

UNIVERSITÉ DU QUÉBEC À MONTRÉAL

COMPARAISON DE LA STRUCTURE ET DE LA COMPOSITION
D'ÉRABLIÈRES ANCIENNES ET AMÉNAGÉES
(COUPE DE JARDINAGE ET COUPE À DIAMÈTRE LIMITE)

MÉMOIRE
PRÉSENTÉ
COMME EXIGENCE PARTIELLE
DE LA MAÎTRISE EN BIOLOGIE

PAR
VIRGINIE-ARIELLE ANGERS

MAI 2004

REMERCIEMENTS

Je ne saurais imaginer meilleur directeur de recherche que Christian Messier. Bien que très occupé, il a su doser supervision et confiance, me laissant beaucoup de latitude dans l'élaboration et la conduite de ce projet. Merci Christian.

Je tiens également à remercier mon co-directeur, Alain Leduc, pour ses conseils théoriques, statistiques (et philosophiques !), ainsi que Marilou Beaudet pour ses multiples révisions en profondeur et ses commentaires toujours pertinents. Merci aussi à Normand Villeneuve, du Groupe de travail sur les écosystèmes forestiers exceptionnels, pour ses commentaires élaborés, et sa précieuse contribution à l'accès aux érablières anciennes et aux données terrain disponibles. Craig Lorimer et Frédérik Doyon, par leurs commentaires à titre de réviseurs externes ont été d'un très grand intérêt dans la finalisation de ce mémoire.

Je ne pourrai jamais remercier suffisamment mes très vaillants aides de terrain, Pascal Côté et particulièrement Stéphanie Côté, pour leur travail efficace et précis, leur curiosité, leur intérêt et leur bonne humeur. Du MRN, unité de gestion de la Basse-Lièvre, merci à Pierrette Cyr et Gaétan Forest qui m'ont accueillis plusieurs jours dans leurs bureaux et m'ont rendu accessibles les documents qui m'ont permis de choisir les sites à l'étude. Merci à Madame Alice Legris, notre hôte de St-André-Avellin pour ses récits et ses bons plats. J'aimerais aussi remercier Jean-Michel Roberge ainsi que les étudiants au laboratoire de Christian Messier pour avoir pris le temps de réviser et commenter très pertinemment une première version du manuscrit.

Merci à ma mère pour son soutien continu et un merci tout particulier à Antoine Martel, dit Le Persévérant, qui a enduré mes étés d'absence, a appris à jardiner et à soigner les orchidées bien malgré lui et m'a supporté en tout temps. Merci à mes amis de la communauté GREFItienne qui pour plusieurs sont devenus plus que des collègues de bureau au cours des trois dernières années.

Finalement, un merci destiné à mon père (1919-1999), écologiste des hommes, qui m'a transmis son amour de la nature, la Flore Laurentienne à la main, à travers nos expéditions en forêt.

AVANT-PROPOS

Ce mémoire constitue le résultat de mes travaux de maîtrise en biologie. J'ai effectué l'essentiel de l'élaboration du projet, de la récolte des données, de leur analyse et de la rédaction. Les résultats de cette recherche ont été présentés oralement lors de trois congrès, dont deux au Québec (AFCAS et GREFi-CRBF) et un en Oregon, à l'occasion du North American Forest Ecology Workshop tenu à Corvallis en juin 2003. Le chapitre principal de ce mémoire est présenté sous la forme d'un article et sera prochainement soumis pour publication scientifique révisée par des pairs. Les coauteurs sont Christian Messier, Marilou Beaudet et Alain Leduc.



Forêt ancienne du Lac La Blanche, mai 2002.

TABLE DES MATIÈRES

REMERCIEMENTS	ii
AVANT-PROPOS	iii
LISTE DES FIGURES	vi
LISTE DES TABLEAUX	vii
LISTE DES APPENDICES	viii
RÉSUMÉ	ix
INTRODUCTION GÉNÉRALE	1
Problématique	1
État des connaissances	2
Objectifs	4
CHAPITRE I	5
COMPARING COMPOSITION AND STRUCTURE IN OLD-GROWTH TO HARVESTED (SELECTION CUT AND DIAMETER-LIMIT CUT) STANDS IN THE HARDWOOD FORESTS OF QUÉBEC (CANADA)	5
1.1 Abstract	6
1.2 Introduction.....	7
1.3 Methods.....	10
1.3.1 Study area and site selection	10
1.3.2 Sampling design and data collection	11
1.3.3 Data analysis	15
1.3.4 Statistical analysis	16
1.4 Results	17
1.4.1 Gaps	17
1.4.2 Vertical foliage profile	17
1.4.3 Sapling diameter distribution	18
1.4.4 Tree species composition	18
1.4.5 Sapling species composition	19
1.4.6 Tree diameter distribution.....	20
1.4.7 Snags	20
1.4.8 Coarse woody debris.....	21
1.5 Discussion	22

1.5.1 Canopy openings.....	22
1.5.2 Wood removal	26
1.5.3 Stand and landscape scale potential impact of management practices on ecosystem dynamics	29
1.5.4 Management recommendations	33
1.6 Acknowledgments	34
1.7 References	35
CONCLUSION GÉNÉRALE	59
RÉFÉRENCES	64

LISTE DES FIGURES

Figure	Page
1.1 Study area showing location of old-growth (OG, n = 6), selection cut (SC, n = 7) and diameter-limit cut stands (DLC, n = 6).....	42
1.2 Canopy gap size distribution in old-growth stands.	43
1.3 Foliage cover profile for old-growth (OG, n = 114 sampled points), selection cut (SC, n = 130 sampled points) and diameter-limit cut stands (DLC, n = 111 sampled points) (± 1 SE).	44
1.4 Dbh distribution of sapling density for old-growth (OG, n = 1331saplings), selection cut (SC, n = 3281 saplings) and diameter-limit cut (DLC, n = 644 samplings) stands (± 1 SE).	45
1.5 Relative basal area of main species and groups of species for a) trees and b) saplings in old-growth (OG, n = 456 trees, 1331 saplings), selection cut (SC, n = 520 trees, 3281 saplings) and diameter-limit cut (DLC, n = 444 trees, 644 samplings) stands (± 1 SE). Only species with more than 5% mean basal area in at least one stand type are presented.....	46
1.6 Tree dbh distribution for old-growth (OG, n = 456 trees), selection cut (SC, n = 520 trees) and diameter-limit cut stands (DLC, n = 444 trees) (± 1 SE) using 10 cm classes.	47
1.7 Snag density by dbh class in old-growth (OG, n = 91 snags), selection cut (SC, n = 95 snags) and diameter-limit cut stands (DLC, n = 216 snags) (± 1 SE).	48
1.8 Decay-class distribution of snag volume in old-growth (OG, n = 91 snags), selection cut (SC, n = 95 snags) and diameter-limit cut (DLC, n = 216 snags) stands (± 1 SE).	49
1.9 Decay-class distribution of CWD (fallen woody debris, logging slash and stumps) in old-growth (OG, n = 357 CWD), selection cut (SC, n = 676 CWD) and diameter-limit cut stands (DLC, n = 395 CWD) (± 1 SE) by origin; N, natural; U, unknown; CS, cut stump; LS, logging slash.....	50
1.10 Synthesis of observed and expected differences between a) old-growth and b) partially harvested stands.....	51
A.1 Evolution of selection cut areas in Québec (1984-2000).....	57
B.1 Trend in species relative basal area for the two main species, sugar maple (a) and beech (b) in old-growth (OG), selection cut (SC) and diameter-limit cut (DLC) stands.....	58

LISTE DES TABLEAUX

Tableau	Page
1.1 Characteristics of study sites and locations.....	52
1.2 Structural characteristics in North America's northeastern hardwoods from published literature (OG, Old-growth; SC, Selection cut; UN, Unmanaged).	54
1.3 Results of comparisons of trees, sapling, dead wood and gaps structural features between old-growth (OG), selection cut (SC) and diameter-limit cut stands (DLC).	56

LISTE DES APPENDICES

Appendice	Page
APPENDIX A.....	57
APPENDIX B.....	58

RÉSUMÉ

Depuis le début des années 1990, la coupe de jardinage (CJ), où environ 30% de la surface terrière est récoltée à tous les 20 à 30 ans, constitue la principale méthode de récolte dans les forêts feuillues du sud du Québec. Plusieurs considèrent que l'impact de cette perturbation est similaire à la dynamique naturelle des micro-trouées, et que l'intégrité des forêts est par conséquent assurée, mais peu d'études détaillées ont été entreprises pour tester cette hypothèse. Par ailleurs, les forêts feuillues ont été modelées au cours des dernières décennies par des coupes sélectives d'intensité variable, le plus souvent des coupes à diamètre limite (CDL). Cette étude visait à caractériser et à comparer la composition (arbres et gaules) et la structure (trouées, distribution du feuillage, arbres, chicots et débris ligneux) de forêt anciennes (ANC), de CJ de 12 ans et de CDL de 28 à 30 ans.

Nos résultats présentent des différences marquées entre les ANC et les peuplements aménagés, et des écarts plus forts entre CDL et ANC qu'entre CJ et ANC. En ce qui a trait à la composition, relativement peu de différences ont été observées, malgré une plus forte abondance relative d'espèces mi-tolérantes à l'ombre dans les cohortes de régénération post-coupe des forêts aménagées, et une plus forte abondance relative de hêtre à grandes feuilles (*Fagus grandifolia* Ehrh.) chez les gaules dans les CDL relativement aux ANC et aux CJ. Davantage de différences ont été observées en ce qui concerne la structure. La synchronisation des ouvertures en forêt aménagée a induit un recrutement massif de régénération post-coupe, ce qui a engendré la formation d'une dense couche de feuillage qui a vraisemblablement entravé les processus de régénération dans la strate adjacente inférieure. Cette dernière présentait de plus des pourcentages de recouvrement du feuillage plus homogènes que les strates correspondantes des autres types de peuplements. Les gros arbres vivants et les arbres défectueux étaient plus rares dans les CJ que dans les ANC. Bien que peu de différences aient été observées chez les chicots et le bois mort, on anticipe une diminution en qualité et en quantité de ces éléments lors des prochaines interventions.

Nous argumentons que même si la CJ semble se rapprocher davantage du régime de micro-trouées qui prévaut dans les forêts feuillues que les CDL, et que par conséquent ce système représente une avancée dans une perspective d'aménagement écosystémique, plusieurs carences subsistent. Aux échelles du peuplement et du paysage, une application étendue, régulière et exclusive de la CJ dans les forêts feuillues pourrait mener à une homogénéisation de la composition et de la structure ainsi qu'à une raréfaction des composantes structurales clés. Des alternatives d'aménagement à la CJ courante sont proposées.

Mots clés: Érablières, forêts anciennes, coupe de jardinage, coupe à diamètre limite, perturbations naturelles, composition, structure, trouées, stratification, chicots, débris ligneux.

INTRODUCTION GÉNÉRALE

Problématique

Depuis un peu plus d'une dizaine d'années, la coupe de jardinage constitue le principal mode d'aménagement dans la forêt feuillue du sud du Québec. Actuellement, on estime que ce mode de récolte prévaut dans 65% des forêts feuillues de la province (Beaulieu 2003). L'instauration de cette méthode a fait suite au constat dressé par le ministère de l'Énergie et des Ressources dans les années 1980 suite à des décennies de coupes à diamètre limite qui ont résultées en une importante dégradation de la qualité commerciale des peuplements. La coupe de jardinage donc a été introduite afin «d'assurer un rendement soutenu en quantité et en qualité lors de l'exploitation des peuplements contenant encore du bois de qualité et d'autre part, à reconstruire et à rendre productifs les peuplements appauvris par les coupes partielles successives » (Majcen 1994).

Cette méthode implique une récolte partielle des tiges, d'environ 30% de la surface terrière, où l'on privilégie les arbres de mauvaise qualité ou peu vigoureux, et ce, avec des rotations d'environ 20-30 ans. Bien qu'elle soit utilisée à grande échelle, la coupe de jardinage n'a fait l'objet que de peu d'études relativement à son impact sur l'intégrité des écosystèmes. Ce projet visait donc à amorcer ce suivi, en utilisant l'approche de l'aménagement écosystémique, qui propose que si l'on aménage la forêt en s'inspirant des processus naturels qui y ont naturellement cours, on devrait garantir la conservation de la majorité des espèces, structures, fonctions et processus qui la caractérise (Hansen *et al.* 1991, Franklin 1993, Attiwill 1994, Angelstam 1998, Bergeron *et al.* 1999). Afin de juger de la durabilité de cette pratique, on devait comparer les régimes de perturbations prévalant dans les forêts naturelles et aménagées.

En forêt feuillue, le régime des micro-trouées constitue le principal type de perturbation naturelle. La création d'ouvertures du couvert causées par la mort d'un

ou de plusieurs arbres (Runkle 1982, 1985) induit des conditions de lumière ponctuelles dans le temps et dans l'espace qui permettent la libération de la régénération pré-établie et assure ainsi le recrutement de nouvelles tiges dans la canopée. Comme la coupe de jardinage crée elle aussi des trouées dans le couvert, plusieurs forestiers prétendent que cette méthode imite les perturbations naturelles. Cette interprétation nous semblait cependant douteuse. D'un point de vue théorique, par rapport au régime des micro-trouées, l'aménagement implique une ouverture synchronisée du couvert qui entraîne une forte augmentation de lumière en sous-couvert, ainsi qu'un retrait de matière ligneuse.

Plutôt que de s'intéresser directement aux processus, on a préféré faire appel à des forêts modelées par les différents types de perturbation. Pour représenter la dynamique des micro-trouées, on a fait appel à des témoins, des érablières anciennes exemptes d'activités anthropiques directes ou de perturbations naturelles majeures récentes. La composition et la structure, des éléments susceptibles d'être modifiés par l'aménagement et qui peuvent en retour avoir un impact sur les processus et les organismes qui leurs sont inférés, ont été utilisés comme descripteurs.

Afin de voir dans quelle mesure les attributs résultants de l'aménagement se rapprochent ou s'éloignent de ceux laissés par les perturbations naturelles, on a donc comparé des érablières anciennes, jardinées et ayant fait l'objet de coupes à diamètre limite. Ce dernier type de coupe n'est en principe plus utilisé, mais l'a tellement été par le passé, et de manière si intensive, qu'il est à l'origine de l'héritage forestier qu'on connaît aujourd'hui en forêt feuillue et il nous apparaissait intéressant de le caractériser (Majcen 1994).

État des connaissances

Selon Franklin *et al.* (1981), une forêt est définie par sa composition, sa fonction et sa structure. La composition est une notion peu ambiguë et réfère à

l'agencement des espèces qui constituent l'écosystème. La structure est quant à elle plus difficile à définir et change souvent selon le point de vue. Dans le cadre de cette étude, en s'inspirant de Kimmins (1997), on définira la structure comme étant l'agencement spatial à la fois vertical et horizontal des plantes et des débris ligneux. Finalement, la fonction des écosystèmes réfère aux processus et aux interactions (Stone et Porter 1998).

La composition et la structure ont été sélectionnées comme les principaux éléments descripteurs dans cette étude parce qu'elles sont les plus tangibles et les plus facilement mesurables sur une courte échelle temporelle que la fonction. Même si on ne mesurera pas directement cette dernière composante, la structure, modelée par les éléments naturels, est à la fois la cause et le produit des processus et peut servir à comprendre le passé, la fonction, voire le futur des écosystèmes forestiers (Spies 1998). La structure constitue un élément particulièrement important de l'habitat. Par exemple, certaines espèces ne sont pas tant sensibles à l'âge ou à la composition d'une forêt, mais à la structure qu'elle recèle (Bunnell *et al.* 1999). L'aménagement a souvent pour effet de réduire la variation dans la structure des forêts (Spies 1998), autant au niveau du peuplement que du paysage.

En forêt feuillue, les connaissances concernant les différences pouvant exister entre forêts anciennes et aménagées selon divers types de coupes partielles proviennent principalement du nord-est des États-Unis, où la coupe de jardinage est d'ailleurs utilisée depuis plus longtemps qu'au Québec (Majcen 1994). Les études sont cependant, pour la plupart, très spécifiques à certains sujets, et considèrent rarement plusieurs facettes de l'écosystème à la fois.

