UNIVERSITÉ DU QUÉBEC À RIMOUSKI

MODÉLISATION DE LA STRUCTURE DES ARBRES POUR EXPLIQUER LA QUALITÉ DU BOIS D'ÉRABLE À SUCRE (*ACER SACCHARUM* MARSH.)

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TREE STRUCTURE MODELING TO EXPLAIN WOOD QUALITY OF SUGAR MAPLE (*ACER SACCHARUM* MARSH.)

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PREFACE

This study was conducted under the direction of Dr. Robert Schneider; co-chair of the Chaire de recherche sur la forêt habitée at the Département de biologie, chimie et géographie, Université du Québec à Rimouski, Rimouski, Québec and under the co-direction of Dr. David Pothier, Département des sciences du bois et de la forêt, l'Université Laval, Québec and Dr. Frank Berninger, University of Helsinki, Helsinki, Finland. This study was financially supported by FQRNT (Fonds de recherche du Québec - Nature et technologies), NSERC (Natural Sciences and Engineering Research Council of Canada), and the Quebec Ministère des Forêts, de la Faune et des Parcs.

Including the general introduction and conclusion, this dissertation consists of five chapters. Among them, chapter II was published in a peer-reviewed journal, and chapter III and IV are ready for submission. All chapters are original contributions. This dissertation being presented as a collection of articles, some repetition between chapters is inevitable. Each chapter is independent and does not require reading the other chapters for understanding.

CHAPTER II - S.K. Baral; R. Schneider; D. Pothier; and F. Berninger (2013). Predicting sugar maple (Acer saccharum Marshall) discoloured wood characteristics. Canadian Journal of Forest Research, 43 (7): 649-657.

CHAPTER III - S.K. Baral; R. Schneider; F. Berninger; and D. Pothier *(In preparation).* Heartwood formation in sugar maple (*Acer saccharum* Marshall). Manuscript.

CHAPTER IV - S.K. Baral; R. Schneider; F. Berninger; and D. Pothier *(In preparation).* Effects of competition on clear wood production in sugar maple (*Acer saccharum* Marshall). Manuscript.

I am the first author of all chapters, as I realized each part of the dissertation from project development, through field work and data analysis, to writing. My supervisors, Robert Schneider, David Pothier and Frank Berninger, are second, third and fourth authors, depending on their contribution to the development of the project and the preparation of the manuscripts.

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RÉSUMÉ

L'érable à sucre (*Acer saccharum* Marshall), est une composante importante des forêts feuillues du nord-est de l'Amérique du Nord. La qualité de l'érable à sucre s'est détériorée à la suite de nombreuses coupes à diamètre limite et d'écrémage. Il est généralement admis que les arbres peu vigoureux ont une faible croissance ainsi qu'une proportion de carie et de coloration plus importante. Cette augmentation de la proportion de coloration chez l'érable à sucre induit une baisse de sa valeur marchande, étant donné qu'il est souvent employé comme bois d'apparence où le bois de couleur blanche est recherché. L'approche sylvicole préconisée pour aménager les érablières est composée d'un système de coupes partielles, où les arbres de qualité inférieure sont récoltés, afin d'améliorer la croissance et la valeur du peuplement résiduel. Toutefois, la relation structurelle-fonctionnelle entre les différentes composantes du bois, et leur évolution a la suite de traitements sylvicoles ne sont pas encore bien comprises.

Le xylème de l'érable à sucre peut être divisé en trois catégories, selon sa couleur et sa fonction : (1) l'aubier (zone de couleur blanche qui réagit au contact d'une solution d'iodure de potassium et d'iode- Iodine), (2) le duramen (zone de couleur blanche ou coloré qui ne réagit pas au contact d'une solution d'iodure de potassium et d'iode, ni colorée), et (3) le bois coloré (zone de couleur foncée causée par une blessure). Le principal objectif de cette étude était de comprendre, grâce à une approche par modélisation empirique, comment les proportions de ces différentes composantes varient d'une tige à l'autre. Le but de la modélisation était de (1) prédire la forme et la taille des colonnes de coloration de même que le volume de bois clair (blanc) dans un arbre en employant des renseignements sur l'arbre, le peuplement et le site; et de (2) recommander une technique sylvicole appropriée visant à minimiser la coloration.

Des échantillons destructifs prélevés sur 109 arbres provenant de 3 sites du sud-est du Québec ont été analysés. Chacun des arbres a été classé selon la classification MSCR (vigueur) et la classification ABCD (qualité du tronc). Les caractéristiques des arbres sur pied et du peuplement ont été déterminées avant l'abattage des arbres-échantillons. Une fois la coupe réalisée, la taille et l'emplacement des principales branches ont été mesurés. Le point d'union entre le tronc et la plus grosse branche était considéré comme une fourche, et la hauteur mesurée du sol à la fourche était définie comme la hauteur de la fourche. Des échantillons de feuillage ont été prélevés sur chaque arbre-échantillonné en utilisant une technique d'échantillonnage aléatoire. Ces échantillons ont par la suite été transportés dans un laboratoire afin d'en déterminer la surface foliaire individuelle précise afin d'estimer la surface foliaire de l'arbre. Des rondelles ont été prélevées à la hauteur de la souche (0,30 m), à la hauteur de la poitrine (1,3 m) et à chaque 2 mètres d'intervalle le long du fût principal jusqu'à la base de la couronne. Par la suite, l'aubier a été délimité en appliquant une solution d'iodure de potassium et d'iode à 2,5 % sur la rondelle fraîchement coupée. Les rondelles ont été transportées au laboratoire, où les composantes claires et colorées de l'aubier ont été mesurées dans huit directions radiales.

Le volume de chaque compartiment (coloré et clair) a ensuite été calculé en utilisant la formule de Smalian. De plus, après avoir poncé les rondelles prélevées à 1.3 m avec du papier abrasif (grains de 80 et 120), le nombre et la largeur de chaque cerne annuel ont été comptés et mesurés dans deux directions radiales perpendiculaires en utilisant le logiciel OSM 3.65b (SCIEM). Les mesures recueillies ont permis de déterminer l'âge et de calculer la croissance radiale et basale annuelle moyenne à hauteur de la poitrine.

Trois caractéristiques associées à la taille et à l'étendue de la coloration ont été analysées afin de comprendre la variation de la proportion de bois coloré (chapitre II). Il a été démontré que la proportion de bois coloré augmente lorsque le volume d'aubier diminue et que l'âge de l'arbre augmente. Les arbres plus jeunes ont une proportion beaucoup moins grande de bois coloré. Le volume de bois coloré augmente rapidement avec le diamètre de l'arbre et variait entre les sites. Le troisième facteur important affectant le niveau de coloration du bois était la vigueur de l'arbre, obtenu avec les caractéristiques de la couronne et le taux de croissance. Ensuite, la coloration a été liée à la formation du duramen (chapitre III). Cette dernière augmente avec la hauteur, l'âge, et la taille de la couronne de l'arbre, mais diminue lorsque le rapport de la surface foliaire sur la surface terrière augmente. De manière générale, la proportion de duramen coloré augmente avec le taux de formation du duramen. Toutefois, pour les arbres classés visuellement comme étant vigoureux, la proportion de duramen coloré semble diminuer lorsque le taux de formation de duramen augmente. Ceci démontre qu'une augmentation de la proportion du bois coloré est associée à la taille et à l'âge de l'arbre, et peut être due à une plus grande probabilité d'être affecté par des maladies et/ou être blessé chez les arbres plus vieux ou plus gros, et par conséquent à un déclin de la vigueur de l'arbre.

Finalement, les effets de la compétition inter-arbre sur la qualité du bois de l'érable à sucre ont été évalués (chapitre IV). La compétition influence la taille de la couronne et ainsi, les propriétés du tronc. Les arbres sous une faible compétition présentent de plus grosses couronnes, ce qui réduit la hauteur de la fourche et le coefficient de forme du tronc. La proportion de bois clair augmente toutefois dans les arbres ayant une couronne plus grande. Ces résultats démontrent la possibilité d'améliorer la qualité du bois en apportant de légères modifications aux traitements sylvicoles employés dans l'aménagement des érablières à sucre. Les résultats de notre étude indiquent que les pratiques sylvicoles actuelles au Québec consistant en un système coupe de jardinage par pied d'arbre permettent de minimiser la proportion de bois coloré dans les tiges résiduelles. Dans ce système, les arbres de catégorie M et S du système de classification MSCR sont récoltés et les arbres vigoureux et en santé (catégorie R) sont conservés. Il faut toutefois aussi considérer la qualité du bois lors de l'établissement des prescriptions sylvicoles. La taille de la couronne et une hauteur de fourche faible, qui représentent les caractéristiques principales des arbres croissant dans de faibles niveaux de compétition, sont positivement corrélées à la proportion de bois clair et négativement corrélées à la longueur de fût de l'arbre et au coefficient de forme. Dans les trouées causées par la coupe de jardinage par pied d'arbre, il est suggéré de conserver une densité de régénération forte jusqu'à ce que la longueur de fût désirée soit atteinte. Par la suite, les tiges vigoureuses de bonne qualité doivent être sélectionnées et dégagées dans le but de faciliter la croissance en diamètre. La croissance rapide qui se produit après le dégagement accélère l'occlusion des branches mortes. Les futures tiges récoltées devraient ainsi avoir des fûts plus longs et exempts de branches, et auront une proportion moins élevée de coloration, ce qui augmentera leur valeur marchande.

Executive summary

Sugar maple, *Acer saccharum* Marshall, is an important tree species of the northern tolerant hardwood forests in North America. Stem quality of these tolerant hardwood forests was reduced due to past high grading and diameter limit cutting. Poor grade trees of low vigour with several injuries do not only have lower growth but also contain larger proportion of decay and discolouration. For sugar maple, the increase in the proportion of discoloured wood reduces timber value as the pale white coloured wood is sought for highly valuable appearance products. Although partial harvesting system in which lower quality trees are removed is found to increase growth and value of the residual trees, residual tree structure development after partial cut and its functional-structural relationship to sapwood, physiological heartwood and discoloured wood components are not yet well understood.

Wood xylem in a sugar maple tree can be categorised as three different components of wood viz. (1) sapwood (white coloured wood zone stained with 2.5% potassium iodide iodine (IKI) solution), (2) physiological heartwood (wood zone that is not stained with IKI solution) and (3) discoloured wood (dark coloured wood zone formed due to physio-chemical response to injury) according to their colour and function. The main objective of this study was to understand how proportions of these three wood components vary within and among trees growing at different sites through an empirical modeling approach. The aim of the modeling was to (1) predict shape and size of discoloured wood column as well as predict amount of clear wood volume (white coloured wood) in a given size tree using tree, stand and site level information; and (2) recommend appropriate silvicultural technique to minimize discolouration in sugar maple trees.

A destructive sample of 109 trees composed of a combination of tree vigour class (MSCR) and stem quality class (ABCD) from three sites of south eastern Quebec was used for analysis. Tree and stand characteristics were determined before felling the trees. Once the trees were felled, size and location of all primary branches were also measured. Foliage samples were collected applying a randomized branch sampling design and transported to the laboratory for determination of leaf area per unit leaf mass. The branch union point between the main stem and the largest branch was considered as a fork, and height from ground to the fork was defined as fork height. Disks were collected at stump height (0.30 m), at breast height (1.3 m), and then at each 2-m interval below the crown base. The sapwood was delineated applying a 2.5% IKI solution on the fresh disk. The stem disks were transported to the laboratory, where sapwood, heartwood and discoloured wood components were measured in eight radial directions. The volume of each compartment (e.g. coloured and discoloured) was then calculated using Smalian's formula (Loetsch et al. 1973). In addition, after the disks were sanded with 80 and 120 grit sanding paper, the number and width of each annual growth ring were counted and measured in two radial perpendicular directions using the OSM 3.65b Software (SCIEM).

This information was then used to determine the age and calculate the mean annual radial and basal area growth at breast height.

At first, tree characteristics that are associated to size and extent of the discoloured wood column was analyzed to understand how discoloured wood proportion varies among different sized trees of a given site (chapter II). It was found that the proportion of discoloured wood increased with decreasing sapwood volume and increasing tree age. Younger trees showed a significantly lower proportion of discoloured wood volume. Discoloured wood volume increased disproportionately with tree diameter, while varying among sites. The third important factor affecting the amount of discolored wood was tree vigour as measured by crown characteristics and growth rate. Then, whether heartwood formation enhances discoloured wood proportion was assessed (chapter III). Heartwood formation increased with tree height, age, crown size but decreased with increasing leaf area to stem basal area ratio. Generally, the proportion of discoloured heartwood increased with increasing rate of heartwood formation. However, for trees visually classed as vigorous, the proportion of discoloured heartwood tended to decline with increasing rate of heartwood formation. This indicates that size/age related increase in discoloured wood proportion in sugar maple is possibly due to increasing likelihood of disease and injuries with increasing tree age or size and subsequent tree vigour decline.

Finally, effects of inter-tree competition on sugar maple wood quality attributes were assessed (chapter IV). Competition influenced crown size and thereby stems properties. Trees with low competition were found to have larger crowns that reduced log length and stem form factor. However, clear wood proportion was found to increase with increasing crown size. These results demonstrate how silviculture can influence wood quality. To minimize discoloured wood proportion in residual trees, the findings of this study support the current Quebec practice of implementing single tree selection system. This consists in harvesting M and S grade trees of MSCR classification system, and healthy and vigorous trees (R class of MSCR) are retained. However, it is important to apply silvicultural prescriptions cautiously while tending tolerant hardwood stands for high quality woods. Crown size and low fork height, the general characteristics of trees growing in lower levels of competition, are positively correlated to clear wood proportion and negatively correlated to bole length and stem form factor. Therefore, in gaps of single tree selection cut, it is suggested to maintain a dense cohort of regeneration until desired clear-bole length is achieved. Then vigorously growing good quality stems must be selected as crop trees and released to promote diameter growth. The vigorous growth after release helps occlusion of dead branch stubs faster (Dănescu et al. 2015). Future crop will thus have longer branch-free bole that contains less proportion of discolouration, which is highly desired for veneer and sawlog quality wood.

CHAPTER I

GENERAL INTRODUCTION

1.1 Introduction

In North America, maple trees are ecologically, economically and socially important (Betts 1959). Ten out of the thirteen maple species (Genus *Acer*) that are native to North America are found in Canada (Canadian Heritage, 2013). Among them, sugar maple (*Acer saccharum* Marsh.) is one of the major components of the northern hardwood forests found in south-eastern Canada (Natural Resources Canada, 2014). Sugar maple trees are economically important for producing maple syrup and high value timber. Sugar maple wood is highly valued for its pale coloured sapwood for appearance products such as veneer, flooring and furniture (Wiedenbeck et al. 2004).

1.1.1 Ecology of sugar maple

Sugar maple is dominant in many northern hardwood and mixed mesophytic forest stands (Burns and Honkala 1990). It is distributed from Nova Scotia and New Brunswick westward to Ontario and Manitoba, southward through Minnesota, and eastern Kansas into north-eastern Texas (Figure 1-1) (Little Elbert 1979; Godman et al. 1990). It is generally found in cool and moist climatic areas, where the temperatures range from -18 ˚C in winter at its northern limit and 35˚C in summer at its southern limit. Average annual rainfall varies from 500 to 1250 mm in its native range (Godman et al. 1990). Although sugar maple is found on a wide variety of soil types, it grows best on deep, moist and well drained soils with medium to fine textures (Luzadis and Gossett 1996). Beech (*Fagus grandijolia* Ehrh.), yellow birch (*Betula alleghaniensis* Britt.), american basswood (*Tilia americana* L.) and red maple (*Acer rubrum* L.) are commonly found with sugar maple (Jarvis 1956).

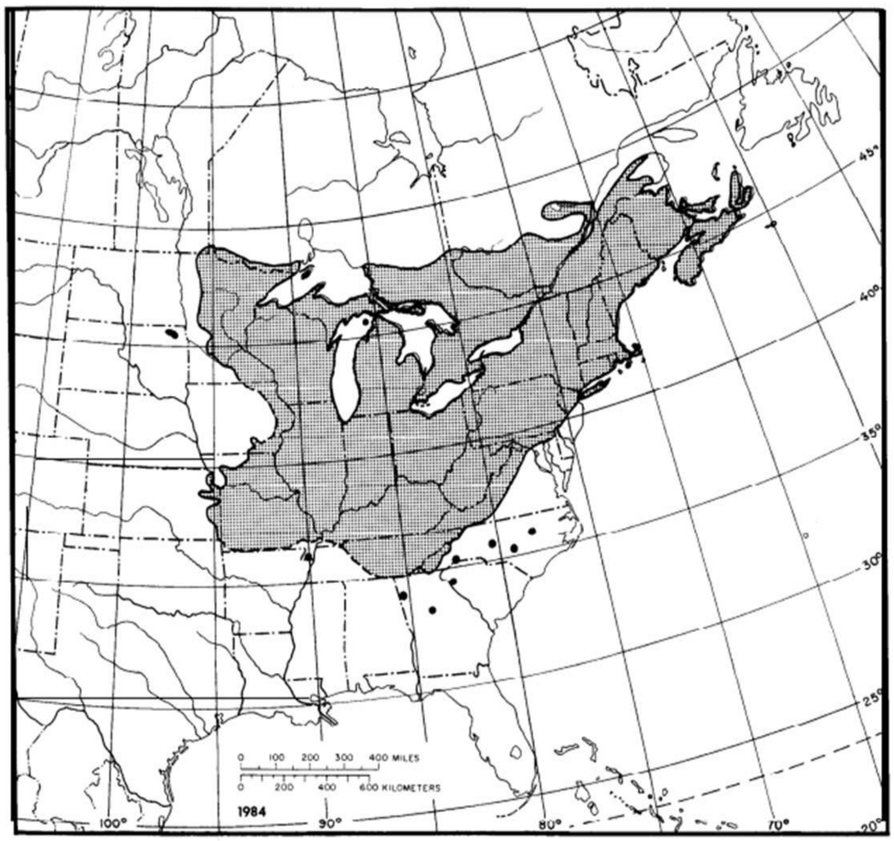

Figure 1-1 Native range of sugar maple in North America

(Source: Godman et al. 1990)

1.1.2 Silvics of sugar maple and hardwood silviculture

Sugar maple regenerates mostly by seeds, but vegetative reproduction is also possible through stump sprouts. It produces abundant seeds every 3 to 7 years (Godman 1965). Seeds require moist stratification at temperatures slightly above 0 ˚C for 35-90 days to germinate (germination capacity>95%) (Yawney and Clayton 1968). Natural seedlings require overstory shade until they reach heights of 0.6 to 1.2 m at which time their root system reaches the mineral soil (Godman and Tubbs 1973). The maximum height growth is observed under intermediate light (Logan 1965). Sugar maple seedlings are very shade tolerant and can survive long periods of suppression (Canham 1988; Godman et al. 1990). After partial harvesting or other disturbances, the tallest seedlings usually develop and constitute the trees of the new cohort as the overstory is gradually removed (Godman et al. 1990). The pole stage trees respond vigorously to canopy gaps created by natural or anthropogenic disturbances (Godman 1965). Sugar maple trees can live up to 400 years and reach heights of 30 m and diameter at breast height of 90 cm (Godman et al. 1990).

Uneven-aged silvicultural systems are commonly applied to manage northern hardwood forests in order to produce high quality products, promoting quality stem development and stand vigour, and ensuring successful natural regeneration of the desired species (Nyland 2002). However, northern hardwood forests were subjected to high-grading, where good quality stems were felled through partial harvesting and thus leaving poor quality trees in the residual stands (Drinkwater 1957; Majcen et al. 2003). The high-grade harvesting practice left a higher number of low vigour and genetically inferior trees in the residual stands (Nyland 1992; Majcen et al. 2003). When low vigour trees are left in residual stands, not only stand productivity declines (Drinkwater 1957) but also tree quality as low vigour is associated with several defects. Moreover, low vigour trees are less capable to withstand biotic and abiotic stresses (Manion 1981). Residual stands composed of low grade trees do not only have lower growth (Duchesne et al. 2003) but also contain larger proportions of decay and discoloration (Drinkwater, 1957; Ohman, 1968; Shigo, 1984). However, partial harvesting systems in which low grade trees were removed with individual or group tree selection methods were found to increase value of the residual stand as growth is accumulated on better quality residual trees (Ondro and Love 1979; Bédard and Majcen 2003; Forget et al. 2007; Swift 2013).

1.1.3 Morphology of sugar maple stems

A tree trunk generally consists of bark, a thin layer of phloem, cambium and xylem (Figure 1-2). A very large proportion of a tree is made up of xylem (Plomion et al. 2001) which can be divided into sapwood and heartwood. There is no apparent difference in colour between sapwood and heartwood in sugar maple (Good et al. 1955). Sapwood is the actively conducting portion of the stem, in which the parenchyma cells are still alive and metabolically active whereas heartwood is not involved in water transport (Wiedenhoeft and Miller 2005). In sugar maple, the outer 30 to 40 growth rings are physiologically active for sap conduction (Sargent 1922; Pausch et al. 2000; Raulier et al. 2002; Ewers et al. 2002) and for storage of reserve materials such as starch (Ewers et al. 2002).

Heartwood is "*the inner layer of the wood, which, in the growing tree, have ceased to contain living cells, and in which the reserve materials (e.g. starch) have been removed or converted to heartwood substances*" (International Association of Wood Anatomists 1964). Heartwood is formed when the vessels are plugged by air (Priestley 1932; Sperry et al. 1991) which is followed by histo-chemical changes (Hillis 1968). A study by Good et al. (1955) provided evidence of heartwood formation in sugar maple. Even though there are very limited studies on heartwood formation in sugar maple, studies on other diffuse porous hardwood species indicate that heartwood formation is a regulatory mechanism for controlling the amount of sapwood (Bamber 1976). Although there are several hypotheses to explain heartwood formation (Taylor et al. 2002), they converge towards two points, viz. (1) sapwood cells have a maximum age and (2) sapwood senescence is related to foliage shedding as the primary function of sapwood is to transport water from the roots to the foliage (Sievänen et al. 1997; Schneider et al. 2011; Hari et al. 2013).

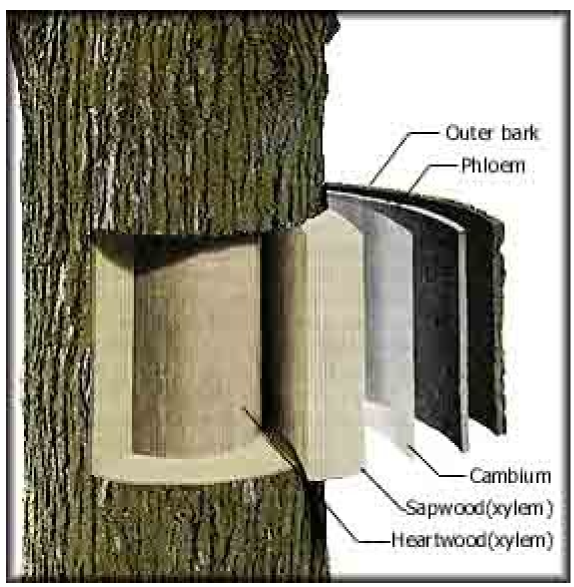

Figure 1-2 Gross structure of a stem cross-section

(Source: http://dendro.cnre.vt.edu/forsite/tait2.htm)

On the other hand, discoloured wood (both discoloured sapwood and heartwood) is not formed due to regular physiological process but is a result of microbial infection of exposed xylem tissue by wounds (Shigo 1965; Ohman 1968). The formation of discoloured wood involves the alteration of wood tissues through vessel plugging, formation of polyphenolic compounds, and the deposition of dark material resulting from injury and infection (Ohman 1968; Shigo et al. 1984). The moisture content of wood cells around the point of injury normally falls as a result of embolisms. These new conditions favour microbial colonisation, which ultimately leads to wood discolouration (Boddy and Rayner 1983; Leben 1985).

