stands (Table 4.2, Fig. 4.2D). No differences in stand maximum tree height were found for any partial harvesting treatment when compared with their respective controls (Table 4.2, Fig. 4.2E). Tree height size variability (standard deviation of tree height) in 400 m^2 gap cuts was significant both initially following treatment and 12 years later (Table 4.2, Fig. 4.2F).

4.4.2.4. Understory structure

Twelve years after harvesting, significantly higher densities of intolerant hardwood saplings were found in the 2/3 partial cuts than in controls of pure aspen stands and in dispersed and gap cuts than in controls of mixed aspen stands (Table 4.2, Fig. 4.3A). Conifer sapling densities were similar across treatments in both pure aspen and mixed aspen stands (Table 4.2, Fig. 4.3C). Over the 12 year period, sapling density of both intolerant hardwoods and shade tolerant conifers increased in all treatments of both stand types (Fig. 4.3A and C). Twelve years after treatment application, a similar high shrub density was found among treatments of pure aspen stands, but higher in gap cuts (not statistically analysed) than controls of mixed aspen stands (Table 4.2, Fig. 4.3E).

4.4.2.5. Snags and downed logs

In both pure aspen and mixed aspen stands, snag density, snag basal area and downed log volume were similar across treatments. Snags density and basal area increased over the 12 year post treatment period in both stand types. In pure aspen stands, total downed log volumes were 134, 94 and 91 $m^3.ha^{-1}$ in controls, 1/3 and 2/3 partial cut treatments, respectively, whereas in mixed aspen stands, downed log volumes were 107, 119 and 156 $m^3.ha^{-1}$ in controls, dispersed and gap cut treatments, respectively (Table 4.2, Fig. 4.3B, D and F).

Table 4.2. Effects of partial harvesting on stand structural attributes at year of treatment application and 12 years later. Significance of fixed effects is based on the contrast among categorical variables. Note. 1/3 PC: 33% BA removal primarily of suppressed and intermediate stems of pure aspen stand, 2/3 PC: 61% BA removal primarily of dominant and co-dominant stems of pure aspen stand, Dispersed cut: 45% BA removal using free thin in dispersed pattern in mixed aspen stands and Gap cut: 54 % basal area removed according to a gap pattern (400 m^2 gap) in mixed aspen stands, NS: p >0.051, -: not included in analysis), PA: pure aspen, MA: mixed aspen.

	Year of treatment application				**12 years after treatment application**			
Response variables	Control, AS Vs 1/3 PC	Control, AS Vs 2/3 PC	Control, AM Vs DC	Control, AM Vs GC	Control, AS Vs 1/3 PC	Control, AS Vs 2/3 PC	Control, AM Vs DC	Control, AM Vs GC
Horizontal structure								
Stand density (≥10 cm DBH)	0.037	0.009	NS	NS	NS	0.012	0.007	0.002
Intolerant hardwood tree density (≥10 cm DBH)	0.018	0.005	NS	0.025	NS	0.005	0.018	0.006
Shade-tolerant conifer tree density (≥10 cm DBH)	NS	NS	NS	NS	NS	NS	NS	NS
Stand basal area (≥10 cm DBH)	0.003	0.000	0.006	0.002	0.019	0.000	0.002	0.000
Mean DBH (≥10 cm DBH)	NS	NS	NS	NS	NS	NS	NS	NS
Standard deviation of DBH (≥10 cm DBH)	NS	NS	NS	0.039	NS	NS	NS	NS
Canopy gap structure								
Percentage of canopy gaps	-	-	-	-	NS	0.003	0.037	0.004
Expanded canopy gap area	-	-	-	-	NS	0.016	NS	0.048
Vertical structure								
Ratio of sub-canopy to canopy basal area	NS	NS	NS	NS	NS	0.022	NS	0.031
Large tree density (≥30 cm DBH)	NS	0.033	0.035	0.015	NS	0.022	0.009	0.008

Table 4.2 continues, Effects of partial harvesting on stand structural attributes at year of treatment application and 12 years later. Significance of fixed effects is based on the contrast among categorical variables. Note. 1/3 PC: 33% BA removal primarily of suppressed and intermediate stems of pure aspen stand, 2/3 PC: 61% BA removal primarily of dominant and co-dominant stems of pure aspen stand, Dispersed cut: 45% BA removal using free thin in dispersed pattern in mixed aspen stands and Gap cut: 54 % basal area removed according to a gap pattern (400 m^2 gap) in mixed aspen stands, NS: p >0.051, -: not included in analysis), PA: pure aspen, MA: mixed aspen.

	Year of treatment application				**12 years after treatment application**			
Response variables	Control, AS Vs 1/3 PC	Control, AS Vs 2/3 PC	Control, AM Vs DC	Control, AM Vs GC	Control, AS Vs 1/3 PC	Control, AS Vs 2/3 PC	Control, AM Vs DC	Control, AM Vs GC
Vertical structure								
Maximum height	NS	NS	NS	NS	NS	NS	NS	NS
Standard deviation of tree height	NS	NS	NS	0.021	NS	NS	NS	NS
Understory structure								
Intolerant hardwood sapling density (2-9.9 cm DBH)	NS	NS	NS	NS	NS	0.032	0.011	0.002
Shade-tolerant conifer sapling density (2-9.9 cm DBH)	NS	NS	NS	NS	NS	NS	NS	NS
High shrub density (2-9.9 cm DBH)	NS	NS	NS	NS	NS	NS	NS	NS
Deadwood structure								
Standing snag density (≥10 cm DBH)	NS	NS	NS	NS	NS	NS	NS	NS
Standing snag basal area (≥10 cm DBH)	NS	NS	NS	NS	NS	NS	NS	NS
Downed log volume	-	-	-	-	NS	NS	NS	NS

Table 4.3. Summary of effects of partial harvesting treatments in terms of promoting structural attributes of old-growth aspen stands or accelerating succession

Stand types	Treatments	No. of structural attributes of natural controls maintained[1]	Accelerated stand development in terms of…[2]	Undesirable changes in terms of…[3]	Effects on succession
Pure aspen	1/3 partial cut (low, light thinning, 33% BA removal)	17	Lower stand basal area	-	Removing smaller stems may prolong simple, even-sized structure
Pure aspen	2/3 partial cut (high, heavy thinning, 61% BA removal)	10	Greater expanded gap area, higher ratio of sub-canopy to canopy basal area, lower hardwood tree density	Too high percentage of canopy gaps and hardwood sapling density and too low stand density, stand basal area and large tree density	Strongly favoring the recruitment of intolerant hardwood sapling may set back canopy succession
Mixed aspen	Dispersed cut (free thinning, 45% BA removal)	12	Higher canopy gap percentage, greater expanded canopy gap area and lower hardwood tree density	Too low stand density, stand basal area and large tree density	Should accelerate stand development of more complex structure in terms of canopy gaps and both intolerant hardwood and tolerant conifer sapling recruitment
Mixed aspen	400 m^2 gap cut (54% BA removal	10	Greater expanded gap area, higher ratio of sub-canopy to canopy basal area and lower hardwood tree density	Too high percentage of canopy gaps and hardwood sapling density and too low stand density, stand basal area and large tree density	Strongly favoring the recruitment of intolerant hardwood sapling may set back canopy succession

[1] Total number of attributes evaluated =18. Number of structural attributes of natural controls maintained = number of attributes that are not statistically different between control and partial harvesting treatment.

[2] Accelerated stand development in terms of… = attributes whose values are statistically different from controls and progressed toward old-growth aspen stand characteristics.

[3] Undesirable changes in terms of… = attributes whose values are statistically different from controls but did not progress toward old-growth aspen stand characteristics.

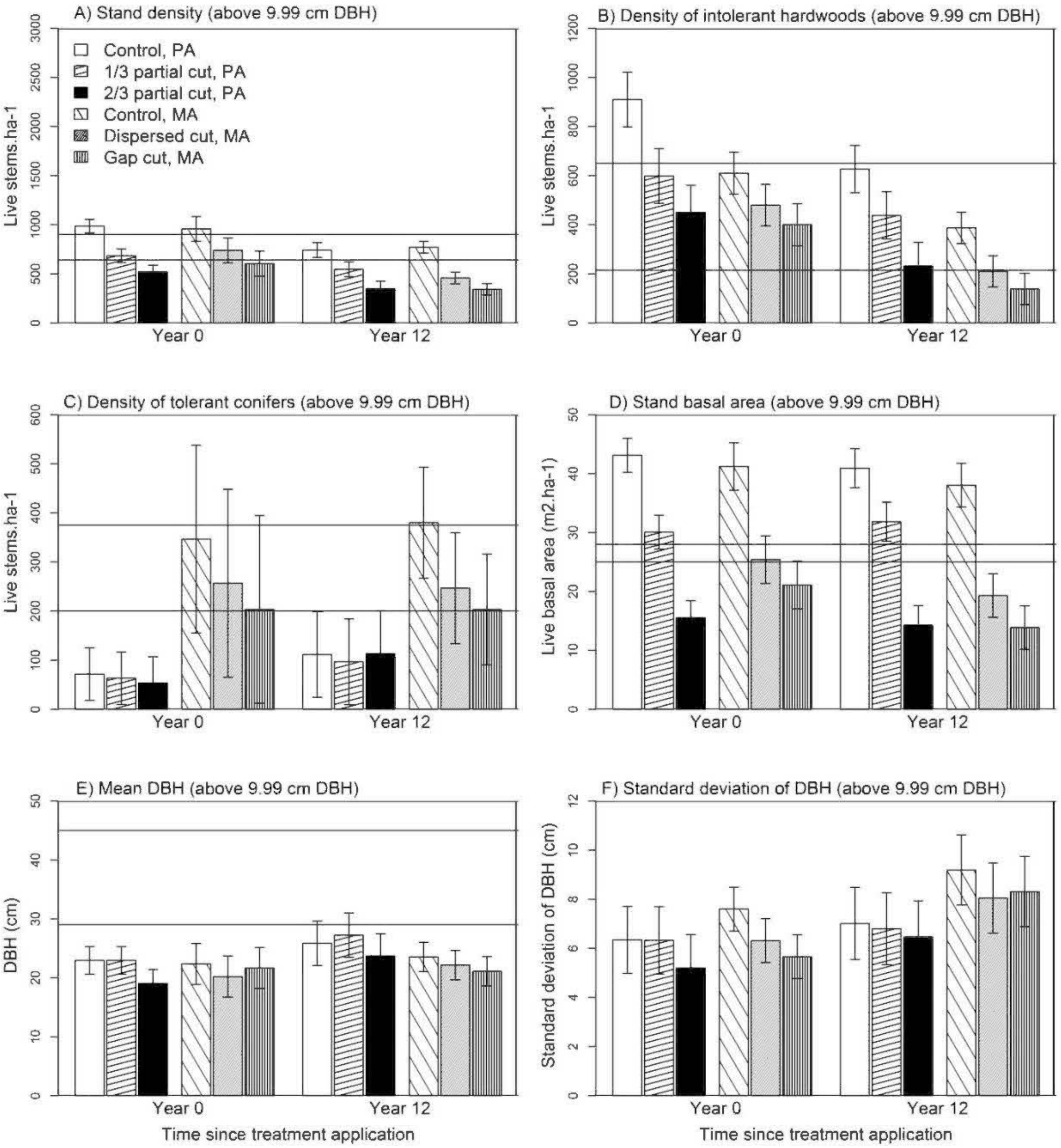

Figure 4.1. Comparisons of stand attributes associated with horizontal structure among six partial harvesting treatments of two stand types. Note. error bars represent mean±95% confidence interval, PA: pure aspen stands and MA: mixed aspen stands. Two parallel horizontal lines represents the range of old-growth structure (Table 4.1), figure-F has no parallel line due to information shortage in literature.

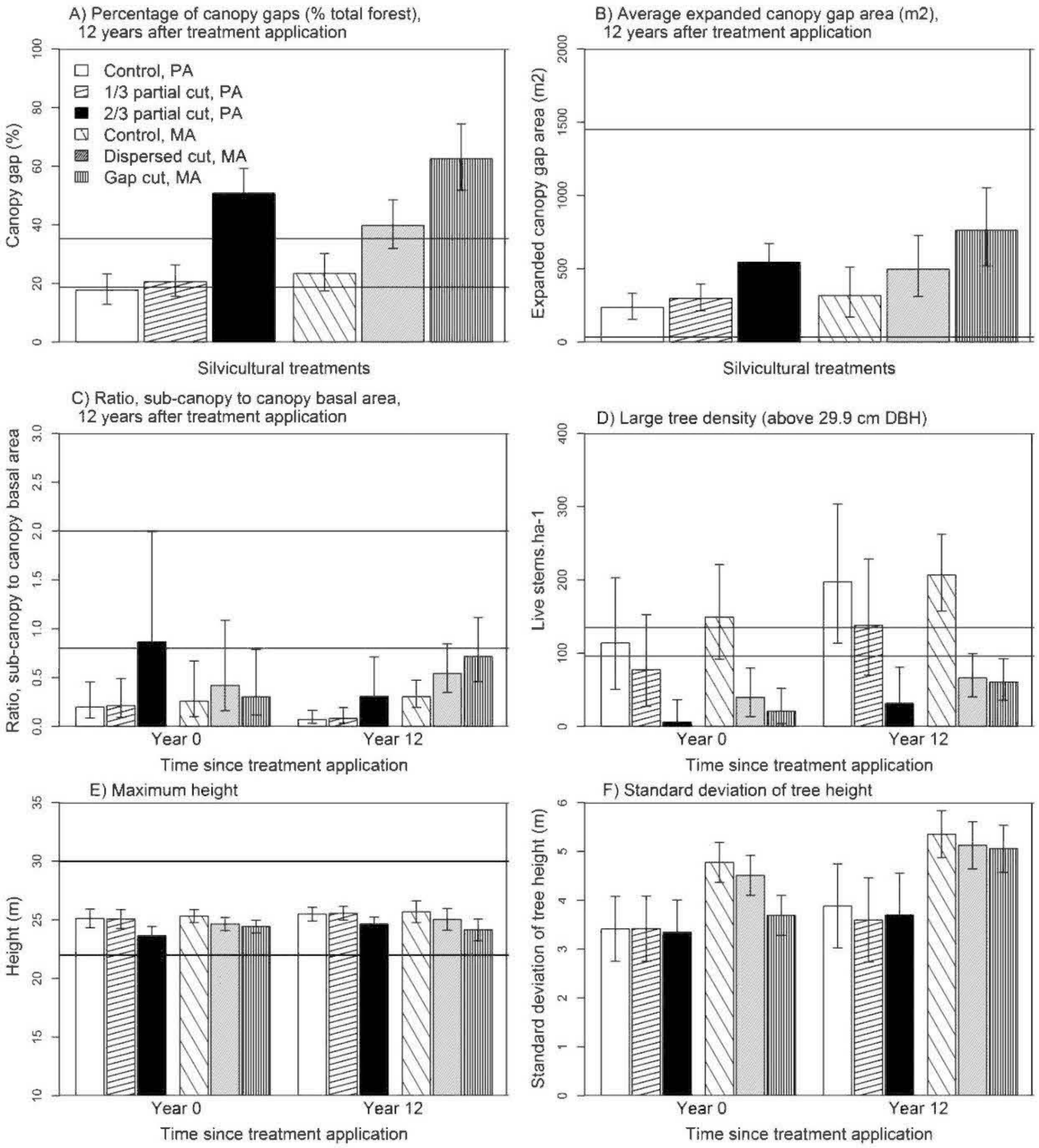

Figure 4.2. Comparisons of stand attributes associated with canopy gap and vertical structure among six partial harvesting treatments of two stand types. Note. error bars represent mean±95% confidence interval, PA: pure aspen stands and MA: mixed aspen stands. Two parallel horizontal lines represents the range of old-growth structure (Table 4.1), figure-F has no parallel line due to information shortage in literature.

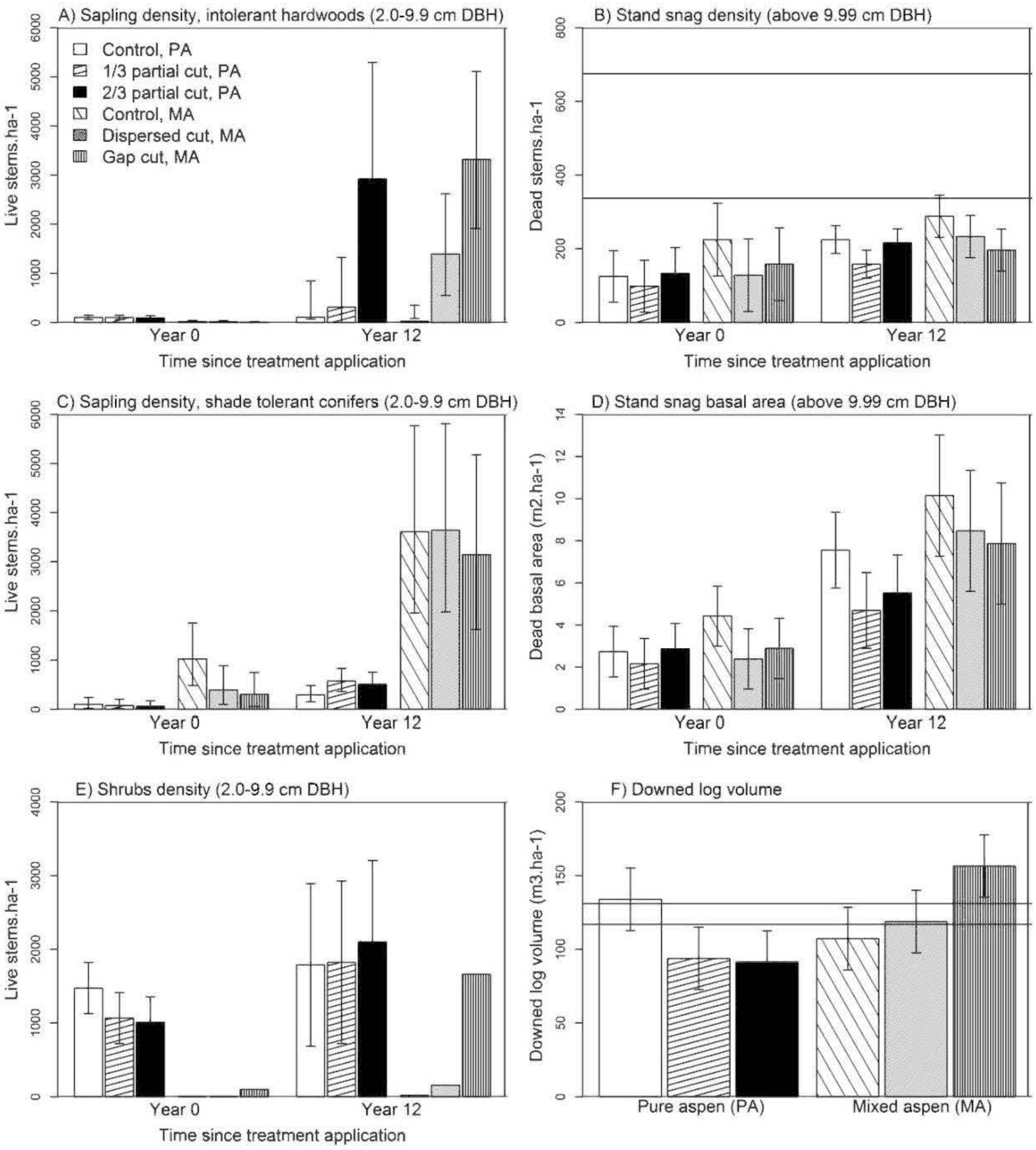

Figure 4.3. Comparisons of stand attributes associated with understory and deadwood structure among six partial harvesting treatments of two stand types. Note. error bars represent mean±95% confidence interval, PA: pure aspen stands and MA: mixed aspen stands. Two parallel horizontal lines represents the range of old-growth structure (Table 4.1), figure-A, C, D and E have no parallel line due to information shortage in literature. No statistical analysis were done with high shrub density in mixed aspen stand (figure E).