En ce qui a trait à la structure, les arbres à valeur faunique et le bois mort sous toutes ses formes (arbres morts sur pied ou chicots, débris ligneux au sol) constituent des sujets très étudiés ces dernières années. La plupart des études notent une diminution des tiges vivantes de gros diamètre et/ou présentant des cavités, du volume de débris ligneux au sol, de la densité ou du volume de chicots et du diamètre des chicots et des débris ligneux au sol dans les forêts ayant fait l'objet

de divers types de coupes partielles par rapport à celles qui ne sont pas aménagées (Goodburn et Lorimer 1998, Hale *et al.* 1999, McGee *et al.* 1999). À notre connaissance, très peu d'études ont porté sur la répartition verticale du feuillage. En général, l'aménagement a pour effet de réduire l'hétérogénéité dans la structure des forêts (Spies 1998), autant au niveau du peuplement que du paysage.

En ce qui concerne la composition, les études sont parfois contradictoires. Alors que certains auteurs ne notent aucune différence de composition entre des peuplements anciens et d'autres ayant fait l'objet de coupes sélectives (Hale *et al.* 1999), d'autres auteurs ayant comparé la composition de peuplements aménagés avec celle de forêts pré-coloniales ont observé une plus forte abondance relative d'érable à sucre et une plus faible abondance relative de hêtre dans les peuplements ayant fait l'objet de coupes (Siccama 1971, McIntosh 1972, Brisson *et al.* 1988).

Objectifs

Cette étude vise principalement à mettre en évidence l'influence qu'a l'aménagement forestier sur la composition et la structure des érablières. Plus spécifiquement, on vise, dans un premier temps, à caractériser la structure et la composition de forêts anciennes, jardinées et ayant fait l'objet de coupes à diamètre limite. Dans un deuxième temps, on vise à comparer ces attributs entre les différents traitements afin de mettre en lumière les différences et similarités rencontrées. Finalement, les résultats obtenus permettront, le cas échéant, de mettre en lumière les principales lacunes de l'aménagement et de formuler des recommandations qui pourraient permettre d'améliorer les pratiques actuelles.

CHAPITRE I

**COMPARING COMPOSITION AND STRUCTURE IN OLD-GROWTH TO
HARVESTED (SELECTION CUT AND DIAMETER-LIMIT CUT) STANDS IN THE
HARDWOOD FORESTS OF QUÉBEC (CANADA).**

1.1 Abstract

Single-tree selection cutting, where approximately 30% of the basal area is removed every 20 to 30 years, has been widely implemented recently in the hardwood forests of Québec (Canada). This system is believed to be similar in some ways to the natural gap disturbance dynamics of hardwood forests and is thus suggested to favor the maintenance of their ecological integrity. However, very few studies have tested this hypothesis. This study characterized and compared the composition (saplings and mature trees) and structure (gaps, foliage distribution, tree diameter and density, snags and coarse woody debris) of old-growth stands (OG), 12-year old selection cuts (SC) (that were probably previously submitted to some forms of partial cut), and 28- to 33-year old diameter limit cuts (DLC).

Our results showed marked structural differences between OG and harvested stands, with stronger differences between DLC and OG than between SC and OG. Synchronization of openings in both SC and DLC induced a massive post-cut regeneration recruitment that created a dense foliage layer that likely impeded the regeneration process in the inferior layer which exhibited a higher homogeneity in foliage cover than other layers. Large living trees and defective trees were scarcer in SC than OG, which can have detrimental impact on species dependent on these elements and on future dead wood characteristics. In composition, relatively few differences were found, although more mid-tolerant species were found in the post-cut recruitment cohorts of harvested stands compared to OG, and beech (*Fagus grandifolia* Ehrh.) was disadvantaged among saplings in DLC compared to OG and SC.

We argue that even if selection cutting is closer to the natural disturbance regime found in hardwood forests than DLC, and therefore represents progress toward an ecosystem management perspective, a wide, regular and exclusive application of selection cutting could lead to homogenization in forest structure and composition, reduction of key structural features and reduction in biological diversity at both the stand and landscape scales. Some management recommendations to the regular selection cutting are proposed.

Key words: hardwood; old-growth; selection cut; diameter-limit cut; disturbance; gaps; foliage cover; structure; snags; coarse woody debris

1.2 Introduction

One of the approaches proposed to implement ecosystem management is to gain insight from the study of natural disturbances and to use that knowledge in managing forests in order to diminish the ecological “distance” separating managed and natural systems. This way, by partially recreating natural conditions, it is thought that the probability of conserving the majority of the attributes, processes and species that are characteristic of natural ecosystems is greatly enhanced (Attiwill 1994, Bergeron *et al.* 1999). Heading towards ecosystem management can be achieved by improving our understanding of the ecosystem natural dynamics and of the impact of our activities on the ecosystem.

When compared to natural disturbance regimes, forest management regimes exhibit many differences in terms of rate of occurrence, size distribution, severity (Bergeron *et al.* 2002) and synchronicity of disturbance events. In natural systems, these disturbance regime properties are known to play a major role in determining patterns of recruitment, growth, and mortality, as well as associated structural patterns observed in forests (e.g. Bormann and Likens 1979, Runkle 1984, 1985ab).

In the northeastern hardwoods, the main natural disturbance is characterized by the regular death or fall of branches, single canopy trees or small groups of trees that creates a gradual or sudden opening in the canopy, and is known as the micro-gap regime (Bormann and Likens 1979, Runkle 1985a). Runkle (1982, 1985a) reported that the average rate of gap creation was about 1% of total land area per year, ranging from 0.5 to 2%/yr.

In the hardwood forests of Québec, single-tree selection cutting has been the most widely used harvesting system since the early 1990's (Appendix A). It is believed that this system is similar in some ways to the micro-gap regime since it creates single and multiple tree canopy openings totaling about 30% of the original basal area, with a return interval of about 25 years, i.e. a mean rate of harvest equivalent to the periodic increment.

Many recent studies have assessed the impact of harvesting in hardwood stands, by focusing on particular features such as snag and coarse woody debris (CWD) abundance (Gore and Patterson 1986, Goodburn and Lorimer 1998, Hale *et al.* 1999, McGee *et al.* 1999), tree size and structure (Hale *et al.* 1999, McGee *et al.* 1999, Solomon and Gove 1999), gap characteristics (Krasny and Whitmore 1992, Kimball *et al.* 1995), light profiles (Beaudet and Messier 2002, Beaudet *et al.* 2004), tree species composition (Majcen 1995, Hardt and Swank 1997, Hale *et al.* 1999, Solomon and Grove 1999), and tree growth (Majcen 1995, Donoso *et al.* 2000). In this study, a more global approach was used to study and compare many structural and compositional features of the hardwood forests between old-growth stands (OG) modeled under the micro-gap regime and two types of partially cut stands. Since selection cutting is relatively recent in Québec, diameter-limit cuts (DLC), a form of partial cutting that has been widely used in the past, were also characterized. This allowed us to assess what forest characteristics were susceptible to recover in the mid-term and what were the biological legacies inherited from that former type of harvesting. Synthetically, compared to the natural micro-gap regime, partial harvesting systems imply among others 1) a synchronization of canopy opening in time and 2) a removal of large quantities of wood.

First, the regeneration process responsible for the future stand composition and dynamic is influenced by canopy openings (Runkle 1984). The rate of canopy gap formation and gap characteristics (size and spatial distributions) will thus influence the species succession and structural path of the future stand (Runkle 1985b, 1989). The micro-gap regime is a type of small-scale disturbance that induces local changes in the light conditions, enhancing regeneration response in a particular location, at a particular moment. At the stand scale, this process induces heterogeneity in structure through the formation of a mosaic of various ages and growth phase patches (Runkle 1984, Lorimer 1989). Mathematically, the harvesting-intensity-to-return-interval ratio of the current selection cutting regime in Québec is similar to the natural gap formation rate (about 1% area/yr), but from a biological perspective, harvesting simultaneously affects large expanses of forests. It therefore

results in a synchronized opening of the canopy that has no natural process correspondence, except possibly heavy ice storm, moderate blowdown or low-severity fire. These more intense disturbance events occur in northeastern hardwoods and play an important role in their natural dynamics (Lorimer et Frelich 1994), but are far less frequent and affect a relatively small fraction of the landscape compared to the micro-gap regime. In this study, we only concentrated on forests shaped by the latter in their recent history.

Second, large and defective living trees as well as dead wood, whether standing (snags) or downed (stumps, CWD) have been recognized as key features for numerous species in all forest ecosystems (Harmon *et al.* 1986, Hunter 1990). Their roles are almost as diverse as their users; in the North American Northeast, more than 25% of wildlife species are associated to them (DeGraaf and Shigo 1985, DeGraaf *et al.* 1992). In addition to be involved in carbon budgets and nutrients cycling, dead wood provides nesting, denning, perching, sheltering, breeding and foraging sites for many vertebrates and invertebrates, as well as germination and growth substrate for many fungi, bryophytes and vascular plants, including tree species such as yellow birch and eastern hemlock (Harmon *et al.* 1986, McGee and Birmingham 1997).

Our main objective was thus to characterize and compare the structure and composition of OG with that of harvested stands to examine the extent of similarities and differences between managed and unmanaged hardwood forests. More specifically, we hypothesized that compared to OG, harvesting induces a higher fraction of area under gaps and a different recovery pattern which includes an enhanced relative basal area of shade-intolerant and mid-tolerant species, and a homogenization in horizontal foliage cover due to higher density of saplings in the lower strata. Also, because logging implies a large removal of live trees that are potential future large trees, defective trees, snags and CWD, we hypothesized that these elements would tend to be scarcer in harvested stands.

1.3 Methods

1.3.1 Study area and site selection

Sampling was carried out from June to August 2002 in the Outaouais region, in southwestern Québec, Canada (45°43'-46°06' N; 75°00'-75°51' W) (Fig. 1.1). The region is mostly characterized by thin glacial till deposits with frequent exposed bedrock and hills reaching about 350-400 m above sea level (Robitaille and Saucier 1998). Mean annual temperature range from 2,5 to 5°C, and mean annual precipitation is about 1000 mm, from which 25% fall as snow (Robitaille and Saucier 1998). Stands were dominated by sugar maple (*Acer saccharum* Marsh) and American beech (*Fagus grandifolia* Ehrh.) with varying but small amounts of yellow birch (*Betula alleghaniensis* Britton), ironwood (*Ostrya virginiana* Mill.), basswood (*Tilia Americana* L.), and eastern hemlock (*Tsuga canadensis* Marsh).

Nineteen study sites were chosen: Six OG, seven selection cut stands (SC) harvested in 1990 and six DLC harvested from 1969 to 1974 (Fig. 1.1). To counteract the bias possibly induced by a geographic gradient that might muddle stand characteristics (Hale *et al.* 1999), we tried to find some representative sites as close as possible from each other. No stand had experienced recent and obvious large-scale natural disturbances. Since the number of available sample sites for each stand type were limited (OG being rare, 1990's SC being relatively scarce, and 30 year-old DLC having often been already reharvested recently), we tried to get environmental characteristics (such as deposit, drainage, slope, aspect) as similar as possible while selecting the sites (Table 1.1).

OG were selected with the help of the Groupe de travail sur les écosystèmes forestiers exceptionnels or GTEFE (Exceptional forest ecosystems working group, free translation), a governmental division that identifies, locates, surveys and protects old-growth forests in Québec. According to the GTEFE (Villeneuve 2000), an old-growth forest is defined as "a forest ecosystem where dominant trees exceed well beyond their biological maturity age, considering their environment and

geographic position. Those forests show a particular dynamic, as indicated by the coexistence of living, senescent and dead trees of various sizes and by lying fallen boles of various decay stages. They have obviously been very slightly affected by human-induced disturbances in recent history” (free translation). The OG sampled were mostly part of relatively large old-growth patches and were representative of the environmental regional conditions. Mean age of dominant trees ranged from 200 to 325 years.

Selection cuts were all conducted at the end of 1990 or beginning of 1991. Stands were managed to favor the production of high quality veneer and saw logs. Low-vigor and low-quality trees were supposed to be logged in priority so the survival, quality and growth of residual trees would improve. No pre-treatment information was available, but various harvesting intensities were used since the harvested basal area, estimated from cut stumps and using dsh-dbh (diameter at stump height - diameter at breast height) conversion table (MRNFP 2003), ranged from 6.8 to 13.2 m²/ha with a mean of 8.7 m²/ha (SE = ± 0.8).

In DLC, timbered at the end of the 60's – early 70's (Table 1.1), no record of volume or species harvested were available, and stumps had often vanished. Actually, diameter-limit cuts practiced in Quebec during this period were not performed following any strict rule. Typically, only merchantable sawtimber trees or certain high value species such as white pine (*Pinus strobus* L.), red oak (*Quercus rubra* L.), yellow birch and sugar maple were removed, and bad quality trees were left behind (Majcen 1994, MRN 2000). As the authorities exerted very few control (Majcen 1994), DLC resulted in a highly variable harvest regime.

1.3.2 Sampling design and data collection

1.3.2.1 Sampling design

At each site, a sampling design consisting of four transects of 190 to 205 m disposed 50 m apart, in staggered rows, was established. That distance was

selected to make it highly improbable to sample the same gap twice given the range of gap sizes reported in the literature for northern hardwoods (see Table 1.2 for a review). The site was visited before installing the transects to avoid falling in patches of undesirable environmental conditions such as humid patches, cliffs, rocky outcrops, and to make sure that there was no particular orientation in CWD. Along each transect, five sampling points were placed 45, 50 or 55 m apart, to avoid any spatial autocorrelation, totalizing 20 sampling points per site.

1.3.2.2 Foliage cover profile

At each sampling point, a 3.57 m radius plot was established and every sapling ($1.1 \text{ cm} \leq \text{dbh} \leq 9.0 \text{ cm}$) was identified to species and its dbh assessed in 2 cm classes. Using the same radius, the vertical profile of foliage cover was visually assessed, always by the same person, using 5 foliage cover classes measured as the horizontally projected percentage of foliage cover (1: 0-5%, 2: 5-25%, 3: 25-50%, 4: 50-75%, 5: 75-100%) in four vertical layers (0.1–2 m, 2-5 m, 5–10 m, >10 m). Ecological features including slope, aspect, and whether the point was located under a gap or a closed canopy were also recorded.

1.3.2.3 Trees

For sampling trees ($\text{dbh} \geq 9.1 \text{ cm}$), an adaptation of the point-centered quarter method was used (Cottam and Curtis 1956, Upton and Fingleton 1985, Leduc and Bergeron 1998). An imaginary line represented by each transect was used to delimitate two quadrats in which the nearest tree on each side was selected. From each of these two trees, the nearest neighbor was also selected, for a total of four trees per sampling point (80 sampled trees per site). The distances from point to tree and tree to tree were noted, as well as the dbh, species and defect class, the latter being used as an indicator of potential use or colonization by organisms that utilize decaying wood, according to the following criteria (adapted from Hale *et al.* 1999): Class I (Localized, minor: Small to medium knot or canker, small lesion with exposed rot, small holes), class II (Localized, moderate: Large knot or canker, small

open split, small to medium healed split, medium lesion with exposed rot), class III (Extensive, spreading: Large knot or canker, medium open split, medium cavity, medium to large lesion with exposed rot, presence of fungi), class IV (Partially hollow or dead tree: Large split with obvious active rot, < 50% of the length of the bole visibly hollow, < 50% crown dead), class V (Hollow or moribund tree: > 50% of the length of the bole visibly hollow, > 50% crown dead).

1.3.2.4 Snags and CWD

Within a 4 m wide continuous strip along each transect, all snags (dead standing trees ≥ 1.3 m tall of dbh ≥ 5 cm) and stumps (cut or broken trees < 1.3 m tall, of diameter at stump height ≥ 5 cm) were sampled. Dead portion of live trees were not measured. Species, origin (cut, natural), diameter (diameter at 30 cm for stumps and dbh for snags), approximate height in the case of snags, and decay stage were recorded, the latter according to the following criteria (Adapted from Lee *et al.* 1997, Goodburn and Lorimer 1998, Doyon *et al.* 1999) : Class I (Recent death or fall, buds and twigs still intact, tight bark and hard wood), class II (Fine parts such as buds and twigs lacking, bark looses, wood still hard), class III (Bark mostly gone, bole periphery softened; a blade can penetrate the outer layer. In snags, tree top is often broken), class IV (Little to no bark remains, bole periphery well rotten and extends in the core; a blade can easily penetrate. In snags, bole is broken), and class V (CWD only, well-decayed wood, incorporating into the forest floor, vegetation has colonized).

