UNIVERSITÉ DU QUÉBEC À MONTRÉAL

CARACTÉRISATION SPATIO-TEMPORELLE DE LA DYNAMIQUE DES TROUÉES ET DE LA RÉPONSE DE LA FORÊT BORÉALE À L'AIDE DE DONNÉES LIDAR MULTI-TEMPORELLES

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SPATIOTEMPORAL CHARATERISATION OF GAP DYNAMICS AND BOREAL FOREST RESPONSES USING MULTI-TEMPORAL LIDAR DATA

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To Arush and Rushat

Its wanting to know that makes us matter!

-Tom Stoppard, Arcadia

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In all the articles presented in this thesis, I was responsible for the problem definition, context, methodological development, data analysis, interpretation as well as writing of the manuscripts. All the authors provided helpful guidance as well as thorough editing of the manuscripts.

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LIST OF ACRONYMS USED

AGL	Above Ground Level
CHM	Canopy Height Model
CRS	Completely Regularised Splines
DTM	Digital Terrain Model
GIS	Geographic Information System
GPS	Global Positioning System
HW	Hardwood
IDW	Inverse Distance Weighted algorithm
IFSAR	Interferometric Synthetic Aperture Radar
INS	Intertial Navigational System
IQ	Inverse Quadratic
LDTRF	Lake Duparquet Training and Research Forest
LIDAR	LIght Detection And Ranging
MSE	Mean Square Error
OK	Ordinary Kriging
RMSE	Root Mean Square Error
SBW	Spruce Budworm
ST	Splines with Tension
SW	Softwood
TIN	Triangulated Irregular Networks
TP	Thin Plate Splines
TSF	Time Since Fire

LIST OF UNITS USED

%	Percentage
cm	Centimeter
deg	Degrees
ha	Hectares
Hz	Hertz
km	Kilometer
km^2	Square Kilometer
m	Meter
m^2	Square meters
Mrad	Micro radians
Nm	Nano meter
Rad	Radians
Yr	Year

RÉSUMÉ

La forêt boréale est un écosystème hétérogène et dynamique façonné par les perturbations naturelles comme les feux, les épidémies d'insectes, le vent et la régénération. La dynamique des trouées joue un rôle important dans la dynamique forestière parce qu'elle influence le recrutement de nouveaux individus au sein de la canopée et la croissance de la végétation avoisinante par une augmentation des ressources. Bien que l'importance des trouées en forêt boréale fut reconnue, les connaissances nécessaires à la compréhension des relations entre le régime de trouées et la dynamique forestière, en particulier sur la croissance, sont souvent manquantes. Il est difficile d'observer et de mesurer extensivement la dynamique des trouées ou les changements de la canopée simultanément dans le temps et l'espace avec des données terrain ou des images bidimensionnelles (photos aériennes,...) et ce particulièrement dans des systèmes complexes comme les forêts ouvertes ou morcelées. De plus, la plupart des recherches furent menées en s'appuyant sur seulement quelques trouées représentatives bien que les interactions entre les trouées et la structure forestière furent rarement étudiées de manière conjointe.

Le lidar est un système qui balaye la surface terrestre avec des faisceaux laser permettant d'obtenir une image dense de points en trois dimensions montrant les aspects structuraux de la végétation et de la topographie sous-jacente d'une grande superficie. Nous avons formulé l'hypothèse que lorsque les retours lidar de tirs quasi-verticaux sont denses et précis, ils permettent une interprétation de la géométrie des trouées et la comparaison de celles-ci dans le temps, ce qui nous informe à propos de leur influence sur la dynamique forestière. De plus, les mesures linéaires prises à différents moments dans le temps permettraient de donner une estimation fiable de la croissance. Ainsi, l'objectif de cette recherche doctorale était de développer des méthodes et d'accroître nos connaissances sur le régime de trouées et sa dynamique, et de déterminer comment la forêt boréale mixte répond à ces perturbations en termes de croissance et de mortalité à l'échelle locale. Un autre objectif était aussi de comprendre le rôle à court terme des ouvertures de la canopée dans un peuplement et la dynamique successionelle. Ces processus écologiques furent étudiés en reconstituant la hauteur de la surface de la canopée de la forêt boréale par l'utilisation de données lidar prises en 1998, 2003 (et 2007), mais sans spécifications d'études similaires. L'aire d'étude de 6 km^2 dans la Forêt d'Enseignement et de Recherche du Lac Duparquet, Québec, Canada, était suffisamment grande pour capter la variabilité de la structure de la canopée et de la réponse de la forêt à travers une gamme de peuplements à différents stades de développement.

Les recherches menées lors de cette étude ont révélé que les données lidar multi-temporelles peuvent être utilisées *a priori* dans toute étude de télédétection des

changements, dont l'optimisation de la résolution des matrices et le choix de l'interpolation des algorithmes sont essentiels (pour les surfaces végétales et terrestres) afin d'obtenir des limites précises des trouées. Nous avons trouvé qu'une technique basée sur la croissance de régions appliquée à une surface lidar peut être utilisée pour délimiter les trouées avec une géométrie précise et pour éliminer les espaces entre les arbres représentant de fausses trouées. La comparaison de trouées avec leur délimitation lidar le long de transects linéaires de 980 mètres montre une forte correspondance de 96,5%. Le lidar a été utilisé avec succès pour délimiter des trouées simples (un seul arbre) ou multiples (plus de 5 m^2). En utilisant la combinaison de séries temporelles de trouées dérivées du lidar, nous avons développé des méthodes afin de délimiter les divers types d'évènements de dynamique des trouées : l'occurrence aléatoire de trouées, l'expansion de trouées et la fermeture de trouées, tant par la croissance latérale que la régénération.

La technique proposée pour identifier les hauteurs variées arbre/gaulis sur une image lidar d'un Modèle de Hauteur de Couvert (MHC) a montré près de 75 % de correspondance avec les localisations photogrammétriques. Les taux de croissance libre suggérés basés sur les donnés lidar brutes après l'élimination des sources possibles d'erreur furent utilisés subséquemment pour des techniques statistiques afin de quantifier les réponses de croissance en hauteur qui ont été trouvées afin de faire varier la localisation spatiale en respect de la bordure de la trouée. À partir de la combinaison de donnés de plusieurs groupes d'espèces (de conifères et décidues) interprétée à partir d'images à haute résolution avec des données structurales lidar nous avons estimé les patrons de croissance en hauteur des différents groupes arbres/gaulis pour plusieurs contextes de voisinage.

Les résultats on montré que la forêt boréale mixte autour du lac Duparquet est un système hautement dynamique, où la perturbation de la canopée joue un rôle important même pour une courte période de temps. La nouvelle estimation du taux de formation des trouées était de 0,6 %, ce qui correspond à une rotation de 182 ans pour cette forêt. Les résultats ont montré aussi que les arbres en périphérie des trouées étaient plus vulnérables à la mortalité que ceux à l'intérieur du couvert, résultant en un élargissement de la trouée. Nos résultats confirment que tant la croissance latérale que la croissance en hauteur de la régénération contribuent à la fermeture de la canopée à un taux annuel de 1,2 %. Des évidences ont aussi montré que les trouées de conifères et de feuillus ont des croissances latérales (moyenne de 22 cm/an) et verticales similaires sans tenir compte de leur localisation et leur hauteur initiale. La croissance en hauteur de tous les gaulis était fortement positive selon le type d'évènement et la superficie de la trouée. Les résultats suggèrent que la croissance des gaulis de conifères et de feuillus atteint son taux de croissance maximal à des distances respectives se situant entre 0,5 et 2 m et 1,5 et 4 m à partir de la bordure d'une trouée et pour des ouvertures de moins de 800 m^2 et 250 m^2 respectivement.

Les effets des trouées sur la croissance en hauteur d'une forêt intacte se faisaient sentir à des distance allant jusqu'à à 30 m et 20 m des trouées, respectivement pour les feuillus et les conifères.

Des analyses fines de l'ouverture de la canopée montrent que les peuplements à différents stades de développement sont hautement dynamiques et ne peuvent systématiquement suivre les mêmes patrons successionels. Globalement, la forêt est presqu'à l'équilibre compositionnel avec une faible augmentation de feuillus, principalement dû à la régénération de type *infilling* plutôt qu'une transition successionelle de conifères tolérants à l'ombre. Les trouées sont importantes pour le maintien des feuillus puisque le remplacement en sous-couvert est vital pour certains résineux. L'étude à démontré également que la dernière épidémie de tordeuse des bourgeons de l'épinette qui s'est terminée il y a 16 ans continue d'affecter de vieux peuplements résineux qui présentent toujours un haut taux de mortalité.

Les résultats obtenus démontrent que lidar est un excellent outil pour acquérir des détails rapidement sur les dynamiques spatialement extensives et à court terme des trouées de structures complexes en forêt boréale. Les évidences de cette recherche peuvent servir tant à l'écologie, la sylviculture, l'aménagement forestier et aux spécialistes lidar. Ces idées ajoutent une nouvelle dimension à notre compréhension du rôle des petites perturbations et auront une implication directe pour les aménagistes forestiers en quête d'un aménagement forestier écologique et du maintien des forêts mixtes.

Mot-clés: perturbation naturelle, dynamique forestière, dynamique des trouées, croissances latérales, régénération, succession, lidar à retours discrets, grande superficie, localisation des arbres individuels, croissance en hauteur

ABSTRACT

Boreal forests are dynamic and heterogeneous ecosystems that are shaped by multiple disturbances occurring in different moments in time like fire, insects, wind and senescence. Canopy gaps play an important role in forest dynamics because they influence the recruitment of new individuals into the forest canopy and the growth of surrounding vegetation through an increase in above and below-ground resources. Although the importance of gaps has been recognised in boreal forests, the knowledge needed to understand the relationships between a gap disturbance regime and their role in forest dynamics, especially growth, is often lacking. It is difficult to observe and measure canopy gap dynamics or changes in forest canopies extensively in both space and time using field measurements or two dimensional remote sensing images (e.g. aerial photos), particularly in complex systems like open and patchy boreal forests. Moreover, most research thus far has been conducted on only a few representative gaps while interactions between gaps and forest structure as well as dynamics of the forest have rarely been addressed across the forest as a whole.

Lidar is an active system that scans the earth surface with a laser beam, resulting in a dense three-dimensional point cloud containing structural aspects of the vegetation canopy and the terrain below it across broad spatial extents. We hypothesized that when accurate and high density lidar returns are acquired at near-nadir angles, a good proportion of them reaching the forest floor, should in combination with the canopy returns enable near perfect interpretation of gap geometry. A comparison over time of perfectly co-registered data will inform us about their influence on forest dynamics. Further, lidar measurements taken at different moments in time should provide a reliable estimate of growth. Thus the focus of this doctoral research has been in developing methods and in improving our understanding of gap disturbance regimes and their dynamics, and how boreal mixedwood forests respond to these disturbances in terms of growth and mortality at local scales. A focus of the research has also been on understanding the role of gap openings on short-term stand and successional dynamics. These ecological processes were studied by reconstructing the canopy height surfaces of boreal forests using discrete lidar data taken in 1998, 2003 and 2007 that have dissimilar survey specifications. The study area chosen was a contiguous 6 km^2 forest around Lake Duparquet, Canada, sufficiently large to capture variability in canopy structure and forest response across a range of stand developmental stages.

Investigations in this study have shown that multi-temporal lidar data should be co-registered *a priori* for any study in change detection, and that optimising grid resolution and the choice of an interpolation algorithm are essential, both for ground and vegetation surfaces, to ensure accurate delineation of canopy gaps. We found that an object-based region growing technique applied to a lidar surface can be used to delineate gaps with accurate gap geometry and to eliminate inter tree spaces that are spurious gaps. A comparison of 29 field-measured gaps along 980 m of transect with lidar delineated gaps showed a strong matching of 96.5 %. Lidar was used to successfully delineate single tree (over 5 m^2) to multiple tree gaps. Using combinatorics of a time series of lidar-derived canopy gaps, methods were developed to delineate dynamic gap events, namely random gap occurrence, gap expansion, and gap closure through both lateral growth and regeneration.

The proposed technique for identifying tree/saplings of various heights on a lidar CHM showed about a 75% match with photogrammetric locations. The suggested unit free growth rates based on raw lidar data after eliminating possible sources of error were used for subsequent statistical techniques to quantify height growth responses that were found to vary by spatial location with respect to the gap edge. Combining data on broad species groups (deciduous and coniferous) interpreted from high resolution images with lidar structural data, we estimated species-group height-growth patterns for trees/ saplings in various neighbourhood contexts.

The results show that boreal mixedwood forests around Lake Duparquet are highly dynamic systems, where canopy disturbance plays an important role, even in a short period of time. The estimated new gap formation rate was 0.6% that resulted in a turnover of 182 years for these forests. The results also show that trees on gap peripheries were more vulnerable to mortality than interior canopy trees resulting in gaps enlarging and coalescing existing gaps. Our results confirm that both lateral growth and regeneration height growth contribute to the closing of canopies at a annual rate of 1.2%. Evidence also shows that both hardwood and conifer trees on the gap edge have similar lateral growth (average of 22 cm/yr) and similar rates of height-growth irrespective of their location and their initial height in boreal forests. The height-growth of all saplings was strongly dependent on the position of the sapling in the gap, tye type of event responsible for the gap and the size of the gap. Results suggest that hardwoods and conifer saplings grow at their highest rates of growth at distances within 0.5 – 2 m and 1.5 - 4 m from the gap edge and in opening sizes less than 800 m^2 and 250 m^2 respectively. Gap effects on height-growth in the intact forest were found up to 30 m and 20 m for hardwood and softwood overstory trees respectively.

Fine-scale analysis of canopy openings shows that stands in different development stages are highly dynamic and do not consistently follow previously conceived successional patterns. Overall, the forest is in a quasi-compositional equilibrium with a small increase in hardwoods, largely due to regeneration in-filling instead of a successional transition to more shade-tolerant conifers. Gaps are important for hardwood maintenance while non-gap replacement is vital for softwoods. The study also noted that the last spruce budworm outbreak that ended 16 years previously has a lasting legacy on old-conifer stands as there continues to be high mortality of conifers in these stands.

The results obtained establish lidar as an excellent tool for rapidly acquiring detailed and spatially extensive short-term dynamics of canopy gaps of complex structure like boreal forests. The findings from the research presented here should benefit ecologists, silviculturists, forest managers and lidar specialists alike. These insights add a new dimension to our understanding of the role of small-scale disturbances, and will have a direct implication for forest managers who are seeking to develop a more ecologically oriented forest management practices aimed at maintaining mixedwood forests.

Key words: natural disturbance, forest dynamics, canopy gap opening and closure, lateral growth, regeneration, succession, discrete lidar, large spatial scale, single tree locations, height-growth pattern.

CHAPTER I

GENERAL INTRODUCTION

1.1. CANOPY GAPS AND FOREST DYNAMICS

Natural disturbances have long been considered an integral component of healthy ecosystems. Many researchers argue that these disturbances should be preserved, enhanced, and even mimicked (Landres et al. 1999). In recent years, there has been increasing interest in developing a forest management system using natural disturbance as a template to ensure that biodiversity and ecosystem functioning are maintained (Perera and Bose 2004). The ecological principle behind this paradigm is that disturbance-driven ecosystems, such as boreal forests, are resilient to natural disturbances, and hence emulating them would ensure the long term maintenance of biodiversity and productivity (Kimmins 2004). Although its importance is realized, the knowledge needed to understand a disturbance regime is often lacking.

Boreal forests are dynamic and spatially heterogeneous ecosystems that are shaped by a complex set of interactions between multiple disturbances that occur at different moments in time. Where fire cycles exceed the longevity of the trees, gap dynamics shape the composition and/or structure of these forests (Kneeshaw 2001). However, given the frequency of large-scale, stand-initiating disturbances like fire and insects the role of small-scale disturbances, like gaps, has until recently been discounted in determining the dynamics of boreal forests (McCarthy 2001).

Gap dynamics are characterized by small or micro-scale disturbances in the mature forest canopy. Trees die standing, snap, blow down, or die due to insects or pathogens which create a “hole” in the canopy. The absence of a single tree or a group of trees in the canopy releases available growing space that is conducive for the release of advance regeneration and the lateral expansion of peripheral trees that eventually close the gap. The array of gaps creates a very heterogeneous canopy, changes biomass accumulation, and also modifies the conditions for tree growth (Messier et al. 1999, Paré and Bergeron 1995). Gap dynamics are considered to be a key process in autogenic succession (Chen and Popadiouk 2002). In view of its importance in regeneration, dynamics and diversity, gap dynamics have been the focus of much research in several forest ecosystems, particularly tropical and temperate systems (Runkle 1998, Yamamoto 1992). Nonetheless, the appreciation of the role of small-scale disturbances in boreal forest dynamics is growing (for e.g., de Romer et al. 2007, Hill et al. 2005, Bartemucci et al. 2002, Cumming et al. 2000, Kneeshaw and Bergeron 1998).

1.1.1. Gap disturbance regimes

A disturbance regime, which is the spatial and temporal characterisation of disturbances affecting a landscape through time, is described by its size and spatial distribution, frequency, shape, rate at which the disturbance occurs and recovery from such events (Denslow and Spies 1990, Pickett and White 1985). Canopy gaps are themselves measurable indicators of past small-scale disturbances. Disturbance characteristics, including those described by studies in boreal forests, are traditionally measured in the field (Kneeshaw and Bergeron 1998, Runkle 1985), but in recent decades conventional remote sensing methods in two dimensions through image interpretation have also been applied (D'Aoust et al. 2004). Although not yet adopted in boreal forests, three dimensional constructions of canopy height models using aerial photos (Fujita et al. 2003) have also been used to characterize gaps. A canopy height model (CHM) is a spatially explicit description of canopy height in three-dimensions over a given area of forest. These provided useful results on gaps, but are limited in their ability to represent spatial and temporal patterns. Ground based methods and manual interpretations of aerial photos are tedious, expensive and cannot be repeated over large areas. Moreover, the quality of the CHM is affected by the accuracy of ground elevation determination, which remains difficult using aerial photos when canopies are closed (St-Onge et al. 2004). Details on more recent and advanced techniques to study canopy gaps will follow in Section 1.2.

1.1.2. Forest response to canopy gap opening

Forests respond to the opening of gaps in many ways, across varying spatial and temporal scales. At a local scale, the vegetation within small canopy openings and in the periphery of these gaps responds to the increase in resources with enhanced growth to eventually close the openings over time (Brisson 2001, Canham et al. 1990, Bongers and Popma 1990, Runkle and Yetter 1987). A response in terms of higher growth rates of saplings in gaps varied with gap size, position and the initial gap size; factors that are directly related to light availability (Canham et al. 1990, Brokaw and Scheiner 1989). Nevertheless, studies on growth have focused mostly on diameter, and more rarely on height. The rates of gap formation and closure can affect the abundance of a species according to it's shade tolerance. However, the influence of gaps on the growth of boreal vegetation is uncertain due to the open and patchy structure of boreal forests (St-Denis 2008).

Competing peripheral trees in hardwood forests forage towards gap openings, often filling smaller gaps, i.e. by lateral growth (Brisson 2001, Runkle 1998, Runkle and Yetter 1987) although this process has not yet been documented in the boreal forest. This may be due to the perception that coniferous trees are unable to respond to canopy openings with significant lateral growth.

Trees at the gap periphery are also vulnerable to mortality through increased exposure to wind and other stresses. Gaps can thus expand in size over time, and could eventually be composed of regeneration in different stages of growth. Gap expansions are reported in wind-prone sub-alpine (Worall et al. 2005) and hardwood forests (Runkle and Yetter 1987) but not directly measured in boreal forests. Moreover, little is known about the impact of gap openings on the intact forest beyond the gap edge.

Species replacement and structural changes studied at the gap level have been used to understand the role of gaps in stand development. In boreal forests, it was suggested that large gaps favour intolerant hardwoods, while shade-tolerants establish in smaller gaps (Kneeshaw and Bergeron 1998). However, other studies found canopy gaps to have limited influence on understory tree establishment and in determining species composition (De Romer et al. 2007, Webb and Scanga 2001).

Thus far, our knowledge on gap disturbances and their influences on forest dynamics, including boreal forests, is based on limited spatial and temporal scales due to limitations in the available tools and methods. In fact, most research has been conducted at the scale of only a few gaps, restricted to evaluating current forest conditions, or has been based on space-for-time substitution. In spite of the insistence by many researchers on the incompleteness in considering a gap / no-gap dichotomy alone to explain the daunting complexity of real forests (for e.g., Lieberman et al. 1989; Brokaw and Scheiner 1989), interactions and dynamics of the forests are rarely addressed across the forest as a whole. Moreover, boreal forests are considered slow growing, and hence monitoring changes, in particular at fine-scales, is very complex using conventional methods. Thus tools are required that can reliably measure forest canopies over time and in great spatial detail over areas sufficiently large to capture variability in forest response.

1.2. CANOPY STRUCTURE

Canopy structure is the complete three-dimensional description of individual structures such as trees, snags and logs of various sizes and conditions (Bongers 2001, Parker 1995). Structure is a surrogate for functions (e.g. productivity) or for habitats (e.g. cavity dwelling animals) that are difficult to measure directly. Furthermore structure is an attribute that is often manipulated to achieve management objectives (Franklin 2002). Hence, characterising the pattern and dynamics of ecological processes requires reliable measurements of the horizontal and vertical arrangement of forest canopies over time (Parker et al. 2004).

Height is a key attribute in understanding canopy structure. Various researchers have proposed a critical regeneration height, adopting relative difference or absolute thresholds, to define and map canopy gaps (Song et al. 2004, Fujita et al. 2003, Tanaka and Nakashizuka 1995, Hubbell and Foster 1986). Hence tools that can provide height in a spatially continuous manner should enable us to map canopy gaps. In a forest canopy, growing space (i.e. gaps in the canopy) is available at places where vegetation does not occupy the vertical structure of the sampled area, for example in the understory (see region B in Fig.1.1), overstory (see region A in Fig.1.1) or gaps extending through all strata (canopy and sub-canopy) to the ground (see C in Fig.1.1). In this research, we study gaps that extend through all strata up to a certain specified height from the ground.

1.2.1. Measuring canopy structure using remote sensing tools

Techniques for collecting data and estimating forest structure, with emphasis on canopy height, range from traditional graduated sticks to analysing remote sensing data using advanced computer algorithms. Acquiring accurate and dense elevation data both of the canopy surface and underlying ground can be difficult, often time and cost intensive using manual or field techniques (Larsen and Franklin 2006, Song et al. 2004, Fujita et al. 2003). Remote sensing is a potential alternative to field based tree height or gap identification, providing a means of scaling measurements across two or more spatial scales of observation (e.g., tree, plot to landscape or region) in multiple time intervals. The primary benefits include synoptic (i.e. spatially complete) coverage, repeat measurements, high cost-effectiveness and coverage of inaccessible areas.

Canopy height models (CHM) are now being extensively used to study the structre of the forests. CHM are computed as the difference between the respective elevations of the canopy surface and the underlying terrain from points that are measured at a high density. The quality and resolution of a CHM is hence a function of the number and quality of measurements. Such measurements are feasible through 3-D remote sensing observations which are then gridded to provide an image visualisation. Such a surface defines the forest canopy as a collection of crowns that are visible from the sky (Fig.1.1 and Bongers, 2000). In other words, at any given geolocation on a grid, a canopy surface describes the elevation at which all the canopy components (within the spatial extension of the grid cell) are found vertically below (St-Onge, 2008). Using a predefined absolute or relative threshold of canopy height (fixed after field observations), it is thus feasible to identify areas occupied by vegetation and areas with canopy gaps.

Optical bi-dimensional images, both airborne and from space, are used for tree height measurements but are limited when canopy cover is dense due to problems discriminating individual crowns and determining ground elevation (St-Onge et al. 2004). Passive sensors are dependent on reflected solar radiation and hence are subject to the effects of shadowing and bidirectional reflectance that severely limit the amount of light reflected from components beneath the canopy surface (Koukoulas and Blackburn 2004, Kimes et al. 1998). Airphoto interpretation is also problematic due to very large errors in tree height estimates on steep slopes (Tanaka and Nakashizuka 1997) and unreliability in detecting smaller or deeper gaps (Betts et al. 2005, Fujita et al. 2003, Miller et al. 2000).

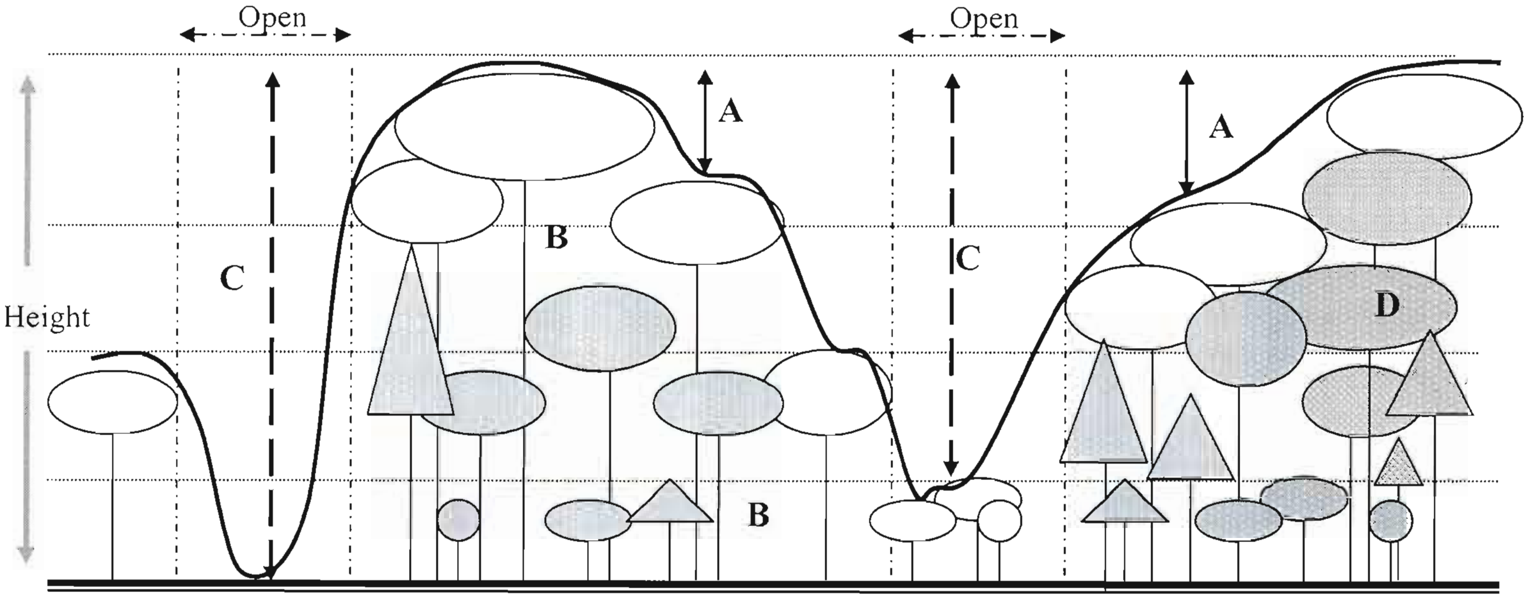

Figure.1.1. A vertical and horizontal cross-section of a forest canopy showing details of vegetation and open spaces. Crowns (empty polygons) are visible from the sky, while shaded crowns are not. The thick line is the possible representation of the forest canopy through remote sensing. This defines the collection of crowns touching the canopy surface. A indicates an Overstory / canopy gap; B: Understory / subcanopy gap; C: Gap extending through all strata (canopy and subcanopy); D: No gap. Current remote sensing technology has the potential to identify A, C and D (in the overstory) types of gaps

Radar sensors operate on the principle that microwave radiation received by the sensor, or backscatter, is proportional to the amount and organization of canopy elements. Shorter wavelengths are more sensitive to smaller canopy elements (foliage, twigs) while longer wavelengths are more sensitive to large canopy elements (trunks). However, vegetation heights are derived indirectly through model based inversions which are subject to uncertainties using radar-based SAR interferometry and signal saturation at relatively low biomass in SAR data (Naeff et al. 2005, Mette et al. 2004, Baltzer et al. 2003)

In recent decades, airborne laser scanning, also known as LiDAR (Light Detection And Ranging, hereafter referred to as lidar), has manifested its role in directly generating high precision 3-D information on land surface characteristics at a high resolution (Lefsky et al. 2002). Due to the capacity of laser signals to penetrate through small openings in the canopy, it is the only technique capable of reliably retrieving ground elevations under a forest cover (Wehr and Lohr 1999). Thus, lidar has attracted much attention in forestry and ecological studies. Lidar has been used to derive biophysical characteristics of vegetation e.g., tree height (e.g., Hyyppä et al. 2001), crown diameter (Popescu et al. 2002), tree density (e.g., Hall et al. 2005), basal area (Lefsky et al. 1999), biomass (e.g., Lim and Treitz 2004). Lidar can be combined with other means of remote sensing to study forest productivity (Vega and St-Onge 2008), biodiversity (Goetz et al. 2007), carbon inventory (Nelson et al. 2004), wild life habitat analysis (Hyde et al. 2006), rangeland vegetation classification (Bork and Su 2007), river bank erosion assessment (Thoma et al. 2005), *etc.*

1.3. LIDAR - AN OVERVIEW

The principle of lidar is based on combining information on range, location and measurement platform to yield the precise location of an object in three dimensional space. Starting as a navigational instrument in 1960, lidar has evolved and is now revolutionizing topographic mapping (St-Onge 2005). A lidar system consists of a laser range finder that has laser emitter / receiver optics, signal detector and amplifier, Inertial Navigational System (INS), scanner and a geodetic quality differential Global Positioning System (GPS) (Baltsavias 1999). A laser system that is mounted on an aircraft emits laser pulses at high frequencies, typically in the infrared wavelengths, to a surface (e.g. ground) that is then reflected back. A scanning mirror is used to direct laser pulses back and forth across a wide swath underneath the path of the airplane. INS that has a very high-accuracy timing device and a gyroscope, records the angle at which the laser signal is sent out, while a GPS determines its exact co-ordinates on the ground (Wehr and Lohr 1999). The swath width is a function of altitude above the ground and scan angle. Typically for land mapping an altitude of 700 m AGL (above ground level) is used to allow an acquisition swath of 300 m (Wehr and Lohr 1999).

The time elapsed between the laser pulse emission and the detection of its return on a surface by the airborne sensor is converted to a range, and combined with differential GPS and inertial data, to calculate the precise *X, Y, and Z* geoposition of each return with accuracies of approximately 15 cm. and 40 cm. or even better, respectively (Krauss and Pfeifer 1998, Davenport et al. 2004). The pulse rates range between 2 kHz to 167 kHz depending on the manufacturer's design and intended application (Fowler 2000). Flying heights can be quite varied, sometimes well over 1 km, depending on the point density and swath width desired by the customer. A laser pulse has a diameter that varies as a function of the AGL altitude of the acquisition system and divergence angle (e.g. 0.1 mrad divergence from 1000 m gives a half-power width footprint of approximately 10 cm). On a well defined horizontal surface, the footprint size of the single return will be that of the pulse diameter, however, when intercepted by a complex volume such as a forest canopy with multiple strata, more than one return will be recorded. Small footprint laser pulses can propagate through small canopy openings to produce dense and accurate (5-20 cm) ground elevation measurements.

Modern airborne lidar sensors are described as either "discrete" (i.e. time-of-flight) or "waveform" depending on how they sample. Discrete systems record one or few returns for each transmitted laser pulse. The first return or pulse is the first interception of the signal that describes the surface visible from the sky, such as the canopy surface. The peak of the last attenuation of the signal is associated with the ground surface. Waveform systems record the amount of energy returned to the sensor over equal intervals of time (called bins). The number of these intervals determines the level of details of a surface within the laser footprint. As the size of the footprint alters the ability of the laser pulse to penetrate the vegetation, the chance of not receiving the last return from the ground increases with a decrease in footprint size (Chasmer et al. 2006). However, for systems such as Optech, the beam divergence can be set for different acquisitions allowing, for example, an increase in the penetration rate into the vegetation. In this study, we use data from Optech small footprint discrete lidar systems.

Discrete laser data point returns are acquired over an area in strips. To avoid data gaps between strips as a result of aircraft movement (roll), overlapping flight lines are flown. The current commercial systems can record upto 10 returns / m^2. The multi-return point clouds are then classified into at least two classes, ground and non-ground returns using special filtering techniques. . The first return point clouds can be readily used as a DSM without processing. The filtering of the last returns, however, is cricital to ensure that they are the ground level echoes. The most popular of the algorithms being currently used is Terrascan (Terrasolid Inc.). The area to be classified is first divided into cells of a coarse size (several tens of meters). Assuming the lowest return to be from the ground, a DEM using TIN is generated. Iteratively, remaining points are examined for inclusion with certain criteria and the DEM is redefined. When a candidate point is examined the algorithm evaluates if a smooth route exists between the current ground and candidate points. A point is accepted when the angle between the underlying triangular plane and a line connecting the candidate point with the closet vertex of a triangle, as well as distance between the candidate point and the triangukar surface, is within the user-defined values. Positional accuracy of the lidar *xyz* data points generated by most lidar systems is assumed to be very high. The altimetric accuracy (z) is evaluated by comparing laser positions to points surveyed in the field using a high grade GPS with sub-centimeter accuracy.

1.4. LIDAR AS A TOOL FOR STUDYING CANOPY STRUCTURE

The classified raw lidar point returns in 3-D space are generally gridded to have an image-like visualization and for the convenience of using image analysis software for further analysis (Fig.1.2.). These irregularly spaced points are interpolated with appropriate techniques and resolution to derive high resolution surface models. Previous studies suggest that a grid resolution should be close to the original point spacing with nearest neighbour, TIN (Behan 2000), bilinear (Smith et al. 2005) interpolations for urban applications and IDW or kriging interpolations for bare-earth models in natural environments (Lloyd and Atkinson 2002). However, optimal interpolation techniques for vegetation surfaces have rarely been studied. The

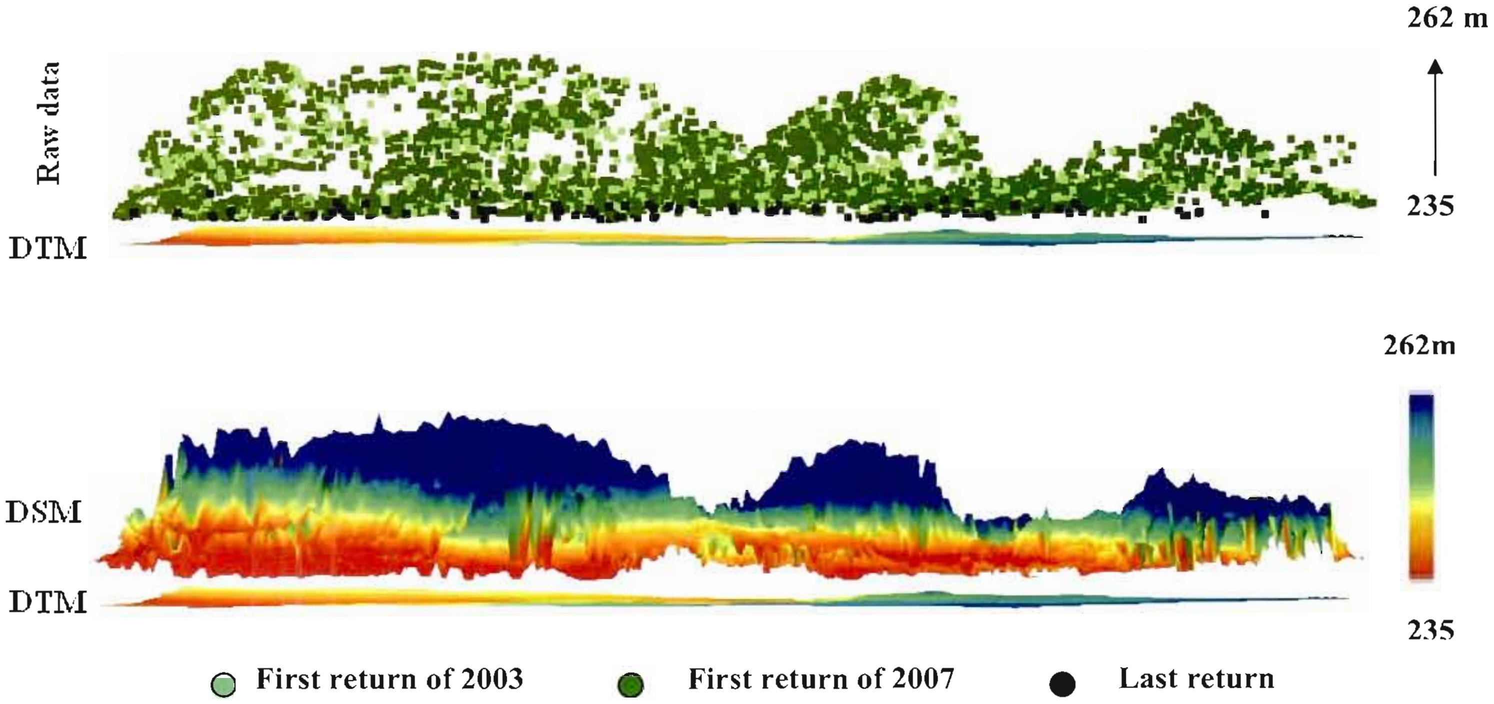

Figure. 1.2. An example of the distribution of raw lidar data points and gridded data in a 40 m X 15 m strip in the study area. (a) First (from two time surveys indicating growth in the vegetation) and last raw laser return data over the gridded DTM. (b) DSM and DTM surfaces

interpolation of a subset of last returns gives bare earth topography (digital terrainmodel, DTM) while that of first returns gives surface height (digital surface model, DSM), for e.g., vegetation or building height. As discussed earlier, the arithmetic difference of the two surfaces is the Canopy Height Model (CHM).

1.4.1. Accuracy of ground elevation, tree identification and tree height estimated from small footprint lidar data

The accuracy of tree height measured from any remote sensing technique requires an accurate ground elevation determination under the canopy (see Section 1.2.). Measurements from remote sensing techniques that are taken from the sky provide the canopy surface height. The accuracy of lidar DTMs is superior to that of other types of DTMs. Comparing lidar DTM, conventional DTMs (USGS levels 1 and 2) and an IFSAR (Interferometric Synthetic Aperture Radar) DTM, and a lidar DTM to accurate field measurement, Hodgson et al. (2003) reported that the lidar DTM had the lowest root mean square error (0.93 m). The mean lidar DTM error under various forest canopies did not exceed 0.31 m in two recent studies using different lidar systems (Reutebuch et al. 2003, Ahokas et al. 2003).

In lidar-based approaches, tree height was measured as individual tree height and average tree height over a given plot or grid. Numerous previous studies have shown a high correlation between tree height measurements acquired from lidar and those acquired using traditional field methods with an r^2 higher than 0.85. On a sampled grid maximum lidar heights of Norway spruce above ground level correlated well ($r^2 = 0.91$) with Lorey's mean tree height (Naesset 1997). Similarly, lidar quantile heights matched within 6% of plot canopy height measured from the ground (Magnussen and Boudewyn 1998). Tree height underestimation due to laser penetration, missing tree apex or ground height inaccuracies was also noted (Nelson et al. 1988, Naesset 1997, St-Onge et al. 2000, Lim et al. 2003)

With advancements in lidar technology, pulse frequency and hence return density has increased our ability to identify individual trees. A semi-automated segmentation algorithm based on pre-filtered local maxima and subsequent dominant coniferous tree height (Hyyppä et al. 2001) and multi-scale segmentation on Gaussian smoothed data in a deciduous forest (Brandtberg et al. 2003) reported an accuracy better than 1 m. The heights of 36 trees identified from a Laplacian of Gaussian filter on the CHM, St-Onge et al. (2000) found a good agreement with corresponding ground measurements (r^2=0.90, significant at 0.01). Tree apices derived from morphological analysis of lidar surface matched to within 1 m of photo-identified ones (Anderson 2001).

1.4.2. Gap detection using lidar

Being an active remote sensing system, which does not rely on sunlight, and having a dense coverage of point clouds of data, lidar overcomes the limitations of conventional remote sensing in detecting canopy gaps. However, so far only two studies have been conducted in delineating canopy gaps (St-Onge and Vepakomma 2004; Koukoulas and Blackburn 2004) and one on harvested trees (Yu et al. 2004). St-Onge and Vepakomma (2004) use a region growing algorithm on the binary grid generated using a gap indicator function to map new gaps that opened during a period of 5 years in mixedwood boreal forests. Selecting a height threshold of 4 m based on the steepest slope values, Koukoulas and Blackburn (2004) used grid morphological functions applied to a lidar CHM to delineate gaps in a semi-natural deciduous woodland. A visual comparison of the results in both studies to those on high resolution optical images indicates the feasibility of detecting a canopy gap. Yu et al (2004) is the only study that verified tree harvest results against ground values, however, none of the studies attempted to address other ecologically important gap dynamic parameters, like gap closure and gap expansion.

1.4.3. Growth assessment using lidar

Research to detect changes in structures using repeat surveyed lidar data is new. Some applications have been made in studying coastal morphological changes (Brock et al. 2004), urban building damage (Vu et al. 2004), snow pack depth (Hopkinson et al. 2004) and characterising landslides (Corsini et al. 2007). Owing to its high accuracy and the improving density of lidar, change detection in forest canopies should be feasible. Although a large quantity of research has been carried out in deriving accurate forest metrics from lidar, studies on monitoring forests using lidar have been limited because high density discrete return surveys are still very recent. Yu et al (2004) effectively detected harvested trees and assessed plot-level growth over two years with 10 to 15 cm precision using a single tree segmentation algorithm in Norway spruce- Scots pine plantations. Co-registering and accounting for discrepancy in lidar ground elevation between the two surveys, St-Onge and Vepakomma (2004) identified new canopy gaps and found expected growth patterns at the individual tree and plot-level over 5 years in a mixedwood boreal forest. Using tree matching techniques on high density discrete small-foot print lidar, Yu et al. (2006) showed a good correspondence of five year tree height growth of Norway spruce and Scots pine with field measurements (r^2 of 0.68 and RMSE of 43 cm.). Similarly, Naesset and Gobakken (2005) assessed lidar metrics over two years at the plot and stand level using mature and immature conifer plots and found that although the predictions were weak, growth was statistically significant. Hopkinson et al., (2008) evaluated uncertainty in measuring growth in conifer plantations using various lidar height percentiles at the plot and stand level. The uncertainty in growth estimates over three years were 42% at the plot and 92% at the tree level. However, they found that lidar was sufficiently sensitive to detect growth at annual steps in conifer plantations.

1.5. CENTRAL OBJECTIVE OF THE RESEARCH PROJECT

The primary contributions of this thesis are in developing methods to detect changes in the forest canopy and in improving our understanding of gap disturbance regimes, their spatiotemporal dynamics and forest responses to these dynamics in boreal mixedwood forests using multi-temporal lidar. This knowledge on structure and species compositional changes is extended to understand how stands affected by different disturbances respond to small gap openings in the short-term. The results from this thesis will hopefully provide new insights for natural disturbance based silviculture and forest management strategies. The methods developed can be replicated easily in other forest ecosystems, and when combined with conventional optical remote sensing, there will also be an increased ability to understand long-term forest dynamics.

1.6. SPECIFIC OBJECTIVES AND THESIS ORGANISATION

This thesis is based on four articles addressing a combination of methodological and ecological questions. Methods necessary to prepare multi-temporal lidar data for canopy gap delineation and height growth are developed in chapters II andIV. Forest responses to canopy openings at local scales in terms of growth are studied in Chapters IV andV, while species replacement and response in terms of mortality in Chapter III. The role of canopy gaps in stand development is investigated in Chapter III.

In Chapter II, our major goal was to evaluate the feasibility and advantages over field techniques of using small footprint lidar to map boreal canopy gaps of various sizes and identify spatial and temporal gap dynamic characteristics like gap expansions, random gap occurrences, canopy closure, regenerating gaps and laterally closing gaps. Hence our objectives were (1) to develop the fundamental methods necessary to compare two lidar datasets that were generated with dissimilar lidar systems (2) find optimal interpolation techniques and grid resolution necessary to delineate gaps reliably with accurate geometry on the resulting lidar surface (3) to propose and verify with field reference data the automated detection of canopy gaps observed on the lidar surface and (4) develop methods to identify gap dynamic characteristics.

In Chapter III, our principal aim was to gain a deeper perception of the response of stands in different developmental stages (i.e. affected by different disturbances in the past; fire and spruce budworm) to small gaps with the aim of understanding the interactions of disturbances on stand development. Hence the objectives were to spatially map and characterise (1) structural and (2) compositional changes occurring in different time-since-fire stands during a short-time window (1998-2003) in 6 km^2 of boreal mixedwood forest. The gap disturbance regimes for each stand were mapped on a lidar surface using the methods developed in Chapter II and object-oriented species group mapping using high resolution images.

In Chapter IV, the principal ecological goals are to gain new insights into (1) how mixed conifer- hardwood boreal forests respond to variously sized canopy openings and (2) the extent to which these canopy gaps influence the growth of saplings growing within a gap and trees ,across the forest matrix. Our aim was also to understand (3) which mechanisms (lateral growth or height growth) of gap closure are important in boreal forests and (4) how growth responses vary with spatial location with respect to the gap edge to determine the optimum opening sizes for maximum growth.

