UNIVERSITÉ DU QUÉBEC EN ABITIBI-TÉMISCAMINGUE

VARIATION DES PROPRIÉTÉS ANATOMIQUES, PHYSIQUES ET MÉCANIQUES DU BOIS DE CLONES DE PEUPLIER HYBRIDE

THÈSE PRÉSENTÉE COMME EXIGENCE PARTIELLE DU DOCTORAT EN SCIENCES DE L'ENVIRONNEMENT

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VARIATION IN WOOD ANATOMICAL, PHYSICAL AND MECHANICAL PROPERTIES OF HYBRID POPLAR CLONES

THESIS PRESENTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY IN ENVIRONMENTAL SCIENCES

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This thesis is dedicated to

my parents and my wife Kaniz Fatema;

especially to my late father, Abdur Rashid SHEIKH,

who passed away on November 17, 2011.

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Une description sommaire des articles scientifiques est proposée ci-après:

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Je suis le premier auteur de chacun des chapitres de cette thèse, ayant réalisé chaque partie depuis la récolte de données jusqu'à la rédaction. Mon directeur Ahmed Koubaa Ph.D, et mon codirecteur Alain Cloutier Ph.D ont toutefois suivi chaque étape de cette thèse et ont réalisé la révision portant autant sur le fond que sur la forme de tous les chapitres. Les autres auteurs ont contribué directement ou indirectement à la réalisation de ce projet et ont participé à la révision des articles.

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LIST OF ABBREVIATIONS

AD	Air-dried density
AFD	Average fiber diameter
AFLA	Average fiber lumen area
ARD	Annual ring density
ARW	Annual ring width
ASTM	American Society for Testing and Materials
AVD	Average vessel diameter
AVLA	Average vessel lumen area
BD	Basic density
CRC-VACAT	Chaire de Recherche du Canada sur la Valorisation, la Caractérisation et la Transformation du bois
CRMR	Centre de recherche sur les matériaux renouvelables
CS	Ultimate crushing strength
CWA	Cell wall area
dbh	Diameter at breast height
EMC	Equilibrium moisture content
EWD	Earlywood density
EWW	Earlywood width
FAO	Food and Agriculture Organization
FL	Fiber length
FP	Fiber proportion
FQA	Fiber quality analyzer
FRQNT	Fonds de recherche du Québec - Nature et technologies
FW	Fiber width
FWT	Fiber wall thickness
G	Genetic gain

GD	Green density
G-layer	Gelatinous fiber layer
H^2	Broad-sense heritability
h^2	Narrow-sense heritability
i	Selection intensity
IPC	International Poplar Commission
L	Longitudinal direction
LSH	Longitudinal shrinkage
LVL	Laminated veneer lumber
LWD	Latewood density
LWP	Latewood proportion
LWW	Latewood width
MC	Moisture content
MDEIE	Québec's Ministère du Développement Économique, de l'Innovation et de l'Exportation
MOE	Modulus of elasticity
MOEC	Compression modulus of elasticity in parallel to grain
MOEF	Flexural modulus of elasticity
MOR	Modulus of rupture
MORF	Flexural modulus of rupture
MRN	Quebec's Ministère des Ressources Naturelles
OD	Oven-dry density
OSB	Oriented strand board
PL	Proportional limit
R	Radial direction
RH	Relative humidity
RLQ	Réseau Ligniculture Québec
RP	Ray proportion
RSH	Radial shrinkage

S	Selection differential
SRIC	Short rotation intensive culture
T	Tangential direction
TD	Transition density
TSH	Tangential shrinkage
TW	Tension wood percentage
UQAT	University of Quebec at Abitibi-Temiscamingue
VP	Vessel proportion
VSH	Volumetric shrinkage

ABSTRACT

To meet increasing wood demand with a dwindling forested land base, there has been a progressive interest in developing productive short rotation tree plantations. In Canada, hybrid poplar plantations are of particular interest because short rotation forestry can contribute to a stronger, more stable and renewable supply of fiber. Moreover, tree breeding is considered one of the best options to accelerate fiber production and improve wood quality. The main objective of this study was to assess the anatomical, physical and mechanical properties of various hybrid poplar clones in a perspective of evaluating the potential of their wood for various end-uses. This study contributes to the Quebec hybrid poplar-breeding program by adding information on wood quality of fast growing clones. For this study, we analysed wood quality of seven hybrid clones from three sites (Pointe-Platon, Saint-Ours, and Windsor) from southern Quebec. Five trees per clone were randomly sampled from each site to measure selected wood anatomical (fiber length, fiber width, fiber proportion, vessel proportion, fiber wall thickness, tension wood, cell wall area percentage), physical (basic density, volumetric, radial, tangential and longitudinal shrinkage), and mechanical (bending and compression strength) properties.

Statistical analyses revealed that the effect of site on the studied properties was highly significant, and was explained by environmental conditions and site quality. All anatomical properties of hybrid poplar wood showed significant clonal variation, indicating the possibility of identifying clones with superior wood properties. All anatomical properties showed variation in their magnitude with increasing cambial age. The variation in radial pattern was characterized by a rapid increase in the first few years in fiber length, fiber width, fiber proportion, wall thickness, and percent cell wall area; in contrast vessel proportion decreased. Pith to bark trends showed that wood density traits increased with cambial age. Heritability values of ring density traits had a tendency to increase with cambial age, and were generally lower near the pith. In contrast, results of ring width traits showed a decreasing trend with cambial age.

All physical and mechanical properties of hybrid poplar wood showed significant interclonal variation, especially for density, flexural modulus of rupture, and ultimate crushing strength. Genetic correlations between all wood properties were higher than the phenotypic correlations. All ring density traits were highly correlated with each other. Strong correlations were also found among fiber proportion, fiber wall thickness, basic density, and mechanical properties. Results from this study further show close genotypic and phenotypic correlations between fiber proportion, fiber wall thickness, and wood density. The genotypic correlations among mechanical properties and density were very strong. As a result, the inclusion of wood density into tree breeding

programs can lead to an improvement of mechanical properties. These high genotypic correlations with MOE and MOR make density a strong candidate for direct genetic improvement of general wood quality. Consequently, the use of this property can ultimately benefit solid wood and fiber-based wood products.

High heritability values for the studied properties indicated that these properties are under moderate to high genetic control. The clonal variation, heritability, and genetic gain values for the properties investigated in this study should help poplar-breeding programs that aim to optimize hybrid poplar clones for solid wood and fiber-based products. However, a future challenge will be to determine whether breeding objectives are compatible with industrial objectives by improving wood properties.

RÉSUMÉ

Pour faire face à la demande croissante de bois avec une diminution des terres forestières disponibles, un intérêt progressif est apparu pour développer des plantations d'arbres productives à rotation courte. Au Canada, les plantations de peuplier hybride sont particulièrement intéressantes puisque la sylviculture intensive courte peut contribuer à un approvisionnement en fibres plus solide, stable et renouvelable. Par ailleurs, l'amélioration génétique est considérée comme l'une des meilleures façons d'accélérer la production de la fibre et d'améliorer la qualité du bois. Le principal objectif de cette thèse était est de caractériser les propriétés anatomiques et physico-mécaniques de plusieurs clones de peuplier hybride dans une perspective d'évaluer le potentiel de leur bois pour diverses utilisations finales. Cette étude contribue au programme d'amélioration des arbres du peuplier hybride du Québec pour une croissance plus rapide en y ajoutant des informations sur la qualité du bois. Pour cette étude, nous avons analysé la qualité du bois de sept clones de peuplier hybride dans trois sites (Pointe-Platon, Saint-Ours, and Windsor) du sud du Québec. Cinq arbres par clone par site ont été échantillonnés aléatoirement afin de mesurer leurs propriétés anatomiques (longueur et largeur des fibres, proportion de fibres et de vaisseaux, l'épaisseur de la paroi des fibres, bois de tension, et pourcentage de la superficie de la paroi cellulaire), physiques (densité basique, et retraits volumétrique, radial, tangentiel et longitudinal) et mécaniques (résistance à la flexion et à la compression) du bois.

Les analyses statistiques ont relevé que l'effet du site sur les propriétés étudiées a été hautement significatif et a été expliqué par les conditions environnementales et la qualité du site. Toutes les propriétés du bois de peuplier hybride ont montré une variation clonale significative, ce qui indique la possibilité d'identification des clones avec des propriétés du bois supérieures. Toutes les propriétés anatomiques ont montré une variation de leur grandeur avec une augmentation en fonction de l'âge cambial. Le patron de variation radiale était caractérisé par une augmentation rapide au cours des premières années de la longueur et la largeur des fibres, la proportion de fibres, l'épaisseur de la paroi cellulaire des fibres, et le pourcentage de la superficie de la paroi cellulaire. En revanche, la proportion de vaisseaux diminuait avec l'âge cambial. Les tendances de la moelle à l'écorce ont montré que la densité du bois et de ses composantes ont augmenté avec l'âge cambial. Les valeurs d'héritabilité de la densité du bois et de ses composantes ont tendance à augmenter avec l'âge cambial et à être généralement plus faibles près de la moelle. En revanche, les résultats de la largeur du cerne et de ses composantes ont indiqué une tendance à diminuer avec l'âge cambial.

Toutes les propriétés physiques et mécaniques du bois de peuplier hybride ont montré une variation interclones significative, ce qui indiquerait une possibilité

d'identification de clones avec des propriétés du bois supérieures, spécialement pour la densité, le module de rupture en flexion et la résistance à l'écrasement. Les corrélations génétiques entre toutes les propriétés étaient plus élevées que les corrélations phénotypes. La densité du cerne et de ses composantes étaient hautement corrélées l'une avec l'autre. Des bonnes corrélations ont été trouvées entre la proportion de fibres, l'épaisseur de la paroi des fibres, la masse volumique, et les propriétés mécaniques. Les résultats de cette étude montrent également des corrélations génétiques et phénotypes étroites entre la proportion de fibres, l'épaisseur de la paroi des fibres et la densité du bois. Les corrélations génotypiques entre les propriétés mécaniques et la masse volumique se sont avérées très fortes. Par conséquent, l'inclusion de la masse volumique du bois dans les programmes d'amélioration génétiques pourrait entraîner une amélioration des propriétés mécaniques. De plus, les corrélations génotypiques étroites entre le MOE et le MOR font de la masse volumique un bon caractère pour l'amélioration génétique directe de la qualité générale du bois. Par conséquent, l'utilisation de cette propriété peut finalement bénéficier au bois massif et aux produits du bois à base de fibres.

Les valeurs d'héritabilité élevées estimées pour les propriétés étudiées indiquent que ces propriétés sont sous contrôle génétique modéré à élever. Les valeurs de variation clonale, d'héritabilité et de gains génétiques pour les propriétés examinées par cette étude indiquant que les programmes d'amélioration génétique du peuplier hybride pour le bois massif et les produits du bois à base de fibres devaient être efficaces. Visant l'amélioration des propriétés du bois, le défi à venir consistera à déterminer si les objectifs de sélection seront compatibles avec les objectifs industriels.

General Introduction

Wood is one of the most important renewable raw materials, which has been used by human beings since early years. World demand for wood is increasing at a rate of approximately 70 million m^3 per year, due in part to the increasing world population (Arseneau and Chiu 2003). Canada's challenge to meet the increasing demand for fiber is also being impeded by a decreasing share in world markets due to new international competitors, mostly from the Southern Hemisphere. The driving force behind these newcomers in the wood fiber market is technology. They possess the scientific expertise to achieve high growth rates and yields from tree species adapted to their conditions as well as the processing technology to use low quality fiber in wood products manufacturing. This trend will continue to gain in prominence over the next century. Fast growing high-yield plantations represent only 7% of the world's total forest area but already provide 30% of timber supply (FAO 2010). By 2020, the global roundwood supply from plantations should increase to 44% (FAO 2001). Several countries have chosen this path, are increasingly competing with Canadian products, and are already ahead of Canadian companies since they have developed and implemented the technology to produce low cost fiber from fast growing high-yield plantations.

Poplars are one of the most widespread and fastest-growing tree species in North America. The genus *Populus* contains over 25 species of deciduous trees including black cottonwood (*Populus trichocarpa*), eastern cottonwood (*Populus deltoides*), lombardy poplar (*Populus nigra*), and aspen, which are frequently the dominant broad-leaved tree species in many forested regions. Poplars have a substantial breadth of distribution across geographic and climatic ecoregions, and are notable for their vigorous growth (Dickmann et al. 2001). *Populus* includes morphologically diverse species of deciduous, relatively short-lived, and fast-growing trees.

Hybrid poplars are progeny from crosses between trees of two or more species within the genus *Populus*. Hybrid poplars are genetically predisposed to grow faster and have wider adaptability than either parent species. Hybrid crosses also create heterosis (hybrid vigor) in which the progeny have increased performance of traits beyond what is capable by either parent. Hybridization can also increase developmental homeostasis, resulting in greater phenotypic stability in varied environments (Stettler et al. 1996). On good sites, hybrid poplars grow faster than any other northern temperate region tree. They can produce 21 to 25 m trees with 20 to 25 cm diameter in 6 to 8 years (Zhao 2006). The hybrid poplar leaves can be four times larger than leaves of either parent at the same age and on the same site. They are easily propagated from stem cuttings, but because of quick re-sprouting, replanting after harvesting may be unnecessary, especially for short harvest cycles (Nesom 2002).