According to the CODIT (Compartmentalisation of Decay in Trees) model that was developed by Shigo and Marx (1977) and which was redefined by Dujesiefken and Liese (2010), trees compartmentalise the discolouration column through four lines of defense (Figure 1-3). The affected area is subsequently isolated from the surrounding tissues by the formation of a watertight compartment. The first line of defense is created by the longitudinal plugging of vessels, the second line is built radially by latewood formation of each growth ring, the third line results from transverse walls made up of ray cells, and the fourth line of defense is formed by the creation of a band of different-sized cells containing antibiotic compounds (e.g., suberin), which inhibits microbial growth. Consequently, a vertical discolouration column is created by the plugging of vessels, which imparts a colour change, whereas inner radial discolouration is provided by the alteration of cell contents in the ray parenchyma (Shigo 1979).

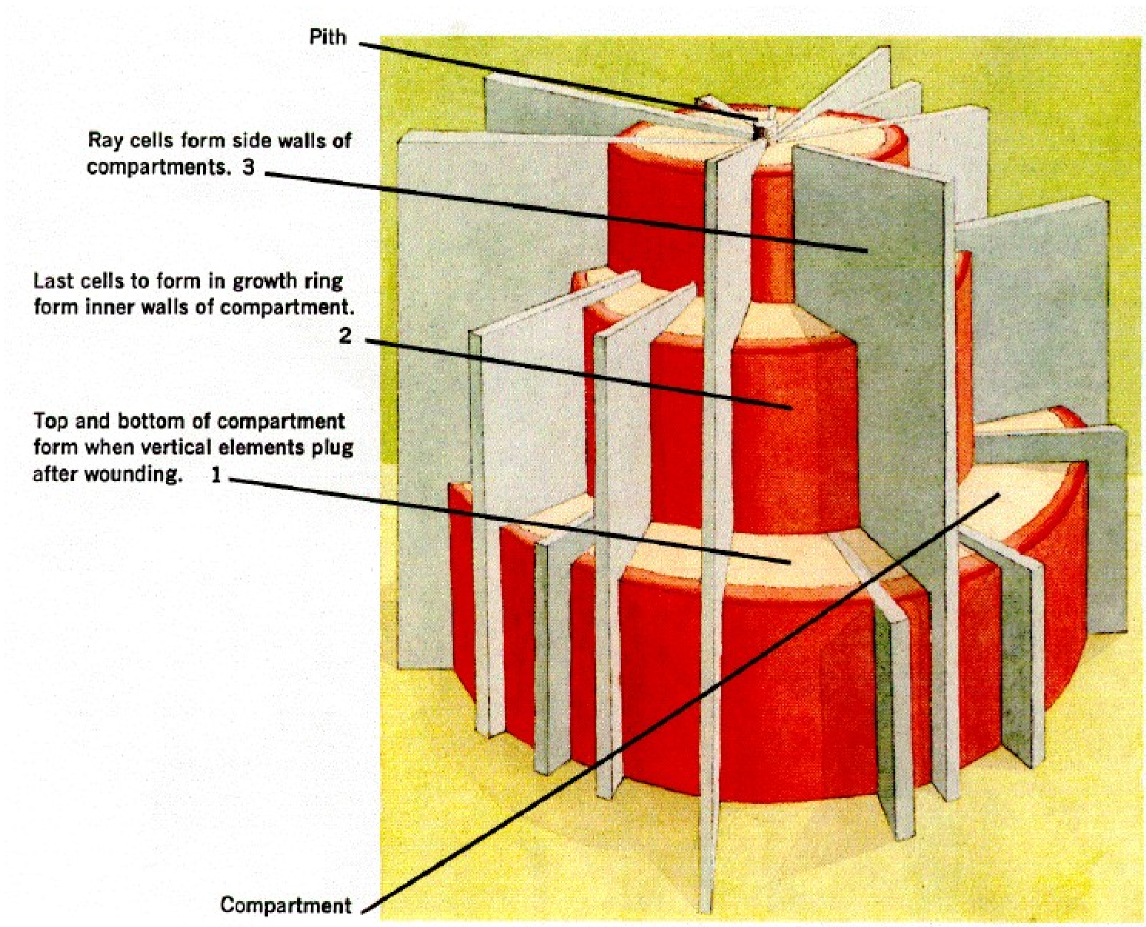

Figure 1-3 Compartmentalization of decay and discoloration in trees

(Adapted from: Shigo and Larson (1969)**)**

Discolouration is the incipient stage of decay when a tree is injured (Shigo and Marx 1977). Shigo (1967) showed a succession of different organisms involved in the process of discolouration and decay of wood. He explained that the wounded area is colonized by bacteria at the beginning. After a certain time, the affected area is colonized by non-decay fungi (Figure 1-4a,b). Finally, decay fungi (hymenomycetes) infects the substrate and wood cells decay completely. The important fungi that are associated to sugar maple discoloration and decay are *Fommes conatus*, *Fommesignarius* and *Polyporusglomeratus* (Shigo 1965; Boulet 2005).

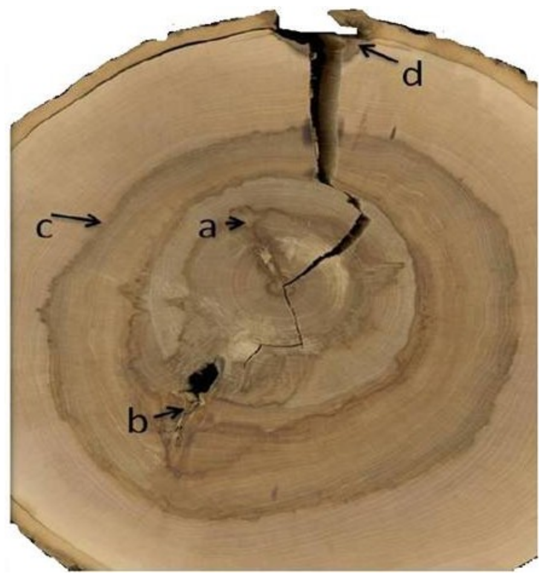

Figure 1-4 Discolored wood formed due to (a and b) successive injuries, 'c' the recent discoloured wood boundary and 'd' discoloured wood compartmentalized in sapwood

Discoloured sapwood (Figure 1-4d) is located at the sapwood injury point and the proportion of such type of discoloured wood is very small at the tree level (Hart 1963). To the contrary, the proportion of discoloured xylem is important in the core. Thus, pale white coloured xylem area in the outer region is designed as clear wood area and dark coloured xylem area in the core which is termed discoloured wood area. However, these clear and discoloured wood areas are not equivalent to physiological sapwood and heartwood areas respectively. Clear wood area would include sapwood and non-discoloured heartwood areas whereas discoloured wood area would include the small discoloured sapwood area and the discoloured heartwood (Hart 1963; Shigo 1967).

Decayed and discoloured wood components are thought to have different anatomical and mechanical properties compared to sound wood (Schwarzee 2007). However, the degree of changes depends on the state of decay and discoloration. For sugar maple, the increase in discoloured wood proportion reduces timber value (D'Eon and Hamilton 2011) as the pale white coloured sugar maple wood is sought for highly valuable appearance products.

1.1.4 Effects of silvicultural systems on wood structure formation

In uneven-aged silvicultural systems, trees are removed partially by mimicking small scale natural disturbances (Seymour et al. 2002). Tree harvesting modifies both above-ground and below-ground resource availability for the residual trees (Hartmann et al. 2009). Trees respond to new environments by increasing their crown size (Rouvinen and Kuuluvainen 1997; Thorpe et al. 2010) to optimize light capture (Valladares and Niinemets 2007). An increase in crown size can be achieved by a reduction of self-pruning and an increase in branch growth or elongation (Maguire et al. 1991).

In selection cutting, not all trees are freed equally from the competition. In each felling cycle, some trees are released and some are not. The early released saplings are more likely to become vigorous canopy trees in the future when compared to saplings suppressed for a long period of time (Landis and Peart 2005). As a result, vigorous trees attain a given diameter at breast height in a shorter time period (Duchesne et al. 2003). To the contrary, long-suppressed trees grow slower and thus take a longer time period to attain the same diameter. Hence, long-suppressed trees are more likely to have been injured repeatedly and have higher proportions of discoloured wood (Erickson et al. 1992).

When dominant and co-dominant trees are removed through selection cutting, the remaining trees get more growing space. As a result, the residual trees will have longer and wider crowns, and thus more foliage. Change in crown size and vigour due to increasing growing space should influence sapwood and heartwood proportions in a tree (Bergstrom 2000; Taylor et al. 2002). Gartner et al. (2000) reported that sapwood area is greatly influenced by tree vigour. The leaf to sapwood area ratio at breast height for sugar maple was found to be 0.51 m^2 cm^{-2} (Chapman and Gower 1991). Studies conducted on other species indicated that leaf to sapwood area ratio changes with height or social position of the tree (McDowell et al. 2002), age (Köstner et al. 2002) and site (Mencuccini and Grace 1994; Berninger et al. 2005). Hence, leaf to sapwood area for sugar maple may also vary with tree height, age and site.

Moreover, wider gaps are more likely to increase crown length and crown diameter of the trees (Drinkwater 1960). In spite of the favourable effects of canopy openings on residual tree growth (Hartmann and Messier 2008), they can also have negative effects on merchantable log volume as they reduce the log length by creating fork (Hein 2009) and by reducing bole volume as main stem tapers sharply above fork (Adu-Bredu et al. 2008; Planck and MacFarlane 2014). In addition, the fork may increase discoloured wood proportion as branch to stem diameter ratio, indicative of the fork size, is positively related to stem discoloration (Eisner et al. 2002).

Selection cuttings can also damage residual tree stems. Indeed, damage was observed on 4 to 40% of trees in residual stands after harvesting operations and this percentage depends on the harvesting method and residual tree basal area (Majcen 1996; Clatterbuck 2006). Among the damaged trees, more than 50% were found to be saplings and pole-sized trees (Davis and Nyland 1991). These logging damages are also the cause of commonly seen frost cracks in northern hardwood stands (Burton et al. 2008). Stem wounds greater than 300 cm^2 are considered to be important injuries as 66% of such injuries were found to be responsible for reducing log value after a 10-year period (Ohman 1970). Root wounds are the major cause of defect in the butt log (Dey 1994). Logging damage, therefore, are responsible of reduction in tree vigour, bole quality and value in the residual stand (Meadows 1993). To overcome these problems, certain techniques of careful logging have been suggested by Coates et al. (1994): (1) trail planning, (2) avoiding excessive brushing, (3) maximizing bunch size and (4) keeping machinery on the trail whenever possible during timber extraction. Experiments have shown that careful harvesting operations reduce the proportion of logging damages, enhance residual tree growth (Ondro and Love 1979; Majcen 1996) and improve stem quality (Ondro and Love 1979; Bédard and Majcen 2003; Swift 2013).

As wood decay and discolouration in sugar maple stems are associated with trauma such as injuries and branch death (Ohman 1968; Shigo and Hillis 1973), we can state that the extent and proportion of discoloured wood in sugar maple may depend on a variety of tree characteristics such as tree age for a given diameter (Knoke 2003; Kadunc 2007), crown recession or branch death (Eisner et al. 2002), injuries or logging damage (Knoke 2003; Belleville et al. 2011), and branching pattern (Eisner et al. 2002). These characteristics can be partly controlled by the silvicultural systems used in northern hardwood stands.

1.1.5 Problem statement and justification

Current challenges of hardwood silviculture in south eastern Canada are, among others, to (i) maintain stem quality and tree vigor of the future stand and (ii) enhance quality of timber harvested in terms of grade and product (Bédard et al. 2010; Swift 2013; Pothier et al. 2013). Tree stand improvement through selective removal of low quality trees (Erdmann 1986; Nyland 1987; Majcen 2001) have indicated the potentiality of improving both residual stand quality (Strong et al. 1995) and volume production (Bédard and Majcen 2003). However, residual tree structure development after partial cuts and its functional-structural relationship to wood structure components are not well understood.

On the one hand, studies have found that heartwood formation is a regulatory mechanism for controlling sapwood (Bamber 1976), which is related to size and vigour of the tree crown (Chapman and Gower 1991; Tucker et al. 1993). On the other hand, the relationship between tree characteristics and dimensions of discoloured wood column remain elusive (Yanai et al. 2009). However, it seems possible to develop good relationships between tree characteristics and size and shape of discoloured wood in a stem (Erickson et al. 1992; Eisner et al. 2002; Knoke 2003; Kadunc 2007; Belleville et al. 2011). Important traits of timber quality of harvested sugar maple trees can be predicted from statistical relationships relating tree and crown characteristics to wood structure components (sapwood, heartwood and discoloured). In addition, such statistical models should be useful in predicting changes in stem quality and tree vigour with changing tree size and crown characteristics. Eventually, better silvicultural decisions for tolerant hardwood forests of North America can be proposed.

1.2 Objectives of the study and structure of the thesis

This thesis aimed at establishing a functional-structural link between tree characteristics and proportions of wood structure components (i.e. sapwood, heartwood and discoloured wood) for understanding clear wood production in stand grown sugar maple trees.

The specific objectives were:

1. to quantify the relationship between discoloured wood proportion and tree characteristics(chapter II);
2. to establish a functional link between tree characteristics and heartwood formation in sugar maple (chapter III); and
3. to understand the effects of crown characteristics and tree growth on clear wood proportions in sugar maple (chapter IV).

Research hypotheses:

The following hypotheses were tested to achieve the research objectives:

1. Discoloured wood proportion in a sugar maple tree increases with age and decreases with tree vigour. It is further hypothesized that width and height of discoloured wood column are positively related to tree diameter and height, respectively, and negatively related to crown ratio.
2. Sapwood proportion in a sugar maple tree decreases with tree height, crown size and increases with leaf area per unit stem basal area. It is further hypothesized that less vigorous trees have lower amount of foliage and higher heartwood and discoloured wood proportion.
3. The ratio of clear wood to merchantable wood volume decreases with tree diameter and increasing presence of defects, and increases with crown diameter, diameter growth rate and log length up to 24 cm diameter of the tree at a site.

This thesis is composed of three articles addressing the relationships between tree crown characteristics and the three sugar maple structural components of interest (i.e sapwood, clear wood and discoloured wood) (Figure 1-5). Chapter II presents statistical models for predicting sugar maple discoloured wood proportion and discoloured wood column tapering using tree and crown size information. Chapter III develops a relationship between functional sapwood to tree characteristics (height, age, crown size, and leaf area) to explain how heartwood formation changes with tree size. This chapter also discusses the relationship between heartwood formation and discoloration among trees of different vigour classes. Chapter IV uses effects of competition on crown characteristics and thereby on clear wood volume in the merchantable section of the log. Finally, Chapter V presents a synthesized review of the results from the previous chapters. It discusses the applicability and limitations of the study and proposes future directions in this field.

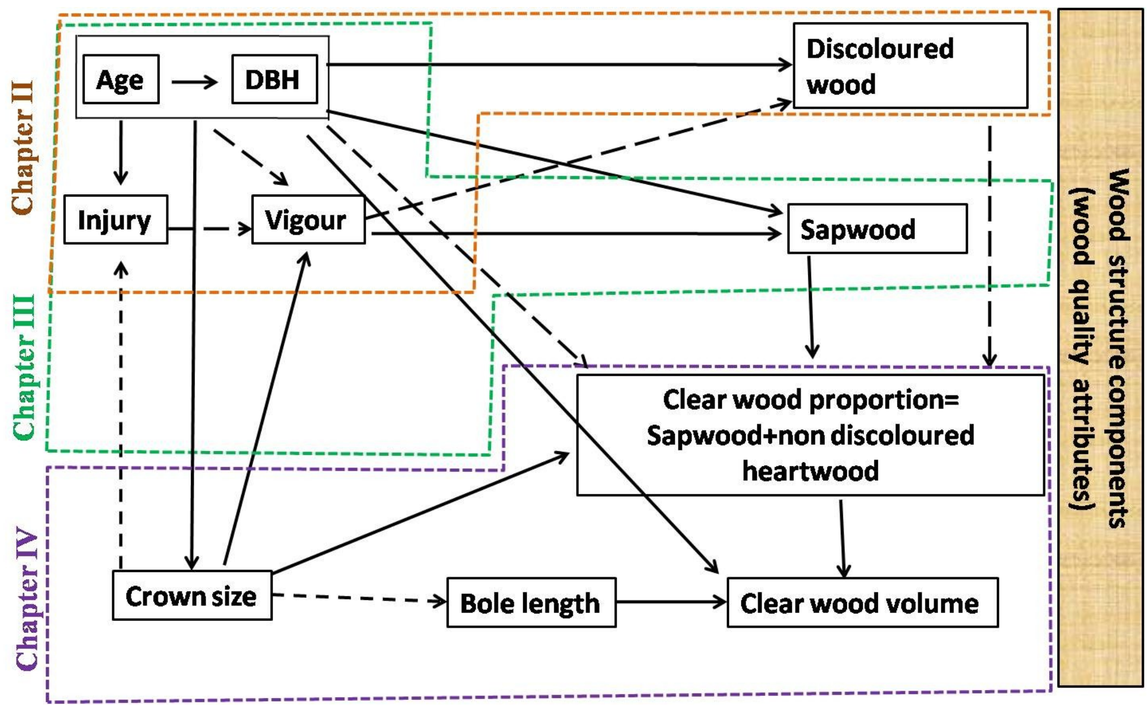

Figure 1-5 Conceptual model showing the organization of the thesis. Solid arrows show positive relationship and dotted arrows show negative relationship

1.3 Study sites

The study sites are located near Mont-Laurier (46° 33' N and 75° 29' W) in the south-western part of Quebec; Duchesnay (46°50' to 47°00'N; 71°35' to 71°45' W), next to Quebec City in the south-central part of Quebec; and Biencourt (48°00’40”N and 68°30’15”W) close to Rimouski in south-eastern Quebec in Canada (Figure 1-6). According to Robitaille and Saucier (1998), mean annual precipitation (1000 mm) and mean annual temperature (2.5 to 5 °C) in Mont-Laurier are more or less similar to mean annual precipitation (1100 mm) and mean annual temperature (2.5 ^{o}C) in Duchesnay. Close to Rimouski, mean annual temperature is similar (2.5^{o}C) and higher mean annual precipitation (1200-1600 mm)(Robitaille and Saucier 1998). Sugar maple (*Acer saccharum* Marsh.)*,* and yellow birch (*Betula alleghaniensis* Britton) dominated the forest canopy at Mont-Laurier and Duchesnay, and sugar maple is associated with balsam fir (*Abies balsamea* (L.) Mill.) and yellow birch at Rimouski.

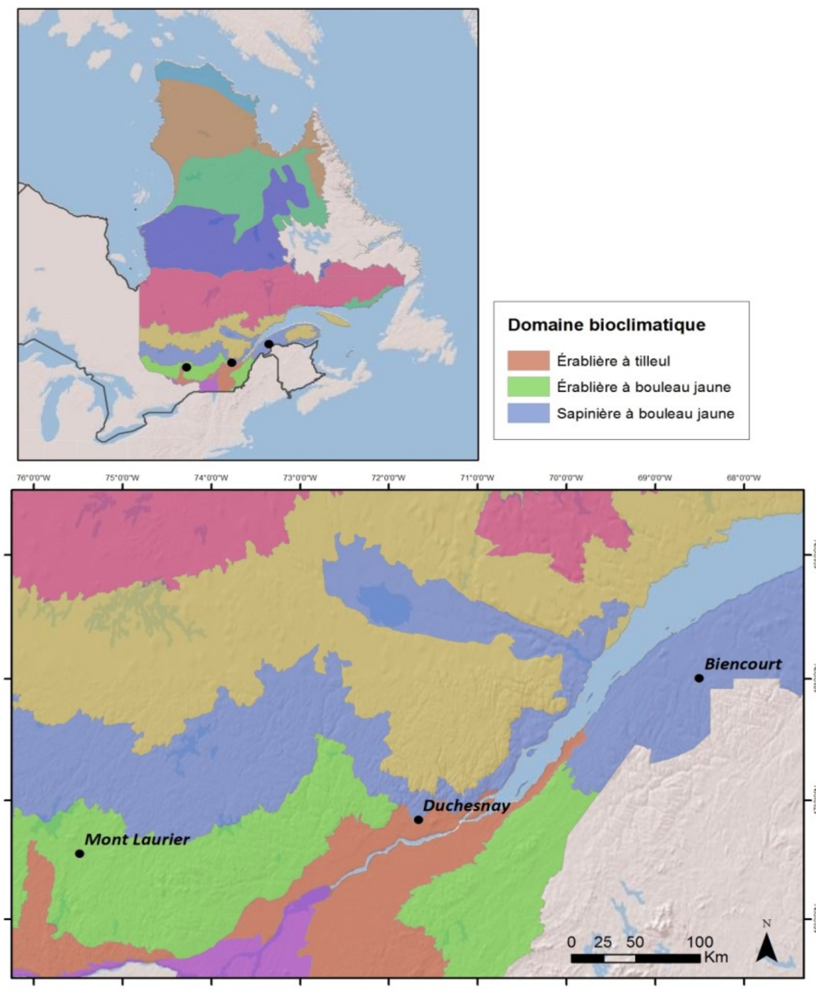

Figure 1-6 Map showing location of three study sites in different bioclimatic domains in Quebec, Canada

1.4 Sampling design

The Quebec Forest, Wildlife and Parks Ministry use both the ABCD (Monger 1991) and MSCR (Boulet 2005) grading systems in their inventory. The ABCD system classifies stem quality according to their potential use. It is done only on living standing trees with a DBH greater than 24 cm. The general principle is to find the best 3.7 m long log within the first 5 m at the base of the stem. In this classification system "A" stands for the good quality stem and "D" stands for the worst category.

The MSCR system classifies the standing trees on the basis of their vigour. M (dead) stands for stems that are very flawed, which could be dead on before the next rotation, S (survival) stands for stems that are defective, in distress and whose timber volume may decrease due to decay, but whose survival is not compromised before the next rotation, C (maintained) stands for stems that have a few defects but the volume of merchantable timber will not deteriorate before the next rotation, and R (retained) stands for stems that have little defects and are future high quality crop trees.

The sample trees used in this studied were thus based on both grading systems (Table 1-1). Altogether 109 trees (40 trees from Rimouski, 39 trees from Mont-Laurier and 30 trees from Duchesney corresponding to each combination (one big and one small tree) of ABCD and MSCR classes and an additional 8 trees -2 trees from every 5 cm interval of trees from 5-24 cm DBH) were selected for detailed examination.

Table 1-0-1 Research design matrix for sample tree selection

Criteria		Stem quality class								Other	
		A		B		C		D		Small Trees	
		DBH (cm)	Sample combination	DBH (cm)	Sample combination	DBH (cm)	Sample combination	DBH (cm)	Sample combination	Diameter class	No. of trees
Tree vigour class	M	<46	A1M1	<40	B1M1	<34	C1M1	<34	D1M1	5-10 cm	2
		>46	A2M2	>40	B2M2	>34	C2M2	>34	D2M2	10–15cm	2
	S	<46	A1S1	<40	B1S1	<34	C1S1	<34	D1S1	15-20cm	2
		>46	A2S2	>40	B2S2	>34	C2S2	>34	D2S2	20-24cm	2
	C	<46	A1C1	<40	B1C1	<34	C1C1	<34	D1C1	Total	8
		>46	A2C2	>40	B2C2	>34	C2C2	>34	D2C2		
	R	<46	A1R1	<40	B1R1	<34	C1R1	<34	D1R1		
		>46	A2R2	>40	B2R2	>34	C2R2	>34	D2R2		

CHAPTER II

Predicting sugar maple (*Acersaccharum*) discoloured wood characteristics

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2.1 Abstract

The presence of wound (strain)-initiated discoloured wood column in the core of sugar maple (*Acer saccharum* Marshall) stems reduces the proportion of white coloured wood and, thus, lowers its commercial value. This study aimed to assess the relationship between tree characteristics, and the extent and proportion of discoloured wood in sugar maple tree stems. Using 109 trees from three different sites in southern Quebec, we found that the proportion of discoloured wood increased with decreasing sapwood volume and increasing tree age. Younger trees showed a significantly lower proportion of discoloured wood volume. Discoloured wood volume increases disproportionately with tree diameter, while varying among sites. The third important factor affecting the amount of discolored wood was tree vigour as measured by crown characteristics and growth rate changes. A non-linear mixed-effects model was used to predict discoloured wood taper. Height along the stem was used as a predictor, along with diameter at 1.3 m (DBH), the ratio of live crown length to tree height, and tree height. Although observed injury surface area was positively correlated to discoloured wood volume, injury information did not explain a large share of discoloured wood proportion variation. Overall, older and larger trees with many injuries on less productive sites are likely to have more discoloured wood.