To achieve these ecological goals in Chapter IV, our primary methodological objectives were to develop methods to explore the potential for multi-temporal lidar data to characterise the height-growth responses of boreal forests to the opening of canopy gaps at the tree level. Specific objectives were to (1) propose a validated scheme to locate individual tree / sapling tops; (2) extract height-growth of trees / saplings over time; and (3) propose methods to quantify the extent of gap influence on height-growth. We combine the strengths of lidar and high resolution multispectral imagery to characterise the different height growth responses of broad species classes (hardwood vs conifer) to canopy openings.

In Chapter V, our main objective was to examine whether height growth patterns of advance regeneration differ according to the type of gap event i.e. old existing gap, expanded gap and random new gap that occurs in boreal forests. Methods developed in chapters 2 and 4 were applied on a time series of three lidar datasets in the study area.

Finally, Chapter VI presents a synthesized review of the results from the previous chapters. It discusses the applicability and limitations in the suggested methods and proposes future directions of this research.

1.7. STUDY AREA

The 6 km^2 study site is located within the Conservation Zone (79°22' W, 48°30' N) of the Lake Duparquet Research and Teaching Forest situated at the southeastern limit of the boreal forest. This is part of the balsam fir – white birch bioclimatic region within Rowe's (1972) Missinaibi-Cabonga forest section. This forest covers part of the clay belt of Quebec and Ontario, a major physiographic region resulting from deposits left by the proglacial Lakes Barlow and Ojibway at the time of their maximum expanse during the post-Wisconsinian period (Vincent and Hardy 1977). Lake Duparquet is part of a vast watershed that drains northward through Lake Abitibi to James Bay. The region has relatively level topography (227 m and 335 m) interspersed with a few small hills. The closest meteorological station to our study area is at La Sarre, approx. 42 km to the north. The regional climate is described as subpolar, subhumid, continental with 0.8° C mean annual temperature, 857mm of average precipitation and a growing season that lasts 160 days (Environment Canada 1993). Snow represents 25% of the total yearly precipitation. Most liquid precipitation falls during the growing season but evaporation can limit plant growth in both June and July. The frost free period lasts 64 days on average, but occasional frost episodes may occur anytime during the growing season. 63% of the study site is covered by forest and nearly 29% of the lands can be flooded in the spring. Surface deposits are largely clays, tills or rocky outcrops.

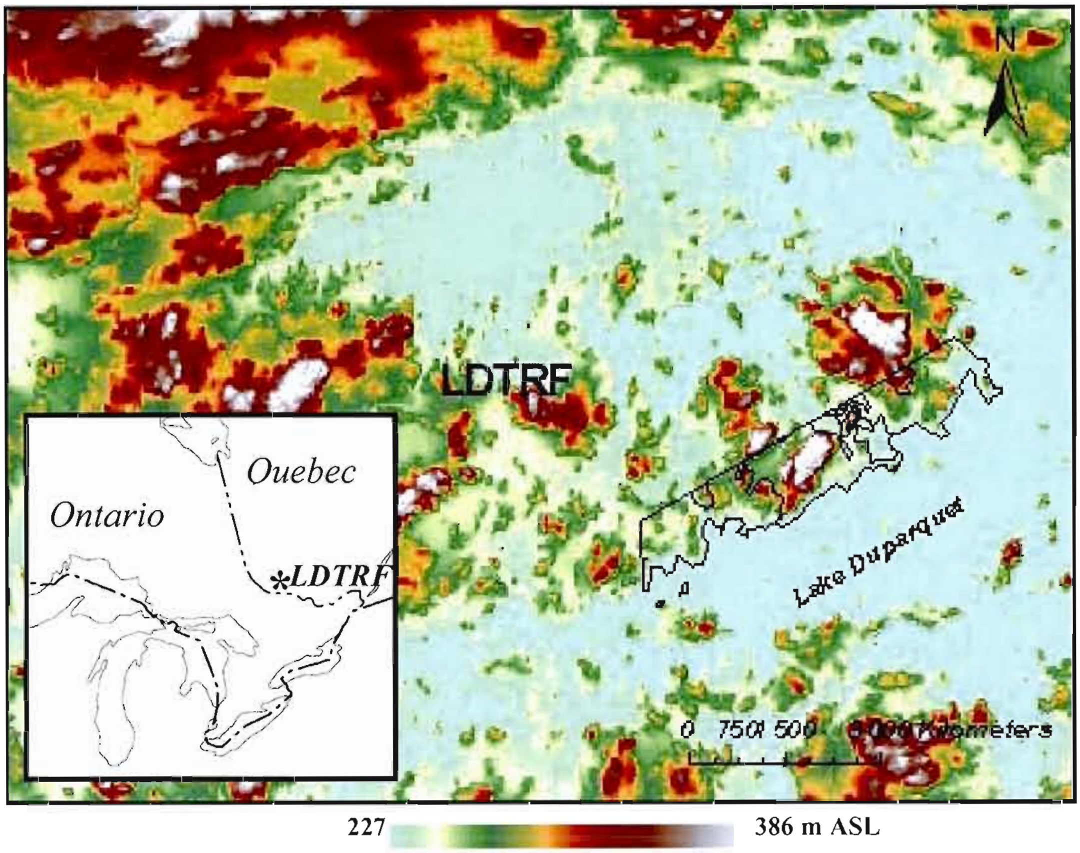

Figure 1.3. Location of the study areas and the Lake Dupartquet Research and Teaching Forest, in western Quebec.

This part of the boreal forest is largely dominated by mixed wood stands which originated from different fires dating from 1760 to 1944 (Danserau and Bergeron 1993). Most stands (98%) in this forest are mature or over mature attaining ages over

50 years. Compositionally, forests within the study area are either mixedwoods (75%) or coniferous (25%). These forests have maximum heights that vary between 20 – 25m. Balsam fir (*Abies balsamea* L. [Mill.]) is the dominant species in mature forests and is associated with white spruce (*Picea glauca* [Moench] Voss), black spruce (*Picea mariana* [Mill] B.S.P.), white birch (*Betula paprifera* [Marsh.]) and trembling aspen (*Populus tremuloides* [Michx]). Eastern white cedar (*Thuja occidentalis* L.) is also a late successional associate of balsam fir on mesic sites and is found on shore lines and rich organic sites. All of the hardwood species found in this part of the boreal forest are shade-intolerant while the softwood species growing on the mesic sites are shade-tolerant (Kneeshaw et al. 2006).

The main disturbances in this area are forest fire and spruce budworm outbreaks (Bergeron 1998; Morin et al. 1993). The fire history of stands surrounding Lake Duparquet was reconstructed using dendroecological techniques (Dansereau and Bergeron 1993) showing a considerable decrease in the frequency and extent of fires since 1850 (Bergeron and Archambault 1983). The fire cycle was estimated as 63 years for the period 1700 - 1870, and more than 99 years for the 1870 – 1990 period (Dansereau and Bergeron 1993). Three major spruce budworm (*Choristoneura fumiferana*) epidemics were recorded for the 20th century by Morin et al (1993), with the 1972-1987 outbreak resulting in the death of most fir trees. Defoliation due to a forest tent caterpillar (*Malacosoma disstria*) outbreak in the 20th century was also reported as causing a decrease in hardwood species (Bergeron and Charron 1994). Although part of the forest was selectively cut, much of the forest in this site is relatively virgin and remains unaffected by human intervention (Bescond 2000).

CHAPTER II

Spatially explicit characterization of boreal forest gap dynamics using multi-temporal lidar data

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2.1 RÉSUMÉ

L'étude des caractéristiques spatiales et temporelles est nécessaire afin de comprendre un régime de perturbation tel que la dynamique de trouées. L'utilisation de données terrain ou d'images de télédétection à deux dimensions permet difficilement d'observer et de mesurer des trouées spatialement et temporellement. Ces difficultés s'accentuent particulièrement en forêt boréale ouverte ou fragmentée. Dans cette étude, nous avons évalué la faisabilité d'utiliser l'altimétrie laser afin de cartographier des trouées de canopée de taille allant de quelques mètres carrés à plusieurs hectares. Deux modèles de hauteur de canopée de résolution optimale ont été créés à partir de données altimétriques laser en 1998 et 2003. Les trouées ont été automatiquement délimitées en utilisant une technique orienté-objet avec une précision de 96 %. La combinaison des deux modèles de hauteur de canopée avec les trouées délimitées a permis d'évaluer la croissance latérale de la végétation adjacente et la croissance verticale de la régénération, et d'ainsi obtenir des informations sur la proportion de la forêt en vieilles ou en nouvelles trouées, sur les taux de fermeture causée par la croissance latérale de la végétation adjacente ou par la croissance verticale, et en nouvelles trouées aléatoires. Les résultats obtenus démontrent que l'altimétrie laser est un excellent outil pour obtenir rapidement des informations spatialement explicites.

Mot-clés: lidar, modèle de hauteur de couvert, dynamique des trouées, forêt boréale

2.2. ABSTRACT

Understanding a disturbance regime such as gap dynamics requires that we study both the spatial and temporal characteristics of disturbance. However, it is still difficult to observe and measure canopy gaps extensively in both space and time using field measurements or bi-dimensional remote sensing images, particularly in open and patchy boreal forests. In this study, we investigated the feasibility of using small footprint lidar to map boreal canopy gaps of sizes ranging from a few square meters to several hectares. Two co-registered canopy height models (CHMs) of optimal resolution were created from lidar datasets acquired respectively in 1998 and 2003. Canopy gaps were automatically delineated using an object-based technique with an accuracy of 96 %. Further, combinatorics was applied on the two CHMs and the delineated gaps to provide information on the area of old and new gaps, gap expansions, new random gap openings, gap closure due to lateral growth of adjacent vegetation or to vertical growth of regeneration. The results obtained establish lidar as an excellent tool for rapidly acquiring detailed and spatially extensive short-term dynamics of canopy gaps.

Keywords: lidar, canopy height models, canopy gap dynamics, boreal forests

2.3. INTRODUCTION

Research in various forest ecosystems has demonstrated that in the absence of large-scale disturbances like fire and insect infestation, forest canopy dynamics in mature and old -growth forests are driven by local gap dynamics (Runkle 1981; Kneeshaw and Bergeron 1998). Small, partial disturbances due to snapping, blow down, insects or pathogens creates canopy openings termed "gaps". They increase space and site resource availability and eventually are closed by tree regeneration or lateral growth of surrounding vegetation determining a new canopy structure (McCarthy 2001; Bongers 2001). Gaps are important for certain tree species to attain canopy status in mature forests (Denslow and Spies 1990). They play an important role in maintaining species heterogeneity and in driving successional dynamics (Payette et al. 1990, Frelich and Reich 1995). Hence the accurate characterization of these disturbances will not only have a direct impact on our perception of ecological processes but also on the quality of management practices when gap dynamics are adopted as a template for ecosystem-based management.

Gaps are characterized by their size, shape, rates at which they open and close and the causes of such events (Denslow and Spies 1990, Runkle 1991). Although traditional ground (Runkle 1991, Lertzman and Krebs 1991, Battles et al. 1995, Kneeshaw and Bergeron, 1998) and conventional remote sensing based methods (Fox et al. 2000; D'Aoust et al. 2004; Jackson et al. 2000; Foody et al. 2003) have provided useful results on tree replacement and resource heterogeneity, they are limited in their ability to represent spatial patterns and temporal dynamics. In fact, most research has been at the scale of only a few gaps, restricted to evaluating current forest conditions, or has been based on space-for-time substitution. Retrospective studies through long-term installations of permanent sample plots or through dendrochronology are costly and time consuming, while simulation models use arbitrary areal units, and often include random initial conditions. Moreover, conventional remote sensing based methods (aerial photography, bi-dimensional analysis of space images) have been criticized for their inadequacy in gap identification due to illumination conditions and spectral inseparability (Tanaka and Nakashizuka 1997, Koukoulas and Blackburn, 2004).

Characterizing and understanding the pattern and dynamics of these ecological processes relies on the study of the horizontal and vertical arrangement of forest canopies over time (Parker 1995). Canopy structure, defined as an organisation of leaves, twigs and branches of a stand of vegetation in space and time (Parker 1995, Bongers 2001), can be described in three-dimensions using a Canopy Height Model (CHM), which is typically a raster surface representing canopy height. A CHM is thus a spatially-explicit description of canopy structure over a given area of forest and is generally obtained by calculating the difference between the elevations of the canopy surface (given by a Digital Surface Models, DSM) and the underlying terrain (Digital Terrain Model, DTM). Ground-based techniques like using graduated height sticks (Fujita et al. 2003), spatial analysis of stem-mapped point data (Song et al. 2004; Larson and Franklin 2006), hemi-spherical photography combined with stem maps (Valverde and Silvertown 1997; Silbernagel et al. 2001), and aerial photography combined with ground measurements of elevation at regular intervals (Tanaka and Nakashizuka 1997; Fujita et al 2003; D'Aoust et al. 2004) have been used to study forest disturbance and their consequences on canopy structure and composition over time by constructing CHMs. Ground methods are costly and tedious, often inaccurate due to the difficulty of GPS positioning in forest environments, and cannot be used extensively. The quality of CHMs and of the gap delineation derived through the analysis of aerial photographs is affected by image texture and contrast, sun-incidence angles during image acquisition, resolution, but most importantly by the accuracy of ground elevation measurements. Assessing ground elevation is critical for determining canopy height but remains very difficult when performed photogrammetrically on aerial images acquired over closed canopies (St-Onge et al. 2004). Various studies using aerial photography noted its unreliability in detecting smaller (< 100 m^2) and deeper gaps (Nakashizuka et al. 1995, Miller et al. 2000, Fujita et al. 2003; Betts et al. 2005). It was also observed that the degree of error in estimating canopy height (or gap depth) increases with higher topographic relief (Tanaka and Nakashizuka 1997).

Recently, the use of new remote sensing technologies like scanning laser altimetry, hereafter referred to as lidar (light detection and ranging), has attracted attention in forestry and ecological studies (Naesset 2002, St-Onge et al. 2004, Hyde et al. 2006). Lidar sensors directly measure the three-dimensional distribution of plant canopies as well as sub-canopy topography, thus providing high-resolution topographic maps and highly accurate estimates of vegetation height, cover, and canopy structure (Baltsavias, 1999, Naesset, 2004, St-Onge et al. 2004). Numerous studies have verified the capacity of lidar, using small (1 m or less) as well as large (10-25 m) diameter footprints, to measure canopy height and canopy vertical structure in a variety of forest ecosystems (e.g., Harding et al. 2001, Parker et al. 2001, Clark et al. 2004). Studies have also shown that retrieval of ground elevations by lidar is superior to that of any other means of remote sensing (Krauss and Pfeifer, 1998, Hodgson et al. 2003, Clark et al. 2004).

Recent studies have demonstrated the potential of LiDAR systems in delineating canopy gaps (Yu et al. 2004, St-Onge and Vepakomma, 2004, Koukoulas and Blackburn, 2004) and could successfully overcome many of the limitations associated with conventional remote sensing methods. Koukoulas and Blackburn (2004) use a rule-based algorithm on a single-time CHM to measure gap sizes (over 50 m^2) and gap shapes. Yu et al (2004) apply a single-tree segmentation using high density (10 returns/m^2) multi-temporal lidar data to identify individual harvested trees reliably (crown radius of over 1 m). Its applicability, however, is restricted to high density lidar data. The early results of these few studies tested on semi-natural forests and plantations (Yu et al. 2004, Koukoulas and Blackburn, 2004) are promising, but still need to be extended to more complex forest structures like old-growth mixed wood forests. St-Onge and Vepakomma (2004) reliably identified newly opened gaps of size less than 1 m^2 in mixed forests. Nevertheless, none of the studies attempt to address other ecologically important dynamic characteristics of gaps, like gap closures and gap expansions.

Gap detection and delineation of its boundaries using any technique is a complex task. A basic assumption is that the gaps are easily distinguishable from the surrounding high canopies. Various researchers, depending on the type and height of forest, have proposed a critical regeneration height (adopting either a relative difference or absolute thresholds on vegetation height) beyond which the gap is considered closed (Nakashizuka et al. 1995, Fujita et al. 2003, St-Onge and Vepakomma, 2004). Such a threshold on a single-time CHM helps in mapping gaps in the canopy at a given time. However, this approach would be ambiguous in distinguishing between gaps created due to tree falls and natural spaces (interstitial space) between tree crowns. This method would be particularly difficult in slow-growing boreal forests as many stands may not have achieved full-grown crown closure, making the canopies appear open and patchy, and because coniferous trees naturally have large inter-tree distances. Moreover, gaps could be considered to be a result of treefall events over successive periods of time (Runkle and Yetter, 1987, Foster and Reiners, 1986) and thus gap formation rates (fraction of ground area converted to new gaps annually) determined based on a single year could lead to an overestimation of true rates.

Given the high accuracy and density of lidar returns, and given the fact that they are obtained from near nadir angles, we hypothesize that the proportion of laser pulses reaching the gap floor should be quite high, enabling the accurate delineation and near perfect interpretation of gap geometry. A new gap of any size resulting from tree fall should create a large negative elevation difference between diachronic CHMs, while a significant height increase over time within a detected gap should indicate canopy closure. Diachronic analysis will also help in filtering out the interstitial spaces between tree crowns to reliably estimate the turnover rates of canopy gap opening and closing that is naturally occurring in old-growth forests. Based on the sensor's characteristics and early studies, the potential to advance our knowledge on gap dynamics through multi-temporal lidar remote sensing appears very high. However, before this can be achieved the necessary fundamental methods need to be elaborated and verified.

The general objective of this study is to evaluate the feasibility of reliably mapping canopy gap opening and closure based on two small footprint lidar datasets separated by a five year interval. This is achieved by first standardizing the lidar datasets through co-registration, selecting an optimal interpolation method and grid resolution suitable for delineating small gaps, and validating the results with ground verification. We then proceed to spatially and temporally characterize gaps in terms of frequency, size and nature of the gap event. The density and rates of gap opening, gap expansion and gap closure (both lateral and vertical) are derived by differentiating recent random gaps from expanded openings and recent gap closures by crown displacement through lateral growth or by regeneration.

2.4. METHODS

2.4.1. Study site

The study was conducted in a 6.0 km^2 area located within the conservation zone (79°22' W, 48°30' N) of the *Lake Duparquet Teaching and Research Forest, LDTRF* (Fig. 2.1). This area is part of Quebec and Ontario's Claybelt and has relatively level topography (227-335 m) interspersed with a few small hills. The climate is described as subpolar, subhumid, continental with 0.8° C mean annual temperature, 857 mm of

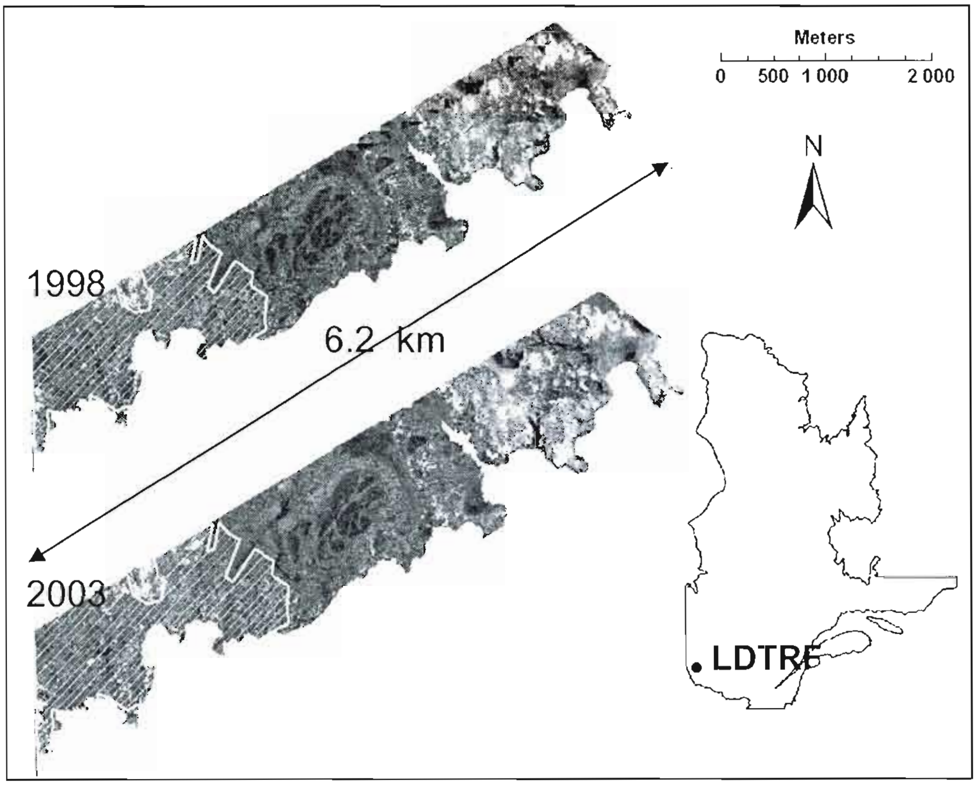

Figure 2.1. Location of the Lake Duparquet Teaching and Research Forest (LDTRF), Quebec and lidar coverage in 1998 and 2003. Hashed polygons indicate the areas where complete analysis was performed.

average precipitation, an average of 64 days of frost and 160 growing season days (Environment Canada, 1993). Stands within the LDTRF originated from different fires dating from 1760 to 1919 (Dansereau and Bergeron, 1993). Most stands are mature or over mature and reach heights of 20-25 m. Balsam fir (*Abies balsamea L.* [Mill.]) is the dominant species in mature forests and is associated with white spruce (*Picea glauca* [Moench] Voss), black spruce (*Picea mariana* [Mill] B.S.P.), white birch (*Betula paprifera* [Marsh.]) and trembling aspen (*Populus tremuloides* [Michx]). The main disturbances in this area are forest fire and spruce budworm outbreaks, while individual or group mortality, and wind throw have also been reported (Dansereau and Bergeron, 1993, Morin et al. 1993, Harper et al. 2002). Although part of the forest was selectively cut during 1920-40, much of the forest is relatively virgin and remains unaffected by human intervention (Bescond, 2002). Canopy gap delineation was conducted for the entire study area while characterisation of gap dynamics was made within a 225 ha area of the 258 year old stand (originated following fire in 1760).

2.4.2. Lidar data acquisition

The study site was surveyed on June 28th 1998 and August 14 to 16, 2003, determining an interval of approximately five growing seasons (Fig. 2.1). The 1998 survey was carried out using an Optech ALTM1020, a single return lidar system, at an altitude of 700 m. Because this lidar could not record both first and last returns in one pass, and had a low impulse frequency, two passes for each flight line were made to acquire the first returns, and one for the last returns. The overlap between adjacent swaths was minimal, resulting in some small data lacunae in the first returns. The data were registered to ground profiles surveyed with a high grade GPS and tacheometer. All returns were classified by the provider as ground or non ground using the REALM software application from Optech Inc. and were assumed correct for the study. First returns not classified as ground were used to generate a vegetation surface (DSM) while first and last returns that were classified as ground were used to generate a bare earth model (DTM).

The 2003 survey was conducted using Optech's ALTM2050 lidar flown at 1,000 m AGL, such that the first and last returns were recorded for each pulse, with a 50% overlap between adjacent swaths. The data was registered to new ground profiles. The inter-swath geometrical fit was improved using the TerraMatch algorithm by Terrasolid Ltd. (Helsinki). The last returns were classified as ground or non-ground using the Terrascan algorithm of Terrasolid. The ground-classified last returns were used to build the DTM, while the DSM was created using all first returns. Table 2.1 presents the key survey and lidar instrument parameters. Although the specifications of the lidar instruments used in the two surveys differed in many aspects, e.g., flight altitude, scan angle, pulse frequency, the most important difference was in terms of point density (Table 2.1).

Table 2.1.
Specification of the lidar data acquisition

Specification	*1998*	*2003*
Lidar	ALTM1020	ALTM2050
Power	140uJ	200uJ
Flight altitude (m AGL)	700	1,000
Divergence (mrad)	0.3	0.2
Footprint size at nadir (cm)	21	20
Pulse frequency (Hz)	4,000	50,000
Max. scan angle (degrees)	10	15
First return density (hits/m^2)	0.3	3
Ground return density (hits/m^2)	0.03	0.19
Classification software	REALM	Terrasolid

Both lidar datasets were assessed for accuracy in two different studies (Coops et al. 2004, Vega, 2006). Clearly identifiable hardwood and softwood trees, 36 (for 1998) and 77 (for 2003) in a height range of 5.6 m – 33.1 m, were field measured for maximum tree height. The relationship between field measured maximum tree height and maximum lidar height for the delineated crowns was found strong (r^2 = 0.88 and 0.86 respectively) with an RMSE of 1.8 m and 1.85 m respectively.

2.4.3. Co-registration of the data sets

Prior to multi-temporal lidar analysis, one has to ensure that the datasets generated in two different surveys are perfectly co-registered as shifts in the *X*, *Y*, or *Z* axes would result in erroneous observations of canopy height change. Although the accuracy of lidar data is known to be very high, with errors below 30 cm for ground hits (Hodgson et al. 2003, Ahokas et al. 2003, Hodgson et al. 2004), a number of factors may affect the positional accuracy of lidar returns. These factors include the quality of the GPS configuration at the time of the survey, mounting errors, reference to ground calibration measurements, etc. (Katzenbeisser, 2003). Overall, these may lead to small systematic shifts or bias in the data. We hypothesized that there could exist a possibility that the two lidar datasets were slightly misaligned and hence verified the *XYZ* fit between them.

Shift in X and Y

First and ground-classified returns were interpolated with a 0.5 m resolution to produce a DTM in grid format for both years. Planimetric shifts were analysed ocularly using a number of visualization strategies (like hill shading, image transparency and swiping) applied to the DTMs and DSMs. The arithmetic difference between DTMs was computed and the resulting image was analysed for trends on sloping terrain, the assumption being that if any horizontal offset existed, it should be apparent as a pattern of negative and positive elevation differences around hills. After establishing that the planimetric shifts were negligible, we measured the average altimetric shift (Z-shift).

Shift in Z

Visual analysis of the DTM difference image indicated a possible shift in *Z*. To quantify and assess this shift, various statistical moments and percentiles were generated using (1) all the corresponding ground returns for 2003 falling within a 10 cm radius of the 1998 hits (matched pairs) and (2) all ground returns within a few rare patches of bare ground. Following these comparisons, the elevation of all the 1998 returns (both vegetation and ground) was lowered to remove the estimated bias (average altimetric difference) observed between 1998 and 2003 ground returns, using the 2003 data as a reference. Subsequently, we merged the 2003 and the adjusted 1998 ground returns to maximise the overall ground density.

2.4.4. Generation of surface models for gap delineation

Theoretically, the quality of gaps derived from lidar should be influenced by the acquisition system (laser instrument, INS and GPS), data characteristics (point density, flight altitude, scan angle) and interpolation errors. Decomposing the observed elevation error in the lidar data that reflected from brush / low trees, Hodgson and Breshanan (2004) found that lidar system errors were dominant (RMSE of 21.3 cm) followed by interpolation error (RMSE of 12.8 cm). System errors can be removed by strip adjustment or error modeling. Furthermore, interpolation of point clouds onto regular grids is a common technique adopted for surface visualization and subsequent extraction of features. Although lidar allows elevation sampling at remarkably high densities, rasterization using elevation data entails a certain amount of uncertainty (Lloyd and Atkinson, 2002, Anderson et al. 2005, Mitasova et al. 2005). The level of uncertainty varies with the interpolation method adopted and so does the accuracy of gap delineation.

Researchers have noted that the magnitude of predicted (interpolation) error has a strong spatial dependence with the greatest error occurring on feature edges (for e.g. Smith et al. 2005). By deriving predicted error, e at each point (x,y), as the difference between the raw lidar height value $Z(x,y)$ and the interpolated lidar height value $Z'(x,y)$ for that location, given as:

$$e(x,y) = Z(x,y) - Z^{'}(x,y) \qquad (1)$$

we also observed a similar trend following preliminary tests. Points well within the canopy area had the lowest prediction error ($e < 1$ m), while the edges of the crowns located on the periphery of gaps had larger predicted errors ($e > 1$ m). The choice of grid resolution also has a strong influence on the errors introduced during interpolation and, consequently, on gap delineation. Previous studies suggested that the optimal grid spacing should be close to the original data point spacing with nearest neighbour, TIN (Behan, 2000) and bilinear (Smith et al. 2005) interpolation techniques for urban applications. Besides, more points in each grid cell would lead to information loss while a smaller grid cell resolution would have more interpolated grid cells. For these reasons, in the context of reliable delineation of canopy gaps we have sought to identify the optimal combination of interpolation method and grid resolution for the DTM (with merged ground returns) and DSMs of both datasets.

The assessment and comparison of interpolation methods was carried out through cross-validation. Cross-validation is a standard validation technique used to identify an accurate surface interpolation algorithm where each measured point is removed and compared to the predicted value location using the remaining data points (Goovaerts, 1997). The prediction errors (e) were plotted against their measured values to observe the distribution graphically and in relation to the interpolated surfaces. In this study, an interpolation method was considered optimal when the Root Mean Square error (RMSE) of its predictions was minimum and the mode of the prediction error distribution was close to zero, specifically within the interval $[-1,1]$. RMSE being a global measure of deviation, as a more robust measure we also check the mode of the prediction error distribution.

Three test windows of approximately 200 m x 200 m representing different site and vegetation characteristics commonly found at the LDTRF were used for selecting the optimal interpolator and grid resolution, namely, low dense vegetation on undulating terrain (A), high and dense vegetation on gentle slope (B) and vegetation (of varying densities and height) with a large number of openings on gentle slope (C). Table 2.2 details the summary statistics of the merged ground and two time vegetation returns for the test windows chosen.

Table 2.2.
Descriptive statistics of the test windows extracted

Window	*Density (points/m2)*	*Minimum height (m)*	*Maximum height (m)*	*Mean height (m)*	*Standard deviation*
A	0.45	244.86	308.84	284.93	18.03
	0.58	245.10	314.89	279.54	17.70
	2.74	244.83	315.13	282.49	18.17
B	0.12	239.62	264.85	255.08	6.40
	0.31	240.17	286.89	264.78	10.04
	1.55	240.34	287.34	267.34	9.81
C	0.27	229.85	266.19	254.68	7.10
	0.42	230.86	280.16	259.60	7.90
	4.21	229.98	281.32	262.20	7.79

Cell vales indicate statistics of the merged ground (top), 1998 first (middle) and 2003 first (bottom) returns.

2.4.4.1. Selection of an optimal interpolation scheme

Data exploration and quantile-quantile plots of the three windows were first used to verify that the data met the assumption of normality (Table 2.2). We tested eight interpolation methods representing deterministic and exact interpolators (inverse distance weighted [IDW], completely regularised splines [CRS], thin plate splines [TP], splines with tension [ST], inverse quadratic [IQ]), deterministic and inexact interpolators (local polynomial [LP]) and a geostatistical interpolator (ordinary kriging [OK]) using the Geostatistical Analyst tool of ArcGIS v9.1 (Environmental System Research Institute, Redlands, CA). Though triangulated irregular networks (TIN) are considered to retain raw values at sample locations and substantially have less error into the surface model, the process of converting TIN into a gridded surface may modify the original lidar return values. This was also observed in our data during preliminary tests and hence TIN was considered unsuitable.

The size and shape of the search neighbourhood, or the number of points to be included determine how far and where to look for measured values used in prediction. We set a maximum of 10 measured points within a circular neighbourhood of radius 1 m. The algorithms within Geospatial Analyst determined the optimal power (which was 2 for all windows and interpolators) by minimizing the RMSE.

2.4.4.2. Selection of an optimal grid resolution

After establishing an optimal interpolator, the optimisation of grid resolution was based on two criteria, (1) to retain maximum number of laser returns in the interpolated grid i.e. minimise the loss of original lidar points in the individual surfaces (DSMs and DTM) generated for each of the test windows and (2) to minimise the number of spurious gaps delineated from the resulting CHMs. For this, we first generated, for each of the lidar datasets, several surface grids with varying grid resolutions (0.1, 0.2, 0.25, 0.5, 0.75 and 1 m) using the optimal interpolator, and compared the percentage of grid cells that had greater than one point per grid cell. Subsequently, we mapped all the new gaps for the surfaces of varying resolutions in each of the windows using the method for delineating new gaps with lidar CHMs (discussed in sections 2.5 and 2.8). Frequency distribution of new gaps and proportionate frequency of spurious new gaps in different resolutions were generated. A minimum grid resolution beyond which the percentage grid cells with more than one point considerably higher is regarded optimal in minimising the loss of lidar points. Similarly, a matching minimum resolution beyond which the percentage spurious gaps increase greatly is considered optimal for reliable gap delineation.

2.4.4.3. Generation of the surface models

The DTM of the merged ground returns was generated by taking the lowest ground point within each grid cell and filling the empty cells with the interpolated ground elevation obtained using the IDW algorithm. Selection of the lowest return reduces the risk of including lidar pulses that reflected from low vegetation but were misclassified as ground returns.

Similarly, the 2003 DSM was created by taking the highest point within each grid cell and supplementing the missing values with interpolated vegetation heights obtained using the IDW algorithm. This eliminated a large number of points that penetrated through the crown while otherwise preserving the original value of the lidar returns. However, due to the low density of points, the 1998 DSM was generated using the (exact) optimal interpolator alone. All the surfaces were generated with 0.25 m resolution within ArcGIS v.9.1. Subtracting the elevations of the merged DTM from the 1998 and 2003 DSMs respectively we created the canopy height models (CHMs) for these two years.

2.4.5. Gap delineation

In this study, a gap is considered as an opening in the canopy caused by the fall of a single or a group of trees of a certain height. Based on field knowledge (and also verified by Daniel Kneeshaw, personal communication) we chose 5 m as the height threshold below which areas would be identified as opening in the canopy, and above which the canopy would be considered closed. The edge of the gap is defined as the vertical projection of the canopy of trees adjacent to the gap. Open-ended systems like bare stream valleys, rock outcrops or marsh lands are not considered to be canopy gaps.

Formally, a gap indicator function G was defined for a given grid cell at (x,y) on the CHM_i as:

$$G_i(x,y) = \begin{Bmatrix} 1 & if\ CHM_i(x,y) < a \\ 0 & otherwise \end{Bmatrix} \qquad (2)$$

where a = 5 m in this study, $CHM_i(x,y)$ is the lidar height of the canopy surface in the ith year, (x,y) is a cell that does not belong to any open-ended system. A region growing algorithm was then applied to the resulting binary grid to identify individual objects of non-null adjacent pixels. We assume that the objects smaller than 5 m^2 in size (chosen arbitrarily) could be a result of spurious low vegetation lidar returns that penetrated deep into the tree crown or that they could correspond to natural interstitial space between tree crowns. Hence they were eliminated. To further ensure that the delineated gap objects are not a result of interpolation artefacts, we set an additional condition that at least three lidar vegetation data points (returns) fall within the gap.

2.4.6. Accuracy assessment of gap identification using lidar

Field verification for the lidar based gap delineation was done only for the 2003 data. Given that the lidar derived 1998 vegetation height is validated, we assume that the gaps delineated using the 1998 lidar data set and following the same procedure as described in Section 2.5, should produce similar accuracies. Despite the lower point density in 1998 this assumption is reasonable as the constraint on minimum number of lidar points and object size should eliminate spurious gap objects.

To validate the accuracy of gap identification using the 2003 lidar data, we conducted ground sampling along four randomly located line transects during September 2004. The total transect length was 980 m. A detailed visual comparison of high resolution panchromatic Ikonos satellite data (acquired in September, 2003) and Quickbird (acquired in June, 2004) made within the 200 m buffer zone around the chosen line transects showed no apparent change in the canopy due to natural disturbances between the 2003 lidar data acquisition and the field survey.

Any opening in the canopy having an average vegetation height of less than 5 m, associated with at least 80% of its perimeter composed of high canopy trees of height greater than 10 m, was recorded as a gap. Openings belonging to open-ended systems (like rivers, trails, wetlands etc.,) were not included. The initial point for each transect was fixed using a differential GPS. The transect was cruised by measuring every 5 m using a well calibrated Vertex III instrument in the set compass direction. All gaps that intersected the transect line were included in the sample. The length of the gap along each transect was measured to the closest decimeter using a Vertex III.

The accuracy assessment of the lidar delineated gaps on the CHM_{2003} was done individually for each transect by computing (i) the percentage number of gaps that were identified on lidar to the total number of gaps found on ground and (ii) the proportion of the total gap length along the transects as derived by the lidar to that of the ground measured length. Overall accuracy was assessed by considering the individual totals of columns (i) and columns (ii).

2.4.7. Improvement of gap geometry quantification using lidar

Deriving the exact gap geometry is fundamental for understanding and quantifying the patterns of gap disturbance (Battles et al. 1995). Gap shapes and size distributions help determine the extent of the disturbance and resource availability (Denslow and

Spies, 1990, Runkle, 1985). But its measurement is often very difficult by any method. Aerial photo based methods used so far (Nakashizuka et al. 1995, Tanaka and Nakashizuka, 1997, Fujita et al. 2003) have adopted a regular grid, the smallest size being 2.5 m X 2.5 m, wherein the scale of mapping restricts the geometry of gaps resulting in either over or under-estimation. When using ground-based methods, gaps sampled along line transects are generally approximated as ellipses by measuring the longest (major) axis and the longest (minor) axis perpendicular to the major axis (Runkle, 1985, Runkle, 1992). Owing to the high density of point cloud representing the elevation and near-nadir incidence angles, we assume that the lidar derived gaps will provide a highly reliable representation of the geometry of canopy gaps. To assess the improvement of gap geometry quantification brought about by lidar, we compared the gap size and shape of 34 automatically derived gaps on the lidar surface to their corresponding manually measured and ellipse approximations.

Area (A_l) and perimeter to area ratio (S_l) of the gap object were used for gap size and gap shape of lidar-derived gaps respectively. To replicate the ground-based measurements, we manually measured the major (a_{major}) and minor (a_{minor}) axes of each of the 34 new canopy gaps randomly selected from the lidar surface. For each of the gaps, we computed the gap area and shape approximated as an ellipse (respectively A_e and P_e) using:

$$A_e = \pi * a_{major} * a_{\min or} \tag{3}$$

$$P_e = 2\pi\sqrt{(a_{major}{}^2 + a_{\min or}{}^2) * (1/2)} \tag{4}$$

Differences in area (ΔA), perimeter (ΔP) and perimeter to area ratios ($\Delta P/A$) between the two methods (with lidar based estimates as a reference) were computed to quantify the gain in using lidar derived methods.

2.4.8 Mapping / studying gap dynamic characteristics

Establishing that the vegetation height and gap delineation using lidar is accurate, the multi-temporal lidar analyses was extended to map other important characteristics of gap dynamics that describe the nature of the gap event, namely, area of new gap opening, gap expansions, random gap opening, gap closures and closures from lateral and vertical growth of vegetation.

A new gap is defined as a gap in the canopy that opened between 1998 and 2003. New gaps that share the edge of a gap existing in 1998 are defined as gap expansions (see region D in Fig. 2.2), while the remaining new gaps are called new random gaps (see region F in Fig. 2.2). We define the vegetation with a height over 5 m as high canopy (see region A in Fig. 2.2). Gap closure occurs when an area with an average vegetation height below 5 m in 1998 increased to over 5 m during the period from 1998 to 2003. An adjacent high canopy can close a gap by crown displacement and lateral growth (see region B in Fig. 2.2), while the regeneration closes the gap vertically (see region E in Fig. 2.2).

We define G^i and G^j as the set of gap objects in the year i and year j respectively, where $i = 1998$ and $j = 2003$. The set of new gaps, N^{ij}, and gap closures, C^{ij}, $i < j$, were mapped using the following combinatorics on the gap objects:

$$N^{ij} = \{g \in G^j \mid g \notin O^{ij}\} \qquad (5)$$

$$C^{ij} = \{g \in G^{i} \mid g \notin O^{ij}\} \tag{6}$$

where O^{ij} is the set of gaps that are common to both years, i.e.

$$O^{ij} = G^{i} \cap G^{j} \tag{7}$$

We defined a spurious new gap as an new gap object that has a minimum size of 5 m^2, but has fewer than 3 lidar vegetation hits in each year.

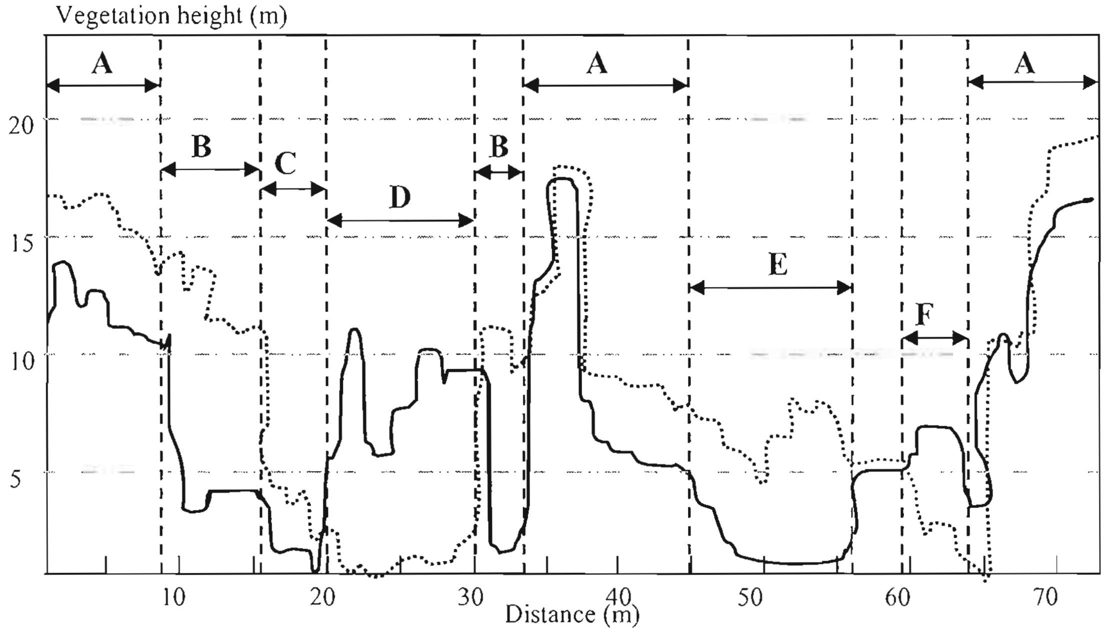

Figure 2.2. Vertical profile (bold line : 1998; dotted line : 2003) along a random transect from the multi-temporal lidar CHMs showing the changes between 1998 and 2003. (A) represents a high canopy where canopy height, h, is over 5 m in both years; (B) Region where a gap present in 1998 is laterally closed by the adjacent high canopy by 2003; (C) An old gap that is still open in 2003; (D) Gap expansion from an old gap; (E) Gap closure from below due to regeneration; (F) Random new gap;

To distinguish the set of gap expansions, E^{ij}, from the set of random new gap objects, R^{ij}, we derived a buffer of 0.5 m (tolerance level sufficient to capture the differences that was fixed by trial and error), B^{L}, around the edge of each gap object of 1998. A buffer is a zone of specified distance around a feature. Objects that are gap expansions are then defined as:

$$E^{ij} = \{g \in N^{ij} \mid g \text{ overlaps with some element in } B^{L}\} \tag{8}$$

and the objects that are random new gaps are:

$$R^{ij} = N^{ij} \setminus E^{ij} = N^{ij} \cap (E^{ij})^{C} \tag{9}$$

Similarly, deriving a buffer of 0.5 m, B^{H}, around the edge of each object of high canopy (canopy height over 5 m) in 1998, we define a set of objects of lateral growth, L^{ij}, i < j, as:

$$\begin{aligned} L^{ij} = \{g \in G^{i} \mid\ & g \text{ overlaps with some element in } B^{H} \\ & \text{and } CHM_{i}(x,y) - CHM_{j}(x,y) > t\ \forall (x,y) \in g\} \end{aligned} \tag{10}$$

where t = 5 m in this study.

And the set of gap objects that are vertically closing, V^{ij}, are

$$V^{ij} = C^{ij} \setminus L^{ij} = C^{ij} \cap (L^{ij})^{C} \tag{11}$$

2.4.9.Calculating gap properties

Gap size and gap perimeter were determined as the gap object area and gap object perimeter using ArcGIS. Perimeter to area ratios are used to assess gap shapes. Gap frequency i.e. the number of gaps and gap fraction i.e. proportion of land area in gaps were calculated based on the standard guidelines on forest gaps proposed by Runkle (1992). Gap size distribution, i.e. frequency of gaps in different gap size classes, are then derived.

Gap fraction for the assessment year i, GF_i, is proportion of forest area under gaps in year i, is derived using:

$$GF_i = \sum_{k=1}^{M} AG_k^i \Big/ aT \qquad (12)$$

where AG_k^i is the area (in m^2) of the kth gap object in the ith year, a is the size of each cell and T is the total number of cells in the study area that do not belong to an open-ended system.

2.5.0. RESULTS

2.5.1. Co-registration in x,y and z between the two lidar datasets

The analyses of the DTM difference image showed no apparent planimetric shift. If one existed, it should be negligible. Comparisons made on spots of bare ground for *Z* discrepancies were not conclusive. The estimated bias (average difference in *Z* between the corresponding ground returns in each of the two years) was 22 cm, with the 1998 data being generally higher than the 2003 data (Table 2.3). The estimated bias did not vary with slope. The first and last returns of the 1998 dataset was thus lowered by 22 cm.