Since CWD abundance exhibits a high spatial variability (Harmon *et al.* 1986, Hale *et al.* 1999), the line intersect sampling method was used (Van Wagner 1968). Multiple directions sample lines were not used, as proposed by Van Wagner (1968), since a visual inspection prior to sampling revealed no bias in CWD orientation. Before field sampling, ten 25 m sections of the transects were randomly selected, for a total of 250 m sampled at each site, where all intersecting CWD ≥ 5 cm at line intercept were sampled. Cross diameter at intersection, larger and smaller end diameter, length and decay class were measured and species was recorded.

1.3.2.5 Gaps

All portions of each transect found under gaps were measured using a clinometer for vertical projection. The canopy gap definition was used (Runkle 1982, 1991, 1992), i.e. the vertical projection of the canopy opening defined by the adjacent trees ($\text{dbh} \geq 9.1 \text{ cm}$). To be considered as a gap, the regeneration under the opening had to be less than half the height of the dominant trees, and evidences of gap maker(s)' presence (stump, snag or fallen branch or log) had to be present. Edaphic conditions creating temporary or permanent openings were not considered as gap makers, except if a gap had mixed origins including edaphic conditions.

For characterizing gaps, the same pre-selected transect sections used in CWD sampling were employed. Using an adaptation of the techniques developed by Runkle (1985b, 1992), only gaps from which at least half the vertical projection on the transect was included in those 25 m sections were characterized. This characterization was done in OG and DLC only, since the spatial pattern of openings in SC consisted in a complex network of multiple interconnected gaps, too complicated to be sampled in a meaningful way, a phenomenon also observed by Kimball *et al.* (1995) and Crome and Richards (1988). The longest axis, as well as perpendicular axes each 3 m along the latter, was measured. When the gap was less than 3 m wide, the perpendicular axis was taken in the middle of the longest axis.

Even if we avoided the most heterogeneous stands and were careful of avoiding extreme conditions in the sampled stands, some transect portions were sometimes located in very steep slopes, rocky outcrops, coniferous or very humid patches. Those transect sections and corresponding points were excluded from the analysis (Table 1.1).

1.3.3 Data analysis

Tree density was calculated using an adaptation by Pollard (1971) of Moore's (1954) estimator (T) based on the distance (r) from a randomly chosen point (n points) to the nearest plant ($n=15$ to 20 trees per site) :

$$T = (n - 1) / \left(\pi \sum_{i=1}^n r_i^2 \right)$$

Since this estimator is known to be very sensitive to deviation from random distribution of plants (Pollard 1971, Upton and Fingleton 1985), we first made sure that this assumption was fulfilled with Eberhardt's E statistic (Upton and Fingleton 1985) :

$$E = n \sum_{i=1}^n r_i^2 / \left(\sum_{i=1}^n r_i \right)^2$$

For each stand, mean dbh and tree composition were calculated using the four trees sampled per point ($n = 60$ to 80 trees per site). Stand basal area was estimated using density and dbh average.

The fraction of area under gaps was calculated as the sum of transects length under gap divided by the total transect length (Runkle 1985b, Battles *et al.* 1996). The individual gap areas were calculated using the ellipse formula (Runkle 1985b, 1992).

To compare variability in foliage cover between stand types in a particular height class, an index of homogeneity (i) inspired from Dale (1999) was developed. Within each site, for each height class, we calculated the difference of foliage cover class (x) between adjacent (horizontal and vertical) and diagonal neighbor points ($n = 111$ to 130 sampling points per stand type, Table 1.1) :

$$i = \sum \left(|x_{ij} - x_{i,j+1}| \right) + \left(|x_{ij} - x_{i+1,j}| \right) + \left(|x_{ij} - x_{i+1,j+1}| \right) + \left(|x_{ij} - x_{i+1,j-1}| \right) / n$$

The higher the index, the lower the homogeneity of foliage cover within a given height class.

Individual CWD volume (V_{ind} excluding stumps) was calculated as a truncated cone using length (L), smaller (r) and larger (R) end radius:

$$V_{ind} = \frac{1}{3} \pi L (r^2 + rR + R^2)$$

CWD volume of stands (excluding stumps) was estimated using Van Wagner's (1968) formula :

$$V = \frac{\pi^2 \sum d^2}{8L}$$

where V is the CWD stand volume, d is the cross-transect diameter and L is the transect length. To calculate total CWD volume, the stump volume calculated as a cylinder and assuming that the mean height was 50 cm was added.

1.3.4 Statistical analysis

For comparison of means between the three stand types, one-way analysis of variance (ANOVA) was performed when the assumptions of homoscedasticity and normality of the residuals were fulfilled. Some variables were log-, square root- or ranked-transformed prior to testing to meet assumptions. When ANOVA indicated a significant difference among stand types, post-hoc Tukey HSD tests were conducted to locate it. Statistical analyses were performed using JMP 4.0.2 (SAS Institute 2000).

When comparing distributions of variables among classes, the chi-square test and the Bonferroni-corrected Freeman-Tukey deviates (Sokal and Rohlf 1981, Legendre and Legendre 1998) were used.

1.4 Results

1.4.1 Gaps

DLC had the lowest percentage of land area under gaps ($4.4 \pm 1.3\%$ land area, based on the fraction of transect directly under gap), followed by OG ($9.4 \pm 1.7\%$) and finally by SC ($32.0 \pm 3.0\%$), with an average canopy opening more than three times higher than in OG. All stands types were significantly different from each other (Table 1.3).

Gap size was only sampled in OG and DLC as explained in the methodology. In OG, 32 gaps were sampled. They were $36.5 \pm 6.0 \text{ m}^2$ in size on average, ranging from 2.3 to 154.2 m^2 and generally followed an inverse J-shaped distribution characterized by a high fraction of small gaps and few large gaps (Fig. 1.2). In DLC, gaps were scarcer and smaller. Only 8 gaps crossed the total 1390 m section of transects sampled. They were $17.4 \pm 6.9 \text{ m}^2$ in size on average, ranging from 2.2 to 58.5 m^2 , and more than 50% of them were less than 10 m^2 .

1.4.2 Vertical foliage profile

Figure 1.3 reveals striking differences in the vertical distribution of foliage cover between the three stand types, especially at heights between 2 and 5 m. Overall, OG showed the most evenly distributed foliage cover among height classes. Both harvested stand types were characterized by highest foliage cover in their vertical foliage distribution corresponding to the post-harvest recruitment cohort (SC: 2-5 m, DLC: > 5 m). In both cases, the foliage cover right beneath those layers was significantly lower.

Higher homogeneity in foliage cover was not observed in the post-harvest recruitment cohort layers for both harvested stand types compared to OG (Fig. 1.3, Table 1.3). However, higher homogeneity was found in the layer right beneath those recruitment cohort layers (SC: 0-2 m, DLC 2-5 m) (Fig. 1.3).

1.4.3 Sapling diameter distribution

Sapling density was significantly different among the three stand types (Table 1.3), being about twice higher in SC and half lower in DLC compared to OG. Figure 1.4 shows the details of that distribution where the major differences occurred in the first few dbh classes. Both OG and SC showed a similar inverted J-shape pattern, typical of an uneven-aged structure with a decreasing density of individuals with increasing dbh classes, a pattern found more strongly in the SC.

1.4.4 Tree species composition

There were very few differences in tree species composition, expressed as percentage of total basal area, among stand types. Sugar maple invariably dominated in all stands, always followed by beech, with only one exception (Fig. 1.5a). The relative basal areas of these two species, as well as that of yellow birch, were not significantly different among stand types. Since no other single species had a mean relative basal area of more than 5% in any stand type, no further mean comparisons were made for individual species. However, we grouped the species according to their shade tolerance (Farrar 1996), grouped conifers, and performed mean comparison tests. No significant difference was observed for the relative basal area of shade-intolerant species and mid-tolerant species among stand types, but conifers exhibited higher basal area in DLC compared to SC, although the relative basal area of this species group is too low (less than 5 % average in every stand type) to deserve further attention.

About thirty years after DLC, the regeneration cohort constituted much of the young tree stratum. To see if the openings had been important enough to allow the establishment and growth of shade-intolerant species, the composition of trees of dbh \leq 21 cm was analyzed. Results showed that there was no greater amount of shade-intolerant species (DLC = $3.9 \pm 2.1\%$, OG = 0%), but significantly more mid-

tolerant species in DLC than OG (DLC = $11.0 \pm 3.3\%$, OG = 1.3 ± 1.3 , $P < 0.01$). In DLC, mid-tolerant species were mostly composed of yellow birch (75% of the mid-tolerant species and 8% of all species).

1.4.5 Sapling species composition

Sapling species composition showed clear differences among stand types (Fig. 1.5b). The two dominant species were still sugar maple and beech (as in the tree strata), but these two species had more similar relative basal area than what was found in canopy trees. For these two species, OG and SC showed no significant differences ($P > 0.05$) and SC significantly differed from DLC in both cases. Sugar maple had a higher relative basal area in DLC compared to SC ($P < 0.01$), whereas beech showed the reverse trend, with a lower relative basal area in DLC than SC and OG ($P < 0.01$). In contrast to the tree strata composition, minor species showed a mean basal area higher than 5% in at least one stand (yellow birch, ironwood and striped maple (*Acer pensylvanicum* L.)). Yellow birch regeneration was very scarce in OG and showed a significantly lower basal area than in SC and DLC ($P < 0.01$).

OG and DLC had similar low relative basal area of shade-intolerant species compared to SC (Fig. 1.5b) ($P < 0.01$). Results are slightly different when looking at mid-tolerant species: the relative basal area in OG was significantly lower ($P < 0.01$) from SC and DLC, the two latter being similar.

Assuming that the composition of shade-tolerant saplings is representative of the stand's future tree composition, the two main species (i.e., sugar maple and beech) showed very similar trends, regardless of stand type: sugar maple was far less represented in saplings than trees whereas beech showed the exact opposite trend (Appendix B).

1.4.6 Tree diameter distribution

Tree basal area was significantly higher in OG than SC (Table 1.3). In DLC, tree basal area was intermediate and not significantly different from OG and SC. The tree density differed significantly among stand types (Table 1.3), with DLC having the highest value followed by OG and SC. In DLC, post-harvest regeneration was responsible for a very high tree density. Mean tree dbh was significantly different among all stand types, being progressively smaller from OG to SC to DLC (Table 1.3). Compared to OG, there was a greater proportion of small dbh trees in DLC and a lower proportion of large dbh trees in DLC and SC (Fig. 1.6). In SC, the reduction of dbh was mostly caused by a decrease in large (≥ 49.1 cm) trees.

For defect classes of trees, too few observations in class 5 constrained us to group classes 4 and 5. The only significant difference in defect class distribution among stand types was found in the higher defect class (4 and 5 grouped), with SC showing less relative abundance of highly defective trees (dying crown or hollow trees) compared to OG and DLC (data not shown).

1.4.7 Snags

Density of snags was about the same in OG and SC, but was more than twice as high in DLC (Fig. 1.7). Mean snag dbh was, however, almost reduced by half in DLC compared to OG and SC, because of significantly higher abundance of small (5.0-9.0 cm) snags (Table 1.3 and Fig. 1.7). In SC, as for trees, mean snag dbh was not significantly different from OG (Table 1.3). Even though the fraction of large snags (dbh ≥ 49.1 cm) in SC was five times lower than in OG, the difference was not significant (Fig. 1.7).

In the analysis of decay stage of snags, there were very few observations in the last class (4), the very decayed snags being rare because they progressively fragment and collapse into stumps and CWD (Goodburn and Lorimer 1998) (Fig. 1.8). In DLC, most of the volume was concentrated in the first decay stage and most

of these snags were small. In SC, most volume was comprised in the second and third decay classes, whereas it was comprised mainly in the first and second classes in OG.

1.4.8 Coarse woody debris

Mean total volume of CWD, excluding stumps, was significantly lower in DLC than OG (Table 1.3). However, mean total CWD volume (stumps included), mean CWD larger end diameter as well as mean piece volume (both excluding stumps) were not significantly different between stand types (Table 1.3).

When looking at the distribution of CWD and stump volume among decay classes (Fig. 1.9), all stand types roughly showed a normal distribution pattern and OG best showed a typical pattern of continuous input. Harvested stands exhibited less flattened distribution than OG, typical of a punctual high input of dead wood in time corresponding to the anthropogenic origin dead wood cohort (Fig. 1.9). The cohorts seemed to evolve through decay stages relatively tightly in both harvested stands, with a visible delay corresponding to time spent between treatments (there was more volume of anthropogenic origins in decay class 3 in SC and more of decay class 4 in DLC).

In harvested stands, logging debris contributed to a relatively large extent to the overall volume of CWD (Fig. 1.9). In SC, almost half (44%) of CWD volume was of anthropogenic origin, from which 23% were stumps. In DLC, slashed debris were very scarce (less than 3%), whereas 36% of volume was represented by cut stumps.

1.5 Discussion

1.5.1 Canopy openings

1.5.1.1 Gaps

Comparison of the fraction of land area under gap and gap characteristics observed in this study with values reported in the literature is often tricky since many different definitions and methodologies are used (Ménard *et al.* 2001, Runkle 1992). Our results in OG are however in agreement with other studies (Table 1.2). The inverse J-shaped distribution of gap size was also observed by other authors, (Runkle 1982, 1985a, Payette *et al.* 1990, Krasny and Whitmore 1992).

Because of the definition of gap used (see methodology), our results suggest that the canopy structure was similar between DLC and OG, which was not actually the case. In DLC, the strong and synchronized opening of the canopy 30 years ago induced a synchronized closing of the canopy, mainly from below, by young trees that now form a nearly even-sized regeneration structure. According to our gap definition, the fraction of area under gaps is thus lower in DLC than in OG. However, although foliage cover was not characterized in the upper height classes (> 10 m class only), DLC's canopy obviously differed from the OG's, being very low, strikingly thinner and thus less opaque, with almost no tree crowns overlapping. Too much time has passed to still be able to detect where the old gaps were created by harvesting in DLC. The very low fraction of area under gap suggests that the gap formation rate seems to be temporarily very low, although most of the recent gaps were of natural origins, suggesting a return to a natural gap formation process.

Our observations also suggested that gaps created by main skid trails take longer to close, probably because of the destruction of pre-established regeneration and soil compaction. In SC, on average, $8.1 \pm 1.7\%$ (range from 2.8 to 13.0%) of the area was occupied by skid trails. It is thus of tremendous importance to evaluate

different strategies in future harvesting operations to limit reduction in productive areas.

In SC, 12 years after harvest, the fraction of land area under gaps was still very high. This is probably due to an initial high harvesting intensity and subsequent mortality of less vigorous trees (Bédard and Brassard 2002), as suggested by a high proportion of gaps of natural origins. Actually, the real area affected by canopy openings was far higher than the fraction of land area under gaps since the latter underestimated the extent to which the understory light regime is modified in the vicinity of the gap, particularly at the relatively high latitudes of our study sites (Canham 1985, 1989, Canham *et al.* 1990). Given that the mean area under gaps in SC 12 years after harvesting was 32%, that extended gaps (canopy gap plus the adjacent area extending to the tree trunks surrounding the gap, Runkle 1990) are about twice as large as canopy gaps (Runkle 1984) and that lateral closing probably occurred since harvest, the area influenced by modified understory light regimes might have been very extensive, i.e. of more than 50% of land area after harvest.

Studies usually characterize the size distribution of gaps at a given moment in time, which provides a snapshot of the situation but does not take into account the fact that gaps are at various stages in their development or closure process. From a management perspective, it would be more helpful to study the size range of recently formed natural canopy gaps, the between years variability in areas of recently formed gaps and the canopy closure rates to get better insights of how to emulate the natural pattern.

1.5.1.2 Sapling recruitment

Following the presumed strong and synchronized enhancement of the light regime in gaps resulting from harvesting, there was a strong response of the regeneration in both SC and DLC. This was noticeable through the peaks in the vertical distribution of foliage corresponding to the post-harvest cohort's crowns (Fig.

1.3) that differed from the fairly evenly-distributed foliage cover observed in OG. It can also be seen by the very high density of small saplings observed in SC compared to OG (Fig. 1.4) and the high proportion of small trees in DLC (Fig. 1.6). This was also observed approximately 10 years after SC (15-30% removal of basal area) by Doyon (2000).

In both types of harvested stands, this dense regeneration layer probably intercepted enough light to impede the continuity of the regeneration process in the underlying stratum, at the stand's scale (Beaudet *et al.* 2004). This is suggested by the diminution of foliage cover in the strata located right below the recruitment cohort in both cases (Fig. 1.3) as well as by the very low density of saplings in DLC (Fig. 1.4). This phenomenon probably also occurs in OG when a gap is formed, but the impact is local and restricted at the gap scale, in opposition to harvested stands where the impact is generalized and observed at the stand scale. In harvested stands, it would be interesting to follow the evolution of the dbh structure of saplings in the future to see if and when it will move towards the one observed in old-growth forests.