The majority of hybrid poplar breeding in Canada utilizes three native species: *Populus deltoides* (eastern cottonwood), *Populus balsamifera* (balsam poplar) and *Populus trichocarpa* (western black cottonwood) and two non-native species: *Populus maximowiczii* (Asian black poplar) and *Populus nigra* (European black poplar) (Demchik et al. 2002). Selected parents are usually inter-mated and superior progeny are selected for the next generation of mating. Selected trees can be vegetative propagated (cloned) and commercially released during any generation of the breeding process.

In Canada, hybrid poplar plantations are of particular interest because short rotation forestry can contribute to a stronger, more stable and renewable supply of fiber. It can also help relieve the pressure on natural forests. In the past, small industrial plantations of hybrid poplar were established in Canada, from Québec to British Columbia. Nurseries of Québec's Ministère des Ressources naturelles produced more than 1.5 million hybrid poplars in 2002, including hybrids of *P. deltoides, P. balsamifera, P. nigra, P. trichocarpa, and P. maximowiczii*. However, plantation sites

Heritability estimates are important to assess the potential genetic gain of the preferred wood properties. Since heritability values and genetic correlations depend on the specific test environment and population of trees (Falconer and Mackay 1996), they should be evaluated in contrasting environments and in different populations. However, it is important for the tree breeders to know the major causes that can affect wood variability and consequences on the genetic parameters. Therefore, the selection phase is generally carried out at young ages to reduce the length of the breeding cycles. Final products are strongly affected by variability of many factors within tree, such as cambial age, growth rate and heartwood formation (Zobel and van Buijtenen 1989). However, from a tree breeding perspective, this provides many opportunities for improvement. In general, it has been reported that wood properties are under strong genetic control (Zobel and Jett 1995).

Mechanical properties of mature wood have relatively high heritability (Zobel and Jett 1995), which indicates that the variability in these properties is under relatively strong genetic control and not much affected by the environment. However, there has been relatively little research on genetic variation in mechanical properties of juvenile wood, their correlations with tree growth and their impact on end-uses products (Zobel and Sprague 1998). According to Hernández et al. (1998), genetic variation in mechanical properties is significant in juvenile wood of hybrid poplar clones. The same conclusion was reached for families of *Eucalyptus grandis* (Santos et al. 2003), clones of *Cryptomeria japonica* (Fujisawa et al. 1994) and provenance of *Tectona grandis* Linn F. (Bhat and Priya 2004). Strength and stiffness are important mechanical properties that determine suitability of wood for specific uses. Wood density is usually a good predictor of mechanical properties (Panshin and deZeeuw 1980). However, these properties can be influenced by other factors including the variability among species, among trees within species and environmental conditions that affect the tree growth (Tsoumis 1991).

This thesis is concerned with the characterization of hybrid poplar wood characteristics and properties, and their utilization in forest industries. This thesis presents estimates for genetic parameters such as genotypic correlations, heritability and genetic gain between properties that are related to wood anatomy, dimensional stability and application for wood industries.

CHAPTER I

LITERATURE REVIEW

1.1 GENERAL INFORMATION ON POPLAR SPECIES

1.1.1 Poplar biology

The genus *Populus* belongs to the family Salicaceae widely known as poplars. The number of species in the genus *Populus* varies among classifications from 22 to 85 (Eckenwalder 1996). Eckenwalder (1996), recognized 29 species subdivided into six sections based on relative morphological similarity and crossability *Abaso*, *Turanga*, *Leucoides*, *Aigeiros*, *Tacamahaca* and *Populus* (Table 1.1; Cagelli and Lefèvre 1995; Eckenwalder 1996). Only 5 among these species are indigenous to Canada: *P. trichocarpa* (black cottonwood), *P. balsamifera* (balsam poplar), *P. angustifolia* (narrowleaf cottonwood), *P. deltoides* (eastern cottonwood and plains cottonwood) and *P. tremuloides* (trembling aspen) (Farrar 1995).

Table 1.1 Species of the sections within the genus Populus with their distribution (Eckenwalder 1996; Dickmann 2001; Taylor 2002).

Section (synonym)	Species	Distribution	Common name
Abaso Eckenwalder	*Populus mexicana* Wesmael	Mexico	Mexican poplar
Turanga Bunge	*P. euhratica* Olivier	NE Africa, Asia	Euphrates poplar
	P. ilicifolia (Engler) Rouleau	E Africa	Kenyan poplar
	P. pruinosa Schrenk	Asia	
Leucoides Spach	*P. glauca* Haines	China	
	P. heterophylla L.	USA	Swamp cottonwood
	P. lasiocarpa Olivier	China	
Aigeiros Duby	*P. deltoides* Marshall	N America	Eastern cottonwood
	P. fremontii S. Watson	USA	Fremont cottonwood
	P. nigra L.	Eurasia, N Africa	Black poplar
Tacamahaca	*P. angustifolia* James	N America	Narrowleaf
Spach	*P. balsamifera* L.	N America	cottonwood
	P. ciliata Royle	Himalayas	Balsam poplar
	P. laurifolia Ledebour	Eurasia	Himalayan poplar
	P. simonii Carrière	E Asia	Laurel poplar
	P. suaveolens Fischer	NE China, Japan	Simon poplar
	P. szechuanica Schneider	E Eurasia	Asian poplar
	P. trichocarpa Torrey &	N America	Szechuan poplar
	Gray	Eurasia	Black cottonwood
Populus (*Leuce*	*P. adenopoda* Maximowicz	China	Chinese aspen
Duby)	*P. alba* L.	Europe, N Africa, Central Asia	White poplar
	P. gamblei Haines	E Eurasia	Himalayan aspen
	P. grandidentata Michaux	N America	Bigtooth aspen
	P. guzmanantlensis Vazques & Cuevas	Mexico	Manantlan white poplar
	P. sieboldii Miquel	Japan	Baja white poplar
	P. simaroa Rzedowski	Mexico	Japanese aspen
	P. tremula L.	Europe, N Africa,	Balasa white poplar
	P. tremuloides Michaux	NE Asia	
		N America	Quaking (trembling) aspen

1.1.2 Poplar morphology

Populus are deciduous tree species generally grown in the boreal, temperate, and subtropical zones of the northern hemisphere (Eckenwalder 1996; Dickmann 2001; Cronk 2005). They have tall and straight single trunks, with bark that tends to remain thin and smooth until more advanced ages than in other tree species (Eckenwalder 1996; Dickmann 2001). They rarely live longer than 100 to 200 years and can reach large sizes. Black cottonwood (*Populus trichocarpa*) can exceed 60 m in height and reach up to 3 m in diameter (DeBell 1990). Leaves are alternate and simple, with pinnato-palmate venation, and petioles are often transversally flattened distally (Eckenwalder 1996).The occurrence of hermaphroditic trees has been reported in multiple poplar species (Rottenberg 2000; Rowland et al. 2002; Cronk 2005; Slavov et al. 2009). Both male and female flowers are grouped in pendent catkins that burst between February and May. After pollination, female flowers develop into capsules that release 2 to 50 light seeds with cottony hairs promoting wind dispersion over greater distance (Schreiner 1974; Boes and Strauss 1994; Eckenwalder 1996). However, many hybrid poplars never produce flowers and therefore to be sterile.

1.1.3 Poplar hybridization

Hybridization is done by crossing two different genera or species to create new individuals with varying degrees of the progenitors' characteristics (Marques et al. 2007; 2014). Hybridization between species has traditionally been examined for its role in finalizing the speciation process through reinforcement of reproductive barriers (Howard 1993). Hybrid poplars are the results of natural and manmade crosses among different poplar species. Interspecies hybridization is one of the common features among many members of the genus *Populus* in the northern hemisphere (Barnes 1961; Eckenwalder 1996; Stettler et al. 1996; Whitham et al. 1996). Several species of the genus *Populus*, particularly the species of the sections *Tacamahaca* and *Aigeiros*, which are represented in North America, are broadly sympatric and known to hybridize extensively (Brayshaw 1965; Eckenwalder 1984*a*, 1984*b*; Rood et al. 1986; Greenaway et al. 1991; Floate 2004).

In North America, hybrid poplars occur naturally wherever compatible species come into close proximity. For example, hybridization between *P. balsamifera* and *P. trichocarpa* occurs in Southeastern Alaska and the Cook Inlet region. Rood et al. (1986) reported tri-hybridization among *P. deltoides*, *P. balsamifera*, and *P. angustifolia*, in Southern Alberta. In addition, natural hybrids occur between *P. deltoides* and *P. balsamifera* in Eastern Canada (Rood et al. 1986; Floate 2004; Hamzeh et al. 2007). However, most hybrid poplars result from artificial hybridization and subsequent planting. An unknown number of hybrids also form between native species and introduced clones, cultivars, and species (Eckenwalder 1996).

1.1.4 Poplar distribution and culture

Poplar species have wide native ranges, often spanning more than 20 degrees of latitude and a great diversity of climates and soils (Eckenwalder 1996; Dickmann 2001). It grows in various habitats, ranging from hot and arid, desert-like sites in central Asia and northern and central Africa to alpine or boreal forests in Europe and North America.

Poplar culture spread across the world at the beginning of last century. In 1947, the International Poplar Commission (IPC) was founded under the patronization of the FAO of the United Nations. The work of the Commission has led to important agreements on nomenclature, registration of clones, and varietal control (Zsuffa et al. 1996). There has been an increase in poplar culture over recent decades as it can provide wood products for fiber, fuels and chemicals while at the same time contributing to a more favourable carbon balance (Klass 1998). In North America, about 50 to 80 clones are currently being used in poplar culture (Dickmann et al. 2001).

1.1.4.1 Poplar culture in Canada

Poplar is an important species in North America. A significant amount of research on fast-growing tree plantations has been carried out in Canada. In Ontario and Manitoba, research was initiated in the 1920s and 1930s (Dickmann and Stuart 1983, Ménétrier 2008). The poplar culture began by Carl Heimburger in Ontario in 1930s, by selecting and breeding poplars for wood production. In Quebec, intensive and large scale efforts began in the late 1960s (Ménétrier 2008). In the 1970s, programs of poplar hybridization became common in Ontario, Quebec, Saskatchewan and British Columbia, whereas, this was initiated in the 1990s in Alberta through private companies and joint efforts with various government agencies across Canada (Poplar Council of Canada 2012). Presently, hybrid poplar crops are almost exclusively on existing farmland or newly cleared agricultural class lands in private ownership, using agronomic methods (Table 1.2). The cultivation approach of short rotation intensive culture (SRIC) for hybrid poplar plantation in Canada are for the purpose of supplying pulp fiber and for engineered wood products, such as OSB, LVL.

The hybrid poplar industry in North America developed around the biomass industry during the oil crises of 1973 and 1979. Then, pulp and paper companies became interested in this species to compensate for fluctuations in the wood fiber and chip markets (Stanton et al. 2002). Hybrid poplar can advantageously replace natural poplar (*Populus* spp.) since its mechanical properties are similar to those of cottonwood (*Populus deltoides* Marsh.), but are slightly lower than those of large-tooth aspen (*Populus grandidentata* Michx.) and trembling aspen (*Populus tremuloides* Michx.) (Hernández et al. 1998). In Canada, 27 559 ha of hybrid poplars were planted in 2011 (Table 1.2) (Poplar Council of Canada, 2012; Derbowka et al. 2012).

Table 1.2 Area of hybrid poplar SRIC crops planted by Canadian Organizations in 2011 (Poplar Council of Canada, 2012).

	Plantation reported in 2011 (ha)
Kruger Products Ltd. - BC	3411
Alberta-Pacific Forest Ind. Inc. - AB	9000
Ainsworth Engineered Canada LP - AB	605
AAFC-AESB – SK	10500
Domtar Inc. – QC	4000
Agro Énergie inc. - QC	43
MRNF – QC	unknown
Total	27,559

1.1.4.2 Poplar culture in Quebec

The poplar-breeding program has been started since 1969 in Quebec (Riemenschneider et al. 2001). The hybrid poplar genetic improvement program led by the *Direction de la recherche forestière, ministère des Ressources naturelles du Québec*, aims at developing high yielding and disease resistant hybrid varieties that can grow well within the range of bioclimatic conditions found in Quebec (Périnet et al. 2012). Selection criteria are vigour, hardiness potential, stem taper, wood quality, and degree of resistance to diseases and insects. A list of about 40 recommended clones exists, and all of these clones originated from hybrids of poplar species from the *Tacamahace* and *Aigeiros* sections (Périnet 2007). The species used include *Populus balsamifera* L., *Populus deltoides* Bartr. Ex Marsh., *Populus maximowiczii* A. Henry, *Populus trichocarpa* Torr. & A. Gray, and *Populus nigra* L. (Périnet et al. 2008).