4.5. Discussion

The principal aim of this study was to identify quantifiable structural attributes of old-growth trembling aspen-dominated stands in the boreal mixedwood forest in order to evaluate the potential of partial harvesting to enhance the development of these attributes in mature even-aged stands. The results of this study indicate that partial harvesting retained many of the structural attributes of mature aspen stands (untreated controls). However, twelve year after harvesting, the resulting stands present few of the attributes that characterize old-growth aspen stands.

4.5.1. Characterization of old-growth forests, a global perspective

Bauhus *et al.* (2009) defined *"old-growth forests as a subset of primary forests that develop only under a limited set of circumstances, mostly associated with long periods without major natural disturbances"*. The old-growth forest has also been defined by a range of structural attributes and processes that illustrate a complex stand structure in both horizontal and vertical dimensions (see details in Spies and Franklin, 1988, 1991; Franklin and Van Pelt, 2004; Zenner, 2004; Bauhus *et al.*, 2009). However, the typical old-growth attributes demonstrated by above studies do not necessarily articulate the old-growth stage of boreal forests (Kneeshaw and Gauthier, 2003; Bergeron and Harper, 2009). Boreal forests in North America are associated with lower species richness, shorter-lived pioneer species, smaller tree sizes and slower decomposition process than forests in temperate and tropical biomes (Kneeshaw and Gauthier, 2003; Bergeron and Harper, 2009); hence, the interest in ecosystem-specific indicators of old-growthness.

4.5.2. Characterization of old-growth trembling aspen boreal mixedwoods

Boreal aspen mixedwoods of stand-replacing fire origin are considered to evolve to an old-growth stage around 100 years after stand initiation when the even-aged post-fire cohort begins to break up (Kneeshaw and Gauthier, 2003; LeBlanc, 2014). The senescence of the initial cohort could start even earlier (Pothier *et al.*, 2004) depending on site productivity and regional factors (Frey *et al.*, 2004). Individual tree or group mortality creates canopy gaps of various sizes (Kneeshaw and Bergeron, 1998; Hill *et al.*, 2005) allowing recruitment of both shade-intolerant hardwoods (Cumming *et al.*, 2000; LeBlanc, 2014) and tolerant conifers (Bergeron, 2000), depending on gap size and conifer seed source and conifer's presence in the understory (Greene *et al.*, 1999). Hence, trembling aspen can maintain its dominance in late-successional stages by persistent regeneration recruitment even in small gaps (Cumming *et al.*, 2000; Bergeron *et al.*, 2014; LeBlanc, 2014). These processes result in uneven-aged stands with multiple cohorts of aspen as well as shade-tolerant coniferous species (Frelich and Reich, 1995; LeBlanc, 2014).

Large trees in old-growth aspen stands derived from the initial aspen cohort. However, aspen trees and other tree species of Canadian boreal forests do not grow into majestic towering form like trees grow in temperate forests (Franklin *et al.*, 1981; Kneeshaw and Gauthier, 2003). In natural even-aged stands, causes and rates of tree mortality change with successionnal status from disturbance-induced mortality to self-thinning, and finally, senescence (Lee *et al.*, 1997). Dynamics of snags and downed logs often follow a “U shaped” successional pattern with higher biomass in young and older stands (Harmon *et al.*, 1986; Brais *et al.*, 2005). Abundance of snags and downed logs are bound to be higher during stand break up. However, due to the slow decomposition characteristics of the boreal forest (Laiho and Prescott, 2004; Brais *et al.*, 2006), some downed logs in boreal stands are legacies from pre-fire events as well as the latest stand replacing fire (Lee *et al.*, 1997). It is expected that old-growth boreal stands should therefore be characterized by a wide range of downed log sizes and decay states (Lee *et al.*, 1997; Kuuluvainen *et al.*, 2001).

Kneeshaw and Burton (1998) and Kneeshaw and Gauthier (2003) proposed two measurements to characterize the progression of cohort replacement in over-mature stands: the cohort basal area ratio (CBAR) and the cohort basal area proportion

(CBAP). These measurements assume that the first even-aged tree cohort still occupies the upper canopy. Mortality of this first cohort promotes recruitment of a second and third tree cohort into canopy gaps that will form the intermediate (sub-canopy) and regeneration layers. The CBAR and CBAP reflect the size and density of saplings relative to remnants of the first cohort. However, these ratios require the identification of the cohort to which each individual stem belongs, which is time consuming (Harper *et al.*, 2003). To address this limitation, Lee *et al.* (2000) proposed a simpler ratio of basal area of sub-canopy trees (intermediate and suppressed) over basal area of canopy (dominant and co-dominant) trees defined by DBH size, irrespective of tree age. The ratio of sub-canopy to canopy basal area reflects the heterogeneity of stand tree size, a recognized attribute of old-growth/late successional stands (e.g., Kneeshaw and Gauthier, 2003; Zenner, 2004; Bauhus *et al.*, 2009). It also provides an indication of the degree of transition from a typical unimodal diameter distribution of the initial cohort toward a broader distribution as mortality occurs in the canopy layer and the sub-canopy increases in importance.

Fire cycles are generally longer in the eastern Canadian boreal forest than in western Canada (Bergeron *et al.*, 2004), and the presence of late-successional species in the east, balsam fir and eastern white cedar specifically, could also be used as an indicator of old-growth stands. While not adapted for regenerating after fire, balsam fir regenerates well by seed under a variety of conditions and can be found in early successional stands; therefore, size of balsam fir trees as well as its abundance in aspen-dominated mixedwood stands is important. In the case of cedar, its frequency of occurrence in the eastern boreal mixedwood landscape is fairly low so old-growth stands will not <u>necessarily</u> contain the species, especially if there are no proximate mature stands to act as seed sources. However, because cedar relies largely on well-decomposed logs for establishment (Simard *et al.*, 2003), it generally recruits decades after stand-replacing fires (Bergeron 2000) so, when present, cedar is generally a very good indicator that a mixedwood stand is old.

Crites and Dale (1998) and Haeussler *et al.* (2007) also demonstrated the importance of understory vegetation (vascular and non-vascular plants) and fungi in defining old-growth boreal mixedwoods. They argued that canopy gaps in old-growth stands facilitate development of a richer understory composition than that found under the closed canopy of younger stands.

Based on these considerations, the identification and characterisation of old-growth boreal aspen mixedwoods should be based on several structural attributes (Table 4.1). These include percentage of canopy gaps, tree size-variability, presence of late-successional species, diversity of tree and non-tree species, large tree density and downed log abundance.

4.5.3. Potential of partial harvesting to enhance de development of old-growth attributes in mature even-aged stands

4.5.3.1. Pure aspen stands

The 1/3 partial cuts prioritized removal of smaller and suppressed stems to emulate tree mortality associated with self-thinning (Harvey and Brais, 2007). The 1/3 partial cuts maintained 17 attributes of untreated mature stands (controls) and reproduced one old-growth attribute of lower stand basal area compared to control stands (Table 4.3). Moreover, this treatment created few and small canopy gaps relative to values reported for old-growth stands (Kneeshaw and Bergeron, 1998; Hill *et al.*, 2005). Hence, canopy opening was insufficient to enhance sapling recruitment of both shade-intolerant and tolerant saplings (Fig. 4.3A and C) or to increase residual tree growth (Bose *et al.*, 2014a). Therefore, 1/3 partial cuts resulted in a lower ratio of sub-canopy to canopy basal area than the ratio reported by Lee *et al.* (2000) for old-growth aspen stands. By removing mostly small trees, the treatment also simplified stand structure by allowing co-dominants and dominants of the initial cohort to fully occupy the canopy growing space and inhibiting recruitment of a new cohort of stems

(O'Hara, 2001). As a result, variability of horizontal and vertical tree size (standard deviation of DBH and height, respectively) was not increased in 1/3 partial cuts 12-years after harvesting. However, the treatment maintained an average of 138 large trees ha^{-1}, or 17% of total stand density, which is within the range for old-growth aspen stands proposed by Lee *et al.* (2000). In addition, the1/3 partial cuts maintained snags and logs abundance within values observed in untreated controls. Hence, a light low thin will clearly delay stand transition from even-sized hardwood dominance to a mixedwood composition with greater vertical variability, but maintains the potential of these stands to evolve towards more structurally complex old-growth stands.

The first step to increasing structural variability using partial harvesting is to create growing space for new cohorts (O'Hara, 2001). The 2/3 (heavy crown) partial cuts, where dominant and co-dominant trees were primarily harvested to emulate senescence mortality or stand break-up (Harvey and Brais, 2007), created more growing space than what is reported for aspen-dominated old-growth stands. The high percentage of canopy gaps (44 - 62%) observed 12 years after harvesting was much higher than values (18.7 - 40.9 %) reported by Kneeshaw and Bergeron (1998) for old-growth aspen stands and promoted higher sapling recruitment of intolerant hardwoods than that reported by these authors. The 2/3 partial cuts did not promote the ratio of sub-canopy to canopy basal area reported for old-growth aspen stands (Lee *et al.*, 2000) but nevertheless caused a significant increase relative to untreated mature stands (controls). The current sapling layer of 2/3 partial cuts showed the potential of this treatment to further increase the ratio of sub-canopy to canopy basal area in following years (Fig. 4.2C). In 2/3 partial cuts, large tree density was lower relative to large tree density of old-growth aspen stands (Lee *et al.*, 1997; Bergeron, 2000).

Nonetheless, like the 1/3 cuts, the 2/3 partial cuts maintained many (10) of the attibutes of untreated mature stands (controls), such as shade-tolerant conifer tree density, DBH variability, maximum tree height and tree height variability, density of shade-tolerant conifer saplings, shrub density and snag and log abundance (Table 4.2 and 4.3). In the short-term, the “stand break-up” condition (300 aspen stems.ha^{-1}, 15 m^2.ha^{-1} BA) artificially generated by the 2/3 partial cuts may reflect senescence plus the exacerbating effects of severe forest tent caterpillar outbreaks on overstory aspen mortality and sapling recruitment rather than stand break-up alone (see in Man *et al.*, 2008b; Moulinier *et al.*, 2011). This treatment resulted in a higher percentage of canopy gaps and recruitment of intolerant hardwood saplings than old-growth aspen dominated stands and may set back successional development.

4.5.2.2. Mixed aspen stands

In the mixed aspen stands, dispersed or diffuse partial cuts were applied to emulate individual-level tree mortality. This treatment could be considered a free thin in which merchantable stems of all size classes were removed. The basal area removed was between that of the 1/3 and 2/3 partial cuts conducted in pure aspen stands and resulted in canopy gap occupancy (32 - 48%) close to that reported for old-growth stands. However, the dispersed cut could not significantly create the ratio of sub-canopy to canopy basal area to a range old-growth aspen stands reported by (Lee *et al.*, 2000). Nonetheless, the dispersed cut maintained 12 attributes of untreated mature stands (controls) and accelerated succession in terms of canopy gap percentage, expanded canopy gap area and intolerant hardwood density. The treatment did not increase, but maintained tree size variability (standard deviation of DBH and height) of mature untreated control stands. However, the dispersed cut reduced the density of large trees: the average of 66 large tree ha^{-1}, 4% of stand density, is much lower than values reported for old-growth aspen stands (Lee *et al.*, 2000; Schieck *et al.*, 2000). Finally, mean volume of downed logs (115 m^3.ha^{-1}), while not significantly different from untreated controls, was close to aspen old-growth volumes (117-131 m^3.ha^{-1}) reported by Lee *et al.* (1997). By creating canopy gaps similar to old-growth aspen stands and promoting recruitment of both intolerant hardwoods and tolerant conifers, this treatment may produce a structurally complex stands in following years.

Similar to 2/3 partial cuts in pure aspen stands, 400 m^2 gap cuts in mixed aspen stands produced higher canopy gap occupancy than values reported by Kneeshaw and Bergeron (1998) and by Hill *et al.* (2005) for old-growth aspen stands. Expanded gap areas were also higher, in part due to subsequent windthrow. This high percentage of canopy gaps resulted in higher sapling densities of intolerant hardwoods relative to those for old-growth stands reported by Kneeshaw and Bergeron (1998). Twelve years after harvesting, the range of the ratio of sub-canopy to canopy basal area was 0.46 - 1.11, which is the highest among all treatments and comparable to that of old-growth aspen stands (0.8-2.0). Similar to the 2/3 partial cut in pure aspen stands, the gap cut maintained 10 attributes of untreatment mature stands (controls) and accelerated stand development in terms of expanded canopy gap area, ratio of sub-canopy to canopy basal area and intolerant hardwood density. Similar to dispersed cuts, large tree density was lower in gap cuts relative to large tree density reported for old-growth aspen mixedwoods (Lee *et al.*, 2000; Schieck *et al.*, 2000). As for other harvesting treatments, gap cuts maintained levels of deadwood (snags and downed logs) comparable to those of mature aspen stands (un-treated controls) and the quantity of deadwood is comparable to deadwoods in old-growth aspen forests (Table 4.1). These results of non-negative effects of partial harvesting to deadwood are contrary to some other studies that have been conducted in the North America (e.g., McGee *et al.*, 1999; Angers *et al.*, 2005; Keeton, 2006).

4.5.4. Management implications

The structural and, potentially, compositional differences between a 60 year old, even-aged, pure or mixed aspen-dominated stand and the same stands 60 year later are enormous. The latter, now old-growth, can be expected to contain fewer but larger stems, greater stem size variability, more canopy gaps of different sizes, multiple tree cohorts, more snags and downed log volume and, in the case of mixedwoods, a greater shade-tolerant conifer component in all layers. It is evident then that managing aspen-dominated mixedwood forests solely on 50 to 80 year rotations will result in a loss of ecosystem (or forest stand type) diversity and habitat diversity. However, with its prolific suckering, fast growth and relatively short lifespan, aspen is perfectly adapted to and generally managed under an even-aged, coppice system. This said, from a forest ecosystem management viewpoint, managing a portion of aspen mixedwoods to develop into more complex stands that contain key structural and compositional attributes of old-growth is not only justifiable, but there is considerable support to indicate that it is also biologically feasible (Man *et al.*, 2008a; Solarik *et al.*, 2010; Bose *et al.*, 2014a). That is, aspen can biologically perform – regenerate, grow well and live long enough to be harvested later - following treatments other than large-gap coppice. Moreover, this consideration of possible alternative silvicultural approaches joins the emerging concept of managing forests for complexity (Messier *et al.*, 2013).

If partial harvesting has its place in boreal mixedwood ecosystems, approaches used to enhance old-growth characteristics should be guided by several factors, notably: 1) composition and structure of stands to be treated (probably most importantly, with respect to the conifer component); 2) ranges of structural and compositional old-growth objectives (how much of what in how many years); 3) a good understanding of tree and understory responses to a variety of partial harvesting intensities and gap sizes under a range of initial stand conditions; and 4) a measure of the implications of different silvicultural options on treatment costs and harvestable volumes at the stand and, cumulatively, management unit levels. While this study looked at medium-term outcomes of single commercial treatments in mature aspen-dominated stands, a variety of single- and multiple-entry options are probably available, particularly to managers working with an overabundance of aspen growing stock. Moreover, treatments should start earlier in stand development than those applied in this study.

Old-growth-oriented partial harvesting prescriptions for these forests could incorporate explicit targets for the following elements. For example (and values are also examples): lower limits for residual merchantable aspen BA (ex. 40-50%; dispersed cut in our treatment) and number of large aspen stems to be retained (ex.15% of total stand density (Lee *et al.*, 2000); range of harvest gap sizes (ex. 400-1,600 m^2) (Bose *et al.*, submitted) and specific thinning prescriptions for between gaps (ex. free thin 1 in 3 stems) (Haeussler *et al.*, 2007); stem size limits on conifer removal (ex. retain stems ≤ 16 cm DBH); and protection measures for snags, dying stems and patches of dense conifer seedlings and saplings (Kneeshaw and Gauthier, 2003; Haeussler *et al.*, 2007). This is clearly more complicated than clear-cutting, but well-trained operators who have been involved in partial harvesting experiments have demonstrated that these treatments can be done and, certainly, the short- to long-term outcomes and ecosystem services are considerably different. These prescriptions should be limited to aspen forests in productive mesic sites.