1.5.1.3 Homogenization of foliage cover

Results from Figure 1.3 may seem contradictory with those from gaps in Table 1.3; DLC exhibited the lowest fraction of area under gaps (Table 1.3) whereas the foliage cover above 10 m was higher in OG than DLC (Fig. 1.3). In fact, much of the trees in DLC were young, and their crowns often overlapped the 5-10 and >10 m height classes. Moreover, those young crowns were fairly translucent compared to those of older trees. Being thin and divided in two height classes, the foliage cover >10 m was consequently lower in DLC than in OG where much of tree crowns were more opaque and located well above 10 m.

Stand-level averaging of foliage cover, as presented in Figure 1.3, gives good insights but may dilute and hide ecologically interesting data (Parker and Brown

2000). The homogeneity index (see methodology) provides complementary information in terms of variability of foliage cover. Since most of the canopy openings were formed synchronously in the harvested stands, we expected that the vegetation response would also be relatively synchronous and uniform and therefore that homogeneity of foliage cover in height classes including the post-harvest recruitment cohort (SC: 2-5 m, DLC: 5-10 m, >10 m) would be higher compared to OG. However, this was not the case. Actually, the layers right beneath those post-harvest recruitment layers were found to be more homogenous in foliage cover in harvested stands than in OG. The process of homogenization in harvested stands would thus not be attributed to the opening in the canopy itself but to the resulting recruitment cohort that might intercept light in a way that homogenizes the light conditions near the forest floor and therefore the establishment and survival of the regeneration. These results contradict those of Doyon (2000) who found no difference between SC and unmanaged stands in horizontal heterogeneity within each regeneration layer. However, this is likely explained by a lower harvesting intensity in SC that would have affected a lower fraction of the area and in turn maintained natural heterogeneity.

1.5.1.4 Composition

Industrial forestry is relatively young and has probably not been intensive and performed over a long enough period to significantly modify the tree species composition. However, the characteristics of the regeneration niches created by human-induced disturbances might differ from those resulting from the micro-gap natural regime. This is suggested by a higher relative basal area of mid-tolerant species in harvested stands and of shade-intolerant species in SC (saplings) and DLC (trees of dbh \leq 21 cm). The relative basal area of these shade-intolerant species was lower than expected in harvested stands, particularly in DLC, and this is likely due to the scarcity of these species among mature trees. In regions where the shade-intolerant species tree component is higher, the post-harvest sapling composition might be different. As described in the literature by authors who

compared the species composition of logged vs. presettlement hardwood forests (Siccama 1971, McIntosh 1972, Brisson *et al.* 1988, Beaudet 2004), a higher relative basal area of sugar maple and a lower relative basal area of beech in DLC stands compared to OG was observed.

The trend observed, suggesting a shift in dominance between sugar maple and beech (towards a higher proportion of beech, Appendix B) in all stand types was not expected and exceeds the scope of this study. However, the growing concern among many foresters about an observed invasion by beech regeneration following selection cutting has to be seen from a more global perspective since the treatment was probably not responsible for this shift, the trend having also been observed in OG. A similar inversion in pole's dominance in sugar maple and beech was observed in unmanaged stands throughout the Québec province by Duchesne *et al.* (2003, pers. comm.), who suggested soil acidification and reduction in soil nutrients as a potential causes.

1.5.2 Wood removal

1.5.2.1 Tree structure

Unlike what was observed in terms of basal area, the density and dbh structure of trees were more similar between OG and SC than between OG and DLC. OG and SC were mainly composed of fewer but larger trees compared to DLC.

Although no lower mean dbh in SC compared to OG (Table 1.3) was observed, there is a significant decrease in large trees abundance after a single entry (Fig. 1.6). More severe reductions of mean dbh and abundance of large trees following selection cutting have been reported in the literature (McGee *et al.* 1999, Hale *et al.* 1999). If the harvest return interval was sufficiently long, this would not constitute a major issue, but given the actual return interval for selection cutting,

trees will probably not be allowed to develop beyond the point of commercial maturity, and the future recruitment in larger stems might not be ensured.

The reduction of highly defective trees in SC compared to the other two stand types was likely due to the preferential removal of defective and low-vigor trees or to their hastened death following harvesting. In DLC, defective trees were often left behind during harvesting, and this might explain the similar abundance of those trees in DLC compared to OG. As old remnant trees from DLC will die and as selection cutting will be applied in those stands, highly defective trees will likely become scarcer in the hardwood forests.

1.5.2.2 Snags

Many authors agree that large snags have a higher biological value than small ones (Evans and Conner 1979, McComb and Lindenmayer 1999). The high density of snags created by self thinning of the regeneration cohort or by the death of short-living species in DLC is thus of low biological interest since most of those snags are less than 10 cm. This also explains why a high fraction of the snags' volume in DLC was in the first decay stages, being mostly composed of recently dead young poles often so small that they fall on the forest floor before entering in the following snag decay classes.

In SC, it is precisely the large and most valuable snags, from a habitat perspective, that tend to become scarcer (although not significantly in this study), as reported by other authors (Table 1.2). The reduction of large living trees dbh in harvested stands and the trend towards a decrease of large dbh snags in SC are evidences of a tendency that could lead to the reduction of large snag availability in the following cutting cycles. Furthermore, selection cutting aims at minimizing tree mortality through the preferential harvest of low-vigor trees that are likely to die in the following rotation. However, in Québec, Bédard and Brassard (2002) reported that post-harvest tree mortality is higher than expected following selection cutting. The

present density of snags may thus be artificially high and only represent a punctual peak in time that might be followed by a future decrease in snag recruitment. Soil compaction, mechanical injuries (Hale *et al.* 1999), and water stresses due to canopy opening may have affected residual trees and hastened tree death. Year of death, and consequently the status of those snags (pre- or post-harvesting creation), could not be determined from the data collected. However, the peak in the abundance of snags in the second and third decay classes suggests a relatively simultaneous mortality event, which may possibly be linked to harvest-related mortality in the first years following selection cutting. This might explain why very few differences in snag abundance between SC and OG were found.

1.5.2.3 Coarse woody debris

Tree and snag characteristics directly influence CWD recruitment and features. Because of the recent application of selection cutting and of the delay of the transition from standing dead wood to CWD, few differences between SC and OG were found. However, if the anticipated reduction in abundance and size of snags in the future occurs, CWD characteristics might be affected in return. As for snags, many authors have actually already noticed a reduction in CWD volume and size in SC compared to OG (Table 1.2).

The overall normal distribution pattern of decay classes observed in OG and to a lesser extent in harvested stands is typical of a continuous input in dead wood (Fig. 1.9), as also observed in Hale *et al.* (1999), McGee *et al.* (1999) and Fraver *et al.* (2002). Residence time is actually known to be much longer in decay classes 3 and 4 than in others because of rapid decay in the beginning and at the end (Harmon *et al.* 1986), where incorporation of CWD to the ground is sometimes difficult to detect. Also, small volumes in the two first classes can be explained by the fact that CWD often comes from snags where the decay process has already begun.

Although the general distribution pattern of CWD among decay classes was similar among stand types, CWD of anthropogenic origin, particularly in stumps, was prominent in harvested stands. If logging residues were absent, the volume in each decay class as well as the total volume, except for decay class 1 in DLC, would be lower in harvested than OG (Fig. 1.9). Stumps were obviously more resistant to decay and persisted longer within the stand than logging residues as suggested by their relative large amount 30 years after DLC. As CWD decays, the continuity of recruitment in poorly decayed wood is not ensured. This is suggested by the very low amounts of CWD in class 1 in SC and in class 2 in DLC, and by the fact that in DLC, class 1 contains mainly small woody debris of low biological value yielded by self-thinning poles.

In DLC, dead wood recruitment now relies only on natural mortality, whether through death of the few old and large residual trees or the death of self-thinning young poles. This gap in recruitment continuity of large, poorly decayed CWD will be dragged through the succeeding decay stages as time goes on. The natural dynamics will return when the stand ages and allows senescence-related mortality, unless it is selectively cut before.

If selection cutting diminishes mortality rates as expected in the coming rotations, dead wood recruitment will principally rely on anthropogenic sources. Shifting from a natural continuous input to a harvested-induced periodic pulse recruitment in CWD may or may not help to maintain a relative representation of all decay stages within stands, depending on the rotation length and residence time in each decay class.

1.5.3 Stand and landscape scale potential impact of management practices on ecosystem dynamics

Even though DLC occurred longer ago than SC, more striking compositional and structural differences were observed between DLC and OG than between SC and OG. In other words, this suggests that the ecological distance between DLC and

OG is larger than between SC and OG, which agrees with what is currently advocated by foresters.

Regarding the micro-gap regime, we have inherited a forest that deviated more from its natural dynamic with diameter-limit cutting than with selection cutting. The latter therefore seems to be a better practice to maintain a more natural structure and composition, but is probably more closely related to moderate severity natural disturbance dynamics and could thus be preserved as a management tool in this perspective. From a historical perspective, some progress has therefore been achieved, but many differences remain between SC and OG, in terms of structure and composition (see Fig. 1.10 for a synthesis of differences between OG and harvested stands). With time, both harvested stand types would likely return to old-growth characteristics if they are left unmanaged for long enough, but this ability to recover from man-made disturbance (i.e. resiliency) may decline over time as we continue our management interventions.

The question from a management perspective is therefore to assess the likely long-term impact of practices such as selection cutting and propose mitigation measures. Results from this study as well as data from the literature already provide useful insights that could be used to identify the problems most likely to occur in the future. A few will be outlined here according to the two main impacts of harvesting assessed in this study.

1.5.3.1 Synchronicity in canopy opening

Beaudet *et al.* (2004) showed that following selection cutting, the light regime below 5 m is greatly modified but recovers to pre-harvest levels within a little more than a decade. This is a great example of the resiliency of the ecosystem to a treatment that may not have a serious impact on habitat in the mid-term. However, from what was found in this study, other elements may be less resilient, or may require more time to recover following selection cutting as it is currently implemented.

Under a regular selection cut harvesting regime, the forest canopy is likely to never be allowed to recover fully, and species associated with open canopy may be favored to the detriment of closed canopy species (Crome and Richards 1988, Bourque and Villard 2001). Moreover, the horizontal homogenization of foliage stratification in specific strata may induce a reduction or increase, dependent of the time elapsed since disturbance, of species that require specific densities of foliage in specific strata. For instance, species requiring a dense shrub layer for nesting, as the black-throated blue warbler (*Dendroica caerulescens*) may be favoured in the short term following selection cutting (Bourque and Villard 2001). However, as the post-disturbance cohort grows, the very open shrub layer will likely not constitute a good habitat until the next entry.

1.5.3.2 Removal of wood

The combination of a lower abundance of large living trees in harvested stands and a reduction in highly defective tree abundance in SC may result in a reduced availability of habitat for species requiring these features (Evans and Conner 1979, Hagan and Grove 1999, Hale *et al.* 1999). Not only is large tree size necessary for large vertebrates, but large trees, snags and CWD provide unique micro-habitats, persist longer in the ecosystem and may thus be used more extensively than smaller ones (Harmon *et al.* 1986, Swallow *et al.* 1986, Doyon *et al.* 1999, Hale *et al.* 1999, Fraver *et al.* 2002).

No difference in total abundance of snags and CWD between SC and OG was found, but only one treatment was applied. One must therefore be concerned that repeated selection cutting would result in a reduction in both the quantity and quality (i.e. large trees) of dead woody material, as many authors have observed in regions that experienced several rotations (Table 1.2). Furthermore, a continuous supply of dead wood is crucial to provide woody material in all decay stages. Different species use different stages of wood decay (Harmon *et al.* 1986, Andersson and Hytteborn 1991, Runkle 1991, Petranka *et al.* 1994) or combine

many stages for different life-history functions (McComb and Muller 1983), and they would be deprived temporarily of habitats if dead wood recruitment was not continuous in time.

1.5.3.3 Impact at the landscape scale

In unmanaged northeastern hardwoods, the micro-gap regime disturbance interval is long relative to the recovery time and only a small fraction of land is affected at a time (i.e. gap scale) (Turner *et al.* 1993). Those types of conditions are considered to provide a landscape equilibrium state (Turner *et al.* 1993). Even though the SC studied have not undergone a complete cutting cycle, it is highly unlikely that the stand will have recovered to old-growth characteristics before the next entry. In other words, time of recovery is longer than average logging return interval, and a relatively large land area is affected simultaneously (i.e. stand scale). According to Turner *et al.* (1993), if the disturbance is sufficiently large and/or frequent, the system may become unstable and change its trajectory from its original path.

At the landscape level, for a broadly implemented disturbance regime such as selection cutting, one of the major consequences of this discrepancy between recovery time and logging return interval might be to lead to an excess of relatively open stands and a deficit in mature and old-growth stand characteristics (Turner *et al.* 1993, Haeussler and Kneeshaw 2003). It thus allows few temporal refuges for old-growth-dwelling wildlife species for which the survival may be impaired. Furthermore, tolerance elasticity of some disturbance-sensitive species may be shorter than what is required by a forest stand to recover. If no adequate habitat is available at hand, given the life history traits of a species (ex. dispersal abilities, home range), the species may be eliminated temporarily or in the long term from the system (Siitonen and Martikainen 1994).

The process of regulating stand age-class distribution has been recognised as problematic in even-aged management of the boreal forest since it allows no space for overmature or old-growth stands (Haeussler and Kneeshaw 2003). This is less evident in an uneven-aged management context since forest cover always remains, but the same concept applies: Given that about 30% of the basal area is harvested at each entry using a selection cutting system, all trees will have been harvested within four entries, which allow no possibility for trees to grow beyond the point of commercial maturity.

Not only does selection cutting not replicate the full range of variability observed in natural conditions, but it restricts the range of variability in disturbances (frequency, size, severity). Implementation of a single management strategy risks to lead to a homogenization of the forest (Haeussler and Kneeshaw 2003). A wide, exclusive and regular application of selection cutting as currently used in most of the hardwood forests of Québec, will likely contribute to a homogenization of stands' structure and composition, yield a reduced forest mosaic diversity at the landscape scale, and possibly impoverish regional species diversity in some groups (Doyon 2000). In its present version, selection cutting can be insidious in the long term by cumulating small effects that could affect the long-term integrity of the forest.

1.5.4 Management recommendations

To address the issue of shorter logging intervals relative to recovery time, we recommend, given the current practice, allowing portions of forest to undergo extended logging return interval. This would provide continuous supply in old-growth characteristics in the landscape by maintaining relatively closed conditions and allowing some trees to get bigger and die before being harvested.

On a stand basis, to mitigate the likely shortage in large trees and highly ecologically valuable dead wood, we recommend to implement a variant of the tree retention approaches advocated in clearcut systems, whether by leaving some

existing snags and large living trees dispersed within stands (Goodburn and Lorimer 1998, Hale *et al.* 1999, McGee *et al.* 1999, Fraver *et al.* 2002) or by leaving small patches of intact forest within harvested areas that permit conservation and production of these structural elements (Hagan and Grove 1999).

Obviously, these recommendations probably imply increased harvesting costs and a lower exploitable volume. To be implemented, an alternative landscape management model would be necessary, as proposed by many authors with the landscape allocation concept, being triad or other (Hunter 1990, Messier and Kneeshaw 1999, Seymour *et al.* 2002). Losses in volume and higher costs associated with extensive management could be compensated by intensive wood production on restricted areas while an extended network of protected areas could be implemented.

Finally, this article only deals with the micro-gap regime at the stand scale. This small-scale disturbance type is the main natural disturbance in the northeastern hardwoods, but other types of less frequent but more intense and larger-scale natural disturbances that are also part of the range of natural events also occur (i.e. ice storms, fires, windstorms). Trying to gain insight from those disturbances in our management would help to preserve landscape diversity as it naturally occurs. However, given that most of these moderate and high severity disturbances are uncontrollable, managers should ensure that their natural representativeness is not excessively multiplied.

1.6 Acknowledgments

We are indebted to S. Côté and P. Côté for assistance in fieldwork and data entry. We also thank N. Villeneuve for helpful comments on the proposal and providing access and information about old-growth stands, P. Cyr and G. Forest from the MRN who provided helpful information about history and location of harvested sites. C. Lorimer, F. Doyon as well as J.-M. Roberge provided helpful comments on

the manuscript. Funding for this project was provided by the Natural Sciences and Engineering Research Council of Canada (NSERC) through a scholarship to the first author and a grant to C. Messier.