Table 2.3.
Comparative statistics (in meters) of the matched ground pairs

Statistic	*1998*	*2003*	*Z-shift*
N	916	916	
Mean	264.07	264.29	-0.22
Median	251.35	251.48	0.24
Modal	Multiple	229.86	-0.32
Minimum	228.05	228.20	-3.24
Maximum	333.10	333.40	2.02
Standard deviation	31.24	31.20	0.46

N is the total number of matched pairs ; Z-shift is the difference in elevation of the matched pair.

2.5.2. Optimal interpolation

This investigation has shown that there is a significant variation in RMSE and individual error distribution between different interpolation algorithms (Table 2.4). Comparing the global characteristics, LP had the lowest RMSE among all the windows of the vegetation returns, but IDW had a similar magnitude of error with the highest mode of individual errors falling within [-1, 1] error interval (Table 2.4). TP had the highest interpolation errors in the vegetation returns. Among the interpolations of the last returns, OK had the smallest RMSE in all windows. However, all the interpolators had a very small magnitude of error in predicting ground elevation (Table 2.4). We also noted that the RMSE in interpolation of the vegetation returns has no correlation with the density of points while the percentage of points with interpolation error less than 1 m increased with the density of points.

2.5.3. Selection of optimal grid resolution

The loss of lidar points caused by the gridding process significantly increases with the grid resolution for all the lidar datasets. Fig. 2.3 shows the result of 2003 DSM

Table 2.4.
Estimated RMSE and distribution of error in the test windows

	RMSE			*% absolute error (<1m)*		
Interpolator	*A*	*B*	*C*	*A*	*B*	*C*
Vegetation returns - 2003						
IDW	2.34	4.49	3.14	55.5	50.3	68.,5
CRS	4.30	4.33	3.03	52.2	40.6	52.7
TP	2.90	19.98	13.08	53.2	40.9	65.8
ST	4.35	4.44	3.08	51.8	40.9	53.4
IQ	2.67	4.32	3.03	56.0	40.4	54.6
MQ	2.60	4.60	3.19	56.4	43.1	59.3
LP	*2.20*	*4.17*	*2.99*	54.5	43.9	51.3
OK	2.33	4.29	3.12	58.0	38.7	44.7
Vegetation returns – 1998						
IDW	3.18	5.41	4.29	50.5	33.6	33.7
CRS	3.13	5.33	*4.08*	33.9	23.7	30.7
TP	4.05	6.92	52.82	45.9	30.2	30.6
ST	3.18	5.43	4.13	37.3	31.8	28.4
IQ	3.57	5.32	*4.08*	37.1	22.7	23.8
MQ	3.37	5.74	4.30	37.0	23.5	33.6
LP	*3.03*	*5.13*	4.11	46.9	26.0	12.4
OK	3.28	5.18	4.27	38.7	23.5	31.5
Ground returns						
IDW	0.39	0.32	0.34	97.3	98.3	97.9
CRS	0.35	0.35	0.32	97.7	97.6	97.9
TP	0.39	0.39	1.31	97.0	97.5	97.6
ST	0.46	0.39	0.34	96.0	97.7	97.7
IQ	0.34	0.35	0.31	98.0	0.0	98.1
MQ	0.35	0.51	0.29	97.8	97.0	98.4
LP	0.39	*0.29*	0.34	97.5	98.9	98.3
OK	*0.33*	*0.29*	*0.28*	98.0	98.8	98.6

Numbers in italics represent minimum RMSE within a window while underlined numbers represent maximum percentage distribution of absolute error within a window.

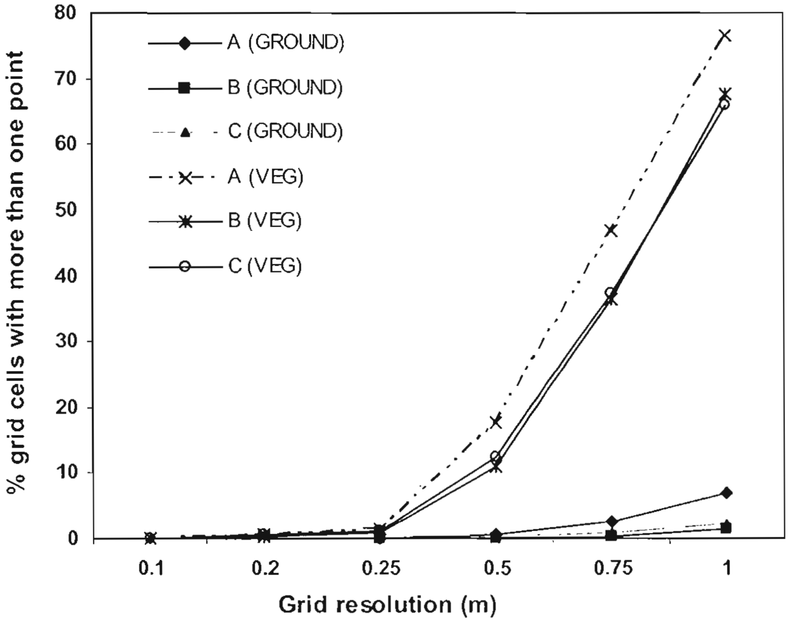

Figure 2.3. Estimated percentage of grid cells having more than one lidar point in varying grid resolutions

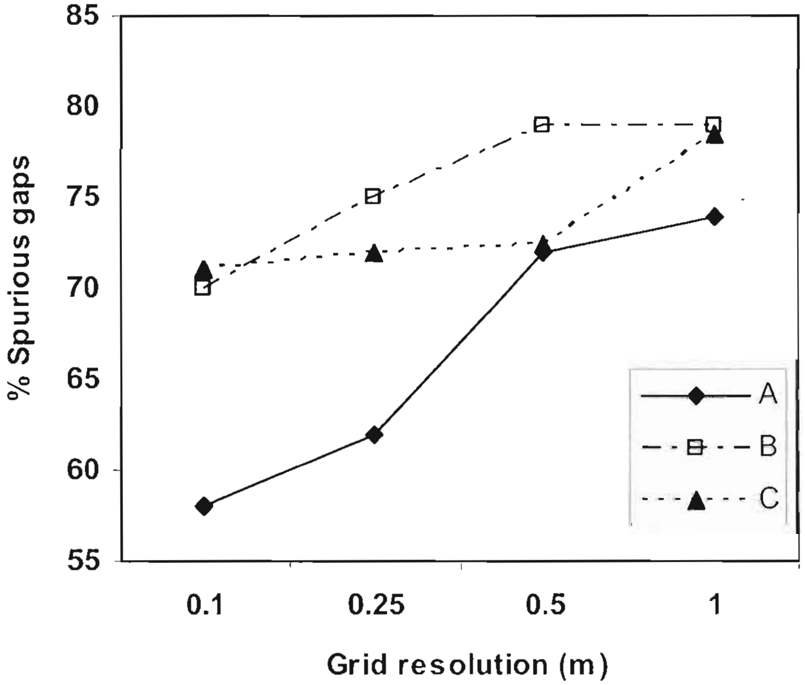

Figure 2.4. Proportionate number of spurious new gaps generated from CHMs of varying grid resolutions

and DTM. Though the point density of the 1998 first returns is slightly better than the merged ground returns, the results of the 1998 DSM are quite similar to that of the DTM. The minimum resolution for both DSMs and DTM beyond which the loss of lidar points increases significantly is 0.25 m. i.e. the loss of data points is over 18% for 2003 DSM and 4% for 1998 DSM and DTM when the grid resolution increases from 0.25 m to 0.5 m. We also note that, for all the test windows, the number of spurious new gaps increased with the increase in grid resolution (Fig. 2.4). As the grid resolution increases from 0.25 m to 0.5 m, there is a considerable increase in the number of spurious gaps from 58 to 75% for the window with low dense vegetation on undulating terrain (A), a steady increase for high and densely vegetated gentle slope (B) and nearly constant for vegetation with openings on gentle slope (C). Comparing the DSMs from all the test windows, we observe that the trend in increase in percentage loss of points and number of spurious gaps against increase in grid resolution did not vary with the point density (Table 2.2, Figs. 2.3 and 2.4). Hence, we chose 0.25 m as the optimal grid resolution for generating the lidar surfaces.

2.5.4. Gap delineation and accuracy assessment

Canopy gaps were automatically delineated from CHM_{2003} (Fig. 2.5). Fig. 2.6 presents an example of the matching of the automatically delineated gaps with the ground identified ones along transect 3. A comparison of the number of automatically identified gaps with the field observed ones showed a good agreement in each of the transects with respect to the number of gaps identified and the total gap length along the transect (Table 2.5). Overall 28 of the 29 gaps with a gap length of 309.1 m of the 423.2 m identified on the field matched the lidar derived gaps.

Small gaps less than 5 m^2 in size were eliminated by the algorithm (for example, gaps 3 and 5 in Fig. 2.6 (b)). The percentage match of the total number of gaps within each

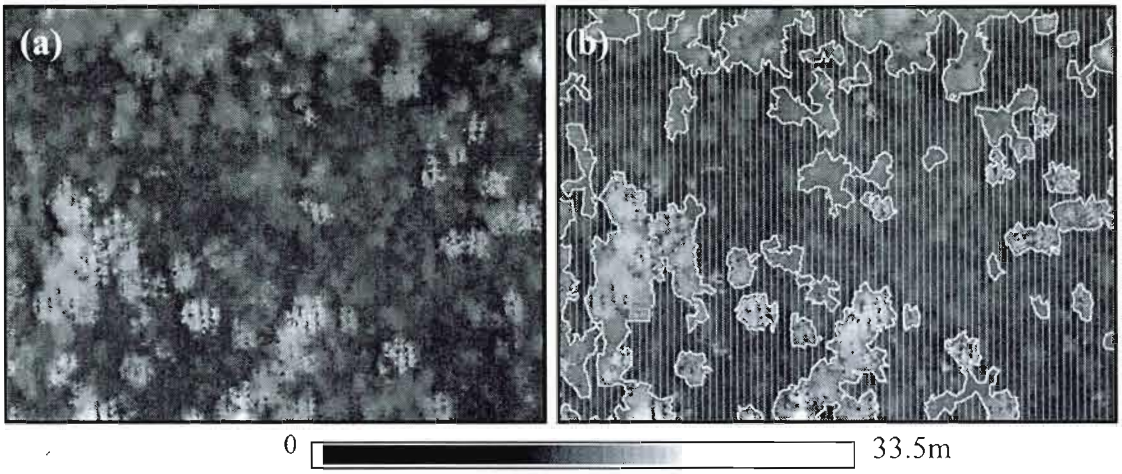

Figure 2.5. An example of automatic gap detection using lidar data. (a) CHM$_{2003}$ (b) Delineated gaps of 2003 overlaid on CHM$_{2003}$

Table 2.5.
Accuracy assessment of gap delineation using lidar

Transect Number	*Transect length (m)*	*Field*		*Lidar*		*% match*	
		# gaps	*Gap length (m)*	*# gaps*	*Gap length (m)*	*# gaps*	*Gap length (m)*
1	300	7	149.96	7	158.50	100.00	105.69
2	160	8	84.99	8	78.81	100.00	92.72
3	240	6	73.01	5	71.80	83.33	98.34
4	280	8	115.20	8	69.06	100.00	59.95
Total	**980**	**29**	**423.2**	**28**	**309.1**	**96.55**	**73.05**

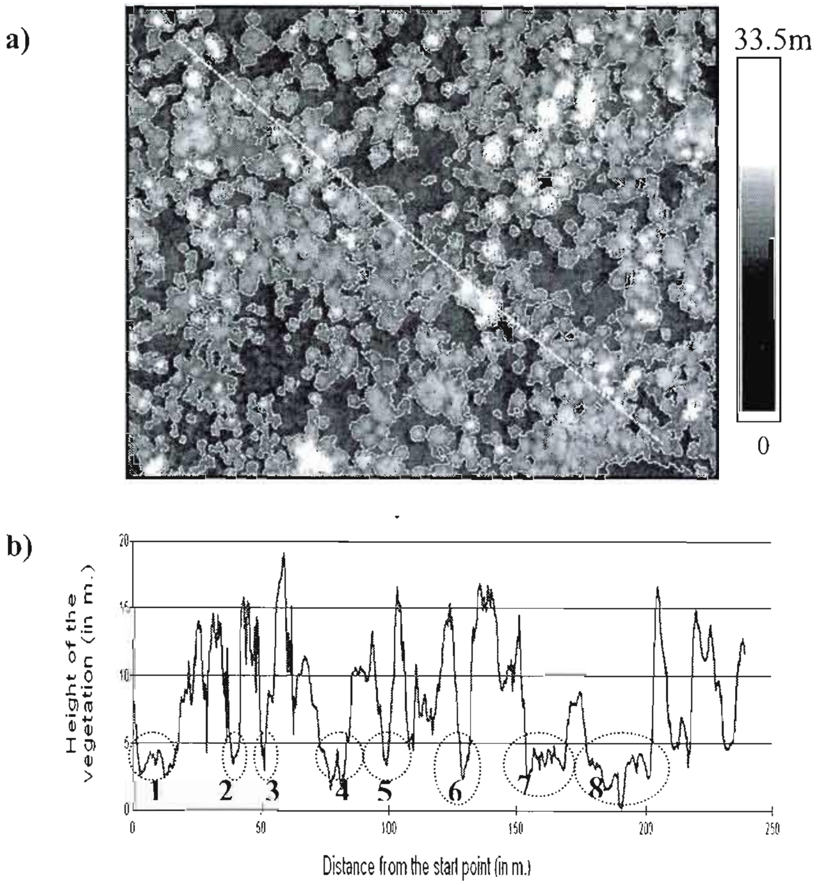

Figure 2.6. A comparison of ground and lidar derived canopy gaps; (a) Transect –3 overlaid on the CHM_{2003} along with the outline of delineated gaps, height gradation is from black (low) to white (high) on the CHM (b) Vertical height profile from S along the transect-3. Dotted ellipses indicate possible gap regions. Gaps 3 and 5 were eliminated due to their size by the algorithm and were also not measured on the ground, and gaps 7 and 8 belonged to the same large gap but were double counted in the field.

transect ranged from 83.3 to 100.0 (Table 2.5). However, the proportion of the gap length along the transect ranged from 60.0 to 105.7% with transect-3 having the poorest match (60.0%). The overall accuracy assessed through the percentage of number of matched gaps was 96.5% and that of the matched gap length was 73.1%.

2.5.5. Gain in the interpretation of gap geometry using lidar

The 34 selected canopy gaps had varying shapes with lidar P/A ranging from 0.35 to 4.16. The area of gaps extracted from the lidar CHMs (A_l) is distributed between 5.0 and 229.3 m^2 and their perimeter$_{\text{lidar}}$ between 14.2 m and 229.3 m. The area as approximated by ellipses A_e (eq. 3) varied between 2.0 to 523.2 m^2 while the corresponding perimeter (P_e , eq. 4) had values from 19.99 m to 226.54 m. On average, A_e is under or over estimated by 8 m^2 while P_e is mostly underestimated by 11.9 m when compared to the lidar-derived ones (Fig. 2.7 a). As a result, the perimeter to area ratio (S_l) is underestimated more often (Fig. 2.7 b).

2.5.6. Gap delineation of 1998 and 2003 lidar data

The maximum heights noted from the derived CHMs are 31.15 m and 33.50 m. respectively with 2.30 m of average increase in vegetation surface height between the two years (Table 2.6). Every gap that has a size over 5 m^2 was mapped in the study area using the proposed method of automatic gap detection from the lidar surfaces. In all there existed 9466 and 7857 gaps in 1998 and 2003 respectively. Large gaps (over 1 ha.) formed due to the impact of spruce budworm infestation in softwood dominated stands and beaver damage in hardwood dominated stands (as evidenced in field observations) were mapped. It was observed that over the 5 year study period, the total area under gaps decreased from 200.0 ha to 180.8 ha resulting in a decline of gap fraction from 0.35 to 0.31. The total gap area includes 156 ha of open area common to both years. The common open areas consist of existing old gaps varying between 5.0 m^2 to 5.9 ha in size.

The average size of the delineated gaps is 156.4 m^2 and 202.3 m^2 respectively for 1998 and 2003. The gap size distribution in both years was consistently negative

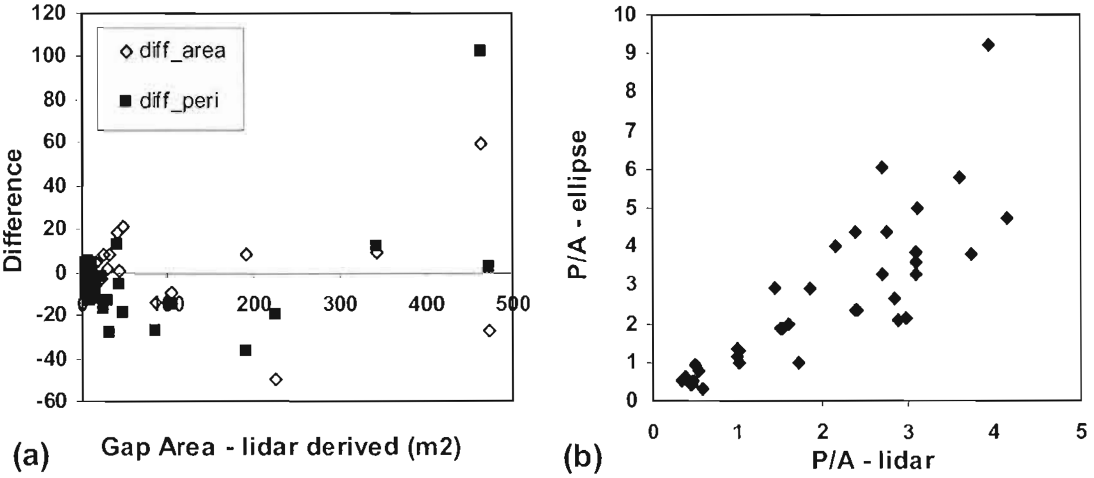

Figure 2.7. Comparing gap geometry of the lidar derived measurements to that of the ground-based ellipse approximations. (a) Difference in gap area and gap perimeter (b) P/A ratio

Table 2.6.
Characteristics of the lidar derived canopy gaps in 1998 and 2003

Statistic	*1997*	*2003*
Max.vegetation height (m)	31.15	33.50
Total number of gaps	9466	7857
Minimum gap size (m^2)	5.0	5.0
Maximum gap size (ha)	9.8	9.21
Mean gap size (m^2)	156.4	202.3
Median gap size (m^2)	19.6	24.5
Total area under gaps (ha)	200.0	180.1
Percentage frequency of gaps < 100m2	86.7	85.1
Number of gaps of size > 1ha.	23	30
Gap fraction	0.38	0.32

exponential with more frequent smaller gaps than larger ones. However, the gap size distribution between the two years is significant (Kolmogorov-Smirnov test, $p < 0.01$). The number of gaps larger than 1 ha increased from 23 to 30, and overall the gap spatial distribution is generally more fragmented in 1998 than in 2003. Nearly 86.7% (in 1998) and 85.1% (in 2003) of the gaps have a size smaller than 100 m^2, possibly due to a single or group tree fall. The average gap perimeter significantly increased from 96.3 m to 141.8 m. The difference between the two years could to some extent be attributed to the variation in lidar point density. The perimeter to area ratio (S_i) of gaps is below 2 for 90% of 1998 gaps and 80% of the 2003 gaps, indicating that most gaps are regularly shaped.

2.5.7. Characterising gap dynamics between 1998 – 2003

New gap openings and gap closures that occurred during 1998-2003 in the 225 ha area of the 258 year old stand of the study area were mapped using the combinatorics on the 1998 and 2003 gap objects as discussed in section 2.8. The results show that old existing gaps and interstitial spaces were completely eliminated. Random new gap openings were easily discernible from gap expansions and lateral closures from regenerating gaps. Fig. 2.8 presents an example of the gap dynamic characteristics identified using the multi-temporal lidar analysis.

Among the 4754 new gaps that opened during the study period, 65% of them are gap expansions from the old existing gaps in 1998 (Table 2.7). The largest random gap opening is 115.6 m2 while 2182.5 m2 is the size of the largest expanded gap. The results indicate that all the new gaps are largely due to the death of one or few trees. Similarly, in this forest more gaps are seen closing from lateral growth of the adjacent matured vegetation (nearly 59%) than from the regenerating vegetation from the floor. The gap size distributions indicate that the recently closed patches are much more fragmented than the recently opened canopy gaps in this old-growth forest. The

Table 2.7.
Characterising gap dynamics between 1998 and 2003

Statistic	***New gap opening***		***Gap closure***	
	Random new gap	***Gap expansion***	***Lateral closure***	***Regeneration***
Number of gaps	1647	3107	4110	2018
Minimum gap area (m^2)	5.0	5.0	5.0	5.0
Maximum gap area (m^2)	115.6	2182.5	55.0	519.3
Average gap area (m^2)	11.4	25.8	8.1	15.8
Stdv. gap area (m^2)	7.7	64.8	65.6	20.7
Minimum gap perimeter (m)	8.66	8.74	2.24	8.60
Maximum gap perimeter(m)	148.7	1367.79	520.53	444.50
Average gap perimeter (m)	20.69	34.09	11.23	27.03
Stdv. gap perimeter (m)	10.10	43.19	9.01	20.81
% number of gaps with P/A < 2	48.5	70	50	78

**Stdv. Stands for standard deviation*

average gap size and the spread of the gap size distribution among all the classes of gap dynamics is variable (Table 2.7). Gap expansions and gap closures due to regeneration are much more regularly shaped than random new gaps or lateral gap closures.

2.6. DISCUSSION

Optimal interpolation and grid resolution

Most studies on quantifying interpolation errors of lidar DEMs have been restricted to analysing global error patterns (using mean, standard deviation or RMSE) within bare-earth models covering urban (Smith et al. 2005, Mitasova et al. 2005) or

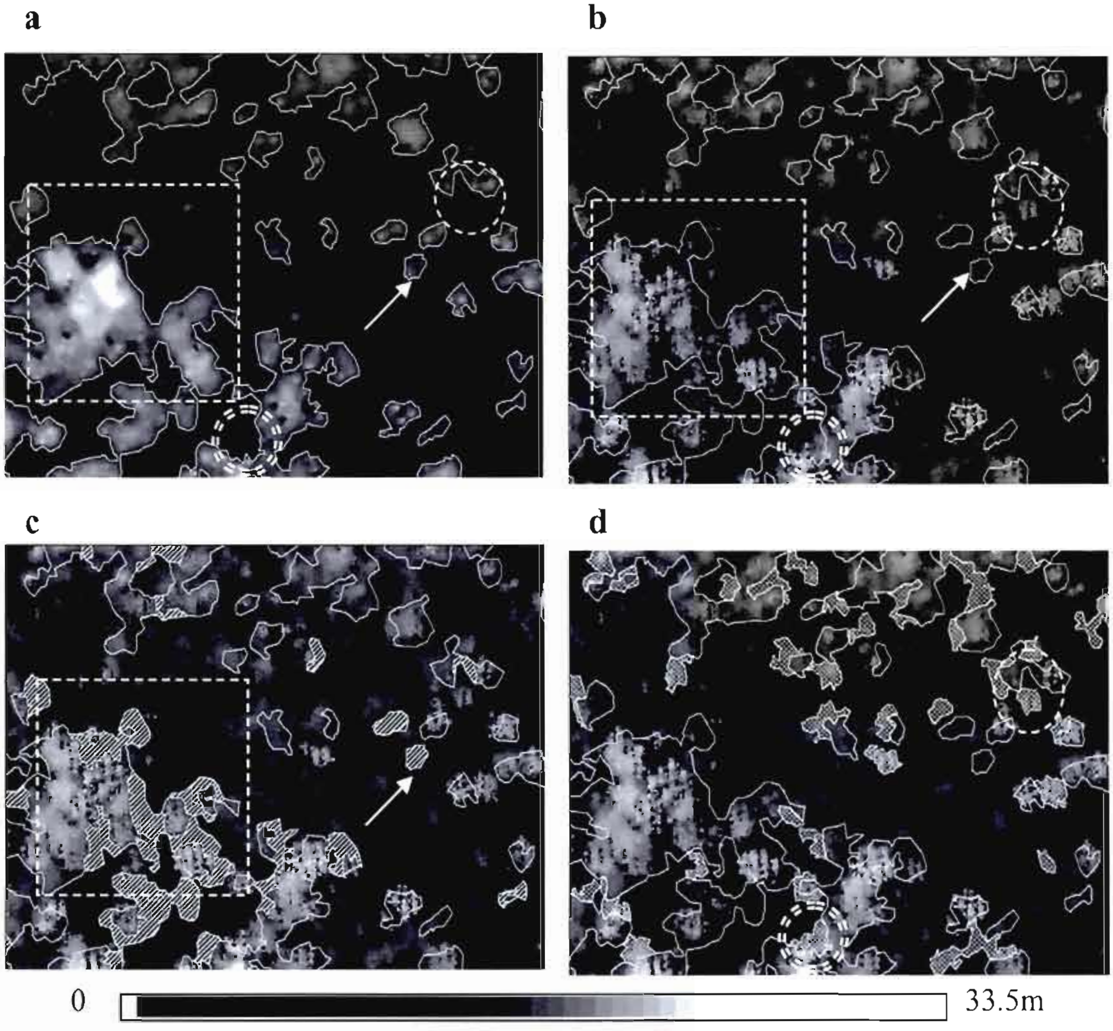

Figure 2.8. Delineating new and closed gaps during 1998 – 2003 using lidar data. (a) Gaps in 1998 overlaid on the CHM_{1998} (b) Gaps in 1998 overlaid on CHM_{2003} (c) Identified new gaps (hashed polygons) formed by multi-tree deaths (square) and single tree death 8.9m^2 in size (arrow) with outline of gaps in 1998 overlaid onto the CHM_{2003} (d) Gaps (checked polygons) closed by regeneration (single dotted circle) and lateral growth of adjacent vegetation (double dotted circle) with outline of gaps in 1998 overlaid onto the CHM_{2003}.

natural environments (Lloyd and Atkinson, 2002, Anderson et al. 2005). Although seen as important and challenging in terms of discontinuities and frequent local changes in elevation, optimal interpolation for vegetation surfaces are rarely attempted, and never in studying canopy gaps. This investigation has shown that optimising grid resolution and choice of interpolation algorithm are essential, both for ground and vegetation surfaces, to ensure accurate delineation of canopy gaps.

Through an analysis of both local and global interpolation errors, our results show that there is minimal loss in accuracy in using a simpler algorithm like IDW for interpolating both vegetation and ground surfaces (Table 2.4). Though kriging methods provide more accurate predictions than IDW, Lloyd and Atkinson (2002) recommend IDW for data with small sample spacing, a finding later corroborated by Anderson et al (2005). Even though local polynomial functions capture short range variation within data well; they are inexact interpolators that are not required to pass through the measured points unlike exact algorithms such as IDW. A further advantage of IDW is that it does not predict beyond maximum or minimum values. We thus chose IDW as the optimal interpolation for this data. Irrespective of the canopy structure and point density that was represented in the different test windows chosen, we also observed that a computationally less intensive algorithm like IDW is optimal for delineating gaps. Our results also indicated that interpolation error is globally not correlated with point density (Fig. 2.6). Comparing the mean error and RMSE, Anderson et al (2005) noted that lidar data can withstand data reduction while maintaining accuracy of the DEM in low relief areas. However in contrast, our results signify that an increase in point density helps minimise the local interpolation bias irrespective of the type of terrain and vegetation structure. Hence, we suggest that noting both the local and global patterns of the interpolation error is essential before deciding upon optimal grid resolution for a given application.

Loss of lidar points and the number of spurious new gaps increased with the grid cell size, with an optimal resolution close to the original point spacing of the 2003 lidar data, similar to the optima noted in previous studies by Behan (2000) and Smith et al (2005) for urban applications. However, the optimal resolution chosen for 1998 lidar set was much smaller than their original point spacing.

Gap delineation using lidar surface

The analysis of the 6 km^2 old-growth mixed boreal forests around lake Duparquet, Quebec, using multi-temporal lidar data gives a reliable estimate of the gap disturbance regime of these forests. Gaps of varying sizes from 5.0 to 2180.0 m^2, resulting from single to multiple tree falls, were reliably delineated. The obtained results fall within the reported characteristics of boreal forests made in earlier studies (a gap size range of 15 to 1245 m^2 as summarized for studies in boreal and subalpine forests by McCarthy, 2001). Tree mortality in old-growth boreal and subalpine forests is largely due to snapping and uprooting (McCarthy, 2001). In the study area, it was noted that tree fall may result from strong winds during violent thunderstorms, snapping under the weight of snow, and beaver activity (as evidenced by field observations and reported by Senecal et al. 2004). The results obtained in this study support this evidence as 98% of the gaps that formed between 1998 and 2003 have a size less than 100 m^2.

An obvious advantage of this method over the rule-based algorithm using single time CHM developed by Koukoulas and Blackburn (2004) and single tree segmentation by Yu et al. 2004, is that canopy gaps as small as 5 m^2 were delineated accurately. Although delineation of individual tree crowns proposed by Yu et al.(2004) could eliminate ambiguities of inter-tree spacing, its applicability and accuracy is largely restricted to high density lidar data and is potentially affected by tree crown delineation errors. Moreover, the objective of their study was to identify individually harvested trees. Koukoulas and Blackburn (2004) found the use of shrinkage and perimeter to area ratios to eliminate inter-tree spacing to be ineffective as they erroneously eliminated some canopy gaps. On the contrary, a multi-temporal data analyses of medium density lidar used in this study enabled the characterization of gaps based on the nature of their occurrence and the distinction of natural tree spacing from small canopy gaps.

The comparison of 29 field measured gaps with automatically delineated gaps on the lidar canopy height surface showed a good matching and high overall accuracy. However, as reported by many researchers, ocular gap delineation on the ground is a much more difficult task than identifying them from an aerial perpective. Large gaps are especially difficult to map on the ground and there is a chance of double counting them due to their convoluted shape. A visual overlay of transects on lidar CHMs showed that the difference that we observed in the number of gaps along transect 3 is because of double counting of a large gap that intersected the transect twice (an example of gaps 7 and 8 is seen in Fig. 2.6-b). Remote sensing techniques with their synoptic and wide coverage are thus definitely advantageous in such situations. Furthermore, owing to the dense point cloud acquisition and active sensors that do not rely on illumination by natural sunlight, and because of the near vertical viewing angles, lidar overcomes the limitations of most of the conventional remote sensing methods such as aerial photography.

In our field validation, the overall match of the lidar delineated total gap length with the field measured length was 73.1% of which transect 4 had the poorest match of 60.0%. This difference in the total gap length in transect 4 is largely due to the position of the transect which passes through the edge of a large gap. Deflection of a few meters from the proposed transect while cruising on the ground could possibly amount to under or over-estimating the gap length along the transect.

Gap measurement using conventional techniques is often difficult. As we noted in most studies (for example Foster and Reiners, 1986, Runkle, 1991, Kneeshaw and Bergeron, 1998, Gagnon et al. 2004), gaps are approximated to an ellipse which may not yield accurate gap geometry. In this study, using an accurate high resolution lidar surface we were able to achieve near perfect interpretation of the gap geometry. Evaluating the gap geometry of 34 lidar-derived new gaps with their respective ellipse-approximated ones, we found that the gap area was either over or underestimated and that gap perimeter was largely underestimated. The more complex the shape of the gaps with irregular perimeter, the greater was the underestimation in gap geometry.

As hypothesized, given the nature of gaps in the study area and the capacity of lidar to detect large changes in elevation, the use of diachronic lidar data has good potential in studying gap dynamics in boreal forests. Characterizing gaps into random new gaps, gap expansions, laterally and vertically closing gaps, helps to better understand the dynamics of the boreal forests. Since the method had been verified in a complex canopy structure of open and patchy mixed boreal forests, we presume that this should be applicable to study gap dynamics in most forest ecosystem.

2.7. CONCLUSION

To the best of our knowledge, this is probably the first study to test the potential feasibility of lidar for spatially explicit mapping of boreal canopy gaps and characterizing temporal canopy gap dynamics. Ground validation shows a very high accuracy of the proposed method in delineating canopy gaps even in a complex canopy structure like that of old-growth mixed boreal forests. The results suggest that lidar is an excellent tool for efficient continuous and complete mapping of canopy gaps that are formed by single to multiple tree falls. The smallest gap that could be reliably delineated was 5 m^2 so far not achieved by any other remote sensing strategy.

The use of a high-resolution DEM to identify and map forest canopy gaps has shown encouraging results, demonstrating that the proposed method has merit as a means for rapidly acquiring information on canopy structure in general, and canopy gaps in particular.

This study is also the first to propose methods to combine datasets acquired by two different sensors with dissimilar point density for ecological applications. By standardizing the two lidar data sets from different sensors we successfully analyse short term dynamic changes in canopy gaps of boreal forests in good detail. We were able to quantify the dynamic gap characteristics in terms of size, and qualify the nature of gap events into gap expansions, random gap occurrence, gap closure due to lateral growth and gap closure due to regeneration. This should enable us to determine rates of gap formation and turnover more accurately for boreal forests.

Although a few constraints persist in using lidar owing to its higher cost of acquisition, large storage and processing complexities, need for special software packages etc., these methods could be adopted on a sample basis to establish reliable estimates of annual rates of gap opening and closures. Recent studies propose precise and effective methods of combining lidar and multi-temporal set of aerial photos to generate retrospective time-series of canopy height models (St-Onge et al, 2007). This establishes an ample potential to extend this study to understand long-term canopy dynamics by integrating lidar with aerial photography. By exploring long term and large scale mortality and recruitment processes, we should be able to validate or improve our understanding of forest successional processes developed from earlier small spatial and temporal studies. Such new insights may have direct implications for forest managers who seek silvicultural and management strategies with a natural disturbance based underpinning but also have spin-offs into key areas of research like carbon sequestration in forests.

CHAPTER III

Interactions of multiple disturbances in shaping boreal forest dynamics – a spatially explicit analysis using multi-temporal lidar data and high resolution imagery

This chapter will be submitted to **Ecology** as: Vepakomma,U., D. Kneeshaw, B. St-Onge, *Interactions of multiple disturbances in shaping boreal forest dynamics – a spatially explicit analysis using multi-temporal lidar data and high resolution imagery.*

3.1. RÉSUMÉ

Afin d'avoir une meilleure compréhension de l'effet à court terme de la dynamique de trouées en forêt boréale mixte le long d'un gradient de peuplements à divers stades de développement, nous avons analysé une surface contiguë de 6 km^2. Nous avons combiné des données d'altimétrie laser et une classification multispectrale de groupements d'espèces feuillues et résineuses obtenue à partir d'images de haute résolution afin de comprendre les changements de composition dans le couvert forestier. Le taux annuel d'ouverture des nouvelles trouées est estimé à 0,16 % dans les peuplements ayant brulé il y a 84 ans contre 0,88 % dans ceux ayant brûlés il y a 248 ans. Les arbres en périphéries des trouées étaient plus susceptibles de mourir que ceux à l'intérieur de la canopée. En raison de la dernière épidémie de tordeuse des bourgeons de l'épinette, le taux de fermeture des trouées était plus élevé que celui d'ouverture, variant de 0,44 % à 2,05 %. La majorité des ouvertures se referme verticalement, bien qu'une mince proportion statistiquement significative se referme latéralement grâce aux arbres de la périphérie des trouées, qu'ils soient feuillus ou résineux. Nous avons aussi noté que les impacts de l'épidémie de tordeuse des bourgeons de l'épinettes, qui a eu lieu 16 ans auparavant, perdurent dans les vieux peuplements conifères en raison de la forte mortalité de la régénération résineuse. En somme, la forêt est en quasi équilibre en ce qui a trait à la composition, avec une augmentation de 6% (de 1 à 11% à travers les divers peuplements) en feuillus causé par la fermeture du couvert par la régénération davantage que par une transition d'espèces vers des résineux tolérants à l'ombre. Les trouées sont vitales au maintien des feuillus tandis que les résineux peuvent s'établir sans la formation de trouées. Nos résultats indiquent que les réponses des vieux peuplements à des perturbations de force modérée ne suivent pas les patrons supposés.

Mot-clés: perturbation naturelle, rotation du couvert forestier, composition du couvert forestier, dynamique des trouées, succession, l'effet continu de l'épidémie de la tordeuse du bourgeon de l'épinette, lidar, images à haute résolution, grande superficie

3.2. ABSTRACT

In order to have a deeper understanding of the short-term gap dynamics of mixedwood boreal forests across a gradient of stand developmental stages, we analysed a large contiguous spatial area of 6 km^2. Here we combine the structural measurements of the canopy from lidar data with spectral classification of broad species group to reliably characterise gap disturbance regime and to evaluate their effect on forest dynamics. Estimated annual gap opening rates based on new gap openings increased from 0.16% for 84 year old time since fire (TSF) stands to 0.88% for 248 year old TSF stands. Trees on gap peripheries were more vulnerable to mortality than interior canopy trees. Due to post spruce budworm outbreak recovery, gap closure rates were higher than opening rates, ranging from 0.44% to 2.05%, but did not show any relationship with stand age. The majority of the openings were filled from below, although a smaller but significant proportion filled from lateral growth of softwood and hardwood gap edge trees. We also note that the last spruce budworm outbreak 16 years previously had a lasting impact on old-conifer stands as its legacy continues with high mortality of conifers in these stands. Overall, the forest is in a quasi-compositional equilibrium with a small 6% increase (1 to 11% in TSF stands) in hardwoods, largely due to regeneration in-filling instead of a successional transition to more shade-tolerant conifers. Gaps are vital for hardwood maintenance while transition to softwoods can occur without perceived gap-formation. Our results indicate that responses to recent moderate to small scale disturbances in these old-growth stands did not follow previously conceived patterns.

Key words: natural disturbance, boreal forests, canopy gap opening and closure, canopy turn over times, canopy composition, succession, spruce budworm legacy effect, lidar, high resolution images, large spatial scale

3.3. INTRODUCTION

Forest dynamics are generated by a complex set of interactions between multiple disturbance events occurring at different moments in stand development. In the attempt to develop a general understanding of forest response, many researchers have assessed dynamics after a single disturbance type, be it fire (Bergeron 2000, Dix and Swan 1971), insect outbreaks (Gray and MacKinnon 2006, Bouchard et al. 2006, Boulanger and Arsenault 2004) or canopy gaps (Parish and Antos 2004, Runkle 1998, Denslow and Hartshorn 1994, Canham 1988). Directional successional patterns have been observed with time since fire such that shade intolerant pioneer species dominate when the time elapsed since fire is short and late successional, shade tolerant species become dominant as time since fire increases (Chen and Popaduik 2002, Oliver and Larson 1996). Structural changes may also be directional such that the forest, as measured in terms of biomass, tends to increase to a maximum before declining to a steady state in which mortality balances growth. However, in terms of canopy opening a number of studies have suggested that boreal forests increase in proportion of gap opening before attaining a plateau at an old-age (Pham et al. 2004, Bartemucci et al 2002, Kneeshaw 2001). It has further been suggested that opening size may determine subsequent response with quick lateral filling of small openings and slower in -filling from regeneration in larger gaps (Kneeshaw and Bergeron 1998). Forest dynamics may thus depend on disturbance history and current structure and composition; although such relationships are poorly defined.

At a landscape scale, forest composition has been directly linked to time since fire such that the forest is dominated by late successional species when intervals between fires are long and by pioneer species when intervals between fires are short (Flannigan and Bergeron 1998, Liu 1990). In forests where fires are rare, insect disturbances control dynamics; with some authors suggesting that insects, such as the spruce budworm, can lead to self-perpetuating systems (MacLean 1988, Baskerville

1975) while others suggest that they aid in maintaining non-host species (Bouchard et al. 2006, Ghent et al. 1957). Results are thus equivocal on forest response although response seems to be linked to forest composition and age. It has also been shown that, when fires and outbreaks interact, forest development patterns may be altered and thus not follow a directional pattern (Bergeron and Dansereau 1993).

Similar patterns of convergent and divergent succession have also been observed for gaps (Kneeshaw and Bergeron 1998, Frelich and Reich 1995, Runkle 1981). However, the role of gaps in influencing forest composition and structure, although important in tropical and temperate forests where they ensure that certain tree species attain canopy status (Runkle 1998, Denslow and Spies 1990), is ambiguous in boreal systems. It has been suggested that large gaps favour intolerant hardwoods while smaller gaps are conducive to the recruitment of shade-tolerant conifers (Kneeshaw and Bergeron 1998). However, the role of canopy gaps in stand development has been questioned in other boreal forests where gaps were found to have limited influence on understory tree establishment and in determining species composition (De Romer et al. 2007, Hill et al. 2005, Webb and Scanga 2001). The interaction between gaps and other disturbances also suggests that gaps may accelerate or retard forest succession depending on the developmental stage of the forest (Kneeshaw and Bergeron 1998).

Stand development stage has also been linked to a linearly increasing size of gap formation followed by recovery from the understory. Random small openings in the canopy due to single tree falls have been shown to close rapidly by adjacent vegetation in the initial stages of development while larger openings due to insect infestation, windthrow or multiple gap makers in the old-growth stage fill- in through advance regeneration (Yamamoto and Nishimura 1999, Oliver and Larsen 1996, Tyrell and Crow 1994). There is also some question as to the distance that gap effects may extend into the understory, with some research suggesting that this should be important in high latitude forests (Ban et al. 1998, Canham et al 1988). Trees on gap edges may also be more vulnerable to disturbances, hence gaps may expand over time. Again this is equivocal as the presence of gaps did not influence gap edge tree mortality rates in hardwood temperate forests (Runkle 1998, Runkle and Yetter 1997) but gap expansions were more frequent in wind-prone sub-alpine forests (Worrall et al. 2005). This phenomenon has not been directly measured in boreal forests.

Furthermore, investigations on disturbance regimes and forest dynamics are often based on a small number of transects, small plots in a limited number of stands or coarse scale analysis at the landscape level. These techniques provide useful results on replacement patterns, compositional and structural changes yet are spatially constrained to sites deemed representative. Large area studies at fine scales of forest dynamics are thus needed to account for spatial heterogeneity within a forest, and thus to provide greater confidence in the rate at which change is occurring.

Our main objective in this study is to evaluate short-term forest dynamics of boreal forest stands in different developmental stages over a large spatial area. Our goal is thus to develop our understanding of how stands affected by different disturbances in the past respond to small gaps with the aim of understanding the roles of gaps at different stages of stand development. We hypothesise that older conifer-dominated stands should be closing to a greater degree than opening due to a delayed response to a spruce budworm outbreak twenty years earlier (i.e. regeneration will now be exceeding mortality). In contrast in the younger, hardwood dominated stands that are approaching the longevity of the dominant species, greater canopy mortality (canopy opening) than closing could be expected. As a corollary we would expect a greater transition to conifers in the hardwood stands as shade-tolerant advance conifer regeneration replaces hardwoods while in coniferous stands we expect conifer dominance to continue as well as the maintenance of a small proportion of hardwoods. These expectations are consistent with the proposed directional succession of these forests (Bergeron 2000). In terms of stand horizontal structure, we will investigate whether gap openings will be due to new (random) mortality or gap expansion as a result of tree mortality at gap edges. Consequently, if there is a legacy effect following the spruce budworm outbreak then we hypothesise that there should be more gap expansions in conifer dominated stands and greater random mortality in hardwood stands. We also expect that the probability of random new openings being observed in closed stands will be much higher than in open stands.

3.4. STUDY SITE

The 6 km^2 site chosen for this study falls within the Conservation Zone (79°22' W, 48°30' N) of the Lake Duparquet Training and Research Forest, situated at the southern limit of the boreal forest in the balsam fir – white birch bioclimatic region of Claybelt forests in Quebec and Ontario, Canada. The region has relatively level topography (227 m and 335 m) interspersed with few small hills. The regional climate is described as subpolar, subhumid, continental with 0.8° C mean annual temperature, 857 mm of average precipitation and a 160 day growing season (Environment Canada 1993). The frost free period lasts 64 days on average, but occasional frost episodes may occur anytime during the growing season. 63% of the study site is covered by forest and nearly 29% is floodlands. Surface deposits are largely clay, tills soils or rocky outcrops.

This part of the boreal forest is largely dominated by mixed wood stands which originated from different fires dating from 1760 to 1944 (Danserau and Bergeron 1993). Most stands (98%) in this forest are mature or over mature reaching an age of over 50 years. The maximum height of the forest is higher when dominated by shade intolerant hardwoods and shorter when dominated by shade tolerant balsam fir. The canopy height thus varies between 20 and 25m. Balsam fir (*Abies balsamea L.* [Mill.]) is the dominant species in the older forests whereas trembling aspen (*Populus* *tremuloides* [Michx]) dominates the younger forests (Bergeron 2000). These species are associated with white spruce (*Picea glauca* [Moench] Voss), black spruce (*Picea mariana* [Mill] B.S.P.), white birch (*Betula paprifera* [Marsh.]). Eastern white cedar (*Thuja occidentalis* L.) is also a late successional associate of balsam fir on mesic sites and is found on shore lines and on rich organic sites. All of the hardwood species found in this part of the boreal forest are shade-intolerant while the softwood species are shade-tolerant (Kneeshaw et al. 2006).