The structural framework for identifying old-growth aspen-dominated mixedwoods (Table 4.1) is based on relatively few studies which highlights the fact that there is still limited information on what actually constitutes old-growth in these stand types. Old permanent sample plots such as those used by LeBlanc (2014) are extremely precious and similar information may exist elsewhere in the boreal mixedwood (and in old boxes and filing cabinets). Certainly, there is a need for long-term (permanent) monitoring of unmanaged aspen mixedwoods. While the successional dynamics of aspen-dominated mixedwoods are reasonably well understood (for example, see Bergeron *et al.*, 2014), the temporal specifics of characteristic stand development stages and transition phases are more elastic in nature and thus contribute to management concerns regarding anticipated outcomes of silvicultural treatments such as partial harvesting. Long-term monitoring of mixedwood silvicultural experiments is therefore also essential to validating novel management practises in these forests.

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CHAPITRE V

MODELLING STAND DEVELOPMENT AFTER PARTIAL HARVESTING IN BOREAL MIXEDWOODS OF EASTERN CANADA

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5.1. Abstract

Multi-cohort-based forest management has been proposed as a strategy to conciliate wood supply and biodiversity conservation objectives. At the stand-level, the approach involves using partial harvesting to generate structurally complex stands, notably in terms of tree age, size and species mixtures, conditions that are not easily integrated into yield tables. Using SORTIE-ND, a spatially explicit stand dynamics model, we simulated 100-year development patterns following different partial harvesting treatments in two trembling aspen (*Populus tremuloides* Michx)-dominated stands in eastern Canada, one 76 years old (pure aspen) and the other 90 years old (mixed aspen). The two stand types differed primarily in the nature of their understory: pure aspen stands had little advance conifer growth and a dense understory of a woody shrub species whereas mixed aspen stands were characterized by a dense regeneration layer of shade-tolerant conifers. To do this, we first evaluated model performance using short (12 years) and long (168 years) term empirical data. We then modelled stand dynamics following a range of simulated partial harvesting treatments of different intensities (33, 61 and 80% basal area removal), and gap sizes (400, 900 and 1600 m^2). Following mortality of the first cohort of aspen, simulations projected dominance of conifer species, white spruce in particular, in unharvested controls of pure aspen stands and balsam fir in mixed aspen stands. Aspen recruitment increased with intensity of partial harvesting. All gap treatments and the 80% dispersed harvesting favored recruitment of aspen over conifer species. After 100 year simulation runs, the 1600 m^2 gap treatment resulted in highest stand basal areas, 38.0 and 34.1 $m^2.ha^{-1}$, of which 18% and 28% consisted of intermediate- to shade-tolerant conifer species in pure aspen stands and in mixed aspen stands, respectively. Concerns surrounding partial harvesting have tended to focus on absolute retention levels and standing residence times of trees; however, our results demonstrate that both stand structure and timber production rates are influenced not only by retention levels after partial harvesting but also by spatial configuration of the residual trees. We identified several model functions that are likely responsible for divergences between empirical conditions and those simulated by SORTIE-ND for the boreal mixedwood and suggested specific empirical studies to improve parameter functions of this modelling tool.

Keywords: Boreal mixedwood, partial harvesting, variable retention, stand modeling, SORTIE-ND and stand dynamics.

Résumé

L'aménagement forestier basé sur la dynamique naturelle a été proposé comme approche permettant de concilier l'approvisionnement en bois et les objectifs de conservation de la biodiversité. À l'échelle du peuplement, les coupes partielles découlant de cette approche visent à générer des peuplements structurellement complexes relativement à leur composition et à l'âge et la taille des arbres. Ces conditions ne sont pas facilement intégrées dans les tables de rendement. En utilisant SORTIE-ND, un modèle spatialement explicite de la dynamique des peuplements, nous avons simulé les patrons de développement de deux types de peuplement de l'est du Canada à dominance de Peuplier faux-tremble (*Populus tremuloides* Michx). Le premier (peuplement de P. faux-tremble) était vieux de 75 ans et le second (peuplement mixte) de 90 ans. Les deux types de peuplements différaient principalement par la nature de leur sous-bois : sous-bois dense en espèces ligneuses arbustives et peu de régénération en conifères dans les peuplements de P. faux-tremble alors que les peuplements mixtes se caractérisaient par une régénération dense en conifères tolérants à l'ombre. Nous avons évalué, en premier lieu, la performance du modèle en recourant à des données empiriques à court (12 ans) et long (168 ans) termes disponibles pour la région. Par la suite, nous avons modélisé la dynamique des peuplements en simulant une gamme de coupes partielles de différentes intensités (prélèvement de 33, 61 et 80 % de la surface terrière (ST)) et selon différents patrons spatiaux (trouées de 400, 900 et 1600 m²). Les simulations projettent, qu'après la mortalité de la première cohorte de P. faux-tremble, l'épinette blanche (*Picea glauca* [Moench] Voss) dans les peuplements non exploités de P. faux-tremble, et le Sapin baumier (*Abies balsamea* (L.) Mill.) dans les peuplements mixtes, deviennent dominants. Le recrutement du P. faux-tremble augmente avec l'intensité de la coupe partielle. L'ensemble des traitements par trouées et le prélèvement de 80% de la ST favorisent le recrutement du P. faux-tremble aux dépens des conifères. Après des simulations avec des pas de temps de 100 ans, la ST des peuplements est maximale à la suite d'un prélèvement par trouées de 1600 m² soit 38.0 m².ha^{-1} dans les peuplements de P. faux-thermale et 34.1 m².ha^{-1} dans les peuplements mixtes, avec respectivement, 18% et 28% en conifères tolérants à l'ombre. Les enjeux relatifs aux coupes partielles ont longtemps touché aux taux et temps de rétention des arbres résiduels. Cependant, nos résultats démontrent que la structure des peuplements et la production de matière ligneuse sont influencées non seulement par les taux de rétention mais aussi par la configuration spatiale des arbres résiduels. Nous avons identifié plusieurs fonctions de modèles qui sont probablement responsables de divergences entre les conditions empiriques et celles simulées par SORTIE-ND de la forêt boréale mixte. Nous avons suggéré des études empiriques spécifiques pour améliorer les fonctions des paramètres de model.

Mots-clés : Forêt boréale mixte, coupe partielle, rétention variable, modélisation des peuplements, SORTIE-ND et dynamique des peuplements.

5.2. Introduction

Mixedwood forests are the most productive and structurally heterogeneous forests in boreal Canada (Rowe, 1972; Chen and Popadiouk, 2002) and an important source of timber supply (Penner, 2008). Mixedwood stands composed of intolerant hardwoods, in particular trembling aspen (*Populus tremuloides* Michx.), and shade-tolerant conifers are abundant across the southern Canadian boreal forest (Nlungu-Kweta *et al.*, 2014). During mixedwood stand development, partial disturbances such as insect outbreaks and windthrow and tree- and stand-level processes such as competition and senescence, facilitate establishment and growth of shade-tolerant conifers by creating small gaps (Bergeron, 2000). However, some studies have shown that trembling aspen can also maintain continuous recruitment even in small gaps (Cumming *et al.*, 2000) resulting in a succession of multi-cohort aspen stands (LeBlanc, 2014). As a result, successional development of boreal mixedwood stands can be extremely complex (Bergeron *et al.*, 2014) and the degree of complexity may be influenced by several factors: pre-disturbance stand attributes and their relative importance, intensity and spatial configuration of disturbances and time since disturbance, and relative importance of post-disturbance attributes (Kneeshaw and Gauthier, 2003).

In boreal mixedwood forests where fire cycles exceed the life expectancy of early successional species, stand-level processes including tree mortality of this first tree cohort and recruitment of mid- and late-successional species tend to transform structurally simple stands into more complex multi-cohort forest structures (Kneeshaw and Bergeron, 1998; Bergeron and Harper, 2009). Based partly on an understanding of these natural dynamics, a multi-cohort-based forest management approach has been proposed for the eastern Canadian boreal mixedwood forest as a means of conciliating industrial demand for wood fibre and biodiversity concerns (Bergeron *et al.*, 2002; Harvey *et al.*, 2002). At the forest-level, the approach uses the regional fire cycle to set objectives for maintaining acceptable levels of forest types associated with different stand development stages on the landscape, and structurally complex old growth forests are of critical importance. At the stand level, the approach proposes greater use of partial cutting treatments to better incorporate natural dynamics associated with canopy succession and partial disturbances to promote the structural attributes associated with over-mature or old growth stands. This concept has led to greater experimentation of novel silvicultural practices including partial harvesting and variable retention (Gauthier *et al.*, 2009). Partial harvesting may retain a range of densities of residual trees, either in aggregated groups, strips or dispersed patterns or a combination of these patterns, depending on stand conditions and management objectives (Franklin *et al.*, 1997; Bose *et al.*, 2014c). Residual trees may serve several functions including maintaining – or eventually producing - key habitat attributes, providing seed sources for future regeneration or reducing the visual impacts of harvesting (Lieffers *et al.*, 1996b; Bergeron and Harvey, 1997). It is expected that partial harvesting will be increasingly applied in boreal mixedwood stands, particularly where intolerant hardwoods reach commercial maturity before more shade-tolerant conifers (Lieffers *et al.*, 1996b; Bose *et al.*, 2014c).

Most partial harvesting experiments have only recently been set up in the Canadian boreal mixedwood forest (e.g., Brais *et al.*, 2004; Man *et al.*, 2008a; Prévost *et al.*, 2010; Solarik *et al.*, 2010). Therefore, little field-based information exists concerning how partially harvested stands develop over long time scales. According to Weiskittel *et al.* (2011), foresters are generally familiar with empirical yield tables and recognize their utility for predicting volume yields for fairly homogenous and simple stand conditions (even-aged, mono-specific or low species mixtures). However, growth estimations of structurally complex stands are not easily or accurately predicted using existing yield tables. Individual tree-based models are generally more flexible than yield tables, allow the exploration of different silvicultural options and can potentially provide more detailed forecasts of tree sizes (Coates *et al.*, 2003; Groot *et al.*, 2004; Papaik *et al.*, 2010). Besides the flexibility generally offered by modelling and the obvious economies in time and resources compared to long-term field monitoring, stand dynamics modelling provides a complementary analysis tool to field trials for investigating and comparing different silvicultural options and outcomes (Thorpe *et al.*, 2010; Ligot *et al.*, 2014).

SORTIE-ND, a spatially-explicit, individual-based stand dynamics model, has been used to explore natural forest dynamics in a number of forest systems, such as mixed aspen boreal forests in eastern (Papaik *et al.*, 2010; Beaudet *et al.*, 2011) and western Canada (Astrup, 2006; Stadt *et al.*, 2007), black spruce forests in eastern Canada (Thorpe *et al.*, 2010; Vanderwel *et al.*, 2011), mixed temperate forests (Haeussler *et al.*, 2013) and elsewhere in the World (Canham *et al.*, 2010; Ameztegui *et al.*, 2012; Yasuda *et al.*, 2013). It is particularly suitable for applications involving mixed species stands and partial disturbances (Coates *et al.*, 2003) and has been used to explore and forecast outcomes under alternative silvicultural systems over longer time scales than those covered by existing empirical studies (Vanderwel *et al.*, 2011).

In this study, we adapted SORTIE-ND for boreal mixedwood stands in north-western Quebec, and evaluated model performance using short and long term empirical data. We then simulated stand dynamics over 100 years following a range of partial harvesting intensities and spatial configurations applied to mature pure aspen and mixed aspen stands. The study aimed to i) evaluate whether SORTIE-ND captures short- and long-term stand dynamics of eastern boreal mixedwood stands, ii) identify the range and configuration of partial harvesting treatments that accelerate the development of multi-cohort complex stands and iii) assess how similar partial harvesting treatments applied to pure aspen and mixed aspen stands with contrasting understories (dense advance conifer regeneration with sparse understory shrubs versus sparse advance regeneration with dense understory shrubs) affect stand development over a period of 100 years.

5.3. Methods

5.3.1. Study area

Field sites were located in the Lake Duparquet Research and Teaching Forest (LDRTF) in the Abitibi region of northwestern Quebec, 45 km northwest of the city Rouyn-Noranda (48°86′N–48°32′N, 79°19′W–79°30′W). This region is characterized by the presence of extensive clay deposits left by proglacial Lake Ojibway (Vincent and Hardy, 1977) and rich clayey soils on upland sites (Canada Soil Survey Committee, 1987a). According to the weather station la Sarre, the climate is continental and cold temperate with a mean annual temperature of 0.7 °C and mean annual precipitation of 889.8 mm (Environment Canada, 2011).

The LDRTF is located within the balsam fir (*Abies balsamea* (L.) Mill.) - white birch (*Betula papyrifera* Marsh) bioclimatic domain (Saucier *et al.*, 1998). Forests of the region are characterized by a mixed composition of boreal conifers, and shade-intolerant broadleaved species. Trembling aspen, white birch, and jack pine (*Pinus banksiana* Lamb.) are the dominant early successional species. Balsam fir is the dominant species in late-successional forests on mesic sites, and is associated with white spruce (*Picea glauca* [Moench] Voss), black spruce (*P. mariana* [Mill.] B.S.P.), and eastern white cedar (*Thuja occidentalis* L.) in this region (Bergeron, 2000).

The natural disturbance regime is characterized primarily by a mix of influences of wildfires and defoliating insect outbreaks. For a *ca.* 16,000 km^2 area surrounding the study sites, Bergeron *et al.* (2001) estimated mean forest age (time since fire) to be 139 years and calculated lengthening fire cycles from 83 to 146 to 325 years for the following three periods: prior to 1850, 1850-1920 and 1920 to 1999, respectively. Three outbreaks of eastern spruce budworm (*Choristoneura fumiferana* (Clem.)), a defoliator of balsam fir and spruce, have been documented in the twentieth century by Morin *et al.* (1993) (See 2.5, Model development.). The forest tent caterpillar

(Malacosoma disstria), a defoliator of broadleaf species, particularly trembling aspen, has shorter outbreak cycles than the budworm (Cooke *et al.*, 2009), but with a more minor effect on host species mortality (Cooke and Lorenzetti, 2006). Gap dynamics associated with these secondary disturbances and successional processes also influence stand-level composition and structure (Kneeshaw and Bergeron, 1998).

5.3.2. Sites used for starting condition and for short-term model evaluation

Empirical data from two separate partial harvesting experiments (SAFE-1 and SAFE-3) established in the late 1990's – early 2000's were used for short-term evaluation of model simulations. Both experiments are part of the SAFE project (*Sylviculture et aménagement forestier écosystémiques*) (Brais *et al.*, 2004; Brais *et al.*, 2013), situated in the Lake Duparquet Forest.

Pure aspen stands of the SAFE-1 project originated from a stand-replacing fire in 1923. Average pre-treatment stand basal area was 44.0 $m^2.ha^{-1}$ of which 92.6% was trembling aspen and 3.3% conifer species, Four harvesting treatments, including a no harvest control, two intensities of partial harvesting and a clearcut, were applied during the winter of 1998-99. The two partial harvesting treatments were designed to remove 33% (1/3 partial cut) and 61% (2/3 partial cut) of merchantable basal area (primarily aspen) in an evenly dispersed spatial pattern. Stands in the 1/3 partial cut were low thinned while stands in the 2/3 partial cut were primarily crown thinned (Brais *et al.*, 2004). Harvesting treatments were applied according to complete randomized block design with three replications (blocks) of each treatment. Forest inventories were conducted in 1998 and 2010 in five 400 m^2 sampling plots per treatment unit.

Mixed aspen stands in the SAFE-3 project originated from a wildfire fire in 1910. Average pre-treatment stand basal area was 41.0 $m^2.ha^{-1}$ of which 80.8% was trembling aspen and 17.8% conifer species. In the winter of 2000, four harvesting treatments including a no harvest control, two intensities of partial harvesting (intermediate-intensity free thin; 45% BA removal and 400 m^2 gap cut; 54% BA removal) and a clearcut were applied. Similar to the aspen stands, treatments were applied according to complete randomized block design with three replications (blocks) of each treatment (see details in Brais *et al.*, 2013). Forest inventories were conducted in 2000 and 2012 in five 400 m^2 permanent sampling plots per treatment unit.

Besides differences in overstory composition, the main difference between the two stand types was in the seedling and sapling layers: balsam fir was very dense in mixed aspen stands, whereas total conifer regeneration was very low and a woody shrub, mountain maple (*Acer spicatum* Lamb.), dominated the regeneration layer in pure aspen stands.

5.3.3. Site used for long-term model evaluation

For long-term (168 years since stand initiation) evaluation of simulations of development of unharvested control stands in SAFE-1 and -3, data were obtained from an area of the LDRTF that originated from a wildfire in 1823. This will be referred to as the "1823 reference stand". The area was inventoried in 1991, which corresponds to 168 years after stand initiation. Sixty temporary quadrants of 256 m^2 (16 m x 16 m) were established at 50 m intervals along transects located within the fire-affected area. In each quadrant, all live and dead (standing) trees greater than 5 cm DBH were identified, measured and categorized by size classes of 5 cm DBH (Bergeron, 2000). To decrease the variability caused by the small size of quadrants, we merged every four consecutive quadrants into 15 larger inventory units (256 x 4 = 1024 m^2).

5.3.4. Simulator

SORTIE-ND is a spatially explicit, individual-based forest stand dynamics model (Murphy, 2011). It originated from model SORTIE developed and tested in the early

1990's for transitional oak-northern hardwood forests in the northeastern US (Pacala *et al.*, 1996). Since then, it has been improved upon with a greater emphasis on forest management considerations being incorporated into the modeling research (e.g., LePage *et al.*, 2000; Astrup *et al.*, 2008; Coates *et al.*, 2009). SORTIE-ND simulates changes in tree populations over time. The model uses a combination of empirical and mechanistic behaviours to predict forest dynamics.

In SORTIE-ND, the forest is represented by a large collection of interacting trees (individuals) that are followed both in time (in steps of one year) and space. Those trees are divided among seedlings, saplings, adult trees and snags. Population-level dynamics are simulated by summing the collective activities of numerous individuals. Each tree is a discrete object that is described with various attributes (size, growth rate, age, crown morphology, and so on). Each tree's (individual) behavior is modeled with rules that describe the interactions with other individuals (e.g., effect of species and distance of neighbors on growth of individual trees) or its environment (e.g., growth of seedlings in relation to available light levels). In SORTIE-ND, many of the interactions have non-linear relationships and/or have random events associated with them. The non-linearity of many interactions, the stochastic behavior of some objects and processes, and the large number of objects, rules and stochastic events makes SORTIE-ND a good example of a modeling approach aimed at being able to represent complex behaviour in forests (Haeussler *et al.*, 2013). See more details on model structure in the appendix or at http://www.sortie-nd.org/help/manuals/help/index.html.