1.7 References

Andersson, L.I. and Hytteborn, H. 1991. Bryophytes and decaying wood - A comparison between managed and natural forest. *Holarctic Ecol.* 14: 121-130.

Angelstam, P.K. 1998. Maintaining and restoring biodiversity in European boreal forests by developing natural disturbance regimes. *J. Veg. Sc.* 9: 593-602.

Attwill, P.M. 1994. The disturbance of forest ecosystems: the ecological basis for conservative management. *For. Ecol. Manage.* 63: 247-300.

Battles, J.J., Dushoff, J.G., and Fahey, T.J. 1996. Line intersect sampling of forest canopy gaps. *For. Sci.* 42: 131-138.

Beudet, M. 2004. Modélisation des effets du jardinage de différentes intensités sur les érablières en Estrie. Rapport final de projet CRSNG-industriel présenté à Domtar, 108 pp.

Beudet, M. and Messier, C. 2002. Variation in canopy openness and light transmission following selection cutting in northern hardwood stands: an assessment based on hemispherical photographs. *Agri. For. Meteo.* 110: 217-228.

Beudet, M., Messier, C., and Leduc, A. 2004. Understory light profiles in northern hardwood stands: recovery process following selection cutting. *J. Ecol.* 92:328-338.

Bédard, S. and Brassard, F. 2002. Les effets réels des coupes de jardinage dans les forêts publiques du Québec en 1995 et 1996. Ministère des ressources naturelles, Québec, 15 p.

Bergeron, Y., Harvey, B., Leduc, A., and Gauthier, S. 1999. Stratégies d'aménagement forestier qui s'inspirent de la dynamique des perturbations naturelles: considérations à l'échelle du peuplement et de la forêt. *For. Chron.* 75: 55-61.

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

Bormann, F.H. and Likens, G.E. 1979. Pattern and process in a forested ecosystem. Springer-Verlag, New-York, 253 p.

- Bourque, J. and Villard, M.-A. 2001. Effects of selection cutting and landscape-scale harvesting on the reproductive success of two neotropical migrant bird species. *Cons. Biol.* 15(1):184-195.
- Brisson, J., Bergeron, Y., and Bouchard, A. 1988. Les successions secondaires sur sites mésiques dans le Haut-Saint-Laurent, Québec, Canada. *Can. J. Bot.* 66: 1192-1203.
- Canham C.D. 1985. Suppression and release during canopy recruitment in *Acer saccharum*. *Bull. Torrey Bot. Club* 112: 134-145.
- Canham, C.D. 1989. Different responses to gaps among shade-tolerant tree species. *Ecology* 70: 548-550.
- Canham, C.D., Denslow, J.S., Platt, W.J., Runkle, J.R., Spies, T.A., and White, P.S. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Can. J. For. Res.* 20: 620-631.
- Crome, F.H.J. and Richards, G.C. 1988. Bats and gaps: microchiropteran community structure in a Queensland rain forest. *Ecology* 69: 1960-1969.
- Cottam, G. and Curtis, J.T. 1956. The use of distance measures in phytosociological sampling. *Ecology* 37(3):451-460.
- Dahir, S.E. and Lorimer, C.G. 1996. Variation in canopy gap formation among developmental stages of northern hardwood stands. *Can. J. For. Res.* 26: 1875-1892.
- Dale, M.R.T. 1999. *Spatial pattern analysis in plant ecology*. Cambridge University Press, Cambridge, 326 p.
- DeGraaf, R.M. and Shigo, A.L. 1985. Managing cavity trees for wildlife in the Northeast. General technical report NE-101.
- DeGraaf, R.M., Yamasaki, M., Leak, W.B., and Lanier, J.W. 1992. New England wildlife: management of forest habitats. U.S. Forest service general technical report NE-144.
- Donoso, P.J., Nyland, R.D., and Zhang, L. 2000. Growth of saplings after selection cutting in northern hardwoods. *NJAF*. 17: 149-152.
- Doyon, F. 2000. Effets de différents types de récolte forestière sur les oiseaux en forêt feuillue à l'échelle de l'habitat et du paysage. PhD Thesis, Université du Québec à Montréal, Montréal, Que.
- Doyon, F., Savard, J.-P.L., Gagnon, D., and Giroux, J.-F. 1999. Snag characteristics

and use as woodpecker drilling sites in harvested and non-harvested northern hardwood forests. Pp. 103-114 *in* Diamond, A. W. and Nettleship, D. N. (eds), *Biology and conservation of forest birds*. Society of Canadian ornithologists, Fredericton, New-Brunswick.

Duchesne, L., Ouimet, R., Moore, J.-D. and Paquin, R. 2003. Diminution de l'abondance de l'éérable à sucre au profit du hêtre à grandes feuilles. Pp.191-200 *in* Grondin, P. and Cimon, A. (eds). *Les enjeux de biodiversité relatifs à la composition forestière*. Ministère des Ressources naturelles du Québec, Direction de la recherche forestière et Direction de l'environnement forestier.

Evans, K. E. and Conner, R. N. 1979. Snag management. pp. 214-225 *in* DeGraaf, R. M. (ed) *Management of north central and northeastern forests for nongame birds*. General technical report NC-51. U. S. Department of Agriculture, Forest service, St-Paul, Minnesota.

Farrar, J. L. 1996. *Les arbres du Canada*. Fides, St-Laurent, 502 p.

Forrester, J.A. and Runkle, J.R. 2000. Mortality and replacement patterns of an old-growth Acer-Fagus woods in the holden arboretum, northeastern Ohio. *Am. Midl. Nat.* 144: 227-242.

Franklin, J.F. 1993. Preserving biodiversity: species, ecosystems, or landscapes? *Ecol. Appl.* 3: 202-205.

Fraver, S., Wagner, R.G., and Day, M. 2002. Dynamics of coarse woody debris following gap harvesting in the Acadian forest of central Maine, U.S.A. *Can. J. For. Res.* 32: 2094-2105.

Goodburn, J.M. and Lorimer, C.G. 1998. Cavity trees and coarse woody debris in old-growth and managed northern hardwood forests in Wisconsin and Michigan. *Can. J. For. Res.* 28: 427-438.

Gore, F.A. and Patterson III, W.A. 1986. Mass of downed wood in northern hardwood forests in New Hampshire: Potential effects of forest management. *Can. J. For. Res.* 16: 335-339.

Haeussler, S. and Kneeshaw, D. 2003. Comparing forest management to natural processes. *In* *Towards sustainable management of the boreal forest*. Burton, P.J., Messier, C., Smith, C. and Adamowicz, W.L. (eds). NRC Research Press, Ottawa, Ontario, 1039 p.

Hagan, J.M. and Grove, S. L. 1999. Bird abundance and distribution in managed and old-growth forest in Maine. Report MM-9901, Manomet Center for Conservation Sciences, Maine, 20 p.

Hale, C.M., Pastor, J., and Rusterholz, K.A. 1999. Comparison of structural and

compositional characteristics in old-growth and mature, managed hardwood forests of Minnesota, U.S.A. *Can. J. For. Res.* 29: 1479-1489.

Hansen, A.J., Spies, T.A., Swanson, F.J., and Ohmann, J.L. 1991. Conserving biodiversity in managed forests. *BioScience* 41: 382-392.

Hardt, R.A. and Swank, W.T. 1997. A comparison of structural and compositional characteristics of southern Appalachian young second-growth, maturing second-growth and old-growth stands. *Nat. Areas J.* 17: 42-51.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K.Jr., and Cummins, K.W. 1986. Ecology of coarse woody debris in temperate ecosystems. *Advances in ecological research* 15: 133-302.

Hunter, M. L. Jr. 1990. *Wildlife, forests, and forestry*. Prentice Hall, Englewood Cliffs, N. J., 370 p.

Kimball, A.J., Withman, J.W., Rudnicky, J.L., White, A.S., and Hunter, M.L.Jr. 1995. Harvest-created and natural canopy gaps in an oak-pine forest in Maine. *Bull. Torrey Bot. Club* 122: 115-123.

Krasny, M.E. and Whitmore, M.C. 1992. Gradual and sudden forest canopy gaps in Allegheny northern hardwood forests. *Can. J. For. Res.* 22: 139-143.

Leduc, A. and Bergeron, Y. 1998. Traits distinctifs des forêts anciennes se développant sur sites mésiques dans le sud du Québec. Direction de l'information et de la coordination de la recherche, Ministère de l'environnement et de la faune et Groupe de recherche en écologie forestière interuniversitaire, Université du Québec à Montréal, Montréal, 139 p.

Lee, P.C., Crites, S., Nietfeld, M., Nguyen, H.V., and Stelfox, J.B. 1997. Characteristics and origins of deadwood material in aspen-dominated boreal forests. *Ecol. Appl.* 7: 691-701.

Legendre, P. and Legendre, L. 1998. *Numerical ecology*. Second english edition. Elsevier, Amsterdam, 853 p.

Lorimer, C.G. 1989. Relative effects of small and large disturbances on temperate hardwood forest structure. *Ecology* 70: 565-567.

Lorimer, C.G. and Frelich, L.E. 1994. Natural disturbance regimes in old-growth northern hardwoods. *J. For.* 33-8.

Majcen, Z. 1994. Historique des coupes de jardinage dans les forêts inéquiennes au Québec. *Rev. For. Fr.* 4: 375-384.

- Majcen, Z. 1995. Résultats après 10 ans d'un essai de coupe de jardinage dans une érablière. Québec. Mémoire de recherche forestière no 122, Direction de la recherche forestière, Ministère des Ressources naturelles, Gouvernement du Québec, Québec, 32 p.
- McComb, W.C. and Muller, R.N. 1983. Snag densities in old-growth and second-growth Appalachian forests. *J. Wildl. Manage.* 47: 376-382.
- McComb, W. and Lindenmayer, D. 1999. Dying, dead and down trees. pp. 335-372 *In* Hunter, M. L. Ed. *Maintaining biodiversity in forest ecosystems*. Cambridge University Press, Cambridge, 698 p.
- McGee, G.G. and Birmingham, J.P. 1997. Decaying logs as germination sites in northern hardwood forests. *North. J. Appl. For.* 14: 178-182.
- McGee, G.G., Leopold, D.J., and Nyland, R.D. 1999. Structural characteristics of old-growth, maturing, and partially cut northern hardwood forests. *Ecol. Appl.* 9: 1316-1329.
- McIntosh, R.P. 1972. Forests of the Catskill mountains, New York. *Ecol. Mono.* 42: 143-161.
- Ménard, A., Dubé, P., Bouchard, A., and Marceau, D.J. 2001. Release episodes at the periphery of gaps: A modelling assessment of gap impact extent. *Can. J. For. Res.* 32: 1651-1661.
- Messier, C.M. and Kneeshaw, D.D. 1999. Thinking and acting differently for sustainable management of the boreal forest. *For. Chron.* 75(6):929-938.
- Moore, P.G. 1954. Spacing in plant populations. *Ecology* 35: 222-227.
- MRN (Ministère des ressources naturelles) 2000. *La forêt feuillue... Au coeur du Québec habité!* Ministère des Ressources naturelles, Gouvernement du Québec, Québec, 8 p.
- MRNFP (Ministère des ressources naturelles, faunes et parcs), 2003. *Méthodes d'échantillonnage pour les inventaires d'intervention (inventaire avant traitement) et pour les suivis des interventions forestières (après martelage, après coupe et années antérieures) Exercice 2004-2005*, Forêt Québec, Direction de l'assistance technique, Québec, 437 p.
- Parker, G.G. and Brown, M.J. 2000. Forest canopy stratification - Is it useful? *Am. Nat.* 155: 473-484.
- Payette, S., Filion, L., and Delwaide, A. 1990. Disturbance of a cold temperate forest as deduced from tree-ring patterns: the Tantaré Ecological Reserve, Québec. *Can. J. For. Res.* 20: 1228-41.

- Petranka, J.W., Brannon, M.P., Hopey, M.E., and Smith, C.K. 1994. Effects of timber harvesting on low elevation populations of southern Appalachian salamanders. *For. Ecol. Manage.* 67: 135-147.
- Pollard, J.H. 1971. On distance estimators of density in randomly distributed forests. *Biometrics* 27: 991-1002.
- Robitaille, A. and Saucier, J.-P. 1998. *Paysages régionaux du Québec méridional. Les publications du Québec, Ste-Foy*, 213 p.
- Runkle, J.R. 1982. Patterns of disturbance in some old-growth mesic forests of eastern North America. *Ecology* 63: 1533-1546.
- Runkle, J.R. 1984. Development of woody vegetation in treefall gaps in a beech-sugar maple forest. *Holarctic Ecol.* 7: 157-164.
- Runkle, J.R. 1985a. Disturbance regimes in temperate forests. Pp. 17-33 *In* Pickett, S. T. A. and White, P. S. *The ecology of natural disturbance and patch dynamics.* Academic Press, New-York.
- Runkle, J.R. 1985b. Comparison of methods for determining fraction of land area in treefall gaps. *Forest Sci.* 31: 15-19.
- Runkle, J.R. 1989. Synchrony of regeneration, gaps, and latitudinal differences in tree species diversity. *Ecology* 70: 546-547.
- Runkle, J.R. 1990. Gap dynamics in an Ohio *Acer-Fagus* forest and speculations on the geography of disturbance. *Can. J. For. Res.* 20: 632-641.
- Runkle, J.R. 1991. Gap dynamics of old-growth eastern forests: Management implications. *Nat. Areas J.* 11: 19-25.
- Runkle, J.R. 1992. Guidelines and sample protocol for sampling forest gaps. General technical report PNW-GTR-283. United States Department of Agriculture, Pacific Northwest Research Station. Portland, Oregon, USA, 44 p.
- SAS Institute Inc. 2000. JMP 4.0.2. SAS Institute Inc., Cary, NC.
- Seymour, R.S., White, A.S., and de Maynadier, P.G. 2002. Natural disturbance regimes in northeastern North America - evaluating silvicultural systems using natural scales and frequencies. *For. Ecol. Manage.* 155:357-367.
- Siccama, T.G. 1971. Presettlement and present vegetation in northern Vermont with special reference to Chittenden County. *Am. Midl. Nat.* 85: 153-172.
- Siitonen, J. and Martikainen, P. 1994. Occurrence of rare and threatened insects living on decaying *Populus tremula*: A comparison between Finnish and Russian

Karelia. *Scand. J. For. Res.* 9: 185-191.

Sokal, R.R. and Rohlf, F.J. 1981. *Biometry*. Freeman, New-York, 859 p.

Solomon, D.S. and Grove, J.H. 1999. Effects of uneven-age management intensity on structural diversity in two major forest types in New-England. *For. Ecol. Manage.* 114: 265-74.

Swallow, S.K., Gutiérrez, R.J., and Howard, R.A. 1986. Primary cavity-site selection by birds. *J. Wildl. Manage.* 50: 576-583.

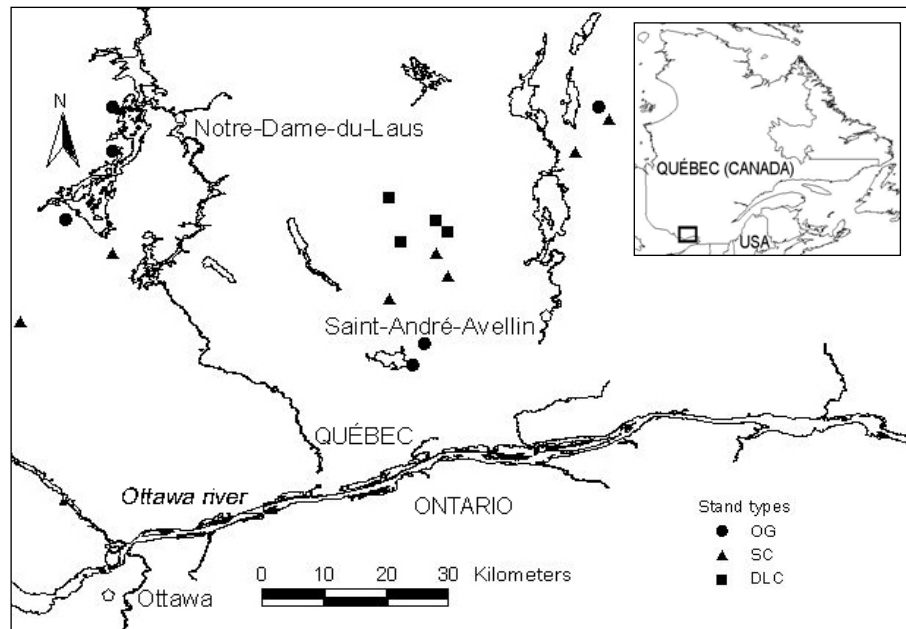
Turner, M.G., Romme, W.H., Gardner, R.H., O'Neill, R.V., and Kratz, T.K. 1993. A revised concept of landscape equilibrium: Disturbance and stability scales landscapes. *Landscape ecol.* 8: 213-227.