Generally, fast-growing hybrid poplar plantations are considered as a potential alternative for producing high yields in temperate region for intensive production (Messier et al. 2003, Bilodeau-Gauthier et al. 2011). According to Messier et al. (2003), the anticipated yields were 14 m^3/ ha.yr on average sites, and 20 m^3/ ha.yr on the best sites of southern Québec in 2003. On the other hand, in the boreal region, the yields were 12 m^3/ ha.yr on the best sites and 10 m^3/ ha.yr on average sites (Messier et al. 2003). Attractive potential yields motivate the Quebec's forest industries to plant hybrid poplar for fiber production. As a result, approximately 10 000 to 12 000 ha of fast-growing poplar plantations are managed by industrials, whereas only 1 000 ha have been planted by small private landowners in the province of Quebec (Derbowka et al. 2012; Fortier et al. 2012). Today, approximately 1 500 ha of land are planted annually with hybrid poplars in Quebec (Périnet et al. 2012) with 1.5 million to 2.0 million plants produced by government nurseries (Fortier et al. 2011).

1.2 WOOD QUALITY AND WOOD PROPERTIES

1.2.1 Wood quality

Wood quality is currently receiving considerable attention from the whole forest industries, because wood quality measures the success of forest growing practices. There are many definitions of wood quality (Keith 1985), but the definition proposed by Mitchell (1961) is widely cited, "*Wood quality is the resultant of physical and chemical characteristics possessed by a tree or a part of a tree that enable it to meet the property requirements for different end products*". Another wood quality defination in broad sense is, "*All wood characteristics that affect the value recovery chain and the serviceability of end products*".

Wood quality can be influenced by several traits, such as wood density, earlywood to latewood ratio, and presence of knots, decay, spiral grain etc. Besides, traits like wood density, fiber length, fiber coarseness, microfibril angle and cell wall chemistry may be a valuable tool when selecting superior clonal material (Mansfield and

Weinseisen 2007). Moreover, wood quality can become valuable for any end uses (Jozsa and Middleton 1994).

Table 1.3 A summary of wood properties that should be assessed for wood quality (Jozsa and Middleton 1994; Raymond 2000; Miller 2002; Zhang 2003; van Leeuwen 2011).

Pulp and paper	Sawn timber	composite
	Wood properties	
Basic density	Stem characteristics and tree age	Basic density
Cellulose content	Microfibril angle	Lignin content
Fiber length	Tension wood	Cellulose content
Extractives content	Knots	Extractives content
	Decay	
	Spiral grain	
	End splits	
	Basic density	
	Shrinkage	
	Products properties	
	Strength and stiffness	Strength and stiffness
	Dimensional stability	Durability
	Lack of internal checking	Gluability
	Crook and bow	Hardness

Small change in material properties of wood affects the process and properties of final products. For this reason, tree breeders do not treat wood quality and wood quantity as independent factors. Wood density is important to the wood technologist for its higher timber strength and a greater yield of pulp (Elliot 1970). Pulp and paper mill requirements for quality wood are long fiber length with low lignin content (Zobel 1961; Zobel and Van Buijtenen 1989). High stiffness is required for structural wood engineering, which is an important wood quality for beam, joints and purlins (Addis Tsehaye et al. 1995).

1.2.2 Properties influences wood qualities

Wood properties are a result of the combination of three characteristics: macroscopic morphology, wood anatomy and chemical composition (Pereira el al. 2003). The macroscopic morphology includes different types of wood tissue, such as reaction wood, growth rings, juvenile wood, and knots, whereas, the anatomical aspects include the types of cells and biometry and the proportions of each comparatively. The chemical composition of wood, the cell wall components and extraneous materials, also have a direct influence on the properties of wood.

Fiber morphology, such as fiber length and coarseness, are attributes of importance to the pulp and paper industry. Fiber length, diameter and cell wall thickness have a direct influence on pulp and paper quality (Seth 1990a; Seth 1990b; Mansfield and Weinseisen 2007). Fiber length impacts inter-fiber bonding and tear strength is proportional to fiber length (Seth and Page 1988). Fiber wall thickness also plays an important role in determining wood quality for the pulp industry. Thin walled cells contribute to burst and tensile strength, whereas, thicker walled cells are favorable to tear strength, breaking length, bulk and absorbance properties, but are less conformable than thinner cell-walled fibers (Da Silva Perez and Fauchon 2003). Fiber wall thickness also has a direct influence on wood density and degree of shrinkage, and indirect influence on the mechanical properties of wood (Polge 1978; Holmberg et al. 1999).

Another anatomical factor that influences the wood quality is reaction wood and compression wood. Reaction wood is generally formed in the upper side of the leaning trees, which is termed as tension wood (Wardrop and Dadswell 1948; Wardrop 1964).

Compression wood in conifers occurs in a range of gradation from near normal wood to the severe compression wood; occurs on the underside of lateral branches and leaning stems. (Low 1964; Yumoto et al. 1983).

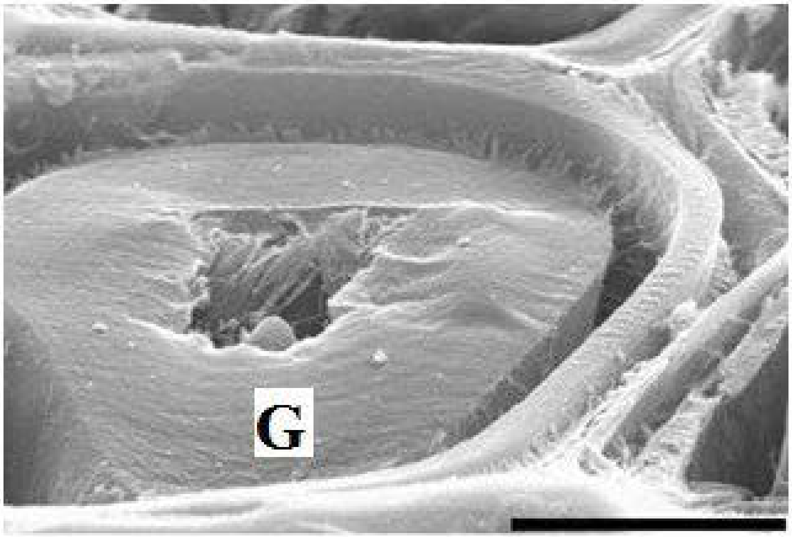

Figure 1.1 Gelatinous fiber layer (G-layer) in hybrid poplar. G: G-layer, Scale bar: 10 μm (Clair 2001).

A gelatinous fiber layer also known as G-layer, certain layer are unlignified or partially lignified and composed of crystalline cellulosic microfibrils in a secondary layer of fibers which are sticky or gelatinous nature (Figure 1.1). Gelatinous fibers are specialized sclerenchyma cells, characterized by their elongated shape and the presence of an inner cell-wall layer (Clair et al. 2008), looks more or less transparent in many types of histological preparations, and hence was called 'the gelatinous layer' (Figure 1.1). Fifty percent of angiosperm wood species surveyed to date produce tension wood, which results of tensional stress (Onaka 1949; Fisher and Stevenson 1981; Clair et al. 2006). However, gelatinous fibers in tension wood can vary significantly even in closely related species; for example, some *Eucalyptus* species produce G-fibers in tension wood whereas others do not have any or little ability to produce. There are sometimes referred to as parts of the secondary cell wall as they replace the secondary S_2 layer or get incorporated into the S_3 layer (Dadswell and Wardrop 1955). Therefore, the structure and composition of tension wood needs to be considered while screening trees for wood quality.

In general, density and microfibril angle are the key determinant factors of wood quality (van Leeuwen 2011). The density of wood is defined as the mass per volume unit. Density is relatively easy to measure and a good predictor of other physical and mechanical properties (Zobel and van Buijtenen 1989). Wood density is most widely used factor to characterize wood quality (Zobel 1961; Yanchuk et al. 1983; Bamber and Burley 1983; Butterfiend 2003). According to Bamber and Burley (1983) "*of all the wood properties, density is the most significant in determining end use as it has considerable influence on wood strength, machinability, conversion, acoustic properties, paper yield properties and probably many others*". Wood density is considered as a determinant factor of wood quality for two reasons: first, suitability of wood to different end-uses purposes, and second, it is a relatively cheap and an easy parameter to measure (Walker and Woolons 1998). Wood density is well correlated to many other physical properties, including strength, stiffness and performance in many end-uses (Panshin and de Zeeuw 1980; Oliveira et al. 2005; Apiolaza 2009). This makes wood density an excellent trait to predict end-use characteristics of wood (Jozsa and Middleton 1995; Pot et al. 2002). Wood with thicker cell walls has a higher density than the same volume of wood with thinner cell walls. Cell wall thickness is species related, but can vary significantly with different factors, such as, cambial age, earlywood and latewood fiber, and growth rings. Latewood cells that produce denser wood have much thicker walls than earlywood cells (Butterfield 2003). On the other hand, wood that has a relatively high fiber to vessel ratio yields more dense wood than wood with a lower ratio (Savidge 2003).

Changes in dimensions, as wood products are exposed to varying relative humidity conditions, cause practical problems. Change in dimensions can be related to dimensional stability of the wood thus considered as an important quality parameter in solid wood products. Wood shrinkage is anisotropic, it shrinks about twice as much tangentially (TSH) as radially (RSH) and shrinkage is generally very low in the longitudinal direction (LSH) (Walker 2006). The TSH, RSH, and LSH together approximate the total volumetric shrinkage (VSH). In general, wood shrinkage from green to oven-dry condition amounts to only 0.1% to 0.3% in the longitudinal direction, while moderate shrinkage in the radial and tangential directions varies from 6-8% and 9-11%, respectively (Zhang and Koubaa 2008). Zhang and Koubaa (2008) prepared a shrinkage classification which represents the dimensional stability of wood listed in Table 1.4.

Table 1.4 Wood shrinkage classification scales (Zhang and Koubaa 2008).

	High	Medium	Low	Very low
Volumetric shrinkage	>17%	13% to 17%	9% to 13%	<9%
Tangential shrinkage	>11%	9% to 11%	5% to 9%	<5%
Radial Shrinkage	>8%	6% to %8	3% to 6%	<3%

Wood quality of solid wood products mainly revolves around stiffness and dimensional stability (Beadle et al. 2008; Sanna 2012). Stiffness or modulus of elasticity (MOE) relates to linear deformation produced by a stress which is completely recoverable after the applied load is removed. Wood is an anisotropic material (Panshin and de Zeeuw 1980); it has three moduli of elasticity in mutually perpendicular axes; EL along the longitudinal axis (parallel to the grain), ER along the radial axis (perpendicular to the grain but normal to the growth rings) and ET along the tangential axis (perpendicular to the grain but tangent to the growth rings) (Kretschmann 2010). Among ER, ET and EL, the value of EL is far larger and this direction is the principal axis for solid wood products. Thus, the EL has been recognized as a key quality standard of wood and timber (Perstorper et al. 1995).

For this study, wood quality of hybrid poplar is expressed as a function of fiber properties (fiber length, width), fiber wall thickness, wood tissue proportions, wood density, dimensional stability and wood mechanical properties.

1.3 HYBRID POPLAR WOOD PROPERTIES

1.3.1 Anatomical properties

The literature addressing variations in anatomical properties of poplars is extensive. Panshin and de Zeeuw (1980) conducted a literature review on longitudinal and radial variations in wood anatomical properties. They found three patterns of radial variation in tracheid and fiber length: 1) a rapid increase followed by constant length from pith to bark; 2) a smooth and continuous increase from pith to bark; and 3) an increase from pith to bark up to a maximum, followed by a smooth decrease. A similar trend was reported for vessel element length and for fiber and vessel diameter, although the increase was moderate. Bendtsen et al. (1981), Bendtsen and Senft (1986) and Koubaa et al. (1998a) observed that fiber length in poplar wood increased from pith to bark and with tree age. In addition, clone type and height significantly affected average fiber length of *Populus* × *euramericana (*Koubaa et al. 1998a). Fiber wall thickness increased from pith to bark in some species and remains constant in others. According to Mátyás and Peszlen (1997), wood properties vary greatly within and among poplar trees. However, the findings on variation in poplar wood properties are inconclusive and in some cases contradictory. More specifically, within-tree variation in anatomical properties in hybrid poplars has not been examined, except for a few studies on fiber length (Holt and Murphey 1978; Murphey et al. 1979; Yanchuk et al. 1984; Bendtsen and Senft 1986; Koubaa et al. 1998a; DeBell et al. 1998).

Information on fiber length is important for several applications. Strength of wood and wood products is related to fiber length. Average fiber length for 40 different poplar clones was reported as 0.86 mm, and significant differences were found between individual trees both within and among clones (Klasnja et al. 2003) (Table 1.5). Geyer et al. (2000) reported that fiber length of eleven four-year old poplar clones ranged from 0.76 mm to 0.87 mm and the average fiber length was 0.84 mm. Bendtsen et al. (1981) and Bendtsen and Senft (1986) reported higher fiber length ranging from 1.02 mm to 1.27 mm for poplar wood.

Table 1.5 Anatomical properties of various *Populus* species and their hybrids (fiber length (FL), fiber width (FW), fiber wall thickness (FWT), fiber proportion (FP), vessel proportion (VP), ray proportion (RP), cell wall area (CWA), and tension wood percentage (TW)).