Key words: discoloured wood, sugar maple, tree characteristics

2.2 Introduction

Sugar maple (*Acer saccharum* Marshall) is a deciduous tree species that is widely distributed throughout eastern North America. Its sapwood is white coloured and is prized by the veneer and flooring industry. Sugar maple is not thought to contain coloured heartwood as a result of aging or maturation (Good et al. 1955). Yet, the trunk of this species frequently has a considerable quantity of reddish-brown coloured wood at its centre, a condition which is referred to as a discoloured wood column (Shigo and Hillis 1973). According to established grading rules, this discoloured wood reduces log value (Erickson et al. 1992).

Discoloured wood formation is due to the alteration of wood tissues through vessel plugging, formation of polyphenolic compounds, and the deposition of dark material resulting from injury and infection (Ohman 1968; Shigo 1984). These changes develop after the wood vascular cambium and phloem have been subjected to wounding or the xylem gets exposed due to branch death (Shortle 1984). The moisture content of wood cells around the point of injury normally falls as a result of embolisation. These new conditions favour microbial colonisation, which ultimately leads to wood discolouration (Boddy and Rayner 1983; Leben 1985). According to the CODIT (Compartmentalisation of Decay in Trees) model that was developed by Shigo and Marx (1977) and which was redefined by Dujesiefken and Liese (2010), trees compartmentalise the discolouration column through four lines of defense. The affected area is subsequently isolated from the surrounding tissues by the formation of watertight compartment. The first line of defense is created by the longitudinal plugging of vessels, the second line is built radially by latewood formation of each growth ring, the third line results from transverse walls made up of ray cells, and the fourth line of defense is formed by the creation of a band of different-sized cells containing antibiotic compounds (e.g., suberin), which inhibit microbial growth. Consequently, a vertical discolouration column is created by the plugging of vessels, which imparts a colour change, whereas inner radial discolouration is provided by the alteration of cell contents in the ray parenchyma (Shigo 1979).

Despite a general consensus that wood discolouration in sugar maple stems is associated with trauma such as injuries and branch death (Ohman 1968; Shigo and Hillis 1973), relationships between the extent of discoloured wood and tree characteristics are not well understood. For example, Yanai et al. (2009) concluded that the proportion of discoloured wood does not increase with tree age or diameter, but others have found that the extent and proportion of discoloured wood in hardwood species may depend on a variety of factors, including tree age (Knoke 2003; Kadunc 2007), bole diameter (Erickson et al. 1992; Kadunc 2007), crown recession or branch death (Eisner et al. 2002); injuries (Knoke 2003; Belleville et al. 2011); branching pattern (Eisner et al. 2002), growth rate (Knoke 2003), and site productivity (Kadunc 2007; Yanai et al. 2009).

It is evident that the proportion of discoloured wood in a tree is regulated by a balance between possible expansion of microbial infections and tree defense capacity. Tree defense is a dynamic process that predominantly takes place in the sapwood, where the wood lumina are saturated by bound and free water (Shigo and Hillis 1973; Schwarze 2007). Ageing processes, in contrast, are associated with a reduction in moisture content of older wood (Good et al. 1955), which could lead to the formation of coloured heartwood in sugar maple. Further, the proportions of functional sapwood declines from 100 to 10-20% as trees mature (Shigo 1982; Schwarze 2007). Therefore, we hypothesise that the proportion of discoloured wood volume increases as trees get older and bigger because of increasing substrate availability for infection by microorganisms.

This study thus aims i) to assess the proportion of discoloured wood volume using various tree grading rules, ii) to quantify the relationship between discoloured wood proportion and tree characteristics, iii) to explore the rate at which discoloured wood expands as trees grow, and iv) to predict the tapering of discolored wood column from base to tree top in a tree bole using tree characteristics. The results should help us to explain the relationship between tree characteristics and the extent of discoloured wood, which could be used to improve northern hardwood forest management.

2.3 Methods

2.3.1 Study sites and tree sampling

Trees were selected from three uneven-aged natural stands, each of which was representative of a different region of the northern hardwood forests of Quebec, Canada (Table 2-1). We selected 39 trees from Mont-Laurier, 30 trees from Duchesnay, and 40 trees from Biencourt, which covered a broad spectrum of tree vigour classes: MSCR (Boulet 2005) and stem quality classes: ABCD (Monger 1991) (Table 2-1).

Tree vigour was measured using the MSCR classification which separates trees into four categories that are assumed to be related to their probability of mortality during the next cutting cycle, i.e. a 20-year period (Boulet 2007). As described by Pothier et al. (2013), the distinction among classes is based on a visual examination of the presence and eventual severity of certain tree defects. These defects are grouped into eight categories: 1) conks and stromata, 2) cambium necrosis, 3) stem deformations and injuries, 4) stem base and root defects, 5) stem and bark cracks, 6) woodworms and sap wells, 7) crown decline, and 8) forks and pruning defects. According to an evaluation grid based on these defects, the tree vigour system classifies standing trees as follows: class M (mortality) corresponds to trees that are likely to die before the next harvest (15-25 years); class S (survival) are trees with significant defects, but that are likely to survive until the next harvest; class C (conserved) are trees with some minor defects that are actively growing and should not deteriorate until the next harvest; and class R (retained) corresponds to vigorous trees that should form the basis of the future stand. The stem quality system (ABCD) is also composed of four classes which aim at predicting the lumber grade and volume recovery (Monger 1991). To this end, the best 3.7-m stem section located in the bottom 5 m of each tree is separated into four faces that are examined to detect the presence and the size of defects. Then, a class is attributed to each tree as a function of its diameter at breast height (DBH), the length of the clear (defect-free) bole on its 3rd best face, an estimated percent of wood rot, and the presence of stem sinuosity and curvature. The four classes, A to D in decreasing order of stem quality, are used to estimate the available wood volume for different types of wood processing industries (i.e. veneer, sawmill or pulp and paper).

Table 2-0-1 Main bio-climatic characteristics (based on Robitaille and Saucier 1998) of the study sites and sample tree characteristics. Range values are given in parenthesis.

		Sites		
S.N.	Description	Mont-Laurier	Biencourt	Duchesnay
1	Location	46.65oN, 75.64oW	48.01oN, 68.50oW	46.94o N, 71.67oW
2	Elevation (m)	475	380	275
3	Topography	High hills, well drained, 15^{o} slope	Hills, well drained, 15^{o} slope	Mountains, well drained, 15^{o} slope
4	Bioclimatic domain	Sugar maple-yellow birch domain	Balsam fir-yellow birch domain	Sugar maple-yellow birch domain
5	Parent bedrock	Igneous or metamorphic	Sedimentary	Igneous or metamorphic
6	Annual rainfall (mm)	1000	1000-1100	1200-1600
7	Mean annual temperature (^{o}C)	2.5-5	2.5	2.5
8	Mean tree age (years)	132 (53-254)	92 (41-152)	105 (74-143)
9	Mean height (m)	18.9 (7.3-24.1)	19.1 (7.8-23)	21.1 (17.5-25.4)
10	Mean diameter at breast height (mm)	338 (71-550)	335 (68-546)	379 (235-585)
11	Mean HFLB (m)	8.5 (1.6-13.3)	6.3 (1.5-9.8)	11.6 (7-18.3)
12	Stand basal area (m^2 ha^{-1})	24.71 (0.83)*	26.73 (1.95)*	23.67 (0.69)*
13	Total number of trees	39	40	30
14	Trees by vigour class			
	M	7	8	6
	S	8	8	8
	C	8	8	8
	R	8	8	8
	O	8	8	0
15	Trees by stem quality class			
	A	8	8	7
	B	8	8	8
	C	8	8	8
	D	7	8	7
	O	8	8	0

A matrix with rows of ABCD classes and columns of MSCR classes was created for the trees that we sampled and which had a diameter at breast height (DBH, 1.3 m) ≥ 23.1 cm.

We tried to include at least two trees in each cell at every site when trees were selected for sampling. Also, trees that were not included in the matrix (i.e. DBH < 23.1 cm) were additionally selected to represent small-sized trees. These small sized trees that were not graded according to the aforementioned classification systems were categorised as other ‘O’.

Prior to felling, sample trees were classified into MSCR and ABCD classes, DBH and the presence, size and type of injuries, scars or damage to the tree stem and crown were recorded. Once the trees were felled, total height (m), and the height of the first living primary branch (HFLB) were measured. Presence of knots, fungi, scars and other marks on each stem were observed thoroughly, and their location and size were measured. Branch location, together with the length and diameter of every primary branch (live and dead), were measured. Stem cross-sectional samples (disks) were taken from each felled tree at 0.3 m (stump height) and 1.3 m (DBH) above the ground, at the crown base, and at every 2 m along the main stem up to about 1.5 m below the tree top. Additional disks were taken below every bifurcation point of six sample branches per tree. The sample branches were selected by a proportional probability sampling technique (see Gregoire et al. 1995).

2.3.2 Sapwood measurements

We took into account three different wood components of sugar maple, i.e. sapwood, clear heartwood, and discoloured heartwood (Figure 2-1). The functional sapwood (starch-storing sapwood cells) compartment was identified by staining each freshly cut wood disk with 2.5% potassium iodide iodine (IKI) solution (Kutscha and Sachs 1962). We then delineated the boundaries of the sapwood, clear heartwood (defined as wood with parenchyma cells that did not contain starch and which was neither discoloured nor stained with IKI solution), and discoloured wood. Bark, sapwood, clear heartwood, and discoloured heartwood radii were then measured in eight radial directions.

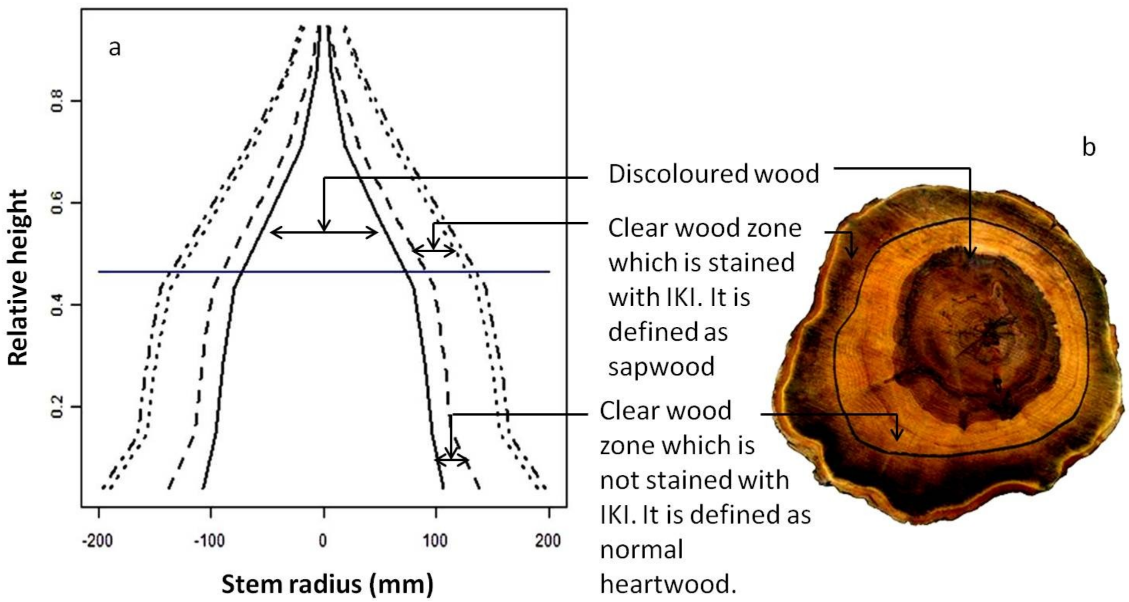

Figure 2-1 (a) Schematic of showing discoloured wood, clear heartwood and sapwood, (b) a wood cross-section stained with I-KI to observe sapwood, clear heartwood and discoloured wood compartments

Quadratic mean radius for each wood component was calculated from the eight radial measurements as suggested by Wieman et al. (2002) to obtain the least biased measurement of the irregular shape of the discoloured heartwood and tree bole. The area of each compartment was then calculated with the quadratic mean radii, assuming the radii of each compartment were concentric rings in the following order from pith to bark: discoloured heartwood, clear heartwood, and sapwood. The volume of each compartment was then calculated using Smalian's formula (Loetsch et al. 1973). In addition, the disk at breast height (i.e., 1.3 m) of each tree was sanded in two perpendicular radial directions with 80 and 120 grit sanding paper and ring width measured, with the OSM 3.65b Software (SCIEM, Brunn, Austria). This information was then used to determine tree age and to calculate the mean annual ring width at breast height. Since the total annual growth rings were counted at breast height for determining tree age, one could use 8-10 years as seedling correction age for estimating the true age of the trees (Beaudet et al. 2007)

2.3.3 Data analysis

2.3.3.1 Proportion of discolored wood

We used the *nlme* library in R statistical software (R Development Core Team 2011) to establish the relationship between discoloured wood volumetric proportion (i.e., the ratio of discoloured wood volume to total tree volume) and tree characteristics using a linear mixed-effects model (Equation 1) with site effects at random intercept. A forward model selection approach that was based on model fit statistics (Akaike Information Criterion, AIC; Bayesian Information Criterion, BIC; likelihood ratio test) was used to select statistically significant covariates. Variance inflation factors (VIF: an index that measures how much the variance of an estimated regression co-efficient is increased because of the collinearity) were used to detect multicollinearity among independent variables. When VIF was > 5 for a given covariate (O'Brien 2007), it was dropped from the model. Multicollinearity was further verified by studying the effect of adding or dropping one variable on the parameter estimate of the remaining variables in the model. Once the main predictors were identified, the sum of the independent and shared variances explained by each significant predictor (i.e., the relative contribution of each covariate) was assessed through hierarchical partitioning (Chevan and Sutherland 1991) using the *hier.part* package in R (Walsh and McNally 2007). The root-mean-squared prediction error (RMPSE) was used as a goodness-of-fit measure for hierarchical partitioning. According to a likelihood ratio test, the optimum random structure was obtained by adding a site random component to the intercept.

$$P_{ij} = a_i + \mathbf{X}_{ij}\boldsymbol{\beta} + \varepsilon_{ij} \quad (1)$$

where:

P_{ij} is the volumetric proportion of discoloured wood of tree *j* in site *i*

a_i is the site random effect, where $a_i \sim N(0, ó_i{}^2)$

$\boldsymbol{\beta}$ is the fixed effects parameter vector

$\mathbf{X}_{ij}$ is the fixed effects covariate vector

ε_{ij} is the unexplained within-group random error, independent of the random effects, $\varepsilon_{ij} \sim N(0, \sigma^2)$

Tree and discoloured wood volume

A linear mixed-effects model was fitted to predict both total stem and discoloured wood volume:

$$\ln(V_{t,ij}) = a_{t,i} + \propto_{t,0} + \propto_{t,1} \ln(DBH_{ij}) + \varepsilon_{t,ij} \quad (2)$$

where:

$V_{t,ij}$ is the volume of tree *j* from site *i* ($t = 0$ for total volume; $t = 1$ for discoloured wood volume)

$\propto_{t,0}$ and $\propto_{t,1}$ are fixed effect parameters

$a_{t,i}$ is the site random effect, where $a_i \sim N(0, {\sigma_i}^2)$

$\varepsilon_{t,ij}$ is the unexplained within-group random error independent of the random effects , where $\varepsilon_{t,ij} \sim N(0, \sigma_t^2)$

Total tree height was tested, and found to be non-significant and thus dropped from the final model. The back-transformed predictions were corrected according to Sprugel (1983). The first derivative of equation (2) with respect to DBH was then calculated as:

$$\frac{\mathrm{d}\,V_t}{\mathrm{d}\,DBH} = CF_t . \propto_{t,0} . (\propto_{t,1} DBH^{\propto_{t,1}-1}) \qquad (3)$$

where CF is the log-transformation correction factor = exp $(SEE^2/2)$ where $SEE = \sqrt{\sum(logV_t - \widehat{logV_t})^2}\,/(N-2)$,

This derivative was then used to predict the difference between total and discoloured wood volume per change in DBH.

$$\Delta = \frac{\mathrm{d}\,V_0}{\mathrm{d}\,DBH} - \frac{\mathrm{d}\,V_1}{\mathrm{d}\,DBH} \qquad (4)$$

2.3.3.2 Discolored wood taper

Discoloured wood radius was plotted against disk height from ground level for each tree to assess the shape of the discoloured wood taper. Preliminary results showed that discoloured wood radius increased from stump height to breast height and then decreased towards the crown for small trees, but not for larger trees. Therefore, we selected a flexible non-linear segmented function to model discoloured wood taper:

$$DR_{ijk} = f(h_{ijk}) + \varepsilon_{ijk} \qquad (5)$$

where:

- DR_{ijk} is the discoloured wood radius of tree *j* at height *k* in site *i* (in mm)
- h_{ijk} is the height of disk k in tree *j* of site *i* (in m)
- ε_{ijk} is the unexplained within-group random error independent of the random effects , where $\varepsilon_{ijk} \sim N(0, \sigma^2)$
- $f(h_{ijk})$ the segmented non-linear function defined as:

$$f(h_{ijk}) = \begin{cases} c_{0,ij} + \beta_0 + \beta_1 \cdot DBH_{ij} \cdot (h_{ijk} - 1.3) & \text{for } h < 1.3 \text{ m} \\ c_{0,ij}\left(1 - \exp\left(-\exp\left(c_{1,ij} \times (h_{ijk} - c_{2,ij})\right)\right)\right)^{c_{3,ij}} & \text{for } h \geq 1.3 \text{ m} \end{cases}$$

(6)

where:

- β_0 and β_1 are fixed effects parameters
- $c_{0,ij}$, $c_{1,ij}$, $c_{2,ij}$ and $c_{3,ij}$ are fixed and random effects parameters:

$$c_{x,ij} = a_{x,ij} + \alpha_{x,i} \text{ for } x = 0,1,2,3, \qquad (7)$$

where:

$$a_{x,i} = (a_{i,1}, a_{i,2}, a_{i,3})^{\tau} \sim N_2\,(0, \boldsymbol{G})$$

where :

$$\boldsymbol{G} = \begin{bmatrix} \sigma_1^2 \\ \sigma_2^2 \\ \sigma_2^2 \end{bmatrix}$$

and,

$$a_{x,ij} = (a_{ij,1}, a_{ij,2}, a_{ij,3})^{\tau} \sim N_2(0, G_{tree})$$

where:

$$\mathbf{G}_{tree} = \begin{bmatrix} \sigma_1^2 & \rho_{12}\sigma_1\sigma_2 & \rho_{13}\sigma_1\sigma_3 \\ \rho_{12}\sigma_1\sigma_2 & \sigma_2^2 & \rho_{23}\sigma_2\sigma_3 \\ \rho_{13}\sigma_1\sigma_3 & \rho_{23}\sigma_2\sigma_3 & \sigma_3^2 \end{bmatrix}$$

The part below 1.3 m height is a linear equation with disk height as the only covariate. Included in this part is the asymptote of the non-linear part (i.e. $c_{0,ij}$) to ensure consistency between the segments. Above 1.3 m height, the model is asymptotic with an offset as proposed by Pinheiro and Bates (2000, p. 512). The $c_{0,ij}$ parameter represents the asymptote of the model and corresponds to the discoloured wood radius at 1.3 m. The $c_{1,ij}$ parameter is the logarithm of the rate of tapering from breast height to stem apex, $c_{2,ij}$ the height at which the discoloured wood radius reaches 0, and $c_{3,ij}$ is a shape parameter.

The model was calibrated with the *nlme* package in R (R Development Core Team 2011). To explain tree-to-tree variability, the random effect estimate for each tree (i.e., $a_{x,ij}$) was plotted against tree characteristics to identify interesting patterns. Strong positive correlations were found between the asymptotic parameter ($a_{0,ij}$) versus DBH, the height at which discoloured wood reaches 0 ($a_{2,ij}$) versus tree height, and the shape parameter ($a_{3,ij}$) versus tree crown ratio. AIC, BIC and likelihood ratio tests were used in a forward stepwise approach to include the new tree level covariates and evaluate the usefulness of each random effect. Strong correlations were observed between $a_{1,ij}$ and $a_{2,ij}$, and led to the exclusion of $a_{1,ij}$ in the final model, as it explained less variability (i.e., $\sigma^2_{1,ij} < \sigma^2_{2,ij}$).

This change in the random effects structure was verified by a likelihood ratio test. Homoscedasticity and normality assumptions for both the error and random variables were verified visually. The final model was as follows:

$$f(h_{ijk}) = \begin{cases} (a_{0,ij} + \alpha_0) \cdot DBH_{ij} + \beta_0 + \beta_1 \cdot DBH_{ij} \cdot (h_{ijk} - 1.3) & \text{for } h < 1.3 \text{ m} \\ (a_{0,ij} + \alpha_0) \cdot DBH_{ij} \cdot \left(1 - \exp\left(-\exp\left(\alpha_1 \times \left(h_{ijk} - (a_{2,ij} + \alpha_{20}) \cdot H_{ij}\right)\right)\right)\right)^{(a_{3,ij}+\alpha_3)\cdot CR_{ij}} & \text{for } h \geq 1.3 \text{ m} \end{cases}$$

(8)

where:

- $a_{0,ij}$, $a_{2,ij}$ and $\beta_{1,ij}$are tree level random effects where $a_{x,ij} \sim N(0, \sigma^2_{x,ij})$ for $x = 0,\ 2;$ and $\beta_{1,ij} \sim N(0, \sigma^2_{1,ij})$
- α_0, α_1, α_2, α_3, β_0 and β_1 are fixed effect parameters
- H_{ij} is the height of the tree

CR_{ij} is the crown ratio, defined as the ratio of crown length to tree height

Heteroscedasticity and auto-correlation were modelled using a fixed variance function and continuous autoregressive correlation, respectively.

$$\varepsilon_{ijk} \sim N(0, \mathrm{V}_{ij}^{1/2} \mathrm{C}_{ij} \mathrm{V}_{ij}^{1/2}) \qquad (9)$$

where:

- V_{ij} is the variance function: $\mathrm{V}_{ij} = DBH_{ij}\,\sigma^2$

- C_{ijk} is a within-tree diagonal correlation matrix with the elements being:

$$\mathrm{corr}(\varepsilon_{ijk}, \varepsilon_{ijk'}) = \rho^{|h_{ijk} - h_{ijk'}|} \text{ for } \forall\, k, k' \qquad (10)$$

2.4 Results

2.4.1 Proportion of discoloured wood

The volume of discoloured wood did not vary significantly among stem quality classes, whereas we observed statistically significant differences among tree vigour classes and among sites. Furthermore, the interaction between site and vigour class was found to be non-significant (Figure 2-2). Tukey's Honestly Significant Difference (HSD) tests on vigour class and site main effects showed trees that were graded M and S have a significantly higher proportion of discoloured wood volume than do trees that were graded R (Figure 2-2). Between-site differences were observed despite similarities in tree size, quality, and vigour (Table 2-1): trees in Biencourt showed the lowest proportion of discoloured wood, followed by those in Duchesnay, whereas trees in Mont-Laurier had the highest proportions (Figure 2-2). Trees sampled in Biencourt were the youngest whereas those in Mont-Laurier were the oldest (Table 2-1).