Upton, G.J.G. and Fingleton, B. 1985. *Spatial data analysis by example - Volume 1 Point pattern and quantitative data*. John Wiley & Sons, Toronto, 410 p.

Van Wagner, C.E. 1968. The line intersect method in forest fuel sampling. *For. Sci.* 14: 21-26.

Villeneuve, N. 2000. Critères et indicateurs permettant la reconnaissance, la localisation et l'évaluation des forêts anciennes à des fins de conservation: Partie 1: Forêt tempérée, sous-zone de forêt feuillue. Ministère des ressources naturelles, direction de l'environnement forestier, Québec, 214 p.

Figure 1.1 Study area showing location of old-growth (OG, n = 6), selection cut (SC, n = 7) and diameter-limit cut stands (DLC, n = 6).



Note: Since diameter-limit stands were very close to each other, they do not all appear separately here.

Figure 1.2 Canopy gap size distribution in old-growth stands.

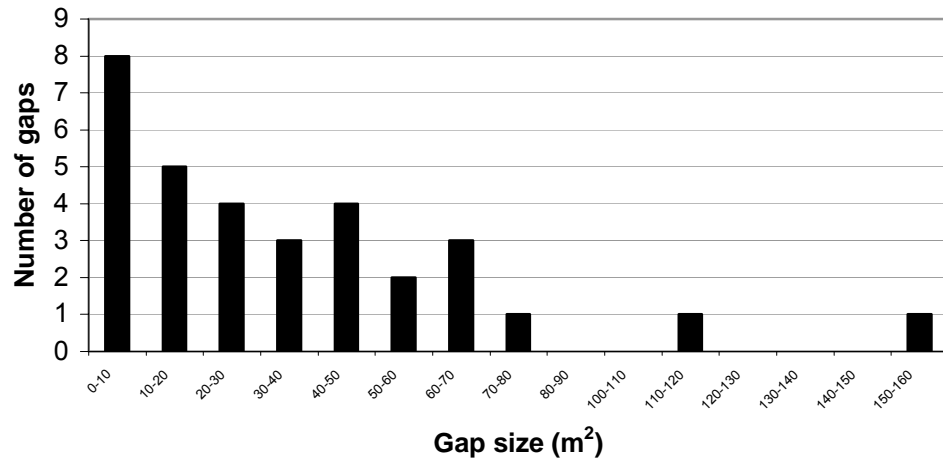
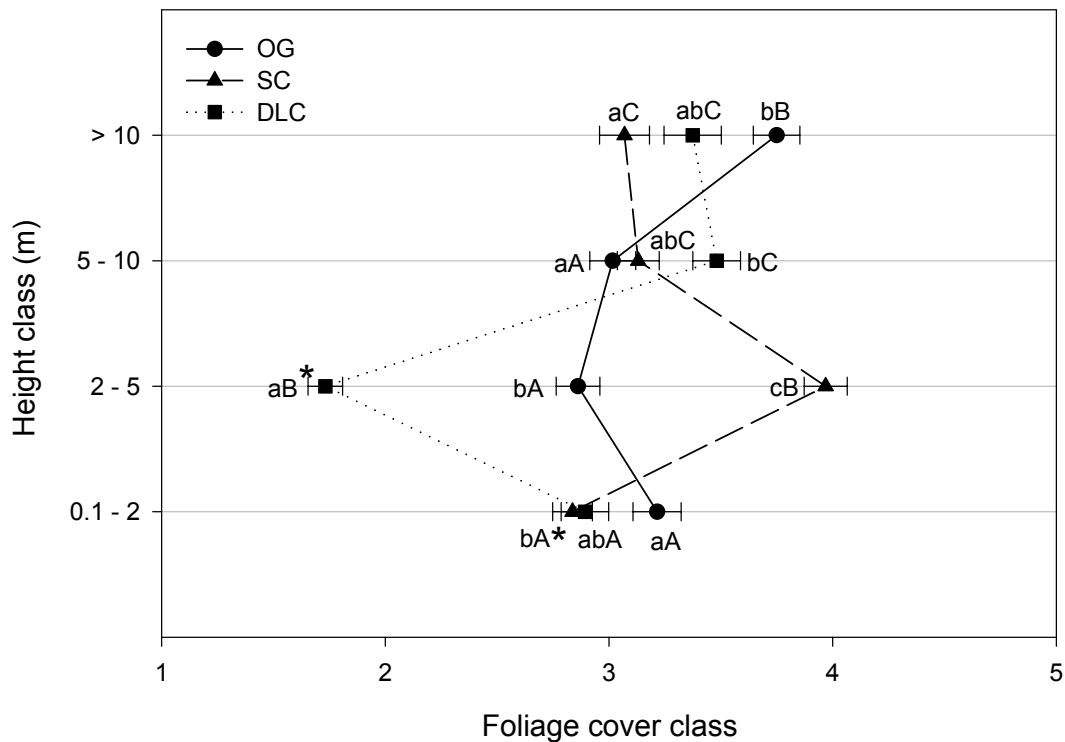


Figure 1.3 Foliage cover profile for old-growth (OG, $n = 114$ sampled points), selection cut (SC, $n = 130$ sampled points) and diameter-limit cut stands (DLC, $n = 111$ sampled points) (± 1 SE).

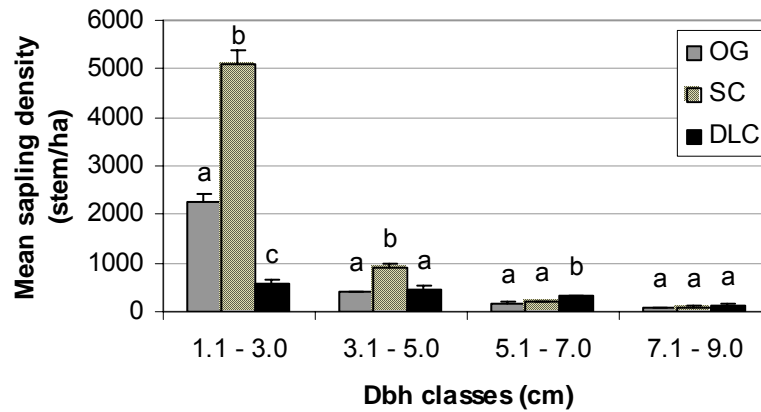


Note: Foliage cover classes are (1) 0-5%; (2) 5-25%; (3) 25-50%; (4) 50-75%; (5) 75-100%.

Different lower-case letters indicate significantly different values among stand types within a given height class at $P < 0.05$, using one-way ANOVA on rank-transformed data (inter-stand type comparison). Different capital letters indicate significantly different values among height classes within a given stand type at $P < 0.05$, using one-way ANOVA on rank-transformed data (intra-stand type comparison).

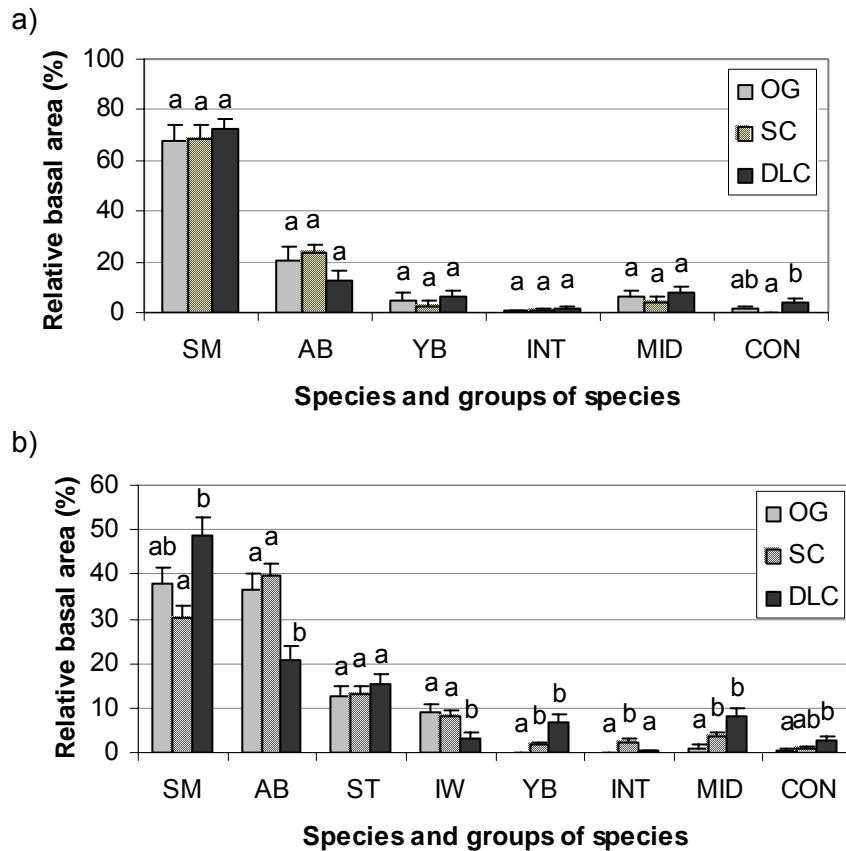
* Foliage cover is more homogenous than in the old-growth stands within this height class ($P < 0.05$).

Figure 1.4 Dbh distribution of sapling density for old-growth (OG, n = 1331saplings), selection cut (SC, n = 3281 saplings) and diameter-limit cut (DLC, n = 644 samplings) stands (± 1 SE).



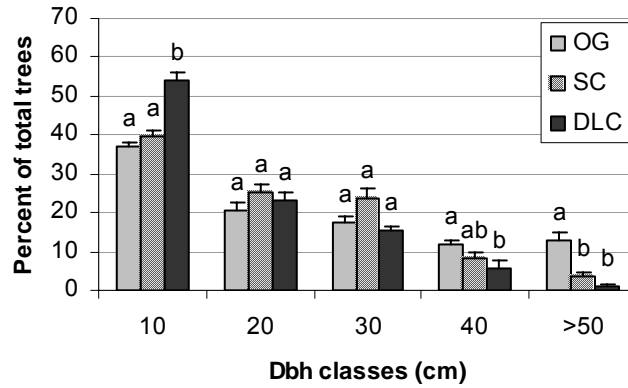
Note: Different letters indicate significantly different values among stand types within a given dbh class at $P < 0.05$, using one-way ANOVA on rank-transformed data.

Figure 1.5 Relative basal area of main species and groups of species for a) trees and b) saplings in old-growth (OG, n = 456 trees, 1331 saplings), selection cut (SC, n = 520 trees, 3281 saplings) and diameter-limit cut (DLC, n = 444 trees, 644 sapplings) stands (± 1 SE). Only species with more than 5% mean basal area in at least one stand type are presented.



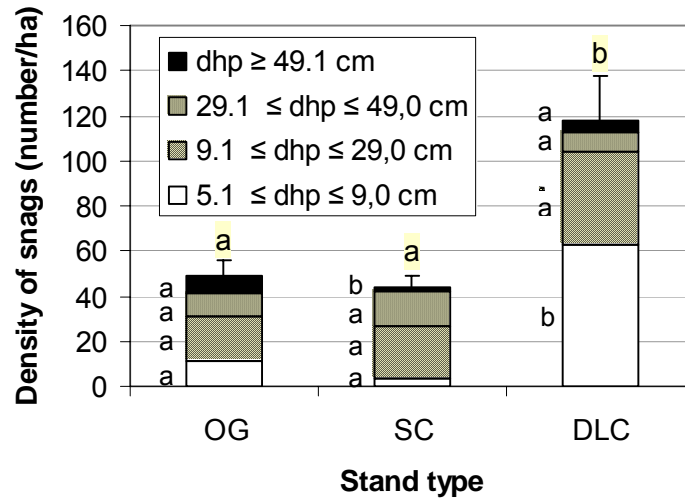
Note : Different letters indicate significantly different values among stand types for a given species at $P < 0.05$, using one-way ANOVA for tree species and one-way ANOVA on rank-transformed data for sapling species. Species and group of species: SM, sugar maple; AB, American beech; YB, yellow birch; ST, striped maple; IW, ironwood; INT, shade-intolerant species: black cherry (*Prunus serotina* Ehrh.), red oak, white birch (*Betula papyrifera* Marsh.), pine cherry (*Prunus pensylvanica* L.f.), bigtooth aspen (*Populus grandidentata* Michx.), trembling aspen (*Populus tremuloides* Michx.), and willow species (*Salix* sp.); MID, mid-tolerant species: yellow birch, red maple (*Acer rubrum* L.), white ash (*Fraxinus Americana* L.), black ash (*Fraxinus nigra* Marsh.) and American elm (*Ulmus Americana* L.); CON, Coniferous species: eastern hemlock, balsam fir (*Abies balsamea* (L.) Mill.), spruce species (*Picea* sp.).

Figure 1.6 Tree dbh distribution for old-growth (OG, n = 456 trees), selection cut (SC, n = 520 trees) and diameter-limit cut stands (DLC, n = 444 trees) (± 1 SE) using 10 cm classes.



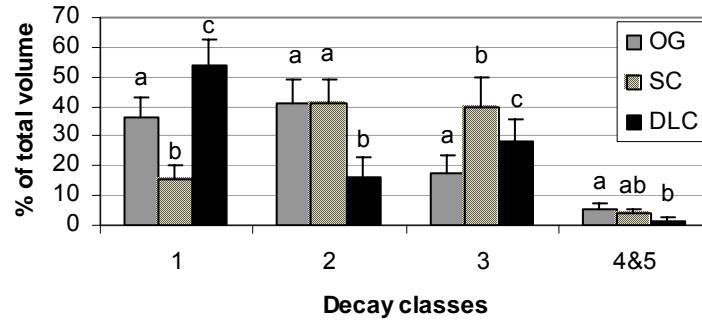
Note: Different letters indicate significantly different values among stand types within a given dbh class at $P < 0.05$, using the Bonferroni corrected Freeman-Tukey deviates procedure.

Figure 1.7 Snag density by dbh class in old-growth (OG, n = 91 snags), selection cut (SC, n = 95 snags) and diameter-limit cut stands (DLC, n = 216 snags) (± 1 SE).



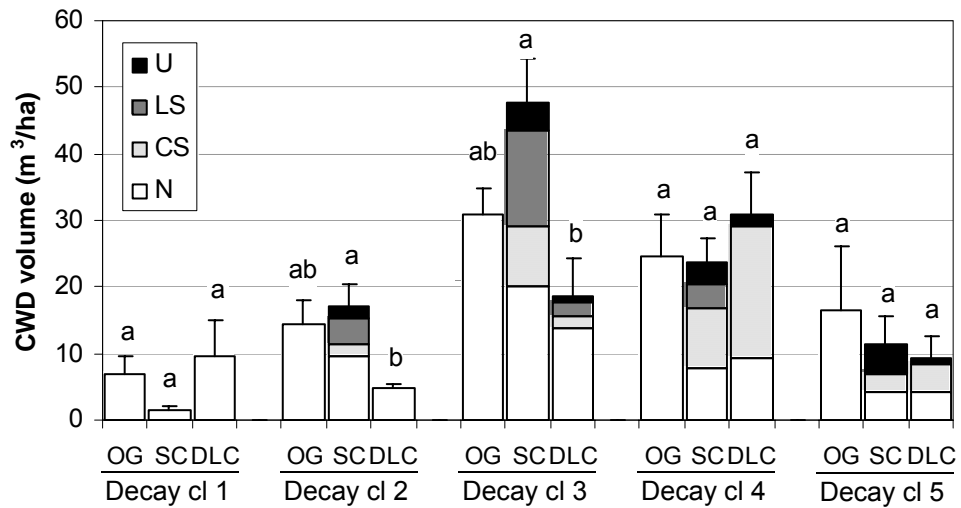
Note: Different letters over columns indicate significantly different mean values among stand types at $P < 0,05$, using one-way ANOVA. Different letters adjacent to size class indicate significantly different mean values among stand types within a given dbh class at $P < 0.05$, using one-way ANOVA.

Figure 1.8 Decay-class distribution of snag volume in old-growth (OG, n = 91 snags), selection cut (SC, n = 95 snags) and diameter-limit cut (DLC, n = 216 snags) stands (± 1 SE).