The main disturbances in this area are forest fire and spruce budworm outbreaks (Morin et al. 1993). The fire history of stands surrounding Lake Duparquet was reconstructed using dendroecological techniques (Dansereau and Bergeron 1993) showing a considerable decrease in the frequency and extent of fires since 1850 (Bergeron and Archambault 1983). The fire cycle was estimated to be 63 years for the period 1700 - 1870, and more than 99 years for the 1870 – 1990 period (Dansereau and Bergeron 1993). Three major spruce budworm epidemics were recorded for the 20th century by Morin et al (1993), with the 1972-1987 outbreak resulting in the death of most fir trees. Defoliation due to a forest tent caterpillar outbreak in 1950 and 2001 has also been documented as causing a decrease in hardwood species. Although part of the forest was selectively cut, much of the study forest is relatively virgin and remains unaffected by human activities (Bescond 2000).

3.5. METHODS

3.5.1. Lidar and gap dynamics

Characterising the pattern and dynamics of ecological processes requires reliable measurements of the horizontal and vertical arrangement of forest canopies over time (Parker et al. 2004). Owing to its ability to directly measure the 3-D distribution of plant canopies as well as subcanopy topography with unprecedented accuracy and consistency, lidar (light detection and ranging) in recent decades has emerged as a superior tool for estimating vegetation height, cover and detailed canopy structure of the forest (St-Onge et al. 2004, Lefsky et al, 2002). With its decimeter accuracy height mapping capability, lidar has the potential for accurate detection of changes in vegetation at a high resolution. Comparing the canopy height models (CHM, a raster surface representing canopy height) over time, a few recent studies have validated its ability to detect tree falls of varying sizes (Vepakomma et al. 2008) and height-growth estimation (St-Onge and Vepakomma 2004, Yu et al. 2004). The evolution of sensor technology and image processing techniques has increased the efficiency in accurately mapping forest species composition with a very high resolution (Clark et al. 2004, Chen et al. 2004). By combining optical remotely sensed data with LIDAR data, the strengths of both data sources can be optimized, especially in monitoring short-term changes in slow-growing forests. In this study, we investigated boreal forest dynamics using a combination of lidar and high resolution multi-spectral imagery over a short-term period of 5 years between 1998 and 2003. Multi-temporal lidar surfaces were used to characterise gap dynamics while broad species compositions were derived from the high resolution images.

3.5.2. Lidar data and canopy surfaces

The study site was surveyed on June 28th 1998 and August 14th to 16th 2003, with an interval of approximately five growing seasons. The 1998 survey was carried out using an Optech ALTM1020 flown at 700 m above ground level (AGL) operating at a pulse frequency of 4 kHz. with two passes for the first returns and one pass for the last returns. The first and last return density was 0.3 and 0.03 hits/m^2 with a maximum scan angle of 10° and a footprint size at nadir of 21 cm. The data was registered to ground profiles surveyed with a high grade GPS and tacheometer. The 2003 survey was done with Optech's ALTM2050 lidar flown at 1,000 m AGL, and the first and last returns for each pulse were recorded with a maximum scan angle of 15 deg. The pulse frequency was 50,000 Hz and the average densities of first and last returns were 3 and 0.19 (hits/m^2). The data was registered to new ground profiles. The inter-swath geometrical fit was improved using the TerraMatch algorithm by Terrasolid Ltd. (Helsinki). All returns were classified by the provider as ground and non ground were assumed correct for the study. Both lidar datasets were assessed for tree height accuracy in two different studies (Vega and St-Onge 2008, Coops et al. 2004). Clearly identifiable hardwood and softwood trees, 36 (for 1998) and 77 (for 2003) with a height range of 5.6 m – 33.1 m, were field measured for maximum tree height. The relationship between field measured maximum tree height and maximum lidar height for the delineated crowns was found to be strong (r^2 = 0.88 and 0.86 respectively) with an RMSE of 1.8 m and 1.85 m respectively. The two datasets were co-registered for temporal comparisons using the methods presented in Vepakomma et al. (2008). The CHM is generated for both years by calculating the difference between the elevations of the respective canopy surface (given by the Digital Surface Models, DSM) and the underlying terrain (Digital Terrain Model, DTM).

3.5.3. Delineation of canopy gaps on lidar surface

In this study we define a gap as an opening in the canopy caused by the fall of a single or group of canopy trees such that the height of any remaining stem is less than 5 m (fixed based on field observations) in height. The edge of a gap is defined as the vertical projection of the canopy crown of trees adjacent to the gap. Open-ended systems like streams, rock outcrops, or marsh lands, are not considered to be a part of canopy gaps. Spatially explicit delineation of canopy gaps for both years surveyed by the lidar were automatically mapped using an object-based delineation technique developed by Vepakomma et al. (2008). A comparison of 29 field measured gaps along 980 m of transect with lidar delineated gaps showed a strong matching of 96.5 %.

Gaps on the lidar surface are individual objects of contiguous binary grid cells determined by a gap indicator function (eq. 1), that have a minimum size of 5 m^2 and which are represented by at least 3 lidar returns. A gap indicator function G is defined for a given grid cell at *(x,y)* on the CHM_i as:

$$G_i(x,y) = \begin{Bmatrix} 1 & \mathit{if}\ CHM_i(x,y) < a \\ 0 & \mathit{otherwise} \end{Bmatrix} \tag{1}$$

where a = 5 m in this study, CHMi(x,y) is the lidar height of the canopy surface in the ith year, (x,y) is a cell that does not belong to any open-ended system. A region growing algorithm applied to this binary grid identified individual objects of non-null adjacent cells. An example of gap identification on lidar surface and the high resolution images is presented in Fig. 3.1

Combinatorics on the two lidar surfaces and gap objects were applied to identify the nature of each gap event: new gap, closed gap, gap expansion, laterally closing or regeneration closing gaps. A new gap is defined as a gap in the canopy that opened between 1998 and 2003. New gaps that share the edge of a gap existing in 1998 are classified as gap expansions, while the remaining new gaps are identified as new random gaps. Areas with vegetation greater than 5 m in height are considered to be closed forest. Gap closure occurs where the average vegetation height increased from below 5 m in 1998 to over 5 m during the period from 1998 to 2003. A gap can be closed by crown displacement or expansion through lateral growth, while regeneration can close the gap vertically. Coalescing gaps form when gap expansions connect two existing gaps (Figs 3.2a and 2b). Shifting gaps are those existing gaps that experience both expansion and also closure over the evaluated time period (Figs 3.2c and 2d).

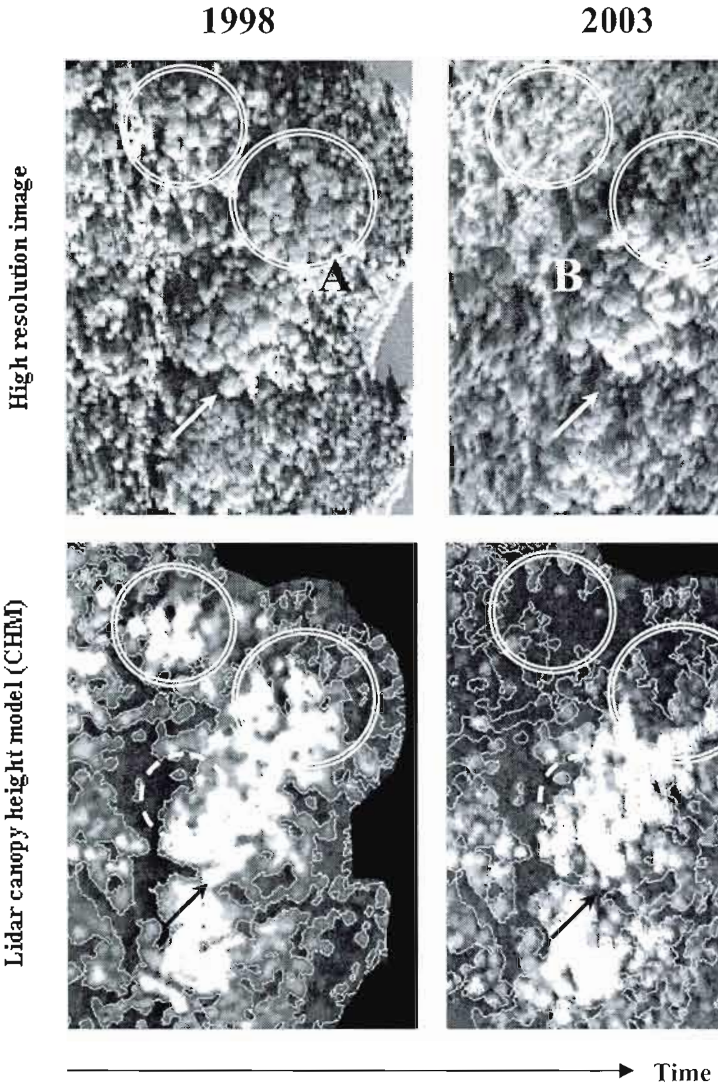

Figure 3.1. An example of delineating gap opening and closure with lidar and high resolution images. Increase in height is given by progressively lighter tones on the CHMs. New single tree (arrow) and group of trees (solid line circle) gaps, and gaps that close (dashed line circle) formed during 1998 -2003 identified on both high resolution images (above) and lidar surfaces (below). "A" on the image indicates hardwood trees that disappeared while "B" indicates softwood trees that are closing a gap.

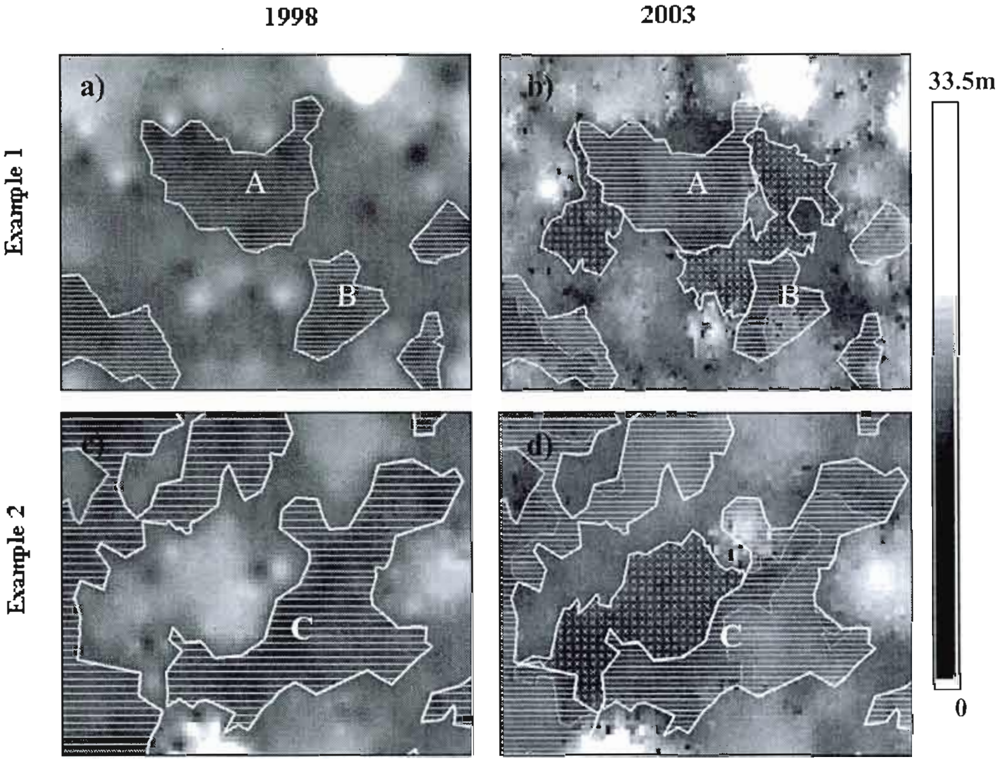

Figure 3.2. Coalescing (top set) and shifting (bottom set) gaps during the period 1998- 2003 delineated on lidar surfaces seen in a 50 m X 40 m window (a) Gaps in 1998 (e.g. A and B) overlaid on CHM 1998 (b) Gap expansion and coalition of A and B during the period 1998-2003, overlaid on CHM 2003 (c) Gaps in 1998 (e.g. C) overlaid on CHM 1998 (d) Gap expansion at the north-west edge and gap closure in the south-east edge of the image during 1998-2003, overlaid on CHM 2003. Polygons filled with horizontal lines show gaps in 1998; polygons with crosses are new gap expansions; dotted line indicates gap closure from 1998-2003.

Calculating gap properties

Gap properties like frequency, percentage of land area in gaps i.e. gap fraction, number of gaps per unit area i.e. gap density, gap size distribution based on frequency of gaps per hectare, annual rates of opening and closure of gaps and turnover were calculated within the ArcGIS 9.2 (Environmental System Research Institute, Redlands, CA) environment based on the standard guidelines on forest gaps (Runkle 1992). Gap size and gap perimeter were determined as the gap object area and gap object perimeter.

Gap fraction for the assessment year *i*, GF_i, is a proportion of forest area under gaps in year *i*, and was derived (Vepakomma et al. 2008) using:

$$\mathrm{GF}_i = \sum_{k=1}^{T} AG_k^i \Big/ aN \tag{3}$$

where AG_k^i is the area (in m^2) of the kth gap object in the ith year, a is the size of each pixel and N is the total number of cells in the study area that do not belong to an open-ended system.

The annual rate of gap opening

$$GO = \text{proportion of land area in new gaps of age} \leq n \text{ years old} / n \text{ years x } 100$$

$$= \left[\sum_{l=1}^{p} AN_l^{ij} \Big/ aNn \right] \text{x } 100, \quad n = 5 \tag{4}$$

where AN_l^{ij} is the area (in m^2) of the l^{th} new gap object during the period *(i,j), i<j, p* is the total number of new gap objects in the study area.

The annual rate of gap closure is

$$GC = \text{proportion of land area where the canopy closed in the gaps / n years x 100}$$

$$= [\ \sum_{f=1}^{q} AC_f^{ij} \Big/ aNn\ ]\, X\ 100,\ n = 5 \qquad (5)$$

where AC_f^{ij} is the area (in m^2) of the f^{th} gap closure object during the period (i,j), $i<j$, q is the total number of gap closure objects in the study area.

Canopy turn over time, the mean time between gap creation events at any point in the forest, was estimated based on total new gap formation and new gap closure independently using:

$$(GO)^{-1} \qquad (6)$$

$$\text{and } (GC)^{-1} \qquad (7)$$

To determine the extent at which new gaps are randomly occurring from a given old existing gap, we adopted the method of plotting average cumulative sums (*CUSUMs)* of the new gap area against the distance from the nearest existing gap edge. *CUSUM* methods are statistical techniques to determine changes or shift over time in a measurement process (Hawkins and Olwell 1998). Distance was calculated as the Euclidean distance from the centroid of a random gap opening to the nearest edge of a gap existing in 1998.

3.5.4. Data on stand initiaton

We used the stand initiation maps created by Dansereau and Bergeron (1993) to identify the different times of origin since fire (TSF) for each stand. The stand chronosequence considered for this study is 248, 206, 133, 123, 96 and 84 years TSF or in other terms the originating stand in 1760, 1797, 1870, 1880, 1907 and 1919 and covering 38%, 30%, 27.5%, 1.4%, 1.69% and 1.85% of the study area respectively. The 248 and 206 year TSF stands are conifer dominated, while the 133 and 123 year TSF stands are mixed forests with a predominance of hardwoods, and the 96 and 84 year TSF stands are dominated by hardwood species.

3.5.5. Classification of species composition

A set of 150 photo captures of near-nadir aerial videography data (0.50 m resolution) acquired on September 27th, 1997 in multi-spectral windows of green (520-600 nm), red (630-690 nm), and near infrared (760-900 nm) bands and orthoready Quickbird satellite images acquired in panchromatic (0.61 m. resolution, 450-900 nm) and multispectral modes (2.44 m resolution, spectral windows similar to videography) on June 13th, 2004 were used to classify vegetation in the study area into conifer or hardwood dominated forest. The Quickbird images were orthorectified with reference to the lidar DSM of 2003 based on modified rational polynomials (for more details refer to St-Onge et al. 2005). A simple first order polynomial rectification was then performed for each of the individual photo captures using the orthorectified Quickbird data as the horizontal geometric reference and then mosaicked in PCI Geomatica v9.01. Canopy height derived from the lidar data was integrated with the spectral signatures of the image data (both years independently) to automatically extract individual image objects using a standard nearest neighbourhood classification procedure in eCognition v. 3.0 (Definiens GmbH, Munich, Germany). This method helped us to successfully separate shadows from vegetation, a problem otherwise inherent in high resolution imagery. We validated the image classification using 40 (and 30 in 2003) hardwood and softwood field identified trees, and 24 non-forest locations. A confusion matrix yielded an overall accuracy of 84% and 87.5%

respectively. The errors were largely due to softwoods mixing with the shadow class. For simplicity, in our further analysis we merged all the non-forest classes into "miscellaneous".

3.6. RESULTS

3.6.1. Gap dynamic characterisation for the period 1998-2003

Extent of canopy opening

In general, we observed that the vegetation surface height increased an average of 2.3 m from 1998 to 2003. Although there was a decrease in the vegetation surface height of almost 5 m across 4% of the area, a significant increase in the vegetation surface height of over 15 m occurred over 6% of the area. Over the 5 year study period the total area under gaps decreased from 200 ha to 180 ha, with 156 ha of the gap area continuing to remain open (Table 3.1 and Fig. 3.3a). Although the total number of gaps per hectare decreased from 17.1 to 13.6, the number of gaps that are larger than 1 ha increased from 23 to 30. Gap closures fragmented a few of the large gaps (over 5 ha) in 1998 into smaller gaps of nearly 1 ha. The mean and median gap sizes are 156.4 m^2 and 19.6 m^2 in 1998 but they increased to 202.3 m^2 and 24.5 m^2 in 2003. The gap size frequency distribution using frequency per unit area for both years is approximately log-normal, with the peak in frequency occurring in the 10 to 100 m^2 size class for all characteristics excepting regeneration and lateral closure where the highest frequency is in the 0 – 10 m^2 size class (Fig 3.3b). The pattern of distribution did not change over time, especially for the existing and new gaps, but the magnitude of frequency varied. Hence, the distributions of gap sizes are significantly different (Kolomogorov-Smirnov test, $p < 0.01$) between all types of gap events.

Table 3.1. Gap dynamic characteristics in a 6 km^2 area of the southeastern boreal forests during 1998 and 2003 as derived from the lidar

Statistic	*Gaps in 1998*	*Gaps in 2003*	*Common open areas*	*New gaps*			*Closed gaps*		
				Expan-sion	*Random*	*Total New gaps*	*Lateral growth*	*Regene-ration*	*Total Closed*
Total number of gaps	9466	7857	9041	6374	452	**6826**	10863	34402	**19329**
Gap frequency per hectare	17.09	13.55	15.83	11.16	0.79	**11.95**	19.02	60.25	**33.85**
Minimum gap size (m^2)	5.00	5.02	5.00	5.00	5.00	**5.00**	3.0	0.5	
Maximum gap size (m^2)	9.8ha	9.2ha	5.9ha	2182.46	223.04	**2182.46**	10.88	402.5	**451.42**
Mean gap size (m^2)	156.37	202.28	149.16	24.64	14.64	**23.98**	7.05	9.25	**17.67**
Median gap size (m^2)	19.6	24.46	23.56	13.72	11.06	**13.43**	5.69	6.63	**12.06**
Standard deviation gap size (m^2)	1708.6	2075.74	1308.75	60.4	14.45	**58.54**	4.41	12.5	**20.31**
95% confidence limit of mean gap size(m^2)	121.9 - 190.9	156.4 - 248.2	122.2- 176.1	23.1- 26.1	13.0 - 15.9	**22.6 - 25.4**	7.1 - 5.7	9.1 - 9.4	**17.4 - 17.9**
Total area under gaps (ha)	200	180.08	156.0	15.71	0.66	**16.37**	7.66	26.49	**34.15**
Percentage of area under gap	38.0	32.0	23.45	2.75	0.11	**2.87**	1.34	4.64	**5.98**
Percentage frequency of gaps < 100 m2	86.7	85.08	85.04	100	97.58	**97.71**	99.99	99.7	**99.04**
Number of gap of size > 1ha.	23	30	17	0	0	**0**	0	0	**0**
Gap fraction (in %)	35.03	31.54	27	2.75	0.12	**2.87**	1.34	4.64	**5.98**
Annual rate of gap formation (opening and closure)	-	-	-	0.55	0.024	**0.57**	0.27	0.93	**1.2**
Turn over time (in years)	-	-	-	-	-	**181.8**	-	-	**83.6**
% hardwood in gap areas that have opened or closed	-	-	-	36	31	**35**	54	50	**50**
% softwood in gap areas that have opened or closed	-	-	-	64	69	**65**	46	50	**50**

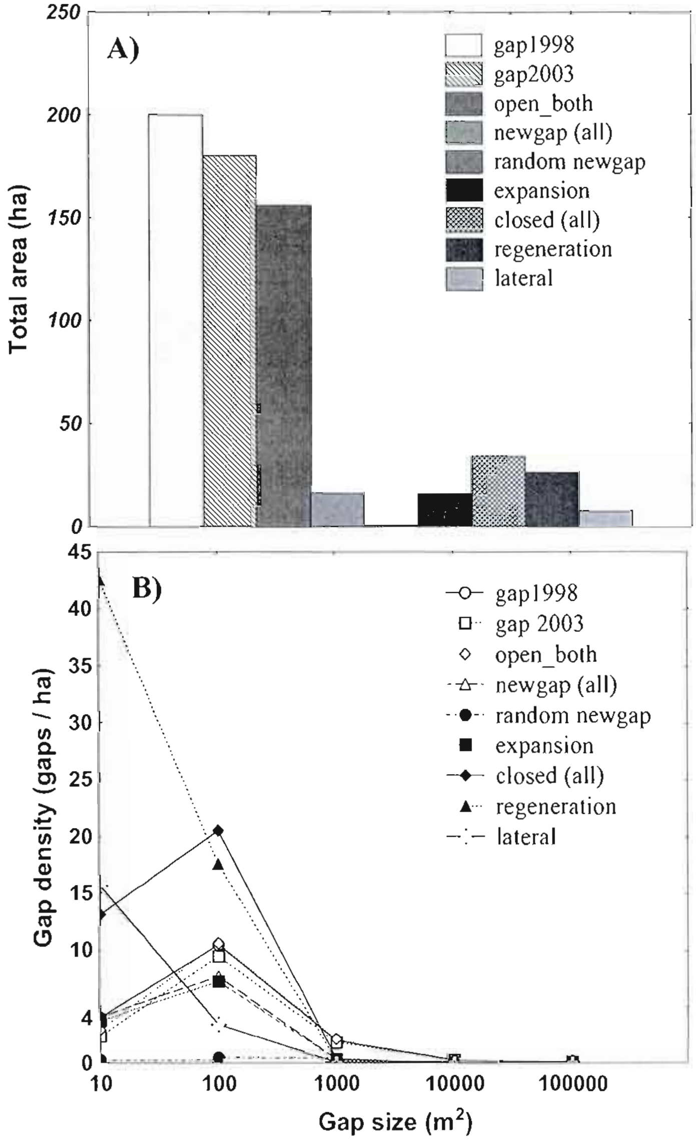

Figure 3.3. Gap processes that occurred from 1998-2003. (A) The area under different gap events; (B) The gap size distribution of different gap events. X-axis shows the upper-limit of the gap-size class.

Gap1998 : gaps in 1998; gap2003 : gaps in 2003; open_both : areas open in both 1998 and 2003; newgap(all) : new openings (random and gap expansions together) that occurred from 1998 – 2003; random new gap : random gap opening during the period 1998-2003; expansion : gap expansion from 1998-2003; closed (all): gap closure (regeneration and lateral closure together) during the period 1998-2003; regeneration: gap closure due to regeneration during the period 1998-2003; lateral :gap closure due to lateral expansion during 1998-2003

New gap openings

A total area of about 16.37 ha in 6826 gaps opened within the canopy during the evaluated 5 year period (Table 3.1). Gap size of the new gaps ranged from 5 to 2182 m^2, with an average size of 25 m^2. Based on their size, 97% of the gaps were formed due to a single or a few trees disappearing from the canopy (Fig. 3.3b). Although the average gap size increased over time, due to gap expansions and gap coalescing, gap size of the new gaps was significantly smaller than the older ones (Mann-Whitney U-test, $p < 0.01$). Based on the recent gap openings, gap density is ~12 / ha, which is slightly lower than the density based on all gaps in 2003. The estimated annual rate of new gap opening is 0.69% with an estimated turn over of 145 years.

Gap expansions vs random gaps

Out of the 6826 new gaps that opened between 1998 and 2003, 94% of them are expansions from existing gaps in 1998 (Table 3.1). There is more area in gap expansions (15.70 ha) than that formed by random gaps (0.66 ha). The mean size of gap expansion is 25 m^2 and that of the random new gaps is 15 m^2. Maximum size of gap expansion is 2182 m^2, while the maximum size of random gaps is 223 m^2. With the exception of two large gap expansions and one large random opening greater than 1 ha in size that opened near streams, nearly 87% of the gap expansions and 90% of the random new openings are less than 55 m^2 in size. This suggests that canopy opening is caused by the death of one or very few trees. However, the size distribution of gaps that expanded is significantly different from those of new random gaps that formed during the study period (Kolmogorov-Smirnov test, $p < 0.001$). Density and annual rates of opening of the gap expansions and random new gap openings are 11.2 per ha and 0.55 and 0.8 per ha and 0.02 respectively.

New gaps coalesced about 409 existing gaps at an annual average rate of 286 m^2 during the study period. It is also noted that about 989 existing gaps with a mean gap size of 1173 m^2 in 1998 have both expanded and closed. Gap size distribution indicates that such coalesced gaps are greater than 100 m^2 in size. Although the overall rate of closure is higher than that of new gap opening in these boreal forests (Table. 3.1), the contrary was noted for the gaps that were both expanding and closing from 1998 to 2003. Of the new gaps that coalesced, over 2.6% of the existing area in canopy opening was closed but another 13% opened as gap expansions.

Gap closures

Overall, in these forests the rate of canopy closure is 1.2%, which is faster than the creation of new canopy openings. Between the two time periods 34.15 ha of canopy closed. Of the 19 329 objects that showed closure, the maximum object size is 451 m^2 but 99% of the closures are smaller than 100 m^2. With a higher gap closure density and smaller average size than that of new gap opening, the recently closed gap objects appear much more fragmented within themselves than the recently opened canopy gaps. The patch size distribution between the recently opened gaps and closed canopy is significantly different (Kolmogorov-Smornov test, $p < 0.01$).

Lateral vs vertical growth

The majority of gaps closed in these forests due to vertical growth of the regeneration (56.5% of the total number of gaps that closed during the 5 years). The total area that closed laterally is 7.7 ha whereas the total area that is closing through regeneration is 26.5 ha (Table 3.1). Gaps that closed due to lateral growth ranged from 5.0 to 10.9 m^2 in size while regenerating gaps ranged from 5 to 403 m^2.

Canopy gaps vs changes in species composition

In general, the percentage of hardwoods increased with a slight decrease in the percentage of softwoods during the study period in this part of the boreal forest (Table 3.2). As noted earlier, open areas (that are merged in the miscellaneous class of image classification) decreased over time (Table 3.1). Generally, softwoods are opening more than hardwoods, with a large proportion (50%) being in gap expansions (Table 3.1). However, hardwoods and softwoods are both closing almost the same number of gaps, with hardwood lateral growth being marginally greater than that of the softwoods. In these forests some short-term shifts in composition were seen, with 4.4% of the hardwoods being replaced by hardwoods, and 8.4% of the softwoods replaced by softwoods (Table 3.2).

Table 3.2.
Broad species compositional changes (given in area ha.) from 1998-2003 in a 6 km^2 area of boreal forests around Lake Duparquet, Quebec, Canada

2003 ***1998***	***Hardwood***	***Softwood***	***Miscellaneous****	***Total***	***% to the total area***
Hardwood	62.76	25.44	21.86	**110.06**	*19.13*
Softwood	48.17	50.86	45.45	**144.48**	*25.11*
Miscellaneous	44.17	45.5	231.19	**273.88**	*55.75*
Total	**155.12**	**121.82**	**298.5**	**575.46**	
% to the total area	*26.96*	*21.17*	*51.87*		

* Miscellaneous class includes shadows and all non-vegetated areas i.e.canopy gaps, water, paths, rocky outcrops.

3.6.2. Gap dynamics in stands in different developmental stages

Gap fraction was reduced in all stands from 1998 to 2003, with the exception of the youngest stand, while the highest decrease occurred in the oldest stand (Table 3.2). New gaps opened more frequently in the oldest stands (burned in 1760 and 1797) than in the remaining younger stands at 0.88% and 0.6% rates of gap opening respectively. Thus the older stands were more dynamic with more area opening and closing. Over 60-80% of the new gaps were formed due to gap expansions. Though the maximum gap sizes varied significantly, the variation in mean gap sizes is not considerable across the stands. The rates of gap closing were consistently higher than the rates of opening in all stands, but gap closures were highly fragmented with a mean size lower than the mean size of new gaps. Gap turnover was shortest in the oldest stands (114 years), and longest in the youngest 84 yr TSF stands (up to 643 years). The percentage of area in gap closures increased with stand age, largely due to regeneration closing gaps from beneath. Closure from the side i.e. lateral expansion is noted in all stands with the most growth occurring in the oldest stands.

The gap density distribution for all gap dynamic characteristics over the range of time since fire stands is approximately lognormal with the peak in frequency mostly occurring in the 10 to 100 m^2 size class, but interestingly the pattern did not differ from the gap density distribution observed at the forest level (Fig 3.4). In all but the youngest stand, gap expansions occur more frequently than random gaps. Gap closures in the oldest stand are the most fragmented compared to the other stands. However, differences in the gap density distributions of all gap dynamics events between the differently aged stands are highly significant (Kruskal-Wallis ANOVA by ranks and Median tests, $p \approx 0$).

Table 3.3. Gap characteristics for different aged stands in the southeastern boreal forest (1998-2003)

Statistic / Time Since Fire (years)	**84**	**96**	**123**	**133**	**206**	**248**
Total area open in 1998 (in ha) *(gap fraction in %)*	1.76 (16.20)	4.26 (42.52)	0.97 (11.59)	26.49 (16.26)	80.92 (45.90)	81.29 (36.10)
Total area open in 2003 (in ha) *(gap fraction in %)*	2.19 (20.19)	3.46 (34.48)	0.72 (8.59)	22.78 (13.89)	70.85 (40.18)	76.34 (33.90)
New Gap Opening						
Number of new gaps (gap density/ha)	55 (5.0)	155 (15.5)	82 (9.9)	1783 (10.9)	3188 (18.1)	4831 (21.5)
Max. gap size (m^2)	289.35	57.4	48.5	2107.63	867.91	2182.46
Mean gap size (m^2)	17.77	13.22	11.86	22.88	16.85	20.83
Median gap size (m^2)	7.68	9.42	9.96	12.46	10.59	11.65
Total area under newgap (ha.)	0.08	0.19	0.09	4.04	5.3	9.9
% area under newgaps	0.78	1.89	1.10	2.47	3.01	4.4
% new gap area that was hardwood	30.00	27.00	24.71	46.96	33.13	30.06
% new gap area that was softwood	70.00	73.00	75.29	53.04	66.87	69.94
Annual rate of gap opening (%)	**0.16**	**0.38**	**0.22**	**0.5**	**0.6**	**0.88**
Gap turnover (years)	643	265	455	202	166	114
Area under gap expansion	0.06	0.13	0.06	3.15	4.11	8.03
Area under random gap opening *(gap density)*	0.02 (2.2)	0.06 (6.29)	0.04 (4.89)	0.89 (4.4)	1.19 (6.23)	1.87 (7.4)
Gap Closure						
Total area of gap closure (ha)	0.02	1.03	0.31	8.08	13.39	13.85
% Area closed to the total area	2.19	10.27	3.68	4.93	7.59	6.15
Annual rate of gap closure (%)	**0.44**	**2.05**	**0.74**	**0.98**	**1.52**	**1.23**
Closure turnover (years)	228	49	136	101	66	81
Area closing from side (in m^2)	0.02	0.13	0.12	1.74	2.63	3.34
Area closing from below(m^2)	0.22	0.9	0.19	6.33	10.7	10.5
% closure that is hardwood	57.50	48.43	54.04	41.63	47.08	48.82
% closure that is softwood	42.50	51.57	45.96	58.37	52.92	51.18

Underlined figures are the highest values for a given statistic

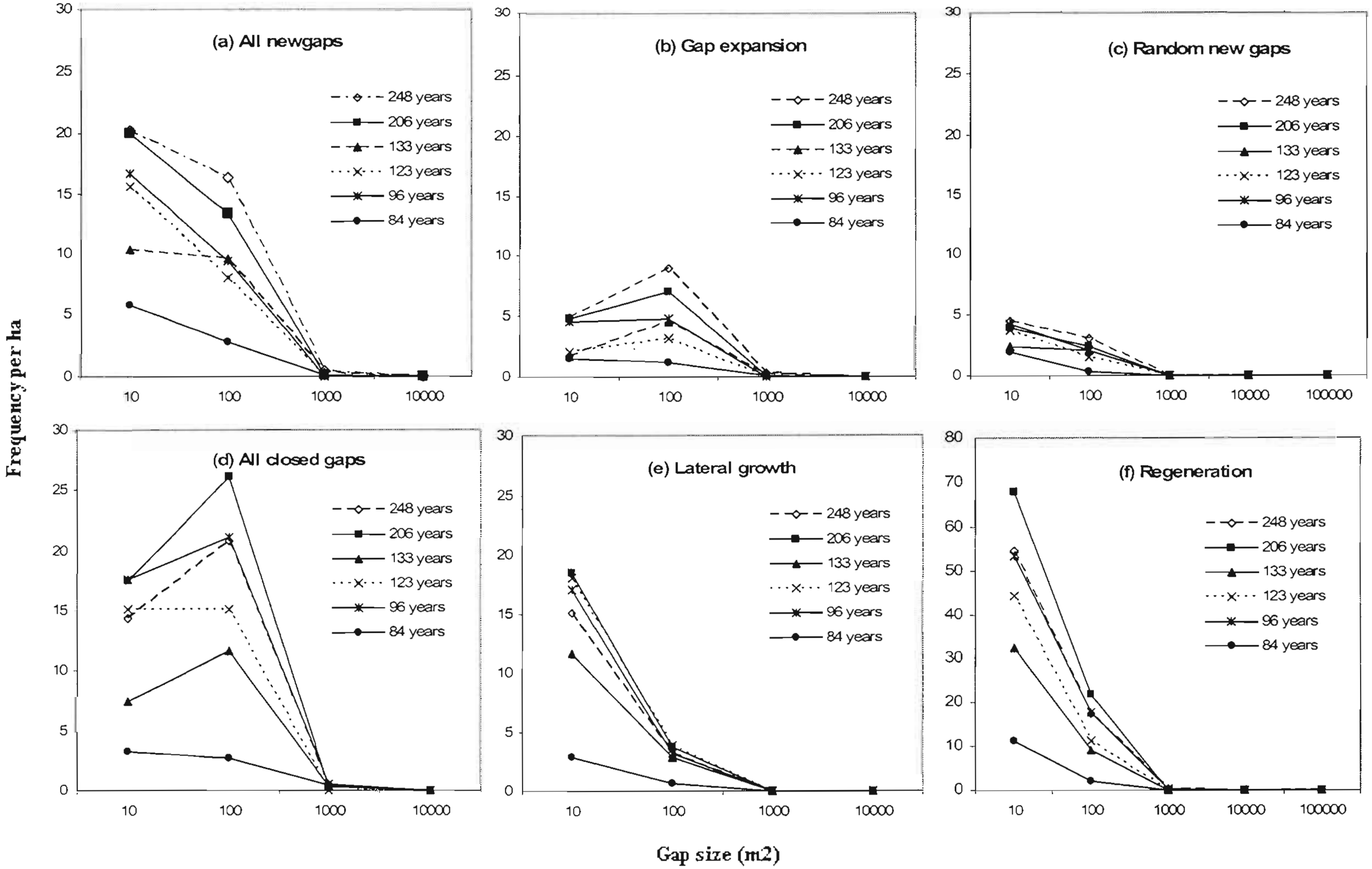

Figure 3.4. Gap density distributions of of various gap dynamical characteristics occured in stands of different origin (times since fire). Gap size class upper-limits are shown on x-axis. Note the difference in the scale on y-axis

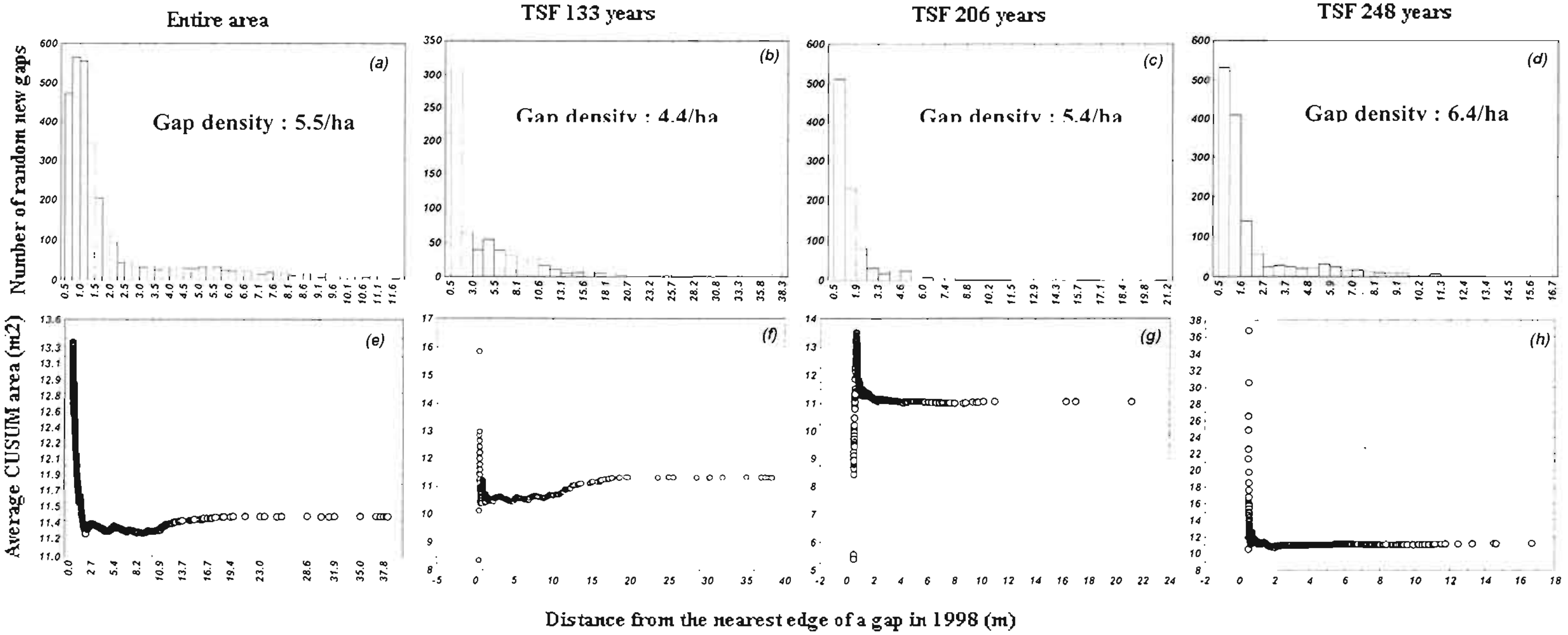

Figure 3.5. Spatial distribution of random new gaps with respect to the distance of their centroid from the nearest edge of a gap in 1998. (a) to (d) Frequency of random gaps occurrences in the entire study area and old stands; (e) to (f) Plots of the average cumulative sum (CUSUM) of random gap area in the entire study area and in old stands

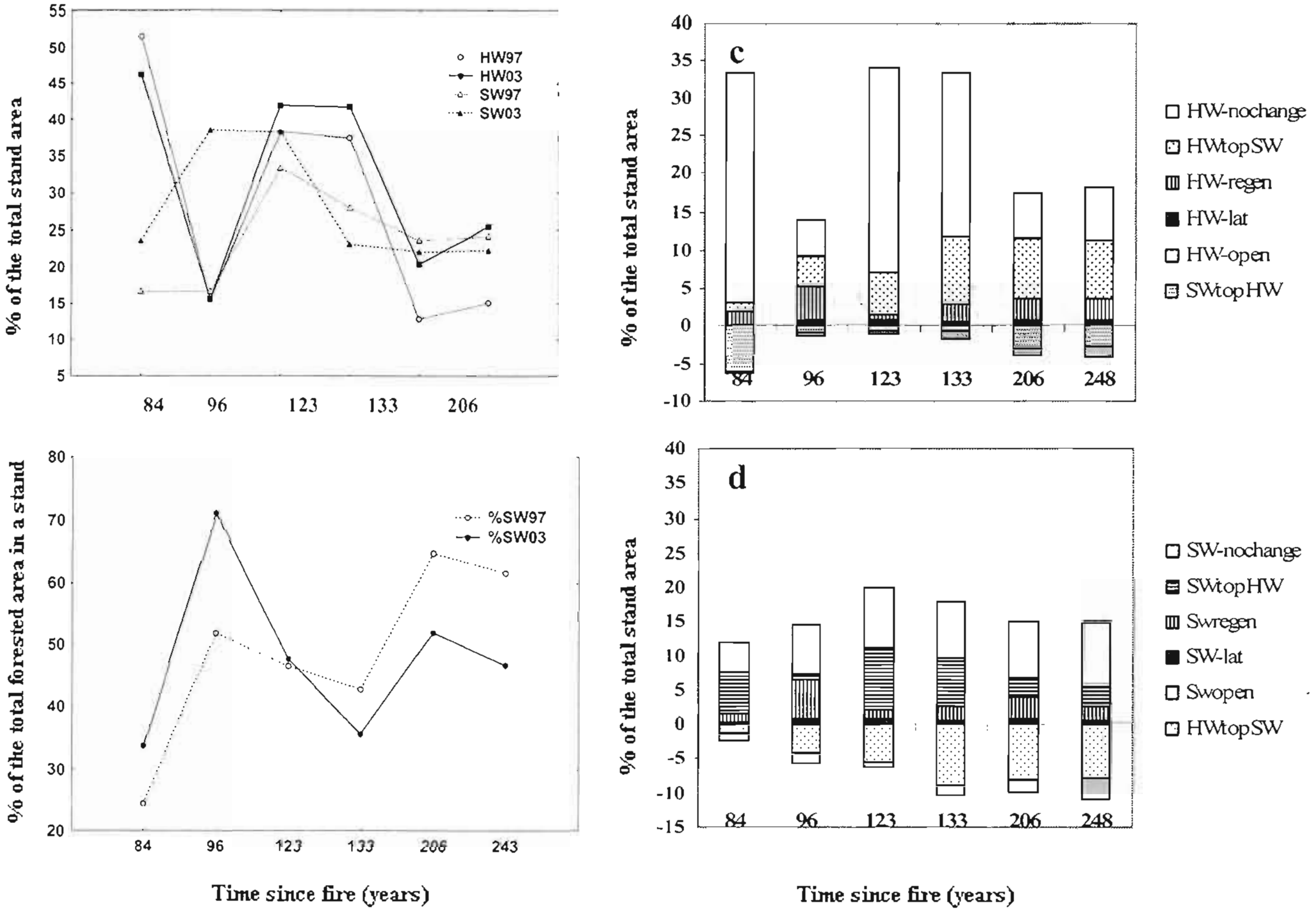

Figure 3.6. Changes in the distribution of hardwood and softwood species during 1998-2003 for stands originating at different times since fire (a) Overall changes in species composition in the stands (b) Percent distribution of softwood to the total forested area per TSF (c) Shows the stacked graph of the percent change in the total area of the hardwood of 1997 to various classesin the stands (d) Shows the stacked graph of the percent change in the total area of the softwood of 1997 to various classes in the stands.

HW : hardwood; SW : softwood; HW-close : Hardwood closure; SW-close : Softwood closure; HW-nochange : unchanged Hardwood; SW-nochange : unchanged softwood; SWtopHW : Softwood topping hardwood; HWtopSW : Hardwood topping hardwood;

Our investigations suggest that the older stands are more open compared to the intermediate and young stands (Table 3.3). Random gaps appeared at a distance of 0.5 m. to 38 m from the edge of an existing gap in 1998 with a range of gap density of 2.9/ha to 6.4/ha. This range increased with stand age. Nonetheless, the majority (75% of random gaps in older stands and 60 to 75% of random gaps in younger stands) of the random gaps appeared within 2.5 m of the existing gap edge irrespective of the openness of the stand (Fig. 3.5a to 5d). The CUSUM (curve of the average cumulative sum of the gap area against the distance from the existing gap edge) also indicates that the size and chance of occurrence of new random gaps in these forests is influenced by the presence of existing gaps (Fig. 3.5e to 5f).

Gaps vs changes in species composition

A comparison of the percentage distribution of species composition over the two years assessed shows that the proportionate area covered by hardwoods increased over time in all stands. Softwoods on the other hand showed a considerable increase in the younger stands with marginal changes in the older ones. Nearly 70% of the newly opened area (mostly composed of gaps smaller than 500 m^2) in all stand types is due to the loss of softwood trees. Gaps created only by hardwood trees were usually found to be large (3 gaps are over 1 ha, 7 are over 500 m^2) and all close to lakes or streams, suggesting that they may have been created by beaver damage (field observations, Senecal et al., 2004). Although a slightly higher proportion of softwoods in the closed gaps is noted in most of the stands, gaps closed by hardwood regeneration in the older stands were observed to be large (exceeding 100 m^2).