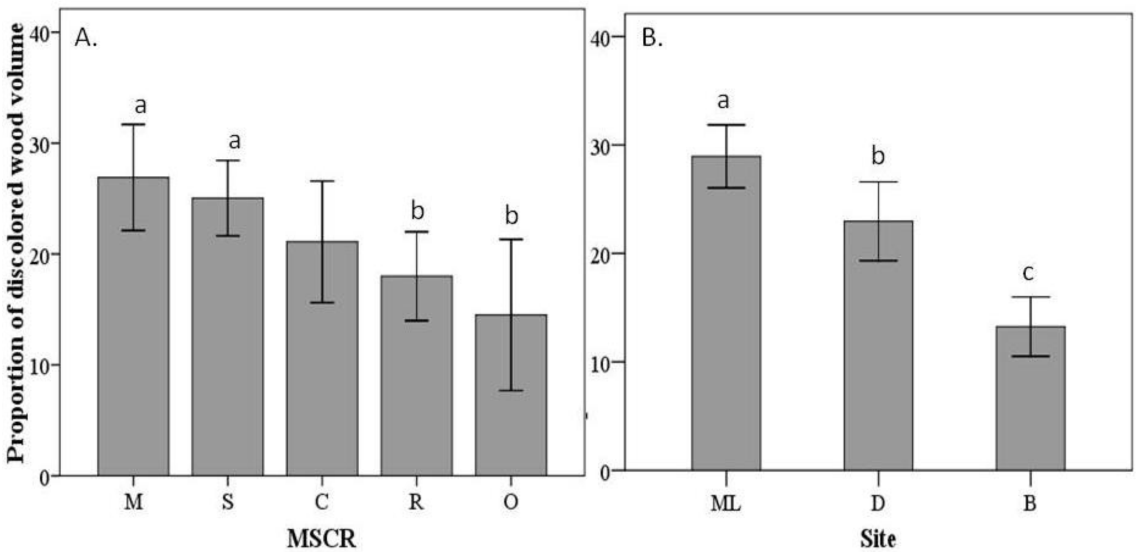

Figure 2-2 Mean proportion of discoloured wood volume among tree vigour classes and site classes. Error bars correspond to 95% level of confidence intervals. Different letters indicate significant differences according to a Tukey HSD multiple comparison test

A preliminary initial correlation analysis showed that the proportion of discoloured wood volume was highly correlated with the proportion of sapwood volume, tree age, DBH, HFLB, radial growth in last 50 years (RG50: mean width of all annual growth rings minus mean width of 50 recent growth rings), the ratio of live branch basal area to stem cross-sectional area at breast height, the ratio of crown length to total height (CR), and the logarithm of open wound area. These covariates were thus included in Eq. 1, with DBH, HFLB and CR subsequently being removed due to collinearity. Hierarchical partitioning analysis showed that the proportion of sapwood volume (negative coefficient), tree age (positive coefficient), the radial growth in the last 50 years (negative coefficient), and the ratio of live branch basal area to stem cross-sectional area at breast height (negative coefficient) contributed 35%, 45%, 5%, and 15%, respectively, of variation in the proportion of discoloured wood volume explained by the model (Table 2-2).

Table 2-0-2 Fit of the mixed effects (random intercept) multiple linear regressions to explain relationships between tree characteristics and the proportion of discoloured wood volume (%) in tree stems (Pseudo R2* with random effects is 0.79; SE indicates the standard error of respective coefficients; Random effects for the intercept are: Biencourt=(a1)=-0.0834, Duchesnay(a2)=0.0433 and Mont-Laurier (a3)=0.0401)

Fixed effects parameters	Variables	Coefficients	SE	*P*-value	Relative contribution (%)
Intercept		0.4851	0.0597	< 0.001	
β_1	Radial growth in last 50 years (mm)	-0.0511	0.0213	0.018	5
β_2	The ratio of total branch basal to stem cross-sectional area	-0.0918	0.0310	0.004	15
β_3	AGE (years)	0.0008	0.0002	< 0.001	45
β_4	Proportion of sapwood volume	-0.5062	0.0521	< 0.001	35

*Calculated as $1 - \sum_{ij}(Y_{ij} - \hat{Y}_{ij}) / \sum_{ijk}(Y_{ij} - \bar{Y}\ )^2$

2.4.2 Tree and discoloured wood volume

Diameter at breast height alone explained large proportions of the observed variability in stem and discoloured wood volumes (Table 2-3). By analysing the unconditional mean, the among-site variability in total and discoloured wood volume was found to be 17 and 37%, respectively. The Biencourt site random effects on tree and discoloured wood volume were the smallest, whereas the Mont-Laurier were the highest.

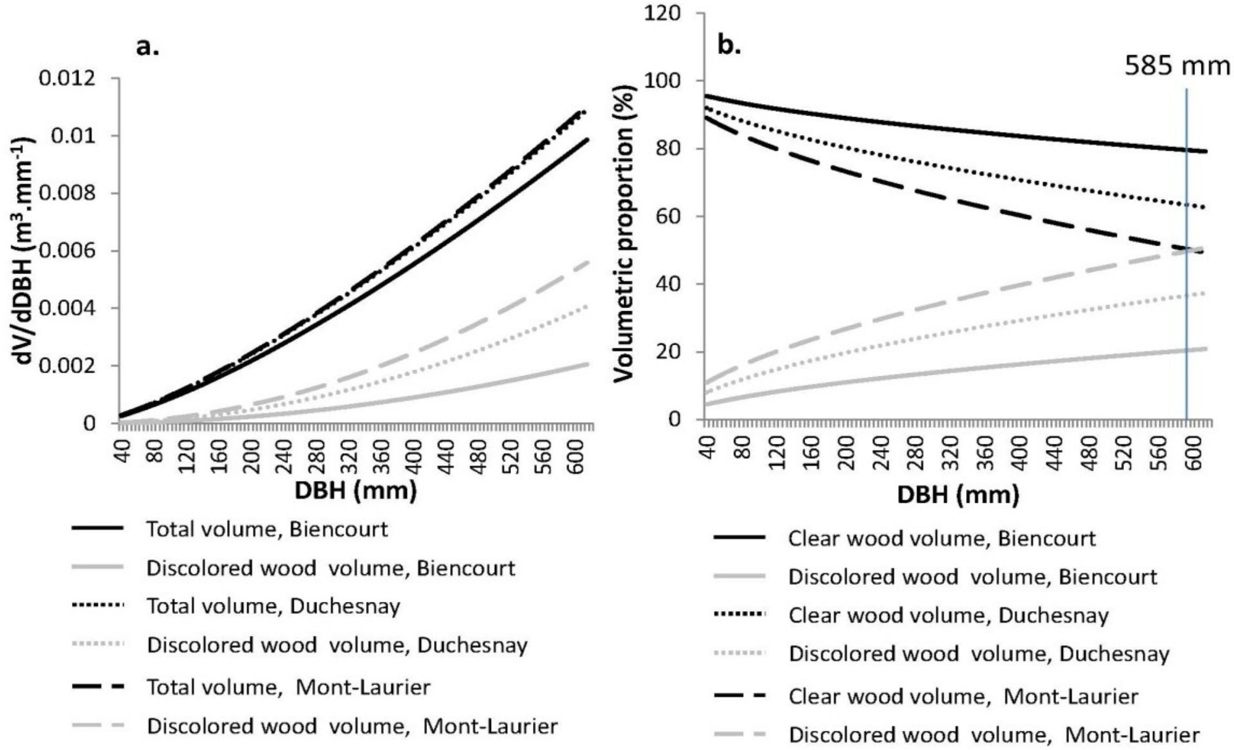

Figure 2-3 (a): Discoloured wood volume (DV) and total stem volume (TV) with increasing tree diameter at breast height (DBH) across sites, (b): proportion of discoloured wood volume (DV) % and proportion of clear wood volume (Total volume under bark-discolored wood volume) % with increasing tree DBH. 'DBH=585 mm' is the threshold points where increase in discoloured wood volume equalizes the increase in clear wood volume at Mont-Laurier. dV= change in volume, dDBH=change in DBH

The slope for discoloured wood volume was greater than that for total stem volume (i.e. $\propto_{1,1} > \propto_{0,1}$), meaning that the rate of increase in discoloured wood volume with increasing DBH is larger than that for clear wood volume (Figure 2-3a). For the Mont-Laurier site, the increase in discoloured wood volume per unit increase in DBH was greater than that for total volume of trees having a DBH > 59 cm (Figure 2-3b). Such a DBH threshold was outside the data range for the other two sites.

Table 2-0-3 Parameters of the linear mixed-effects model fitted to explain the change in total stem volume and discoloured wood volume as tree DBH (mm) varies. Standard error of the corresponding value is given in parenthesis.

Predicted	Random effect parameters			Fixed effect parameters		SD of random effects		Pseudo R^2*
Variables	$a_{0,Biencourt}$	$a_{0,Duchesnay}$	$a_{0,Mont-laurier}$	$\alpha_{t,0}$	$\alpha_{t,1}$	$a_{t,i}$	$\epsilon_{t,ij}$	
Total volume (m^3) (t = 0)	-0.0706	0.0294	0.0412	2.1558 (0.0604)	2.3576 (0.0407)	0.0664	0.3181	0.90
Discoloured wood volume (m^3) (t = 1)	-0.5610	0.1219	0.4391	1.1361 (0.3481)	2.9314 (0.1894)	0.5164	194.6364	0.82

* Includes random effects.

The residuals of total volume and discoloured wood volume were weighted by (DBH) ^ (-0.1157) and (DBH) ^ (-1.0286) respectively with varPower function available in nlme package (Pinheiro and Bates 2000).

2.4.3 Discoloured wood taper

The discoloured wood column can be divided into two sections: below breast height and above breast height (Figure 2-4). In the lower section, discoloured wood radius remained stable or even decreased from stump to breast height for large trees, whereas it increased for small diameter trees. Above breast height, discoloured wood tapered off towards the stem apex. The segmented model accounts for these trends by adjusting the shape of the taper below breast height as a function of DBH. Hence, the negative value of $\beta_1(-0.0437)$ indicates that discoloured wood at stump height is positively related to DBH (Table 2-4). Moreover, the maximum value of the non-linear segment (i.e., above 1.3 m) is also influenced by DBH ($\alpha_0 = 0.2231$), indicating that discoloured wood radius at breast height is positively related to DBH (Table 2-4).

Table 2-0-4 Parameter estimates of nonlinear mixed-effects model for explaining discoloured wood column taper in tree stems

Fixed effect parameters	Estimate	SE	*t*-value	*P*-value
α_0	0.2231	0.006	36.27	<0.001
α_1	-0.1946	0.019	-9.00	<0.001
α_2	0.6330	0.045	13.11	<0.001
α_3	6.2986	1.420	4.29	<0.001
β_0	22.012	5.368	4.08	<0.001
β_1	-0.0437	0.017	-2.60	0.0094
Random effect parameters				
$\sigma_{a0,ij}$	0.056			
$\sigma_{a2,ij}$	0.095			
$\sigma_{\beta1,ij}$	0.054			
σ_{ijk}	11.308			
Autocorrelation parameter				
Φ	0.155			
Fit statistics				
R^{2*} (without random effects)	0.75			
R^{2*} (with random effects)	0.93			

*Calculated as $1 - \sum_{ij}(Y_{ij} - \hat{Y}_{ij}) / \sum_{ijk}(Y_{ij} - \bar{Y}\ )^2$

The negative value for the rate of taper parameter ($\alpha_1 = -0.1946$) indicates that discoloured wood radius is negatively related to height within the tree. The maximum height of the discoloured wood column is positively related to tree height since the offset coefficient is positive ($\alpha_2 = 0.6330$). Finally, the slope of discoloured wood radius is negatively related to the crown ratio ($\alpha_3 = 6.2986$). Visual inspection of the residuals (not shown) and plots of predicted and observed discolouration radii (Figure 2-4) indicate that the model generally followed the trends observed in the data.

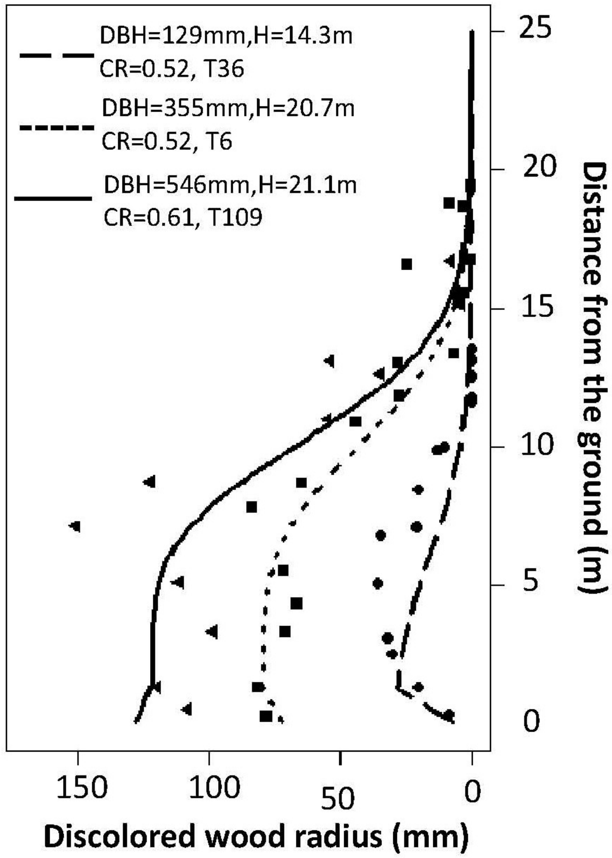

Figure 2-4 Predicted discoloured wood taper in three different sized tree stems. Lines are the predicted values using fixed effects parameters only, circles, squares and triangles are the observed values of the respective trees (tree number: 36, 6 and 109 respectively)

2.5 Discussion

The inverse relationship between the measure of tree vigour (sapwood proportion, live branch basal area supported by per unit stem cross-sectional area and radial growth in last 50 years) and the proportion of discolored wood volume in sugar maple tree stems substantiates the hypothesis: anything that lowers vigour of a tree will then lower the repairing capacity of a tree against wounds and injuries (Shigo 1971), and thus increases discolored wood proportion. The amount of sapwood largely determines the discoloured wood proportion. It was found that the younger trees that have higher proportion of sapwood volume have small proportion of discoloured wood. These trees might have been well able to compartmentalize injuries within small areas because they have a larger proportion of younger tissues, which contain active parenchyma cells with large energy reserves which can be mobilized for tree defense. On the other hand the presence of heartwood in the injured zone accelerates the spread of discoloration (Shortle 1979).

Tree age is another important variable that helped to explain the observed variability in discoloured wood. Older and thus larger trees likely supported bigger (e.g., large dead branches) and older wounds that can increase the coloured heartwood column, where compartmentalisation seems to be harder to implement (Dujesiefken and Stobbe 2002). In addition, the reaction zone formed at the time of wounding can be penetrated by microorganisms after several years, resulting in new discolouration surrounding the initial discoloured wood (Pearce 1991; Dujesiefken and Stobbe 2002).

Some measures of tree vigour such as the ratio of branch to stem basal area and the diameter growth rate were negatively correlated with the volumetric proportion of discoloured wood. Generally, trees that have higher branch basal area per unit of stem cross-sectional area support larger foliar mass (Raulier et al. 1998) and, thus have higher diameter growth (Waring et al. 1981). The higher diameter growth enables faster overgrowth of injuries, thereby making discoloured wood formation less probable (Kadunc 2007). Moreover, tree vigour classification was significantly related to the proportion of discoloured wood, while the stem quality classification was not. This indicates that vigorous trees are able to compartmentalise the wounds effectively.

Entry points for discolouration microorganisms are produced by mechanical injuries exposing the wood, by branch death or by cambial injuries, the occurrence of which likely increases with increasing tree age. One possibility for the introduction of microbes into the stem is through dead branches, given that sugar maple follows area-preserving rule, i.e., trees conserve total cross-sectional area across every branching point (Arastu 1998). The live branch area to stem cross-sectional area at breast height ratio can be used as an indicator of branch mortality because the trees with a larger ratio will have fewer dead branches. The relationship between mechanical injury and discolouration, however, is harder to identify with our dataset. We observed a correlation (r = 0.42, P-value <0.001) between cross-sectional area of discoloured wood columns at breast height and cumulative area of injuries present on tree, regardless of the height from the ground.
However, cumulative area of injuries present on tree was weakly correlated with the proportion of discoloured wood volume (r = 0.22, P-value = 0.03), as has been previously observed by Mishler (2009). The reason could be that the cumulative injury area present on a tree does not convey information about the time since the injury. But the time since injury might be important for explaining discolored wood proportion. Having detailed injury information (e.g., type, size, locale, and time-since-injury) could help reduce the unexplained variation of the discoloured wood column taper, but this would necessitate vertically dissecting the stems.

The rate of increase in discolouration volume with DBH was higher than that of total stem volume. This result is only valid for trees with discolouration, as all of our trees had some. This result is compatible with the findings of Wieman et al. (2004), who concluded that the discoloured wood in sugar maple disproportionately increases as trees get older. Similarly, Erickson et al. (1992) concluded that the proportion of discolouration increases with increasing tree diameter in sugar maple. Kadunc (2007) and Knoke (2003) found similar results for *Acer pseudoplatanus* L., and *Fagus sylvatica*. Likewise, red heartwood occurrence in *Betula papyrifera* was highly correlated with DBH and tree height (Giroud et al. 2008). These results are contrary to those presented by Yanai et al. (2009) for *Acer saccharum*. It could be due to the different history of injury events that might have created different amount of discolored wood proportion as a function of tree age within a site.

The use of grading systems to quantify the amount of discolouration is unclear. We were able to discriminate between tree vigour grades, where healthy trees have lower proportions of discoloured wood, on average, compared to low vigour trees. Although Belleville et al. (2011) did not find any differences in the proportion of discoloured wood volume between tree vigour classes in *Betula papyrifera*, their sample size (n = 12) might have been far too small to make such an inference. In contrast, no statistical differences were observed between the different stem quality grades, although these have been linked to wood product volume recovery (Schneider et al. 2008; Fortin et al. 2009). We thus expected that high quality trees would have lower proportions of discoloured wood than low quality ones since the former have few to no visible defects within the first 5 m. Our statistical analysis did not give any differences in the proportion of discolored wood for different stem quality grades, even if we accounted for the effects of diameter.

The volumetric proportion of discoloured wood was highest at the Mont-Laurier site, followed by the Duchesnay site, and then the Biencourt site. The difference can be partly explained by the average age of the sample trees (Mont-Laurier, 132 years; Duchesnay, 105 years; Biencourt, 92 years) which is consistent with the results of Havreljuk et al. (2013). In addition, this result can be explained by the calcium richness of the Biencourt site since a higher level of calcium availability improves canopy health by reducing branch dieback and enhances the rate of wound closure (Horsley et al. 2002; Huggett et al. 2007). This is consistent with the results of Yanai et al. (2009), who found the lowest mean discoloured wood ratio on carbonate parent material.

2.6 Conclusions

The results consistently converge towards the fact that the proportion of discoloured wood in sugar maple stems increases disproportionately with tree size and age. Vigorous trees characterized by a large volume of sapwood and a limited number of small-sized injuries are likely to contain lower proportions of discoloured wood. Therefore, selection cutting, the principal silvicultural treatment applied in uneven-aged forests dominated by sugar maple, should target the removal of low-vigour trees to concentrate the site growth potential on high-vigour trees with few defects. As proposed by Pothier et al. (2013) in the case of stands containing numerous low-vigour trees, selection cutting should target smaller trees (< 65 cm) of low vigour to reduce the amount of discoloured wood and thus increase the value of harvested trees, without compromising the silvicultural objective of improving the vigour of future stands. In addition, while the intensity of tree removal should be large enough to be financially profitable, it should be kept as low as possible to allow the self-pruning of small branches on pole-stage trees.

2.7 Acknowledgements

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CHAPTER III

Heartwood formation in sugar maple (*Acer saccharum* Marshall)

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Manuscript

3.1 Abstract

Sugar maple heartwood is more susceptible to decay and discoloration than the sapwood. In order to understand heartwood formation, foliage, sapwood, heartwood and discoloured wood areas as well as other biometric variables were measured on 79 trees sampled in two sites in south eastern Quebec, Canada. The data were used to connect tree growth to heartwood formation and discoloration through a modelling approach. Heartwood formation increased with tree height, age and crown size, but decreased with increasing leaf area to stem basal area ratio. Generally, the proportion of discoloured heartwood increased with increasing rate of heartwood formation. However, for trees classed visually as vigorous, the proportion of discoloured heartwood tended to decline with increasing rate of heartwood formation. This indicates that size/age related increase in discoloured wood proportion in sugar maple is possibly due to increasing likelihood of disease and injuries with increasing tree age (or size) and subsequent tree vigour decline. Thus, residual stands composed of high vigour trees can likely maintain higher growth while minimizing discoloured wood proportion in stem logs.

Key words: Discolouration, Heartwood formation, Quebec, Sapwood area, Sugar maple

3.2 Introduction

Sugar maple (*Acer saccharum* Marshall) is an important tree species of North-American temperate deciduous forests. Its quality logs (i.e. free of defects) are used to manufacture veneer, furniture and panelling whereas low grade logs are used for pulp and fire wood (Majcen et al. 2003). Discoloration is one of the most important defects that reduces timber grade (Ohman 1968) and timber value (Erickson et al. 1992; D'Eon and Hamilton 2011; Havreljuk et al. 2014) since discoloured wood is not sought after by consumers. Generally, the discoloured wood column is located in the heartwood area as sapwood is unfavourable to micro-organisms responsible for discoloration (Boddy and Rayner 1983).

The heartwood area is composed of xylem tissues, which contains little or no starch (Hillis 1987). It is formed when a vessel is plugged by air (Priestley 1932; Sperry et al. 1991a) which is followed by subsequent histo-chemical changes (Hillis 1968). Although there are several hypotheses to explain heartwood formation (Taylor et al. 2002), they converge towards two points, viz. (1) parenchyma cells in sapwood have reached a maximum age and (2) their senescence is related to foliage death that eliminates the need for water transport from roots to leaves (Sievänen et al. 1997a; Schneider et al. 2011; Hari et al. 2013).

Unlike the heartwood of tropical hardwoods and some native species of Quebec (e.g. *Prunus serotina*, *Juglans nigra*), dark coloured sugar maple wood (e.g. discoloured wood) is composed of tissues that are altered in color when cell constituents are changed

(Shigo et al. 1984) through plugging of vessels, formation of polyphenols and deposits of dark material as a result of injury and infection (Ohman 1968; Shigo et al. 1984). It appears after the wood vascular cambium and phloem are exposed by wounds or branch death (Shortle and Dudzik 2012). However, the amount of discoloured wood depends on the efficiency of the tree's defense system (Shigo et al. 1984). The extractives found in the heartwood generally provide a weak and static defense against pathogen spread in the heartwood tissues. On the other hand, sapwood has a strong dynamic defense system which consists of compartmentalizing wood discolouration (Shigo and Marx 1977). As detailed by Shigo and Marx (1977), trees compartmentalize wounds or injuries by developing four walls of defense to isolate the affected area by forming a watertight compartment. Boddy and Rayner (1983) added that the high moisture content and associated restriction of aeration in sapwood limits microorganism's activity and provides strong defense.

Defense capacity is normally high as long as wood lumens are saturated by bounded and free water (Shigo and Hillis 1973; Pearce 1996; Schwarzee 2007). In sugar maple, sapwood is only composed of a certain proportion of the outer layer of wood which is physiologically active for sap conduction (Pausch et al. 2000; Raulier et al. 2002) and for storing reserve materials such as starch (Ewers et al. 2002). The physiologically inactive heartwood is more susceptible to discolouration because of reduced moisture content and presence of dead cells (Good et al. 1955). Once old tissues of trees are infected by microorganisms, the discolouration may thus expand radially and longitudinally due to a gradual succession of microorganisms over time (Shigo and Hillis 1973). As a result, the proportion of discoloured heartwood in maples increases with tree age (Kadunc 2007; Havreljuk et al. 2013). In addition to the accumulation of old tissues with time, tree vigour generally decreases with tree age (Binkley et al. 2002). Hence, a smaller amount of discoloured heartwood is generally observed in young trees (Shigo et al. 1984; Baral et al. 2013) as such trees are more resistant to stress (Dobbertin 2005).

To understand whether the disproportionate increase of discoloured heartwood with tree size (and/or age) is related to heartwood formation, the following hypotheses were tested. Compared to less vigour trees, we expect that the larger leaf area of vigorous trees can reduce the rate of sapwood turnover and increase the sapwood formation. We further hypothesized that: (1) the rate of sapwood formation is greater for vigorously growing trees, which means that the ratio of heartwood formation to tree growth is smaller for more vigorous trees; and (2) the lower rate of heartwood formation in more vigorous trees is associated with a lower proportion of discoloured wood. Hence, this study aimed at establishing a functional link between tree characteristics and heartwood formation and discoloration in sugar maple trees. Such relationships can support the development of silvicultural treatments to promote diameter growth while minimizing discoloured wood proportion in sugar maple stems.