SORTIE-ND is driven by a parameter file based on local conditions and field data. The Lake Duparquet Forest parameter file has been developed, tested and modified over the course of the last number of years. This has been done either through individual field experiments or studies that have allowed parameterization of specific functions in the different sub-models constituting SORTIE-ND (tree allometry, light, tree growth, tree mortality, and recruitment) or through concerted efforts to calibrate the model to adhere to our current understanding – based on empirical studies - of natural stand dynamics (Poulin and Messier, 2008; Beaudet *et al.*, 2011; Leduc and Coates, 2013). The parameterized model for LDRTF includes six tree species trembling aspen, balsam fir, white spruce, white birch, eastern white cedar and jack pine and one woody shrub, mountain maple.

5.3.4.1. Growth

SORTIE-ND is designed to provide growth predictions for individual seedlings, saplings and adult trees in multi-species, complex-structured stands (Fig. 5.1). Seedlings and saplings grow as a function of understory light availability (e.g., Wright *et al.*, 1998) to a size of 3-10 cm diameter (DBH), depending on species, and then shift to adult tree growth functions based on tree size and neighborhood competition (e.g., Coates *et al.*, 2009). In cases where there is insufficient data on neighborhood competition a simple species-specific diameter increment function is used (e.g., Pacala *et al.*, 1996). This was the case for jack pine and mountain maple in our northern Quebec simulations. For the other species, a neighborhood competition index (NCI) reduces the predicted maximum potential growth rate of a tree based on the species, size and proximity of neighbors. The NCI sums up the competitive effect of all neighbors out to the estimated maximum distance of effect, in m. The competitiveness of a neighbor increases with the neighbor's size and decreases with distance to the neighbor. It also incorporates species-specific competitive effects, with the effect depending on the relationship between the target species and the neighbor species. Once diameter growth is determined, and incremented on to an individual tree, tree height is calculated using species-specific allometric equations based on DBH. The list of parameters of different model behaviors (e.g., growth, mortality, substrate) used in the present study are described in the appendix.5.1

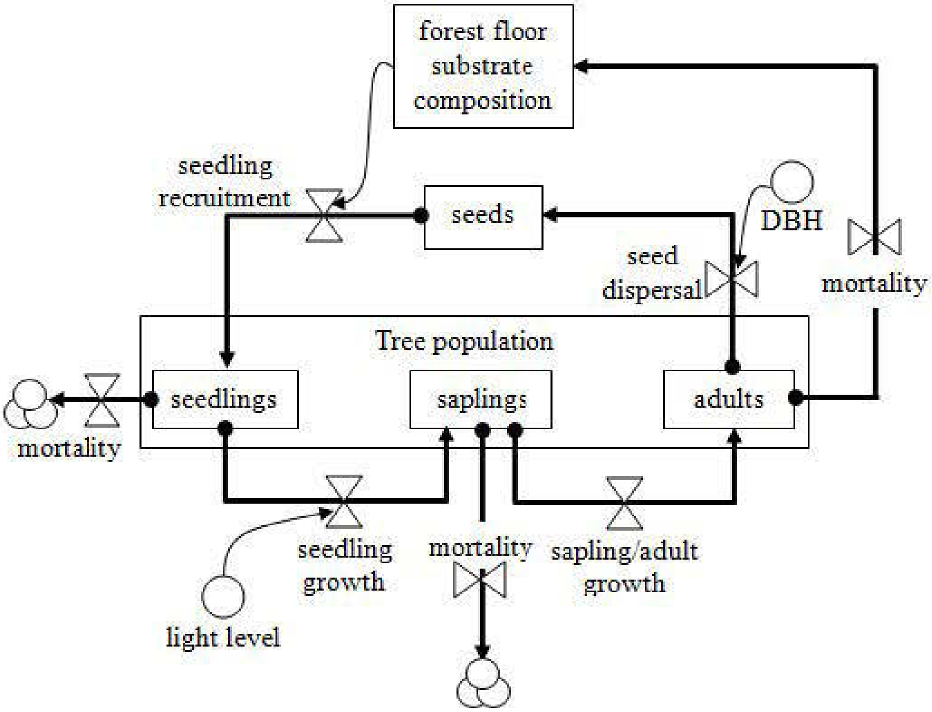

Figure 5.1. Conceptual modelling diagram of SORTIE-ND (Source: Lora Murphy, http://www.sortie-nd.org/help/manuals/help/index.html)

5.3.5. Model development

In addition to the model development described above, using repeated measurements data from the SAFE project (Brais *et al.*, 2004; Robert *et al.*, 2012; Bose *et al.*, 2014b), we tested and calibrated the following parameters: senescence mortality of mountain maple, juvenile mortality of trembling aspen, white spruce and balsam fir, competition mortality of trembling aspen and sucker recruitment of trembling aspen.

We also accounted for conifer mortality caused by spruce budworm (episodic mortality in SORTIE-ND). The frequency of budworm incidents over a 100 year period was based on the chronology of three outbreaks that occurred in the region during the 20th century from 1919 to 1929, 1930 to 1950 and 1970 to 1987 (Morin *et* *al.* (1993). As mentioned previously, the pure aspen stands originated from a fire in 1923; therefore, we simulated budworm mortality at years 2024, 2040 and 2078, that is, at stand ages 101, 117 and 155 years, respectively. The mixed aspen stands originated from a fire in 1910 so we induced budworm mortality at years 2011, 2027, 2065 and 2095, or stand ages of 101, 117, 155 and 185 years, respectively. We simulated an additional budworm mortality episode for aspen mixedwoods because we expected another budworm occurrence in the remaining 35 years of simulation.

In each time step, the budworm induced mortality was based on Bergeron *et al.* (1995) for balsam fir in the region and on Blais (1981) for white spruce in the eastern Canadian boreal region. For balsam fir, we set different mortality rates for the following three diameter classes, 5-10, 10-15 and ≥15 cm DBH, and we also accounted for stand composition (relative proportions of budworm-susceptible conifers and non-host hardwoods) that influence the magnitude of mortality according to Bergeron *et al.* (1995). We assumed deciduous-dominated stand conditions during the first budworm occurrence (101 years), mixed-deciduous during the second budworm occurrence (117 years) and conifer-dominated stand conditions during third budworm occurrence (155 years). These stand compositions at different time steps were adjusted by noting relative (to total) basal area of each species in simulation outputs. For white spruce, we set the mortality for only one size class (>10 cm DBH) but for two stand compositions, mixedwood and conifer (see Table 1 of Blais (1981)). We adjusted stand composition (mixedwood or conifer) for white spruce following a procedure similar to that described above for balsam fir.

5.3.6. Simulation runs

Simulations were conducted using a 4 ha (200 m×200 m) plot (stem map) (Beaudet *et al.*, 2011; Vanderwel *et al.*, 2011) with a time step = 1 year. Harvest episodes (Table 5.2) were created at time step 1. The SORTIE-ND simulation plot is a torus, where each edge connects to the edge of the opposite side (see http://www.sortie-nd.org/help/manuals/help/data/plot.html).

5.3.6.1. Model evaluation

Short term evaluation

We used inventory data from 15 permanent sample plots (PSP - 400 m^2) of pre-treatment conditions of unharvested controls and the 1/3 partial cuts in the aspen stands and unharvested controls and 400 m^2 gap cuts in aspen mixedwoods (60 PSPs in all). Therefore, we created 15 starting conditions for each of the four treatments based on inventory data collected in 1998-1999 in the pure aspen stands and in 2000 in the mixed aspen stands. For the 1/3 partial cut in pure aspen stands and the 400 m^2 gap cuts in the mixed aspen stands, we implemented basal area removal by partial harvesting treatments (harvest episode in SORTIE-ND) (Table 5.1). We then compared empirical values of stem density and stand's basal area from 12-year post-treatment field measurements in permanent sample plots with simulated values for the same year.

Long term evaluation

We also used the 15 permanent sample plots of pre-treatment conditions of unharvested controls of both the pure aspen and mixed aspen stands for long-term evaluation of model simulations. We simulated each plot for a 100-year period and evaluated the simulation outputs at 168 years since stand initiation of the pure aspen stands (76 years initially + 92 years simulated = 168 years) and mixed aspen (90 years initially + 78 years simulated = 168 years) using empirical data of the 1823 reference stand (168 years old when inventoried in 1991). We ran two separate simulations for each study site: one including and the other excluding spruce budworm outbreak “incidents” (Table 5.1).

Simulated silvicultural treatments over a 100-year period

Using pre-treatment data from the 15 permanent sample plots of un-harvested controls in pure aspen stands and un-harvested controls in mixed aspen stands, we implemented six different partial harvesting scenarios: three dispersed partial cut patterns with 33%, 61%, and 80% BA removal and three aggregated cut scenarios that removed trees in 400 m^2, 900 m^2 and 1600 m^2 gaps corresponding to 37%, 43% and 54% BA removal, respectively (Table 5.2*)*. An un-harvested 15 m wide band was maintained between adjacent gaps in all gap-harvested stands. We averaged and calculated 95% CI of replicate model outputs ($n = 15$) for each harvest scenario and post-harvest time interval to account for the random variability in stand composition, structure and dynamics.

5.3.7. Analysis of model simulated outputs

For both short- and long-term evaluations, we examined tree size distribution, live stem density ($\geq$ 5 cm at DBH) and total live stem basal area ($\geq$ 5 cm at DBH) for trembling aspen, white birch, balsam fir and white spruce. Additionally, we examined the effect of spruce budworm outbreaks (included in or excluded from simulations) on stand dynamics for long-term simulations. For the 100-year simulation following partial harvesting, we analysed separately live merchantable trees ($\geq$ 10 cm at DBH) and the live sapling layer (5-10 at DBH). We averaged and calculated 95% CI of replicate model simulated outputs ($n = 15$) for each treatment to account for the variability among the 15 plots (starting conditions). We compared the average with 95% CI between simulated treatments at years 25, 50 and 100.

Table 5.1. Short and long term evaluation of simulated outputs using empirical data

Stand types	Treatment	Starting condition (years)	Simulation period (years)	Empirical data used to validate
		Short term evaluation		
Pure aspen	Control	76	12	Same treatment
Pure aspen	1/3 partial cut	76	12	Same treatment
Mixed aspen	Control	90	12	Same treatment
Mixed aspen	Gap cut	90	12	Same treatment
		Long term evaluation		
Pure aspen	Control	76	92	168 years old growth stand
Mixed aspen	Control	90	78	168 years old growth stand

Note: For long term evaluation, two separate simulations were used for both study area by including and excluding spruce budworm outbreak "incidents" that affected for balsam fir and white spruce (see details in method's section, 5.3.5 Model development)

Table 5.2. Simulated harvesting scenarios applied to pure aspen stands and mixed aspen stands

Silvicultural treatments	Scenario No.	Scenario description		
		Spruce budworm	Basal area removed	Harvesting pattern
Control	1	x	x	x
Control	2	√	x	x
Partial cut	3	√	33%	Dispersed
	4	√	61%	Dispersed
	5	√	80%	Dispersed
Gap cut	6	√	37%	400 m2
	7	√	43%	900 m2
	8	√	54%	1600 m2

Notes: All stems of ≥5 cm dbh in size were considered in harvesting prescriptions. Same simulated treatments applied in both aspen and aspen mixedwood stands with a replication of n=15 for each site.

5.4. Results

5.4.1. Model evaluation

5.4.1.1. Short term evaluation

At the end of 12 year simulation runs, simulated unharvested controls in both the pure aspen and mixed aspen stands showed good agreement with empirical data in terms of tree size distribution (Fig 5.2A, B, C and D for the pure aspen stands and I, J, K and L for the mixed aspen stands), live stem density and live stem basal area of whole stand, aspen, birch, fir and spruce (Table 5.3). Higher mortality (expressed in terms of BA) of trembling aspen was the most notable difference between simulated outputs and the empirical results (7% and 13% higher mortality for the pure aspen stands and mixed aspen model results, respectively). This resulted in slightly lower aspen and total stem density and BA values in simulated outputs compared to empirical data (Table 5.3).

In the 1/3 partial cut (low-light thinning) in pure aspen stands, 12 year simulated outputs captured all dynamics of tree size distribution with the exception of mortality associated with smaller stems (5-10 cm DBH) of white birch (Fig 5.2E, F and G). Simulated density and BA for total stand, aspen, fir and spruce showed good agreement with the empirical data (Table 5.3). The simulation did, however, project somewhat lower sapling recruitment of aspen saplings (5-10 cm DBH) than the empirical data, although sapling densities of other species were in good agreement with empirical data (Fig. 5.2H).

Simulated outputs of 400 m^2 gap cuts in mixed aspen stands did not capture initial logging-induced mortality of residual trembling aspen and spruce, and showed higher survival of these two species than empirical data (Fig. 5.2M, N and O). Such survivability of residual trees translated into 9.3 $m^2.ha^{-1}$ more BA in simulated outputs (Table 5.3). Balsam fir regeneration (< 5 cm at DBH) recruitment into sapling layer (5-10 cm DBH) was slightly lower in simulated outputs than in empirical data (Fig. 5.2P).

5.4.1.2. Long term evaluation

Simulations that incorporated periodic spruce budworm “incidents” (punctual outbreaks) showed closer agreement with empirical data of the 1823 reference stand than simulations that did not (Fig. 3A vs 3B and 3C for pure aspen stands, Fig. 5.3A vs 5.3D and 5.3E for mixed aspen). Hence, we retained simulations that included spruce budworm dynamics for long-term model evaluation and also for running 100 year simulations of partial harvesting scenarios (Table 5.2).

At the end of 92-year simulation runs of pure aspen stands (76 years at starting condition + 92 year simulation = 168 years), the overall stand basal area, aspen density, balsam fir density, birch basal area, balsam fir basal area and the dynamics of balsam fir showed a good agreement with the 1823 reference stand (Table 5.3). The major differences between the 1823 reference stand and the simulated pure aspen stands appeared in the dynamics of spruce and aspen (Fig. 5.3A vs 5.3B). Higher densities of small sized (5-15 cm at DBH) spruce in the simulated aspen stands resulted in higher stand density at 168 years than in the1823 reference stand (Table 5.3). Additionally, aspen appeared in all size classes of the 1823 reference stand, whereas simulated outputs showed aspen only in small size classes (5-15 cm at DBH) (Fig. 5.3A vs 5.3B).

At the end of the 78 year simulation of mixed aspen stands (90 years at starting condition+78 year simulation=168 years), stand BA and birch BA and the dynamics of balsam fir showed good agreement with the 1823 reference stand (Table 5.3). The main difference between the 1823 reference stand and simulated output of the mixed aspen stands appeared in the dynamics of spruce and aspen (Fig. 5.3A vs 5.3D). The simulations projected higher densities of small-sized (5-15 cm at DBH) spruce than empirical data of the 1823 reference stand (Table 5.3). Additionally, while aspen appeared in all size classes of the 1823 stand, simulated outputs of the mixed aspen stands presented virtually no aspen (Fig. 5.3A vs 5.3D).

5.4.3. Simulated stand dynamics of unharvested controls

After the mortality of first cohort aspen, simulations projected dominance of conifer species, white spruce in particular, in unharvested controls of pure aspen stands and balsam fir in mixed aspen stands. At the end of 100 year simulation runs, these intermediate and shade-tolerant conifers had accumulated 13.9 $m^2.ha^{-1}$ and 18.6 $m^2.ha^{-1}$ of BA, or 51% and 78% of total stand BA in pure aspen stands and in mixed aspen stands, respectively. The sapling layer (5-10 cm DBH) was equally dominated by balsam fir and white spruce in the pure aspen stands, but balsam fir occupied a larger proportion of saplings in the mixed aspen stands at the end of 100 simulations (Table 5.4 and 5.5). In addition, balsam fir maintained a higher proportion of merchantable BA in mixed aspen stands than in the pure aspen stands whereas the second cohort of aspen was more important in the pure aspen stands than in the mixed aspen stands (Table 5.4 and 5.5, Fig 5.4 and 5.5).

5.4.4. Stand dynamics following simulated partial harvesting treatments

Simulated gap harvesting, in particular 1600 m^2 gaps, (54% BA removed), produced the highest merchantable BA of all simulated treatments at years 50 and 100 (Fig. 5.4 and 5.5). At year 100 of simulations, total stand BA values for pure aspen stands and mixed aspen stands were 38.0 and 34.1 $m^2.ha^{-1}$, of which conifer species accounted for 18% and 28%, respectively (Table 5.4 and 5.5).