Species or hybrid	FL (mm)	FW (μm)	FWT (μm)	FP (%)	VP (%)	RP (%)	CWA (%)	TW	References
Hybrid poplar	0.92-0.94	20.0-27.2	1.2-2.4	54.1	27.5	18.5	39.4	38.8	Rydholm (1965).
P. x euramericana	0.62-1.02	-	-	-	-	-	37.1-45.9	15.3	Peszlen (1994); Mátyás and Peszlen (1997); Koubaa *et al.* (1998a); Jourez et al. 2001
Poplar clones	0.68-1.27	23-26	-	53-68.5	25.9-34.0	8.4-14.0	-		Geyer et al. (2000); Klasnja et al. (2003); Cheng and Bensend (1979); Fang and Yang (2003)
Poplar spp.	1.32-1.38	-	-	53-60	28-34	11-14	-	29.1-42.3	Kaeiser and Boyce 1965; Panshin and de Zeeuw (1980); Kroll et al 1992
P. tremuloides	-	-	2.3-2.4	-	-	-	41.9-42.2		Sutton and Tardif (2005)

The wood element proportion of poplar wood is dominated by a relatively high proportion of fibers (57 to 69 %) followed by vessel elements (23 to 33 %), ray cells

(6 to 12 %) and a negligible proportion of axial parenchyma (0.1 to 0.3 %) (Cheng and Bensend 1979; Bendtsen et al. 1981; Balatinecz et al. 2001). Panshin and de Zeeuw (1980) reported 53 to 60% fiber proportion, 28 to 34% vessel proportion and 11 to 14% ray proportion, respectively, for poplar species (Table 1.5).

Peszlen and Molnar (1996) investigated the fraction of fiber lumen, vessel lumen, cell wall and ray area on cross sections. Average fiber lumen diameter was reported as 16.2 μm and 18.8 μm for cottonwood and its hybrid NE-237, respectively, although both species had the same average vessel lumen diameter at 107 μm (83 to 131 μm) (Bendtsen et al. 1981). A similar fiber lumen diameter range of 15.2 μm to 17 μm was found in three *P.* × *euramericana* clones from two different sites, but with a smaller vessel lumen diameter ranging from 76 μm to 86 μm (Mátyás and Peszlen 1997).

In many species such as poplar, oak or chestnut, tension wood contains fibers with a special morphology and chemical composition due to the development of the so-called gelatinous layer (G-layer) (Onaka 1949) replacing the S_3 layer and a part or the whole of the S_2 layer (Saiki and Ono 1971). The G-layer is known to have high cellulose content with a high degree of crystallinity (Norberg and Meier 1966; Côté et al. 1969) and to contain microfibrils oriented along the axis of the cell (Fujita et al. 1974). Data on tension wood in poplars and hybrid poplar clones are summarised in Table 1.5.

1.3.2 Physical properties

Wood density is considered as the most important wood property as it has a major impact on other wood properties and their end uses. Wood density of hybrid poplar in North America ranges from 0.30 to 0.39 (Balatinecz et al. 2001). This is consistent with the density of poplar wood documented in other studies (Yanchuk et al. 1983; Hernández et al. 1998; Goyal et al. 1999; Klasnja et al. 2003). Beaudoin et al. (1992) reported significant differences in wood density among poplar clones according to the height at which samples were collected. In the longitudinal direction, density is usually higher at breast height (dbh), decreases until mid-height then increases upward (Beaudoin et al. 1992; De Boever et al. 2007). On the other hand, in the radial direction, density increases from the pith outwards (Yanchuk et al. 1983; Beaudoin et al. 1992; Hernández et al. 1998).

Considering their low density compared with other species, poplar species have high volumetric shrinkage (Balatinecz et al. 2001). Koubaa et al. (1998b) reported 11.9–13.5 % total volumetric shrinkage for ten *P.* × *euramericana* clones, which is consistent with some other native poplars. Koubaa et al. (1998b), found 7 % to 8.3 % partial volume shrinkage, whereas, Pliura et al. (2005) found slightly lower values in hybrid poplar clones. Averages of 1.8 % and 4.8 %, and 2.3 % and 5.1 % were for radial and tangential shrinkage for hybrid and native poplar, respectively (Pliura et al. 2005). They also reported that longitudinal shrinkage was the lowest in all three principle directions, ranging from 0.1 % to 0.24 % for hybrid poplars.

Table 1.6 Physical properties of poplar species.

Species/Hybrid	Density (kg/m^3)	Volumetric shrinkage (%)	Longitudinal shrinkage (%)	Radial shrinkage (%)	Tangential shrinkage (%)	References
Hybrid poplar	300-390	5.2-8.0	0.1-0.4	1.8-2.6	4.9-5.0	Balatinecz et al. (2001); Pliura et al. (2005).
P. x euramericana clones	276-407	11.9–13.5	-	9.5	3.5	Bendtsen et al. (1981); Beaudoin et al. (1992); Koubaa et al. (1998b)

1.3.3 Mechanical properties

Wood may be described as an orthotropic material. It has unique and independent mechanical properties in the directions of three mutually perpendicular axes: longitudinal, radial and tangential. The most commonly measured properties that represent wood strength include the modulus of rupture in bending, the modulus of elasticity parallel to the grain, the compressive stress parallel and perpendicular to the grain, and shear strength parallel to grain (Green and Evans 1987). Additional measurements are often made to evaluate other mechanical properties such as work to maximum load in bending, impact bending strength, tensile strength perpendicular to grain, and hardness.

Hybrid poplar is a fast growing tree and it is important to know the mechanical properties of its wood for optimum end-uses. Several researchers have studied the potential of using hybrid poplar for lumber manufacturing (Hall et al. 1982; Hernández et al. 1998; Kretschmann et al. 1999; De Boever et al. 2007).The mechanical properties values of hybrid poplar clones are summarized in Table 1.7.

Table 1.7 Mechanical properties of poplar species.

Species/Hybrid	MOE (MPa)	MOR (MPa)	CS (MPa)	References
Hybrid poplar	3781-7130	50.4-75.4	41.9	Peters et al. (2002); Yu et al. (2008).
P. deltoides	7000	37	-	Balatinecz and Kretschmann (2001).
P. x euramericana clones	5380-7540	33.6	31.4	Bendtsen et al. (1981); Hernández et al. (1998)

1.4 RELATIONSHIP BETWEEN WOOD ANATOMICAL, PHYSICAL AND MECHANICAL PROPERTIES

1.4.1 Growth effect on wood properties

The relationship between tree growth rate and wood quality is an important issue when designing a breeding strategy. Growth rate, expressed as ring width and the number of growth rings per measure unit, is closely correlated with wood density. This relationship is of an extreme importance in most breeding programs, since most programs are driven by the selection of superior growth trees, and should a negative relationship exist, this selection could be on the detriment of other characteristics. The relationship between growth rate and fiber and wood properties is controversial and confusing mainly due to the complexity caused by the various factors that impact both wood and tree growth (Zobel and van Buijtenen 1989).

Correlation of growth rate with wood properties has been widely investigated. Many studies have shown that there is an increase in the proportion of juvenile wood and earlywood percentage in rapidly grown trees, and wood properties of these trees are poor in comparison with the slow growth trees (Bendsten 1978; Zobel 1981; Zobel and Talbert 1984; Megraw 1985).

The growth rate, which is expressed as ring width, has been positively correlated to wood density, for example, wider growth rings are associated with higher wood densities (Zobel and van Buijtenen 1989; Dobrowolska et al. 2011) but this relationship is species dependent. Ivkovich (1996) found a slight negative correlation between growth rate and density in *Populus balsamifera.*

The impact of the growth rate of different Hybrid poplarson mechanical properties is still a matter of controversy, largely because most studies include only one hybrid with a limited number of clones at a single site (Yu et al. 2008). A previous study noted no significant correlations between growth rate and MOE or MOR in static bending for diffuse porous hardwoods (Zhang 1995). Yu et al. (2008) reported the effect of diameter at breast height (dbh) growth on mechanical properties was negative but inconsistent.

1.4.2 Relationship between wood properties and anatomical properties

The variation in anatomical properties has influences on wood properties (Dadswell 1957; Burley and Palmer 1979). Fiber and vessel element dimensions, proportion and arrangement of different wood elements and density are the features of interest in this connection. However, the general pattern of variation in wood element dimensions is found not only within a species but also observed within tree in different species (Zobel 1965; Pande et al. 1995). Only few reports are available on the variation in wood anatomical properties and other wood properties in different poplar clones (Phelps et al. 1982; Koubaa et al. 1998a).

As fiber length depends on the rate of transverse division of the initial cambial cells, the result in fast-growing trees is a possible decrease in fiber length (Zobel and Talbert 1988). For poplars, most of the studies found no relationship between fiber length and growth rate. While, some reported a positive correlation between these two variables (DeBell et al. 2002; Cisneros et al. 2000; Yu 2001; Zhang et al. 2003).

Fiber length is generally short near the pith, increases rapidly during the early years, and then continues to increase at a lower rate towards the bark (Peszlen 1994; Mátyás and Peszlen 1997; DeBell et al. 1998; Koubaa et al. 1998a). The increase in fiber length from pith to bark could be explained by the increase in length of cambial initials with increasing cambial age, as discussed in previous studies (Peszlen 1994; Koubaa et al. 1998a, DeBell et al. 1998; Jorge et al. 2000; Fang and Yang 2003; Fang et al. 2004).

Isebrands (1972) reported that with the increase in volume of vessels percentage, fibers percentage decreased in eastern cottonwood (*Populus deltoides* Bart.). She also found that wood formed in the juvenile crown of eastern cottonwood usually had a lower percentage of vessels than wood in more mature crowns, and a noticeable decrease in the percentage of fibers with increasing distance from the pith and with tree height.

Most reports on radial patterns in hardwoods described the fiber length and wood density. The fibers are short, and density is low near the pith (Zobel and Buijtenen 1989). Similar pattern in *Populus* was also reported by Boyce and Kaiser (1961) and in *Eucalyptus* by Bisset and Dadswell (1949). Specific gravity and fiber dimensions are important wood traits, because they have strong relationship with both the yield and the quality of end products. Therefore, they are recommended as secondary traits for selection, and tree improvement programs are taking this route (Zobel and Buijtenen 1989).

There is no agreement in the literature regarding the length of tension wood fibers in comparison to normal fibers. Compared to normal fibers, tension wood fibers were reported sometimes as being longer (Onaka 1949; Ollinmaa 1959; Polge 1984; Jourez et al. 2001). As normal wood formation, the fiber length is intensively related to growth rate (Kennedy 1957; Koubaa et al. 1998a; Fang et al. 2002). If eccentricity of tension wood is produced from an increase division rate in the cambium, then tension wood fiber length would be expected to be shorter (Wardrop 1956, 1964). Concerning cell wall thickness, many researchers have reported that tension wood had thicker cell walls (Onaka 1949; Dadswell and Wardrop 1955; Wardrop 1964). In previous studies, there was a general agreement that tension wood contains lower vessel proportion than normal wood (Onaka 1949; Jourez et al. 2001; Ruelle et al. 2006), but some studies also showed a higher proportion (Kaeiser and Boyce 1965; Kroll et al. 1992). The decrease in vessel proportion with height in tension wood could partially be explained by the auxin concentration. Considering these results, it is easy conclude that fiber proportion increases in tension wood. Onaka (1949) and Jourez et al. (2001) reported that ray proportion did not vary with normal or tension wood.

Panshin and de Zeeuw (1980) and Jourez et al. (2001) reported a higher basic density for tension wood. Washusen et al. (2001) stated a positive correlation between microdensity and tension wood fiber percentage. Similar results were also reported by Kroll et al. (1992) and Clair et al. (2003). Shrinkage was reported to be higher in tension wood than normal wood (Onaka 1949; Dadswell and Wardrop 1955; Jourez et al 2001; Clair et al. 2003; Yamamoto et al. 2005).

1.4.3 Relationship between wood properties and physical properties

Variation within annual ring is of an important influence on overall wood density. Similarly, the variation in earlywood and latewood density can be the greatest amount of variation in a tree (Zobel and van Buijtenen 1989). Earlywood is generally produced during the first part of the growing season; whereas, latewood production occurs later in the growing season, during and after bud resting (Kennedy 1971; Zobel and van Buijtenen 1989). With the increase of cambial age, the percentage of latewood production also increases and results of an increase in the overall density. Previous research has shown that the proportion of latewood to earlywood influences the density, as does the variation in the density of earlywood and latewood (Zobel and van Buijtenen 1989).

The wood density of poplars and their hybrids was found to be high near the pith to drop at mid diameter and to increase afterword outwards, as reported for *P. albe* L., *P. grandidentata* Michx., and *P. tremuloides* Michx. (Johnson 1942; Beaudoin et al. 1992), *P. trichocarpa* (Okkonen et al. 1972), *P. euramericana* Dole. (Hernández et al. 1998), and *P. trichocarpa* x *P. deltoides* (DeBell et al. 2002). A slight negative correlation between the fast-growing habit of poplar clones and density was also found

(Beaudoin et al. 1992; Hernández et al. 1998). Blankenhorn et al. (1988) reported increasing specific gravity of wood with age. Whereas, Murphey (1979) and Bendtsen and Senft (1986) reported that specific gravity did not change significantly with age. A recent study (Pliura et al. 2005) found highly significant site effects on wood density. Cambium age and ring width were able to explain a large part of the radial variation in wood density within trees and that the cambial age explains more variation than does the ring width (Zhang and Zhong 1991).