By examining the changes that occurred in the two broad species groups with respect to their status in 1998, we noted that the gain in the proportion of hardwoods is much higher than its loss, and that these gains steadily increase with stand age (Fig 3.6). Although hardwoods and softwoods have similar rates of closing, softwoods gained less area than they lost, and the area gained decreased with the age of stands. Hardwoods top softwoods at a greater rate in the older stands while softwoods tend to outgrow hardwoods in the younger stands. A higher proportion of hardwood gain occurs through lateral gap closures while softwood gain by overtopping is observed mostly in the younger stands, while the opposite was found in the older stands.

3.7. DISCUSSION

Gap dynamical characteristics in boreal forests

Canopy openings varied in sizes from 5m^2 to 9.8 ha, thus falling beyond the reported range of gap characteristics of boreal forests made in earlier single-time observations (de Romer et al. 2008, Bartemucci et al. 2002, Kneeshaw and Bergeron 1998, Frelich and Reich 1995). A gap size range of 15 to 1245 m^2 was summarized for studies in boreal and subalpine forests by McCarthy, 2001. Their shapes were also noted to be highly complex and irregular in our study unlike the ellipsoid forms described in much of the literature (examples in Figs 3.1 -3.3). Dense and contiguous coverage of lidar data enabled a near-complete census of gaps in 6 km^2 of forest area, which improved the chance of identifying both small and large gaps. Owing to dense point cloud acquisition at near vertical viewing angles and active sensing that does not rely on illumination by natural sunlight, lidar methods provide an effective way of identifying canopy gap dynamics (Vepakomma et al. 2008).

Random occurrence of canopy gaps as well as expansions from previously disturbed canopies is seen in all stands. Though gap expansion is also a prominent feature in tropical and temperate forests (Worall et al. 2005, Runkle 1998, Lertzman and Krebs 1991, Foster and Reiners 1986), gap expansions have not been noted in other parts of the boreal forest. Previous single-time studies assumed that younger boreal stands due to their age did not undergo gap expansions and thus they attributed abundant small gaps to random senescence and death of early successional species (Hill et al.

2005, Bartemucci et al. 2002, Kneeshaw and Bergeron 1998). Based on our multi-temporal lidar data analyses we found that trees bordering canopy gaps were more vulnerable to mortality compared to interior canopy trees in all stands regardless of gap fraction. Gap expansions reported in most studies (Quine and Malcom 2007, Worall et al. 2005, Rebertus and Veblan 1993, Worall and Harrington 1988, Foster and Reiners 1986) were due to windthrow. Although very large expansions were observed, the majority of gap expansions and formation of random gaps were smaller than 55 m^2 unlike in wind-driven *Picea-Abies* forests of New Hampshire (Worall et al. 2005) and Sitka spruce plantations in Britain (Quine and Malcom 2007) where gap expansions were also as frequent but larger in size compared to random gaps.

The majority of the openings are filled from below, with a smaller but significant proportion of the closures due to lateral growth of the gap edge trees. In hardwood forests it has generally been acknowledged that small gaps close from the sides while large ones fill from below (Van der Meer and Bongers 1996, Runkle 1981). In boreal forests, gap closure from lateral in-filling has not been thought to be important due to the determinate growth and crown form of conifer trees (Nagel and Svoboda In-Review). However both types of canopy closure were observed in our study across a gradient of gap size, although gaps closing due to regeneration attain larger closure sizes (403 m^2 vs 11 m^2 maximum closed gap size). Furthermore, both hardwoods and softwoods close gaps laterally which supports the conclusion made by Umeki (1995) that the foraging ability of gap edge canopy trees towards gap centre did not differ amongst species groups.

Dynamic structural changes of stands in different developmental stages

This study of a fine scale process of individual tree mortality over a large spatial area (6 km^2) reveals that boreal forests of all developmental stages (i.e. recruited after different stand replacing disturbances and then affected by one or multiple spruce budworm outbreaks (Campbell et al. 2008, Bergeron 2000, Morin et al. 1993)) are changing quickly even within a short period of time. Canopy gaps in these forests are dynamically expanding, coalescing old gaps to form large openings and closing rapidly during the study period. Openness in all stands generally decreased over time, however, older stands (i.e. those that have had a longer period of development since the last fire) had higher rates of new gap formation. Increased openings with stand development were also noted in 60-120 year old stands in aspen dominated boreal forests (Hill et al. 2005). Our results indicated that the gap closure rate is higher than the rate of canopy opening in these boreal forests, especially in the older stands. Since the older stands were primarily dominated by balsam fir and thus most opened following the last spruce budworm outbreak (Kneeshaw and Bergeron 1998), this is in agreement with suggestions made by researchers that structural changes are faster during the first stages of gap closure (Valverde and Silvertown 1997, Brokaw 1985). Older forests in this study area have been regenerating for 10-20 years following the last SBW outbreak (Morin et al. 1993). Despite higher rates of closure, the forests appear patchy and open as 78% of the old-gaps did not fill and thus continue to be open. Short growing seasons and persistent snow accumulation may delay the filling of the gaps in the northern latitudes (Parish and Antos 2004, Bartemucci et al. 2002, Lertzman et al. 1996).

Gap density of random new gaps showed no pattern with respect to stand development and gap expansion is reportedly high in all the stands. In fact, from the analysis on the distance of random new gaps to the nearest old gaps of 1998 in the conifer dominated stands it emerges that irrespective of the level of openness in stands occurrence of random gaps is to a large extent influenced by the presence of an existing gap. Evidence also shows that both random gaps and gap expansions are mostly formed by late successional conifers, with an exception of two large new openings of hardwoods that occur in the proximity of streams. Comparing the results from previous studies in this forest, we note that the last spruce budworm outbreak had a significant and severe impact on old-conifer stands that even 16 years after the last outbreak they are not closer to their pre-outbreak canopy structure (Fig 3.7a). Since no exogenous disturbances like windthrow or root rot are reported in this forest during the study period, we conclude that these parts of the boreal forests are still experiencing the legacy of the last spruce budworm outbreak.

In contrast to the expectations, responses to the last moderate to small scale disturbances in these stands did not follow the previously conceived patterns. Old-conifer dominated stands recovering from the last infestation of spruce budworm outbreak are closing at a greater rate than young hardwood dominated stands as hypothesised, except in the case of the 96 year TSF stand. However the rates of new openings in the canopy continue to be high in both young and old stands. In comparison, the younger stands appear more dynamic with a slight increase in gap fraction due to a new opening rate of 0.16 and a closure rate of 0.44 in 84 year TSF stand rates which are slower than in the older stands. In contrast, there is a considerable decrease in gap fraction and a high rate of closure of 2.05 in the 94 year TSF stand.

Compositional shifts of stands in different developmental stages

Previous research suggested that large gaps favour intolerant hardwoods while shade tolerant softwoods successfully regenerate in small gaps (Kneeshaw and Bergeron 1998) however this relationship was not observed here. An evaluation of gaps that totally closed from regeneration between observations in 1998 and 2003 did not show a correlation between species groups of the regeneration and gap opening size. Overall a proportion of softwood and hardwood regeneration within gaps was almost balanced with only a slight variation between the stands (Fig. 3.7b). The exception was in the oldest stand where a considerable number of the large closures (over 100 m^2) were, in contrast to our expectations, closed by hardwood regeneration.

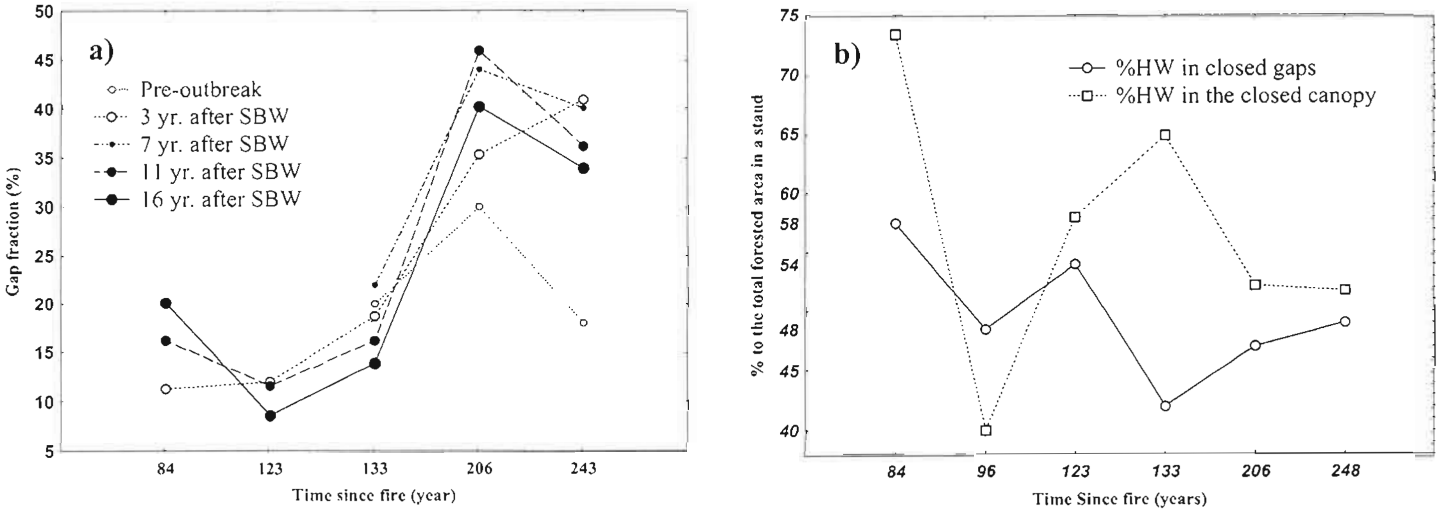

Figure 3.7(a) Comparison of gap fraction over time in different time since fire stands of the boreal forests. "SBW" stands for spruce budworm outbreak. Results of pre-outbreak conditions and 7 years after SBW adopted from D'Aoust et al (2002), while 3 years after SBW from Kneeshaw and Bergeron (1998). (b) Comparison of species composition between regenerating gaps and closed canopy.

In general, there is an increase in the presence of hardwood in this forest over the study period; however, the softwood component is still maintained. Hardwoods continue to be predominant in the canopy of younger stands although conifer regeneration was abundant only in the 96 years TSF stand. In contrast, as seen in earlier studies in boreal forest (Bouchard et al. 2006, Kneeshaw and Bergeron 1998) gaps created by spruce budworm outbreaks seem to be the mechanism for hardwood maintenance in older conifer forests. Nonetheless, as we noted in this study, shifts in species composition in all stands are not just a result of gap closures but are also due to species replacement in the canopy without gap formation (Fig 3.6). As the canopy dies, understory softwoods assume dominance in younger stands without the formation of a gap although a decrease in canopy height is observed. In the older stands such transition, without our recording of a gap, can occur from conifers to hardwoods. These transitions both support and oppose earlier studies from chronosequences in this region that have shown a slow progression from hardwood dominated, younger TSF stands to mixed coniferous-deciduous stands due to small-scale disturbances and a continued increase in conifer dominance in mid-late aged stands (Bergeron 2000). However, most studies based on the chronosequence approach are made using single-time measurements based on a few representative sites from each stand to infer general patterns. An obvious advantage of using lidar and high resolution image analysis of canopy gaps is the ability to repeat this near-complete census of canopy openings through time and over an extensive spatial area and hence can capture variations at local scales and across stands.

3.8. CONCLUSION

This spatially explicit fine scale and short-term study of old-growth boreal forest dynamics counters earlier assumption that transition in boreal forests is slow, directional and influenced by the period of development since the last fire. Gaps are important for hardwood maintenance while non-gap replacement is the main mechanism for softwood recruitment in these forests. These results stress the need for temporally analysing large contiguous spatial areas to alleviate uncertainty in interpreting and extrapolating dynamics from few representative sites. The study also provides a promising illustration of the strengths of combining lidar and high-resolution imagery in rapidly evaluating detailed and spatially extensive (a near-complete census of gaps in a large area) short-term dynamics of boreal forests. However, further analysis over a long time period is necessary to verify whether these observed dynamics are a temporary phenomenon or a characteristic that fluctuates with spruce budworm outbreaks.

CHAPTER IV

Boreal forest height growth response to canopy gap openings – an assessment with multi-temporal lidar data

This chapter will be submitted **to Ecological Applications** as: Vepakomma,U., B. St-Onge, D. Kneeshaw, *Boreal forest height growth response to canopy gap openings – an assessment with multi-temporal lidar data.*

4.1. RÉSUMÉ

Suivant l'ouverture de la canopée en forêt boréale, l'évaluation à l'échelle fine de la croissance en hauteur d'un arbre est difficile à déterminer à partir de données terrain, et elle est d'autant plus difficile à partir d'images à deux dimensions étant donné les limites de précision dans la détermination de la hauteur photogrammétrique de la couronne et de la taille des individus. Toutefois, connaître la réponse en hauteur des arbres selon la taille d'ouverture d'une trouée est nécessaire au développement d'une sylviculture basée sur la dynamique de trouées. Dans cette étude, nous démontrons le potentiel de l'utilisation de données d'altimétrie laser prises sur un intervalle de cinq ans afin de caractériser les arbres et les gaules selon leur croissance en hauteur et en largeur à la suite de l'ouverture de la canopée. En combinant les groupements d'espèces feuillues et résineux obtenues à partir d'images de haute résolution avec les informations structurales provenant de l'altimétrie laser, nous avons estimé des groupements d'espèces selon des patrons de croissance en hauteur des arbres et des gaules dans une matrice de forêt mixte boréale canadienne de 6 km^2. Par la suite, nous avons utilisé des techniques statistiques afin d'évaluer la réponse de la croissance selon localisation spatiale dans la trouée. Les résultats démontrent que les mécanismes de fermeture des trouées s'effectuent à un taux de 1,2% par année. Les feuillus et les conifères en périphérie des trouées semblent avoir une croissance latérale similaire (en moyenne de 22 cm/an), ainsi qu'un taux similaire de croissance en hauteur indépendamment de la localisation et de la taille initiale. La croissance en hauteur des gaules était fortement influencée par leur localisation dans la trouée et par la taille de la trouée. Les résultats suggèrent que les gaules feuillues et résineuses croissent à un taux plus élevé à une distance de 0,5 – 2 m et 1,5 - 4 m de la périphérie de la trouée pour des trouées plus petites que 800 m^2 et 250 m^2 respectivement. Dans les forêts intactes, l'effet des trouées était notable sur la croissance en hauteur des feuillus et des conifères dominants jusqu'à une distance de la trouée de 30 m et 20 m respectivement. Nos résultats suggèrent que les forestiers devraient considérer le développement de techniques sylvicoles engendrant de petites ouvertures de la canopée dans la forêt mixte boréale afin de maximiser la croissance des arbres résiduels et de la régénération.

Mot-clés: dynamique des trouées, la fermature de la canopée, croissances latérales, localisation des arbres individuels, croissance en hauteur, taille d'ouverture minimale, lidar à retours discrets

4.2. ABSTRACT

Fine scale height-growth responses of boreal forests to canopy gap openings are difficult to measure from the ground, and photogrammetric height measurements using bi-dimensional images have limitations in accurately defining gaps and determining individual crowns and height. The precise knowledge of height growth response to different openings will be critical in refining gap-based single or multiple tree silviculture. In this study, we demonstrate the potential of discrete multi-temporal lidar acquired over a 5-year time interval to characterise tree / sapling height and lateral growth responses to canopy openings. Combining data on broad species classes interpreted from high resolution images with lidar structural data, we estimated species-class height-growth patterns of trees / saplings in various neighbourhood contexts across a 6 km^2 matrix in Canadian boreal mixed deciduous-coniferous forests. We then use statistical techniques to probe how these growth responses vary by spatial location with respect to the gap edge. Results confirm that both mechanisms of gap closure contribute to the closing of canopies at a rate of 1.2% per annum. Evidence also shows that both hardwood and softwood gap edge trees have similar lateral growth (average of 22 cm / yr) and similar rates of height-growth irrespective of their location and initial height in boreal forests. Height-growth of all saplings, however, was strongly dependent on their position within the gap and size of the gap. Results suggest that hardwood and softwood saplings grow at highest rates at distances within 0.5 – 2 m and 1.5 -4 m from the gap edge and in openings smaller than 800 m^2 and 250 m^2 respectively. Gap effects on the height-growth of trees in the intact forest were evident up to 30 m and 20 m for hardwood and softwood overstory trees respectively. Our results thus suggest that foresters should consider silvicultural techniques that create multiple small openings in mixed coniferous deciduous boreal forests to maximise growth response of both residual and regenerating trees.

Key Words: canopy dynamics, gap closure, lateral growth, regeneration, single tree locations, height-growth pattern, minimum opening size, discrete lidar

4.3. INTRODUCTION

Tree mortality causing canopy opening leads to an increase in resources that ostensibly increases with opening size (Pickett and White 1995, Denslow and Spies 1990). These enriched environments not only accelerate the height growth of saplings within gaps but also the lateral growth of edge trees; eventually closing the canopy gaps from below or from the sides (McCarthy 2001, Denslow et al. 1990, Brokaw 1985). Gaps can also have a positive influence on the growth of trees in the forest surrounding the opening although they may also have negative effects through increased stress and thus mortality of edge trees. There is also some question as to the distance gap effects may extend into the interior tree layer with research showing edge effects to be important in artificial openings like agricultural fields, or clearcuts (Burton 2002, Chen et al. 1992). Furthermore, different species groups (hardwoods or conifers) may respond differently to canopy openings especially in mixed deciduous-coniferous boreal forests as conifers have determinate growth and hardwoods have indeterminate growth. These differences may thus limit or enhance the growth responses of adult vs regenerating trees of these different species groups to canopy openings. As forest managers explore alternative treatments, knowledge on growth responses will be critical for evaluating the efficacy of different partial harvest treatments, especially in sub-boreal forests that have been traditionally managed with large clearcuts. However, thus far, fine-scale ecological knowledge on lateral *vs* vertical height growth or mortality responses to canopy gap openings and application of this knowledge to gap-based silviculture is based on limited spatial and temporal scales (Hausseler and Kneeshaw 2003, Landres et al. 1999, Coates and Burton 1997).

Studies on height-growth responses are few and rarely document spatial variability due to the difficulty in collecting data and limitations in available techniques.

Specifically, measuring tree height-growth responses can be complex using conventional methods (Vepakomma et el. 2008, McCarthy 2001). Moreover, most studies focus largely on species-specific diameter growth rather than height-growth, in small plots within a few ground measured gaps of particular stands (Fajvan et al. 2006, Pedersen and Howard 2004, Canham 1988). The response of the whole forest is thus interpreted from only a few representative gaps at local scales. Photogrammetric measurements using bi-dimensional images for canopy height and to some extent canopy gaps have been used in the past across larger spatial scales (Miller et al. 2004, Fujita et al. 2003, Tanaka and Nakashizuka 1997). However, the quality of photo-measurements is affected by image texture and contrast, sun-incidence angles during image acquisition, resolution and most importantly by the accuracy of ground elevation which remains difficult when canopies are closed (St-Onge et al. 2004, Koukoulas and Blackburn 2004). Ground elevation is critical in determining the canopy height from digital surface models. Traditionally we are thus left with a limited choice between great precision for a few small plots that must be extrapolated or from imprecision at larger scales. In recent decades, evolution of laser pulse technology has increased the efficiency in describing forest canopies in three dimensional (3-D) space with finer spatial details and also across broad extents. Air borne laser scanning, hereafter referred as "lidar" (for LIght Detection And Ranging), data has emerged as a tool to estimate vegetation height, cover, detailed canopy structure and changes in forest height in a variety of forest (Vepakomma et al. 2008, Clark et al. 2004, Harding et al. 2001). The potential to measure growth using repeat lidar measurements has been suggested in a few studies (Hopkinson et al. 2007, Yu et al. 2006, St-Onge and Vepakomma 2004). In this study we develop methods to explore the potential of lidar for characterising the height-growth responses of boreal forests to the opening of canopy gaps across a large forest area by measuring height-growth at tree level.

Many factors contribute and interact to affect the height-growth of individual trees and saplings in and surrounding canopy gaps (Oliver and Larson 1996). Thus mode of gap closure depends on how rapidly saplings can grow before gaps are closed laterally. Trimble and Tryon (1966) and Hibbs (1982) showed that few saplings reach the canopy in smaller openings in temperate forests because of quick closure by the surrounding trees. Furthering these observations through repeat measurements (Runkle and Yetter 1997), tree ring data analysis (Canham 1985) and simulations (Cole and Lorimer 2005) it has been shown that most saplings in temperate forests require two or more gap episodes to reach the canopy. Because the process of gap closure is slow and difficult to monitor except in a limited number of gaps, optimum opening sizes and the time required for successful recruitment of tree saplings to the canopy are not well known (Webster and Lorimer 2004). Moreover, these studies suggest the effect of lateral growth may be more important than height growth in filling smaller gaps, especially in hardwood forests. Although softwoods have shown similar foraging for resources as hardwoods in Fennoscandinavian boreal forests (Umeki 1995), and to a lesser degree in mixed hardwood stands of Massachusetts (Muth and Bazzaz 2002), research on lateral growth of the softwoods has attracted less attention than hardwoods. Little is known about the capacity of either conifer or hardwood trees in North American boreal forests to grow laterally.

Research in many forests shows that height growth responses of gap saplings varies with gap size, position and initial sapling size; factors that are directly related to light availability (Canham et al. 1990, Brokaw and Scheiner 1989). In boreal forests, however, the role of canopy gaps in enhancing the growth of vegetation is ambiguous. Studies in the eastern boreal forest suggested that large gaps favour intolerant hardwoods, like aspen or birch, while smaller gaps are conducive to the recruitment of shade-tolerant conifers, like fir and spruce (Kneeshaw and Bergeron 1998). Not all shade-tolerant conifers, however, responded to gap size in the coniferous forests of Oregon-Washington forests (Gray and Spies 1996). It has also been shown that light levels differ little between non-gap and gap environments in boreal forests (Bartemucci et al. 2002, Ban et al. 1998). Furthermore, growth rates differed little between conifer saplings in full-light and in partial shade (Claveau et al. 2002). Despite growing recognition of boreal canopy gap dynamics in the recent past, gap filling processes in boreal forests have attracted much less attention than gap formation (for e.g., De Romer et al. 2007, Drobyshev and Nihlgård 2000, Kneeshaw and Bergeron 1998).

The central objective in this study is to develop a deeper understanding of how mixed conifer- hardwood boreal forests respond to various sized openings of the canopy created by the removal of overstory trees and to what extent these canopy gaps influence the height growth of trees and saplings across the forest matrix. We will then investigate whether lateral growth or height growth of regenerating vegetation is more important in closing different sized gaps. We expect a greater lateral and height growth response from intolerant, indeterminate growth hardwoods than from shade-tolerant conifers in large gaps but those conifers would out grow hardwoods in the forest interior and in the smallest canopy openings. By individually locating trees and saplings, and stratifying the whole forest, we investigate whether gap openings influence the height growth of vegetation (a) within canopy openings and (b) in the neighbourhood of canopy openings. Consequently, we should be able to assess (c) the distance to which the effect of openings extends into the interior of intact canopies in terms of height-growth of overstory trees. Similarly, we will also examine the impact of the position of gap sapling within a gap with respect to (d) the gap edge and (e) the gap opening size on the height-growth of the gap sapling. This information will provide us with a greater understanding of how canopy openings affect growth and forest structure within and surrounding gaps and will thus allow us to evaluate whether silvicultural strategies based on gap openings could play an important role in a forest managers tool kit in similar boreal forests.

4.4. LIDAR AND HEIGHT GROWTH OF VEGETATION

Remote sensing data provides a means of scaling measurements across two or more spatial scales of observation (e.g., tree, plot to landscape or region) at multiple time intervals. Lidar is an active remote sensing technology now being commonly used to generate high resolution spatially explicit 3-D surfaces of ground elevation (digital elevation model, DEM), vegetation surface (digital surface model, DSM), and canopy height (Canopy Height Model, CHM = DSM - DEM)) in a variety of forest ecosystems (e.g., Vepakomma et al. 2008, Clark et al. 2004, Harding et al. 2001). A lidar sensor is a measurement system that emits and receives laser pulses at high frequencies (over 160,000 pulses per second) of which a significant proportion (nearly 20 to 40% in dense canopies) of laser pulses propagate through small canopy openings to the ground (Krauss and Pfeifer 1998). Current systems can collect up to and exceed 10 hits per m^2, and positional accuracy is typically at a decimetre to metre level (Fowler 2001). Detailed description of lidar can be found in Baltsavias (1999), and Wehr and Lohr (1999), while lidar sensing of forests and ecology can be found in Dubayah and Drake (2000) and Lefsky et al. (2002). Investigations in many studies found a good relationship (r^2 ranging between 0.85 and 0.95) with field measures (St-Onge et al. 2008, Coops et al. 2004, Magnussen and Boudewyn 1998).

Lidar's high density and accuracy has permitted it to detect tree falls of varying sizes (Vepakomma et al. 2008) and using multi-temporal lidar data sets to provide height-growth estimation was also shown in a few recent studies (St-Onge and Vepakomma 2004, Naesset and Gobakken 2005, Yu et al. 2006, Hopkinson et al. 2008). Vepakomma et al. (2008) validated the feasibility of lidar to map several gap dynamic characteristics like canopy gap opening and closure of sizes ranging from 5 m^2 to 9.8 ha.in boreal forests. The suggested methods could successively eliminate inter-tree spaces and restore the accurate gap geometry. St-Onge and Vepakomma (2004) confirmed the change in forest height of mixedwood boreal forests in 5 years is acceptable with expected results. Using tree matching technique on high density discrete small-foot print lidar, Yu et al. (2006) showed a good correspondence of five years tree height growth of Norway spruce and Scots pine with field measurements (r^2 of 0.68 and RMSE of 43 cm.). Naesset and Gobakken (2005) performed similar growth analyses at plot and stand level and found that though the predictions were weak, growth was statistically significant. Hopkinson et al. (2008) found that lidar is sufficiently sensitive to detect growth at annual steps in conifer plantations. Despite its high level accuracy and effective tool for change detection, no studies have so far been made to characterise height growth response to canopy gaps using lidar techniques. Moreover, with fast changing technology like lidar, datasets acquired with dissimilar specifications are likely to become more common. Based on earlier studies, the potential to assess the height growth responses to canopy opening using multi-temporal lidar when survey specifications are dissimilar is very high.

Modern optical sensors with high spatial and spectral resolution for earth observation, like IKONOS, Quickbird, enable distinction of tree species and patterns at finer scales (Leckie et al. 2005, Wang et al. 2004, Asner and Warner 2003). Consequently, advanced image processing techniques have been developed to provide better capabilities of mapping and monitoring forest ecology; specifically, species composition of forests over large areas (Foody et al. 2005, Clark et al. 2004, Kerr and Ostrovsky 2003). Hence, we characterise the differential height growth responses of broad species classes to canopy openings by combining the strengths of lidar and high resolution multi-spectral imagery.

4.5. METHODS

4.5.1. Study area

The study site is located within the conservation zone of the Teaching and Research Forest of Lake Duparquet (TRFLD, 79° 22'W, 48° 30'N), in the Province of Quebec, Canada (Fig. 4.1). The 6 km^2 sector is essentially covered by lacustrine clay deposits. The area is characterized by small hills with elevations varying between 227 m and 335 m. The climate is subpolar, subhumid, continental with an average annual temperature of 0.8°C and annual precipitation of about 857 mm. The frost free period lasts for nearly 64 days, while the length of the growing season is on average 160 days (Environment Canada 1993).

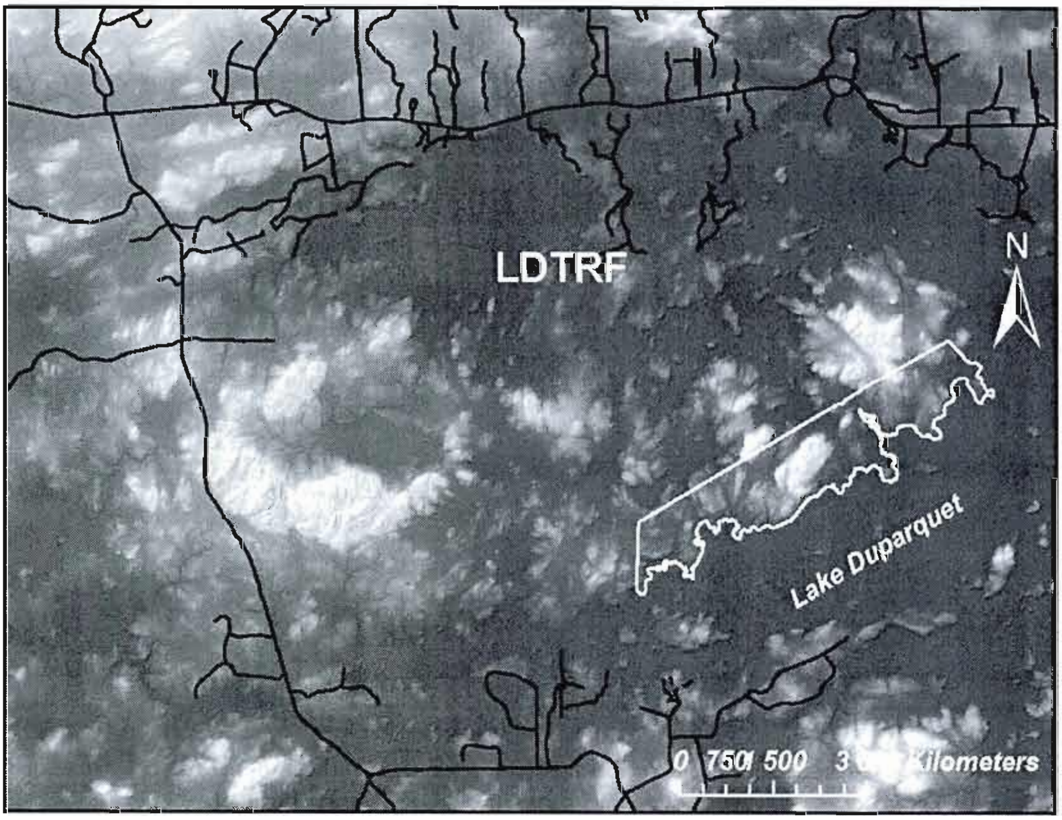

Figure 4.1. Location of the study area, Conservation zone, LDTRF, Quebec, Canada

The forest age structure found in the study area results from a series of fires occurring between1760 and 1919 (Danserau and Bergeron 1993). However, spruce budworm infestation (*Choristoneura fumiferana* [Clem]), also affects age and stand structure and the most recent outbreak occurred from 1970-1987 and resulted in death of most fir trees (Morin et al. 1993). Defoliation due to a forest tent caterpillar outbreak in 1950 has also been documented as causing decrease in hardwood regrowth while windthrow has been identified as only leading to the mortality of individual trees (Senecal et al. 2004). Most stands are considered mature or over mature reaching an age over 50 years and heights of 20-25 m. The vegetation is composed of common boreal species, dominated by balsam fir (*Abies balsamea* L. [Mill.]), and trembling aspen (*Populus tre*muloides [Michx]) with minor amounts of paper birch, white spruce and cedar. Although part of the forest is selectively cut, much of the forest is relatively virgin and remains unaffected by human intervention (Bescond 2002).

4.5.2. Lidar datasets and surface generation

Multi-temporal lidar surveys were conducted using Optech's ALTM 1020 (in 1998) and ALTM 2050 (in 2003) with an interval of five growing seasons. The technical specifications of the lidar acquisitions is summarised in Table 4.1. In 1998, due to low pulse frequency of the system, two passes for each flight line were made for the first returns and one pass to acquire the last returns. With minimal overlap between swaths the resulting point density was 0.3 and and 0.03 hits/m^2 respectively. While in 2003, due to 50% overlap between swaths and higher pulse frequency, the resulting point density of the lidar data was much greater at 3 and 0.19 hits/ m^2.

The two datasets were then co-registered for effective temporal comparisons using the methods discussed in Vepakomma et al. (2008). Canopy structure can be described in three-dimensions using a Canopy Height Model (CHM), which is usually a raster surface representing canopy height. Canopy height distribution or CHMs were generated by calculating the difference between the elevations of the respective canopy surface (given by a Digital Surface Models, DSM) and the underlying terrain (Digital Terrain Model, DTM). The lidar surfaces were generated following the optimised techniques described in Vepakomma et al. (2008) for accurate and reliable delineation of gap geometry. The DTM was generated by using the combined last returns from both datasets. A surface of 0.25 m was interpolated using the lowest ground point within each grid cell and filling the empty cells with the IDW (inverse distance-weighted) interpolation algorithm. Similarly, the DSMs of 0.25 m resolution were created by taking the highest point within each grid cell and supplementing the missing values with interpolated vegetation heights obtained using the IDW algorithm. Accuracy assessment of lidar derived canopy heights for both years was carried out in two different studies using 36 (1998) and 77 (2003) field measured trees of height range between 5.6 m – 33.1 m and yielded r^2 of 0.88 and 0.86 with an RMSE of 1.8 m and 1.85 m respectively (Véga and St-Onge 2008, Coops et al. 2004).

4.5.3. Image data and species composition

A set of 150 frames of near orthographic vertical multi-spectral aerial videography data (0.50 m resolution) acquired on September 27th, 1997 and a single image of orthoready Quickbird image acquired on June 13th, 2004 in panchromatic (0.61 m. resolution) and multispectral modes (2.4 m resolution) were used to map the broad species groups within the study area (Table 4.1). We first orthorectified the Quickbird images based on modified rational polynomial coefficients (for more details refer to St-Onge et al. 2005). A simple first order polynomial rectification was then performed for the individual videography frames using the orthorectified Quickbird data as reference and then mosaiced in Geomatica OrthoEngine v10.0.3 (PCI Geomatics).

Table 4.1.

Technical specifications of the spatio-temporal data used

Data characteristics	***1998***	***2003***
A. Lidar		
Lidar system	ALTM1020	*ALTM2050*
Acquisition date	June28	*Aug 14-16*
Power (µJ)	140uJ	*200uJ*
Flight altitude (m AGL)	700	*1,000*
Divergence (mrad)	0.3	*0.2*
Footprint size at nadir (cm)	21	*20*
Pulse frequency (Hz)	4,000	*50,000*
Max. scan angle (degrees)	10	*15*
First return density (*hits/m*^{2})	0.3	*3*
Ground return density (*hits/m*^{2})	0.03	*0.19*
Classification software	REALM	*Terrasolid*
B. Optical Images		
Acquisition system	Super VHS video	*Quickbird*
Acquisition date	Sept. 27, (1997)	*June 13*
Acquisition altitude (km AGL)	1.9 (airborne)	*450 (spaceborne)*
Spatial resolution (m)	0.50	*PAN : 0.60* *MSS: 2.40*
Multi-Spectral windows (nm)		*450-520*
	520-600	*520-600*
	630-690	*630-690*
	760-900	*760-900*

Researchers have noted that although increased spatial resolution should provide an excellent source of data suitable for various scales of study, it can negatively affect the accuracy of pixel-based classification due to increased intra class spectral variability (Franklin 2001) and a greater degree of shadow (Laliberte et al. 2004, Asner and Warner 2003). Alternately, object-based classifiers that exploit semantic information in the image that identify individual objects by segmentation (e.g., patch of a landscape, or a tree crown) as opposed to single pixels are found to be more accurate (Benz et al. 2004, Thomas et al. 2003). Image segmentation is a way of summarizing information as objects from a contiguous cluster of homogeneous pixels. Each image object then becomes a unit of analysis for which a number of attributes like spectral response, texture, shape, and location can be measured.

In this study, canopy height derived from the lidar data was integrated with the spectral signatures of the image data to automatically extract individual tree objects of broad species composition classes, namely, hardwood (HW) and softwood (SW) (i.e. a differentiation of trees at the Class level into angiosperms and gymnosperms), shadows and other non-forested areas using object-oriented image analysis in eCognition v. 3.0 (Definiens GmbH, Munich, Germany). Based on a reconnaissance survey of the study site in 2004 and consultation of the ecoforestry maps generated by the Quebec Ministry of Natural Resources and Wildlife (QMRNW), Quebec, Canada, we identified the training sites. Classification was performed using the method we detailed in St-Onge et al. (2005). Accuracy assessment of both datasets was accomplished using well distributed field data collected on 81 and 54 distinctly identifiable single trees in 1999 and 2005 respectively. The overall accuracy of the image classification based on a comparison matrix with field data was 84% and 87.5% for 1997 and 2003 respectively. The errors observed were largely due to softwood objects inter-mixing with the shadow class.

4.5.4. Gap dynamic characteristics

We define a gap as an opening in the canopy caused by the fall of a single or a group of trees such that the height of remaining stems is less than 5 m (height threshold determined based on field observations). The edge of the gap is defined as the vertical projection of the canopy crown of trees adjacent to the gap. Following the method proposed in Vepakomma et al. (2008), open-ended systems like streams, rock outcrops and marsh lands, were eliminated to explicitly map canopy gaps on the lidar CHMs in both years. Mapped gaps are individual objects of contiguous binary grid cells determined by a gap indicator function (Eqn. 1).

$$G_i(x,y)=\begin{Bmatrix}1 & if\ CHM_i(x,y)<a \\ 0 & otherwise\end{Bmatrix} \tag{1}$$

where a = 5 m in this study, $CHM_i(x,y)$ is the lidar height of the canopy surface in the ith year, (x,y) is a cell that does not belong to any open-ended system. This method has previously been validated using 29 field measured gaps along 980 m of transect to show a strong matching of 96.5% with lidar delineated gaps.

Important dynamic characteristics that describe gap processes like gap closure, and how this occurs, i.e. closure from the side (due to lateral growth) and closure from below (due to regeneration) were identified by applying combinatorics on the individual objects generated from multi-temporal lidar CHMs with the following definitions. We define gap closure as areas where the vegetation height that was less than 5 m in 1998 increased to or over 5 m during the period 1998 and 2003 (regions B and C in Fig.4.2). A gap is assumed to close from the side (region B in Fig.4.2) when the difference in the vegetation height between 1998 and 2003 (Δh) within the gap is greater than 5 m, as this is assumed to be smallest height difference that is too

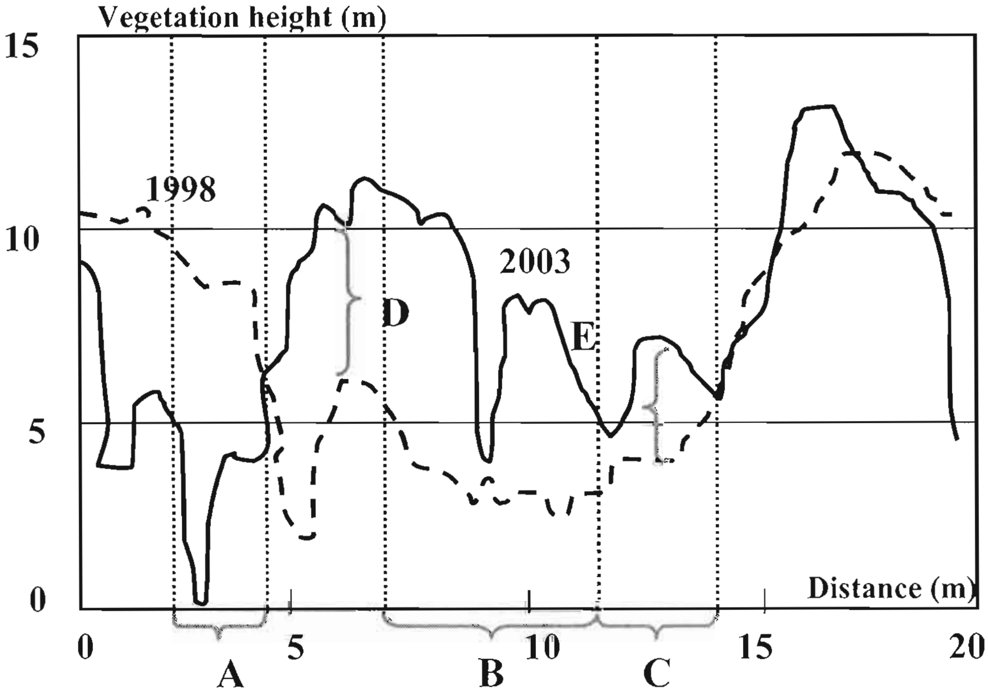

Figure 4.2. Vertical profile (1998 dashes, 2003 thick line) along the transect shown in Fig.3. (white arrow) from the multi-lidar CHMs showing dynamical changes between 1998 and 2003. (A) represents a new gap; (B) a region where the gap that was open in 1998 closed from side during 1998-2003 and Δh > 5 m; (C) a region where the gap in 1998 is closing from below and Δh < 5 m; (D) shows the height growth of the vegetation in the gap edge; (E) shows the height-growth in the regenerating gap.

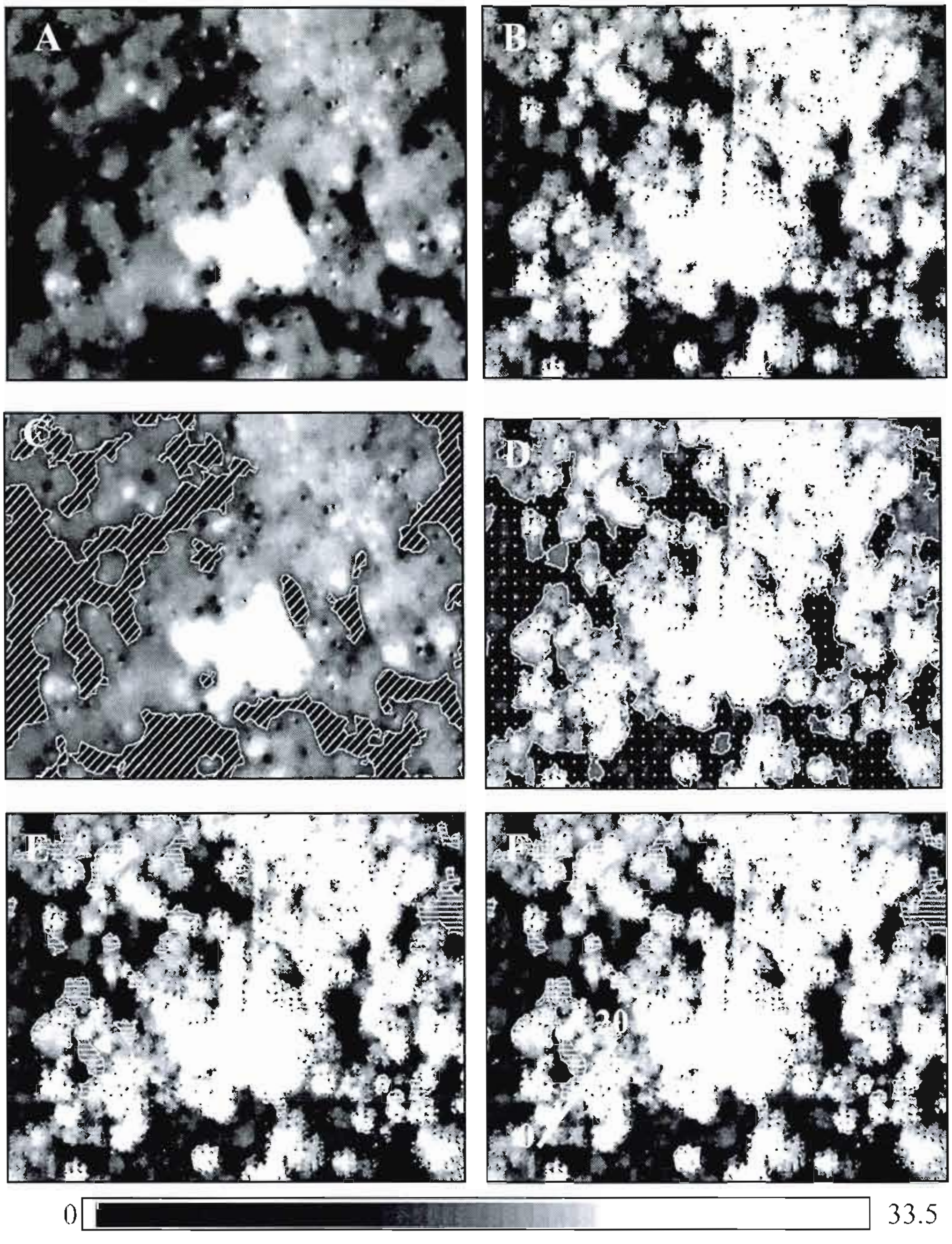

Figure 4.3. An example of automatic detection of gaps and gaps that have closed between 1998-2003 using multi-temporal lidar data. (A) CHM$_{1998}$; (B) CHM$_{2003}$; (C) Gaps delineated (hashed object) in 1998; (D) Delineated gaps (dot filled objects) in 2003 (E) Delineated gaps that have closed (objects filled with horizontal lines) (F) Identification of gaps that have closed from the side (mesh filled objects); the white thick is the 20 m transect chosen for the vertical profile in Fig.1.

too high for a vertical growth (and is contiguous with the gap edge). Lateral extension of tree growth into gaps was computed directly in ArcGIS v9.3. (Environmental System Research Institute, Redlands, CA). A gap is considered to close from below when Δh is both positive and less than 5 m (region C in Fig.4.2). A canopy surface in which the canopy height is over 5 m represents high canopy zones. Fig. 4.3 presents an example of gap dynamic characteristics identified using the multi-temporal lidar analysis. The minor axis of each polygon identified as laterally growing, i.e. contiguous area where $\Delta h > 0$, is estimated based on the ellipsoidal approximation. These minor axes are considered as the length of the lateral extension of gap edge trees into the gap. The analyses and computation of statistics was accomplished within ArcGIS v9.3.