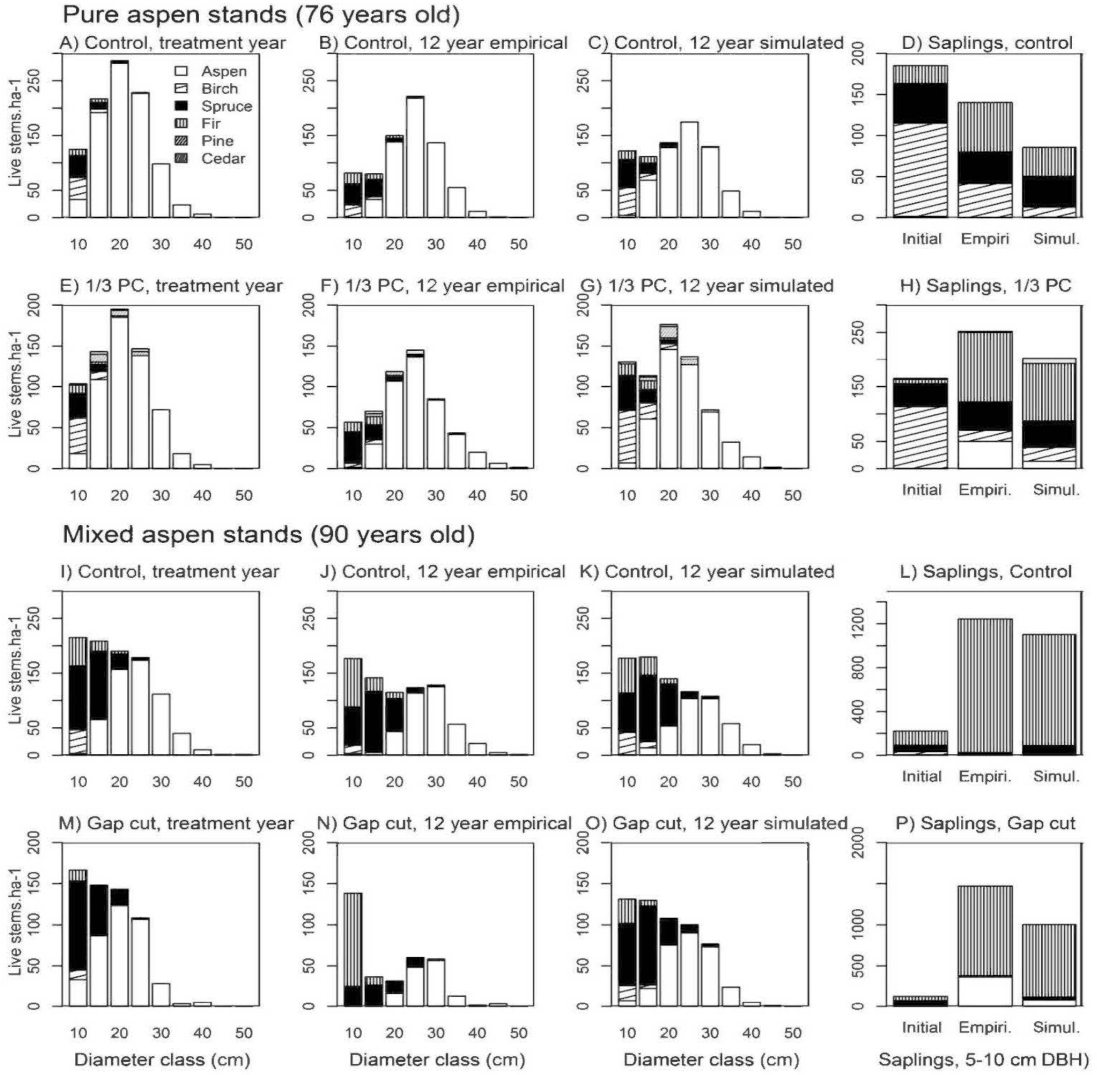

Figure 5.2 Comparison between empirical and model simulated results of DBH size distribution 12 years after partial harvesting treatment application of two stand types, pure aspen stands and mixed aspen stands. Fig A-C: merchantable trees (≥ 10 cm DBH) and D: sapling layer (5-10 cm DBH), of control (no harvesting) in pure aspen stands, Fig E-G: merchantable trees (≥ 10 cm DBH) and H: sapling layer (5-10 cm DBH), of 1/3 PC (partial cut: 33% harvesting) in pure aspen stands, Fig I-K: merchantable trees (≥ 10 cm DBH) and L: sapling layer (5-10 cm DBH), of control in mixed aspen stands and Fig M-O: merchantable trees (≥ 10 cm DBH) and P: sapling layer (5-10 cm DBH), of Gap cut (400 m^2) in mixed aspen stands. Initial: Treatment year, Empiri: Empirical, Simul: Simulated. Note. each graph represents the average condition of 15 permanent sample plots.

Table 5.3: Results of short term (12 years) and long term (92 years and 78 years for pure aspen stands and mixed aspen stands respectively) model evaluation: comparison between empirical and simulated outputs. PA: Pure aspen, MA: Mixed aspen and RS: reference stands

Stand types and treatments		Live stem density ≥ 5 cm at DBH (stems.ha^{-1})					Live basal area ≥ 5 cm at DBH (m^2.ha^{-1})				
		Stand	Aspen	Birch	Fir	Spruce	Stand	Aspen	Birch	Fir	Spruce
					Short term evaluation						
Control, PA	Treatment-year	1190±97	857±88	161±41	40±22	102±36	44.0±2.4	40.6±2.4	1.2±0.3	0.4±0.3	1.0±0.4
	12 year empirical	895±106	592±76	73±23	95±36	117±39	41.5±3.4	37.7±3.1	0.7±0.3	0.9±0.5	1.7±0.6
	12 year simulated	822±73	566±69	76±25	64±29	114±42	38.3±1.6	35.0±1.8	1.0±0.3	0.6±0.3	1.5±0.6
1/3 partial cut, PA	Treatment-year	856±82	545±79	168±67	23±26	80±51	30.9±3.1	27.3±3.7	1.3±0.8	0.3±0.3	0.7±0.5
	12 year empirical	813±119	478±89	30±25	153±76	115±54	32.8±4.2	29.0±4.2	0.3±0.3	1.0±0.5	1.5±0.7
	12 year simulated	818±147	459±76	**115±60**	83±67	112±63	31.9±2.2	26.5±3.0	**1.6±1.1**	0.9±0.7	1.3±0.8
Control, MA	Treatment-year	1178±128	568±81	75±55	205±88	330±94	42.2±4.9	33.7±4.8	0.8±0.4	1.7±0.8	6.1±1.3
	12 year empirical	2013±262	377±74	17±16	1343±310	277±89	42.3±4.3	29.3±4.4	0.2±0.2	6.1±1.1	6.7±1.8
	12 year simulated	1902±292	357±55	59±33	1120±231	366±131	41.9±3.5	26.8±3.3	**0.9±0.4**	5.3±1.2	8.2±1.8
Gap cut, MA	Treatment-year	653±194	387±99	22±16	67±33	257±152	21.7±4.3	17.2±4.2	0.2±0.2	0.4±0.2	3.9±2.0
	12 year empirical	1750±347	503±249	7±8	1200±322	103±52	19.1±3.1	11.2±2.3	0.0±0.0	5.4±1.7	2.5±1.4
	12 year simulated	1579±127	384±47	**27.4±23**	921±149	246±125	**28.4±2.0**	**19.1±2.2**	**0.4±0.3**	3.6±0.8	5.4±2.4
					Long term evaluation						
168 RS	Empirical	1210±186	472±122	206±58	430±131	86±23	20.7±2.4	10.3±2.2	3.6±0.8	3.7±1.3	2.7±0.8
76 years old PA	92 year simulated with budworm	**1583±83**	635±169	**101±43**	269±120	**571±174**	22.5±2.0	**6.3±1.4**	5.6±1.9	2.4±1.2	**8.1±2.4**
76 years old PA	92 year simulated without budworm	**2185±153**	456±182	**75±30**	715±269	**932±260**	**37.4±5.4**	**4.6±1.6**	5.4±1.9	**10.2±4.4**	**17.1±4.6**
90 years old MA	78 year simulated with budworm	**1659±198**	**37±17**	**49±29**	**1037±179**	**536±109**	24.1±1.0	**0.9±0.3**	4.2±2.0	**10.3±1.0**	**8.6±1.5**
90 years old MA	78 year simulated without budworm	**1802±89**	**7±4**	**48±28**	**1424±140**	**323±70**	**51.9±3.1**	**0.8±0.3**	3.7±1.7	**26.2±2.9**	**21.2±5.3**

Note. All values presented in table represents, Mean± 95% Confidence Interval (n=15), elements in bold indicate significant difference (mean±95% confidence interval) between simulated and empirical field data

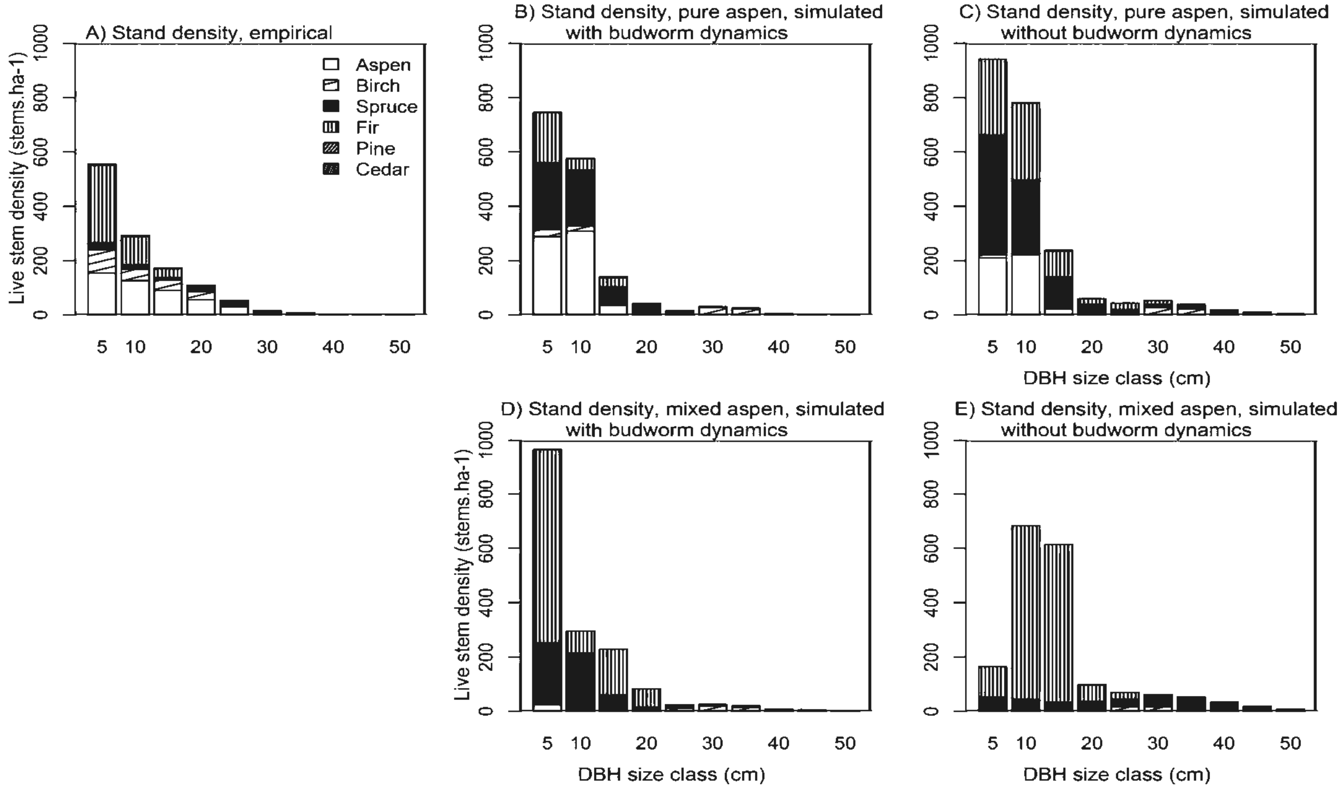

Figure 5.3. Comparison between empirical and model simulation results of DBH size distribution for long term model evaluation. Fig A presents 168 years old growth stand using empirical data from Bergeron (2000), Fig B and C show 76 years old pure aspen stands simulated 92 years to 168 years (76+92=168) using empirical data from pure aspen stands. Fig D and E show 90 years old mixed aspen stands simulated 78 years to 168 years (90+78=168) using empirical data from mixed aspen stands. Each graph represents the average condition of 15 permanent sample plots of each study site.

Total stand regeneration, and in particular aspen suckers, responded proportionally to simulated gap size at both stand types. Sucker recruitment into the sapling layer (5-10 cm DBH) started between 12-15 years of simulation runs and aspen sucker density increased with gap size (Fig. 5.4 and 5.5). Simulated gap cuts created higher aspen sucker densities than dispersed partial cuts in both stand types. Aspen sapling recruitment into merchantable tree size (≥ 10 cm DBH) began 40 years after partial harvesting (Fig. 5.4B and 5.5B). Similar to sucker density, merchantable aspen stems responded proportionally, in terms of both density and BA, to gap size (Fig. 5.4B, C and 5.5B, C) in both stand types. No differences appeared between unharvested controls and the 33% dispersed cut in the case of pure aspen stands or among unharvested controls, 33 and 61% dispersed cuts in the mixed aspen stands in terms of aspen and conifers density and basal area (Fig. 5.4A, B, C and 5.5A, B, C).

At years 25, 50 and 100 of simulation runs, mixed aspen stands had higher balsam fir sapling density and higher merchantable stem density and BA than pure aspen stands. Contrary to the response of aspen to gap size, balsam fir decreased in simulated gap cuts in both stand types. Compared to gap cuts, unharvested controls and dispersed partial cuts favored balsam fir (Table 5.4 and 5.5, Fig 5.4D, E, F and 5.5D, E, F). Between spruce and fir, the latter dominated the sapling layer of the mixed aspen stands whereas white spruce dominated in the pure aspen stands (Fig. 5.4D, G and 5.5D, G). At simulation years 25, 50 and 100 in the pure aspen stands, white spruce produced higher stem density and BA (≥ 5 cm DBH) than balsam fir, irrespective of simulated treatments (Table 5.4). In the mixed aspen stands, stem density and BA values were higher for balsam fir at years 25 and 50, but white spruce dominated at year 100 year, regardless of simulated treatments (Table 5.5).

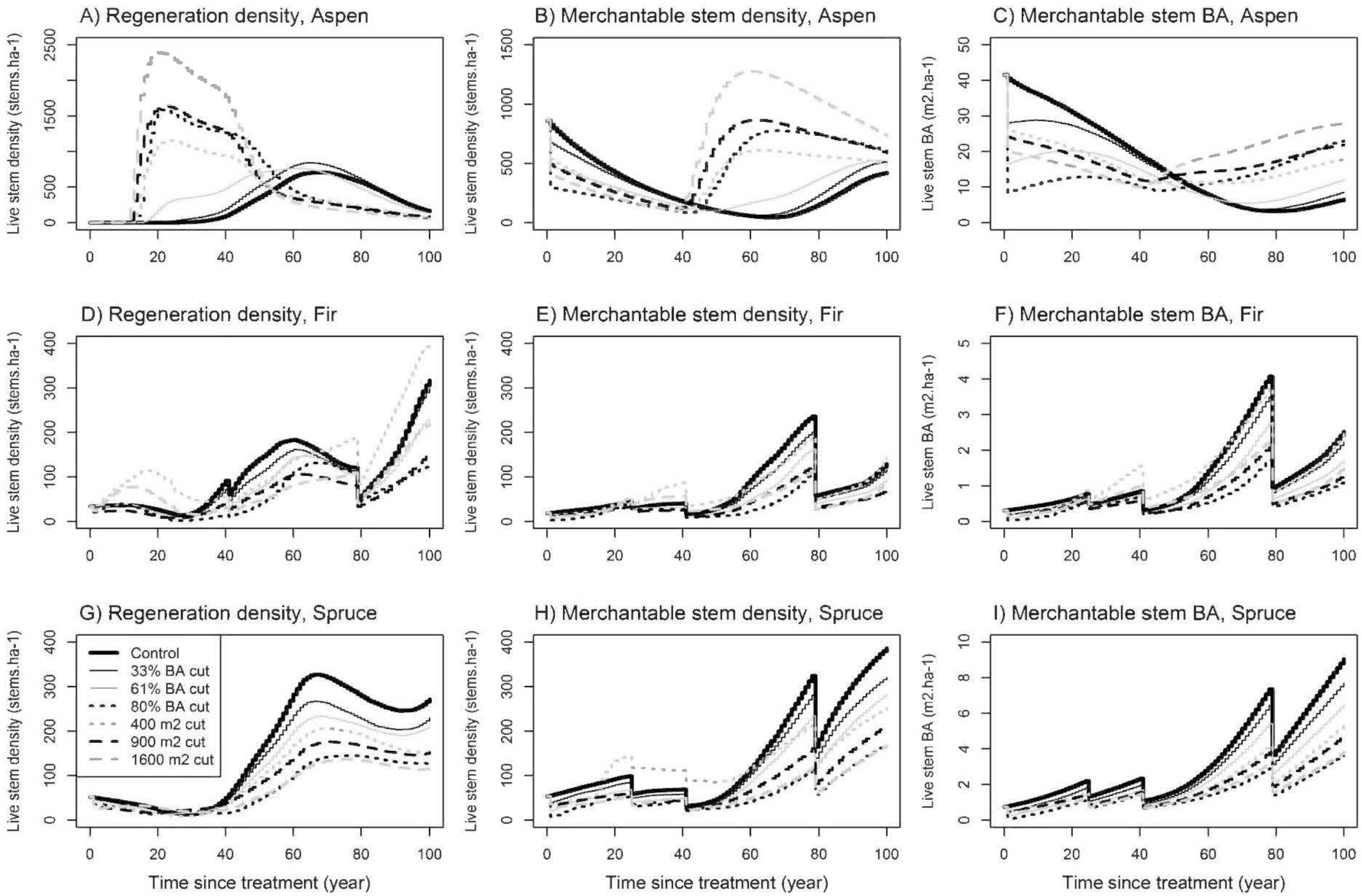

Figure 5.4: Stand dynamics of live stems after six levels of partial harvesting and unharvested controls in pure aspen stands. Note. Each graph represents the average condition of 15 permanent sample plots. Regeneration size: 5-10 cm at DBH, Merchantable stem: ≥ 10 cm at DBH. Sharp declines at the year of 25, 41 and 79 are due to spruce budworm mortality manually invoked by outbreak "incidents" that affected for balsam fir and white spruce (see details in method's section, 5.3.5 Model development).