The relationship between shrinkage and wood density has been discussed by many authors (Siau 1984; Skaar 1988; Koubaa et al. 1998b). Koubaa et al. (1998b) reported that the correlation between basic density and shrinkage was generally significant for hybrid poplar. However, Shupe et al. (1995) reported no significant correlation between wood density and shrinkage in cottonwood trees. Poplars also have a high ratio of tangential to radial shrinkage (Balatinecz et al. 2001).

1.4.4 Relationship between wood properties and mechanical properties

Mechanical properties show a marked improvement with age as the tree progresses through juvenile wood to maturity (Bendtsen and Senft 1986). Peszlen (1997) reported no clone effect on wood mechanical properties of hybrid poplar, such as MOR, MOE and crushing strength. However, age significantly influenced mechanical properties, which increased consistently with age, except for ultimate tensile strength, with no significant differences in early growth. Hernández et al. (1998) identified a negative but inconsistent relationship between growth rate and mechanical properties in *P.* × *euramericana*. Static flexural strength is the most frequently investigated mechanical property of wood, and strength varies across clones and within clone age groups. Mature wood generally has stronger mechanical properties due to its longer fibers, higher density, and smaller microfibril and spiral grain angle (Cisneros et al. 2000).

Mátyás and Peszlen (1997) reported that the average MOE and MOR of 10 and 15 years old *P.* x *euramericana* hybrids increased from pith to bark by 30%. Roos et al. (1990) reported MOE and MOR of quaking aspen (*Populus tremuloides* Michx.) in static bending to be 31 and 18 % higher, respectively, in mature wood then in juvenile wood. For *P. deltoides,* Bendtsen and Senft (1986) found a 10% increase in wood density from juvenile wood to mature wood, but this increase was not sufficient to account for the increases of 38% observed in MOE and of 21% found for MOR.

1.5 GENETIC CONTROL OF WOOD PROPERTIES

The field of genetics offers perhaps the greatest potential for improvement of wood yield and quality (Bowyer et al. 2007). However, knowledge on the mode of genetic control (heritability) of wood traits and their genetic relationships is essential for effective selective breeding programs. The aim of breeding programs is to maximize the genetic gain in industrially important wood traits and, concurrently, to effectively manage undesirable trait correlations whilst sustaining genetic variability for future selection and adaptation. For this, a better understanding of the inheritance and relationships among traits of interest is needed. With the exception of fiber length and wood density, which are commonly studied and generally show moderate to high heritability (Yanchuk et al. 1984; Pliura et al. 2007; El-Kassaby et al. 2011), little is known about the genetic parameters for other wood-related properties in poplar.

1.5.1 Genotypic and phenotypic variation

In breeding programs, it is essential to understand the relationship between the characteristics. The evaluation of genotypic and phenotypic variation among individuals is the first step in genetic research on a species. Genetic correlation measures the genetic similarity between two characteristics. It is expressed as the ratio of the two characters' genetic covariance to the products of the two characters' genetic standard deviations (Falconer 1981). Pleiotropic effects are the main reason for genetic variation (Wagner 1989). However, pleiotropy does not always cause a detectable correlation, because some genes may increase both characters, while others may increase one and reduce the other. The former tends to cause a positive correlation and the latter tends to cause a negative correlation (Falconer 1981; Namkoong et al. 1988). However, even if phenotypic correlation between two properties is not found, genetic correlation between them may be estimated.

In a breeding programs, genetic correlation plays an important role in the prediction of correlated responses and development of effective selection indexes. Several studies have focused on the fiber morphology, density, and growth properties (Yanchuk et al. 1984; Beaudoin et al. 1992; Koubaa et al. 1998 a, b; Zhang et al. 2003; Pliura et al. 2005; Pliura et al. 2007; Zhang et al. 2012), but there is no or little information available about mechanical properties.

When studying genetic and phenotypic variability, one observes that populations, provenances or progenies may perform differently when they are moved away from their site of origin natural stand. This is related to different environmental influences and a different interaction between the tree genotypes and the environment in different locations. To fully understand the effect of this variation, it is useful to acquire a clear understanding of environmental and genetic control of wood traits.

1.5.2 Heritability

Heritability is the proportion of the phenotypic variation in a population that is due to the average effects of genes. In other words, it measures the strength of the relationship between performance and breeding value of individuals. It is also defined as a ratio indicating the probability with which parent trees transmit their characteristics to their offspring (Falconer 1981; Zobel and Talbert 1984). Heritability also indicates the reliability of the total phenotypic values as a guide to the breeding value. However, its value will change for certain characteristics of given species, because heritability is the ratio between genetic variances and phenotypic variances. Heritability should only be considered as the estimated value that gives a general idea about the ability of inheritance. Estimates change with age, environment, trait, and even test design and plantation (Zobel and Talbert 1984). There are two types of heritability used in tree improvement programs. The first is broad-sense heritability (H^2) defined as the ratio of total genetic variation in a population to phenotypic variation. The second is narrow-sense heritability (h^2) defined as the ratio of additive genetic variance to total variance (Falconer 1981). Broad-sense heritability is normally greater or equal to the narrow-sense heritability.

$$H^2 = \sigma_G^2 / \sigma_P^2 \quad (1.1)$$

$$h^2 = \sigma_A^2 / \sigma_P^2 \quad (1.2)$$

where σ_A^2, σ_G^2 and σ_P^2 are the additive, genotypic and phenotypic variance, respectively.

Heritability is used to help plant breeders to determine management strategies, estimate breeding values of individuals and predict response to selection.

Heritability values for fiber length in for *Populus tremuloides* clones were reported at 0.43 by Yanchuk et al. (1984), and at 0.61 by Klasnja et al. (2003) and for *Populus deltoides* clones at 0.36 (Farmer and Wilcox 1968). These results confirm that fiber length in poplar is only moderately genetically determined, as suggested by Koubaa et al. (1998a). Heritability for wood density of *Populus* clones was reported at 0.51 by Peszlen (1998), and at 0.35 by Yanchuk et al. (1983) for *Populus tremuloides*, and at 0.69 by Farmer and Wilcox (1968) and Beaudoin et al. (1992) for *P. euramericana* clones, and at 0.22 to 0.52 by Pliura et al. (2007) for hybrid poplar clones. Hernández et al. (1998) observed a broad-sense heritability of 0.34 for MOE and 0.47 for crushing strength.

1.5.3 Genetic gain

The aim of each breeding program is to improve one or more traits of interest. The output of the results of breeding programs or genetic can be understood by its achievement for future plantations through higher yields, for example by increased growth, or higher values of wood quality attributes (White et al. 2007). This is often useful to express the results in terms of response to selection or gain from selection, also known as genetic gain. According to Zobel and Talbert (1984), the response to selection results when the mean of a population subgroup is greater than the mean value of the entire population of the previous generation. In selection response during breeding cycle, the breeders try to find out superior quality traits by selection, mating and propagation of the best individuals. This improvement can be made as a function of the variation that exists within a trait, the heritability of that trait and the selection intensity. The expected genetic gain in the traits is calculated by using the equation for direct response defined by Falconer and Mackay (1996).

$$G = h^2 * S \qquad (1.3)$$

$$S = i * \sigma_P \qquad (1.4)$$

where G is the genetic gain, h^2 is the heritability, S is the selection differential, i is the selection intensity, and σ_P is the phenotypic standard deviation.

This improvement can be expressed in absolute values or in percentage of the original value. The gain of selection or genetic gain distinguishes between expected and realized genetic gain. The realized gain is based on actual measurements of both base and improved populations. The expected gain is estimated a priori using information of a population that is considered for selection.

This genetic information is very limited for poplar species. Pande and Dhiman (2011) reported genetic gain for 16 clones of *P. deltoides* of 2.8% for fiber length, 8.6% for fiber width, 4.8% fiber wall thickness, and 16.6% for specific gravity.

1.6 POTENTIAL USES OF HYBRID POPLARS IN WOOD PRODUCTS MANUFACTURING

There is an increasing need to improve tree quality and growth rates as the demand for raw material rises globally. Hybrid poplars have been extensively used for paper manufacturing following the shortfall of conventional raw material supply from softwood species like spruce, pine, fir and tamarack (Shi 2006). Its light density and moderate strength to density ratio position poplar wood between softwoods and other hardwood species (Rijsdijk and Laming 1994; Karki 2001; De Boever et al. 2007). Poplar wood holds the potential to be used for composite panel manufacturing as well. It continues to be an important raw material in the traditional lumber, veneer and plywood, oriented strand board and structural composite lumber industries in North America. The other applications of this material include lumber, pallets, furniture components, fruit baskets, containers, match splints and chopsticks (Balatinecz et al. 2001). Some developments have already been made and research is underway for further improvement of wood properties and quality of products made of this material for different end uses. However, it requires careful consideration of several physical and mechanical properties for their utilization in other commercial wood products. Relatively small changes in the properties of wood affect the profitability of the process and the properties of the final products.

1.6.1 Anatomical properties and potential applications in paper manufacture

The quantity and quality of wood and fiber properties of trees affect the suitability of genotypes as raw material for pulp and paper, and for mechanical wood processing

(Zobel and van Buijtenen 1989). Spruce, pine and fir have been the conventionally used softwood species for paper and composite panel products (e.g., hardboard, medium density fiber board) industries. Due to softwoods slow growth, the industry has responded by increasing the use of hardwoods despite the significant influence of fiber length and fiber properties on processing and on product quality. Hence, use of hybrid poplars created an impact on pulp and paper industries because of its fast growth. Annual growth increment for hybrid poplar is 5-10 times larger than the other species (Holder et al. 1979). The average length of vessel elements of mature poplar wood ranges from 0.58 to 0.67 mm, and the average fiber length ranges from 1.3 to 1.4 mm. Poplar wood contains relatively high proportion of fibers (53% to 60%), followed by vessel elements (28% to 34%) (Panshin and de Zeeuw 1980). Poplar fibers are shorter and finer than those of softwoods, which offer excellent optical properties of paper. Blending of poplar fibers with softwood pulp is recommended for overall sheet strength (Keays et al. 1974). Selection for density would have negative impact on fiber diameter and thus have an impact on pulp and paper properties such as smoothness and opacity (Zhu et al. 2008). Nevertheless, the vessel elements of poplar significantly enhance the smoothness and opacity of sheets, making poplars well suited for printing papers. Vessel elements enhance the smoothness and opacity and suitable for printing papers.

The lower fiber wall thickness of hybrid poplars compared to other poplar species appears to be responsible for a higher degree of fiber collapse and presumably, a higher relative bonded area. Similarly, clones with higher density would result in higher fiber yield for the pulp industry (Mahdavi et al. 2013).

Tension wood is characterized by the lack of cell wall lignification, the presence of a gelatinous layer in the fibers, higher cellulose and ash content, but lower lignin and hemicelluloses content (Isebrands and Parham 1974; Holt and Murphey 1978). Parham et al. (1977) found that during paper formation, tension wood fiber leads to inferior bonding strength. Hence, the proportion of tension wood in poplar clones is also important for their more efficient utilization for pulping.

As discussed above, fiber length, cell diameter and the ratio between them are important wood quality attributes especially to the pulp and paper industry. The bigger the ratio, the more flexible are the fibers and the better is the pulp and paper quality (Balodis 1991). The absolute value of cell diameter is not meaningful for pulp and paper manufacture, but the length to diameter ratio is an important indicator for quality.

1.6.2 Physico-mechanical properties: potential application in solid wood products

Wood dimensional stability is considered to be the most significant physical property for the manufacture of solid wood products, where drying and seasoning is mandatory. Tangential shrinkage (across the grain shrinkage in width of a flat-sawn piece) is responsible for cupping in wide flat sawn timber. Defects like warping and splitting arise from excessive longitudinal shrinkage (Panshin and de Zeeuw 1980). The best suited wood for uses involving critical dimensional stability is one with low tangential to radial shrinkage and normal longitudinal shrinkage. Koubaa et al. (1998b) reported the shrinkage values of a hybrid poplar as 12.8% (volumetric), 9.5% (tangential) and 3.5% (radial). The commercially used poplar species like black cottonwood and eastern cottonwood have been reported to have volumetric shrinkage values in the order of 12.4% and 14.1% (FPL 2010).

Siau (1984) and Skaar (1988) discussed the relationship of shrinkage and wood density as $S_V = \rho f$, where S_V is volumetric shrinkage, ρ is wood density based on green volume and oven-dry weight, and f is fiber saturation point based on the volume of water. Koubaa et al. (1998b) also used this relationship to evaluate the dimensional stability of hybrid poplars and reported a significant correlation between basic density and shrinkage. However, they recommended direct measurement of shrinkage values for poplar since several anatomical features like ring angle, fibril angle or lumen diameter might significantly influence the shrinkage of juvenile poplar wood.