3.3 Methodology

3.3.1 Study sites

We sampled trees from two sites around Mont-Laurier and Biencourt located in south-eastern Quebec, Canada. These two sites are respectively located at 46.65º N and 75.64º

W, and 48.01º N and 68.50º W. The topography of both sites is hilly with slopes up to 15º, which comes with well-drained soils. According to Robitaille and Saucier (1998), average annual precipitation is approximately 1000 mm for both sites whereas the mean annual temperature at Mont-Laurier is 2.5 to 5 ºC, and 2.5 ºC at Biencourt.

Table 3-0-1 Main bio-climatic characteristics (based on Robitaille & Saucier, 1998) of the study sites and sample tree characteristics. Range values are given in parenthesis. '*' indicates standard error of the corresponding value.

		Sites	
S.N.	Description	Mont-Laurier	Biencourt
1	Location	46.65°N, 75.64°W	48.01°N, 68.50°W
2	Elevation (m)	475	380
3	Topography	High hills, well drained, 15° slope	Hills, well drained, 15° slope
4	Bioclimatic domain	Sugar maple-yellow birch domain	Balsam fir-yellow birch domain
5	Parent bedrock	Igneous or metamorphic	Sedimentary
6	Annual rainfall (mm)	1000	1000-1100
7	Mean annual temperature (°C)	2.5-5	2.5
8	Mean tree age (years)	132 (53-254)	92 (41-152)
9	Mean height (m)	18.9 (7.3-24.1)	19.1 (7.8-23)
10	Mean diameter at breast height (mm)	338 (71-550)	335 (68-546)
11	Mean HFLB (m)	8.5 (1.6-13.3)	6.3 (1.5-9.8)
11	Mean crown diameter (m)	6.4 (3.2-10.4)	6.6 (2.7-10.6)
12	Mean leaf area (m^2)	130.3 (10.2-388.2)	186.2 (17.3-464.2)
13	Mean leaf area leaf mass ratio (m^2 Kg^{-1})	12.13 (8.39-23.15)	18.51 (13.17-45.5)
14	Mean sapwood area (cm^2)	369.4 (8.8-799.0)	337.3 (7.0-617.5)
15	Mean stand basal area (m^2 ha^{-1})	24.71 (0.83)*	26.73 (1.95)*
16	Total number of trees	39	40

The forest type at Mont-Laurier belongs to the sugar maple (*Acer saccharum*Marsh.)-yellow birch (*Betula alleghaniensis* Britt.) whereas that of Biencourt belongs to the balsam fir (*Abies balsamea* (L.) Mill.)-yellow birch forest type. Both sites are considered to be at the northern limit of the temperate forest. The stand basal areas at Mont-Laurier and Biencourt were 24.7 and 26.7 m^2 ha^{-1}, respectively (Table 3-1).

3.3.2 Field measurements and calculations

We sampled 39 trees from Mont-Laurier and 40 trees from Biencourt (Table 3-1), so as to have a large range of tree diameters at breast height (DBH between 68 and 585 mm), and properly represented all tree vigour classes of the MSCR classification (Boulet 2005).The MSCR system classifies the standing trees on the basis of their vigor: the M class (mortality) corresponds to trees that are likely to die before the next harvest (15-25 years); the S class (survival) to trees that are defective, whose timber volume may decrease, but likely to survive until the next harvest; the C class (conserved) to trees whose merchantable volume should not deteriorate until the next harvest; and the R class (retained) to vigorous trees. Moreover, trees with a DBH smaller than 23.1 cm were not graded and assigned to class 'O' (Other).

Before felling the sample trees, tree height, DBH and height of the first living primary branch (HLFB) were noted. Then, crown radii along four radial directions (N, E, S, and W) were measured from the centre of the bole of each tree to the edge of its crown, which was determined by vertical sighting (Russell and Weiskittel 2011). Quadratic mean crown radius was calculated from the four measured crown radii.

Once the trees were felled, we measured the diameter and height of all primary branches. Then, a randomized branch sampling (RBS) technique was applied for foliage mass estimation (Valentine et al. 1994). The sample tree crowns were divided into thirds. Two first order branches were selected at random from each third with probability proportional to the diameter squared. These branches were further sub-sampled using RBS. Two paths were followed in each selected first-order branch so as to have two foliage samples per branch. Each path consisted of a randomly chosen branch emanating from each node from the beginning of the selected first-order branch. In each branch, the first segment of each path was the first segment of the first-order sampled branches. Foliage, when shoot diameter was less than 15 mm, was picked off, tagged and bagged with an identifying code and its unconditional probability of selection was recorded. Five fresh leaves were randomly selected from each shoot sample and pressed in newspaper and transported to the laboratory for leaf area and leaf-mass ratio measurement. In the laboratory, leaves and twigs were separated from the terminal shoots and we weighed the air dry mass. Twenty subsamples of known mass of leaves and twigs were selected and dried at 70 °C until a constant mass was obtained. Leaf area of the pressed leaves was determined using WinFolia (2005) software and then the samples were dried and weighed to get the dry leaf mass. Leaf area for each sample branch was estimated using Eq. 1. An inflation factor (the ratio of total primary branch basal area to sample branch basal area) times sample branch leaf area provided an inflated tree level leaf area. The inflated leaf area obtained from all the sample branches of a sample tree were averaged to obtain leaf area estimate of the tree.

$$\widehat{B_{LA}} = 1/2 \sum_{i=1}^{2} \frac{y_i}{p_i} \quad (1)$$

where,

$\widehat{B_{LA}}$= Leaf area of sample branch

y_i= Leaf area of the foliage sample (i)

= (leaf mass of the sample (i) × leaf area to leaf mass ratio of sample (i))

p_i= Unconditional probability of sample (i)

Disks were cut from each sample tree at breast height (1.3 m) and transported to the laboratory. We defined three different wood types on these disks i.e. sapwood, clear heartwood, and discoloured heartwood (Figure 3-1a). The sapwood (defined here as starch storing sapwood cells) compartment was identified by staining each freshly cut wood disk with 2.5% potassium iodide iodine (IKI) solution (Kutscha and Sachs 1962). This allowed us to delineate the boundaries between sapwood, clear heartwood (defined as the parenchyma cells that are devoid of starch which was neither discoloured nor stained with IKI solution) and discoloured wood. Bark width, sapwood, clear heartwood and discoloured heartwood radii were then measured in eight radial directions. Quadratic mean radius for each wood component was calculated from the eight radial measurements as suggested by Wiemann et al. (2002) to obtain the least biased measurement of the irregular shape of the discoloured wood and tree bole. The area of each compartment was then calculated with the quadratic mean radii, assuming that the radii of each compartment were concentric rings in the following order from pith to bark: discoloured heartwood, clear heartwood and sapwood. In addition, after the disks were sanded with 80 and 120 grit sanding paper, we counted and measured the number and width of each annual growth ring in two radial directions perpendicular to each other using the OSM 3.65b Software (SCIEM). This information was then used to determine the age and calculate the mean annual radial and basal area growth at breast height.

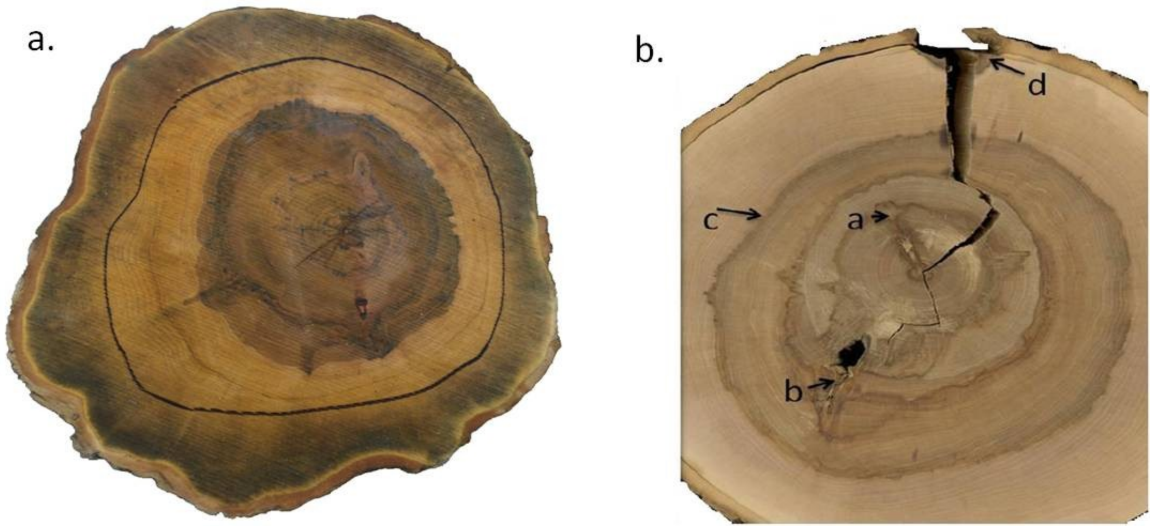

Figure 3-1 (a) Delineation of Sapwood, heartwood and discoloured wood boundaries after staining with 2.5% IKI solution (b) Discoloured wood at different stages ('a', 'b' and 'c' indicate different injuries and associated discolouration, 'd' indicates compartmentalized injury at functional sapwood, not connected to discoloured wood column

3.3.3 Data analysis

3.3.3.1 Sapwood area

As the preliminary analysis indicated that sapwood area increases nonlinearly with increasing tree size, a non-linear model was fitted using generalized least squares method in the *nlme* package (Pinheiro et al. 2015) to establish the relationship between sapwood area and tree characteristics:

$$A_{s,ij} = BA_{ij} \times H_{ij}^{(X\beta)} + \varepsilon_{ij} \quad (2)$$

where:

$A_{s,ij}$ is the sapwood area (cm^2) at breast height (1.3 m) of tree j in site i

BA_{ij} is the inside bark basal area (cm^2) at breast height (1.3 m) of tree j in site i

H_{ij} is the tree height (m)of tree j in site i

β is the parameter vector

X_{ij} is the covariate matrix

ε_{ij} is the random error, $\varepsilon_{ij} \sim N(0, \sigma^2)$

Statistical significance of the site was verified by inserting a site random component in the exponent term. The changes in AIC, BIC and likelihood ratio were used to assess its usefulness. The AIC, BIC and likelihood ratio tests were used in a forward stepwise approach to include tree level covariates. Homoscedasticity and the assumptions of normality of the residuals were verified visually. The exponent term of equation (2) was found to be equation (3), which included tree age, crown surface area (computed from crown length and crown radius assuming a parabolic crown shape) and the leaf area per unit basal area.

$$X\beta = \beta_0 + \beta_1 \times Age_{ij} + \beta_2 \times CSA_{ij} + \beta_3 \times \left(\frac{A_{L,ij}}{BA_{ij}}\right) \quad (3)$$

where:

β_0, β_1, β_2 and β_3 are the parameters to be estimated.

Age_{ij} is the total number of annual rings counted at breast height (years) of tree j in site i

CSA_{ij} is the crown surface area of the tree (m^2) of tree j in site i

$A_{L,ij}$ is the leaf area (m^2) of tree j in site i

Heteroscedasticity was modelled using a constant plus power variance function (Pinheiro and Bates 2000):

$$Var\ (\varepsilon_{ij}) \sim \sigma^2 (\delta_{1,ijl} + |BA_{ij,l}|^{\delta_{2,ijl}})^2 \quad (4)$$

where: k=1 and 2, and l=M, S, C, R and O of the MSCR class as a grouping factor.

3.3.3.3 Heartwood formation

Heartwood formation of a tree for a given time period is given by :

$$dA_H = dBA - dA_S \quad (5)$$

where:

$$dBA = BA_{(t)} - BA_{(t-1)} \quad (6)$$

$$dA_S = A_{S(t)} - A_{S(t-1)} \quad (7)$$

dBA was obtained from the measurement of basal area growth at breast height whereas $dA_S$was estimated from Eq. (7) in which $A_{S(t)}$ and $A_{S(t-1)}$ were computed as shown in Eq. (8).

$$dA_S = (BA_t \times \widehat{H}_t^{(b_0 + b_1 AGE_t + b_2 \widehat{CSA}_t + b_3 (\frac{\widehat{A_{L,t}}}{BA_t})}) - (BA_{t-1} \times \widehat{H}_{t-1}^{(b_0 + b_1 AGE_{t-1} + b_2 \widehat{CSA}_{t-1} + b_3 (\frac{\widehat{A_{L,t-1}}}{BA_{t-1}})}) \quad (8)$$

Eq. (8) requires prediction models for tree height, leaf area and crown surface area to estimate the corresponding values of these variables at time (t) and (t-1). Thus, the prediction models (Appendix 1, Eq. 1, 2, 3) for tree height, leaf area and crown surface area were calibrated with either nonlinear (Appendix 1, Eq. 1) or linear equations (Appendix 1, Eqs. 2 and 3). H , A_L and CSA were estimated for time (t) and (t-1) from equations 1, 2 and 3 (Appendix 1) using $BA_{(t)}$and $BA_{(t-1)}$ as the predictors.

3.4 Results

3.4.1 Sapwood area and sapwood proportion

Tree sapwood area at breast height for a given basal area was found to scale allometrically with tree height (Eq. 5). The model describes adequately the data (Figure 3-2) and no serious departures from the model assumptions were noticed (result not shown).

Table 3-2 Parameter estimates of sapwood area model (equation 5, R2=0.77*)

Parameters	Estimates	SEE	t-value	P-value
β_0	-0.1779	0.0375	-4.7499	0.000
β_1	-0.0004	0.0002	-1.9857	0.050
β_2	-0.0006	0.0002	-3.3217	0.001
β_3	0.1855	0.0829	2.2366	0.028

$* \, Pseudo \; \mathrm{R}^2 = 1 - \sum_{\mathrm{ij}} (\mathrm{Y_{ij}} - \hat{\mathrm{Y}}_{\mathrm{ij}}) / \sum_{\mathrm{ijk}} (\mathrm{Y_{ij}} - \overline{\mathrm{Y}} \;)^2$

The amount of sapwood area for a given basal area and tree height decreased with tree age ($Table\ 3-2, b_1 = -0.0039$) and crown surface area ($Table\ 3-2, b_2 = -0.0006$) and increased with leaf area per unit stem basal area ($Table\ 3-2, b_3 = 0.1855$).

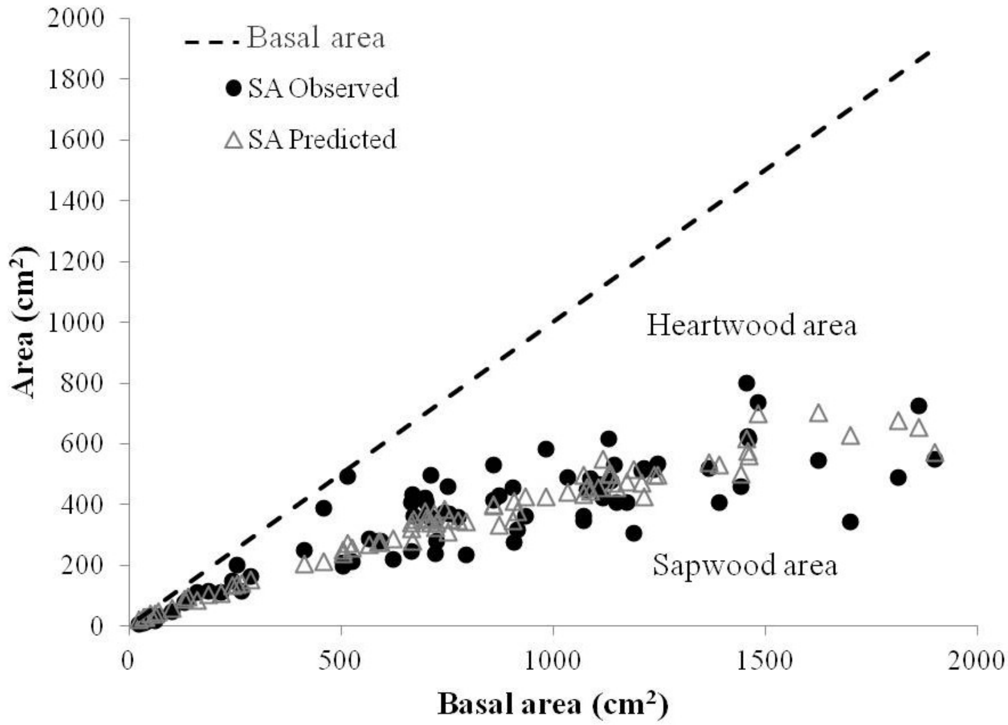

Figure 3-2 Observed and predicted sapwood area as a function of tree basal area.

Sapwood proportion in a tree can be estimated by dividing both sides by stem basal area inside bark using Equation 2. Figure 3-3 shows that observed and predicted sapwood proportion followed similar trends with four different tree characteristics except for four supressed trees (H<10 m). Sapwood proportion decreased with tree age (Figure 3-3A), height (Figure 3-3B), and crown surface area (Figure 3-3C); and increased with leaf area to tree basal area ratio (Figure 3-3D).

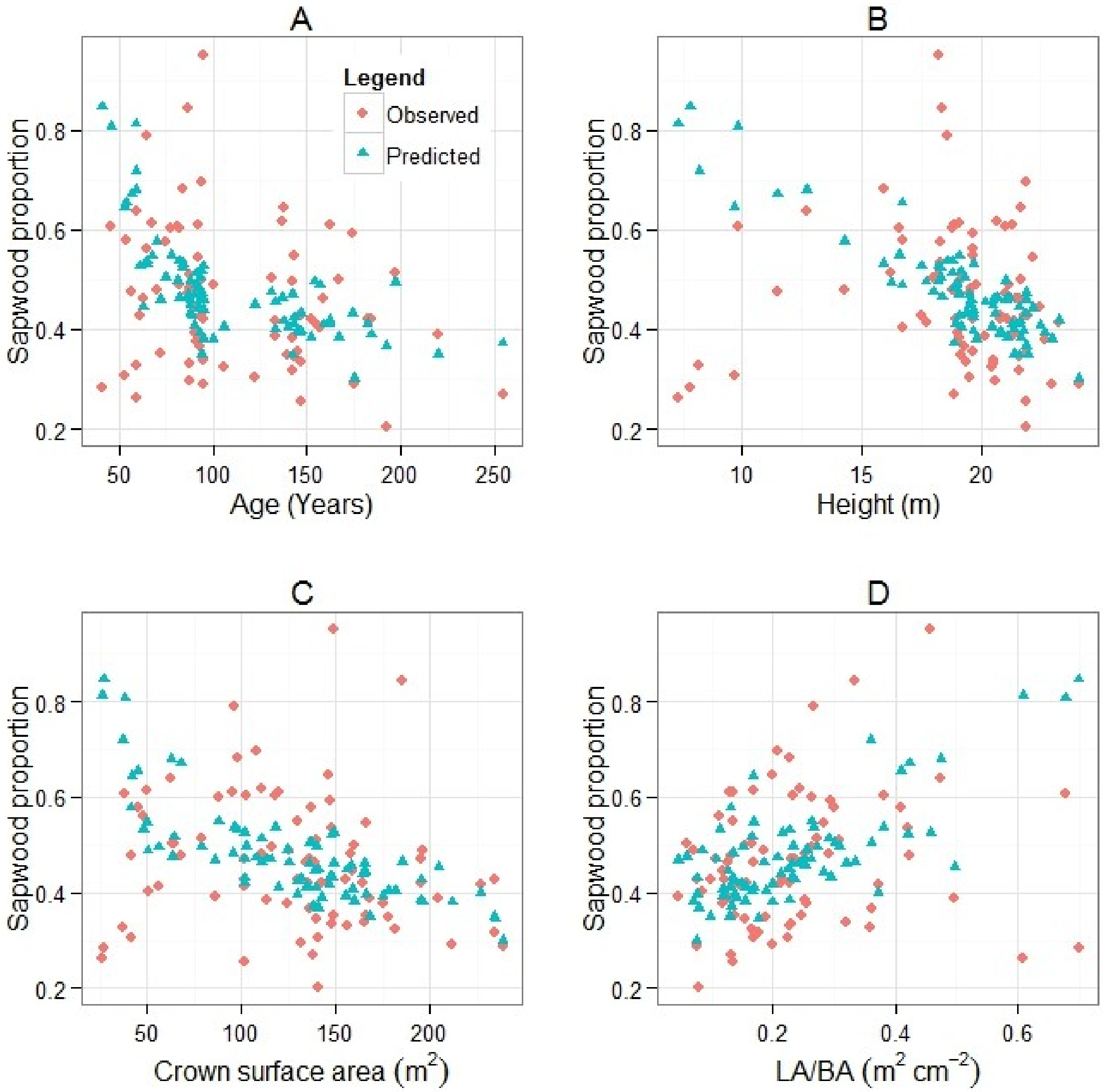

Figure 3-3 Variation of sapwood proportion with different tree characteristics (A) age of the tree, (B) tree height, (C) crown surface area, and (D) leaf area per unit stem basal area (filled circles= observed values, open triangles= predicted values)

3.4.2 Heartwood formation

Heartwood area at breast height was found to increase with tree basal area as the difference between the 1:1 line and the sapwood area curve increases with BA (Figure 3-2). The estimated rate of heartwood formation (dHA), calculated from equations 5 to 8, per basal area increment was smaller (40-60% of dBA) for small trees ('O' class<230 mm DBH) whereas it increased up to 60-90% of dBA for larger trees (DBH>230 mm) (Figure 3-4). The increasing pattern of the ratio of heartwood formation to basal area growth with tree size (BA) was similar for all MSCR categories irrespective of site (Figure 3-4).

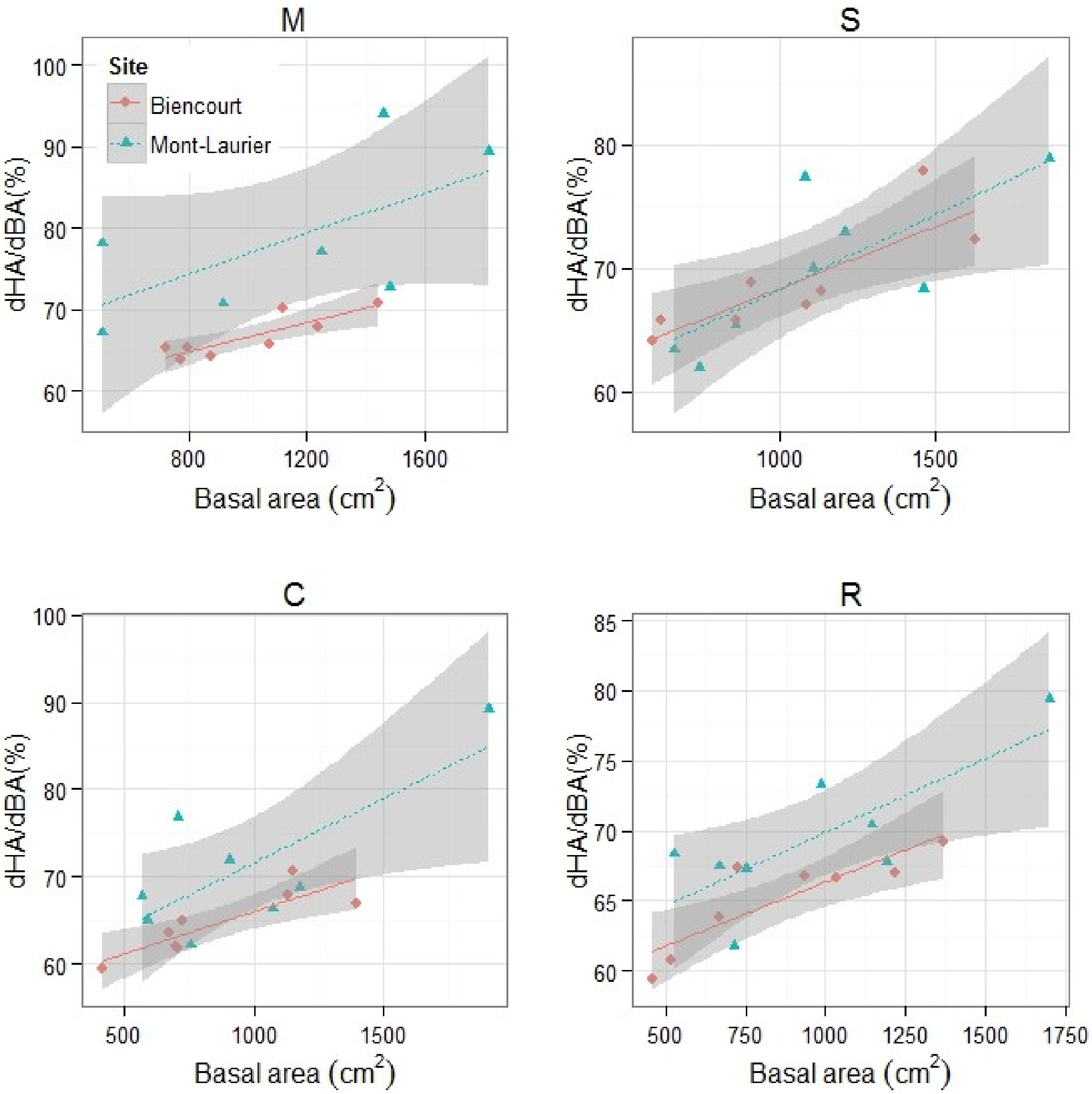

Figure 3-4 Relationship between the ratio of heartwood growth to tree growth (dHA/dBA) and tree size among the trees of different vigour classes per site (MSCR: M=Mortality, S=Survival, C= Conserved and R=Retained). The shaded area represents the confidence interval at 95% significance level.