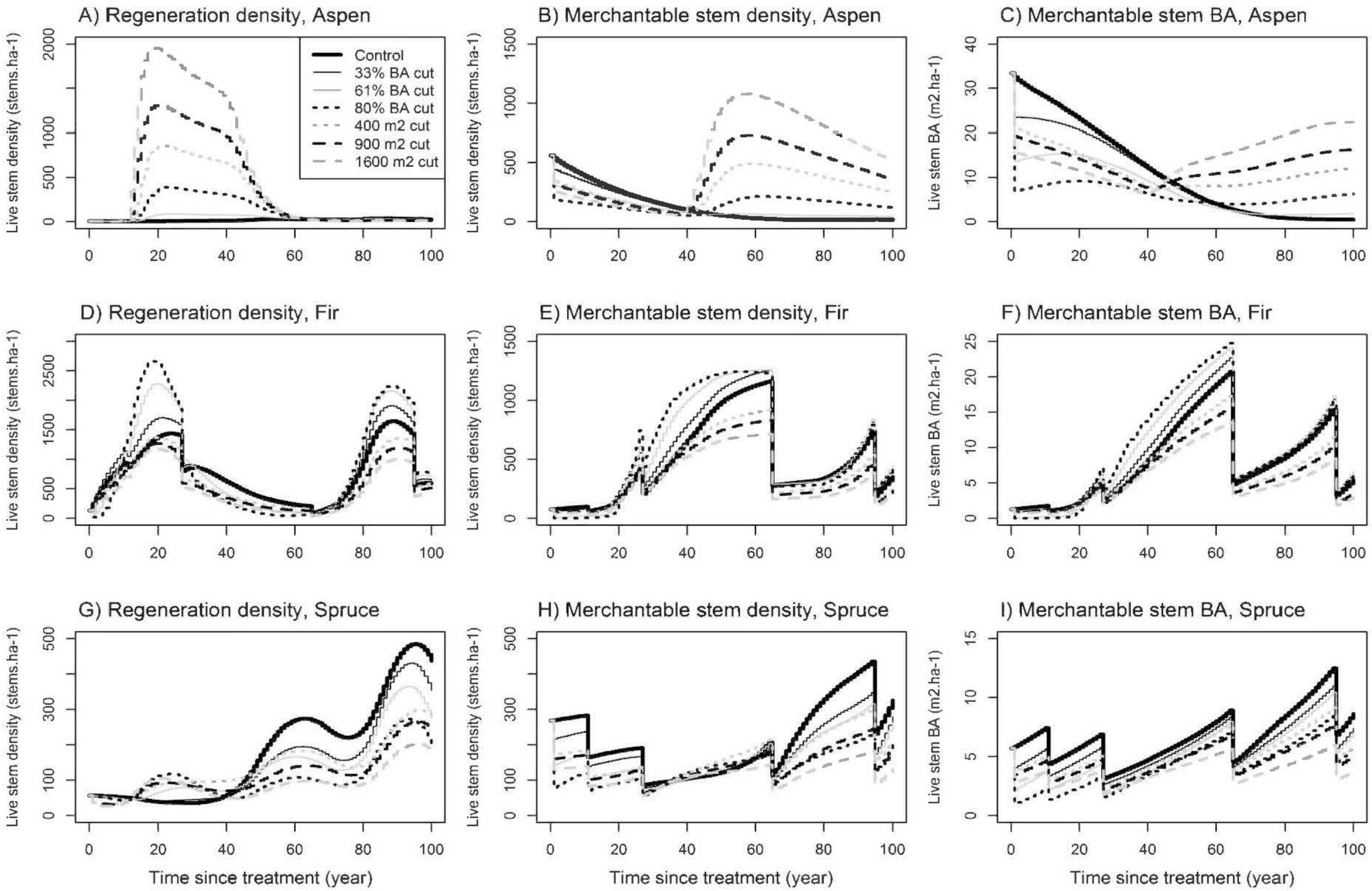

Figure 5.5: Stand dynamics of live stems after six levels of partial harvesting and unharvested controls in mixed aspen stands. Note. Each graph represents the average condition of 15 permanent sample plots. Regeneration size: 5-10 cm at DBH, Merchantable stem: ≥ 10 cm at DBH. Sharp declines at the year of 11, 27, 65 and 95 are due to spruce budworm mortality manually invoked by outbreak "incidents" that affected for balsam fir and white spruce (see details in method's section, 5.3.5 Model development).

Table 5.4: Comparison among seven simulated partial harvesting treatments in pure aspen stands at time steps 25, 50 and 100 years of simulations

	Live stem density ≥ 5 cm at DBH (stems.ha^{-1})				Live basal area ≥ 5 cm at DBH (m^2.ha^{-1})			
	Stand	Aspen	Fir	Spruce	Stand	Aspen	Fir	Spruce
				25-year simulation				
Un-cut	548±54	347±49	44±22	74±31	31.6±1.9	28.1±2.1	0.5±0.3	1.4±0.5
33% dispersed cut	535±47	351±34	40±20	62±29	28.4±1.6	25.4±1.9	0.5±0.2	1.1±0.5
61% dispersed cut	754±104	572±91	33±18	55±26	23.3±0.9	20.7±1.2	0.4±0.2	0.9±0.4
80% dispersed cut	1855±165	1676±210	28±18	53±38	20.9±0.3	18.5±0.7	0.4±0.2	0.8±0.3
400 m^2 gap cut	1606±66	1371±54	114±70	48±20	26.5±1.0	23.3±1.2	0.9±0.4	0.9±0.4
900 m^2 gap cut	1963±43	1811±45	28±13	55±27	26.4±0.9	23.8±1.1	0.4±0.2	1.0±0.4
1600 m^2 gap cut	2637±143	2457±129	75±41	55±16	26.3±1.1	23.8±1.1	0.6±0.3	0.8±0.2
				50-year simulation				
Un-cut	915±150	461±94	172±116	204±81	20.6±1.5	14.0±1.9	1.1±0.7	2.2±0.8
33% dispersed cut	1005±127	620±124	133±93	177±69	19.9±1.4	14.1±1.7	0.9±0.5	1.9±0.7
61% dispersed cut	1125 ±114	807±131	93±67	151±55	18.7±1.1	13.4±1.4	0.8±0.4	1.6±0.6
80% dispersed cut	1446±92	1262±102	50±36	73±30	19.0±0.9	14.9±0.7	0.5±0.3	1.1±0.5
400 m^2 gap cut	1320±83	993±70	131±68	126 ±55	19.9±1.8	14.7±1.1	1.2±0.5	1.3±0.6
900 m^2 gap cut	1546±60	1281±61	82±52	118±44	21.6±0.8	17.0±1.1	0.6±0.3	1.4±0.5
1600 m^2 gap cut	1931±128	1719±129	81±37	85±26	23.8±1.1	19.9±1.1	0.8±0.3	1.2±0.3
				100-year simulation				
Un-cut	1790±156	579±154	446±210	658±190	27.1±2.5	7.5±1.7	3.7±1.8	10.2±3.0
33% dispersed cut	1727±163	669±162	415±206	551±187	26.9±2.4	9.6±2.0	3.4±1.7	8.6±2.9
61% dispersed cut	1558±165	649±123	326±174	494±172	27.9±2.5	12.8±2.0	2.8±1.4	7.2±2.5
80% dispersed cut	1210±126	660±56	194±102	299±115	32.7±2.1	23.4±2.4	1.6±0.8	4.2±1.5
400 m^2 gap cut	1592±174	566±76	553±212	400±139	32.6±1.9	18.7±1.3	4.1±1.4	5.6±2.1
900 m^2 gap cut	1330±98	672±70	220±96	365±110	33.8±1.6	22.4±1.3	1.9±0.8	5.4±1.6
1600 m^2 gap cut	1427±125	785±73	360±149	283±73	38.0±0.8	28.1±1.3	2.4±1.0	4.3±1.1

Note: All values presented in table represents mean± 95% confidence interval (n=15). All simulations incorporated spruce budworm outbreak "incidents" that affected for balsam fir and white spruce (see details in method's section, 5.3.5 Model development)

Table 5.5: Comparison among seven simulated partial harvesting treatments in mixed aspen stands at time steps 25, 50 and 100 years of simulations

	Live stem density ≥ 5 cm at DBH (stems.ha^{-1})				Live basal area ≥ 5 cm at DBH (m^2.ha^{-1})			
	Stand	Aspen	Fir	Spruce	Stand	Aspen	Fir	Spruce
25-year simulation								
Un-cut	2298±278	216±33	1794±248	225±73	38.8±2.7	20.3±2.9	10.3±1.6	6.8±1.6
33% dispersed cut	2601±315	213±29	2126±287	209±68	38.0±2.6	18.8±2.6	12.4±1.5	5.8±1.4
61% dispersed cut	2997±365	233±112	2514±391	207±78	34.1±2.4	14.3±1.6	14.4±1.6	4.5±1.1
80% dispersed cut	3363±331	437±271	2695±459	200±131	30.7±2.0	10.4±1.1	16.0±2.2	3.6±1.0
400 m^2 gap cut	2878±242	957±130	1647±322	228±100	32.9±2.3	16.6±1.7	10.1±1.3	5.2±1.2
900 m^2 gap cut	3121±211	1352±180	1511±326	218±112	32.7±2.1	17.6±1.7	9.4±1.4	4.9±1.1
1600 m^2 gap cut	3497±171	1898±287	1359±374	206±128	31.2±1.9	17.9±1.4	8.4±1.8	4.2±1.0
50-year simulation								
Un-cut	1769±169	78±19	1339±165	294±74	32.8±1.8	7.5±1.6	15.7±1.7	6.8±1.6
33% dispersed cut	1808±146	82±30	1425±153	251±74	33.2±2.1	7.2±1.5	17.5±1.6	6.2±1.5
61% dispersed cut	1797±138	120±88	1373±201	262±84	32.5±2.2	5.8±1.0	18.9±2.1	5.8±1.3
80% dispersed cut	1861±151	272±194	1348±237	211±112	32.2±2.2	5.7±1.5	19.8±2.6	5.2±1.7
400 m^2 gap cut	2021±100	625±98	1057±167	296±82	31.0±2.0	9.5±0.9	13.5±1.8	6.1±1.3
900 m^2 gap cut	2115±74	900±129	941±165	236±86	31.1±1.8	11.8±1.2	12.2±1.9	5.3±1.3
1600 m^2 gap cut	2307±68	1286±204	800±182	189±89	31.2±1.7	14.4±1.5	10.7±2.3	4.5±1.3
100-year simulation								
Un-cut	1800±105	43±14	945±79	764±156	23.7±1.2	0.6±0.4	7.8±0.8	10.8±1.9
33% dispersed cut	1784±95	45±16	1066±68	633±137	22.9±1.1	0.8±0.7	9.0±0.8	9.2±1.5
61% dispersed cut	1791±81	61±37	1158±71	539±119	23.1±1.9	2.0±2.3	9.6±0.9	8.5±1.4
80% dispersed cut	1743±104	117±79	1205±128	397±116	24.9±2.8	6.3±4.4	9.5±1.4	7.0±1.4
400 m^2 gap cut	1627±82	257±40	847±68	490±101	28.7±1.2	12.1±2.1	6.3±0.7	7.2±1.2
900 m^2 gap cut	1561±85	365±51	743±71	425±95	30.8±1.4	16.3±2.4	5.6±0.7	6.3±1.1
1600 m^2 gap cut	1479±81	520±81	619±85	315±86	34.1±1.9	22.4±3.4	4.7±0.7	4.7±1.0

Note: All values presented in table represents mean± 95% confidence interval (n=15). All simulations incorporated spruce budworm outbreak "incidents" that affected for balsam fir and white spruce (see details in method's section, 5.3.5 Model development)

5.5. Discussion

The two central questions of this study were: 1) Does the SORTIE-ND reasonably simulate short- and long-term stand dynamics of aspen-dominated mixedwoods and 2) Can partial harvesting accelerate the development of complex, multi-cohort stands and, if so, which treatments perform best? To do this, we used the SORTIE-ND model which has been parameterized for the study area. Short-term (12 year) simulation outcomes were very similar to empirical values of species composition and size distribution, and although long-term simulations showed some unexpected trends, these were not solely due to problems with model parameter functions or values (discussed below). Stand dynamics similar to those of unharvested controls occurred in both stand types following the simulated 33% partial harvesting. All gap harvesting and the 80% dispersed harvesting promoted aspen recruitment and maintained mixed compositions with higher stand productivity than that in 33% and 61% dispersed harvesting treatments.

5.5.1. Short term evaluation

Over the short term (12 years), simulated treatments generally agreed with field data for most parameters including species-level stem density and basal area, but showed higher survival of residual aspen trees in the forest matrix of the 400 m^2 gap cuts in mixed aspen stands. The observed short-term mortality not captured by the model was likely both endogenous (death of small, low-vigour residual aspen stems) and exogenous. These latter sources of mortality include combined effects of harvesting machinery on some residual stems, two years of partial defoliation of aspen by the forest tent caterpillar and dry summers in 2001 and 2002, and moderate windthrow, particularly in the mixed aspen stands (Harvey and Brais, 2007; Bose *et al.*, 2014a). None of these sources of mortality are incorporated into the model, and occurring individually, their effects may not be very important to overall stand dynamics;

however, their combined and cumulative effects probably contributed to discrepancies between field observations and simulations.

5.5.2. Long term evaluation

Simulated development of un-harvested controls of 76 year old pure aspen stands and 90 year old mixed aspen stands forecasted conifer dominance in the old stands with lower basal areas than those at starting conditions of simulations. Old stands (150-200 years) in this region are generally composed of at least two cohorts of shade-tolerant conifers (balsam fir, white and black spruce, eastern white cedar), possibly with some residuals of the initial intolerant hardwood cohort and minor subsequent cohorts of intolerant hardwoods (Bergeron, 2000; Harvey *et al.*, 2002; Pothier *et al.*, 2004). The degree to which intolerant hardwoods recruit into older stands generally depends on several factors: density of advance conifer regeneration; canopy composition at the time of budworm or tent caterpillar outbreaks; defoliation severity and the extent of subsequent canopy mortality (Bergeron, 2000; D'Aoust *et al.*, 2004; Bouchard *et al.*, 2005; Moulinier *et al.*, 2011, 2013). The 1823 stands used as a reference for the study contained small amounts of white spruce in all size classes, abundant small-sized balsam fir and decreasing densities of trembling aspen from the 5 cm diameter class (ca. 150 stems) to the 25 cm size class (ca. 50 stems), thus suggesting a multiple cohort age structure for aspen (Fig. 5.3A). This stand structure would appear to be driven by spruce budworm-induced mortality and recurrent aspen and fir recruitment into budworm gaps (Morin *et al.* (1993). We recognize, however, that the 1823 reference stands represent one portrait of a ca.190 year old boreal mixedwood stand on a spectrum of possible structural and compositional conditions. Indeed, numerous factors, including initial stand conditions, severity of the stand-establishing fire and subsequent budworm and tent caterpillar disturbances, seed sources and succession processes, could all influence stand development in these boreal mixedwood landscapes.

Given the occurrence of three spruce budworm outbreaks of variable duration and intensity in this region during the twentieth century (Morin et al., 1993), it is understandable that the punctual budworm “outbreak incidents” induced in the simulations deviate in their effect on stand structure and composition from the 1823 reference conditions. Certainly, the approach to incorporating budworm-induced mortality was hindered by data shortage on spruce mortality from outbreaks in the study area, and our simulated output showed higher survival of spruce than observed in the reference stand. The data that we used to estimate white spruce mortality (Blais, 1981) were from a site situated 600 km southeast of the study area so it is possible, even likely, that real budworm mortality in the 1823 reference stand was different. In addition to this, while we accounted for the percentage of budworm-induced fir and spruce mortality, we did not consider size of gaps created by this mortality. As demonstrated by the partial harvesting simulations, if conifer mortality had been imposed in the form of medium to large gaps (900 – 1,600 m^2 and larger) rather than in a random (dispersed) distribution, this would have resulted in higher aspen recruitment and survival and, like the 1823 reference stand, more aspen in intermediate diameter classes.

5.5.3. Multi-cohort management and stand productivity in pure aspen and mixed aspen stands

A multi-cohort based forest management approach proposed for the eastern boreal forest (Bergeron and Harvey, 1997) involves, at the stand level, integrating natural stand dynamics into silviculture with the objective of developing structural and compositional attributes characteristic of old growth stands. In this context, variants of partial harvesting have been suggested to promote the old-growth attributes. Our results suggest that, in the two stand types, virtually all simulated partial harvesting treatments maintained multi-cohort mixedwood compositions with a second generation of aspen and first and second generation shade tolerant conifers. The sole exception was the 33% dispersed removal (and to a certain extent, the 61% dispersed removal) in mixed aspen stands which almost eliminated aspen by year 100 of the simulations

By creating more area with high light incidence in the sub-canopy and forest floor, gap harvesting favored trembling aspen and increased stand productivity in terms of basal area, regardless of stand type. In contrast, dispersed harvesting promoted shade tolerant conifers (Fig. 5.4 and 5.5). A simulation study by Beaudet *et al.* (2011) using the light resource module of SORTIE-ND in similar forest cover types showed that dispersed removal of 30% BA created no sub-canopy microsites with > 50% light availability, and only 2-3% of microsites had > 50% light availability after 60% BA dispersed removal. SORTIE-ND predicts regeneration recruitment and growth as a function of light and neighborhood competition (Coates *et al.*, 2003) and our results indicate that dispersed partial harvesting as high as 60% of BA still benefits shade tolerant conifers over trembling aspen but results in lower total stand basal area than gap harvesting of similar intensity (Table 5.4 and 5.5). Similar low understory light conditions have been observed after dispersed partial harvesting in aspen mixedwood stands in other studies of the eastern Canadian boreal forest (e.g., Prévost and Pothier, 2003; Man *et al.*, 2008a). Understory light could further decrease following dispersed tree removal due to crown expansion of residual neighbors in the years following partial harvesting (Man *et al.*, 2008a).