Regenerating gaps and high canopy zones were stratified based on species composition (hardwood or conifer) by overlaying the2003 species classification layer. Gap properties like gap size distribution, percentage land area in gaps (i.e. gap fraction), rates of opening and closure of gaps, were calculated based on standard guidelines for measuring forest gaps (Runkle 1992) within ArcGIS v9.3.

4.5.5. Identification of tree tops

In this study, we used the 2003 CHM to locate tree / sapling tops from which we subsequently extracted the original raw lidar returns for estimating all growth statistics. The location of individual tree / sapling tops was determined by assuming that the pixel associated with the peak of a tree will be higher than the surrounding pixels on the CHM within the defined buffer. A local maxima filter with a circular non-overlapping (moving) window was applied to the CHM_{2003}, to determine local peak points, *LMAX (x,y)*. Local maxima filtering is a common technique first adopted to identify trees in high resolution optical imagery (e.g., Pinz, 1999) that is also

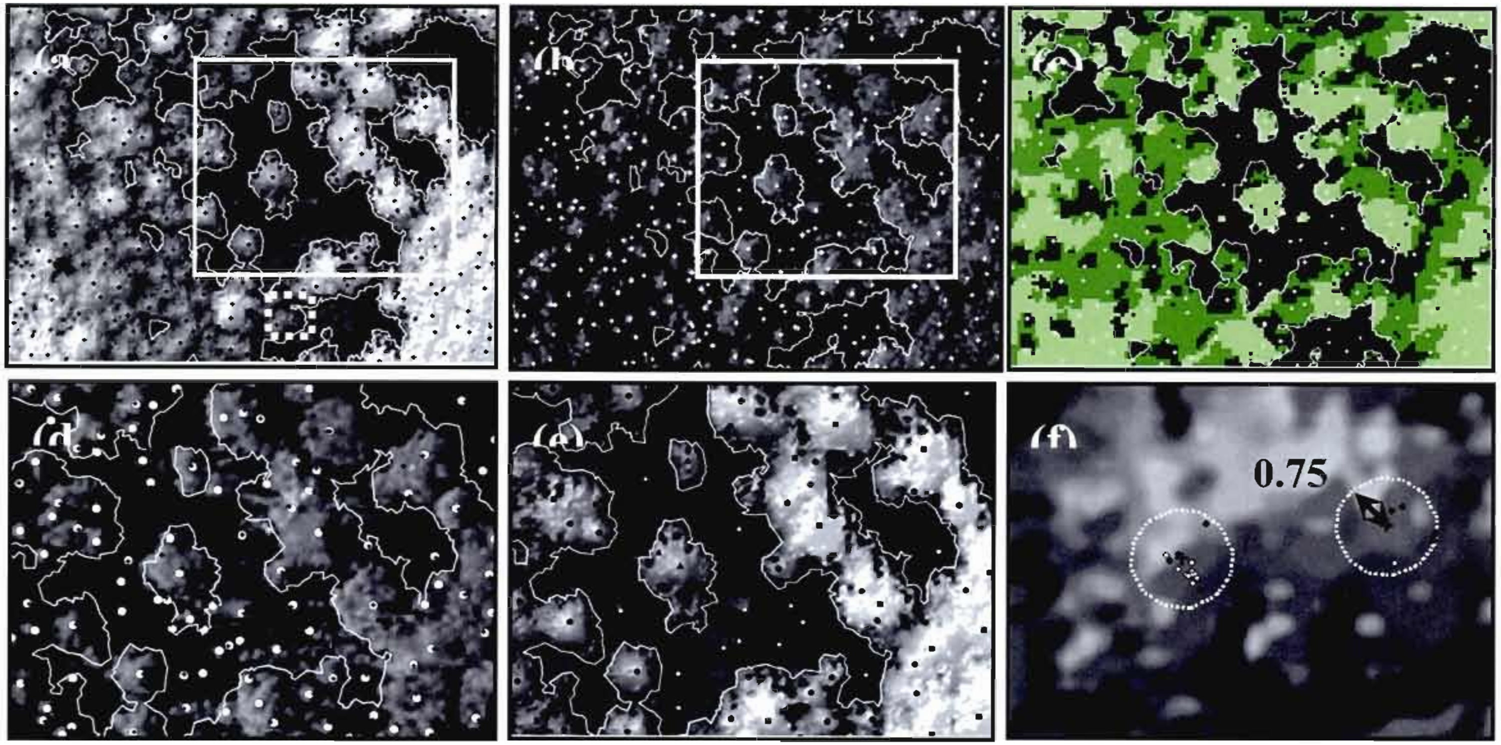

Figure 4.4. An example of automated identification of tree / sapling location shown as crosses in all figures. Increase in height is given by progressively lighter tones. (a) automatically identified tree locations overlaid on lidar CHM_{2003} (b) photo-measured tree locations overlaid on orthorectified panchromatic digital areal image of 2007 (c) automatically identified tree locations overlaid on the image of broad species classification from Quickbird satellite data of 2003; light green: hardwood; dark green: softwood; black: shadow and non-forest (d) Accuracy assessment of automatically identified tree locations (enlarged window – box of white thick line in (a)) : Crosses represent automated identification of trees / saplings; circles represent 0.5 m error around photo-measured locations (e) Enlarged window (box of white thick line from (a)) showing tree / sapling categorization. Black patterns represent trees while white are saplings; Circles : Gap edge trees; Squares: Interior closed crown trees; Triangles: Gap island trees; Stars: Gap saplings. (f) Enlarged window (box of dotted white line in (a)) showing an example of matching sampling lidar densities between the two years. Dotted circles indicate the 0.75 m buffer around the tree top from which the number of lidar first returns of 1998 (black dots) are matched with those of 2003 (white dots) for growth estimation.

extended successfully to lidar surfaces (e.g., Popescu and Wynne 2004). Here, the chosen search radius of 7 pixels (1.25 m) which is based on the average crown radius of 200 field-measured trees of varying maximum heights (5-25 m) in the study area. A local maximum within a search window that matches the height on the CHM i.e. $LMAX(x,y) = CHM_{2003}(x,y)$, is assumed to be the maximum height ($TMAX(x,y)$, hereafter *TMAX*) of the tree crown.

We validated whether a tree / sapling top (*TMAX*) automatically identified on the lidar surface corresponds to a reference tree / sapling peak by using manual photogrammetric methods. Identification of the exact (X, Y, Z) location of a tree top in the field is difficult due to the size of tree crowns and the density of the forest. Tree bases need not necessarily represent the centre of canopy as trees may be inclined or exhibit asymmetric growth. Hence, for verification we considered clearly visible photogrammetric locations of the tree / sapling peak as our reference. A 2.5 ha window at near-nadir angles from a very large resolution (10 cm) orthorectified panchromatic digital aerial photograph obtained from large format Vexcel UltraCam D taken in 2007 was used to maximise the accuracy of photo measurements. After ensuring that there was no apparent change in the canopy due to natural disturbances between the 2003 lidar data acquisition and the 2007 aerial photo, the planimetric geolocation of the tree tops visible in the study window were measured on the orthophoto and stored as $P_i(x,y)$ point coordinates in a file. Error in identifying a tree location was estimated as the Euclidean distance of the nearest $TMAX(x,y)$ to $P_i(x,y)$. We assume an automatic tree location is a correct match if the error in identification is within 0.5 m. Accuracy is computed as the proportion of correct matches to the total identified locations within the study window.

Among the 940 automatically identified trees in the 2.5 ha window, 74.6% were correctly matched with the corresponding photo-locations (Table 4.2). Tree locations that had either an error of over 1 m or had no tree/ sapling visible on the photo

Table 4.2.
Accuracy assessment of automatic tree / sapling top location.

Distance or error 'e' (m)	*# points match*	*Cum. # point match*	*Cum. % point match*
$e \leq 0.2$	203	238	25.32
$0.2 < e \leq 0.25$	102	340	36.17
$0.25 < e \leq 0.3$	93	433	46.06
$0.3 < e \leq 0.35$	81	514	54.68
$0.35 < e \leq 0.4$	66	580	61.70
$0.4 < e \leq 0.45$	63	643	68.40
$0.45 < e \leq 0.5$	58	701	74.57
$0.5 < e \leq 0.6$	159	860	91.49
$e \geq 0.6$	80	905	96.27
No match (i.e. error > 1m)	*35*	*35*	*3.72*

constituted 3.72 % of locations. It was noted that hardwood and softwood trees had an equally likely chance of having an error ranging between 0.5 – 1 m. An example of photo-identified locations and the automatically identified tree locations with respect to the 0.5 m error circles can be seen in Figures 4.4b and 4d respectively.

4.5.6. Extraction of growth statistics

Tree top objects were created by defining a 0.75 m buffer zone around each point of *TMAX* (Fig.4.4f). Tree top objects whose image-classified species composition did not match between the two years were eliminated. This can happen when the trees are shadowed, when one tree overtops the shorter tree, or when trees fall between the two measurement years. Lidar raw point clouds of the vegetation (first returns) in 1998 and 2003 were then extracted for each tree object. The data was further constrained for height and point density to achieve a more reliable assessment. Previous studies of lidar have indicated a possible underestimation of tree heights (e.g., Hopkinson et al. 2008, Lim et al. 2003) due to ground height over-estimation as a result of minimal point density in dense vegetation (Reutebuch et al., 2004), laser penetration into foliage (Hopkinson et al. 2008) and insufficient representation of canopy apices (St-Onge et al. 2004). In this study we tried to minimise these possible errors. We increased the ground lidar density by combining the two lidar datasets. From each of the datasets, we eliminated the lidar first returns whose elevation was 2 m lower then their respective *TMAX* with the assumption that they may have penetrated deep into the crown. Since the density of lidar points in 2003 was higher than in 1998 we suppose that any comparison of statistics between the datasets could be biased. In order to make the data sets comparable, we matched the point densities of both years within each tree object i by randomly selecting n_i sample points for both years such that

$$n_i = \min\,(n_i^{1998}, n_i^{2003}) \tag{2}$$

where n_i^{1998} and n_i^{2003} are the number of first returns within the i^{th} tree object in 1998 and 2003 respectively (Fig. 4.4d). All tree objects that had a minimum point density of 3 hits (chosen arbitrarily) and growth (positive values of both *MGTH* and *AGTH* as defined below) were selected for further analysis.

Canopy height of all sampled raw lidar returns was calculated by taking the difference of the elevation of the first lidar return and the interpolated ground elevation at that corresponding (*X*, *Y*) position. For each of the i^{th} tree top object delineated, the maximum tree / sapling height ($h^i_{MAXj}, j= 1998, 2003$) and average tree / sapling height ($h^i_{AVGj}, j = 1998, 2003$) were computed using the n_i sampled raw lidar returns within the 0.75 m buffer as:

$$h^i_{MAXj} = \max\,(h^{i1}_j, h^{i2}_j, \ldots\ldots\, h^{ini}_j) \tag{4}$$

$$h^i_{AVGj}, = \text{average}\,(h^{i1}_j, h^{i2}_j, \ldots\ldots\, h^{ini}_j) \tag{5}$$

Height growth rates $MGTH_i$ and $AGTH_i$ of the i^th^ tree were then computed as follows:

Rate of maximum growth per unit height ($MGTH_i$)

$$MGTH_i = \frac{\Delta h^i_{\max}}{h^i_{\max}} = \frac{h^i_{MAX2003} - h^i_{MAX1998}}{h^i_{MAX1998}} \tag{6}$$

Rate of average growth per unit height ($AGTH_i$)

$$AGTH_i = \frac{\Delta h^i_{avg}}{h^i_{avg}} = \frac{h^i_{AVG2003} - h^i_{AVG1998}}{h^i_{AVG1998}} \tag{7}$$

It is to be noted that MGTH and AGTH as computed here are the rates of growth of each sampled tree over the 5 growing seasons;that being a proportional growth they are unit free measures. Thus a MGTH value of 0.2 of a sampled tree / sapling signifies a 20% increase of its determined maximum growth from its 1998 maximum reference height.

4.5.7. Categorisation of the tree objects

The identified tree objects in the whole forest were categorised according to their neighbourhood context and position. An identified tree object is heuristically considered a sapling when $h_{MAX1998} < 5$ m, and a mature tree otherwise. A sapling growing within a canopy gap of 1998 is a gap sapling. High canopy zones that have an area less than 50 m^2 are considered as high canopy islands within a canopy gap. Trees that are within the gap island are gap island trees (Figs 4.4e). Further, mature trees outside the gap were categorised as gap-edge trees when they lie within 10 m of a gap edge, and otherwise they were considered to be an interior canopy tree (Figs 4.4e). According to the above criteria and validity rules, we sampled 98 hardwood and 58 softwood gap saplings, 57 hardwood and 137 softwood gap island trees, 239 hardwood and 247 softwood gap edge trees and 117 hardwood and 32 softwood interior trees.

In all categories, the correlation between the average and maximum tree height generated by the two lidar datasets is very high at over 0.98 (Table 4.3). The change in the lidar derived maximum tree height estimates of both hardwoods and softwoods (all trees and saplings combined) is relatively consistent over the gradient of height over time (Fig 4.5). We already noted that the predicted tree heights from these lidar data sets were accurate. The results thus strongly suggest that the growth between the two years can be measured using multi-temporal lidar data.

4.5.8. Influence of canopy gap opening on height growth

To understand the role of opening of a canopy gap on the height growth we compared MGTH and AGTH between and within the categorised trees and gap saplings using (1) exploratory statistics (2) histograms and (3) scatterplots against the reference tree height i.e. $h_{MAX1998}$ and $h_{AVG1998}$, hereafter refered as MAX_{1998} and AVG_{1998}. Since the scatterplots of MGTH against initial tree heights indicated a non-linear relationship, we fitted non-parametric predictive models (described below) of the MGTH given the initial tree height.

In higher latitudes, due to low sun angles (for e.g., Canham et al. 1990) and shadow from the gap edge vegetation, the position of a sapling inside a canopy gap and gap size can have a significant impact on the resource levels and micro-climatic conditions, and thus on the sapling's growth rate. The release of resources for the growth of gap saplings should thus be directly proportional to the gap size. We believe that the farther the sapling is positioned away from the gap edge, i.e., towards

Table 4.3.
Correlation between lidar return 1998 and 2003

Tree strata	*Average r(98,03)*	*Maximum r(98,03)*
Regeneration	0.99	0.99
Gap Island trees	0.98	0.98
Gap edge trees	0.99	0.99
Interior trees	0.98*	0.98*

** significant at p < 0.001*

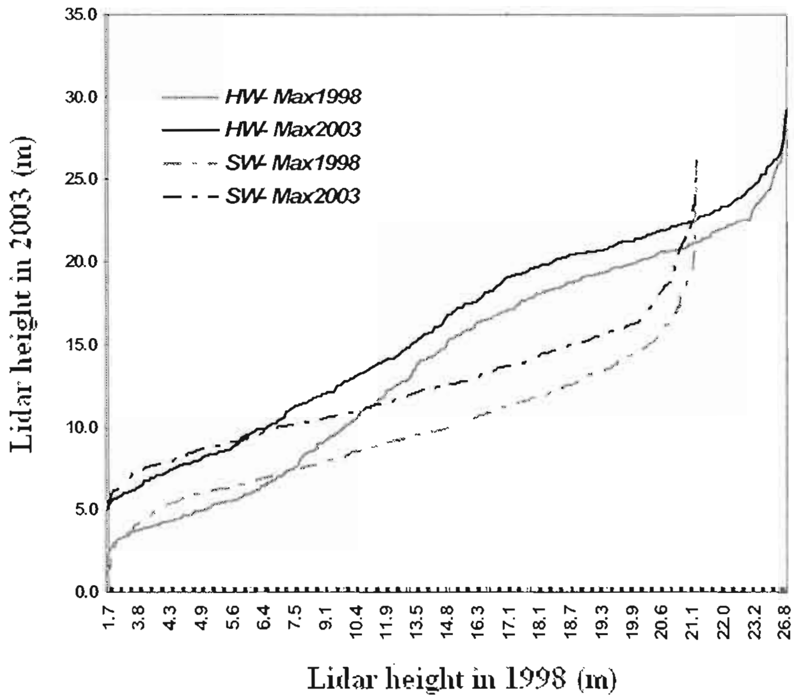

Figure 4.5. Maximum height 1998 and 2003 of the 511 hardwood and 494 softwood trees/saplings derived from the lidar

the center of the gap, the greater should be the resources (above and below ground) available to enhance its growth. Similarly, we assume that mature trees closest to the gap edge should benefit most from the available site resources in the canopy gap.

To determine the extent of influence of gap opening on mature tree outside the gap edge, the effect of gap size and gap sapling position within a gap, we adopted the method of plotting average cumulative sums (*CUSUMs*) of the response variable (*MGTH* here) against the nested explanatory variable (e.g., gap size, distance from the gap edge). *CUSUM* methods are process control statistical techniques to determine changes or shift over time in a measurement process (Hawkins and Olwell 1998). Normal control charts usually do not detect small shifts in a process, say observed by measuring a change in statistic Q from a desired value k that could appear more like noise around the mean. Alternately, the slope of the curve from the cumulative sum of such small shifts (as defined below), may be more indicative of how average Q differs from k.

$$CUSUM_i = (Q_i - k) + CUSUM_{i-1} \tag{8}$$

The *CUSUM* is hence an asymptotic function that could increase or decrease to a finite point where the rate of change of the response variable will slow down with respect to an increase in the explanatory variable. CUSUM curves have applications in many areas i.e. learning curves and assessing doctors' competence to network surveillance (Barratt et al. 2007, Park 2005, Lim et al. 2002).

In this study, we extended their use to establish the zones of influence of the opening of a canopy gap on height growth. The point where the rate of change of the response variable converges to zero is considered to be the point where the explanatory variable (e.g., rates of growth) ceases to have an influence on changes in the response variable (e.g., gap area, distance of a tree from the edge of a gap). Here we computed *CUSUM* as:

$$CUSUM_l = CUSUM_{l-1} + AMGTH_l \qquad (9)$$

where

$$AMGTH_l = MGTH_l / n \qquad (10)$$

is the average maximum rate of growth of n sampled trees at the l^{th} distance from the gap edge

or

$$AMGTH_l = MGTH_l / GAPAREA_l \qquad (11)$$

is the average maximum growth per unit gap area for a gap sapling growing within gap of l^{th} gap size.

To further strengthen and verify the extent of influence of gap opening on height growth, we fitted a non-parametric regression of (1) *MGTH* against distance from the gap edge, (2) *MGTH* against gap size and (3) *MGTH* against position (in terms of distance) of gap sapling from the gap edge.

Non-parametric predictive models:

Non-parametric regression is a form of regression analysis where the predictor does not take a predetermined form but is constructed according to information derived from the data. To predict the maximum rate of growth in 5 years for a given initial height we used a non-parametric regression estimator for non-negative random variables proposed by Chaubey et al. (2008) which converges to the true regression function *m(x)* defined as

$$m(x) = E(Y \mid X = x) \qquad (12)$$

The non-parametric regression estimator is:

$$m_n(x) = \frac{n^{-1}\sum_{1}^{n}(Y_i)Q_{x+\varepsilon_n,v_n}(X_i)}{n^{-1}\sum_{1}^{n}Q_{x+\varepsilon_n,v_n}(X_i)}, x \geq 0 \qquad (13)$$

which is of the form of a weighted average $\sum Y_i W_i(x)$, $\sum W_i(x) = 1$. Here $Q_{v_n,x+\varepsilon_n}(\cdot)$ is a gamma density function with mean $x+\varepsilon_n$ and variance $v_n^2(x+\varepsilon_n)^2$. Namely, for $x \geq 0$,

$$Q_{x+\varepsilon_n,v_n}(t) = \frac{1}{\beta^{\alpha}_{x+\varepsilon_n}\Gamma(\alpha_n)} t^{\alpha_n-1} e^{-\alpha_n t/(x+\varepsilon_n)} \qquad (14)$$

where $\alpha_n = 1/v_n^2$, $\beta_{x+\varepsilon_n} = v_n^2(x+\varepsilon_n)$ and ε_n and v_n goes to 0 at an appropriate rate as $n \to \infty$. Since the mean of this gamma density tends to x and the variance tends to zero, it can be shown that the weighted average $\sum Y_i W_i(x)$ converges to $m(x)$. Unlike commonly used kernel regression estimators, this estimator does not provide biased values near the boundary. Often, as in the case of tree heights, we may need to predict values beyond the range of sample observations.

4.6. RESULTS

4.6.1. Gap filling and overall growth statistics in boreal forests

An example of automatically delineated opened and closed (from sides and below) gaps from 1998 and 2003 is seen in Fig. 4.3. The results indicate that a higher annual rate of canopy closure, 1.2 %, compared to 0.52% of annual rate of gap formation, reduced the total area under gaps from 38% in 1998 to 32% in 2003. Overall the average area of gap closure during 1998 - 2003 is 29.6 m^2 in these forests. Though there is more area closing due to regeneration than lateral growth, a significant area, nearly 22% of the total area closed, was found to be closing due to lateral growth. Average annual lateral extension of the bordering tree into a gap is 24 cm, such that SW are growing at a slightly faster rate (24 cm) when compared to HW that are growing at a rate of 21 cm/yr. Lateral extension ranged between 10 cm to 2 m over the 5 growing seasons.

Distribution of the lateral extension of border trees during the 5 growing seasons is near normal around 1 m (Fig 4.6a), while the distribution of lateral and regeneration patch areas is exponential (Fig 4.6b). Though 83% of the lateral closures occurred in gap openings less than 200 m^2 in size, where 12% of the gaps are predominantly closed from the sides, lateral extension was also noted in gap openings up to a size of 1 ha. As expected, the area that closed due to either regeneration or lateral growth increased with an increase in the size of gap opening in 1998 (Fig 4.6c). The correlation between gap opening in 1998 and patch sizes of regeneration and lateral growth is 0.4 and 0.5 respectively (both significant at $p < 0.05$).

Comparing the two canopy height surfaces between the 5 growing seasons, we observed that 56.6% of the total area had positive vegetation height-growth of which 4.6% is regenerating vegetation that closed the canopy gaps from below, 1.3% is lateral growth of gap edge vegetation that closed the gap from the side, 20% is regenerating vegetation that has yet reached the canopy and 30.6% is mature vegetation that is still growing laterally into a gap. There were 413 hardwood and 416 softwood trees identified that have a maximum tree height of at least 5 m. Our data indicates that nearly 65% of the trees are below 15 m in height and that these are largely composed of softwoods (Fig. 4.7). During the 5 years, we observed that softwood trees have greater height growth compared to that of hardwoods along the entire gradient of tree height (Fig. 4.7).

4.6.2. Comparison of height growth of gap edge, interior closed canopy and gap island trees

Gap edge HW trees overall have significantly higher growth rates compared to interior HW trees (K-S- test $p < 0.001$). Particularly, gap edge HW trees in the height range of 5.3 to 11.0 m are observed to be growing faster than those HW in the canopy interior, indicating that the opening of gaps influence the height-growth of gap edge HW trees up to a height of 15 m (Table 4.4 and Fig 4.8, 4.9 and 4.10). In fact, interior HW trees are growing at a consistent rate of 0.1, i.e. 10% of their initial height in the five years, which is slower than gap edge and gap island HW trees over the entire range of height. However, it should be noted that although no samples of interior HW trees were found below 13.9 m in height, the estimated regression models are expected to be unbiased near the boundaries (Chaubey et al. 2007). Comparatively, gap island HW trees have the highest growth rate on average with nearly 75% of the trees having a growth over 0.25.

On average, gap edge and interior SW trees are growing almost similarly but much slower than gap island trees (Table 4.4). Although the average and maximum growth of SW gap edge trees is higher than interior SW trees, growth rates and their distributions are not significantly different (K-S test $p > 0.1$). Nearly 60% of the gap island SW trees have an MGTH of over 0.5, while the majority of the gap edge and interior SW trees have an MGTH of 0.25 (Fig. 4.8). However, gap edge and gap island trees below 11 m in height benefit from gap openings with higher growth rates compared to the interior SW trees which are growing at a consistent rate of 0.25 m/yr (Figs. 4.9 and 4.10). On average, MGTH of gap edge and interior SW trees are

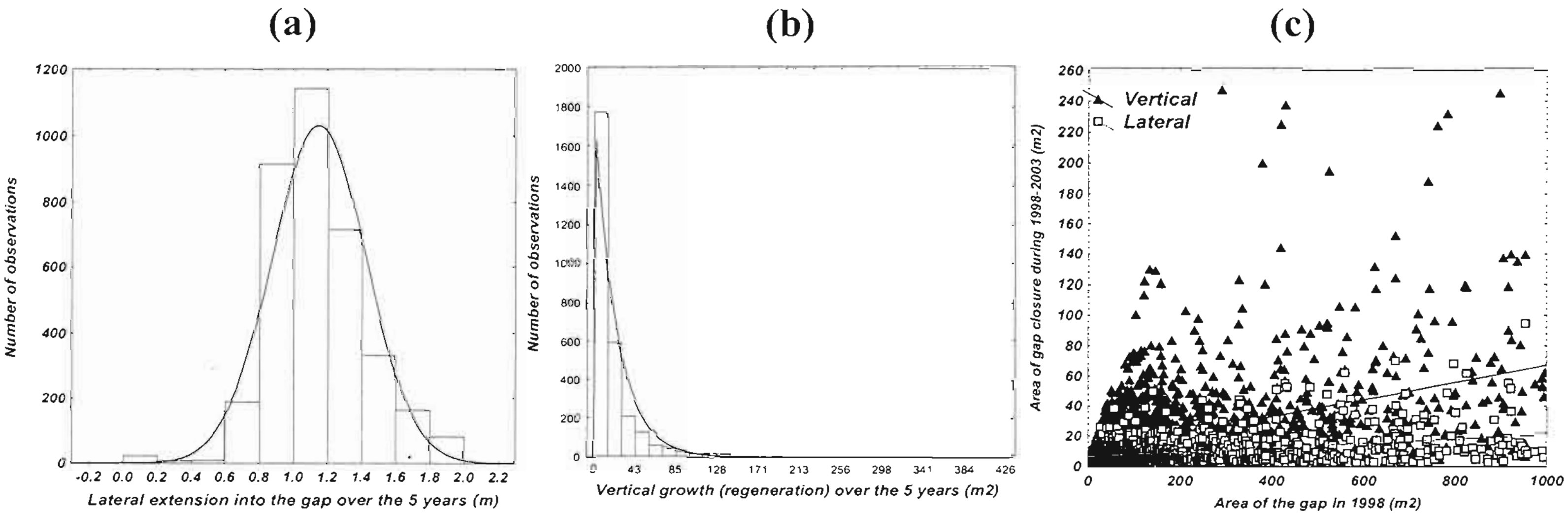

Figure 4.6. Gap filling in boreal forests during the 1998-2003 period (a) Size (length) distribution of lateral extension (b) Size distribution of regeneration (c) Size distribution of closures along increasing gradient of gap openings in 1998.

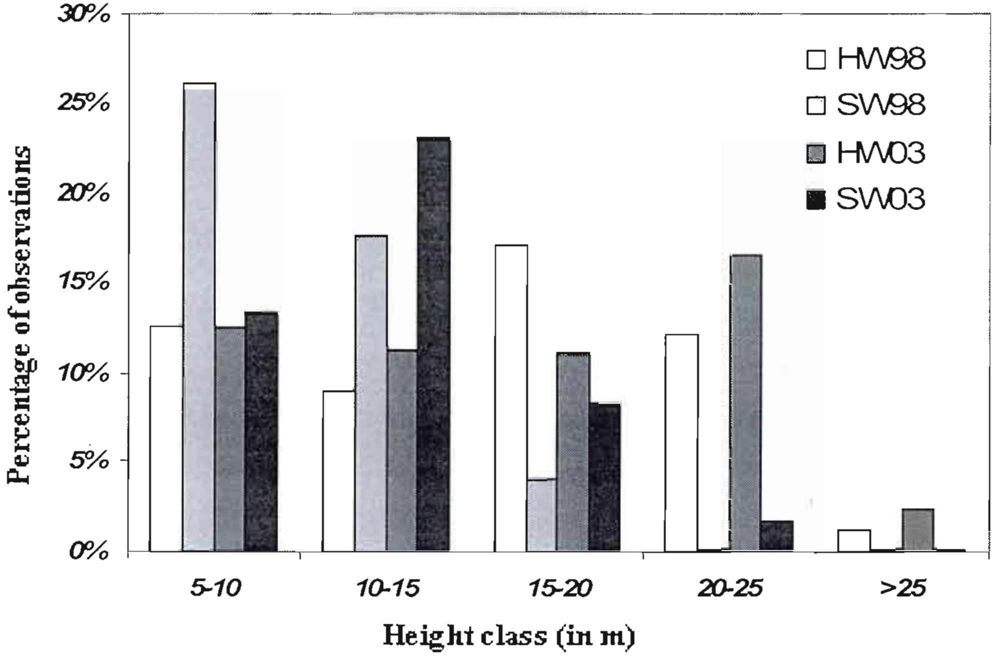

Figure 4.7. Tree height distribution of the species classes in 1998 and 2003

similar (Table 4.4), however, the distribution of *MGTH* along the initial heights show that the gap edge trees do have higher growth rates compared to their interior counter parts (Figs. 4.8 and 4.9).

On the whole, AVG_{1998} and MAX_{1998} of HW's are higher than that of SW's for the gap saplings and gap island trees, while the contrary was observed for gap edge and interior trees (Table 4.4). In general, the *AGTH* rates are higher than the *MGTH*, as AVG_{1998} is lower and the difference in AVG_{1998} and MAX_{1998} is higher than that of AVG_{2003} and MAX_{2003}. The HW and SW gap island trees are growing with similar average and maximum growth rates (Table 4.4 and Fig. 4.8). Otherwise, SW trees are growing at a much higher rate than HW trees. In fact, 9-10% of the SW trees that are outside the gap have a growth over 50% of their respective initial heights i.e. over 0.5 of *MGTH* (Fig. 4.8), while fewer than 4% of the HW trees have a similar growth rate. Over the entire gradient of initial height, SW trees are growing at significantly faster rates than HW (Fig. 4.9). A large number of HW (33%) and SW (24%) gap island trees have an *MGTH* over 0.5 (Figs. 4.8 and 4.9). The growth rates of gap edge and gap island trees over 9 m in height are similar.

Trees of all strata, except those of interior HW, have high growth rates (MGTH) of at least 0.15, although they seem to be declining at a faster rate beyond a certain initial height (Fig. 4.10A). Both SW and HW trees, especially in the 5 – 10 m height class benefit from the opening of gaps as seen by the predictive models (Fig. 4.10B). Canopy opening influences hardwood trees that are within 20 m of the edge of the gap, as seen on the CUSUM plot of the average MGTH per tree and further confirmed by estimating the regression (Fig. 4.11). SW trees growing beyond 15 m of a gap edge do not seem to benefit from the gap opening (Fig. 4.11). Maximum effects

Table 4.4 Summary of the growth statistics of different vegetation during 1998-2003 based on lidar observations

Regeneration in the canopy gaps

 # Hardwood saplings . 98; # Softwood saplings . 58

	Hardwood		*Softwood*		
Variable	*Mean*	*SD*	*Mean*	*SD*	*KS Test*
AVG98	3.91	0.91	3.73	1.19	p > .10
MAX98	4.45	1.02	4.21	1.21	p > .10
AVGGTH	3.23	1.79	4.34	2.39	p < .005*
MAXGTH	3.29	1.86	4.49	2.41	p < .005*
AGTH	0.94	0.65	1.43	1.19	p < .025*
MGTH	0.82	0.60	1.29	1.11	p < .01*
Range of Max98	1.7 - 5.9		1.3 - 5.9		

Hardwood Trees

 # Gap edge trees : 239; # Interior trees : 117

	Gap Edge		*Interior*		
Variable	*Mean*	*SD*	*Mean*	*SD*	*KS Test*
AVG98	15.28	5.14	19.42	3.01	p < .001*
MAX98	15.76	5.12	19.91	3.05	p < .001*
AVGGTH	1.85	2.03	1.58	1.84	p > .10
MAXGTH	1.88	2.08	1.52	1.92	p < .10
AGTH	0.18	0.39	0.12	0.42	p < .001*
MGTH	0.18	0.39	0.12	0.43	p < .001*
Range of Max98	5.3 - 26.7		13.9 - 29.04		

Gap Island Trees

 # Hardwood trees : 57; # Softwood trees . 137

	Hardwood		*Softwood*		
Variable	*Mean*	*SD*	*Mean*	*SD*	*KS Test*
AVG98	8.60	3.32	8.22	2.68	p > .10
MAX98	8.96	3.27	8.65	2.68	p > .10
AVGGTH	2.47	1.59	2.44	1.86	p > .10
MAXGTH	2.54	1.63	2.40	1.87	p > .10
AGTH	0.35	0.27	0.34	0.31	p > .10
MGTH	0.34	0.26	0.31	0.29	p > .10
Range Max1998	4.9 - 21.7		4.8 - 21.7		

Softwood Trees

 # Gap edge trees . 247; # Interior trees . 32

	Gap Edge		*Interior*		
Variable	*Mean*	*SD*	*Mean*	*SD*	*KS Test*
AVG98	10.35	3.39	12.36	2.64	p < .001*
MAX98	10.86	3.38	12.79	2.64	p < .001*
AVGGTH	2.17	1.76	2.75	2.20	p > .10
MAXGTH	2.18	1.81	2.85	2.34	p > .10
AGTH	0.25	0.24	0.21	0.35	p > .10
MGTH	0.23	0.23	0.22	0.34	p > .10
Range of Max98	5.9 - 25.11		7.9 - 17.3		

*AVG98 and MAX98 are the average and maximum reference tree heights (in m) respectively; AVGGTH and MAXGTH are the average and maximum height growth (in m); AGTH and MGTH are the average and maximum rates of growth per unit height respectively; SD : standard deviation (in m);KS-Test ; Kolmogorov Smirnov two independent sample test; * indicates that the test was significant.*

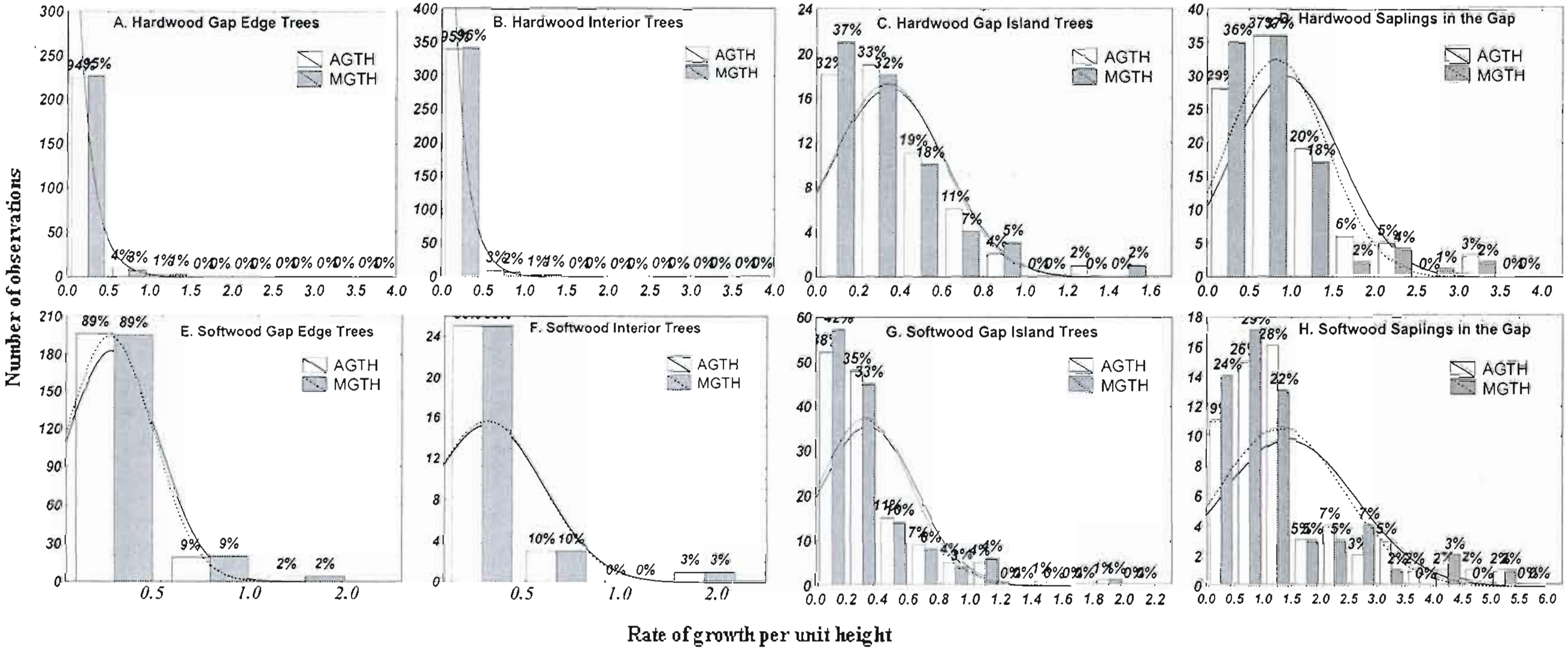

Figure 4.8. Height growth variation between hardwood and softwood gap edge, interior trees and regeneration within gaps shown using histograms of rates of growth per unit height, average (AGTH) and maximum (MGTH).

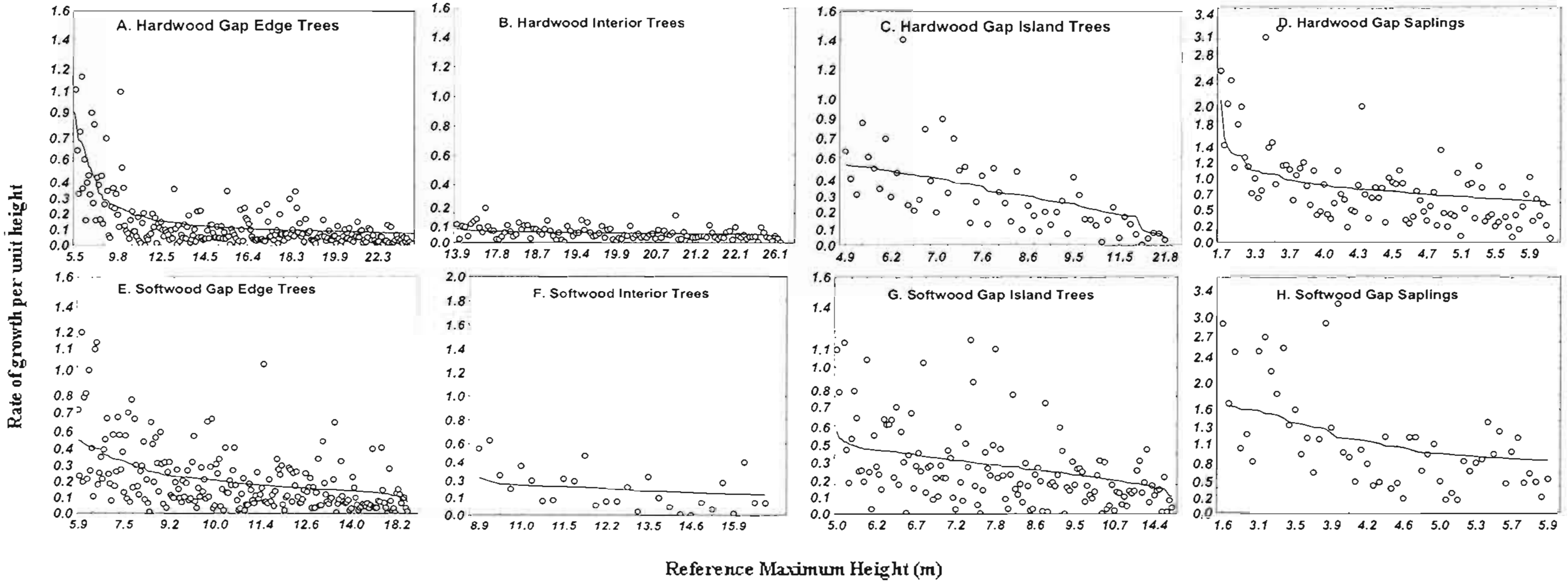

Figure 4.9. Height growth variation between hardwood and softwood gap edge, interior trees and regeneration within gaps shown in terms of the distributions of rate of maximum growth per unit height (MGTH) along the reference maximum height gradient (MAX_{1998} in meters). The curves in the graph are the estimated non-parametric regressions.

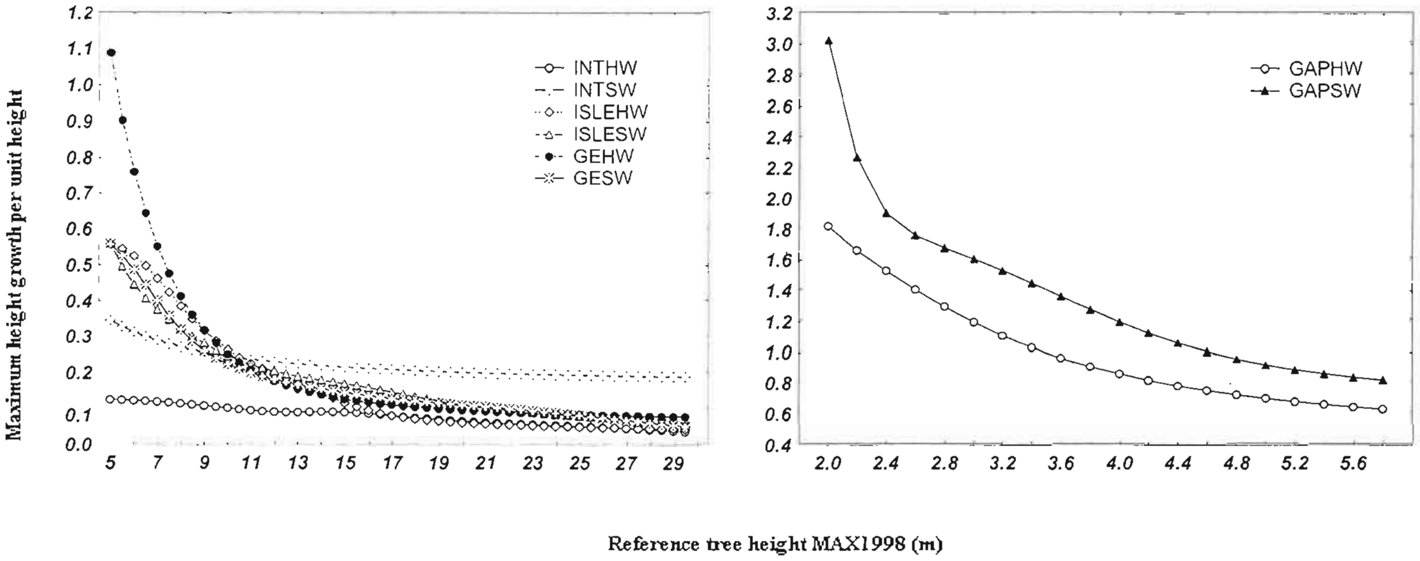

Figure 4.10. Estimated regressions of MGTH. given the reference (initial) tree heights. (A). Predicted functions of hardwood and softwood gap edge, interior and gap island trees (B) and Predicted functions of hardwood and softwood regenerating saplings within gaps

on growth occur within the first 2 to 4 m for both SWs and HWs respectively.

4.6.3. Influence of canopy gap opening on height growth of regeneration within gaps

The identified 98 HW and 58 SW saplings within the canopy gaps show that HW and SW average initial heights are very similar, but their average and maximum growth are significantly different with SW saplings growing at a much higher rate (on average over 100% of the initial sapling height in five growing seasons) than the HW saplings (Table 4.4). Over 46% of the sampled SW saplings have an *MGTH* over 1.0 but only 23% of the HW sampled saplings are growing with an *MGTH* over 1.0 (Fig. 4.8). However, the growth rates of all the young saplings occurs at a consistently higher rate of over 0.5 along the height gradient up to 5 m (Figs. 4.9 and 4.10).

The gap size where saplings were sampled varied from 27 m^2 to 10 ha. The *CUSUM* plots of both gap size and position of the gap sapling (i.e. distance of the gap sapling from the nearest gap edge) for both HW and SW show consistent and strong trends in height growth response with a distance to a plateau (Fig. 4.12). The rate of height growth (*MGTH*) increased rapidly up to 100 m^2 and then gradually but consistently until about 1000 m^2 for the hardwood saplings (Fig. 4.12A). On the other hand, softwood sapling growth responds well for small gap sizes, to about 400 m^2. (Fig. 4.12B). The significant impact on the height growth of both hardwood and softwood saplings is seen for those saplings that are positioned almost 5 m in to gap centre, consistently adding at least 10% more height growth to the sapling for every 0.2 m distance after 1 m from the gap edge (Fig. 4.12C and D).