3.4.3 Heartwood discolouration

The proportion of discoloured heartwood (DA/HA) generally increased with increasing ratio of heartwood formation to basal area growth (dHA/dBA) (Figure 3-5).

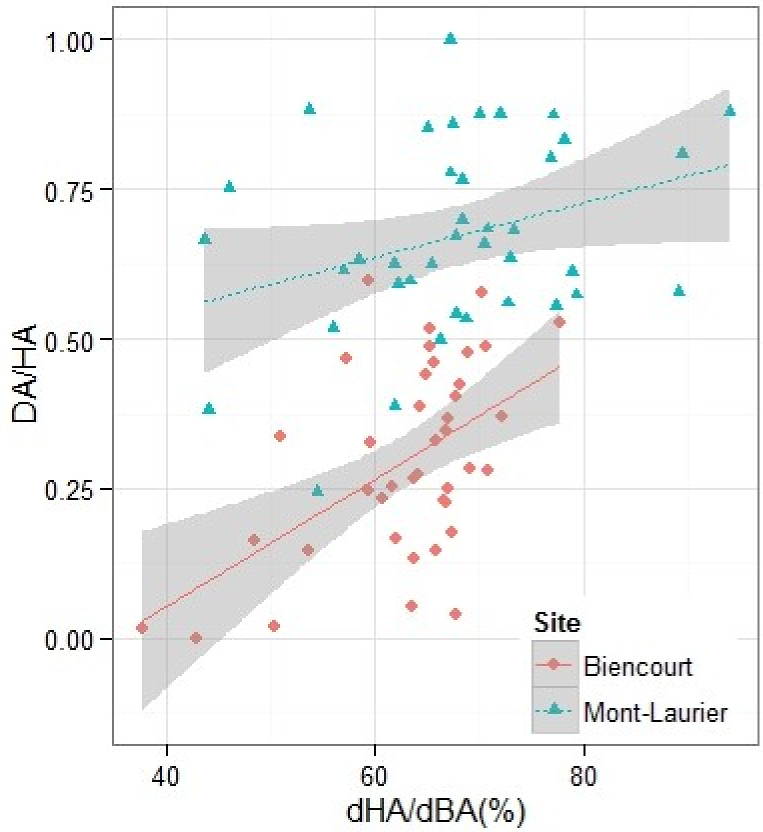

Figure3-5 Proportion of discoloured heartwood with the rate of heartwood formation. The shaded area represents the confidence interval at 95% significance level.

However, the proportion of discoloured heartwood was found to decrease with increasing ratio of heartwood formation to basal area growth for more vigorous trees (class R) for both sites unlike trees classified in M, S and C classes (Figure 3-6).

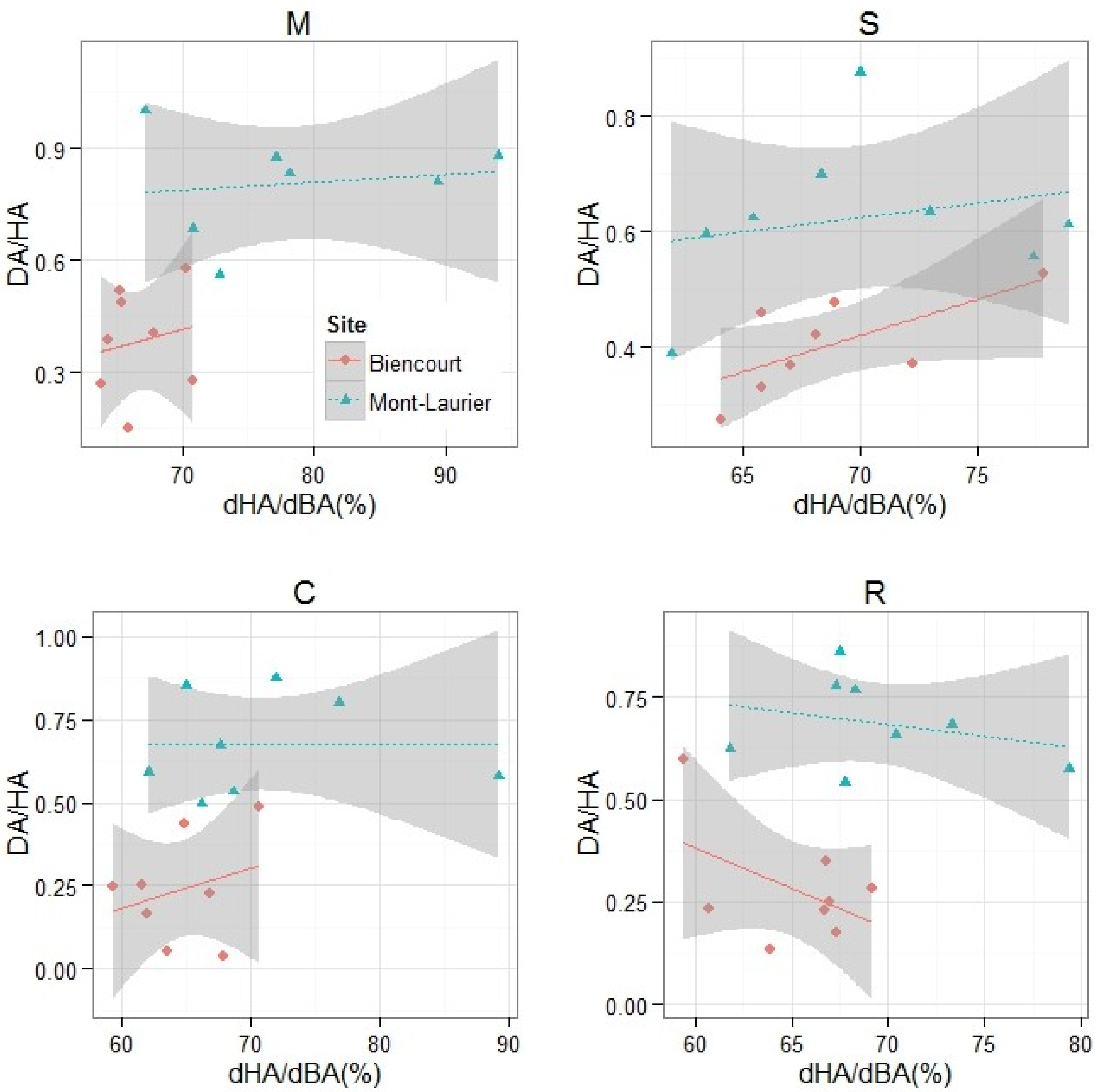

Figure 3-6 Relationship between proportion of heartwood discoloured (DA/HA) and ratio of heartwood growth to tree growth (dHA/dBA) among different vigour class trees growing at two different sites of Quebec, Canada (MSCR: M=Mortality, S=Survival, C= Conserved and R=Retained). The shaded area represents the confidence interval at 95% significance level.

3.5 Discussion

We established a link between tree and crown dimensions, sapwood area, sapwood to heartwood conversion, and discoloured heartwood. To achieve this, a nonlinear model was calibrated to predict the cross-sectional area of sapwood at breast height using tree height, age, crown surface area and leaf area per unit stem basal area as predictors. Proportion of sapwood area decreased with tree height, age and crown surface area and increased with foliage area per unit stem basal area. This is in accordance with results showing that the rate of heartwood formation increases with tree height (Hölttä et al. 2013), age (Hillis 1968; Schneider et al. 2011), and crown size (Stokes and Berthier 2000) while it decreases with increasing leaf area (Sievänen et al. 1997a; Schneider et al. 2011). Calculating the change in sapwood area from time *t-1* to *t*, we were able to quantify the heartwood formation for different tree sizes using average basal area increment of the last five years. The relationships between basal area growth, heartwood formation and discoloration among different tree vigour categories were thus established.

The positive relationship between sapwood proportion and leaf area per unit stem basal area and the negative relationship between sapwood proportion and tree height and age indicate that the hydraulic supply not only depends sapwood area but also depends on sapwood permeability (England and Attiwill 2007). Dominant trees with larger crowns have higher rates of transpiration which is quite likely to lead to higher rates of embolism (Zimmermann and Brown 1971; Maherali and de Lucia 2000; Cochard 2006; Ogasa et al. 2013). However, such trees are more vital and can support higher leaf area per unit sapwood area because vital trees have higher hydraulic conductivity (McCulloh et al. 2003) as they form wider growth rings that consist of larger diameter vessels (Fan et al. 2012; Tulik 2014).

As trees grow, the amount of sapwood is adjusted to the tree requirements by forming heartwood (Bamber 1976). Indeed, the vessels located at the sapwood-heartwood boundary experience higher hydraulic constraints with tree size and age (Sperry et al. 1991a) because taller trees require higher tension to move water up from the roots if stomatal conductance and sapwood to foliage ratio remain constant (Dixon and Joly 1894; Ryan and Yoder 1997; Tyree 1997). Although tall trees can reduce resistance to water transport by producing more permeable xylem elements (Pothier et al. 1989; Ogasa et al. 2013), still the gravitational resistance cannot be fully compensated (Mencuccini and Grace 1996). Tension beyond the limit of xylem endurance causes embolisms (Cochard 2006) which are more frequent in older vessels located near the sapwood-heartwood boundary since they have larger openings due to degradation of their pit membrane (Sperry et al. 1991a). This will consequently lead to dysfunction of older sapwood and initiate heartwood formation.

In accordance with our observation of higher ratio of heartwood formation to basal area growth with increasing tree basal area, higher heartwood formation rates were reported for larger trees (Selin 1994; Taylor et al. 2002; Morais and Pereira 2007; Beauchamp 2011; Tewari and Mariswamy 2013). Hence, our second hypothesis stating that the ratio of heartwood formation to tree growth is smaller for more vigorous trees was not supported by our results as no such trend was observed in each tree vigour class. This suggests that heartwood formation is a size related process regardless of tree vigour.

The proportion of discoloured heartwood generally increases with increasing heartwood proportion likely because the non-functional heartwood tissues are more susceptible to discoloration (Shigo and Hillis 1973; Boddy and Rayner 1983). However, despite a higher rate of heartwood formation in vigorous trees (i.e. R class), their proportion of discoloured heartwood was lower than in less vigorous trees, as expected in our third hypothesis. This indicates that the basal area growth rate of trees with little or no injuries is higher (Hartmann et al. 2008) than their discoloured wood growth rate. The reason is that the rate of heartwood formation is strongly correlated to the basal area growth rate ($r=0.81$, $p<0.01$) but discoloured wood growth rate is limited due to lower levels of oxygen in trees without injuries (Shortle and Dudzik 2012). The increase in discoloured wood proportion with tree size/age for sugar maple trees (Erickson et al. 1992; Havreljuk et al. 2013; Baral et al. 2013) is likely due to an increasing likelihood of disease and injuries (biotic and abiotic) with increasing tree age or size and subsequent decline on tree vigour with increasing tree size (Pothier et al. 2013). Thus, a silvicultural treatment that can maintain a high proportion of vigorous trees (R class) in the residual stand is likely to have higher growth (Hartmann et al. 2008) while minimizing heartwood discolouration. However, this conclusion may not be applicable for stands composed of very large trees as we sampled trees with DBH<60 cm.

3.6 Conclusion

As trees grow, the amount of sapwood is adjusted by heartwood formation. Therefore, the rate of heartwood formation increases with increasing tree size. Although the rate of heartwood formation is higher for larger trees, the proportion of discoloured heartwood does not necessarily increase with increasing rate of heartwood formation. The proportion of discoloured heartwood increases with the rate of heartwood formation only for trees that are associated with several apparent stem damages (M, S and C classes). Thus, the disproportionate increase in discoloured heartwood proportion with tree size observed by Baral et al. (2013) is most likely due to the higher likelihood of tree damage with increasing tree size/age and subsequent tree vigour decline, rather than the increasing rate of heartwood formation with increasing tree size. Therefore, selection cutting using advisedly a tree vigour classification system would likely maintain or improve stand vigour while keeping a minimum rate of change of discoloured heartwood proportion.

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3.9 Appendix 1: Supplementary information

Supplementary information related to (a) tree height and stem basal area relationship, (b) leaf area and stem basal area relationship, and (c) tree height and crown surface area relationship

The prediction models (Eq. 1, 2, 3) for tree height, leaf area and crown surface area using basal area were calibrated with either nonlinear (eq. 11) or linear (eq. 12and 13) regressions.

$$H = b_{1,0} \times \left(1 - e^{\left(-e^{(b_{1,1})} \times \left(\sqrt{BA} - b_{1,2}\right)\right)}\right) + \epsilon_{1,i} \tag{1}$$

$$Ln(A_L) = (b_{2,0} + b_{2,ML}) + b_{2,1} \times Ln(BA) + b_{2,2} \times Ln(H) + \epsilon_{2,i} \tag{2}$$

$$Ln(CSA) = (b_{3,0} + b_{3,ML}) + b_{3,1} \times Ln\ (BA) + \epsilon_{3,i} \tag{3}$$

where:

$b_{1,0}$,$b_{1,1}$,$b_{1,2}$,$b_{2,0}$,$b_{2,1}$,$b_{2,2}$,$b_{3,0}$,$b_{3,1}$ are the parameters to be estimated.

$b_{2,ML}$,$b_{3,ML}$are Mont Laurier site specific parameters

$\epsilon_{1,i}$,$\epsilon_{2,i}$,$\epsilon_{3,i}$ are the residuals related to the corresponding models, $\varepsilon_{ij} \sim N(0, \sigma_{ij}^2)$

Log transformation bias was corrected for the predictions of equations (2) and (3) according to equation 14 (Sprugel 1983).

$$CF = e^{\left(\frac{SEE^2}{2}\right)} \tag{4}$$

where,

CF is the log transformation correction factor, and

$$SEE = \sqrt{\sum(\text{Ln}\, Y_i - \widehat{LnY_i})^2 / (N - K)} \tag{5}$$

where,

LnY_i= Natural logarithm of observed dependent (Y) variable

$\widehat{LnY_i}$=Natural logarithm of corresponding predicted(Y) variable

N= number of observations

K= number of parameters in the model

Parameter estimates for equation 1, 2 and 3 are presented in following table.

Model	Parameters	Estimates	SEE	CF	R^2
Height	$b_{1,0}$	21.0364	0.3223	NA	0.83
	$b_{1,1}$	-2.0620	0.1268		
	$b_{1,2}$	2.0293	0.7250		
Leaf area	$b_{2,0}$	1.9705	0.7922	1.11	0.74
	$b_{2,ML}$	-0.4522	0.1021		
	$b_{2,1}$	0.9721	0.1126		
	$b_{2,2}$	-1.0947	0.4657		
Crown surface area	$b_{3,0}$	2.0785	0.1990	1.04	0.73
	$b_{3,ML}$	-0.2232	0.0601		
	$b_{3,1}$	0.4326	0.0305		

CHAPTER IV

Effects of competition on clear wood production in sugar maple (*Acer saccharum* Marshall) trees

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Manuscript

4.1 Abstract

The white coloured, clear wood of sugar maple (*Acer saccharum* Marsh.) is highly sought after for appearance products. With the aim of being able to explore silviculture techniques to increase clear wood volume for a given sugar maple diameter tree, we investigated the effects of competition on tree crown and stem characteristics. Tree characteristics were determined for 91 sample sugar maple trees from three uneven-aged stands in eastern Canada. Stem disks were collected to determine the proportion of clear and discoloured wood at different heights along the main stem. Linear and non-linear mixed effects models were developed to assess the effects of competition on tree crown and clear wood volume. Results indicate that competition reduces crown diameter. Percent clear wood volume is positively affected by crown diameter and negatively by tree size. Bole length and stem form factor increased with height of the biggest branch. From these results, we expect that clear wood volume would be optimized by exposing sugar maple trees to high levels of competition during sapling and pole stages to promote height growth and self-pruning, and by decreasing competition at later stages to help develop vigorous crowns.

Key words: tree competition, crown characteristics, clear wood volume, northern hardwood stands

4.2 Introduction

In North America, sugar maple (*Acer saccharum* Marshall) is widely distributed in the northern hardwood forests that extend from New England and the Great Lakes of the United States to the St. Lawrence River Valley and Acadian regions of Canada (Pond et al. 2014). Sugar maple stands are economically important for supplying high quality timber (Majcen et al. 2003). However, the financial value of sugar maple logs depends upon their quality, with higher values associated with high quality veneer logs (207-218 USD m^{-3})[1] compared to low quality saw logs (72 USD m^{-3}) (Keys and McGrath 2002; D'Eon and Hamilton 2011).

Higher quality sugar maple wood is generally obtained from the stem section below the first branch. To produce a veneer quality log, a sugar maple tree must have very little sweep and a high proportion of white-coloured wood (Wiedenbeck et al. 2004), hereafter referred to as clear wood. Accordingly, dark-coloured wood (hereafter referred to as discoloured wood) strongly reduces log values when present (Ohman 1968; Erickson et al. 1992). The proportion of clear wood volume generally increases with tree vigour (Baral et al. 2013), and decreases with tree age (Erickson et al. 1992; Havreljuk et al. 2013; Baral et al. 2013). Moreover, bole injuries that are induced by branch mortality are likely to reduce the proportion of clear wood (Ohman 1968; Shigo and Marx 1977; Shortle and Dudzik 2012).

[1] Dollar values are based on July 2008.

Northern hardwood forests are often managed through selection cutting to improve both tree vigour and stem quality, while mimicking the general tree-scale mortality that is observed in these stands (Nyland 2002). This treatment provides more growing space for the residual trees and promotes the establishment of shade-tolerant tree seedlings. Trees respond to the larger growing space by increasing their crown size (Rouvinen and Kuuluvainen 1997; Thorpe et al. 2010) to optimize light capture (Valladares and Niinemets 2007). An increase in crown size can be achieved through a reduction in self-pruning (Nicholson et al. 2010) and/or an increase in branch growth or elongation (Maguire et al. 1991; Groot and Schneider 2011). From a wood production standpoint, this increase in crown size can be significant, since it can improve both wood growth (Wyckoff and Clark 2005) and properties (Larson 1969). For example, the larger diameter growth associated with large crown trees corresponds to wider sapwood to maintain a balance between transpiring leaves and transport tissues (Shinozaki et al. 1964; Whitehead et al. 1984). In addition to having a white colour, this larger quantity of sapwood is thought to improve the compartmentalization efficiency when trees are injured, which in turn can further reduce the proportion of discoloured wood (Shigo and Marx 1977).

Understanding the interactions between aboveground competition, crown characteristics, and clear wood proportion can provide important guidelines for increasing the production of high quality sugar maple trees. This paper thus explores these interactions in relation to clear wood volume up to different merchantable limits (9 and 24 cm top diameter). In this context, we assumed that under high competition, trees have shorter and narrower crowns, and lower stem diameter growth compared to low competition trees. As a result, a tree of a given diameter growing under more competition will be older and have more injuries due to branch death. We thus hypothesize that trees growing under high level of competition have lower proportion of clear wood volume as older trees are associated with a higher proportion of discoloured wood volume.

4.3 Materials and methods

4.3.1 Study sites

The data for this study was collected from three different sites that were located in south-eastern Quebec, Canada (Mont-Laurier: 46.65 ºN, 75.64 ºW; Duchesnay: 46.65 ºN, 75.64 ºW; and Biencourt: 48.01 ºN, 68.50 ºW). The topography of all sites is hilly, with slopes up to 15º and soils that are well-drained. According to Robitaille and Saucier (1998), average annual precipitation is about 1000 mm at Mont-Laurier and Biencourt and 1200-1600 mm at Duchesnay; mean annual temperature at Mont-Laurier is 2.5 to 5 ºC, and 2.5 ºC at the other two sites. The forest type at Mont-Laurier and Duchesnay belongs to the sugar maple-yellow birch (*Betula alleghaniensis* Britt.) domain, whereas that of Biencourt belongs to the balsam fir (*Abies balsamea* (L.) Mill.)-yellow birch domain. Stand basal area was 24.7m^2 ha^{-1}at Mont-Laurier, 23.7 m^2 ha^{-1} at Duchesnay, and 26.7m^2 ha^{-1}at Biencourt (Table 4-1).

4.3.2 Field measurements

A total of 31 trees from Mont-Laurier, 28 trees from Duchesnay, and 32 trees from Biencourt were felled. A wide range of tree sizes (diameter at breast height (DBH) ranged from 25 to 58.5 cm) were sampled, with an appropriate representation of tree vigour and stem quality classes. Tree vigour was measured using the MSCR classification (Boulet 2005) based on live crown percentage, bole characteristics and presence of wounds and defects on tree stem. The tree vigour system classifies standing trees as follows: class M (mortality) corresponds to trees that are likely to die before the next harvest (15-25 years); class S (survival) are defective trees, whose timber volume may decrease, but likely to survive until the next harvest; class C (conserved) are trees, whose merchantable volume should not deteriorate until the next harvest; and class R (retained) corresponds to vigorous trees. The stem quality system (ABCD) is composed of four classes (Monger 1991), with the class A being the highest grade (straight stem, no injuries and branches, round stem, and DBH at least 40 cm) and class D (curved or forked stem section, different kinds of damages, and DBH at least 23.1 cm), the lowest grade. B and C are the intermediate quality classes.

Before felling, tree height, DBH and height to the first living primary branch (HLFB) were recorded. Each sample tree was classed according to four social statuses: (1) dominant (free-standing trees with upper crown above the general level of the canopy), (2) co-dominant (trees with crowns forming the general upper level of the canopy), (3) intermediate (trees extending into the canopy and receiving some light from above, but shorter than the dominant and co-dominant classes) and (4) suppressed (trees with crowns below the general level of the canopy, receiving little direct light from above). Crown radii in the four cardinal directions were measured from the centre of the bole of each tree to the edge of its crown, as determined by vertical sighting. Quadratic mean crown radius was calculated from the four crown radii that were measured (Gregoire and Valentine 1995; Wiemann et al. 2002; Russell and Weiskittel 2011). Stand basal area (m^2 ha^{-1}) was measured around each sample tree using an angle count method with a basal area factor of 2 m^2 ha^{-1} $tree^{-1}$.

Once the trees were felled, we measured the size and location of all primary branches. The branch union point between the main stem and the largest branch was considered to be a fork, and height from ground to the fork was defined as fork height. Stem disks were collected at stump height (0.30 m), at breast height (1.3 m), and then at each 2-m interval below the crown base. The stem disks were transported to the laboratory, where clear and discoloured wood components were measured in eight radial directions. The volume of each compartment (e.g. coloured and discoloured) was then calculated using Smalian's formula (Loetsch et al. 1973).

4.3.3 Data analysis

A series of models were calibrated in order to estimate the effect of competition on clear wood volume. The first step was to relate crown characteristics to stand and tree level variables. Total stem volume as well as clear wood volume up to top end diameters (e.g. 9 cm and 24 cm top diameters) was then predicted using tree characteristics. Linear and non-linear equations were chosen through preliminary inspection of the data and prior knowledge of the biological relationship between the response and explanatory variables.