Simulations indicate that low-level (33- 66%) dispersed partial harvesting impedes trembling aspen recruitment and survival. Overall results suggest that, over the long-term and after successive budworm outbreaks, these treatments would create stands with the lowest stand BA (≈23-28 m^2) but with the highest proportion of shade-tolerant conifers (36-45% in pure aspen stands and 78-80% in mixed aspen stands). The level of ingress of intolerant species depends on initial canopy opening by treatments and on the extent of subsequent canopy tree mortality induced by spruce budworm and other partial disturbances. In contrast, high intensity partial harvesting

($\geq$ 80% BA) and particularly gap cuts $\geq$ 400 m^2 favor trembling aspen recruitment immediately after harvesting. Large gaps, in particular, have the sustained effect of maintaining high stem densities of aspen in both stand types. At year 100 of simulations, unharvested controls, 33% and 61% dispersed harvestings created more simple stand structures in both stand types, with only merchantable trees and regeneration of tolerant conifers. In contrast, by favoring a continuous recruitment of trembling aspen as well as tolerant conifers, all gap treatments and 80% dispersed harvesting created more complex stand structures in both stand types (Fig. 5.4 and 5.5 and Table 5.4 and 5.5). Although, we did not measure the size variability/heterogeneity, graphics of stand dynamics (regenerations and merchantable stems) illustrate a more complex stand structure with regeneration and merchantable stems of both trembling aspen and tolerant conifers in all gap harvesting treatments at year 100 of simulations (Fig. 5.4 and 5.5). Pretzsch and Schütze (2009) also demonstrated the importance of mixed compositions of Norway spruce and European beach for long-term stand-level productivity. According to Pothier *et al.* (2004), a second generation aspen recruitment in even-aged natural aspen stands is generally delayed until stand senescence. At this point, mortality is less density-dependant and, especially in clonal aspen stands, is probably more contagious (aggregated). If this is the case, gap cuts would certainly better mimic senescence mortality in aspen and aspen mixedwood stands than dispersed partial harvesting.

5.5.4. Dynamics of pure aspen versus mixed aspen stands

After 25 and 50 years of simulation runs, unharvested controls of the two stand types showed different development patterns, largely as a result of differences in pre-treatment understory conditions (Table 5.4 and 5.5). Besides the low initial densities of conifer regeneration in the pure aspen stands, the presence of mountain maple impaired the recruitment of shade tolerant conifers into larger tree layers and is likely at least partly responsible for lower stand basal area than the mixed aspen stands after 25 and 50 years of simulation. The adverse impact of high woody shrubs such as mountain maple on shade tolerant conifer recruitment and growth has been well documented for eastern Canadian boreal mixedwood (MacDonald *et al.*, 2004; Kneeshaw and Prévost, 2007; Bose *et al.*, 2014b). Moreover, the pure aspen stands in the study site had fewer conifer seed trees than the mixed aspen stands, which also would affect conifer recruitment over the long term. Our results suggest that the differences in pre-treatment stand characteristics, that is, abundance of advance conifer regeneration, conifer seed trees and mountain maple in the understory were the primary factors driving tree and stand responses to the simulated treatments. Results showed that such differences in pre-treatment stand conditions could continue to influence stand dynamics for up to 100 years. However, at year 100, simulated 1600 m^2 gap cuts decreased over all stand and species specific differences between the two stand types (Tables 5.4 and 5.5).

5.5.5. Management implications

Forecasting stand growth and development is not an exact science and, after partial harvesting, is additionally complicated because this type of intervention generally introduces more stand-level structural complexity (Zenner, 2000). This study provides insight into how partial harvesting treatments of different intensities and spatial configurations can influence dynamics in pure aspen and mixed aspen stands. Our results demonstrate - or at least strongly suggest - that the spatial configuration of residual overstory trees, the amount of residual conifer seed trees and advance conifer regeneration, conifer mortality by spruce budworm and the presence of woody shrubs like mountain maple are all factors that, ideally, should be taken into consideration when making harvest prescriptions, and particularly partial harvesting prescriptions. To promote aspen regeneration, our long-term simulations corroborate the overwhelming body of knowledge on the subject: large gaps favor aspen recruitment and growth, small gaps and low intensity canopy removal tend to be much less favorable. This is generally true for both pure aspen and mixed aspen stands. To promote conifer recruitment into the canopy layer, the contrary is generally true: small gaps and a range of intensities of dispersed harvesting will favor spruce and fir at the expense of aspen. This said, these treatments are best applied in mixedwood stands, like the ones simulated in this study, where dense conifer understories are present.

Three of the simulated gap harvesting treatments (400 m^2, 900 m^2 and 1600 m^2) removed less than 60% of basal area but generated higher basal area values at 100 years of simulation than dispersed partial harvesting of 60% and 80% basal area removal. Such high basal area retention by gap harvesting could potentially also retain more favorable wildlife habitat than dispersed harvesting with low basal area retention. A review by Vanderwel *et al.* (2009) indicated that high intensity partial harvesting (70% BA removal) created unsuitable habitat for about one fourth of all late-successional species, including most forest raptors, pileated and black-backed woodpeckers, brown creeper, northern flying squirrel and woodland caribou.

5.5.6. Further model development and calibration

This study allowed us to identify a number of gaps in our understanding of the dynamics and interrelationships occurring within these ecosystems. The model simulations also identified areas in which the parameters estimated in SORTIE-ND could be improved upon or where more empirical studies should be undertaken to improve our understanding of specific dynamics of the eastern Canadian boreal mixedwood.

The fact that white spruce appears to have superior seedling recruitment and survival to that of balsam fir does not reflect the reality of our region in the eastern Canadian boreal forest. Therefore, there is clearly a need to better understand spruce recruitment and dynamics at the juvenile (seedling and sapling) stage. Installation of long-term monitoring plots would allow the quantification of relationships between spruce seed production, seed dispersal, and germination and seedling survival rates for specific seedbed types as well as mortality at different stages (seedlings, saplings and pole size). A better understanding of the competitive effects of woody shrubs on survival is also very much of interest. In this study, we considered the competition effect of mountain maple, a high, woody shrub, but not other species in the herb and shrub layers. It should be noted that SORTIE-ND does not incorporate below-ground effects of competition for water and nutrients on growth or regeneration recruitment.

Currently, the integration of punctual, non-catastrophic disturbances such as insect outbreaks can only be done manually with SORTIE-ND, by converting selected live trees species and tree sizes to snags at pre-determined specific time-steps. Due to the already complex nature of the model, this manual approach to integrating budworm dynamics may be a more reasonable way to go than endeavoring to model them. Budworm-forest dynamics are complex and other non-spatial models have been developed solely for the purpose of characterizing and forecasting forest dynamics under budworm-driven disturbance regimes and developing management options for optimising wood supply (MacLean *et al.*, 2001). Nonetheless, similar to work by D'Aoust *et al.* (2004), aerial photographs could be used to improve understanding of the spatial dimensions of canopy gap formations following insect outbreaks such as spruce budworm and forest tent caterpillar in mixed forest types of different ages and with varying proportions of vulnerable species. SORTIE-ND could also benefit from monitoring of budworm-induced canopy gap formation and closure and associated regeneration dynamics.

Several studies have reported on initial logging induced mortality after partial harvestings in Canadian boreal mixedwoods (e.g., MacDonald and Thompson, 2003; Bladon *et al.*, 2008; Solarik *et al.*, 2012). A better understanding of initial pulses of mortality after a range of partial harvesting treatments (different intensities and spatial configurations) could contribute to capture a source of mortality otherwise missed by SORTIE-ND. For example, Thorpe *et al.* (2010) simulated a range of partial harvesting treatments for black spruce forests of boreal Ontario and reported initial logging induced mortality for several harvesting scenarios and Arii *et al.* (2008) employed a complex harvesting algorithm to investigate a broader range of partial harvest scenarios.

This said, we believe that SORTIE-ND has already proved its utility for the eastern Canadian boreal mixedwood forest and will continue to be improved as new data specific to key ecosystem processes become available.

5.6. Acknowledgements

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Appendix 5.1. Major modelling behaviors of SORTIE-ND used in present study

Growth behaviors

Three sub-models were used to predict growth,

i) Non limited absolute diameter-growth for seedlings and sapling

$$Y = SF\left(\frac{A\times GLI}{\frac{A}{S}+GLI}\right) \text{.......} (1)$$

where, Y = *log10(radial growth + 1)*, SF is the suppression factor, A is the asymptotic diameter growth, S is the slope of growth response and GLI is the gap light index, calculated by a light behavior. A Gap Light Index (GLI) value is calculated for each individual tree by accounting for minimum solar angle in radians, number of altitude sky divisions, number of azimuth sky divisions, beam fraction of global radiation (0 to 1), clear sky transmission coefficient, first day of growing season, last day of growing season, amount of canopy light transmission (0 to 1) and amount of light transmission through snags (0 to 1). GLI values range from 0 (no sun) to 100 (full sun).

Amount of diameter growth per timestep is calculated as

$\text{Growth} = (((10^{Y} - 1) * 2)/ 10) * T$ ....(2)

where Y = log10 (radial growth + 1) and T is the number of years per time step.

ii) constant radial growth, $Y = \frac{g4}{10} \times 2 \times T$ ....(3)

where, Y is the amount of diameter growth, in cm, to add to the tree, $g4$ is the species-specific adult constant radial growth parameter in mm.yr^{-1} and T is the number of years per timestep.

iii) NCI (neighborhood competition indices) growth,

*Growth = Max Growth * Size Effect * Shading Effect * Crowding Effect*.................(4)

Max Growth is the maximum diameter growth the tree can attain, in cm.yr^{-1}, entered in the NCI Maximum Potential Growth, cm.yr^{-1} parameter. *Size Effect, Shading Effect* and *Crowding Effect* are all optional factors which act to reduce the maximum growth rate and will vary depending on the conditions a tree is in. Each of these effects is a value between 0 and 1.

$$\text{Size Effect, } SE = e^{-0.5}\left[\frac{ln(\frac{DBH}{X_0})}{X_b}\right]^2 \quad \text{.. (5)}$$

where, *DBH* is the DBH of the target tree in cm, X_0 is the NCI size effect mode in cm and X_b is the NCI size effect variance in cm.

$$\text{Shading Effect, } ShE = e^{-m.s^n} \quad \text{...(6)}$$

where, *m* is the NCI shading effect coefficient, *n* is the NCI shading effect exponent and *S* is the amount of shade cast by neighbors, from 0 (no shade) to 1 (full shade).

$$\text{Crowding Effect, } CW = e^{-C*DBH^{\gamma}*NCI^{D}} \quad \text{...(7)}$$

where, *C* is the NCI crowding effect slope, *DBH* is the DBH of the target tree in cm, *γ* is the NCI size sensitivity to target tree species type, *D* is the NCI crowding effect steepness and *NCI* is the individual based tree NCI value (equation below),

$$NCI_i = \sum_{j=1}^{S}\sum_{K=1}^{N}\lambda_{iK}\,\frac{\left(\frac{DBH_{jk}}{q}\right)^{\alpha}}{dist_{ik}^{\beta}} \quad \text{...(8)}$$

where, the calculation sums over $j = 1...S$ species and $k = 1...N$ neighbors of each species of at least a DBH of NCI minimum neighbor DBH, in cm, out to a distance of NCI max radius of crowding neighbors, in m, α is the NCI alpha parameter for the target tree's species, β is the NCI beta parameter for the target tree's species, DBH_{jk} is the DBH of the kth neighbor, in cm, q is the NCI DBH divisor, λ_{ik} is the species j NCI Lambda parameter for the target species relative to the kth neighbor's species, $dist_{ik}$ is distance from target to neighbor, in m.

Mortality behaviors

Five sub models are used to predict mortality,

i) Juvenile mortality, $m = 1 - e^{-(T \times m1)e^{-m2 \times G}}$ ....(9)

where, m is the probability of mortality, T is the number of years per timestep, $m1$ is the mortality at zero growth parameter, $m2$ is the light-dependent mortality parameter and G is amount of radial growth, in mm.yr^{-1}, added to the tree's diameter during T.

ii) Senescence, $m_s = \frac{e^{(\alpha+\beta(DBH-DBHs))}}{1+e^{(\alpha+\beta(DBH+DBHs))}}$ .... (10)

where, m_s is the probability of mortality, α (senescence mortality alpha parameter) and β (senescence mortality beta parameter) control the magnitude of the uptick, DBH is the tree's

DBH, in cm and $DBHs$ is the DBH at onset of senescence, in cm parameter.

iii) Adult stochastic mortality, $= \frac{Max}{1+(\frac{Age}{X_0})x_b}$ ....(11)

p is the probability of mortality, Max is the suppression duration mortality - max mortality rate (0-1) parameter, X_0 is the suppression duration mortality - X_0 parameter, X_b is the suppression duration mortality - X_b parameter, Age is the tree's age, in years.

iv) Weibull snag mortality, $s = e^{-(a \times T)^b}$ ....(12)

where, S is proportion of snags still standing, between 0 and 1, a and b are weibull parameters (weibull annual "a" parameter for snag size class X mortality parameter and weibull annual "b" parameter for snag size class X mortality parameter), T is the snag age in years.

v) Competition mortality: competition mortality is a growth-based mortality behavior. It uses the results of the NCI growth behavior (equation-2). Trees killed by this behavior have a mortality reason code of "natural".

Substrate behaviors

Substrates are what seedlings germinate on. Six types of substrates of variable and species-specific suitability are incorporated into the model: forest floor litter, forest floor moss, scarified soil, tip-up mounds, decayed logs and fresh logs.

Fresh log area, $FL = \frac{DBH \times h}{2}$ ....(13)

where, *FL* is new fresh log area, in square meters, *DBH* is the DBH of the fallen tree, in m and *h* is the height of the fallen tree, in m.

Newly exposed tip-up mounds, $OA = \pi \times (r \times F)^2$ ....(14)

where, *OA* is the new tip-up mounds area in square meters, *r* is the tree trunk radius in meters and *F* is the uprooted tree radius increase factor for root rip-out parameter, which accounts for the effects of root disturbance.

Relationships among fresh logs, decayed logs, tip-up mounds and scarified soils represent the decay of the different substrates as a function of substrate age according to the following equation, $Y = e^{\alpha \times t^{\beta}}$ ....(15)

where t is time in years, α and β are the parameters.

Spatial disperse behaviors

We used the methods of to fit functions that predict the density (numbers/m^2) of seedlings (R_i) in quadrat *i* using an equation of the form:

$Ri =$

$STR \sum_{j=1}^{S} Cifi \sum_{k=1}^{T} \left(\frac{dbh_k}{30}\right)^2 \frac{1}{n} e^{-Dm_{ik}^3}$.. (16)

where STR ("standardized total recruits") is the potential number of seedling recruits produced by a 30 cm DBH parent tree, c_j and f_j are the cover and favourability, respectively of the $j = 1..S$ substrate types, dbh_k is the DBH (in cm) of the $k = 1..T$ parent trees within the specified radius of quadrant i, n is a normalizer (described below), D is a species-specific dispersion parameter and m_{ik} is the distance (in meters) from the i^{th} quadrant to the k^{th} parent tree. The normalizer (n) serves two functions. It reduces parameter correlation between STR and the dispersion parameter (D); and scales the distance-dependent dispersion term so that STR is in meaningful units - i.e., the total number of seedlings produced in the entire seedling shadow of a 30 cm DBH parent tree.

CHAPTER VI

GENERAL CONCLUSION

This study was conducted to enhance our understanding of the potential use of partial harvesting in the context of natural disturbance-based forest management in trembling aspen-dominated mixedwoods of eastern Canada. Compared to most previous studies done in similar forest types, this thesis provides longer-term stand and tree-level responses to partial harvesting treatments. The research evaluated partial harvesting treatments on three major areas of management concern: growth of residual trees, mortality of residual trees and regeneration recruitment. It also examined the potential of partial harvesting in terms of promoting structural attributes associated with the old-growth development stage. Additionally, the modelling chapter demonstrated the use and utility of a stand dynamics simulation tool adapted for the aspen-dominated mixed forest type of eastern Canadian boreal forest. This chapter also revealed that by applying partial harvesting using different intensities and gap sizes, one could generate various structural and compositional configurations of mixed forests.

6.1. Main results

6.1.1. Recruitment of regeneration

In pure aspen stands (92% of aspen basal area), aspen sapling recruitment follows a gradient of canopy opening (clearcut > 2/3 partial cut (heavy, high thinning) > 1/3 partial cut (light, low thinning) > control). Twelve years after treatment application, the 1/3 and 2/3 partial cuts respectively generated 5% and 56% of the density of aspen sapling (2-9.9 cm DBH) densities in clearcuts. No aspen suckers recruited into the sapling layer of controls. The cumulative recruitment of aspen saplings 12 years after treatments was ≈ 5,000, ≈ 2,850 and ≈ 250 stems ha^{-1} in clearcut, 2/3 and 1/3 partial cut treatments, respectively (Table 2.3 and Fig. 2.2A, B and C, Chapter 2).

There was no conifer recruitment into the sapling layer in the first three years following harvesting treatments. The peak of conifer sapling recruitment occurred at a different period for each treatment. Conifer sapling recruitment was significantly higher in partial cuts than clearcuts in terms of sapling basal area. No difference appeared in terms of conifer sapling recruitment between the two partial cuts or between partial cuts and controls (Table 2.3 and Fig. 2.2D, E and F, Chapter 2).

Although mountain maple regeneration ($\leq$ 2m) density was higher in partial cuts and highest in the clearcuts in the year following treatments, very few stems (180 stems ha^{-1}; not statistically analysed) actually recruited into the sapling layer in clearcuts. Twelve years after treatment application, mountain maple maintained a similarly dense multi-stemmed condition in the understory of un-harvested controls and of both partial harvesting treatments (Table 2.2, Chapter 2), possibly influencing the recruitment of conifer regeneration into the sapling layer.

6.1.2. Mortality of residual and recruited stems

In pure aspen stands, the mortality of residual trees was significantly affected by partial harvesting treatments and time since treatment applications. The 2/3 partial cut generated significantly higher mortality during the first three years following treatment application. This can partly be explained by the nature of the treatment which was essentially a heavy high thinning that targeted dominant and co-dominant stems. In all treatments, the highest mortality levels were observed during the initial periods 1-6 years following treatments and decreased thereafter. The mortality of residual aspen stems occurred mostly in the smaller size classes (10-19.9 cm DBH). The cumulative mortality of trembling aspen over the entire study period reached 250 stems $ha^{-1}12yr^{-1}$ in controls, compared to 106, and 170 stems $ha^{-1}12yr^{-1}$, respectively in the 1/3 and 2/3 partial cut treatments which translated into a relative mortality of 29, 20 and 43% respectively in the controls, 1/3 and 2/3 partial cut treatments. The higher mortality in controls was largely due to higher merchantable stem densities which induced more mortality in smaller, less vigorous stems. The fact that stems in these size classes were preferentially harvested in the 1/3 partial cut (low light thinning) accounted for lower tree mortality in this treatment, whereas these low vigour stems formed a good part of residual stems in the 2/3 treatment and probably were negatively affected by the radical change in the growing environment following the treatment. No significant mortality of aspen or conifer saplings or conifer trees occurred over the 12 year post-treatment period (Table 2.4 and Fig. 2.3, Chapter 2).