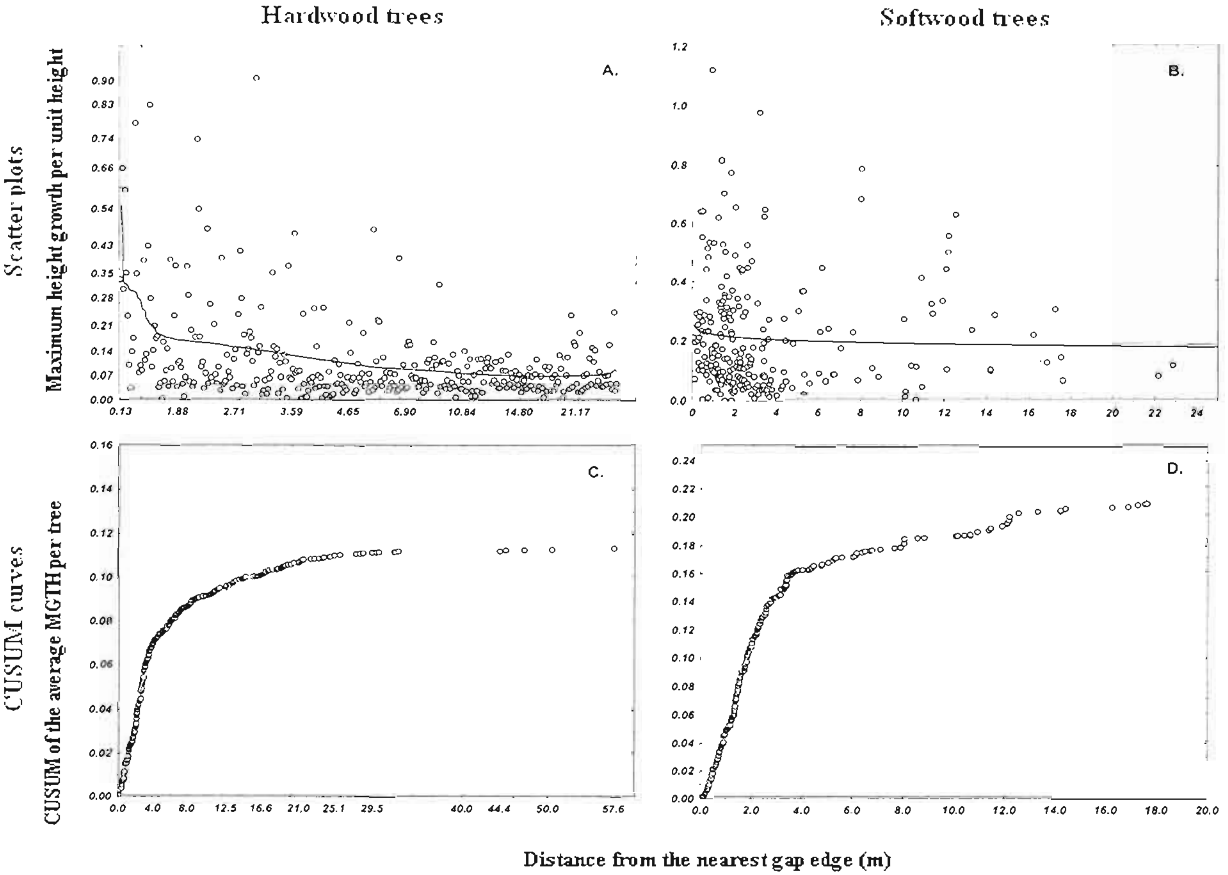

Figure 4.11. Extent of influence of canopy opening on the height growth of the closed canopy hardwood and softwood trees. A and B show the scatterplots of MGTH and the estimated regression, C and D show the scatterplots of CUSUM of the average MGTH per tree along the distance from the gap edge.

4.6. DISCUSSION

Measuring canopy closure in boreal forests

Studies on canopy closure are rare and to the best of our knowledge, none exist in boreal forests, yet this is crucial for understanding turnover times. The rate of gap closure estimated in this study based on the gap characterization of multi-temporal lidar data covering the 6 km^2 boreal forests is 1.2% per annum. The few studies conducted in other forest biomes (e.g. in rainforests using hemi-spherical photos by van der Meer and Bongers (1996), temperate forests using hemi-spherical photos by Valverde and Silvertown (1997), deciduous forests using repeat ground measurements by Runkle and Yetter (1997), Runkle (1998)), may not be directly comparable primarily because of the difference in definitions and measurements adopted. We defined canopy closure based on attaining a certain canopy height (i.e. 5 m) rather than change in percent openness (e.g. as in van der Meer and Bongers (1996)) or rate of expansion or growth of gap edge vegetation (e.g. as in Runkle and Yetter (1997)) to predict the time required for gap capture. Gaps closed through both height and lateral growth in the study area. Studies with retrospective ground based measurements focused mainly on lateral extension in filling small gaps (Runkle 1998, Runkle and Yetter 1997), while others with hemispherical photos were restricted to gap centres (Valverde and Silvertown 1997, van der Meer and Bongers 1996). In addition, because they were conducted at the scale of only a few representative gaps, the chance of underestimation could be due to the limitations of the techniques, especially with hemispherical photos. Since the photos are taken at gap centres, there is an uncertainty in estimating gap closures with repeated measurements in and around the gaps.

Our estimated rate of gap closure using a lidar surface for boreal forests is higher than the closure rates estimated using a 15 m threshold on aerial photo based CHM of

0.62% in mixed deciduous forests (Tanaka and Nakashizuka 1997), 0.5% in evergreen broad-leaved forests (Fujita et al. 2003), and 0.39% in temperate forests (Henbo et al. 2004). This finding is surprising since gap recruitment and gap filling in cold, slow-growing northern forests is considered to be very slow compared with that occurring in most temperate and tropical forests (Bartemucci et al. 2002, McCarthy et al. 2001). It should also be considered that estimates from other studies based on photo-CHM are at a coarser grid (the finest being 2.5 m X 2.5 m) wherein the scale of mapping restricts the geometry of gaps resulting in either under or over estimation (Vepakomma et al. 2008). Identification of small gaps in these other studies is poor as gaps appear shallower on aerial photos, hence erroneously merging two gaps in close proximity as one large gap that can be ambiguous in monitoring over time (Koukoulas and Blackburn 2004, Henbo et al. 2004). Moreover, the quality of the CHM is most importantly affected by the accuracy of ground elevation measurements, which remains difficult over closed forest canopies using aerial photos alone (St-Onge et al. 2004).

Influence of canopy gaps on height-growth

Species classified as early successional are believed to have more rapid height-growth compared to those classified as late-successional (Claveau et al. 2002, Messier et al. 2000) In general, we found that late successional SW trees/saplings in this part of the study area, irrespective of their location and initial height, are growing at similar rates compared to the early successional HWs. These findings are in agreement with the observations made by Gutsell and Johnson (2002) in boreal forests in Saskatchewan. However, they included jack pine, a fast growing early succesional species that is also found in the the neighbouring forests.

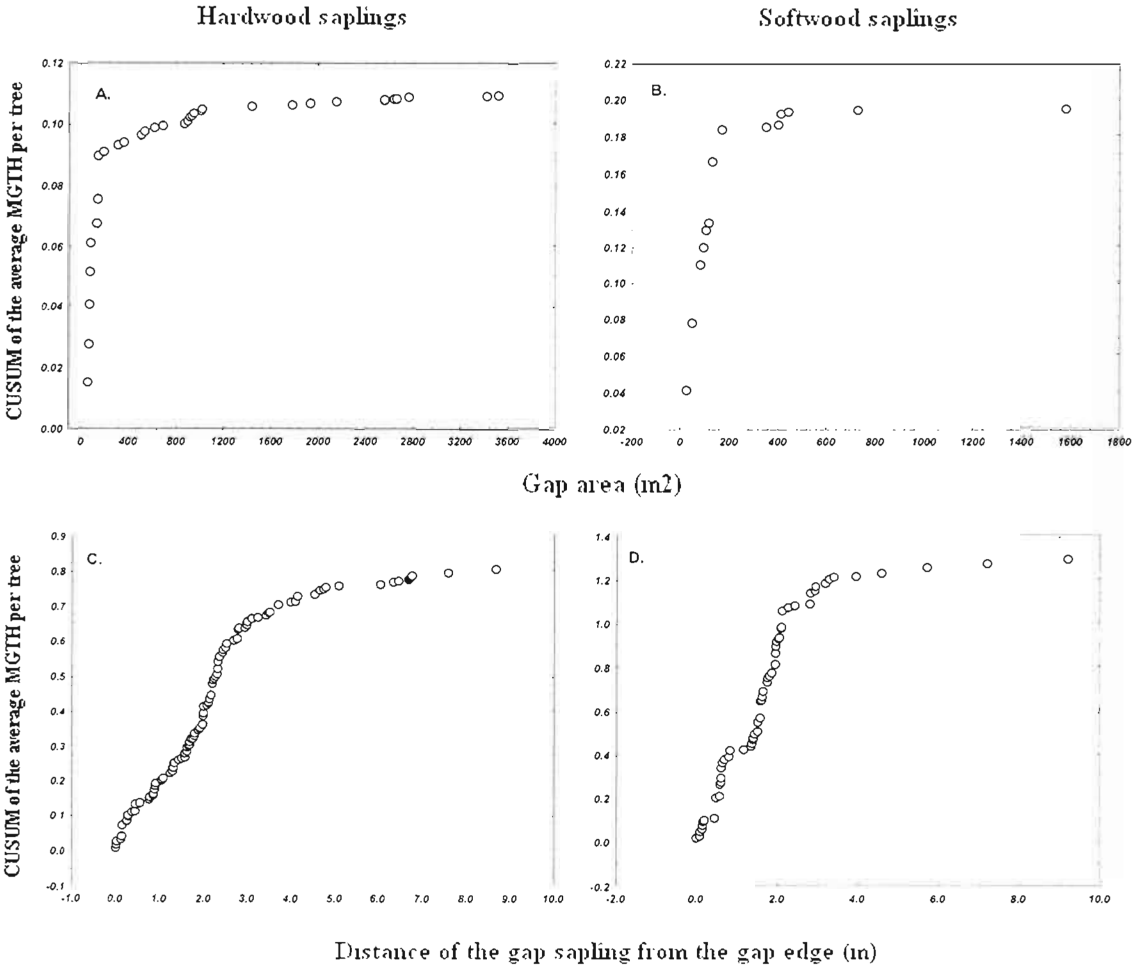

Figure 4.12. Effect of gap size and position of the sapling within the gap on the height growth. A and B are the scatterplots of CUSUM MGTH per unit area along increasing gap size, C and D are the scatterplots of average MGTH per gap sapling.

In this research, we noted that irrespective of the initial height, the position of a sapling in a gap and the size of the canopy opening have a strong influence on height growth. Conifer saplings in gaps were found to have a better growth within 0.5 – 2 m of the gap edge. Previous studies have also noted that the regeneration of shade tolerant conifers is generally more abundant under or in the proximity of intact forest canopies (Drobychev and Nihlgard 2000, Burton 2002) or in the southern shaded part of gaps (Kneeshaw and Bergeron 1999). On the other hand, as HWs in these forests are light demanding species, it is not surprising to find that height-growth is greatest at distances greater into the gaps i.e. 1.5 - 4 m from the gap edge. Analysis of cumulative growth per tree with an increasing gradient of gap sizes shows that HW saplings optimize their height growth in gap openings less than 800 m^2 in size, whereas the optimal gap opening for SW saplings to attain maximum height growth is much smaller and occurs around 250 m^2.

Although more area is closing due to regeneration than lateral growth, canopy gaps in boreal forests have a strong influence on the growth of gap edge vegetation with nearly 22% of the total area being closed due to lateral closure alone. 54% of this lateral closure is due to the expansion of hardwood crowns which although not documented in boreal forests is common in tolerant hardwood forests to the south (Runkle 1998, Runkle and Yetter 1997) while 46% of the closure is due to the expansion of conifers which has previously been considered to be minor due to the determinate growth of coniferous stems.

Both mechanisms of closure occurred across a large range of gap sizes (up to 1 ha.) despite the expectation that lateral expansion would be more important in small gaps. However, lateral closures were predominant in small gaps (below 200 m^2) as noted in previous studies (Runkle 1985, 1998). Evidence from this study also shows that both hardwood and conifer trees had similar lateral growth. These findings agree with those of Umeki (1995) who concluded that lateral growth, expressed as foraging, did not differ between hardwood and softwood species groups. In other studies, canopy displacement in tolerant conifer species was noted to be similar to that of intolerant hardwoods (Getzin and Wiegand 2007, Muth and Bazzaz 2002, Stoll and Schmid 1998).

Many species in a variety of forest systems, especially those with indeterminate growth, are known to have morphological plasticity in their horizontal growth in response to an opening (Muth and Bazzaz 2002, Brisson 2001, Rouvien and Kuuluvainen 1997). This has been measured in terms of asymmetry in crowns in relation to availability in space or lateral extension of branches (Runkle and Yetter 1997, Runkle 1998, Perdersen and Howard 2004). Based on a large sampled area in this study, the rate of average lateral extension of gap edge trees was estimated to be 24 cm/ yr with a maximum length of 40 cm/yr and did not vary much between the two species groups. This estimate is higher than the average 18 cm/yr reported (although their maximum was 58.6 cm/yr) for hardwood temperate forests by Runkle and Yetter (1997). The difference is probably due to the large sample size and the fact that we included small sized gaps in our study.

Gap edge trees also respond to canopy gaps with an increase in height-growth. The estimated rate of maximum growth (MGTH) of fifty two gap edge laterally growing trees with an average height of 15.2 m (mainly consisting of hardwoods) is 0.3 m over 5 years, a rate similar to those of gap island trees. Comparing the growth of interior trees with those growing in gap edges we found that HW and SW gap edge trees, smaller than 15.0 m and 11.0 m in height respectively, benefit greatly from gap openings. This influence decreases with the height of trees. Larger trees on the gap edge may be less physiologically capable of responding to increased resources in the gap (Oliver and Larson 1996). A positive response of stem radial growth of gap edge trees was also seen in most of the tree species studied in American beech forests (Pedersen and Howard 2004).

In fact, gaps not only influence the immediate vicinity of their edges, but also into forest interiors. Significant differences in natural regeneration, seedling establishment and tree growth are known to be associated with distance from the gap edge (Burton 2002, Coates 2000). In our analysis based on CUSUM of the average maximum rate of growth per tree, we noted that canopy gaps have an influence on the height-growth of both HW and SW trees at a distance less than 30 m and 20 m respectively from the gap periphery. The highest growth rates (30% increase over 5 years) occurred in trees close to the gap edge and gradually decreased to 7% at around 25 m from the gap edge. The gap effect on height growth of overstory trees in the intact forest from an edge of naturally occurring canopy gaps has rarely been examined. Nevertheless, the radial growth of sugar maples in the understory was noted to increase as far as 30 m into the uncut stand from the opening edge of clear cuts (Tyron et al. 1992). Similarly, increased irradiance due to windthrows following a clearcut enhanced the growth of understory *Picea* and *Abies* seedlings, to a distance of 60 m and caused a decrease in the radial growth of adult trees up to 45 m into the sub-boreal forest from opening edges (Burton 2002).

4.7. CONCLUSION

This study demonstrates the ability and prospective use of discrete multi-temporal lidar to characterise filling of canopy gaps and to provide information on the effect of canopy openings on the productivity of boreal forests at fine scales. The separation of laterally closing gaps from vertically closing gaps shows that the silvicultural creation of canopy gaps should be greater than 200 m^2 to favour seedling height growth instead of lateral growth. Our results also demonstrate that foresters should consider lateral growth from both hardwoods and conifers. Gap based silviculture will also have benefits of increasing tree growth not only within gaps but also up to 30 m fro gap edges into the interior forest. The improved understanding of spatially explicit forest responses to canopy openings will not only improve long-term monitoring of forest productivity, and thus an improved evaluation of optimal rotation ages but also will permit improved carbon budgeting through a better estimation of biomass fluctuations.

CHAPTER V

Height growth of regeneration in boreal forest canopy gaps – does the type of gap matter? An assessment with lidar time series

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5.1. RÉSUMÉ

Dans les vieilles forêts, les grandes trouées de canopée engendrées par la chute de plusieurs arbres au fil des années se composeraient d'une régénération étant à différents stades de croissance. Bien qu'il soit important de comprendre la dynamique découlant de processus complexe de mortalité, suivi est rarement effectué en raison de certaines limites techniques. En appliquant des techniques orientées objets à une série de trois jeux de données altimétriques laser sur une période de neuf ans en forêt boréale, nous avons distingué les types suivants : anciennes trouées, des expansions de trouées existantes et nouvelles trouées aléatoires. En combinant le type d'essence (feuillu ou résineux) obtenu à partir d'images de haute résolution à la localisation des gaules par altimétrie laser, nous avons pu estimer la croissance en hauteur des espèces le long d'un gradient de hauteur. Les résultats indiquent qu'il existe des patrons de croissance en hauteur distincts pour les feuillus et les résineux selon l'événement perturbateur créateur de la trouée. Les méthodes développées pourraient éventuellement s'appliquer à l'évaluation précise du développement des patrons de croissance juvénile.

Mot-clés: croissance en hauteur, lidar multi-temporelle, dynamique des trouées, régénération

5.2. ABSTRACT

Large canopy gaps in old-growth forests, formed as a result of tree fall events over time, could be composed of regeneration in various stages of growth different from that of single mortality events. Though important to understand forest dynamics such complex processes are rarely monitored due to limited techniques. Applying object-based techniques to a series of three lidar datasets acquired over nine years in boreal forests, we characterised gap events into old gaps, gap expansions and new random gaps. Combining broad species class from high resolution images, and individually locating gap saplings on the lidar surface, species-specific height growth across gradients of sapling height was estimated. The results indicate distinct height growth patterns of both hardwood and softwood gap saplings in different gap events. The methods can potentially be extended to develop accurate juvenile growth patterns.

Key words: height-growth, multi-temporal lidar, gap dynamics, advanced regeneration

5.3. INTRODUCTION

Canopy gaps created by the fall of one or more overstory trees are important for regeneration dynamics in old-growth forests (Pickett and White 1995). The availability of increased site resources enhances the height growth rates of all species within canopy gaps. Research in various forest systems showed that sapling height growth is a function of gap characteristics, such as gap size (Kneeshaw and Bergeron 1998). Due to the vulnerability of gap edge trees to mortality, some larger canopy gaps could be a result of tree fall events over successive periods of time (Runkle and Yetter 1987, Foster and Reiners 1986). As a consequence, such large gaps in an old-growth forest could be composed of regeneration in different stages of growth whereas gaps formed from a single mortality event should have a single regeneration cohort. Hence it is important to characterise the type of gap events to forecast growth patterns of the regeneration. However, gap formation (expansion vs a single event) is rarely investigated due to the difficulty in collecting data and the limited techniques available for monitoring canopy gaps over time. Moreover, measurement of a canopy gap, gap dynamic characteristics like gap expansions and closure and reliable measurement of height-growth in the field is complex. Conventional remote sensing based methods using aerial photos have been criticized for inadequately identifying gaps (Koukoulas and Blackburn 2004) while assessment of vegetation height is prone to error in closed canopies (St-Onge et al. 2004).

In recent decades lidar has emerged as a powerful tool in remote sensing to accurately measure canopy height and vertical structure (Lefsky et al. 2002). Owing to its high sampling density and accuracy, the potential to detect tree fall and growth estimation using multi-temporal discrete small-foot print lidar data sets has also been shown in a few recent studies (Hopkinson et al. 2008, Yu et al. 2006, Naesset and Gobakken 2005, St-Onge and Vepakomma 2004). Using tree matching techniques on high density lidar, Yu et al. (2006) showed a good correspondence with field measurements. Lidar was effective in recording significant growth changes at plot and stand levels (Naesset and Gobakken 2005) and in detecting annual conifer growth (Hopkinson et al. 2008). St-Onge and Vepakomma (2004) compared and confirmed results of dissimilar density lidar data for expected forest height growth. Vepakomma et al. (2008a) validated the feasibility of using medium density small-foot print lidar to map gap dynamic characteristics like canopy gap opening and closure of sizes ranging from 5 m^2 to 9.8 ha. Nonetheless, no studies using lidar have yet been conducted to characterise height growth patterns of vegetation in canopy gaps.

Assuming lidar accuracy and the potential to estimate changes in forest growth with similar and dissimilar densities from earlier studies, we characterise the height growth patterns of gap saplings growing following different gap events by analysing a time series of lidar data. Using a validated method to locate individual trees/ sapling tops and to identify their species class (hardwood or softwood), we quantified the height growth rates of saplings over four years in canopy gaps. By delineating the canopy gaps and identifying gap events as old existing gaps, new gap expansions and new random gaps, we investigated whether height growth patterns varied between gap events.

5.4. METHODS

5.4.1. Study area

The study site is within the conservation zone of the Teaching and Research Forest of Lake Duparquet (TRFLD, 79°22'W, 48°30'N), in the Province of Quebec, Canada. This area is characterized by small hills that vary in elevation between 227 m and 335 m. The mixed vegetation of this part of forest is composed of common boreal species, dominated by balsam fir (*Abies balsamea L.* [Mill.]), paper birch (*Betula papyrifera* [Marsh.]), and trembling aspen (*Populus tremuloides* [Michx]). The stand level age structure found in the study area results from a fire driven disturbance regime (1760-1919), and a recent infestation of a defoliating insect (1970-1987) called the spruce budworm (*Choristoneura fumiferana* [Clem]). Most stands are mature or over mature reaching heights of up to 25 m. The climate is cold temperate with an average annual temperature of 0.8° C with annual precipitation of 857 mm The frost free period lasts for nearly 64 days, while the length of the growing season is on average 160 days (Environment Canada 1993).

5.4.2. Lidar data

A time series of lidar data in three time steps was collected on June 28th 1998, August 14 to 16, 2003, and July15th, 2007. The 1998 survey was carried out using an Optech ALTM1020 flown at 700 m above ground level (AGL) operating at a pulse frequency of 5 kHz. with two passes for the first returns and one pass for the last returns, resulting in 0.3 and 0.03 hits/m^2 respectively. The 2003 survey was done with Optech's ALTM2050 lidar flown at 1,000 m AGL, with 50 kHz and 50% overlap between adjacent swaths resulting in 3 and 0.19 hits/ m^2. The 2007 survey was conducted using ALTM 3100 flown at 700 m AGL with 67 kHz and over 50% overlap between adjacent swaths resulting in 10 hits/ m^2 for the first returns. All returns were classified by the provider as ground and non ground and were assumed correct for the study.

Accuracy assessment of lidar derived canopy heights for 1998 and 2003 was carried out in two different studies with 36 (1998) and 77 (2003) field measured trees ranging in height from 5.6 m – 33.1 m that yielded an r^2 of 0.88 and 0.86 with an RMSE of 1.8 m and 1.85 m respectively (Véga and St-Onge 2008, Coops et al. 2004). It is to be noted that at the time of this study, the accuracy assessment of the 2007 data using field measurements was not performed. However, visual and statistical comparisons of the 2007 CHM with high resolution images from the 2007 and 2003 lidar data sets showed a good match.

5.4.3 Lidar surface and gap characterisation

The three datasets were co-registered for temporal comparisons using the methods suggested by Vepakomma et al. (2008a). The Digital terrain model (DTM) was generated by combining the last returns in 1998 and 2003. The time series of canopy height distributions or canopy height models (CHMs) were generated using an optimised grid resolution (0.25 m) and an interpolation algorithm (a combination of local maxima and an inverse distance method) for accurate and reliable delineation of gap geometry. Defining a gap as an opening in the canopy caused by the fall of a single or a group of trees of a height, greater than 5 m (determined in the field), a highly accurate ground validated algorithm on the lidar CHMs was used to explicitly map canopy gaps for each of the years. Mapped gaps are individual objects of contiguous binary grid cells determined by a gap indicator function (Eq. 1). The comparison of 29 gaps measured in the field along 980 m of transect with lidar delineated gaps showed a good match with 96.5% overall accuracy.

$$G_i(x,y) = \begin{Bmatrix} 1 & \textit{if } CHM_i(x,y) < a \\ 0 & \textit{otherwise} \end{Bmatrix} \qquad (1)$$

where a = 5 m in this study, $CHM_i(x,y)$ is the lidar height of the canopy surface in the *ith* year, (x,y) is a cell that does not belong to any open-ended system.

Gap objects were delineated on 1998 and 2003 lidar surfaces. We define old gaps as those gaps that are open in 1998 and 2003 while gaps that opened between 1998 and

2003 are new gaps. New gaps that share the edge of an existing gap in 1998 are gap expansions, otherwise they are considered new random gaps. Areas within a gap where the difference in vegetation height between 1998 and 2007 is greater than 5 m, i.e. the smallest difference that is considered to be too high for vertical growth, and contiguous with the gap edge, are classified as lateral growth of adjacent vegetation. Separating laterally growing gaps from regenerating areas reduces ambiguity in height growth patterns of regeneration. We performed various combinatorics on the delineated gap objects of 1998 and 2003 to define the nature of the gap events, namely, old gaps, new gap expansions and new random gaps. An example of automatically delineated canopy gap events is shown in Fig. 5.1

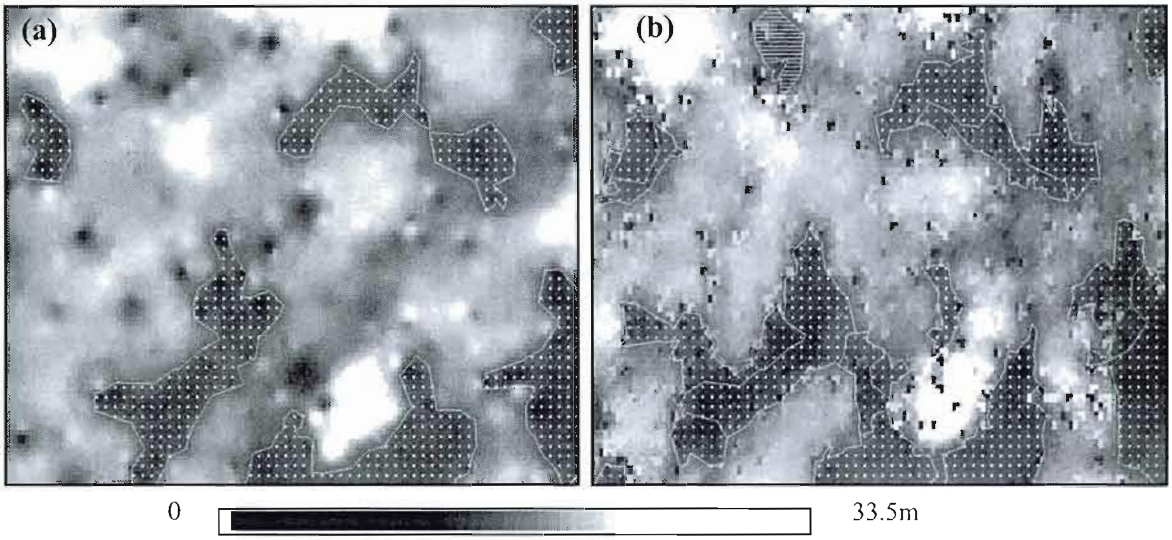

Figure 5.1. An example of automatically delineated canopy gaps. (a) Gaps in 1998 (dotted objects) overlaid on CHM_{1998} (b) Old gaps (dots), new gap expansions (crosses) and new random gaps (lines) that appeared between 1998 – 2003 overlaid on CHM_{2003}

5.4.4. Species class delineation

Orthorectified high resolution multi-spectral Vexcel UltraCamD image data acquired five weeks prior to the 2007 lidar data was used to classify the vegetation of the study area into broad species classes, namely, hardwood (HW) and softwood (SW). Canopy height derived from the lidar data was integrated with the spectral signatures of the image data to automatically extract individual image objects using eCognition v. 3.0. The overall accuracy of the image classification based on a comparison matrix with 25 hardwood and softwood field-identified trees, and 15 open, non-forest locations is 91.5%, while softwood class showed the least (73.3%) of the classification accuracies.

5.4.5. Identifying maximum tree height locations and extraction of growth statistics

Height growth statistics for individual saplings were estimated based on raw lidar returns from 2003 and 2007 extracted after identification of sapling tops on the CHM_{2007}. A local maxima filter with a circular non-overlapping (moving) window was applied to the CHM_{2007} to derive a layer of sapling apices, *LMAX (x,y)*. Local maxima filtering is a common technique first adopted to identify trees in high

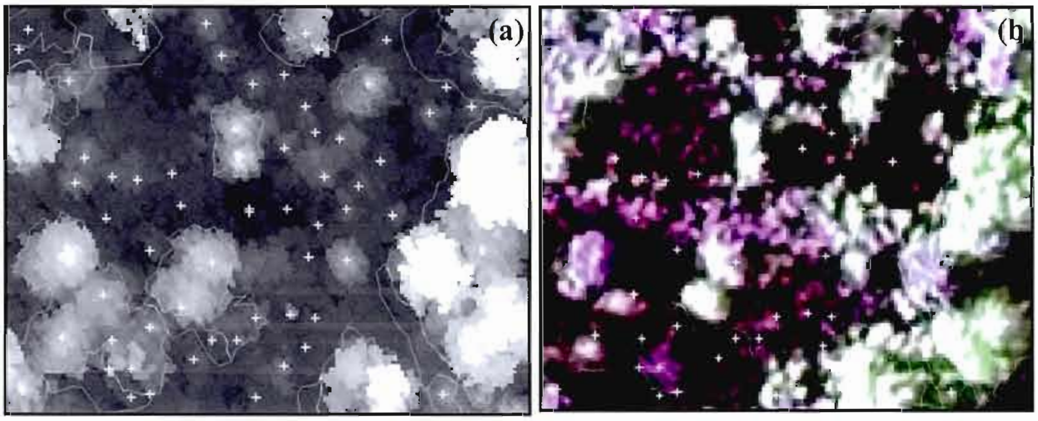

Figure 5.2. Identification of sapling tops (crosses) along with gap edges (solid line) shown on (a) the CHM_{2007} (b) UltraCam D Image of 2007. Brightness on the CHM is proportional to canopy height.

resolution optical imagery and successfully extended to lidar surfaces (Popescu and Wynne 2004). We selected a search radius of 5 pixels (1.25 m). This is equal to the average crown radius of 30 saplings (with maximum heights between 3-5 m) visually interpreted on the lidar surface. A local maximum within a search window that matches the height on the CHM i.e. $LMAX(x,y) = CHM_{2007}(x,y)$, is assumed to be the maximum height ($TMAX(x,y)$, hereafter $TMAX$) of the sapling crown. This method applied on CHM_{2003} was previously validated with 940 trees and saplings identified using manual photogrammetric methods on UltraCamD images of 2007 elsewhere in the study area (Vepakomma et al. 2008b). An example of identified sapling tops is seen in Fig. 5.2.

Lidar raw point clouds of the 2003 and 2007 vegetation (first returns) were extracted within a buffer zone of 0.5 m radius around each sapling top of *TMAX*. In order to make the lidar datasets of varying densities comparable, the lidar sampling point densities within these buffers were made equal by randomly selecting n_i sample points for both years such that

$$n_i = \min\,(n_i^{2003}, n_i^{2007}) \qquad (2)$$

where n_i^{2003} and n_i^{2007} are the number of first returns within the i^{th} buffer zone in 2003 and 2007 respectively. All buffer zones were further constrained to have a minimum point density of 3 hits /m^2 and a lidar-determined height to be not less than 2 m of the zonal maxima such that possible errors due to insufficient representation of canopy apices and lidar penetration into the foliage is minimised.

Sapling height growth was calculated as the differences in height of the sample maximum (MAXGTH) and sample average (AVGGTH) for the first returns in 2003 and 2007 Reference average (AVG03) and maximum (MAX03) sapling height for each buffer zone are the sample average and sample maximum of the difference in the height of the 2003 lidar first returns and their respective ground elevation extracted from the DEM. Growth rates in terms of average growth per unit height (AGTH), i.e. (AVGGTH / AVG03), and maximum growth per unit height (MGTH), i.e. (MAXGTH / MAX03) were used to assess growth. It is to be noted that MGTH and AGTH computed here are the rates of growth over the four growing seasons and being proportional growth they are unit free measures. Thus a MGTH value of 0.2 signifies a 20% maximum growth increase from its 2003 maximum reference height.

5.4.6. Height growth patterns of regeneration in canopy gaps

To understand if height growth patterns differ based on the nature of the gap events, we considered three windows with varying gap fraction (percentage of gap area) that constituted a total size of 26 ha. Since hardwood and softwood trees have different architecture and respond differently to available resources, we assessed AGTH and MGTH based on species class across gradients of sapling height and also between the gap events using (1) exploratory statistics (2) scatterplots and (3) non-parametric regression estimation of MGTH given the initial height of the sapling. To investigate whether distinction of the type of gap events is important for understanding growth patterns of regenerating saplings in gaps, we compare the statistics and models generated separately by pooling the sapling data.

5.5. RESULTS

5.5.1. Canopy gap characteristics and sapling height

Delineation of canopy gap events indicates that about 16.8% of the study area is in canopy gaps during 1998 – 2003 of which 13.1% is composed of old gaps that opened before 1998 (Table 5.1). During the period 1998-2003, gaps are seen to be expanding at a higher rate and more frequently than the formation of random gaps. Average gap size of gap expansion is almost twice the average size of old gaps and seven times the average size of new random gaps. However, average gap size of pooled data is largest at 6024.5 m^2.

Table 5.1.

Gap characteristics in the study area

Statistic	*Old gaps*	*Expansion**	*Random**	*Pooled*
# Gaps	420	617	80	483
Total area in gaps (m^2)	34028.7	8667.5	861.4	43557.6
% area in gaps	13.1	3.3	0.3	16.8
Minimum gap size (m^2)	5.0	5.0	5.3	5.0
Maximum gap size (m^2)	2988.7	288.9	87.3	6024.5
Mean gap size (m^2)	80.9	149.8	28.7	104.9
# of saplings identified	388	52	12	452
Avg. sapling height (m)	3.28	3.06	2.1	3.23
Mean MGTH (AGTH)	0.4 (0.7)	1.23 (0.76)	1.14 (0.6)	0.76 (0.6)

* Gaps qualified as expansions and random are new gaps that opened between 1998-2003

In all, 452 gap saplings with a height ranging between 0.5 – 5.0 m were automatically identified in the 26 ha study area, of which 85% belong to old gaps (Table 5.1). On average, the saplings in new gap expansions are fast growing compared to those in new random and old gaps. In all cases, the correlation between average and maximum sapling height generated by the two lidar datasets (2003, 2007) is very high at over 0.97 suggesting that growth between the two periods can be measured using multi-temporal lidar data.

5.5.2. Height growth patterns in canopy gaps

The average and maximum height of saplings in old gaps are higher than in new gaps (Table 5.2). The range of sapling height in old gaps is greater than that of saplings in new gaps. Except for saplings in old gaps, the maximum growth rates are higher than average growth rates. However, the height growth of HW and SW saplings within old

Table 5.2
Summary of growth statistics between 2003 – 2007 in various gap types

A. Hardwood sapling (# Saplings in Old gaps : 138; new gap expansions: 23; new random gaps : 6)

	Old gaps			*New gap expansions*			*New random gaps*			*Pooled*		
Variable	*Min*	*Max*	*Mean*	*Min*	*Max*	*Mean*	*Min*	*Max*	*Mean*	*Min*	*Max*	*Mean*
AVG03	0.42	6.53	3.25	0.30	4.34	2.34	0.82	2.94	1.43	0.30	6.53	3.06
MAX03	0.42	6.65	3.39	0.30	4.85	2.42	0.82	2.94	1.43	0.30	6.65	3.19
AVGGTH	0.10	4.8	0.90	0.01	5.45	1.26	0.01	2.02	0.50	0.12	19.60	1.25
MAXGTH	0.02	4.7	1.31	0.09	4.76	1.67	0.60	3.53	0.97	0.10	19.60	1.83
AGTH	0.10	4.8	0.40	0.02	2.72	1.15	0.50	2.13	0.62	0.01	5.45	0.61
MGTH	0.00	4.7	0.52	0.02	3.78	1.23	0.20	3.73	1.01	0.02	4.79	0.79

B. Softwood saplings: (# Saplings in Old gaps : 250; new gap expansions: 29; new random gaps : 6)

	Old gaps			*New gap expansions*			*New random gaps*			*Pooled*		
Variable	*Min*	*Max*	*Mean*	*Min*	*Max*	*Mean*	*Min*	*Max*	*Mean*	*Min*	*Max*	*Mean*
AVG03	0.41	6.31	3.49	0.98	6.06	2.71	0.76	5.09	2.68	0.06	6.31	3.39
MAX03	0.41	7.19	3.71	0.98	6.99	2.84	0.76	5.78	2.79	0.06	7.19	3.60
AVGGTH	0.01	4.86	0.66	0.10	2.78	0.83	0.19	2.42	1.14	0.10	4.86	0.69
MAXGTH	0.00	4.74	1.08	0.08	4.63	1.33	0.67	4.49	2.46	0.00	5.00	1.12
AGTH	0.10	3.10	0.25	0.01	1.74	0.46	0.04	1.27	0.58	0.01	7.06	0.31
MGTH	0.00	3.78	0.36	0.02	2.01	0.61	0.14	4.47	1.26	0.00	3.78	0.58

AVG03 and MAX03 are the average and maximum reference tree heights (in m) in 2003 respectively; AVGGTH and MAXGTH are the average and maximum height growth (in m); AGTH and MGTH are the average and maximum rates of growth per unit height respectively; Min is minimum; Max is Maximum;

and new gaps and between gap events is highly significant (Kruskal-Wallis ANOVA by ranks and Median tests, $p \approx 0$). SW saplings are taller than HWs in all the gap events (Table 5.2). The results indicate that HW saplings in old gaps and gap expansions are growing at a faster rate than SWs, but the contrary is noted in new random gaps. Though maximum MGTH is noted for HW saplings in old gaps, HWs are growing only slightly faster than SWs. On the other hand, HWs

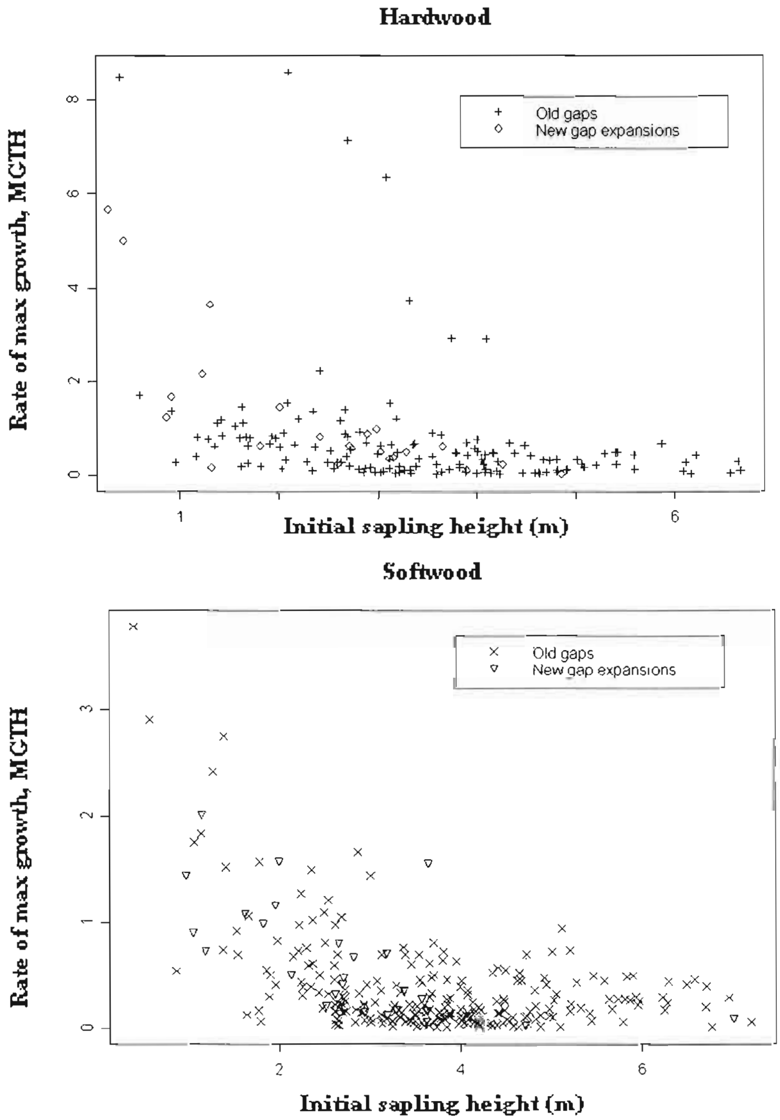

Figure 5.3. Scatterplot of the rate of maximum growth per unit height during 2003 - 2007in old gaps and gap expansions

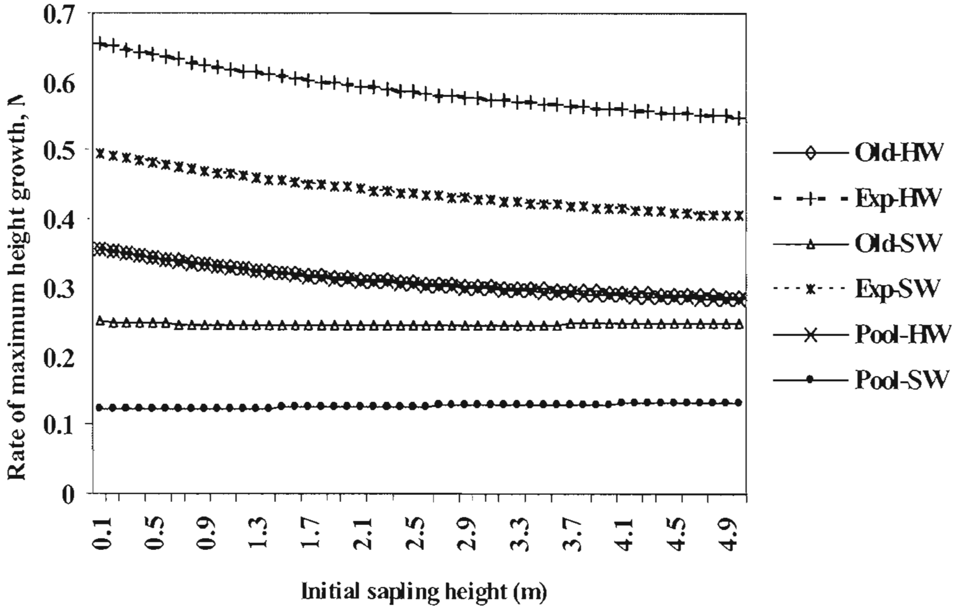

Figure 5.4. Estimated non-parametric regressions of the rate of maximum growth per unit height based on the growth in 2003 – 2007 in old gaps and gap expansions (*Old stands for old gaps; Exp for new gap expansions, Pool for pooled dataset*)

are growing at twice the rate of SWs in new gap expansions. Scatter plots and predictive models (Figs. 5.3 and 5.4) indicate that the height growth of saplings in all gap events is considerably different.

5.6. DISCUSSION

The ability of lidar to reliably estimate gap disturbance regimes is well established (St-Onge and Vepakomma 2004, Koukoulas and Blackburn 2004). Estimated gap sizes and gap fraction in this study fall within the reported range of characteristics of boreal forests found in earlier studies (Vepakomma et al. 2008 , McCarthy 2001). Gap expansion is a prominent feature in a number of forest ecosystems (Worall et al. 2005, Runkle 1998). In the part of boreal forests we studied, gap expansions are more frequent than random new gaps (Table 5.1). Though less frequent in hardwood forests, similar to the boreal forests around Lake Duparquet, trees bordering an old gap are more vulnerable to mortality compared to interior canopy trees in wind fall prone *Picea-Abies* forests of New Hampshire (Worall et al. 2005).

The identification of saplings in old gaps was more successful than in new gaps. Owing to the longer period of opening, the range of sapling height in old gaps is wider than that in new gaps. A higher average height of 3.9 m in older gaps also enabled easy identification on the lidar surface (Table 5.1). Identification of saplings within new random gaps was difficult due not only to their small sizes but also to the lateral growth of adjacent vegetation.

The HWs in this forest are all shade intolerant while SWs are all shade-tolerant (Kneeshaw et al. 2006). Previous research in boreal forests has suggested that large gaps favour intolerant hardwoods while shade tolerant softwoods successfully regenerate in small gaps (Kneeshaw and Bergeron 1998). The present analyses support this evidence as HWs grow faster in old gaps whose average gap size is larger than new gaps (Tables 5.1 and 5.2). SWs are growing faster in new random gaps that are smaller in size. The resources within gaps, especially light, increases with gap expansion, which primarily benefits the HW saplings growing in old gaps adjacent to the new gap openings. The dominant conifers on the other hand are shade tolerant and they have been found to be successful in smaller gaps and in the shadier southern portions of gaps due to their requirement for higher moisture (McLaren and Janke 1996).

The present results clearly indicate distinct growth patterns of saplings in different gap events. This suggests the need to characterise the type of gap events to forecast growth patterns of the regeneration. The use of a time-series of lidar data for documenting the height- growth differences of advance regeneration in canopy gaps spanning the full range of height gradients is particularly relevant given the complexity of field based methods. This establishes multi-temporal lidar as an excellent tool to characterise gap dynamics, and thus provide insight into boreal forest dynamics. With rigorous field verification for height of regeneration, these methods can be extended to develop accurate height growth models for juvenile vegetation in a non-destructive way.