Wood density strongly affects pulp yield and solid wood product performance (Barnett and Jeronimidis 2003). The basic density values of commercially used poplars range from 320 kg/m^3 to 400 kg/m^3 (Table 1.8). Several researchers have studied the potential of using hybrid poplar for lumber manufacture (Hall et al. 1982; Hernández et al. 1998; Kretschmann et al. 1999; De Boever et al. 2007). Wood strength properties are closely related to wood density. Thus, the fast grown hybrid poplars would generally produce wood having inferior strength properties. The relationship is attributed to the ease of reducing fiber length; lower density improves the fiber compressibility within a sheet. However, high wood density is directly related to increased pulp yield, though affects pulp properties. The preferred wood density for the production of OSB and particleboard is from 250 kg/m^3 to 450 kg/m^3 (Zhang and Koubaa 2008). Nevertheless, lower density and thinner cell walls, are preferred for OSB manufacture as they facilitate greater compressibility and thus greater inter-strand contact surface area, which improves the internal bond strength and ultimately the board strength (Woodson 1976). Similarly, an increase in wood density results in decreased MOE, MOR and tensile strength in medium density fiberboard (Woodson 1976).

Strength properties of the studied hybrid poplar clones show lower density values compared to the other commercially used poplars like eastern cottonwood and other wood species like spruce, pine and fir (Balatinecz and Kretschmann 2001). The mechanical properties of wood tends to improve as the tree grows older. Geimer and Crist (1980) studied the properties of structural flake-board panels made from five hybrid poplar clones and reported effects of clonal variation on panel properties. Peter et al. (2002) reported the properties of oriented strand boards made from eleven hybrid poplars and the good potential of such panels. De Boever et al. (2007) tested the potential of four hybrid poplars for manufacturing of veneer-based products. They recommended a poplar hybrid having MOE to density ratio or specific strength of 18.75 (weighed average) as suitable for both plywood and sawn wood production. In addition, hybrid clones having a minimum specific strength of 17.45 was recommended for sawn wood-based products. Therefore, the low strength and hardness of hybrid poplar species precludes a number of structural applications. However, when poplar is combined with polymer, the potential opportunities are much greater (Yildiz et al. 2005).

Table 1.8 Wood properties of poplars and their clones in comparison to other commercial wood species.

Species or hybrid	FL (mm)	FP (%)	VP (%)	FWT (μm)	TW (%)	BD (kg/m^3)	VSH (%)	LSH (%)	RSH (%)	TSH (%)	MOEF (MPa)	MORF (MPa)	CS (MPa)	References
P. x euramericana clones	0.62-1.02	36.1-44.1	14.9-22.6	-	15.3	335-350	12.8	-	3.5	9.5	7540	-	31.4	Mátyás and Peszlen 1997; Hernández et al. 1998; Koubaa et al. 1998(a, b); Jourez et al. 2001; Badia et al. 2006.
Balsam poplar	0.62-1.16	64.9	32.0	-	42.3	360-370	10.5-16.2	0.42-0.65	3.0-5.7	7.1-10.5	9651-11500	60.7-70	34.6	Kellogg and Swan 1986; Micko 1987; Kroll et al 1992; FPL 2010.
Trembling Aspen	0.67-0.97	-	-	2.3-2.4	-	320-400	11.5	0.16-0.72	3.5	6.7	8136	58	29.3	Yanchuk et al. 1984; Sutton and Tardif 2005; FPL 2010.
Eastern cottonwood	0.86	-	-	3.7	29.1	342-380	11.8-14.1	-	3.1-3.9	7.8-9.2	7800	52	26.5	Kaeiser and Boyce 1965; Klasnja et al. 2003; FPL 2010.
Black spruce	3.00-4.50	-	-	1.5	-	363-455	11.1-11.3	-	3.8-4.1	6.8-7.5	10500	71.1	36.7	Jang and Seth 1998; Zhang and Koubaa 2008; FPL 2010.
Jack pine	1.50-5.70	-	-	2.5-2.9	-	313-449	9.6-10.4	-	3.4-4.0	5.9-6.5	9300	68.3	37.2	Seth 1990; Zhang and Koubaa 2008; FPL 2010.
Balsam fir	1.90-5.60	-	-	-	-	305-348	10.7-11.2	-	2.7-2.9	6.9-7.5	10000	63.4	43.9	Zhang and Koubaa 2008; FPL 2010.
Tamarack	1.70-5.60	-	-	-	-	430-485	11.2-13.6	-	2.8-3.7	6.2-7.4	11300	80	49.4	Zhang and Koubaa 2008; FPL 2010.

FL fiber length, FP fiber proportion, VP vessel proportion, FWT fiber wall thickness, TW tension wood, BD basic density, VSH volumetric shrinkage, LSH longitudinal shrinkage, RSH radial shrinkage, TSH tangential shrinkage, MOEF flexural modulus of elasticity, MORF flexural modulus of rupture, and CS ultimate crushing strength parallel to the grain.

1.7 RESEARCH OBJECTIVES AND HYPOTHESES

This chapter presents an introductory overview of poplar species and illustrates the need and intention to include wood properties into breeding programs. Some of the challenges facing the wood industry were discussed and the implications that wood quality may have on the utilization of the potential material were highlighted. There is an increase interest in fast-growing tree species and their utilization in the fiber based industries. Thus, it became obvious that a more comprehensive and detailed understanding of different wood properties and their genetic control or genetic correlation would be of considerable value both to breeding programs and to end uses. Essential information such as the genetic variation and parameters (heritability, geneotypic correlation) among wood properties of hybrid poplar clones is still lacking. Therefore, the general objective of this thesis is to elucidate the variation of anatomical, physical and mechanical wood properties of seven hybrid poplar clones grown in Southern Quebec. The experimental layout of wood properties also allowed investigating their radial variation from pith to bark and for estimation of genetic parameters such as heritability and correlations between wood properties. The characterized wood properties may offer insight into whether or not clonal variation of these hybrid poplar clones can be exploit to improve in breeding strategy for potential future hybridisation of poplar species for specific uses in Quebec.

The specific objectives were:

1) To investigate site, clonal, and within-tree variations in selected anatomical properties of hybrid poplar clones.

   Hypothesis:

   a. Fiber length, width, wall thickness and fiber proportion vary with clones and sites.

b. Fiber length, width, wall thickness and fiber proportion increase and vessel proportion decrease with radial and longitudinal position within trees.

2) To examine the radial patterns of wood density along stem height and to determine the variation dependencies between earlywood and latewood.
   Hypotheses:
   c. Radial and longitudinal variation of wood density vary due to tree age.
   d. Variations in earlywood are greater than those in latewood.

3) To investigate the site and clonal variation in the physical and mechanical properties of selected hybrid poplar clones.
   Hypotheses:
   e. Density, shrinkage and flexural properties vary with clones and site quality.
   f. Heritability of wood properties is moderate to high.

4) To estimate the genotypic and the phenotypic interactions among wood anatomical, physical, and mechanical properties and their implication in hybrid poplar breeding programs for wood quality.
   Hypotheses:
   g. There are strong correlations among wood properties.
   h. Wood density depends on fiber cell wall thickness, fiber and vessel proportion.
   i. Mechanical wood properties are closely related to wood density.
   j. Tension wood has impact on wood quality.

Based on the results presented in this thesis, we believe that it will be a valuable contribution to the Quebec's hybrid poplar clones breeding program, which aims to increase wood quality and reduce rotation age as the demand for wood fibers increases. To our knowledge, this Ph.D study is the first study that conducted:

1) a detailed investigation of wood anatomical properties in hybrid poplar clones and their variations between sites and clones and within trees with cambial age. This could good opportunities for selecting the best performing clones in terms of anatomical properties, both for breeding and for processing for specific end uses;

2) a detailed investigation of the clonal variation of selected physical and mechanical properties of fifteen-year-old clones (previously done with younger age) and provided evidence of site quality effect on different responses;

3) a study of genotypic and phenotypic correlations of all wood properties of hybrid poplar clones that have key effects for developing defferent selection and breeding strategies;

There is no extensive study that reported on the genetic parameters of wood quality attributes of hybrid poplar. These parameters are important for the continuing development of the hybrid poplar breeding programs. The findings of this thesis should contribute to a better understanding of hybrid poplar wood quality and will contribute to improving the efficiency of the breeding programs for future forest growth and productivity for specific end-uses in Quebec.

Note: This thesis is written in the form of a collection of articles published or submitted to peer-reviewed scientific journals. Hence, there are repetitions in the text between the General introduction, Literature review, Martial and methods, General conclusion and the Chapter's papers as well as the Appendix A paper.

CHAPTER II

MATERIALS AND METHODS

2.1 MATERIALS

2.1.1 Study area

Materials for this study were collected from three hybrid poplar clonal trials established by the *Direction de la recherche forestière, Ministère des Ressources Naturelles du Québec* (Research Branch at Quebec's Ministry of Natural Resources) between 1991 and 1995. Trees for hybrid clones trials were planted at the Saint-Ours and Windsor sites in 1993, and in 1991 at the Pointe-Platon site (Table 2.1). Trees for clone DNxM-915508 were obtained from a 1995 trial at the Pointe-Platon site (Table 2.2). In this study, five clones of *P. deltoides* x *P. nigra*, one clone of *P. trichocarpa* × *P. deltoides*, and one clone of (*P. deltoides* × *P. nigra)* × *P. maximowiczii* were selected. The trial sites are located in Pointe-Platon (46°40'N 71°51'W), Saint-Ours (45°54'N 73°09'W), and Windsor (45°42'N 71°57'W) in southern Quebec, Canada (Figure 2.1). The sites represent major soil types in which hybrid poplar clones are expected to be planted in Southern Quebec. The Saint-Ours site is located in the Champlain marine deposit, where the soil consists of a silty clay deposit (40% clay). The two other sites consist of sandy loam soil (Pliura et al. 2007). All sites were originally used for agriculture, but had been abandoned for several years before the hybrid poplar clones were planted. All tree plantation trial sites had a randomized block design with ten blocks each. Clones were planted in row plots containing four trees each. One systematic thinning was carried out in 1995 at the Platon site and in 1996 at the Windsor and Saint-Ours sites. Early in 2006, a thinning operation was carried out, removing two-thirds of the trees from these plantation sites.

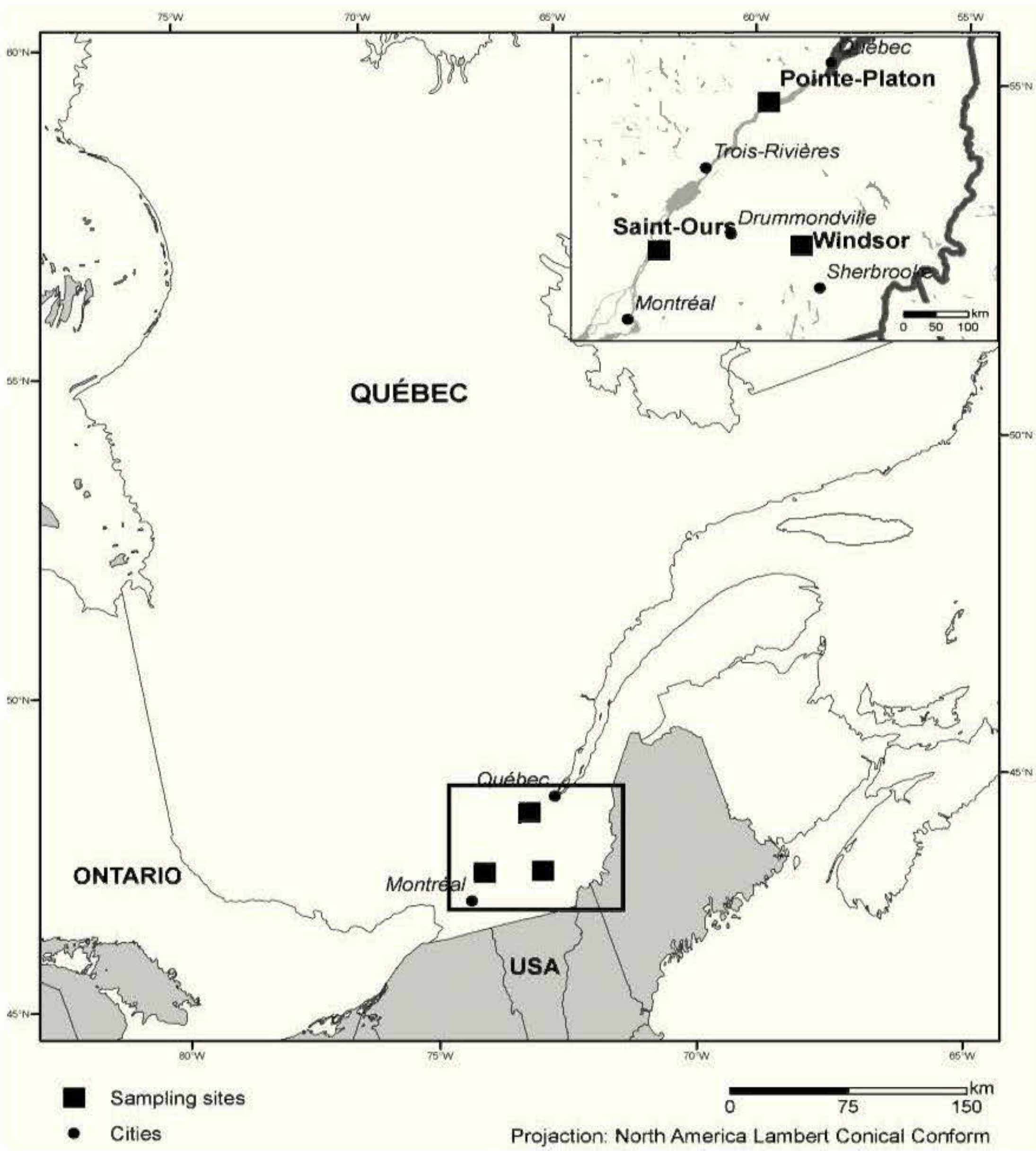

Figure 2.1 Map of sampling sites located in the southern part of the province of Quebec, Canada.