Statistical significance of the site was verified by inserting a site random component in the linear or nonlinear mixed effect models. The changes in AIC, BIC and likelihood ratio were used to assess its usefulness. Variable selection was based on a forward stepwise approach. Homoscedasticity and the assumptions of normality of the residuals were verified visually. The list of potential covariates tested in this study is presented in Table 4-1.

Table 4-1 Main bio-climatic characteristics (based on Robitaille and Saucier 1998) of the study sites and stand characteristics. Ranges of variables are given in parentheses.'*' Indicate potential candidate covariates.

S.N.	Description	Sites: Mont-Laurier	Biencourt	Duchesnay
1	Location	46.65°N, 75.64°W	48.01°N, 68.50°W	46.94° N, 71.67°W
2	Elevation (m)	475	380	275
3	Topography	High hills, well drained, 15° slope	Hills, well drained, 15° slope	Mountains, well drained, 15° slope
4	Bioclimatic domain	Sugar maple-yellow birch	Balsam fir-yellow birch	Sugar maple-yellow birch
5	Parent bedrock	Igneous or metamorphic	Sedimentary	Igneous or metamorphic
6	Annual rainfall (mm)	1000	1000-1100	1200-1600
7	Mean annual temperature (°C)	2.5-5	2.5	2.5
8	DBH (cm)*	38.7 (26.5-55)	38.2 (26.4-54.6)	38.9 (28.0-58.5)
9	Height (m)*	20.3 (16.3-24.1)	21.2 (17.5-25.4)	20.3 (18.2-23.0)
10	Height of first live branch (HFLB, m)*	9.5 (6.6-13.3)	10.1 (5.1-16.0)	6.5 (2.5-9.4)
11	Fork height (m)*	10.8 (7.4-14.3)	10.3 (5.1-16.3)	9 (2.5-12.3)
12	Height up to 24 cm top diameter (m)*	10.13 (3.3-15.6)	10 (3.3-16.0)	7.9 (2.3-12.7)
13	Mean crown diameter (m)*	6.8 (3.6-10.4)	7.6 (4.5-11.6)	7.3 (4.0-10.6)
14	Mean stand basal area (m^2 ha-1)*	26.6 (14-38)	27.4 (14-36)	23. 7 (14-32)
15	Average annual diameter growth (mm/year)*	2.72 (1.80-4.10)	3.88 (2.45-5.05)	3.64 (2.30-4.95)
16	Total number of trees	31	32	28

4.3.3.1 Crown diameter model

Crown diameter was related to stand basal area, DBH, social status and MSCR grade with a linear model:

$$CD_{ij} = \beta_0 + b_i + \beta_1.BA_{ij} + \beta_2.DBH_{ij} + \beta_3.SP_{\boldsymbol{Int,ij}} + \beta_{\boldsymbol{4}}.MSCR_{R,ij} + \varepsilon_{ij} \quad (1)$$

where;

CD_{ij}= Crown diameter (m) of tree *j* in site *i*

BA_{ij} = Stand basal area (m^2 ha^{-1}) at the point of tree *j* in site *i*

DBH_{ij}= Diameter at breast height of tree *j* in site *i*

$SP_{\boldsymbol{Int,ij}}$ = tree *j* in site *i* grouped as intermediate social position, e.g. $SP_{\boldsymbol{Int}} = 1$ for intermediate trees, 0 for the other social classes

$MSCR_{R,ij}$ = tree *j* in site *i* grouped as class R as R (vigorous) trees and M, S, and C as other (non-vigorous) trees of the MSCR classes

β_0 to β_4=Estimated fixed-effect parameters

b_i= Site specific random effects, $b_i \sim N(0, \sigma_i^2)$

ε_{ij} = Unexplained within-group random error, independent of random effects,$\varepsilon_{ij} \sim N(0, \sigma^2)$

4.3.3.2 Height up to 24 cm top diameter

Height up to 24 cm outside bark diameter (H_{24}) is asymptotic to tree height (H):

$$H_{24,ij} = H_{ij}.\left(1 - e^{(\beta_0 + \beta_1.FH_{ij} + \beta_2.DBH_{ij})}\right) + \varepsilon_{ij} \quad (2)$$

where,

$H_{24,ij}$= Height up to 24 cm outside bark diameter (m) of tree *j* in site *i*

H_{ij}= Tree height (m) of tree *j* in site *i*

FH_{ij}= fork height of tree *j* in site *i*, which is defined as the height up to the biggest branch

β_0 to β_2= Parameters to be estimated

ε_{ij}= Random error, $\varepsilon_{ij} \sim N(0, \sigma^2)$

4.3.3.3 Stem volume

Volume up to a given top end diameter was modelled with a form factor approach:

$$V_{ijk} = \left(\frac{\pi}{4}\right).DBH_{ij}^2.H_{ijk}.FF_{ijk} + \varepsilon_{ijk} \quad (3)$$

where,

V_{ijk}= volume (m^3) up to the point of interest k of tree *j* in site *i* to a top end diameter *k* (*k*=1 and 2 for volume up to 9 cm top diameter and 24 cm top diameter respectively, and *k*=3 and 4 for clear wood volume up to 9 cm top diameter and 24 cm top diameter respectively)

H_{ijk}= Height up to the point of interest k of tree *j* in site *i*, where $H_{ijk} = H_{ij}$ when *k* =1 and 2, and $H_{ijk} = H_{24,ij}$ for k = 3 and 4

FF_{ijk}= Form factor (ratio between stem volume to volume of the same size cylinder) for volume k of tree *j* in site *i*, defined as:

$$FF_{ijk} = \left(1 - e^{(\boldsymbol{X}_{ij}\boldsymbol{\beta}_{ij})}\right) \quad (4)$$

$\boldsymbol{\beta}_{ij}$= Vector of estimated fixed-effect parameters

$\boldsymbol{X}_{ij}$= Covariate matrix

ε_{ijk}= Random error, where $\varepsilon_{ijk} \sim N(0, \sigma^2)$

For stem form factor up to a top end diameter of 9 cm (FF_{V9}), the linear combination of FH and DBH was used in Eq. 4 (Eq. 5a), whereas only the parameter for DBH was statistically significant for stem form factor up to a top end diameter of 24 cm (FF_{V24}, Eq. 5b). To predict clear wood form factor to a top end diameter of 9 cm (FF_{CWV9}), FH, predicted crown diameter (Eq. 1) and ABCD grade (ABCD =0 for D grade trees, and 1 for A, B and C grades) were used with DBH (Eq. 5c). In order to predict clear wood form factor to a top end diameter of 24 cm diameter (FF_{CWV24}), predicted crown diameter (Eq. 1) and ABCD grade (ABCD =0 for D grade trees, and 1 for A, B and C grades) were used with DBH (Eq. 5d). A site random effect was also included in equations 5c and 5d, as indicated with a likelihood ratio test (e.g. $b_i \sim N(0, \sigma_i^2)$).

$$\boldsymbol{X_{ij}\beta_{ij}} = \beta_0 + \beta_1.FH_{ij} + \beta_2.DBH_{ij} \quad \text{(5a)}$$

$$\boldsymbol{X_{ij}\beta_{ij}} = \beta_0 + \beta_2.DBH_{ij} \quad \text{(5b)}$$

$$\boldsymbol{X_{ij}\beta_{ij}} = \beta_0 + b_i + \beta_1.FH_{ij} + \beta_2.DBH_{ij} + \beta_3.\widehat{CD_{ij}} + \beta_4.ABCD_{ij} \quad \text{(5c)}$$

$$\boldsymbol{X_{ij}\beta_{ij}} = \beta_0 + b_i + \beta_2.DBH_{ij} + \beta_3.\widehat{CD_{ij}} + \beta_4.ABCD_{ij} \quad \text{(5d)}$$

4.4 Results

Crown diameter was found to be negatively related to stand BA around each sample tree (β_1 = -0.0507, Table 4-2) and positively related to DBH (β_2 = 0.1356, Table 4-2). Intermediate trees were found to have smaller crown radii (β_3= -0.8254, Table 4-2) whereas R vigour class trees had larger crowns (β_4 = 0.7066, Table 4-2). The site random effect estimates indicated that trees from Biencourt had the widest crowns and trees from

Mont Laurier the narrowest crowns, all other covariates being held constant ($b_{Biencourt}$=0.1144, $b_{Duchesnay}$=0.0066 and $b_{Mont\ Laurier}$=-0.1210, Table 4-2: eq 1).

Table 4-2 Parameter estimates and fit statistics of the fitted models (Standard error of the corresponding values are given in parenthesis)

Regression parameters	CD (Eq. 1)	H_{24} (Eq. 2)	FF_{V9} (Eq. 5a)	FF_{V24} (Eq. 5b)	FF_{CWV9} (Eq. 5c)	FF_{CWV24} (Eq. 5d)
Fixed effects						
Intercept	3.2050 (1.0433)	0.6641 (0.0911)	-0.4705 (0.0495)	-2.5423 (0.1942)	-0.3185 (0.0496)	-0.9731 (0.1322)
DBH	0.1356 (0.0201)	-0.0237 (0.0024)	0.0032 (0.009)	0.0330 (0.0039)	0.0086 (0.0018)	0.0263 (0.0044)
BA**	-0.0507 (0.0192)					
$SP_{Intermediate}$	-0.8254 (0.3623)					
$MSCR_R$	0.7066 (0.3065)					
$ABCD_O$					-0.0354 (0.0164)	-0.0955 (0.0437)
FH		-0.0348 (0.0056)	-0.0132 (0.0025)		-0.0053 (0.0025)	
$\widehat{CD}$					-0.0371 (0.0112)	-0.0837 (0.0291)
Random effects						
$b_{MontLaurier}$	-0.1210				0.0118	0.0563
$b_{Duchesnay}$	0.0066				0.0107	-0.002
$b_{Biencourt}$	0.1144				-0.0225	-0.0545
σ^2_{site}	0.1972				0.0183	0.0508
$\sigma^2_{residuals}$	1.2330				0.1108	0.1172
R-squared*	0.52	0.73	0.91	0.89	0.85	0.84

* Calculated as : $R^2 = 1-(\frac{\sum_{i=1}^{m}(\hat{Y}_i-Y_i)^2}{\sum_{i=1}^{m}(Y_i-\bar{Y})^2})$, ** BA=Stand basal area

Note: As the functional form of equations (2 and 5a,5b,5c and 5d), was set to quantify the deviation from H for eq. (2) and cylindrical volume for (eqs. 5a,5b,5c and 5d), positive parameter estimates give lower estimate of y variable and negative parameter estimates give higher estimate of y variable. FF_{V9} and FF_{V24} represent form factor for stem volume up to 9 cm and 24 cm top diameter respectively. Similarly, FF_{CWV9} and FF_{CWV24} represent form factor for clear wood volume up to 9 cm and 24 cm top diameter respectively.

H_{24} was found to increase with DBH (β_2 = -0.0237, Table 4-2) and fork height (β_1 = -0.0348, Table 4-2). V_9 also increased due to increase in FF_{V9} with FH (β_1 = -0.0132,

Table 4-2). The effect of fork height on V_{24} was however indirect. As V_{24} was predicted with H_{24}, and that H_{24} increased with FH, V_{24} also increased with FH (Figure 4-1).

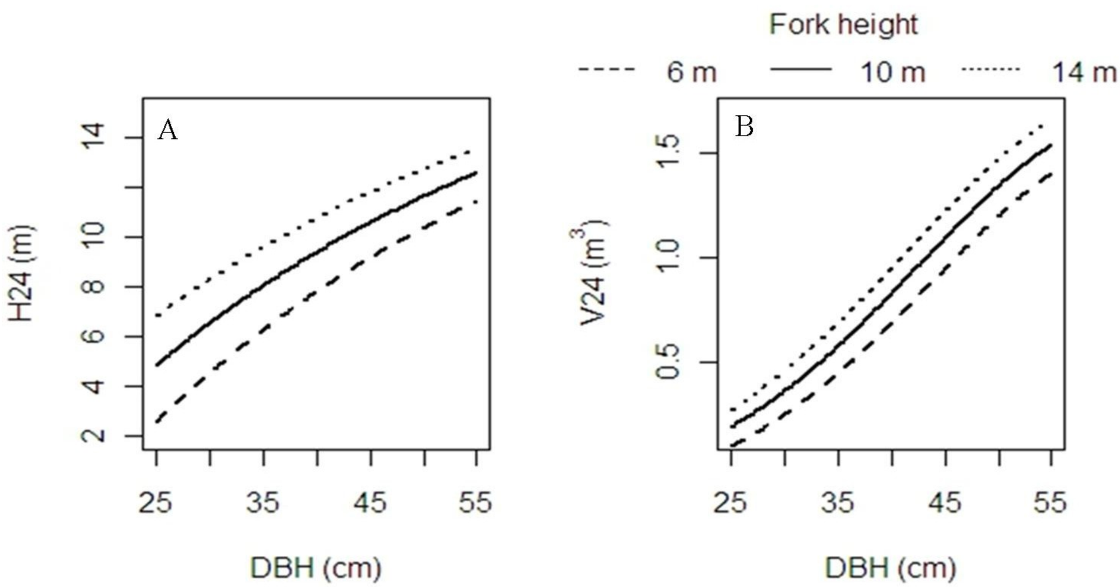

Figure 4-1 Effects of fork height (FH: 6, 10 and 14 m) on (A) height up to 24 cm top diameter (H24) and (B) volume up to 24 cm top diameter (V24)

Form factors for all volumes (e.g. V_9, V_{24}, CWV_9, CWV_{24}) decreased with DBH (β_1 positive for each FF, Table 4-2). However, the rate of decrease in form factor for clear wood volume with DBH was more important than the decrease in tree volume (Figure 4-2). Moreover, the form factor value for V_9 and CWV_9 was lower than those associated with V_{24} and CWV_{24}.

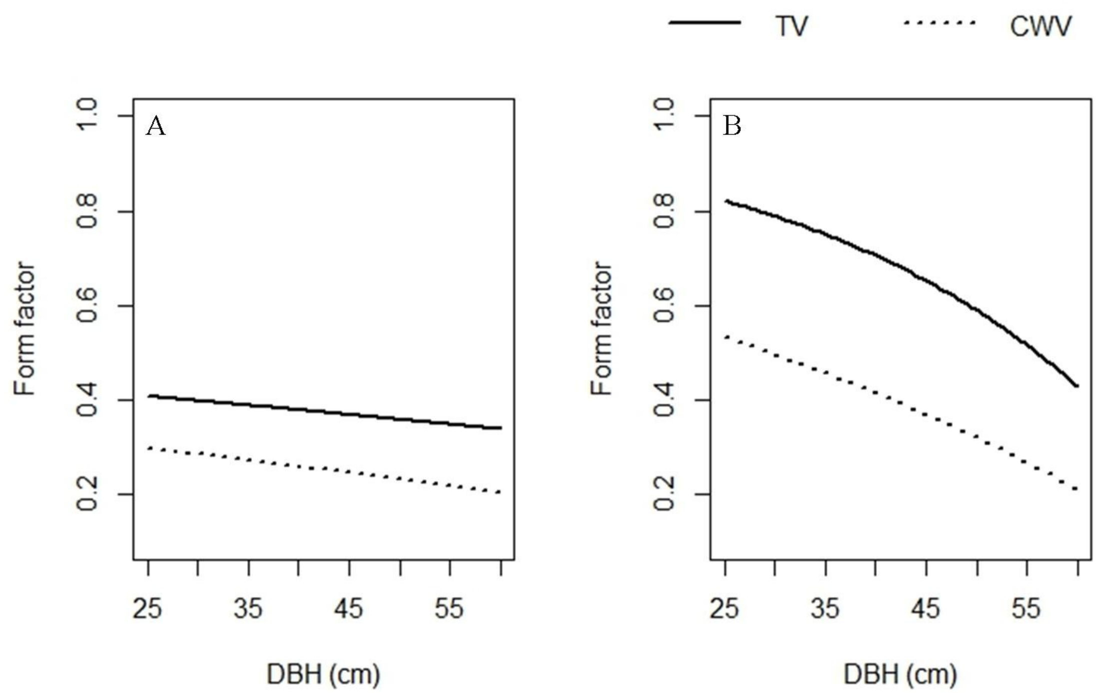

Figure 4-2 Form factor of stem (TV) and clear wood column (CWV) with tree size (A) 9 cm top diameter and (B) 24 cm top diameter

Clear wood form factor was positively related to crown diameter (β_3 negative for CWV_9 and CWV_{24}, Table 4-2). However, the effect of CD on CWV form factor was more pronounced for larger DBH: the difference in FF for small sized trees (e.g. DBH = 25 cm) between small and large crowns was smaller than the difference in FF for large sized trees (e.g. DBH = 60 cm) (Figure 4-3). The effect of CD on form factor for CWV9 was less pronounced.

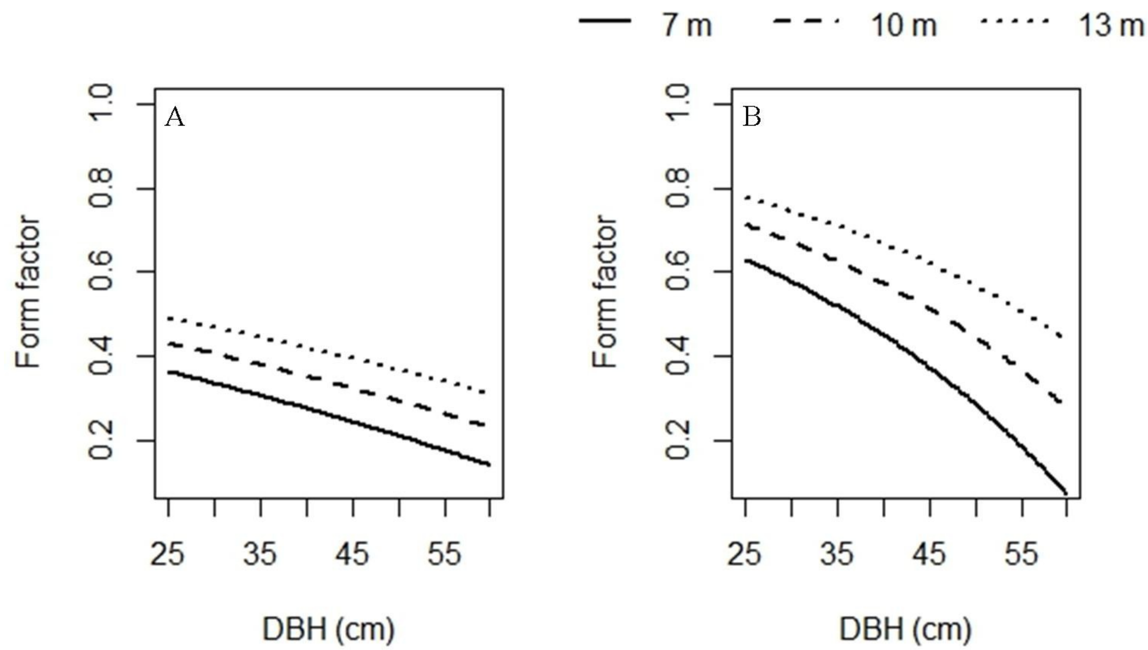

Figure 4-3 Effects of crown diameter (7 m, 10 m and 13 m) on form factor of clear wood column (A) 9 cm top diameter, (B) 24 cm top diameter

The effect of competition on clear wood volume was found to be indirect. Competition, quantified by stand basal area, was negatively related to crown diameter while form factor of CWV was positively related to crown diameter. Hence, trees growing in low basal area stands were found to have larger crowns, CWV and % CWV for a given diameter tree (Figure 4-4). Moreover, the effect of competition on CWV for small trees was not apparent (Figure 4-4C and D) but the % CWV visibly increased for these trees in low BA stands (Figure 4-4A and B). Effects of competition on CWV and % CWV was found larger for larger DBH trees (Figure 4-4), as have been found for CWV form factor. The differences on CWV among stand BAs was more important for larger trees, particularly for CWV24 (Figure 4-4C), CWV9 (Figure 4-4D), and % CWV24 (Figure 4-4A), but not for % CWV9 (Figure 4-4B).

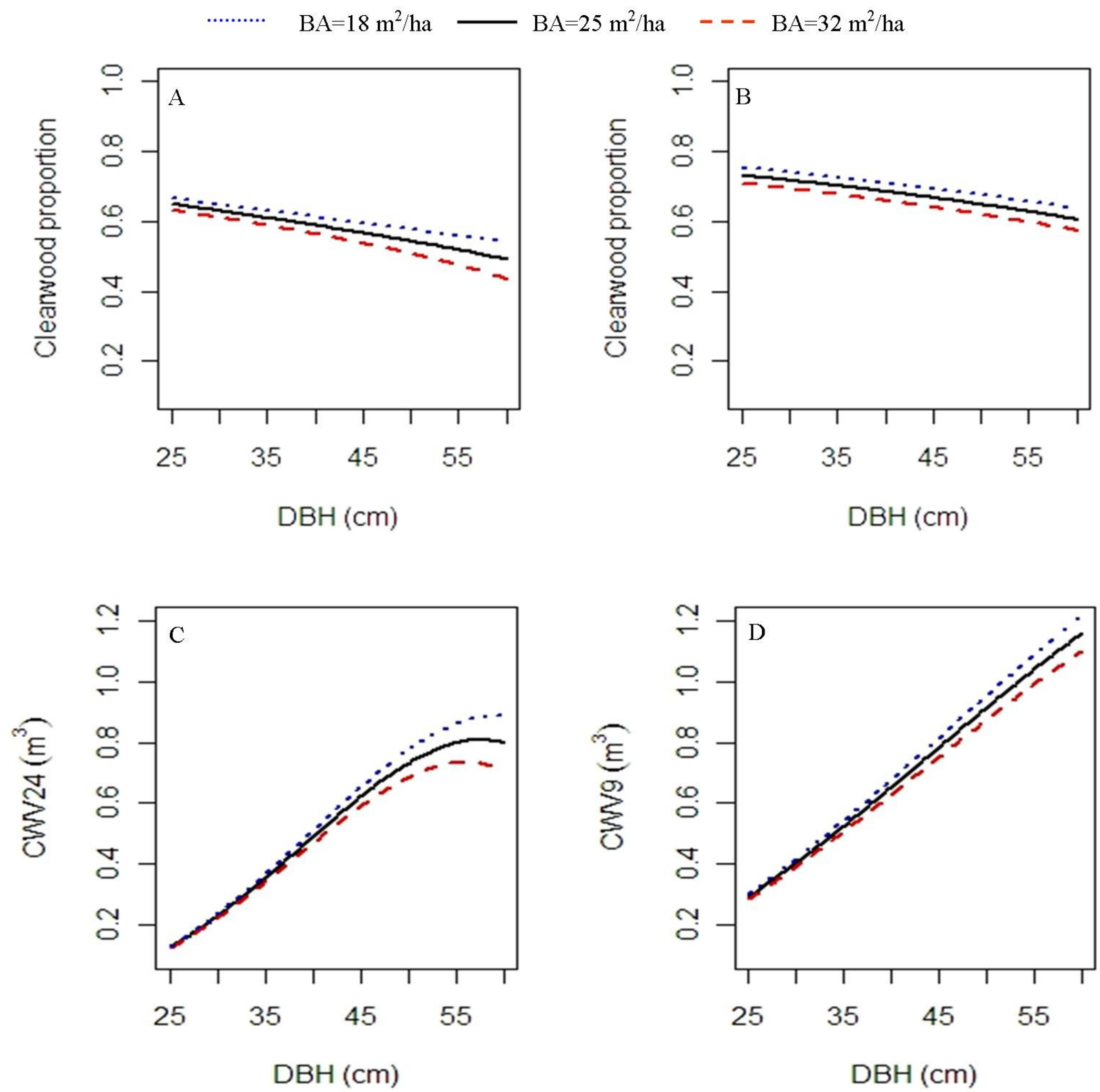

Figure 4-4 Effects of stand basal area (BA: 18, 25 and 32 m2/ha) on clear wood proportion and clear wood volume up to different height of interest (A) %CV up to 24 cm top diameter, (B) %CV up to 9 cm top diameter, (C) CV up to 24 cm top diameter and (D) CV up to 9 cm top diameter (Predicted crown diameter for a given diameter tree of 20 m height at different stand basal area was used to predict CV9 and CV24, fixed effect parameters were only used to make predictions)

Finally, the amount of clear wood volume for a tree of given dimension (height or diameter) was higher for stem quality classes A, B and C compared to class D (Table 4-2, equations 5c and 5d: coefficient for $ABCD_O$=-0.0955, p<0.05, and $ABCD_O$=-0.0354, p<0.05). It also varied between sites (Table 4-2, equations 5c and 5d).