Note: Different letters indicate significantly different values among stand types within a given decay class at $P < 0.05$, using the Bonferroni corrected Freeman-Tukey deviates procedure.

Figure 1.9 Decay-class distribution of CWD (fallen woody debris, logging slash and stumps) in old-growth (OG, n = 357 CWD), selection cut (SC, n = 676 CWD) and diameter-limit cut stands (DLC, n = 395 CWD) (± 1 SE) by origin; N, natural; U, unknown; CS, cut stump; LS, logging slash.



Note: Different letters indicate significantly different values among stand types within a given decay class at $P < 0.05$, using one-way ANOVA on rank-transformed data.

Figure 1.10 Synthesis of observed and expected differences between a) old-growth and b) partially harvested stands.

a)



b)



Note: Compared to partially harvested stands, old-growth stands include 1) Large and defective living trees; 2) Large snags and CWD; 3) Few openings. Compared to old-growth, partially harvested stands include 4) Stratified under story foliage distribution due to high foliage cover from recruitment cohort; 5) Homogeneity in underlying foliage layer adjacent to recruitment cohort.

Table 1.1 Characteristics of study sites and locations

Site name ^a and abbreviation used	Stand type ^b	Deposit ^c	Drainage ^d	Slope ^e	Main aspect	Year of last known harvest	% area under gaps ^f	Coordinates	Nb sampled points	Transect length sampled (sections length) ^g
Old-growth stands (n=6)										
La Blanche Lake	SM	R	2	D	SE	-	13	45°43' N, 75°17' W	19	745 (250)
Britannique Lake	SMTH	R	2	C	NE	-	15	45°45' N, 75°16' W	19	740 (250)
Marie Lefranc Lake	SM	1aR	2	D	N	-	8	46°06' N, 75°01' W	20	795 (250)
O'Hara Lake	SM	1aR	3	C	S	-	8	46°02' N, 75°43' W	20	795 (250)
Petit Poisson Blanc Lake	SMTH	1a	3	B	SW	-	3	46°06' N, 75°43' W	16	740 (225)
Tucker Lake	SMTH	R	2	D	NE	-	7	45°56' N, 75°47' W	20	795 (250)
Selection cuts (n=7)										
Clark Lake	SM	1aR	3	D	SW	1990	33	45°53' N, 75°15' W	18	750 (225)
Escalier Lake	SMTH	1aR	2	C	W	1990	30	45°53' N, 75°43' W	20	795 (250)
Falcon Lake	SM	1aR	2	D	SW	1990	25	45°49' N, 75°19' W	15	707 (225)
Marie Lefranc Lake	SM	1aR	3	D	E	1990	32	46°05' N, 75°00' W	20	795 (250)
Petit Preston Lake	SM	1aR	3	C	N	1990	48	46°02' N, 75°03' W	20	795 (250)
St-Charles Lake	SM	R	2	D	NE	1990	22	45°47' N, 75°51' W	20	795 (250)
Vert Lake	SMTH	1aR	2	D	SW	1990	32	45°51' N, 75°14' W	17	775 (250)

^aSites were named according to the nearest lake or pond.

^bAccording to the Québec's MRN classification rules. SM, sugar maple occupies $\geq 66\%$ of the basal area; SMTH (sugar maple and shade-tolerant hardwood), sugar maple is the main species (33%-66% of the basal area), and shade-tolerant hardwood species occupy 33%-50 % of the basal area.

^cR, No or very thin glacial till; 1aR, Thin glacial till (< 50 cm); 1a, Thick glacial till (> 1m).

^d2, Well drained; 3, Moderately well drained (six classes total).

^eB:4-8%; C:9-15%; D:16-30%.

^fPercentage of transect length located under gaps.

^gActual portion of the transect sampled due to extreme environmental conditions (sections designed for CWD and gap sampling)

Table 1.1 Characteristics of study sites and locations (continued)

Site name ^a and abbreviation used	Stand type ^b	Deposit ^c	Drainage ^d	Slope ^e	Main aspect	Year of last known harvest	% area under gaps ^f	Coordinates	Nb Sampled points	Transect length sampled (sections length) ^g
Diameter-limit cuts (n=6)										
La Bécasse Lake	SM	1aR	2	C	NW	1971	4	45°56' N, 75°15' W	19	795 (250)
Écorces Lake	SM	1aR	3	C	NW	1974	5	45°54' N, 75°18' W	20	795 (250)
Lanthier Lake	SM	1aR	2	C	N	1969	2	45°58' N, 75°19' W	17	685 (225)
Mulet Lake	SM	1aR	2	C	NE	1971	2	45°56' N, 75°15' W	19	740 (250)
Du Parc Pond	SMTH	1aR	2	C	W	1972	10	45°55' N, 75°14' W	18	770 (225)
Sayabec Pond	SM	1a	3	C	W	1974	3	45°56' N, 75°15' W	18	705 (190)

Table 1.2 Structural characteristics in North America's northeastern hardwoods from published literature (OG, Old-growth; SC, Selection cut; UN, Unmanaged).

Reference	Region, stand type	Results \pm 1 SE (range)
Mean individual gap size		
This study ^a	Southwestern Québec, OG	36.5 \pm 6.0 m ² (2.3-154.2 m ²)
Runkle (1985a) ^a	Eastern US, OG and mature	\approx 31 m ² (1 to 1490 m ²)
Krasny and Whitmore (1992) ^a	New York, mature	42.8 \pm 6.7 m ²
Dahir and Lorimer (1996) ^b	Northwestern Michigan, OG	44.8 m ²
Pourcentage of land area under gaps		
This study ^a	Southwestern Québec, SC vs OG	SC : 32 ^a \pm 3.0% (23.4-48.2) OG : 9.4 ^b \pm 1.7% (3.5-14.6)
Krasny and Whitmore (1992) ^a	New York, mature	8.4 \pm 0.8%
Runkle (1985b) ^c	Eastern US, OG	10.1 \pm 0.7% (3.3-26.1%)
Runkle (1990) ^a	Ohio, OG	7.0%
Snags (density and size)		
This study	Southwestern Québec, SC vs OG	SC: 43.9 ^a \pm 4.9/ha (18.9-59.7) OG: 49.3 ^a \pm 6.7/ha (20.1-64.2)
McComb and Muller (1983) ^d	Eastern Kentucky, OG	OG: 42.8/ha
Forrester and Runkle (2000) ^d	Northeastern Ohio, OG	OG : 27.5/ha
Runkle (1991) ^e	New-York, OG	OG: 54–73.8/ha
Doyon <i>et al.</i> (1999) ^f	Southwestern Québec, SC	SC: 94 \pm 8.8/ha
Hale <i>et al.</i> (1999) ^d	Minnesota, SC vs OG	SC: 24/ha ^a (0-88) OG: 34/ha ^a (0-75)

Note: Different letters indicate significantly different values among stand types at $P < 0.05$ according to respective authors. For dead wood, only studies using a dbh cutoff similar to the one used in this study are presented.

^aAccording to the canopy gap definition; ^bOriginal canopy gap area; ^cAccording to the line intersect method; ^dSnags ≥ 10 cm dbh; ^eSnags ≥ 11 cm dbh; ^fSnags ≥ 5 cm dbh; ^gLogs and stumps; ^hLogs only; ⁱCWD ≥ 15 cm; ^jCWD ≥ 10 cm; ^kCWD ≥ 1 cm.

Table 1.2 Structural characteristics in North America's northeast hardwood forests from published literature (OG, Old-growth; SC, Selection cut; UN, Unmanaged) (continued).

Reference	Region, stand type	Results \pm 1 SE (range)
Snags (density and size) (continued)		
McGee <i>et al.</i> (1999) ^d	New-York, SC vs OG	SC: 42.8 ± 25.3 /ha (16.7-71.7) OG: 59.7 ± 21.7 /ha (35.0-80.0) Lower density in ≥ 25 cm in SC
Goodburn and Lorimer (1998) ^d	Wisconsin and Michigan, SC vs OG	SC: ≈ 37 /ha ^a OG: ≈ 38 /ha ^a Lower density in ≥ 30 cm in SC
Coarse woody debris (volume and size)		
This study ^g	Southwestern Québec, SC vs OG	SC: $100.9^a \pm 8.5$ m ³ /ha (62.5-133.7) OG: $93.4^a \pm 11.9$ m ³ /ha (39.5-120.3)
Doyon (2000) ^f	Southwestern Québec, SC	SC: 60.7 ± 7.1 m ³ /ha
Hale <i>et al.</i> (1999) ^{hi}	Minnesota, SC vs OG	SC: 40^a m ³ /ha (12-89) OG: 55^b m ³ /ha (12-121)
Goodburn and Lorimer (1998) ^j	Wisconsin and Michigan, SC vs OG	SC: $\approx 61^a$ m ³ /ha OG: $\approx 102^b$ m ³ /ha Lower volume in ≥ 40 cm in SC
Leduc and Bergeron (1998) ^j	Southeastern Québec, OG	OG: 40.4-84.1 m ³ /ha
Forrester and Runkle (2000) ^j	Northeastern Ohio, OG	OG: 80.2 m ³ /ha
McGee <i>et al.</i> (1999) ^k	New-York, SC vs OG	SC: $69.1^a \pm 16.7$ m ³ /ha (55.3-100.9) OG: $138.5^b \pm 22.0$ m ³ /ha (120.6-180.9) Lower volume in ≥ 25 cm in SC
Gore and Patterson (1986)	New-Hampshire, SC vs OG	Lower proportion in ≥ 15.2 cm in SC

Table 1.3 Results of comparisons of trees, sapling, dead wood and gaps structural features between old-growth (OG), selection cut (SC) and diameter-limit cut stands (DLC).

Variables	Old-growth (n = 6)			Selection cuts (n = 7)			Diameter-limit cuts (n = 6)			Transformation used
	Mean ± SE	Range	n	Mean ± SE	Range	n	Mean ± SE	Range	N	
Gaps										
Area under gaps (%)	9.4 ± 1.7 ^a	3.5-14.6	104	32.0 ± 3.0 ^b	23.4-48.2	228	4.4 ± 1.3 ^c	1.8-10.3	71	Log
Vertical foliage profile										
Foliage cover homogeneity index (FCHI) 0-2 m ¹	24.8 ± 1.2 ^a	0-85	114	19.6 ± 1.1 ^b	0-72.5	130	25.4 ± 1.2 ^a	0-72.5	111	Rank
FCHI 2-5 m	22.7 ± 1.1 ^a	0-72.5	114	20.4 ± 1.2 ^a	0-85	130	12.7 ± 0.3 ^b	0-60	111	Rank
FCHI 5-10 m	27.1 ± 1.3 ^a	0-85	114	26.2 ± 1.2 ^a	0-85	130	29.7 ± 1.4 ^a	0-85	111	Rank
FCHI >10 m	26.8 ± 1.3 ^a	0-85	114	29.9 ± 1.3 ^a	0-85	130	32.3 ± 1.6 ^a	0-85	111	Rank
Saplings										
Density (stems/ha)	2919 ± 184 ^a	250-9500	1331	6310 ± 330 ^b	500-19 750	3281	1491 ± 112 ^c	250-6250	644	Log
Trees										
Density (stems/ha)	438.0 ± 18.0 ^a	392.1-511.5	114	334.9 ± 41.7 ^a	250.2-554.8	130	578.5 ± 41.9 ^b	429.9-691.5	111	None
Basal area (m ² /ha)	27.1 ± 2.1 ^a	20.1-35.4	114	16.2 ± 1.7 ^b	11.5-24.6	130	20.2 ± 2.3 ^{ab}	13.6-30.5	111	None
Dbh (cm)	28.0 ± 0.7 ^a	9.1-89.0	456	24.9 ± 0.5 ^a	9.1-65.4	520	21.0 ± 0.5 ^b	9.1-58.8	444	Rank
Snags										
Density (stems/ha)	49.3 ± 6.7 ^a	20.1-64.2	91	43.9 ± 4.9 ^a	18.9-59.7	95	118.1 ± 19.8 ^b	60.8-173.0	216	Square root
Dbh (cm)	24.6 ± 1.8 ^a	5.4-68.0	91	26.6 ± 1.4 ^a	6.6-74.5	95	14.0 ± 0.9 ^b	5.0-101.0	216	Rank
Coarse woody debris (CWD)										
CWD volume (without stumps) (m ³ /ha)	78.4 ± 9.6 ^a	33.0-96.6	254	72.7 ± 6.4 ^{ab}	43.9-96.2	332	41.6 ± 12.0 ^b	27.3-101.5	140	None
Stumps volume (m ³ /ha) ²	15.0 ± 2.7 ^a	6.6-20.2	103	29.3 ± 2.4 ^{ab}	18.6 - 37.3	244	35.7 ± 7.5 ^b	11.4 - 57.6	255	None
Total volume (CWD and stumps) (m ³ /ha)	93.4 ± 11.9 ^a	39.5-120.3	357	100.9 ± 8.5 ^a	62.5-133.7	676	77.3 ± 17.3 ^a	43.5-150.0	395	None
Large end diameter (cm)	19.5 ± 0.9 ^a	5.0-61.0	254	17.8 ± 0.7 ^a	5.4-66.0	332	18.5 ± 1.0 ^a	5.4-56.0	140	Log
Mean piece volume (cm ³)	24.7 ± 3.1 ^a	0.1-343.3	254	19.0 ± 2.4 ^a	0.1-346.9	332	15.3 ± 2.1 ^a	0.1-140.9	140	Log

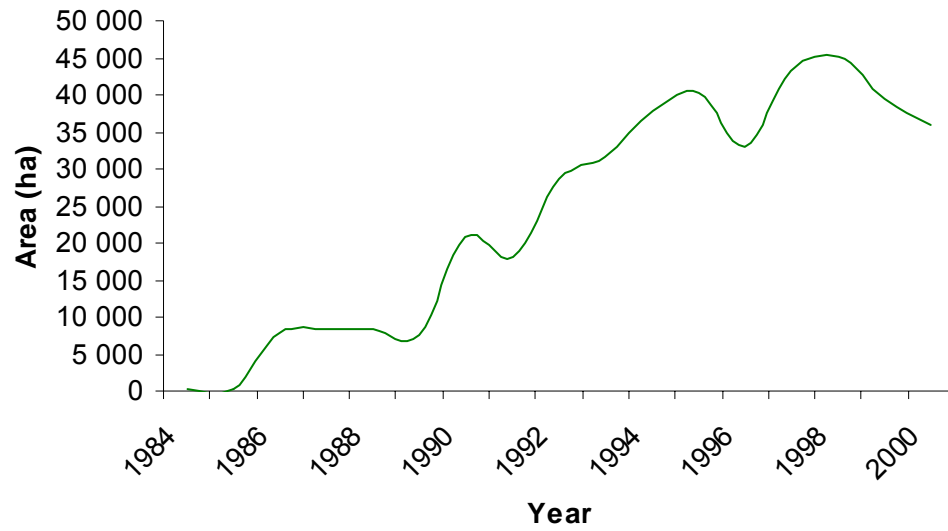
Note: Different letters indicate significantly different values among stand types at P < 0.05

¹See methodology for index calculation. Homogeneity was inversely proportional to the index.

²Natural and cut stumps

APPENDIX A

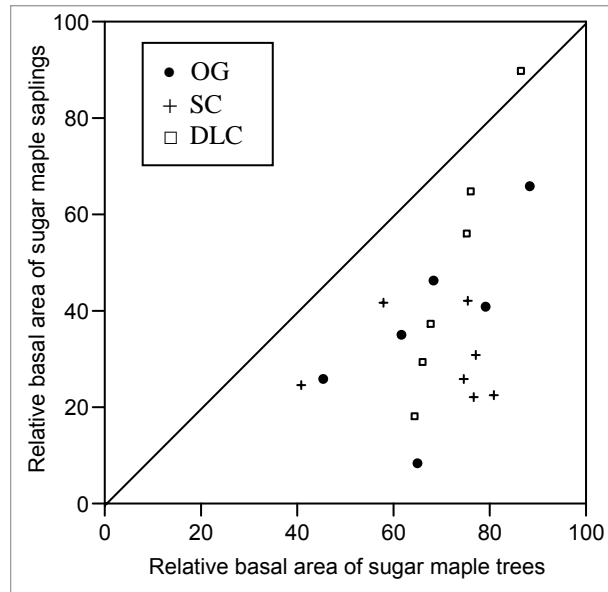
Figure A.11 Evolution of selection cut areas in Québec (1984-2000)



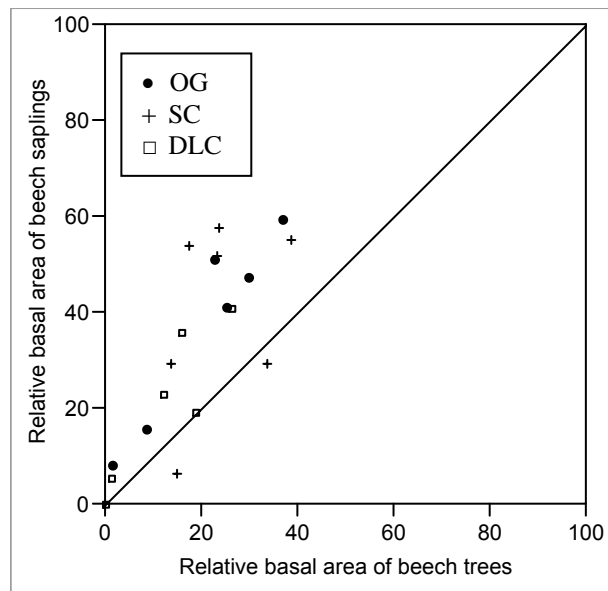
APPENDIX B

Figure B.1 Trend in species relative basal area for the two main species, sugar maple (a) and beech (b) in old-growth (OG), selection cut (SC) and diameter-limit cut (DLC) stands.

a)



b)



Note: Lines at 1:1 slope show steady state between saplings and trees abundance.