Table 2.1 Site characteristics of hybrid poplar clonal trials.

	Site		
Characteristics	Pointe-Platon	Saint-Ours	Windsor
Trial number	PLA01791	STO10893	WIN10593
Establishment year	1991	1993	1993
Geographic coordinates	46⁰40'N, 71⁰51'W	45⁰54'N, 73⁰09'W	45⁰42'N, 71⁰57'W
Elevation (m)	60	15	260
Ecological sub-region –bioclimatic domain	Sugar maple – basswood domain	Sugar maple – bitternut hickory domain	Sugar maple – basswood domain
Degree-days above 5°C	1722	1889	1611
Surface deposit	Sandy clay loam soil (marine)	Champlain marine deposit with silty clay soil	Sandy loam soil (deep till)
Initial spacing	1 m x 3 m	1.2 m x 3.5 m	1.5 m x 3.5 m
Spacing after 1st Thinning	2 m x 3 m	2.4 m x 3.5 m	3 m x 3.5 m

2.1.2 Sample collection

Seven hybrid poplar clones (Table 2.2) were selected for this study. Five trees per site were randomly sampled for each clone, for a total of 105 trees. Trees were cut from the St-Ours and Windsor sites after 15 growing seasons. Trees were cut from the Pointe-Platon site after 17 growing seasons, except for clone DNxM-915508, which was felled after 13 growing seasons. Felling of trees from three sites were conducted during the months of July, August and early September 2007 (Figure 2.2).

Table 2.2 Studied hybrid poplar clones.

Clone	Hybrid	Female parent	Male parent	Note
DxN-131	*Populus deltoides* × *P. nigra*	*P. deltoides*	*P. nigra* 'Italica' as the putative father	A natural hybrid selected from the Montréal area, Québec
TxD-3230	*P. trichocarpa* × *P. deltoides* Syn.: *P.* × *generosa* 'Boelare'	*P. trichocarpa* 'Fritzi Pauley' (from Washington)	*P. deltoides* S.1-173 (from a cross between *P. deltoides* V.5 from Iowa and V.9 from Missouri)	Clone S.910-8 from Belgium. Cultivar 'Boelare'
DxN-3565	*P. deltoides* × *P. nigra* Syn.: *P.* × *canadensis*	*P. deltoides* S.513-60 (from a cross between *P. deltoides* V.5 from Iowa and V.12 from Illinois)	*P. nigra* S.157-3 (from a cross between *P. nigra* V.220 from Italy and V.450 from Belgium)	Family/tree from Belgium: 78.017/164
DxN-3570	*P. deltoides* × *P. nigra*	*P. deltoides* S.513-60	*P. nigra* S.157-4 (from a cross between *P. nigra* V.220 from Italy and V.450 from Belgium)	Family/tree from Belgium: 78.018/204
DxN-3586	*P. deltoides* × *P. nigra*	*P. deltoides* S.513-60	*P. nigra* S.132-4 (from a cross between *P. nigra* V.441 from Italy and V.450 from Belgium)	Family/tree from Belgium: 78.016/156
DxN-4813	*P. deltoides* × *P. nigra*	*P. deltoides* 226 (from Trois-Rivières, Québec)	*P. nigra* 'Italica'	A controlled cross selected from Québec
DNxM-915508	(*P. deltoides* × *P. nigra)* × *P. maximowiczii*	*P. deltoides* × *P. nigra* (from Québec City)	*P. maximowiczii* (from Japan)	A controlled cross selected from Québec

* Trees for the clone DNxM-915508 at Pointe-Platon were sampled from another trial PLA16495.

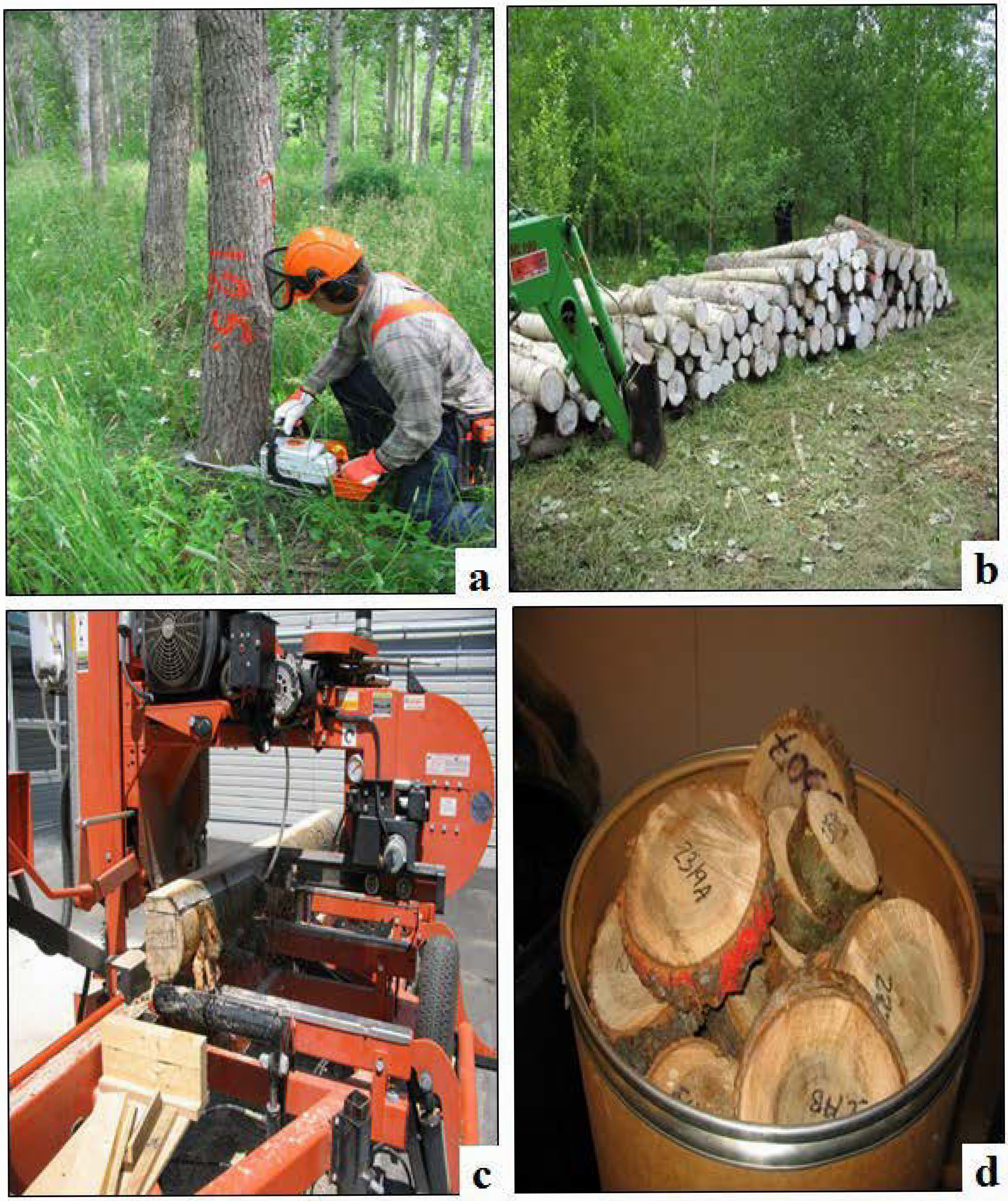

Figure 2.2 a) Hybrid poplar trees felling at Pointe-Platon site, b) logs of hybrid poplar, c) sawing logs with Wood Mizer, d) 10 mm thick disks for wood anatomical properties.

Disks 10 cm thick were collected from each tree from breast height upward at 2.5 m intervals (Figure 2.2) and used for anatomical analysis. A log of 800 mm in length with its base at a height of 0.5 m above the ground was collected for physical and mechanical property measurements from each tree stem after felling. Each disk and log was labelled to indicate the source of clone, tree, stem and position. Wax was applied to the disk and log edges to limit drying and prevent decay and other environmental alterations. Samples were then transported to the Wood Research Centre, Laval University, Quebec, Canada and kept frozen (-5°C) until test sample preparation. Logs were sawn into 2.5 cm thick planks (bark-to-bark passing through the pith) with Wood Mizer. The planks were then dried with kiln drying method to systematically remove moisture from wood and to reach the 12% target moisture content within a reasonable drying time. Specific drying schedule was prepared for hybrid poplar to reduce deformation such as twisting and warping (Table 2.3). After drying, planks were planned to remove surface defects. Then, the selected planks for physical and mechanical tests were placed in a conditioning room set at 20°C and 60% relative humidity (RH) in order to keep a nominal equilibrium moisture content (EMC) of 12%. The disks selected for anatomical tests were also placed in conditioning room to reach the same equilibrium moisture content (EMC).

Table 2.3 Drying schedule used for hybrid poplar clones.

Stages	Duration (h)	Average moisture content (%)	T_s (°F)	T_h (°F)	H_{equi} (%)
Initial temperature	4		140	136,4	18,1
Dry stage 1		> 60	140	132,5	14,0
Dry stage 2		60-12	150	135,8	10,0
Equalized condition	48		150	139,5	12,0
12- cooling stage	3		40		

2.2 METHODS

2.2.1 Anatomical properties

2.2.1.1 Image analysis for fiber morphological property measurements

To determine wood anatomical properties, thin strips approximately 2 cm wide and 1 cm thick were sawn from each disk (bark-to-bark passing through the pith) at three different heights. The age of each strip was determined using a binocular microscope. A series of radially oriented sample blocks sized 1 (T) x 1 (R) x 2 (L) cm was systematically cut from annual growth rings (3, 6, 9, and 12) using a precision saw and a chisel. At the annual growth ring with a cambial age of 15, there was insufficient wood to prepare samples for properties measurement by WinCELL, an image analysis system specifically designed for wood cells analysis, from Regent Instruments, Québec, Canada. Each wood block contained a ring pair and several surrounding rings. Before sectioning, samples were put in a cup of water and soften with microwave oven. Then samples were soaked into water-glycerine solution until sectioning. Cross sections of 20 µm were cut using a rotary microtome with a disposable blade positioned at approximately 15 degrees. Sections were then bleached with sodium hypochlorite solution (80 mL water + 5 drops of bleach) for 1 minute and washed in a distilled water bath for 1 minute. Sections were then double stained with 1% safranin stain for 5 minutes and 0.1% astra blue stain for 15 minutes. Excess stain was removed by washing sections successively in 50, 80, and 100% ethanol solution. Safranin stains all tissues, and astrablue replaces safranin in purely cellulosic G-layers of tension wood. Double-staining is used to detect and confirm tension wood. Thin sections were further dehydrated using toluene and then permanently mounted on microscope slides with cover slips using mounting medium. The finished slides were placed on an electric warming plate at approximately 50°C and were firmly secured using a small magnet to prevent bubble formation under the cover slip. Samples were left for two weeks to allow the mounting medium to dry thoroughly. From each block, 2 sections were used to prepare slides and a total of 2520 slides were prepared for the image analysis.

Samples were photographed at ×50 magnification using a Leica compound microscope (DM 1000) equipped with a PL-A686 high resolution microscopy camera to capture black and white images (tiff electronic file format) at 1200x1600 resolution using a green filter to maximize contrast (Figure 2.3). From each slide, 3 images were taken, thus a large number of images (about 7500) were taken for the WinCELL analysis. WinCELL Pro 2004a (Régent Instruments Inc. 2004) was used to measure average fiber wall thickness, fiber lumen area, vessel lumen area, fiber diameter, and vessel diameter. Average fiber diameter accounts for average fiber lumen diameter and the respective two-sided fiber wall thickness. Cell wall area (%) was estimated by subtracting the percent areas of the vessel lumen, ray, and fiber lumen from the image area (Peszlen 1994).

Table 2.4 Wood properties measured for anatomical properties with units.

Property	Abbreviation	Unit	Method of measurement
Fiber length	FL	mm	Fiber quality analyzer
Fiber width	FW	mm	Fiber quality analyzer
Fiber wall thickness	FWT	μm	Image analysis system
Average fiber lumen area	AFLA	μm^2	Image analysis system
Average fiber diameter	AFD	μm	Image analysis system
Average vessel lumen area	AVLA	μm^2	Image analysis system
Average vessel diameter	AVD	μm	Image analysis system
Fiber proportion	FP	%	Image analysis system
Vessel proportion	VP	%	Image analysis system
Ray proportion	RP	%	Image analysis system
Cell wall area	CWA	%	Image analysis system
Tension wood	TW	%	Image analysis system

The proportion of tissue in the different cell types was estimated from two cross-sections of each wood block. Vessel cells were distinguished from fiber and ray by analyzing 570 μm^2 fields (corresponding to four squares of the grid) and noting the tissue types within the field. Fiber proportion was measured using the same method. Ray proportion was obtained by subtracting from unity the vessel and fiber areas.