4.5 Discussion

This study demonstrates the link between inter-tree competition and three important wood quality attributes, viz. log length, form factor and clear wood proportion of sugar maple. As was hypothesized, trees growing under more competition were found to have smaller crowns and lower proportions of clear wood volume. Although it is well-known that competition affects crown diameter (Krajicek et al. 1961) and the height of the first fork (Nicholson et al. 2010), we explored how these crown characteristics influence wood quality attributes of sugar maple.

Besides competition, crown diameter was also related to tree vigor class and site. Although crown diameter of a tree is strongly related to its DBH (Lamson 1987; Russell and Weiskittel 2011), the CD-DBH relationship is also modified by the competitive status of the trees (Krajicek et al. 1961; Russell and Weiskittel 2011; Hao et al. 2015). A reason could be that sugar maple responds to reductions in competition (or canopy openings) through lateral extension of the crown (Runkle and Yetter 1987). Furthermore, trees without any serious visual damage to the crown (such as trees of vigor class R) have significantly wider crowns.

It has long been known that stem taper is influenced by crown characteristics (Larson 1963). Moreover, taper and form factor are by definition related, where trees with more taper will have lower form factors: a cone (e.g. large taper) has a form factor of 0.3 whereas a cylinder (e.g. no taper) has a form factor of 1. Thus, the variables which influence taper will also play a role on the form factor. In our study, the form factor decreases with tree diameter and increases with competition because trees growing under more competition have smaller crowns for a given DBH. Fork height also influences stem form because the stem diameter decreases rapidly above a fork (Adu-Bredu et al. 2008; Anderson 1996). Thus, stem volume increases with fork height.

While total tree volume is linked to stem taper, clear wood volume depends on tree vigour (Baral et al. 2013). Generally, trees with wider crowns are more vigorous as they are able to incept more light per unit of foliage (Zarnoch et al. 2004; Schomaker et al. 2007) and consequently have higher rates of basal area increment (Hocker 1979). Such trees have larger proportions of sapwood (Berninger and Nikinmaa 1994) as well as better defences against infections due to micro-organisms (Shigo 1979). Because of the effects of tree vigour, the form factor for clear wood is actually larger in vigorous trees than in suppressed trees, in spite of an opposite trend for the form factor of total wood.

It is less likely that the observed variation of competition effect on clear wood volume for different sized trees is related to the social position of the tree in an uneven-aged stand as only the trees that are greater than 24 cm were used in the analysis. Therefore, we argue that the more pronounced effect of competition on clear wood volume for larger diameter trees than in small diameter trees can be explained via the interactions of tree vigour and tree size. Firstly, trees with larger stems need to allocate more resources to the crown to maintain a positive carbon balance because maintenance cost increases with stem volume (Waring and Schlesinger 1985). However, the radial expansion of the crowns is limited by competition. Consequently, larger diameter trees growing under high competition are less vigorous (Hartmann et al. 2009). Secondly, wood discoloration is related to the trees ability to compartmentalize injuries to the wood (Shigo et al., 1984). This ability declines with tree age (Shigo 1979). Since diameter growth and crown diameter are correlated (Duchesne et al. 2003; Hartmann et al. 2009; Zarnoch et al. 2004), our dataset compares younger and older trees at a given diameter. Consequently the effects of competition are more pronounce for larger diameter trees.

Interestingly, our results show that the effect of competition on clear wood volume is larger when CWV was measured up to a top end diameter of 24 cm compared to a top end diameter of 9 cm. This can be explained by the variation of inside-crown stem form factor among trees of different crown widths growing under different competition levels. For a given DBH, wider crown trees have bigger branches in the lower part of the crown than narrower crowned trees (Sumida and Komiyama 1997; Ishii and McDowell 2002). In addition, narrower crowned trees growing in denser stands have higher proportions of branch basal area (and thus foliage) distributed in the upper part of the crown (Valladares and Niinemets 2007). Since the sapwood area at any height is proportional to the amount of foliage above that height (Shinozaki et al. 1964), the form factor of the upper stem section between H_9 and H_{24} of narrow-crowned trees must be higher than for wider-crown low-competition trees. Thus, stem volume located in the stem section with diameters between 9 and 24 cm (V_9-V_{24}) should be higher for trees with a narrower crown. This wood will be almost in its totality clear wood since discoloured wood column tapers out very rapidly within crown (Baral et al. 2013). Therefore, the “addition of larger stem volume containing a higher clear wood proportion” may explain the small dependence of CWV on competition when a top end diameter of 9 cm is used rather than that of 24 cm.

Our results also indicate that vigorous trees (vigor class R) with minimum stem damage (stem quality classes A, B and C) have higher clear wood volume for a given sized tree. Although the effect of tree vigour on clear wood volume is not direct; it can be inferred by the increasing CWV with decreasing competition level, which corresponds to trees with larger crown and, thus more vigorous. Even though the large proportion of between-site variability of clear wood volume for a given sized tree was explained by the variation in the CD-DBH relationship among sites, still small but statistically significant proportion of between-site variability of clear wood volume for given sized trees remained unexplained.

From our results, we infer that sugar maple wood quality can be improved by exposing trees to different levels of competition during their developmental stages. Sapling to pole stage trees need to grow in denser stands until the desired bole length is obtained. At this phase, trees have low maintenance cost and small sized branches. Death of small branches (that do not contain heartwood) are less likely to cause discolouration in the main stem as wounds resulting from branch abscission are usually sealed quickly (Smith et al. 1997; Dănescu et al. 2015). In contrast, a higher level of competition is detrimental to large sized canopy trees. On the one hand, the death of larger branches are likely associated with larger trees under higher competition that induce discoloration more easily in the stem, thereby reducing the clear wood proportion. On the other hand, large diameter trees under higher competition are likely to have smaller diameter crowns and thus are less vigorous and the injuries from branches will reach the heartwood. As a result, such trees are more likely to increase the size of discoloured wood column and thus have a smaller clear wood proportion. Hence, reducing competition for large sized trees should produce vigorous crowns, while limiting the development of discoloured wood. This would help maximize clear wood volume.

4.6 Acknowledgements

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Chapter 5: GENERAL CONCLUSION

5.1 Background

Sugar maple value comes from unblemished white colored veneer and saw-log quality logs that are used for appearance wood products (Wiedenbeck et al. 2004). Generally, logs that are free from major defects, and have a minimum proportion of discoloration are graded as veneer and saw-log quality (Myers et al. 1986; NLGA 2014). As stem quality is very important for high-value hardwoods, stem quality improvement has been one of the important goals of hardwood silviculture in north-east America over the last six decades (Eyre and Zillgitt 1953; Arbogast 1957; Erdmann 1986; Nyland 1987; Bédard and Majcen 2003; Nolet et al. 2013). Although implementation of the selection systems in tolerant hardwood stands have been successful in increasing the proportion of better grade trees (Strong et al. 1995; Gronewold et al. 2012), the link with observable defects used for tree grading to invisible features related to wood quality (e.g.: decay and discoloration) is still poorly understood (Belleville et al., 2011; Drouin, 2010; Erickson et al., 1992; Germain et al., 2015; Giroud et al., 2008; Havreljuk et al., 2013; Schneider et al., 2008;Yanai et al., 2009).

There are ample studies on the causes of wood discolouration in living trees of temperate hardwoods (Ohman 1968; Shigo and Hillis 1973; Shigo et al. 1984; Schwarzee 2007; Dujesiefken and Liese 2010; Shortle and Dudzik 2012; Smith 2015). Wood discolouration in living trees initiates when trees get injured due to branch death or mechanical damage on tree stems (Ohman 1968; Shortle and Dudzik 2012). Immediately after injury, the process of compartmentalization begins by plugging the vessels above and below the injury point to prevent the loss of physiological functioning (Shigo and Hillis 1973). As a result, the cambium and sapwood cells present at the injury point die due to loss of physiological connection (Shigo et al. 1984; Schwarzee 2007; Shortle and Dudzik 2012; Smith 2015). In the dead sapwood tissues, pathogens begin discoloration by secreting enzymes which spread into the heartwood zone (Shortle and Dudzik 2012). As trees grow, a new layer of sapwood (callus) is added outside of the injury point that eventually encapsulates the injury (Dujesiefken and Liese 2010). A strong compartmentalization boundary isolates the infected wood inside the newly formed sapwood zone (Shigo et al. 1984; Schwarzee 2007). Fast growing trees seal the injury (or stem damage) faster (Dujesiefken and Liese 2010; Shortle and Dudzik 2012; Smith 2015). When the injury points are sealed, it obstructs aeration and reduces the oxygen level (Dujesiefken and Liese 2010). This prevents further expansion and degradation of the discolored wood (Shigo et al. 1984; Dujesiefken and Liese 2010; Shortle and Dudzik 2012).

This theoretical explanation of the discoloration process indicates that regulation of tree growth by applying appropriate silvicultural practices likely influences discolored wood proportion in a given sized tree. On the one hand, stand density influences stem geometry (Hein 2009). On the other hand, it reduces tree growth by limiting crown size (Hartmann et al. 2009). Slow growing trees delay wound closure and have weak compartmentalization (Leben 1985; Dănescu et al. 2015). As a result, such trees tend to have a higher proportion of discolored wood. While discolored wood proportion is considered to be a grading defect, poor geometry of the log is considered to be a scaling defect (NLGA 2014). Therefore, a complete understanding of the effects of stand density on tree crown and stem properties, discoloured wood formation, its link to tree vigour, and the development of a discoloured wood column with tree size is necessary to understand what management scenarios should be used to increase standing timber wood quality. Without such information, it is difficult to make management decisions such as: (a) how long a tree associated with certain visible damage (i.e. as observed through various grading rules such as the MSCR or ABCD used in Quebec) would grow without further deteriorating wood quality? (b) What is the maximum tree size at which maximum high-value merchantable timber volume can be obtained? (c) How does stand density influence wood quality attributes? In this context, this study was designed to understand these vital issues in the context of managing tolerant hardwoods in north-east America. This study, thus, aimed to:

(1) predict extent and proportion of discolored wood within and between trees;

(2) explore the link between tree vigor, heartwood formation and discolored wood proportion in different sized trees; and

(3) assess effects of competition on tree crown characteristics and thereby wood quality.

The findings of the thesis contribute to a better understanding of how discoloured wood proportion changes with tree size/or age, and the scientific basis to predict wood quality attributes (log length, stem form factor and discolored wood proportion) of sugar maple.

The findings also provide the basis for recommending necessary amendments to current northern tolerant hardwood silviculture for wood quality development. In line with these objectives, the main conclusions are discussed in the subsequent section.

5.2 Important results, general discussion and management implication

5.2.1 Size/or age related change of discolored wood proportion

The relationships between tree dendrometric information and composition of wood structure components (sapwood, heartwood and discolored wood) of different sized sugar maple trees were established using an empirical modeling approach. This modeling approach allowed us to understand how sugar maple wood quality is linked to tree and stand characteristics. The findings of chapter II, III and IV collectively help clarify the dilemma whether discolored wood proportion increases with tree size or age. Although several studies indicate that discolored wood proportion in tolerant hardwoods increases with tree size (Erickson et al. 1992; Kadunc 2007) and/or age (Havreljuk et al. 2013), some studies strongly disagree with this statement (Yanai et al. 2009; Germain et al. 2015). In an attempt to clarify this confusion, this thesis concludes that size related increase in discolored wood proportion is due to the increased likelihood of damage and subsequent tree vigor decline with tree size.

The discolored wood proportion increases with tree age, and decreases with tree vigor and sapwood proportion. This indicates the possibility of increasing discolored wood proportion with heartwood formation (Chapter II). However, discolored heartwood proportion increases with the rate of heartwood formation except for R category trees (Chapter III). Heartwood formation increases with tree size and age as have been reported elsewhere (Yang and Hazenberg 1991; Sellin 1993; Gjerdrum 2003; Morais and Pereira 2007), but not necessarily the proportion of discolored wood. Microbial infection through wounds and injuries is necessary for heartwood discoloration, which is generally smaller in R category trees. R category trees have significantly wider crowns (Chapter IV), which increases tree growth (Chapman and Gower 1991; Duchesne et al. 2003; Punches 2004; Hartmann et al. 2009). Due to faster growth of vigorous trees (e.g. R trees); injuries associated to branch death seal faster and thus have lower discolored wood proportion (Leben 1985; Dănescu et al. 2015).

Discolored wood proportion is positively correlated to tree size or age (Chapter II). However, it is better correlated to tree age than tree size, which is analogous to Havreljuk et al., (2013). Variation in tree age for a given tree diameter makes the effect of diameter on discolored wood proportion weaker. Sugar maple, a shade tolerant species, can remain suppressed from a few decades to a century before they reach to canopy (Canham 1990). Early released vigorous trees in a productive site attain a given diameter faster. However, longer suppressed trees are generally less vigorous as they are likely to be associated with several damages (branch death and mechanical damages) and thus take centuries to attain the same diameter. Such trees have weaker compartmentalization ability that make them more vulnerable to microbial-induced expansion of the discolored wood column. In addition, early released trees (or trees in less competition) tend to be relatively younger at a given diameter, thus have lower proportion of discolored wood volume. Hence, tree size per se does not to have effect on discolored wood proportion. The observed relationship is due to its correlation with tree age.

Based on the above finding, it can be presumed that the inconsistencies on the relationship between tree size and discolored wood proportion among sites must be related to site factors. It is well accepted that site factors affect discolored wood proportion (Yanai et al. 2009; Havreljuk et al. 2013; Germain et al. 2015). However, the factors leading to an increase in discolored wood proportion are not well understood. Studies suggest three possible explanations: (1) soil factors (Horsley et al. 2002; Germain et al. 2015), (2) climatic factors (Wiedenbeck et al. 2004; Havreljuk et al. 2013), and (3) effect of past management (Shigo and Hillis 1973; Erickson et al. 1992). Although the influence of site on discolored wood proportion was not investigated in this study, its effect was controlled using sites as a grouping variable in the model.

5.2.2 Prediction of wood quality attributes

High quality sugar maple trees used for veneer and sawn timber are characterized by trees with less tapered and longer branch-free boles. This study has developed regression models to predict these wood quality attributes for sugar maple using tree and stand characteristics as predictors.

5.2.2.1 Prediction of discolored wood column

The taper equation for discolored wood column presented in Chapter II provides the shape of discolored wood column in sugar maple trees. Prediction of the width of discolored wood column at different heights helps identify and segregate different grade logs found in a tree that are suitable for different end products. The observed shape of discolored wood column is similar to the shape of red heart in *Fugus sylvatica* by Wernsdörfer et al., (2006) and in *Betula papyrifera* by Drouin (2010). In general, the shape of discolored wood column is similar to the shape of heartwood observed elsewhere (Knapic, 2006; Moya et al., 2014): maximum at base, tapers slightly up to crown base, and tapers rapidly in the crown. However, pole sized trees have spindle shaped discolored wood column (e.g. maximum at crown base and tapering off towards top and bottom). This can be inferred as branch death is one of the most important factors responsible for initiating discoloration in sugar maple trees.

5.2.2.2 Prediction of sapwood area at breast height and heartwood formation

Heartwood formation provides a physiological link to discoloration. The expansion of the discolored wood in the heartwood is more rapid than in the sapwood, as the compartmentalization in heartwood is the weakest (Dujesiefken and Liese 2010). In addition, process-based modeling approaches also need to quantify sapwood turnover (Sievänen et al. 1997b; Hari et al. 2013). The sapwood prediction model (Chapter III) provides the basis for estimating sapwood turnover using age, crown surface area, and leaf area as predictors for a given height and diameter tree. Furthermore, such dynamics are difficult to measure experimentally. Leaf to sapwood area relationship for sugar maple was quantified by Chapman and Gower, (1991), which is within the observed range of this study. In addition, this study provides how leaf to sapwood area relationship varies according to different tree characteristics for a given height and diameter. This information is useful to quantify sapwood turnover allometrically. There are two competing hypotheses to explain sapwood turnover, 1) ageing (Yang 1990; Yang and Hazenberg 1991) and/or (2) foliage death (Kaipiainen and Hari 1985; Sievänen et al. 1997b). However, this study (Chapter III) suggests that sapwood turnover is related to both cambial age and foliage death. In addition, leaf to sapwood area ratio is influenced by the crown surface area indicating that sapwood area is not only related to amount of foliage but also related to foliage distribution pattern within the crown as previously observed by Schneider et al., (2011) in jack pine.

5.2.2.3 Prediction of log length, stem form and clear wood volume

Merchantable volume up to any height of interest can be estimated either using stem profile models (Zakrzewski 2011) or using merchantable volume equations restricted to specific top diameters (Alemdag 1988**).** To model highly irregular tree profiles precisely, taper equations are generally developed using complex functions (Westfall and Scott 2010; Zakrzewski 2011). Due to the complexity of stem profile models, accurate but easy-to-use merchantable volume equations are always sought for practical application in the field. Therefore, merchantable volume equations for total stem volume and clear wood volume up to 9 and 24 cm top diameters for sugar maple trees growing in south-eastern Quebec are presented in chapter IV. Being easy-to-use models, volume prediction ability of these models is superior or equally precise to the complex models developed elsewhere for sugar maple (Ormerod 1953; Hart 2009; Zakrzewski 2011). Moreover, these models allow assessing the influential tree characteristics on both stem form factors and clear wood column form factors.

Sugar maple crown characteristics influence bole length, stem tapering and clear wood proportion in main stem. On the one hand, height to the biggest branch influences stem tapering. In addition to height and DBH of the tree, position of the biggest branch is another important variable that has significant influence on stem tapering and thus useful for predicting bole length and merchantable volume. When the fork is in the crown (as opposed to the crown base), the trees have longer and less tapered bole and thus have higher stem to branch volume ratios (Planck and MacFarlane, 2014). Low forked trees not only have lower merchantable volume (Adu-Bredu et al. 2008; Planck and MacFarlane 2014) but also have lower lumber volume recovery due to stem tapering (Steele 1984; Missanjo and Magodi 2015). On the other hand, crown diameter is related to clear wood volume and clear wood proportion. Crown diameter is an important tree characteristic which is positively related to clear wood volume in a given sized tree. Wider crown trees are more vigorous (Morrow 1955) and therefore such trees have higher diameter growth (Duchesne et al. 2003; Hartmann et al. 2009). As a result, wider crown trees are younger for the given diameter, thus have lower proportion of discolored wood volume which is similar to the findings of chapter II of this study as well as Kadunc, (2007) and Havreljuk et al. (2013). Therefore, in addition to DBH, tree grade and site; crown diameter is important variable to predict clear wood volume in sugar maple trees.

5.2.3 Silvicultural prescription for wood quality development

Analyzing effects of stand and tree characteristics on tree crowns and wood quality attributes demonstrated the possibility of wood quality development by slight modification of existing tolerant hardwood silviculture. Since sugar maple is a shade tolerant tree species, sugar maple stands for timber production are generally being managed by single tree selection system (Nyland 2002). Generally, in the selection system, individual trees of all size classes more or less uniformly throughout the stand are felled to maintain an uneven-aged stand with felling cycles of 20 to 25 years. The current Quebec practice of implementing single tree selection system is to remove M and S grade trees of MSCR classification system (Boulet 2005). Findings of this study indicate that rapidly growing vigorous trees without any damages (R class trees) have low proportion of discoloured wood volume regardless of tree diameter. This supports the current Quebec practice of implementing single tree selection system, which is likely to minimize discolored wood proportion in residual trees in future. Hence, removing M and S grade trees during selection felling is a good silvicultural strategy to maintain healthy stand of vigorously growing trees with low proportion of discolored wood in future.

In addition to discolored wood proportion, log length and stem form factor are the other important wood quality attributes that are related to lumber recovery (Steele 1984). When self-pruning is promoted to increase bole length (Hein 2009), injuries related to branch death are likely to introduce discoloration (Ohman 1968; Dănescu et al. 2015). Therefore, it is important to apply silvicultural prescriptions cautiously while tending tolerant hardwood stands for high quality woods. Stand density influences crown characteristics of pole sized trees (Nicholson et al. 2010). Crown size and low fork height, the general characteristics of trees growing in lower level of competition (Hein 2009), are positively correlated to clear wood proportion and negatively correlated to bole length and stem form factor (Chapter IV). Therefore, in gaps of single tree selection cut, it is suggested to maintain a dense cohort of regeneration as has been suggested by Gasser et al. (2010) until desired clear bole length is achieved (Hein 2009). Then vigorously growing good quality stems must be selected as crop trees and released to promote diameter growth (Perkey et al. 1994). The vigorous growth after release helps occlusion of dead branch stubs faster (Dănescu et al. 2015). Future crop will thus have longer branch-free bole that contains less proportion of discolouration, which is highly desired for veneer and sawlog quality wood.

5.3 Limitations of the study

Since the aim of this study was to develop tree structural models to predict wood quality of sugar maple, the scope of this study was limited to three sites of Quebec, Canada. Moreover, the sample trees were subjectively selected using MSCR tree classification system and ABCD tree classification system to compare wood quality attributes among different grade trees. It is important to note that this delimitation of scope and non-randomness of the sample may limit the generality of the results. In addition, the dynamic variables such as change in discoloration, bole length, and competition were assessed comparing single measurement information among different sized trees growing in uneven aged forest. This static measurement might not fully represent the dynamic growth process.

5.5 Future directions

This study contributed towards a better understanding of the relationship between tree and stand characteristics, and wood quality attributes of sugar maple. In addition to this, it is important to link discoloration to heartwood formation and probability of a tree being injured (related to branch death and mechanical injuries) in a functional-structural growth model so that discolored wood dynamics as trees grow could be better understood. To do this, it is necessary to quantify how the competitive environment changes for shade tolerant trees growing in uneven-aged stands during different developmental stages (sapling, pole and tree), and its effects on tree crown characteristics (specially, crown recession and lateral crown expansion). On the one hand, this tree structural dynamics has physiological implication to tree vigor and heartwood formation. On the other hand, crown recession induces discoloration in tree stem. This dynamic two-way relationship between tree structure and function in different growth conditions provides the link between silviculture and wood quality. In this direction, this study was limited with the static information about tree and stands characteristics and links them to wood quality attributes. As a result, the findings of this study have limited implications. Therefore, future studies should be directed towards the following three important themes.

Firstly, although between tree variations on discoloured wood proportion in sugar maple is relatively known, the reason behind between site variations of discoloured wood proportion in a given sized tree still remains unexplained. A recent study by Havrejluk et al. (2013) found inter-site climatic variation (annual minimum temperature) as a possible cause. However, this problem still needs a comprehensive study covering a wide range of geographical area. In addition, the taper equation developed for predicting discoloured wood column in sugar maple trees also needs to be validated with independent data from other locations. Besides this, vertical dissection of some trees would help link discoloured wood dynamics to branch death and other mechanical injuries.

Secondly, dynamic growth modelling approach requires a basis to quantify sapwood turnover (heartwood formation). Heartwood formation, in this study, was quantified using an allometric relationship between tree characteristics and stem basal area. This needs to be verified experimentally. Besides this, the variation of leaf to sapwood area ratio with crown size for a tree of given sized tree (chapter III) indicates that leaf area as well as leaf distribution in the crown is related to sapwood area at the given height. Therefore, study on sapwood tapering along the main stem and branching of sapwood and heartwood at the branching points will be useful for parameterizing the growth model. Moreover, although the biochemical assay of physiological heartwood in sugar maple was done by Good et al. (1955), biochemical and anatomical examination using recent technologies would help to define physiological heartwood in sugar maple as well as other diffuse porous hardwoods.

Lastly, prediction models for wood quality attributes presented in this thesis were based on limited sample size coming from three different sites of south-eastern Quebec, Canada. Therefore, it is important to validate/or re-calibrate these model before using them to predict for the trees that are outside the observed range or study area.

5.6 References (General Introduction and General Conclusion chapters)

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