CONCLUSION GÉNÉRALE

L'objectif principal de cette étude consistait à mettre en évidence l'influence qu'a eu l'aménagement forestier sur la composition et la structure des érablières en comparant des peuplements anciens et aménagés. Or, nos résultats indiquent des différences marquées entre les forêts ayant été modelées par les perturbations naturelles et anthropiques.

Même si la période écoulée depuis les CDL était beaucoup plus longue que suite aux CJ étudiées, on observe globalement des différences plus marquées en termes de structure et de composition entre les CDL et les ANC qu'entre CJ et ANC. En d'autres termes, on peut dire que nous avons hérité d'une forêt qui a probablement passablement dévié de sa dynamique naturelle suite à l'utilisation à grande échelle de la coupe à diamètre limite, et que l'aménagement par coupe de jardinage a permis d'amoindrir les différences entre coupes et perturbations naturelles en termes d'effets sur la structure et la composition. Ceci dit, de nombreuses lacunes ont été observées et d'autres sont à prévoir.

Impact à l'échelle du peuplement

En ce qui a trait à la composition en espèces, peu de différences ont été observées entre les peuplements jardinés et les forêts anciennes. Notons toutefois une augmentation faible mais significative de la surface terrière relative des gaules d'espèces peu tolérantes à l'ombre dans les peuplements aménagés.

C'est en regard de la structure que l'on observe le plus de différences. D'une part, on remarque en forêt aménagée la présence d'une dense couche de feuillage. Cette strate de feuillage s'est probablement développée suite à l'ouverture forte et synchronisée du couvert causée par la récolte qui a vraisemblablement entraîné une augmentation marquée de la lumière en sous-couvert et a pu provoquer un

recrutement massif de la régénération (Beudet *et al.* 2004). La continuité des processus de régénération sous cette strate formée par la cohorte de régénération post-coupe semble être entravée, probablement à cause d'une faible disponibilité de lumière qui entraînerait une forte mortalité (Hane 2003), puisqu'on y observe très peu de feuillage. De plus, le pourcentage de recouvrement du feuillage situé dans la couche sous-jacente à cette strate est beaucoup plus homogène dans les peuplements aménagés par rapport aux forêts anciennes. Ces différences, directement liées à une synchronisation des ouvertures lors de la récolte, pourraient avoir des impacts sur les organismes forestiers qui sont associées à des densités de feuillage particulières à certaines strates (Crome et Richards 1988, Bourque et Villard 2001).

Pour ce qui est du bois mort (chicots, débris ligneux au sol), nous n'avons pas observé de différence significative en ce qui concerne leur taille, leur volume et leur abondance, bien qu'une tendance ait été notée concernant la raréfaction des gros chicots en CJ. Cette absence de différence est vraisemblablement en partie due à la mortalité naturelle après coupe qui serait relativement élevée suite au jardinage (Bédard et Brassard 2002). On anticipe cependant que la combinaison de la raréfaction des arbres de gros diamètre et la réduction de la mortalité suite à plusieurs rotations successives de jardinage auront des conséquences directes sur le recrutement de chicots puis sur la création de débris ligneux à forte valeur écologique (i.e. de gros diamètres, et avec une représentation dans toutes les classes de décomposition). Aux Etats-Unis, de nombreuses études ont fait état de la raréfaction des gros arbres et du bois mort de haute valeur écologique suite à quelques rotations de jardinage (Goodburn et Lorimer 1998, Hagan et Grove 1999, Hale *et al.* 1999, McGee *et al.* 1999). La présence de chicots et de débris ligneux est pourtant essentielle à la survie d'une foule d'espèces animales et végétales qui les utilisent entre autres comme sites d'alimentation, de reproduction, ou comme substrat d'établissement, sans parler des processus dans lesquels le bois mort est impliqué, comme le cyclage des éléments ou le stockage du carbone (Harmon *et al.* 1986, McComb et Lindenmayer 1999).

En forêt naturelle, si l'on considère le régime des micro-trouées, l'intervalle séparant l'occurrence de deux perturbations au même endroit est relativement long par rapport au temps de récupération (refermeture du couvert) et la superficie affectée est généralement très limitée. Même si les sites jardinés qui ont été étudiés ici n'ont pas encore complété un cycle entier de jardinage, la proportion d'ouvertures (moyenne de 32% d'ouverture après 12 ans) suggère que la canopée ne sera probablement pas refermée à un degré similaire à celui des forêts anciennes (9% en moyenne) avant la prochaine intervention, ou si c'est le cas, pour une très courte période seulement. En d'autres termes, le temps de récupération après coupe est plus long que l'intervalle entre les coupes.

Impact à l'échelle du paysage

On s'est surtout intéressé aux conséquences de l'aménagement à l'échelle du peuplement, mais les résultats de cette étude permettent aussi de réfléchir sur l'impact à l'échelle du paysage. L'application à grande échelle de la coupe de jardinage, associée à ce déséquilibre entre l'intervalle entre les perturbations et le temps de récupération, pourrait entraîner, à l'échelle du paysage, une augmentation de la proportion de peuplements relativement ouverts et un déficit en forêts matures et anciennes (Turner *et al.* 1993, Haeussler et Kneeshaw 2003). Les espèces associées à ces types de forêts et dépendant de leurs caractéristiques structurales (couvert relativement fermé, abondance de bois mort, structure horizontale et verticale du feuillage diversifiée) pourraient donc être défavorisées.

Bien que moins fréquentes et affectant de moins grandes étendues que le régime des micro-trouées, d'autres types de perturbations naturelles ont aussi cours en forêt feuillue et jouent un rôle essentiel dans la dynamique de ces forêts (ex. : chablis, verglas, feu, épidémies) (Lorimer 1977, Lorimer et Frelich 1994). Le recours presque exclusif à la coupe de jardinage comme mode d'aménagement en forêt

feuillue ne permet pas de reproduire toute la variabilité des perturbations observées en forêt naturelle en termes de fréquence, de grandeur et de sévérité et pourrait entraîner une homogénéisation de la structure et de la composition des peuplements, à l'échelle du peuplement et du paysage, ainsi qu'une raréfaction des peuplements de début de succession (Haeussler et Kneeshaw 2003).

Implications pour l'aménagement

Même si toutes les contraintes économiques étaient levées, viser une reproduction exacte de la dynamique des micro-trouées serait utopique opérationnellement. Dans le contexte économique et opérationnel actuel et à venir, quelques mesures d'atténuation des différences entre coupes et perturbations naturelles sont cependant envisageables.

Afin d'amoindrir le déséquilibre entre l'intervalle de coupe et le temps de récupération, des portions de forêt pourraient être aménagées en ayant recours à des périodes de rotation allongées, ce qui permettrait de favoriser le développement et la disponibilité continue d'attributs de forêts anciennes à l'échelle du paysage.

À l'échelle du peuplement, afin d'atténuer la raréfaction anticipée des gros arbres et des débris ligneux, une variante de l'approche de rétention variable proposée pour les systèmes de coupe totales pourrait être mise en œuvre. Elle consisterait à laisser des chicots et des arbres de fort diamètre sur pied en permanence à même les peuplements (Goodburn et Lorimer 1998, Hale *et al.* 1999, McGee *et al.* 1999, Fraver *et al.* 2002) ou encore des îlots résiduels de forêts matures intactes à l'intérieur des aires de récolte (Hagan et Grove 1999).

Évidemment, la mise en pratique de plusieurs de ces recommandations entraînerait vraisemblablement des coûts de planification et d'exploitation supplémentaires et une diminution du volume exploitable. Afin que l'implantation de

telles recommandations puisse être envisageable opérationnellement et économiquement, on pourrait considérer le recours à un modèle d'allocation du territoire. Les pertes économiques associées à un aménagement plus extensif et à la mise de côté de portions du territoire sous forme d'aires protégées seraient alors comblées par un aménagement intensif visant une production accrue de matière ligneuse sur des portions restreintes de territoire (Hunter 1990, Messier et Kneeshaw 1999, Seymour *et al.* 2002).

Dans le cadre d'un aménagement écosystémique, l'échelle du paysage doit aussi être considérée. Pour progresser dans cette voie, on devrait adopter une stratégie de planification des coupes à l'échelle du territoire qui permettrait de contrôler les proportions de territoire soumises aux différents systèmes sylvicoles de façon à ce que ces proportions soient, dans la mesure du possible, représentative du régime de perturbation naturelle de ce type d'écosystème. Évidemment, ceci nécessiterait une étude approfondie de la représentativité naturelle des différents types de perturbations pour la forêt feuillue du Québec puisque la plupart des connaissances proviennent du nord-est des États-Unis.

RÉFÉRENCES

Angelstam, P.K. 1998. Maintaining and restoring biodiversity in European boreal forests by developing natural disturbance regimes. *J. Veg. Sc.* 9: 593-602.

Attwill, P.M. 1994. The disturbance of forest ecosystems: the ecological basis for conservative management. *For. Ecol. Manage.* 63: 247-300.

Beaudet, M., Messier, C., and Leduc, A. 2004. Understory light profiles in northern hardwood stands: recovery process following selection cutting. *J. Ecol.* 92:328-338.

Beaulieu, C. 2003. Tembec et Commonwealth Plywood en ont marre du jardinage forestier. *La terre de chez nous*, 13 novembre, p. 19.

Bergeron, Y., Harvey, B., Leduc, A., and Gauthier, S. 1999. Stratégies d'aménagement forestier qui s'inspirent de la dynamique des perturbations naturelles: considérations à l'échelle du peuplement et de la forêt. *For. Chron.* 75: 55-61.

Bourque, J. et Villard, M.-A. 2001. Effects of selection cutting and landscape-scale harvesting on the reproductive success of two neotropical migrant bird species. *Cons. Biol.* 15: 184-195.

Brisson, J., Bergeron, Y., et Bouchard, A. 1988. Les successions secondaires sur sites mésiques dans le Haut-Saint-Laurent, Québec, Canada. *Can. J. Bot.* 66: 1192-1203.

Bunnell, F.L., Kremsater, L.L., et Wind, E. 1999. Managing to sustain vertebrate richness in forests of Pacific Northwest: relationships within stands. *Environ. Rev.* 7: 97-146.

Bédard, S. et Brassard, F. 2002. Les effets réels des coupes de jardinage dans les forêts publiques du Québec en 1995 et 1996.

Crome, F.H.J. et Richards, G.C. 1988. Bats and gaps: microchiropteran community structure in a Queensland rain forest. *Ecology* 69: 1960-1969.

Franklin, J.F. 1993. Preserving biodiversity: species, ecosystems, or landscapes? *Ecol. Appl.* 3: 202-205.

Franklin, J. F., Cromack, J.F., Dension, W., McKee, A., Maser, C., Sedell, J., Swanson, F. et Juday, G. 1981. USDA Forest Service general technical report PNW-118. Portland, 48 p.

Fraver, S., Wagner, R.G., et Day, M. 2002. Dynamics of coarse woody debris

following gap harvesting in the Acadian forest of central Maine, U.S.A. *Can. J. For. Res.* 32: 2094-2105.

Goodburn, J.M. et Lorimer, C.G. 1998. Cavity trees and coarse woody debris in old-growth and managed northern hardwood forests in Wisconsin and Michigan. *Can. J. For. Res.* 28: 427-438.

Haeussler, S. et Kneeshaw, D. 2003. Comparing forest management to natural processes. *In* Towards sustainable management of the boreal forest. Burton, P.J., Messier, C., Smith, C. and Adamowicz, W.L. eds. NRC Research Press, Ottawa, Ontario, 1039 p.

Hagan, J.M. et Grove, S. L. 1999. Bird abundance and distribution in managed and old-growth forest in Maine. Report MM-9901, Manomet Center for Conservation Sciences, Maine, 20 p.

Hale, C.M., Pastor, J., et Rusterholz, K.A. 1999. Comparison of structural and compositional characteristics in old-growth and mature, managed hardwood forests of Minnesota, U.S.A. *Can. J. For. Res.* 29: 1479-1489.

Hane, E. N. 2003. Indirect effects of beech bark disease on sugar maple seedling survival. *Can. J. For. Res.* 33:807-813.

Hansen, A.J., Spies, T.A., Swanson, F.J., et Ohmann, J.L. 1991. Conserving biodiversity in managed forests. *BioScience* 41: 382-392.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K.Jr., et Cummins, K.W. 1986. Ecology of coarse woody debris in temperate ecosystems. *Advances in ecological research* 15: 133-302.

Hunter, M.L.Jr. 1990. *Wildlife, forests, and forestry*. Prentice Hall, Englewood Cliffs, N. J., 370 p.

Kimmins, J.P. 1997. Biodiversity and its relationship to ecosystem health and integrity. *For. Chron.* 73: 229-32.

Lorimer, C.G. 1977. The presettlement forest and natural disturbance cycle of Northeastern Maine. *Ecology* 58: 139-148.

Lorimer, C.G. et Frelich, L.E. 1994. Natural disturbance regimes in old-growth northern hardwoods. *J. For.* 33-8.

Majcen, Z. 1994. Historique des coupes de jardinage dans les forêts inéquiennes au Québec. *Rev. For. Fr.* 4: 375-384.

McComb, W. et Lindenmayer, D. 1999. Dying, dead and down trees. *In* Maintaining

biodiversity in forest ecosystems. Hunter, M. L. Jr. ed. Cambridge University Press, Cambridge. pp. 335-372.

McGee, G.G., Leopold, D.J., et Nyland, R.D. 1999. Structural characteristics of old-growth, maturing, and partially cut northern hardwood forests. *Ecol. Appl.* 9: 1316-1329.

McIntosh, R.P. 1972. Forests of the Catskill mountains, New York. *Ecol. Mono.* 42: 143-161.

Messier, C.M. et Kneeshaw, D.D. 1999. Thinking and acting differently for sustainable management of the boreal forest. *For. Chron.* 75: 929-938.

MNR (Ministère des ressources Naturelles) 2000. La forêt feuillue... Au coeur du Québec habité! Ministère des Ressources naturelles, Gouvernement du Québec, Québec, 8 p.

Runkle, J.R. 1985. Disturbance regimes in temperate forests. *In* The ecology of natural disturbance and patch dynamics. Pickett, S. T. A. and White, P. S. eds. Academic Press, New-York. pp. 17-33.

Runkle, J.R. 1982. Patterns of disturbance in some old-growth mesic forests of eastern North America. *Ecology* 63: 1533-1546.

Seymour, R.S., White, A.S., et deMaynadier, P.G. 2002. Natural disturbance regimes in Northeastern North America - Evaluating silvicultural systems using natural scales and frequencies. *For. Ecol. Manage.* 155: 357-367.

Siccama, T.G. 1971. Presettlement and present vegetation in northern Vermont with special reference to Chittenden County. *Am. Midl. Nat.* 85: 153-172.

Spies, T.A. 1998. Forest structure: A key to the ecosystem. *Northwest Science* 72: 34-39.

Stone, J.N. et Porter, J.L. 1998. What is forest structure and how to measure it? *Northwest Sc.* 72: 25-26.

Turner, M.G., Romme, W.H., Gardner, R.H., O'Neill, R.V., et Kratz, T.K. 1993. A revised concept of landscape equilibrium: Disturbance and stability scales landscapes. *Landscape Ecol.* 8: 213-227.