6.1.3. Volume growth of residual aspen trees

In aspen stands, annual volume increment of individual residual trembling aspen trees increased linearly with time since partial harvesting over the 12-year period. Annual volume increment increased significantly in the 2/3 partial cut starting in the first growing season after treatment application. Considering both dominants and co-dominants, the average annual increment in the 2/3 partial cut was 25.6% higher than in controls over the 12-year period. No significant difference occurred between the 1/3 partial cut and controls. In all treatments, including controls, annual volume increment of dominant trees was higher than that of co-dominants by an average of 16.2 $dm^3.tree^{-1}.yr^{-1}$ over the 12 year post-treatment period. Harvesting did not induce any initial growth reduction (growth shock) in aspen residual trees (Table 3.3 and Fig 3.2, Chapter 3). In addition, aspen tree-level volume increment response in the last three years of the monitoring period was independent of neighborhood competition, but dependent on pre-treatment size, irrespective of harvesting treatments (Table 3.5, 3.6 and Fig 3.2, Chapter 3).

6.1.4. Emulating or accelerating stand development through partial harvesting

In pure aspen stands, 1/3 and 2/3 partial cuts promoted respectively lower and higher canopy gap percentages than the old-growth stage of aspen mixedwoods. In 1/3 partial cuts, canopy opening was insufficient to promote new tree cohorts and eventually produced less variability in tree size classes. Although the 1/3 partial cuts retained large trees similar to old-growth aspen mixedwoods, by removing smaller, low-vigour stems ("imminent mortality"), this treatment may delay stand transition from hardwood dominance to mixedwoods and from even-sized to a more complex vertical stand structure. The 2/3 partial cuts, where dominant and co-dominant trees were primarily harvested to emulate senescence mortality, created more growing space than what is reported for old-growth aspen mixedwoods. Although, 2/3 partial cuts created a higher percentage of canopy gaps than old-growth aspen mixedwoods, this treatment showed its promise of increasing tree size varibility by promoting regeneration recruitment and growth of residual trees.

In mixed aspen stands (81% of aspen basal area), the 45% BA dispersed cut resulted in canopy gap occupancy (32 - 48%) closer to those reported for old growth stands. By protecting the advanced balsam fir regeneration, the dispersed cut increased the ratio of sub-canopy to canopy basal area. The dispersed cut did not "accelerate succession", but maintained tree size variability of mature untreated controls. However, the dispersed cut reduced the density of large trees. Nonetheless, the mean downed log volume in dispersed cuts was 115.5 $m^3.ha^{-1}$, which is close to the volume (117-131 $m^3.ha^{-1}$) of aspen old-growth stands reported by Lee *et al.* (1997). Similar to 2/3 partial cuts of pure aspen stands, the 400 m^2 gap cut in mixed aspen stands created higher canopy gap occupancy than old-growth aspen mixedwoods. Twelve years after harvesting, the range of the sub-canopy to canopy basal area ratio was

0.44 - 1.11, which is comparable to the ratio (0.8-2.0) of old-growth aspen mixedwoods. Similar to dispersed cuts, large tree density was lower in gap cuts relative to large tree density reported for old-growth aspen mixedwoods (Lee *et al.*, 2000; Schieck *et al.*, 2000). Similar to other harvesting treatments, gap cuts maintained deadwood material of mature aspen stands (untreated controls) and a quantity of deadwood comparable to that of old-growth aspen mixedwoods.

6.1.5. Simulating long-term development of mixedwood stands

The spatially explicit stand dynamics model SORTIE-ND appeared to capture short-term dynamics well, but showed more deviation from the empirical reference for longer-term simulations (Table 5.3, Fig. 5.1 and 5.2, Chapter 5). After the mortality of first cohort aspen, long-term simulations projected dominance of conifer species in controls, in particular white spruce in pure aspen stands and balsam fir in mixed aspen stands. Outcomes of 100 year simulations of untreated controls indicated that shade tolerant conifers would accumulate ≈ 14 $m^2.ha^{-1}$ and ≈ 18.5 $m^2.ha^{-1}$ of BA, representing 51% and 78% of total stand BA of pure aspen stands and of mixed aspen stands, respectively (Table 5.4 and 5.5, Chapter 5).

Simulated gap harvesting, particularly 1,600 m^2 gaps (54% BA removal), produced the highest merchantable BA of all simulated treatments at years 50 and 100. Total stand regeneration, particularly aspen suckers, responded proportionally to simulated gap size in both stand types. Sucker recruitment into the sapling layer (5-10 cm DBH) started between 12-15 years of simulation runs, and aspen sucker density increased with gap size. According to simulations, aspen sapling recruitment into merchantable tree size class (≥ 10 cm DBH) began 40 years after partial harvesting. In terms of aspen and conifer density and basal area increases following treatments, no differences occurred between controls and the 33% dispersed cut in pure aspen stands or among controls, 33 and 61% dispersed cuts in mixed aspen stands (Fig. 5.4A, B, C and 5.5A, B, C, Chapter 5).

Over the 100-year simulation period, mixed aspen stands had higher balsam fir sapling densities, merchantable tree densities and BA than aspen stands. Contrary to the response of aspen to harvesting treatments, balsam fir and white spruce responses were more linked to pre-treatment condition than harvesting intensities and spatial configurations. Between spruce and fir, long-term simulations suggested that the latter dominate in mixed aspen stands whereas white spruce dominate in pure aspen stands, a result of their pre-treatment occupation in the two stand types (Table 5.4 and 5.5,Chapter 5).

The overall results of the thesis indicate that partial harvesting is a viable silvicultural option for trembling aspen-dominated boreal mixedwoods of eastern Canada. This practice can be used to improve the growth of large aspen trees and to promote certain attributes of old-growth stands. However, residual tree mortality immediately after treatments and limited conifer recruitment, particularly in pure aspen stands with understories of woody shrubs, could reduce the potential of partial harvesting. I argue that adapting partial harvesting treatments (intensity, size classes and spatial configuration) based on pre-harvest stand conditions (e.g., stand age, size distribution, presence of conifer seed trees, advanced regeneration and woody shrubs) is the key to the success of partial harvesting treatments.

6.2. Management recommendations

In ecosystem management, forest practitioners use natural disturbance dynamics as templates or references to set management strategies and develop or adapt silvicultural practices. Silvicultural approaches that emulate natural disturbance or stand dynamics should decrease differences between managed and natural forest ecosystems (Bergeron and Harvey, 1997; Franklin *et al.*, 1997, 2007). In boreal mixedwoods of eastern Canada, partial harvesting has been promoted to emulate stand-level disturbances and to accelerate natural succession (Bergeron and Harvey, 1997), but three major concerns associated with partial harvesting have been identified: growth of residual trees, mortality of residual trees and recruitment of regeneration (Coates, 1997; Messier *et al.*, 1999; Ruel *et al.*, 2000; Bose *et al.*, 2014c). This thesis used two stand types, aspen stands (92% of aspen basal area) and aspen mixedwoods (81% of aspen basal area), and evaluated their responses to partial harvesting treatments. Based on our results and the relevant literature, the following recommendations are put forward to improve mixedwood management in the eastern Canadian boreal forest.

1. Ecosystem management: emulating or accelerating natural succession

Based on the principles of ecosystem management, partial harvesting should emulate – or be inspired by – natural stand-level dynamics (Bergeron and Harvey, 1997). Regional knowledge of mortality dynamics associated with forest tent caterpillar (FTC) outbreaks could be emulated for partial harvesting in aspen stands. In eastern Canada, FTC outbreaks may occur every 9 to 13 years (Cooke and Lorenzetti, 2006) and may last 1 to 6 years (Cooke *et al.*, 2009). Outbreaks are often associated with growth reduction only (Frey *et al.*, 2004, chapter 3), but by killing large aspen trees, they may also create large canopy gaps representing 11% to 47% of stand area (Moulinier *et al.*, 2013). Aspen trees are less vulnerable to FTC outbreaks on productive sites (Frey *et al.*, 2004, Chapter 3). In addition to aspen mortality by FTC, the timing of aspen senescence needs to be better understood and should be integrated into designing partial harvesting scenarios. Aspen senescence generally begins around 60 years (Pothier *et al.*, 2004), but may be delayed up until 100 years on productive sites (Frey *et al.*, 2004, Chapter 2).

Stand-level mortality associated with natural succession creates irregular stand structure (Franklin *et al.*, 2007). Therefore, partial harvesting should be designed to create irregularities both in horizontal and vertical structural dimensions. Horizontal stand irregularity can be achieved by retaining trees in dispersed patterns and in groups, whereas retaining trees of all available size classes would ensure vertical irregularity. Results from our study as well as studies done elsewhere (e.g., McGee *et* *al.*, 1999; Angers *et al.*, 2005; Keeton, 2006) show an immediate adverse impact of high-intensity partial harvesting on potential habitat substrates such as large overstory trees. To address this limitation, a certain proportion of large trees as well as potential deadwood structures (future snags) should be retained during partial harvesting treatments.

2. Enhance growth of residual trees

If management objectives include improving growth of aspen trees (which is generally *not* the case), our results show that high-intensity partial harvesting (61% BA removal) can increase the volume growth of large (dominant and co-dominant) aspen trees, and that growth increases can been maintained for at least 12 years. Employing treatments much earlier than those applied in the aspen stands of the SAFE Project (76 years), would likely produce greater positive growth responses as a result of younger tree age, higher vigor and growth potential, as well as provide more time for residual trees to accumulate volume. Concerns regarding initial growth shock and neighbourhood competition reported for other species (e.g., Jones and Thomas, 2004; Thorpe *et al.*, 2007; Hartmann *et al.*, 2009) do not appear to apply to large aspen trees (Chapter 3).

3. Reduce mortality of residual trees

Although residual tree mortality is a concern in partial harvesting, results from this study suggest that, on productive sites, vigorous dominant and co-dominant aspen trees - even 75 to 85 years old - are not susceptible to mortality following treatment, whereas small, non-vigorous aspen trees are (Chapter 2). Partial harvesting, other than salvage cutting, should be avoided in aspen stands recently affected by forest tent caterpillar defoliation because weakened stems appear to be more vulnerable to logging shock (Man *et al.*, 2008b). Mortality due to windthrow after partial harvesting can be minimized by avoiding large open areas of road clearings or clear-cut stands (Williamson and Price, 1971) and by leaving residual trees in large patches or groups (Lavoie *et al.*, 2012). Also, partial harvesting should not be applied to stands that, because of topographical or soil conditions, are naturally prone to windthrow.

4. Facilitate recruitment of shade tolerant conifer regeneration

Pre-treatment stand condition is the key to increasing sapling recruitment of shade tolerant conifers. In stands with dense understories of conifer regeneration and adequate conifer seed trees (like the mixed aspen stands in this study), virtually any (careful) partial harvesting treatment could favour establishment and maintain growth of conifer regeneration. However, high-intensity ($\geq$ 50% of BA removal) partial harvesting or gap cuts (400 m^2 or 900 m^2) in mixed aspen stands would promote both shade-tolerant conifer and intolerant hardwood regeneration (Chapters 4 and 5) and could be appropriate in ecosystem-based silviculture unless minimizing aspen recruitment is a primary treatment objective.

In stands on rich sites with low conifer regeneration, few conifer seed trees and a dense woody shrub layer (like the pure aspen stands in this study), partial harvesting should be avoided if the primary objective is to promote conifer recruitment. High intensity partial harvesting under these conditions mostly benefits intolerant species like trembling aspen and low intensity partial harvesting (<50% basal area removal) tends to benefit woody shrubs already established in the understory. Shade-tolerant woody shrubs like mountain maple are efficient in occupying small gaps and impairing conifer recruitment and growth (MacDonald *et al.*, 2004; Kneeshaw and Prévost, 2007). However, in the context of FEM and if the management objective is to promote tree size variability and retention of biological legacies, a non-uniform or irregular partial harvesting treatment (rather than removal of small or large trees only) could be applied to create adequate growing space (see Kneeshaw and Bergeron, 1998) for new cohorts and also maintain a certain proportion of large trees (see Lee *et al.*, 2000). (This sort of treatment was not applied in the aspen stands of SAFE project.)

6.3. Limitations of the study

The results reported here on partial harvesting effects on trembling aspen-dominated mixedwood stands cannot be generalized to late successional mixedwoods dominated by shade-tolerant conifers or to other boreal forest types. Similarly, only two stand types and four partial harvesting treatments were tested in this study (although others were simulated) and should not be generalized to other partial harvesting treatments. The two stands were primarily different in terms of understory composition, rather than stand age (only 13 years difference) or overstory composition (both $\geq$ 80 % aspen basal area). However, stand dynamics models such as SORTIE-ND allow exploration of other silviculture options on a wider range of stand conditions.

In the course of the study, I was not able to identify the exact causes of residual tree mortality and of low recruitment of conifer regeneration following partial harvesting treatments in aspen stands. Moreover, the fact that light availability and regeneration below 2 cm DBH were not re-measured in the latter years of the 12-year post-treatment period limited our ability to attribute possible mechanisms that influenced regeneration dynamics in the study. Similarly, continuous monitoring was not carried out on canopy gap dynamics or on neighborhood competition of stems used for growth analyses.

The stand dynamics model SORTIE-ND revealed a number of anomalies with respect to what we know of medium- to long-term mixedwood stand dynamics. The fact that white spruce appears to have superior seedling recruitment and survival to that of balsam fir does not reflect the reality of our region in the eastern Canadian boreal forest. Therefore, there is clearly a need to better understand spruce recruitment and dynamics at the juvenile stage. Currently, the integration of punctual, non-catastrophic disturbances such as insect outbreaks can only be done manually with SORTIE-ND, by “harvesting” specific species and tree sizes, and therefore is rather simple and crude. Moreover, a better understanding of initial pulses of mortality after a range of partial harvesting treatments (different intensities and spatial configurations) could contribute to capture a source of mortality otherwise missed by SORTIE-ND.

6.4. Knowledge gaps and research avenues

Regeneration recruitment, particularly of shade-tolerant conifers, is an important criterion for evaluating the potential of partial harvesting. Although the sapling stage was monitored in this study, to really understand regeneration dynamics, it is probably equally important to examine factors affecting the success rate of conifer seedling recruitment into the sapling stage. To this end, it would be interesting to design an experiment to investigate factors influencing species-specific seedling survival rates including partial harvesting intensity and spatial configuration, relative importance of seed trees, substrate quality and quantity and competitive effects of woody shrubs and other understory vegetation. As well, to increase our understanding of mechanisms involved in seedling growth and recruitment responses to partial harvesting, eco-physiological approaches could be applied. For example, a greater species-specific understanding of light requirements and plasticity of crown architecture at different growth stages, the saturation point of photosynthesis, stomatal control and rooting characteristics would provide functional explanations to treatment responses. A greater understanding of these parameters would contribute to improving the design of partial harvesting treatments for a variety of stand conditions and species compositions.

Large, vigorous aspen trees benefited from partial harvesting treatments with no indication of growth shock or mortality. However, small suppressed individuals had much higher mortality in high-intensity partial harvesting treatments during the first three years after treatment application. It would be interesting to examine the exact causes of their mortality, specifically, whether treatments, competition, disease or combination of these factors were at cause. Although, neighbourhood competition was insignificant for large aspen trees, projecting forward 40 to 60 years, when shade-tolerant conifers approach commercial maturity, and overstory aspen are in senescence, it would be interesting to examine the effect of neighborhood competition on growth of shade-tolerant conifer trees.

Several authors have suggested that mixedwoods are the most structurally complex and most productive forest ecosystems of the Canadian boreal forest (De Grandpré and Bergeron, 1997; Chen and Popadiouk, 2002; Haeussler *et al.*, 2007). However, no research has been conducted to compare the degree of complexity among different forest types of the Canadian boreal forest. A complex system generally exhibits various properties such as heterogeneity, hierarchy, self-organization, openness, adaptation, memory, non-linearity, and uncertainty (Filotas *et al.*, 2014). Among these, non-linear dynamics have been highly reported as being the major characteristic of any complex system (e.g., Wiggins *et al.*, 1990; Waldrop, 1993; Barnes *et al.*, 2003; Messier *et al.*, 2013). For example, May and Leonard (1975) proposed empirical methods to test non-linear dynamics in terms of competition among species, Canham *et al.* (2004) proposed several non-linear mathematical equations to describe competition among tree individuals and Zenner (2000) demonstrated a three-dimensional structural complexity index that accounts for non-linear dynamics of tree size variability. In all cases, because spatial data is necessary for theses analyses, it would be interesting to map mixedwood stands as well as other boreal stand types and compare the non-linear dynamics in terms of competition and size variability among tree individuals. Moreover, the manner in which non-linear behavior influences forest productivity (i.e., tree volume growth) and other ecosystem functions (i.e., wildlife habitat and plant and animal diversity) would be an interesting avenue of research.

Current knowledge on partial harvesting in eastern Canadian boreal mixedwoods is largely based on relatively recent experimental trails (≤ 15 years old). Therefore, individual-based stand dynamics models like SORTIE-ND can be tremendously useful but obviously require adequate parameterization to make credible projections of long-term stand- and tree-level dynamics. This study identified potential limitations of SORTIE-ND and some areas where model parameters could be improved upon to better project stand development of eastern Canadian boreal mixedwoods. Empirical studies should be designed to improve our knowledge of stand dynamics, particularly dynamics related to white spruce survivability at juvenile stage (seedlings and saplings) and trembling aspen sucker recruitment following overstory tree mortality (either in dispersed or in patchy layouts). Moreover, stand-level mortality due to insect outbreaks (spruce budworm and forest tent caterpillar) and other minor disturbances or stresses (windthrow and drought) need to be better understood and integrated into model calibration and parameterization. Using modelling approaches to investigate partial harvesting not only saves the operational costs of long-term experimental trials - which are nonetheless important and complementary-, but provides flexibility to modify and explore entire silvicultural systems that includes stand renewal, pre-commercial and commercial treatments and final harvests.

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