CHAPTER VI

SYNTHESIS, CONCLUSIONS AND FUTURE RESEARCH

Boreal forests are heterogeneous ecosystems that are a result of multiple disturbances over time. Identifying and quatifying this spatial heterogeneity helps in understanding forest resource availability and distribution across the forests. This dissertation contributes to improving our understanding of gap disturbance regimes and their dynamics, and how boreal mixedwood forests respond to these disturbances in terms of growth and mortality at local scales. A focus of the research has also been on understanding the role of gap openings on short-term stand and successional dynamics. Thus far most research was conducted at the scale of a few gaps, restricted to current conditions or based on space-for-time substitution. Although many researchers highlighted the incompleteness in considering gap / no gap dichotomy alone to explain the complexity of forests (Lieberman et al. 1989, Brokaw and Scheiner 1989), interactions and dynamics of forests are rarely addressed across the forest as a whole. In this study we analysed a contiguous 6 km^2 forest around Lake Duparquet, Canada, a area sufficiently large to capture variability in canopy structure and forest response (Fig.1.3). Ecological processes were studied by reconstructing the canopy height surfaces of boreal forests using discrete lidar data taken in 1998, 2003 and 2007 that has dissimilar survey specifications. The findings from the research presented here should benefit ecologists, silviculturists, forest managers and lidar specialists alike. In this chapter we briefly summarize the results and highlight some of the major contributions this doctoral research project has made in developing methods and understanding gap dynamics in boreal forests. The direction that this research should take in the future is also discussed.

6.1. SYNTHESIS, MAIN FINDINGS AND CONCLUSIONS

6.1.1. Methodological innovation

Mapping of canopy gaps and their dynamics using lidar data

This study demonstrates the gains made by using tools like lidar in mapping canopy gaps which are otherwise limited by traditional means. Lidar provides spatially continuous high resolution measurements of canopy height over large spatial coverages. Canopy openings delineated in this boreal forest varied considerably in sizes from 5 m^2 to 9.8 ha. (Chapter III) thus widely expanding the range presented in previous studies based on a few sampled gaps (e.g., Bartemucci et al. 2002, Kneeshaw and Bergeron 1998, Frelich and Reich 1995). Canopy gaps can be large and could be a result of treefall events over time (Foster and Reiners 1986). Hence results and interpretations on forest dynamics made following measurements in a few gaps with a single time observation or by indirect means (e.g., by dating fallen stems) to note past disturbances may misrepresent long-term gap dynamics. The gaps in this study area were also seen to be complex and irregularly shaped with a perimeter-to-area ratio between 0.35 and 4.16 (Chapter II). Measuring gaps with such complex geometry, which can also be confused with inter-tree spaces in coniferous forests, can be difficult with conventional field or optical remote sensing techniques (e.g., de Romer et al. 2008, D'Aoust et al., 2004, Fujita et al., 2003). These conventional methods have limitations in studying, monitoring or replicating gaps at large spatial scales. Moreover, the assumption of an ellipsoidal shape used to measure canopy gaps in most studies could under –estimate or overestimate gap geometry.

The primary contribution of this project has been in greatly increasing our capacity to measure and study the dynamics of canopy gaps using multi-temporal lidar data. As a corollary to this development, the major contributions have been (1) demonstration of the feasibility of identifying gaps using lidar (Appendix-I), (2) the *a priori* preparation of multi-temporal lidar data for forest change assessment and gap detection (Chapter II) and (3) the development of a validated algorithm to automatically map canopy gaps and their dynamic characteristics (Chapter II).

The proposed object-based region growing technique on lidar surface can delineate gaps with accurate gap geometry and eliminate inter tree spaces that are spurious gaps (Chapter II). A comparison with 29 field measured gaps estimated accuracy to be over 96% in identifying the number of gaps and 74% in matching gap length along transects. It was found that gap area was either over or underestimated and that gap perimeter was largely underestimated when gap geometry of 34 lidar-derived gaps was compared to their respective ellipse approximated ones. This confirms our hypothesis that when accurate and high density of laser returns are acquired at near-nadir angles, with a good proportion of them reaching the floor should in combination with the canopy returns, will permit the precise reconstruction of gap geometry (Chapter II). Further, methods used to delineate dynamic gap events, namely random gap occurrence, gap expansion, and gap closure through lateral growth and regeneration, were developed using combinatorics of time-series of lidar-derived canopy gaps based on this technique (Chapter II). Being fully automated, this method can be applied to larger areas without much effort. Since this method had been verified in a complex mixed coniferous deciduous species canopy structure, we presume that it should be applicable in most forest ecosystems.

The investigations conducted in this research have also shown that datasets generated from different surveys should be perfectly co-registered in X, Y and Z prior to any multi-temporal lidar analysis to eliminate erroneous observations of canopy height change (Chapter II). It has also been shown that optimizing grid resolution and the choice of an interpolation algorithm are essential, both for ground and vegetation surfaces, to ensure accurate delineation of canopy gaps (Chapter II). Analysing the global (RMSE) and local (mode) of the predicted error based on cross-validation of eight interpolation techniques, and the number of spurious gaps delineated there after, (IDW with 0.25 m grid resolution) resulted in a minimal loss in accuracy for interpolating both vegetation and ground surfaces. Though similar optima were noted in previous studies on bare-earth models (Anderson et al. 2005, Smith et al. 2005, Lloyd and Atkinson 2002), optimal interpolation for vegetation surfaces has rarely been investigated.

Methods to characterize height growth response to canopy gap openings using multi-temporal lidar data

The capability for single tree identification using lidar is well established in studies conducted in various forest systems (Andersen et al. 2001, Popescu et al. 2002, Brandtberg et al. 2003). Owing to its high density and accuracy, theoretical feasibility in observing an increase in height from two perfectly co-registered datasets is also demonstrated in recent studies (Appendix-I, Yu et al. 2006). However, the ability to use multi-temporal lidar data to characterise growth response to canopy gaps, in general, and when survey specifications are dissimilar has not previously been established. The second major contribution of this project is in exploring the potential of lidar for measuring forest growth (Appendix-I), developing a robust approach in automating height increase measurement using lidar and characterising the growth responses of a tree/sapling to the opening of canopy over a short-term period of 5 years (Chapter IV). The proposed technique for identifying trees / saplings of various heights on a lidar CHM showed about a 75% match with photogrammetric locations. This greatly expands the possibility of measuring various forest biophysical parameters like biomass, net primary productivity, in finer details, thus enlarging the scope of addressing several ecological questions. In this study we demonstrated its utility in examining forest growth responses to canopy openings.

Unit free growth rates were reliably estimated using raw lidar data after eliminating possible sources of error due to minimal point density of ground returns, laser penetration and different pulse densities between years. The advantage of this method is in its measurement of spatially explicit tree tip locations and height growth over large spatial scales. This provides insights into understanding growth patterns that occur across gradients of initial tree heights in different neighbourhood contexts present in the forest matrix (Chapters IV and V).

Measurements of growth being spatially explicit, distance effects on growth can be determined by applying statistical techniques. For this purpose, we proposed a novel method of establishing the zones of influence of opening of a canopy on height growth by extending the technique of CUSUM functions (Chapter IV). CUSUM functions determine changes over time in a measurement process (Hawkins and Olwell 1998). The modified CUSUM method we proposed has a great potential in studying change in any response variable with respect to a change in the nested explanatory variable.

6.1. 2. Ecological insights

Spatio-temporal dynamics of gap formation in mixedwood boreal forests

Boreal mixedwood forests around Lake Duparquet are highly dynamic systems, where canopy disturbance plays an important role, even over a short period of time (Chapters III-V). Gaining knowledge of the dynamics and creating a huge database on gap disturbance in boreal mixedwood forests over five years through a near-complete census of canopy openings (over 5 m^2) in a 6 km^2 forested area has been one of the major contributions of this study (Chapter III). Gap disturbance in these forests is a dominant, continuous and highly dynamic process. Contrary to the assumptions of previous studies in boreal and coniferous forests that canopy gaps may not be subject to gap expansion, especially in younger stands (Bartemucci et al. 2002, Kneeshaw and Bergeron 1998, Lertzman and Krebs 1991, Runkle 1990), the results from our study show that the gap disturbance regime in the study area is characterized by both random occurrence of tree mortality as well as disturbance on the gap periphery that enlarges and coalesces existing gaps. In fact, trees bordering gaps are more vulnerable to mortality compared to trees in the interior forest as nearly 95% of the new opening is due to gap expansions. Further analysis in conifer dominated stands shows that irrespective of the level of openness in stands occurrence of random gaps is to a large extent influenced by the presence of an existing gap.

Mapping of the spatio-temporal dynamics of gap formation is important, especially in estimating gap formation rates or turnover times that are critical for developing silvicultural rotations that emulate natural disturbances. Ecologically, it also provides us with an understanding of the length of time that individuals may remain in the canopy and thus the length of time required for a change in forest composition or structure to occur. Gap formation rates, the fraction of ground area converted to new gaps annually is 0.6% resulting in an estimated turnover time of 145 years in this part of the boreal forest. Gap turnover rates estimated based on single-time analysis are probably over-estimates as there is no information on the spatial extent of new gap formation and thus turnover is calculated based on average growth rates to fill gaps (Chapter II).

Moreover, large gaps could be the result of tree falls over successive periods of time such that they may be composed of regeneration in different stages of growth whereas gaps formed by a single mortality event should have a single regeneration cohort. Distinction of old from new openings that are either gap expansions or randomly formed, and their spatial extents can help in correctly characterizing height growth patterns of regeneration (Chapter V) and in understanding why shade intolerant species can recruit in some gaps but not in others that share a similar characteristic such as gap size. Large gaps in old-growth forests are also indicators of the etiology of the disturbance and recovery (Nagel and Svoboda Accepted).

Forest response to canopy opening

Studies on canopy closure are rare and to the best of our knowledge, none exist in boreal forests. This study has demonstrated that boreal forests experience not only the negative effects of gaps through increased stress and thus mortality of edge trees (Chapter III), but also positively influence growth vertically and laterally. This growth, which varied between species groups, resulted in canopy closures by different mechanisms depending in part on gap size but not due to species group (Chapters IV andV). Gap fraction decreased over the 5 year study period, despite a new gap opening rate of 0.6%, due to a high closure rate of 1.2%. The majority of the openings that closed are filled from below with a maximum growth rate (MGTH) of 1.0 (i.e. 100% growth of its initial height) over 5 years, with a smaller (22%) but significant proportion of the closures due to lateral growth of gap edge trees (a rate of 22 cm / yr) (Chapters III andIV). Furthermore, lateral growth occurred over a gradient of gap sizes in which both hardwoods and softwoods closed gaps laterally at nearly similarly rates (Chapter III). This is an important finding as it was previously assumed that lateral in-filling occurred primarily in small gaps and was insignificant in conifer trees due to their morphology and determinate growth (e.g. Runkle and Yetter 1987).

In general, softwood saplings were found to be growing at a faster rate than hardwood saplings in gaps (Chapter III). However, the study shows that height-growth of all saplings was strongly dependent on position, type of gap event and gap size (Chapters IV andV). Hardwood saplings in gap expansions and softwoods in random new gaps grow at nearly twice the rate compared to saplings in old gaps (Chapter V). Results suggest that hardwood and conifer saplings grow at their greatest rates within a distance of 0.5 – 2 m and 1.5 - 4 m from the gap edge and in openings smaller than 800 m^2 and 250 m^2 respectively (Chapter IV).

Indeed, gaps in boreal forests not only influence the immediate vicinity of their edges, but also forest interiors (Chapter IV). In our analysis based on the CUSUM of the average maximum rate of growth per tree at increasing distance from the gap edge, we noted that canopy gaps have an influence on the height-growth of both HW and SW trees at distances up to 30 m and 20 m respectively from any gap periphery. The highest growth rates (30% increase over 5 years) occurred in trees close to the gap edge and gradually decreased to 7% at around 25 m from the gap edge. The gap effect on height growth of overstory trees in the intact forest from a naturally occurring gap edge has rarely been examined. This is an important ecological finding that will be of interest to both foresters and biologists alike. Our results thus suggest that foresters should consider silvicultural techniques that create multiple small openings in mixed coniferous deciduous boreal forests to maximise growth response of residual as well as regenerating trees.

Based on 829 trees and 166 gap saplings that were clearly discerned with geo-location of their tips on the lidar surface, the study shows that the boreal forest around Lake Duparquet is not slow growing as previously believed, as 65% of the forest is growing with an annual average rate of 8% of its initial height, while the remaining regenerating area is growing at an even faster annual rate (20% of its initial height) (Chapters III andIV). Moreover, the spatial mapping of canopy gaps over the entire 6 km^2 forest swath suggests that boreal mixedwood forests can be characterized as a gappy matrix

(Chapter III) with a maximum of 60 m (and more frequently 30 m) of forest interior from any gap edge (Chapter IV). Hence the study also suggests that height growth dynamics of boreal mixedwood forests are influenced notably by the presence and dynamics of canopy openings.

Role of canopy gaps in stand development

Fine-scale analysis of canopy openings shows that stands in different development stages (recruited after stand replacing disturbances that occurred at different times) that were also impacted by spruce budworm infestations are highly dynamic and do not consistently follow previously conceived successional patterns (Chapter II). Gap density and rates of closure did not show any relationship with stand age. Contrary to our hypothesis, though old-conifer dominated stands had high closure due to recovery from insect infestation, we also noted that they have higher rates of opening. In fact, this study also noted that the last spruce budworm outbreak that ended 16 years previously has a lasting legacy on old-conifer stands as there continues to be high mortality of conifers in these stands.

The proportion of softwood and hardwood regeneration within gaps was balanced in all stands, with the exception of the older stand where most large gaps, in contrast to our expectations, were closed by hardwoods. Overall, though there is an increase in hardwoods due to in-filling from regeneration, the forests are thus at compositional equilibrium. In our study, we noted that species replacement, especially recruitment of softwoods into the canopy, has also occurred without gap formation when understory trees emerged in the canopy as dominant trees die. This is a major ecological finding in our study that should trigger more questions into non-gap replacement of species in the canopy.

In summary, the four chapters presented in this thesis show the complexity in structure and dynamics of the gap processes in boreal forests, and techniques that can quantify and evaluate these processes at the scales at which they occur. Multi-temporal lidar was found to be an excellent tool for rapidly acquiring information on the dynamics of canopy structure in general, and canopy gaps in particular. It also expanded the possibility of combining datasets acquired by different sensors with dissimilar point density for ecological applications.

6.2. FUTURE DIRECTIONS

Future efforts should be focused on extending this research to larger spatial and temporal scales and to other forest ecosystems by improving the proposed methods, fusing alternate data sources with lidar data and gaining more thorough understanding of the mechanisms that drive the forest dynamics.

This spatially explicit fine scale and short-term study of old-growth boreal forest dynamics counters earlier assumptions that transition in boreal forests is slow, directional and influenced by the period of development since the last fire. In fact, boreal mixedwood forests around Lake Duparquet were found to be highly dynamic systems, where canopy disturbance plays an important role, even in a short period of time. These results stress the need for temporally analysing large contiguous spatial areas to alleviate uncertainty in interpreting and extrapolating dynamics from few presumably representative sites. However, we would like to extend this analysis further over a longer time-period, i.e. through intergration with the aerial photos, to minimise the bias that may have occurred in the results due to the short time-window studied. Furthermore, consideration of sub-or-micro stands in these large TSFs would probably bring out within-stand variability that may have been generalized here.

This thesis was motivated by a need to understand ecological processes occurring at scales that could be evaluated by studying the 3-D arrangement of forest canopies and the ability of lidar to accurately describe them. Lidar data are becoming less costly, and with improved technology multi-temporal lidar datasets encompassing longer time intervals will become more common. We presume that the methods developed in this thesis will help to bring new insights based on such improved datasets.

The applications of the methods developed here can also be extended to fusion datasets of lidar and optical photogrammetric data. Recent developments in photo-lidar and IKONOS-lidar fusion showed a great promise in determining accurate canopy structure. Applications of this kind of model can be useful in retrospective analysis especially since aerial photographs have been taken for 60 to 80 yrs across many areas in the boreal forest. A fusion of techniques would thus permit the long-term assessment of forest dynamics and thus the validation of theory developed from space-for-time substitution or from extrapolations from very limited sets of permanent plots.

For practical reasons and generality, the species in this study were classified into broad groups of hardwoods and softwoods. However, more detailed species data at the tree level will improve our understanding of tree to tree species-level interactions. Combination of very high resolution images like those generated at low altitude from Vexcel Ultracam with lidar data will facilitate future research in that direction. Also, in this study we did not directly validate the height growth of trees / saplings with field data. Although we assume that an independent validation of tree height is sufficient to reliably assess gap influences on height growth, growth validation will give greater confidence in the development of accurate height growth models.

Since the object-based algorithm that was tested accurately identified gaps up to 5 m^2 using medium density lidar data (3 hits / m^2), there would be merit in determining the optimal density that would be sufficient to accurately describe gaps and their dynamic characteristics and effects on forest development. The study area has a fairly flat terrain interspersed with small hills hence it would also be of value to test whether the developed algorithm is efficient in highly undulating terrain. Such an evaluation will be critical in applying the developed methods to other ecosystems. Other research has suggested that lidar has performed well in providing forest structural measurements in all types of terrain and ecosystems.

Apart from suggestions made to foresters, the results and discussion presented in this thesis may also have broader implications for a wide readership and researchers working in other special fields related to forest ecology. Forest engineers, conservation biologists and those interested in modeling of complex systems, may be interested in the results of our studies.

In conclusion, advanced tools such as lidar reveal the unrecognized or difficult to measure dynamics of boreal forests in reponse to the dynamics of canopy gaps. Due to the recentness of high-resolution of 3-D and image sensors, we are only starting to uncover such processes in boreal canopies. We hope future research will bring greater insights into these processes and thus help us to better manage our forests.

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APPENDIX I

Assessing forest gap dynamics and growth using multi-temporal laser-scanner data

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A.1. ABSTRACT

Research on lidar change detection is at its inception with a few studies to monitor coastal erosion and almost none for forest dynamics. While long-term installations and dendrochronology are cost and time intensive, this study highlights potential use of multi-temporal medium density lidar data for studying forest dynamics in a spatially explicit manner, particularly in identifying new canopy gaps and assessing height growth. It also underlines some of the challenges of co-registering multi-temporal lidar datasets, working with large differences in return densities, and developing methodological approaches to compute growth. Two laser-scanner datasets, acquired in 1998 and 2003 over a 6 km2 area of the mixed boreal forest in Quebec, Canada, were analysed. After co-registration, an automated method to accurately identify new gaps was developed which showed an overall accuracy of 96% when compared with high resolution images. Mean gap size, gap density and rate of gap openings have been in accordance with the reported statistics for the boreal forests. Forest growth was assessed by comparing various lidar statistics for hardwoods and softwoods in three height classes. The measured growth was in general consistent with expected height growth for the concerned species, however, improvements will be needed to increase the accuracy and reliability of results.

A.2. INTRODUCTION

During the last decade, it was clearly demonstrated that many forest structure attributes can be measured, or estimated with a high accuracy, using high density scanning laser altimetry data. Diverse studies have shown that height, volume, biomass, and to a lesser extent, crown diameter, stem density, or diameter at breast height estimates can be produced using lidar data (Magnussen and Boudewyn, 1998 Naesset 2002, Lim et al. 2003, Zimble 2003). Though further research efforts are still needed in this area, nonetheless the technology and methods are sufficiently matured to study the changes in forest using multi-temporal lidar datasets. Until recently, standard methods for studying fine scale forest changes were mostly based on space-for-time substitution (Kneeshaw and Bergeron 1998), which is restricted to inferring from current forest conditions, or analysing data collected at long term permanent plots which is labour, time and cost intensive. Studies documenting both spatial and temporal characteristics are rare as necessary field data is difficult to collect.

Research on lidar change detection has only begun with a few studies using topographic change mapping to monitor coastal erosion (http://www.csc.noaa.gov/crs/tcm/, last consulted on July 12th 2004). In forested environments, the high accuracy and density of lidar data would theoretically allow the detection of tree falls, and the estimation of growth. This has been demonstrated in Yu et al. (2004), which is currently the only published study on forest dynamics based on lidar data. Although the time interval between the two lidar surveys was of only two-year, this study could effectively detect harvested trees and assess growth at the individual tree level using very high density, low altitude, Toposys multitemporal lidar data (about 10 returns/m2). Excepting the short time interval, the conditions of this study were ideal as the lidar instrument used for both surveys was the same, the density was very high and homogeneous, and only one species was studied. Due to the fast technological changes, most future multi-temporal lidar datasets are likely to be generated using different sensors, hence could have different densities, especially for longer time intervals. Indeed, most of the existing lidar data that could compose future multitemporal datasets have a density that is quite lower than what is achievable with a TOPOSYS lidar flown at a low altitude. This paper aims at developing methods for the detection of new gaps resulting from tree falls, and to assess tree growth using heterogeneous, medium density (up to 3 returns/m^2) lidar data acquired over a sector of the mixedwood boreal forest. Although these new techniques could be useful for industrial forest management, our prime interest lies in the development of new knowledge on the dynamics of natural forests. This paper focuses on the development of methods for the co-registration of multi-temporal lidar datasets, manual and automated methods for detecting tree falls and estimating growth.

A.3. STUDY SITE AND DATA

A.3.1. Study site

The study site falls within the conservation zone of the *Training and Research Forest of Lake Duparquet* (TRFLD, 79 ° 22'W, 48 ° 30'N), in the Province of Quebec, Canada. The 6 km^2 sector is characterized by small hills and is essentially covered by lacustrine clay deposits (Brais and Camiré 1992) with elevations comprised between 227 m and 335 m. The mixed vegetation is composed of common boreal species, and dominated by balsam firs (*Abies balsamea L.* [*Mill.*]), paper birch (*Betula papyfifera* [Marsh.]), and trembling aspen (*Populus tremuloides* [Michx]). The age structure found at this site results from a fire driven disturbance regime (Bergeron et al. 2000), and a recent infestation of a defoliating insect (1970-1987, Morin et al. 1993) called the spruce budworm (*Choristoneura fumiferana* [Clem]). Most stands are mature or over mature and reach heights of 20-25 m. The climate is cold temperate with an average annual temperature of 0.8 C and a number of degree days of approximately

2000, while the length of the growing season is on an average 160 days (Environment. Canada 1993)

A.3.2. Lidar data

The study site was surveyed on June 28th 1998, and again, as part of a larger coverage, on August 14 to 16 2003, thus determining an interval of approximately five growing seasons. The 1998 survey was carried out using an Optech ALTM1020 flown at 700 m above ground level (AGL) operating at a pulse frequency of 4 kHz. Because this lidar could not record both first and last returns in one pass, and had low impulse frequency, two passes for each flight line were done to acquire the first returns, and one for the last returns. The overlap between adjacent swaths was minimal, resulting in some small data gaps in the first returns. The data was registered to ground profiles surveyed with a high grade GPS and tacheometer. All returns were classified as ground and non ground using the REALM software application from Optech Inc. Only the ground-classified last returns were used to generate a bare earth digital terrain model (DTM). In 1998, the provider had also classified the first and last returns into ground and non-ground categories, but had delivered only the non-ground (vegetation) first returns and the ground classified last returns. The latter ones were used to generate a digital surface model (DSM). Note that a true lidar DSM should be created using all first returns. At the time of writing this paper, the full set of first returns was being recovered from the original raw data, but remained unavailable for this study.

The 2003 survey was done with Optech's ALTM2050 lidar flown at 1,000 m AGL, and recorded the first and last returns for each pulse, with a 50% overlap between adjacent swaths. The data was registered to new ground profiles. The inter-swath geometrical fit was improved using the TerraMatch algorithm by Terrasolid Ltd. (Helsinki). The last returns were classified as ground and non-ground using

Terrasolid's Terrascan. The ground-classified last returns were used to build the DTM, while the DSM was created using all first returns. Table A.1 presents the key survey and lidar instrument parameters. It shows that the surveys differed in many aspects, but most importantly in terms of density.

Table A.1.
Specification of the lidar data acquisition

	1998	*2003*
Lidar	ALTM1020	ALTM2050
Power	140uJ	200uJ
Flight altitude (m AGL)	700	1,000
Divergence (mrad)	0.3	0.2
Footprint size at nadir (cm)	21	20
Pulse frequency (Hz)	4,000	50,000
Max. scan angle (degrees)	10	15
First return density (hits/m^2)	0.3	3
Ground return density (hits/m^2)	0.03	0.19

A.3.3. Image data

High resolutions images were used to visualise the forest canopy structure, identify tree species, and verify the appearance of new gaps. An aerial videography survey was carried out on September 27th 1997 using a video camera equipped with a zoom lens connected to a Super VHS video recorder. The plane was flown at 1890 m AGL and acquired image data in the green (520-600 nm), red (630-690 nm), and near infrared (760-900 nm) bands. Frame grabs from the video playback yielded digital 50 cm resolution images covering the 1998 lidar area. A field survey done in 1998 allowed building an interpretation key of tree species. Theoretically, only minimal changes occurred between the acquisition of the September 1997 videographies and the June 1998 lidar data. A panchromatic IKONOS image of 1 m resolution (0.45-0.9μm), acquired on September 5th 2003, and a QuickBird image, in panchromatic

(0.61 cm. resolution, 450-900 nm) and a multispectral modes (2.44 m resolution), acquired on June 13th 2004, were also used to give image context to the 2003 lidar dataset. The spectral bands of the QuickBird image used in this study are the same as those of the videographies. The multispectral QuickBird image was pan-sharpened with the panchromatic image by running an arithmetic combination technique in Geomatica v. 9.01 (PCI Geomatics) for better visualization.

A.3.4. Age-height tables

Due to the unavailability of growth measurements for precisely geopositioned trees in the studied sector, age-height tables, developed by Pothier and Savard (1998) for the most common tree species found in Quebec, were consulted to derive the expected specific height growth values. These tables were developed from field measurements performed in several thousands permanent and temporary 400 m2 plots by the Forest Inventory Service of the Province of Quebec. For each species, average dominant height at a given age is given, from age 20, with a step of 5 years for four site index and three density classes.

A.4. METHODS

A.4.1. Co-registration

Standardization of the heights is obligatory for comparison of the height of the forest canopy at different dates. The first level of standardization consisted of using the same DTM for both years in order to avoid DTM differences causing false canopy height changes. This approach was also used by Yu et al. (2004). To allow the use of the same DTM, the lidar data generated in two different surveys must be perfectly co-registered. Shifts in the X, Y, or Z axes would result in erroneous canopy height change observations. The accuracy of lidar data is known to be very high. Recent studies reported elevation errors below 30 cm (Hodgson et al. 2003) for ground hits. However, a number of factors may affect the positional accuracy of lidar returns, like the quality of the GPS configuration at the time of the survey, mounting errors, INS errors, fluctuation of the scanning mirror speed, reference to ground calibration measurements, etc. Note that, unlike the 2003 dataset, no inter-swath fitting was performed on the 1998 data. We hypothesized that the error level and bias may be different for the two lidar surveys, and hence checked the XYZ fit between the two datasets. First returns and ground-classified returns were interpolated using a TIN algorithm to produce respectively a DSM and a DTM in grid format for both years. Planimetric shifts were analysed by visualizing the DTMs and DSMs. The arithmetic difference between DTMs was computed and the resulting image was analysed for trends on sloping terrain. No apparent shift was evidenced in all the analyses, and if one existed it was too negligible to be detected. Therefore, no further numerical analysis for planimetric shift was performed. The DTM difference image had however indicated a possible shift in Z. To assess this shift, all the corresponding ground returns of 2003 falling in a 10 cm radius of the 1998 ground returns were compared. The elevation of the 1998 ground returns was on average 22 cm higher than the corresponding 2003 returns. This may be due to errors in the GPS data, or in referencing the lidar data to ground profiles. The discrepancy could also be caused by differences in the ground classification. Comparisons on spots of stable bare ground (rock outcrops) were not conclusive to that regard. The 2003 data was chosen as the reference, and the elevation of all the 1998 returns (first and last) was accordingly adjusted.

A.4.2 Ground elevation and canopy height models

The density of the ground hits in 2003 was significantly higher than that of the 1998 data. However, there were some small gaps in the 2003 DTM point coverage for which 1998 points existed. We thus merged the 2003 and 1998 ground returns to maximize the overall return density of the DTM. After adjusting the 1998 last returns, preliminary grids of DTMs were created using TIN interpolation of the ground classified returns independently for both years. Wherever the difference in the interpolated grids was higher than 1m, the higher values were replaced with the lower ones under the assumption that the higher ones were caused by reflection of the lidar pulses on low vegetation that were not removed by the ground classification algorithm. The DTM was regenerated using tthe merged last return dataset and converted to a 50 cm grid. DSM grids of 50 cm pixel were generated by taking the highest point within each pixel and supplementing the missing values (pixels with no returns) with interpolated heights obtained using the inverse distance weighted algorithm. This eliminated a large number of points that penetrated through the crown while otherwise preserving the original value of the DSMs. All interpolations were carried out using ArcGIS v. 8.3 routines. Both the 1998 and 2003 DSMs were transformed into canopy height models (CHMs) by subtracting the corresponding elevations of the merged DTM. Point CHMs (XYH, where H is canopy height) were created by subtracting the underlying DTM elevation from the Z value of individual XYZ returns.

A.4.3 Detecting new gaps

In the study area, it was noted that tree fall may result largely from strong winds during violent thunderstorms, snapping under the weight of snow, and beaver activity (Daniel Kneeshaw, personal communication). Thus, new gaps resulting from tree fall should indicate large elevation differences between the CHMs of 1998 and 2003. We define a new gap as an opening in the canopy caused by the fall of a single or of a small group of trees of a certain height during the study period. To automatically identify the new gaps in a grid environment, a new gap indicator function G(x,y) is defined as:

$$G(x,y)=\begin{Bmatrix}1 & \textit{if } CHM98(x,y)\geq 10\,\mathrm{m}\ \mathrm{AND}\ CHM03(x,y)<10\,\mathrm{m}\\ 0 & \textit{otherwise}\end{Bmatrix}$$

where CHM98(x,y) and CHM03(x,y) are respectively the lidar height of the forest cover in 1998 and 2003. A region growing algorithm was then applied to the resulting binary grid to identify individual patches of non null G(x,y) adjacent pixels. Patches having an area less than 5 m2 were eliminated under the hypothesis that they were due to chance occurrence of spurious low returns. Finally, only patches having a minimum of 3 hits in 1998 were considered for a reasonable representation and meaningful comparison with high density data of 2003. A window of 250m X 290m, were significant changes were appeared was tested for delineating the new gaps. All the accepted non null G(x,y) patches identified in this window were further verified for tree falls by visually comparing the high resolution images of 1997 and 2003-04. To quantify the accuracy of gap identification, a systematic grid of 94 sampling points was overlaid onto the test window and each point was visually inspected on the registered high resolution images for probable gap occurrence. Commission and omission errors are reported in a confusion matrix.

A.4.4 Assessing growth

The height growth of trees corresponds to the vertical elongation of crown tips over time. Repeated measurements of individual tree height are traditionally used to measure tree growth. In Yu et al., 2004, a method for measuring this elongation was applied which can only be employed if the probability of lidar pulses hitting at or near the tip of any tree is high, i.e. if the return density is very high. Such lidar coverages are however rare, and the cost to cover large forested areas on a regular basis at such a density are presently prohibitive. As the lidar coverages considered in this study are of a lesser density, it was necessary to use all the returns falling on crowns to assess height growth, as many tree tips may be missed. This, however, brings the problem of translating canopy height increase into average tree height increase. Conifer trees grow by elongating their tips vertically, and by elongating existing branches horizontally, while the crowns of the most common hardwood species found in the study area grow like expanding ellipsoids or semi-ellipsoids. In the hardwood and softwood cases, points falling on the crown in 1998 will be slightly higher in 2003 if significant growth occurred, while points that have hit on low surfaces near the crown periphery in 1998 will be much higher as the result of hitting on the crown in 2003 due to lateral growth. Based on age-height tables (Pothier and Savard 1998), it is expected that smaller, and presumably younger, trees grow faster than higher, older ones. The following three experiments were carried out to assess the feasibility and better define the problem of measuring small amount of growth using multitemporal lidar data characterized by different densities.

Manually delineated crowns

Eighteen individual crowns of hardwood trees (trembling aspen) were delineated manually using the CHM grid of 2003. These were discriminated from other species based on the hue of the QuickBird pan-sharpened multispectral image. Manual delineation insured that lidar returns from single crowns could be isolated with certainty. An inner buffer of 0.5m was automatically created from the delineated outline to discard lidar hits falling on the irregular periphery of the crown and to isolate vertical growth. The difference in the maximum and mean heights between the 1998 and 2003 XYH points falling within the inner crown (inside of the buffer) were compared to the expected height growth of trembling aspen for the prevailing site index and density found in the study sector using the age-height tables (Pothier and Savard, 1998). The maximum height of the 2003 lidar XYH point cloud within each inner crown was used as a proxy for tree height in 2003. The height closest to this one in the age-height table was identified, and the height increase in the last five years was read from the table. The correlation between the observed and expected height increases, as well as between the logarithm of the maximum lidar height and growth, were calculated. The logarithm of tree height was used to linearize the relationships with growth.

Object-oriented crown delineation

As a first attempt to automate the abovementioned procedure, we used image segmentation methods in eCognition v3.0 to extract individual tree crowns on the 2003 grid CHM. Segmentation was done with height as the "theme" using the following parameters: scale=5, homogeneity criterion=0.7, shape=0.3, smoothness=0.5 and compactness=0.5. Subsequently, these segments were classified within eCognition based on the "mean" object feature in height classes 5-10 m (low), 10-15 m (medium), and >15 m (high), and two broad species classes: hardwood and conifers. This delineation was performed twice: once for a hardwood stand, and once for a softwood stand. The vector segments were later buffered inside by 0.5 m and the lidar XYH points of both years falling within the inside buffer were analysed as in 3.4.1. Only the polygons which had at least two lidar points were considered for analysis. For each height-species class, the average height changes were calculated for the maxima and mean lidar heights between 1998 and 2003. Again, the results were compared to expected growth values.

Window based

Overall height increases, i.e. those resulting from vertical and lateral growth, were also studied. The maximum, mean, 90th and 95th percentile lidar height differences of all lidar points (Z) falling within 20 x 20 m plots were compared between 1998 and 2003. The use of percentiles is justified by their effectiveness in predicting the height of stands or plots (Magnussen and Boudewyn, 1998, Naesset 2002). Five plots each corresponding to the low, medium, and high classes of hardwoods, and low and medium height classes of conifers were compared to expected values.

A.5. RESULTS AND DISCUSSION

A.5.1 Detecting new gaps

Examples of the appearance of new single- and multi-tree gaps is illustrated in figure 1. Inside the 6.8 ha study site, 88 new gaps with a minimum size of 0.5 m2 were identified. The largest gap covered 0.17 ha and the mean gap size was of 79.4 m2.

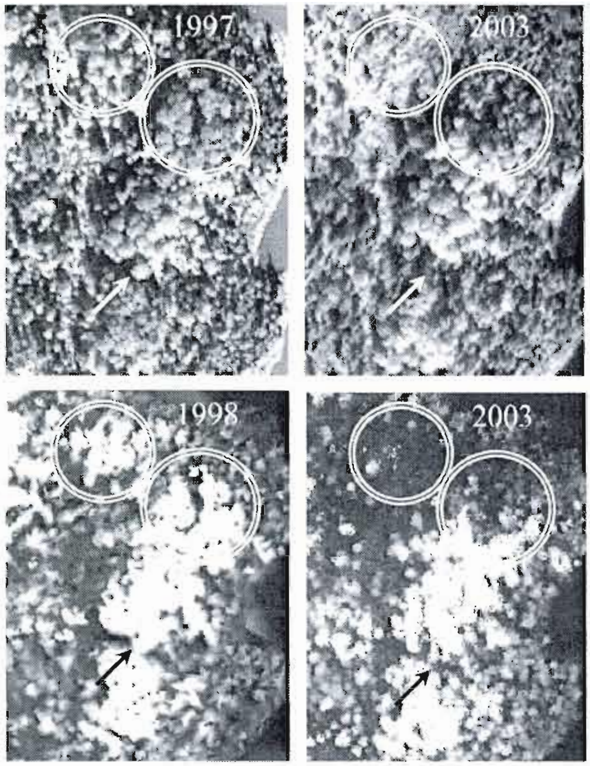

Figure A.1. New single-tree (arrow) and multi-tree (circle) gaps between 1998 and 2003 identified on the high resolutio Figure 2.A.

Gap size distribution is negative exponential with nearly 62% of the gaps being single-tree falls. The total new gap area is 0.71ha, which is about 10.4% of the highly disturbed study site with 2.08% annual rate of new gap opening. Large gaps of size 1,721 m2, 1,743 m2 and 798 m2 were seen within 20-30m of the lake shore in the northern part of the site, perhaps a result of severe wind storms. A large number of gaps were also seen in the neighbourhood of the existing large openings, verifying that new gaps are more likely to occur adjacent to pre-existing gaps. The accuracy of the identification of new gaps was high at 96% when compared visually with the registered images of Ikonos/Quickbird and Videography (Table A.2). User's and producer's accuracies were very similar, and omission and commission errors of gaps were 2% and 8% respectively.

A.5.2 Growth assessment

Manually delineated crowns

The statistics relative to the 18 manually delineated crowns of various heights are presented in Table A.3. Lidar estimated height growth is rather variable between trees, but the general trend indicates that presumably younger trees have a faster growth rate than older ones, as is expected. The mean difference, and mean absolute difference (deviation), between the maximum lidar height increase and the

Table A.2.
New gap error matrix

		High resolution images (reference)			
		NO-GAP	GAP	TOTAL	USER'S ACC.
LIDAR	NO-GAP	56	1	57	98%
	GAP	3	34	37	92%
	TOTAL	59	35	94	
	PROD.'S ACC.	95%	97%		OVERALL 96%

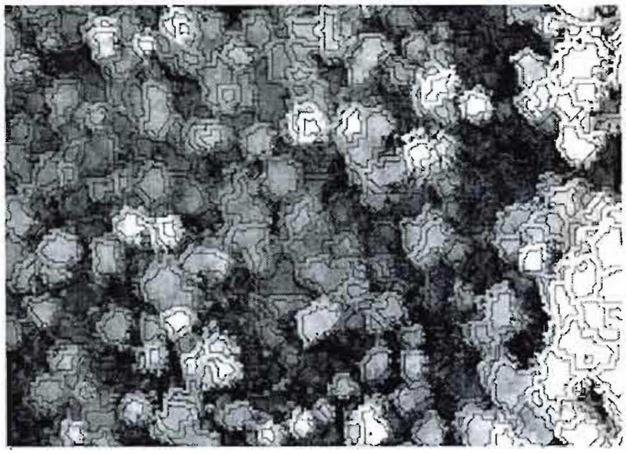

Figure A.2. Sub-image of the 2003 lidar grid CHM with overlaid eCognition segments.n images and lidar CHMs.

corresponding age-height table value are respectively 0.42 m, and 1.09 m. These values decrease to –0.08 m and 0.67 m when the two first cases are removed. These two undoubtedly erroneous height growth values (5.42 and 7.42 m) probably result from a poor evaluation of height in 1998 due to the low density of returns. The correlation between the maximum, and mean height of tree crowns in 1998 and 2003, on the one hand, and, on the other hand, the lidar maximum, lidar mean, and expected growth is given in Table A.4. The highest correlations are seen between logHmax98, logHmax98, dHmax, and dHmean. All correlations are highly significant. Correlations are notably lower for the 2003 height values. The relationship between dHmax and dHtable is significant at □ = 0.1 while the one between dHmax and dHtable is not. A two-sided test revealed that the two correlations are not statistically different. The fact that expected values come from a table in which heights are given for 5 year increments reduces the variance of dHtable and may cause the correlation to be lower than if actual field growth measurements had been used. All these results suggest that growth over five years could be measured with lidar. The accuracy however still needs to be assessed thoroughly.

Object-oriented crown delineation

Figure A.2. shows an example of the eCognition individual crown segments automatically extracted from the 2003 lidar grid CHM. The resulting objects represented individual crowns in the majority of cases. Conifers corresponding to only the low and medium height classes could be found. In the case of the hardwoods, the expected growth trend is reversed: higher trees appear to grow faster than larger trees (Table A.5). Both the maximum and mean height differences have the same behaviour. In the case of the softwoods, the expected trend is observed, and the growth values obtained from lidar are close to those given in the age-height tables. It should be noted that these results were pooled per height class, and not by individual segments

Window based

The differences in maximum, mean, 90th and 95th between 1998 and 2003 inside 400 m2 windows are shown in Table A.6. For hardwoods, both dHmax and dH95 behave as expected. Variation in the other difference statistics is rather erratic. Height increases are close to the age-height table values (average deviation of 0.42 m). Trends in the hardwoods are contrary to expectations for difference statistics. Observed growth values are however still close to the expected ones.

A.6. CONCLUSION

Automated delineation of the new individual gaps has been straightforward, as expected. The detection accuracy has been very high as the changes in the study sector have generated height differences larger than the possible lidar elevation errors. The results are similar and comparable to those reported in Yu et al. (2004) for the harvested trees. Mean gap size, gap density and rate of gap openings have been in accordance with the reported statistics for the boreal forests (Pham et al., 2004). The study suggests that lidar is an excellent tool to map gaps and estimate gap characteristics.

Growth was evaluated on manually delineated individual crowns, on automatically delineated crowns, and for all the returns inside 400 m2 windows. Results in the case of the manually delineated crowns show that multi-temporal lidar offers a high potential for estimating growth on an individual tree basis as observed values were in general close to the expected ones, even if the density was rather low in 1998. The automated delineation of crowns on the 2003 lidar CHM were highly satisfactory, however, the trend in average growth by broad height class (low, medium, high trees) were not conclusive. Nonetheless, the general growth rate corresponded well to what is expected within five growing seasons. Finally, average growth computed for 400m2 plots behaved as expected for hardwoods, but not for softwoods. All statistics, i.e. mean, maximum, height at the 90th and 95th percentile showed the same trend. In general, results show that multitemporal medium density lidar enables the detection of new gaps with a very high accuracy, and can potentially be used to measure growth on an individual crown, or window basis. A number of issues however need to resolved to improve estimation of growth: a more robust estimation of tree height based on lower density data, unmixing the effects of vertical and lateral growth, and automation of measurements. Future work building on this initial study will compare field measurement of growth to observed lidar values, and will recourse to geometrical tree models to better predict individual heights.

Table A.3.
Height changes of individual crowns between 1998 and 2003.

H_{max03}	dH_{max}	dH_{mean}	dH_{table}
11.89	5.42	4.54	2
14.11	7.49	3.77	2
10.63	1.58	0.73	2
12.23	2.72	0.97	2
12.75	2.9	1.9	2
14.74	2	1.35	2
15.24	0.88	0.94	2
15.79	1.38	1.75	1.7
16.23	1.78	1.13	1.7
14.4	0.37	-0.21	2
15.86	1.11	1.54	1.7
18.99	1.89	2.86	1.3
16.54	0.05	0.06	1.7
24.17	1.6	1.75	0.5
23.62	0.63	0.87	0.6
25.1	1	0.54	0.4
24.88	1	1.1	0.4
25.15	0.09	-2.44	0.4

H_{max03}: maximum lidar height in 2003, dH_{max}: difference in the maximum lidar heights, dH_{mean}: difference in the mean lidar heights, and dH_{table}: expected difference from the age-height tables.

Table A.4

Correlation coefficient (and p values) for the logarithm of maximum and mean height in 1998 and 2003 $\log H_{max03}$, $\log H_{mean03}$, $\log H_{max98}$, $\log H_{mean98}$), maximum and mean height differences, and expected height increase (dH_{table}).

	dH_{max}	dH_{mean}
$\log H_{max03}$	-0.46 (p=0.053)	-0.39 (p=0.113)
$\log H_{mean03}$	-0.59 (p=0.010)	-0.43 (p=0.074)
$\log H_{max98}$	-0.78 (p=0.000)	-0.62 (p=0.006)
$\log H_{mean98}$	-0.79 (p=0.000)	-0.66 (p=0.003)
dH_{table}	0.41 (p=0.088)	0.37 (p=0.127)

Table A.5.

Summary of the object-oriented crowns for low, medium and high trees (see table 3 for symbols).

	Hardwoods			*Softwoods*	
	Low	Med	High	Low	Med
H_{max03}	10	15.6	21.3	13	14.5
dH_{max}	0.08	0.38	1.39	1.64	0.78
dH_{mean}	0.3	0.68	1.44	1.09	0.62
dH_{table}	2	1.7	1	1.6	1.4

Table A.6.

Summary of the window based growth analysis statistics, including difference between the heights at the 90th and 95th percentiles, respectively dH_{90} and dH_{95} (see table 3 and 5 for other symbols).

	Hardwoods			*Softwoods*	
	Low	Med	High	Low	Med
H_{max03}	16.1	17.2	30.2	11	16.2
dH_{max}	3.36	1.31	0.47	0.13	0.82
dH_{mean}	0.74	0.2	0.69	0.04	0.57
dH_{90}	0.21	0.42	0.35	0.03	0.87
dH_{95}	1.55	0.7	0.41	0.02	0.95
	1.7	1.5	0.1	1.4	1.1