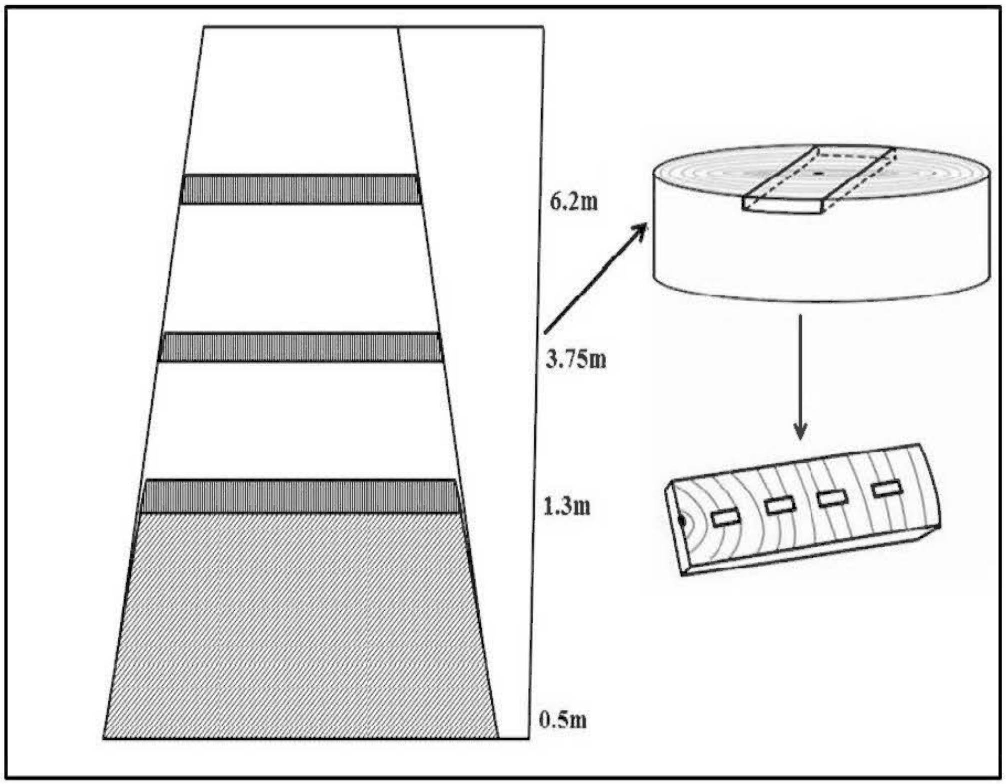

Figure 2.3 Schematic diagram of the sampling procedure for the analysis of hybrid poplar wood anatomical properties.

2.2.1.2 Fiber length and width

The same slabs used for wood anatomy image analysis were used to analyze fiber properties from pith to bark at different tree heights A series of radially oriented thin tangential sections was systematically cut from annual growth rings 3, 6, 9, 12, and 15 for fiber length and fiber width measurement. Tangential sections were macerated using Franklin's method. Sections were soaked in Franklin solution (1:1, glacial acetic acid: 30% hydrogen peroxide) and heated at 70 °C for approximately 48 hours. The solution was decanted and the remaining fibrous material was washed under vacuum with deionized water until reaching neutral pH. A total of 1500 samples were prepared for the fiber length and width measurements.

Fiber length and width were measured automatically using a Fiber Quality Analyzer (FQA, OPTEST, Canada). Based on image analysis (Robertson et al. 1999), the FQA allows rapid determination of tracheid length, width, and several other morphological properties. The FQA measures the true contour length, and not the projected length. A total of 5 000 fibers were measured for each sample. To determine the length, the FQA computes three parameters: mean length, length-weighted mean, and weight-weighted mean fiber length (Robertson et al. 1999). The last parameter was used in this study because it gives more weight to the fibers and reduces the potential impact of fines on length determination. Individual tracheid length and width are reported to a precision of 0.01 mm and 1 µm, respectively (Robertson et al. 1999).

2.2.2 Physical properties

2.2.2.1 Density with X-ray densitometer

To determine wood density with X-ray densitometry, thin strips approximately 20 mm wide and 1.57 mm thick were sawn from each disk (bark to bark passing through the pith). Samples were then conditioned to 12% equilibrium moisture content (EMC) before measurement.

Ring and wood density components were measured using a QTRS-01X Tree-Ring X-Ray Scanner (QMC, Knoxville, Tennessee). A linear resolution step size of 20 µm was used for X-ray densitometry. The density calculation required knowledge of the mass attenuation coefficient (cm^2/g) of the wood. The calibration to the appropriate mass attenuation coefficient was conducted using a set of 25 radial strips from cores. The 25 mass attenuation coefficients were averaged to provide the final value used to calculate the wood density. In order to run the QMS X-ray densitometer, some values need to be known such as wood moisture content, dimension of wood samples, ages of wood samples and target density. Target density was measured at 10.20% moisture content. After conditioning, rings from pith to bark were scanned in air-dry condition. During scanning, precautions were taken to eliminate incomplete or false rings and rings with compression wood or branch tracers. False and missing rings were detected by cross-dating ring width chronologies.

From the wood density profiles, annual (ARD), earlywood (EWD), and latewood (LWD) density were calculated for each annual ring. Demarcation between earlywood and latewood was determined for each annual ring by the maximum derivative method using a six-degree polynomial (Koubaa et al. 2002). The density at the demarcation point on the polynomial curve was defined as the transition density (TD). From the same density profiles, annual (ARW), earlywood (EWW), and latewood (LWW) ring width were determined. Latewood proportion (LWP) was calculated as the ratio of latewood width to annual ring width. Cross-dating was numerically verified using COFECHA software (Holmes 1983). A total of 315 strips were analyzed by X-ray densitometry.

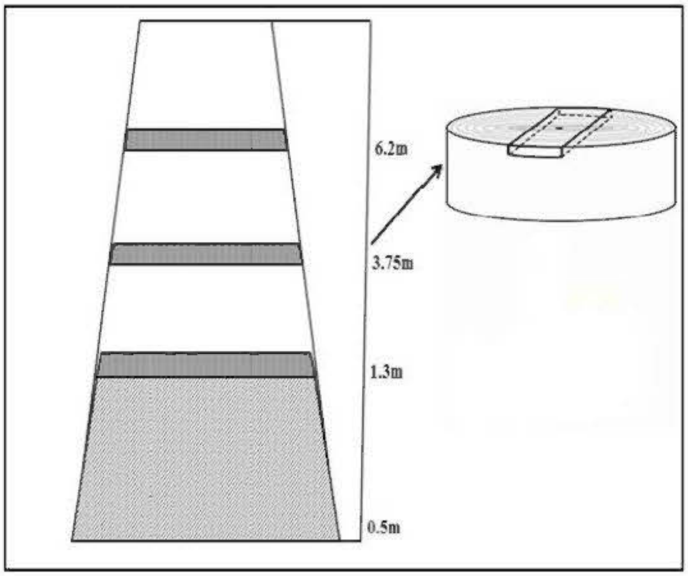

Figure 2.4 Schematic diagram of the sampling procedure for the analysis of hybrid poplar wood for ring density properties.

2.2.2.2 Moisture content

Moisture content (MC) was measured in all physical and mechanical tests. The MC was determined by oven-dry method, which is the most satisfactory for most purpose. The MC was obtained as follows:

$$MC = \frac{m_t - m_0}{m_0} \times 100 \qquad (2.1)$$

Where, m_t is the actual weight at the time of test, and m_0 is the weight of samples after it has been oven dried at a temperature of 103 ± 2°C for 48 hours.

2.2.2.3 Basic density

The density of wood is its single most important physical characteristics (Haygreen and Bowyer 1982) and also a good indicator of other wood properties (Guitard and

Amri 1987). Basic density was calculated as the oven-dry mass to green volume ratio. Several densities were measured in this study: basic density, green density, air-dried density and oven-dried density. The dimensions of wood samples for measuring densities were 20 mm (T) x 20 mm x 100 mm (L). A number of 315 defect free samples were carefully selected for the study. Samples were oven dried at a temperature of 103 ± 2°C for 48 hours. The specimens were weighed in an analytical balance and a digital micrometer was used to determine their T, R, and L dimensions. Dimensions were determined in all three principle directions to the nearest 0.01 mm using a digital micrometer, and specimens were weighed to the nearest 0.01 g. The basic density (BD, kg/m^3) was calculated as follows:

$$BD\ (kg/m^3) = \frac{oven\ dry\ mass\ (kg)}{green\ volume\ (m^3)} \tag{2.2}$$

Green density (GD, kg/m^3) was calculated as the ratio between the green mass and green volume

$$GD\ (kg/m^3) = \frac{green\ mass\ (kg)}{green\ volume\ (m^3)} \tag{2.3}$$

Oven-dry density (OD, kg/m^3) calculated as the ratio between the oven-dried mass and oven-dried volume

$$OD\ (kg/m^3) = \frac{oven-dry\ mass\ (kg)}{oven-dry\ volume\ (m^3)} \tag{2.4}$$

Air-dried density (AD, kg/m^3) calculated as the ratio between the air-dried mass and air-dried volume

$$AD\ (kg/m^3) = \frac{air-dry\ mass\ (kg)}{air-dry\ volume\ (m^3)} \tag{2.5}$$

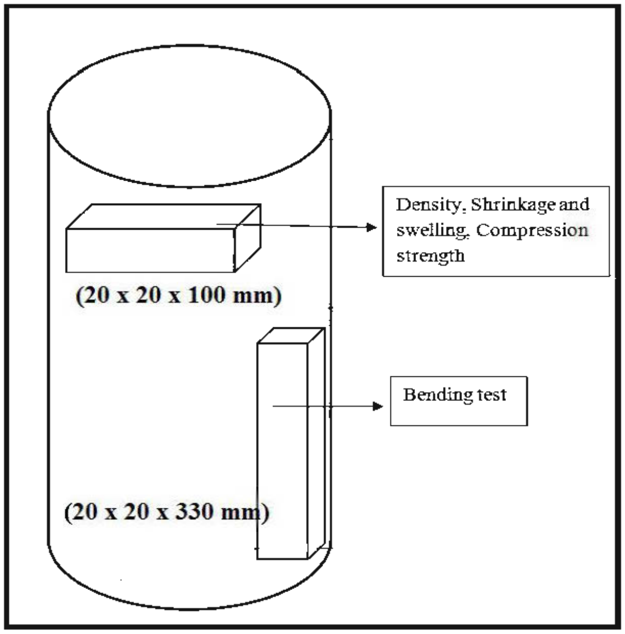

Figure 2.5 Schematic diagram of the sampling procedure for the analysis of hybrid poplar wood for physical and mechanical properties.

2.2.2.4 Shrinkage and swelling properties

Hybrid poplar wood samples with dimensions 20 mm × 20 mm ×100 mm (tangential × radial × longitudinal) were used to determine shrinkage and swelling properties. A number of 315 defect free samples were carefully selected for the study. Samples were submerged into water for water absorption with submersion period of 168 hours. After saturation period, dimensions were determined in all three principle directions to the nearest 0.01 mm using a digital micrometer, and specimens were weighed to the nearest 0.01 g. Samples were then oven-dried for 48 hours at 103 ± 2°C until constant weight was reached. The same measurements were taken again on oven-dried samples. In order to minimize error, on each surface of the sample a point was marked at the center and measurements were always taken on these points precisely.

The shrinkage and swelling were measured with following formula:

$$\text{Shrinkage / swelling (\%)} = \frac{change\ in\ dimension\ or\ volume}{initial\ dimension\ or\ volume} \text{ x } 100 \quad (2.6)$$

2.2.3 Mechanical properties

2.2.3.1 Static bending test

Three-point static bending tests were carried out using a universal testing machine (Zwick/Roell Z020) with a maximum load of 20 kN. The sample size for the test was 20 mm (T) × 20 mm (R) x 330 mm (L), with actual height and width at the center measured before the test (Figure 2.5). Span length was assumed at 300 mm. The remaining procedures were conducted according to ASTM D 143-94 (ASTM 2007), except for dimension of samples. A total of 315 samples were measured. Modulus of elasticity (MOE, MPa) and modulus of rupture (MOR, MPa), proportional limit (PL, MPa), strain at MOR (S_{MOR}, %) and work to MOR (W, Joule) were recorded.

2.2.3.2 Compression test

According to the relative angle of the applied load and the longitudinal axis, two types of compression tests, parallel and perpendicular, were performed on a universal testing machine (Zwick/Roell Z100) with a maximum load of 100 kN. Compression specimens were machined to 20 mm (T) × 20 mm (R) x 100 mm (L) and to 50 mm (T) × 20 mm (R) ×50 mm (L) for parallel and perpendicular to grain tests, respectively. Actual cross-section area length was measured before testing. Both operations were conducted in accordance with ASTM D 143 (Reapproved 2007), except for dimension of samples. A total of 315 number of samples were measured. MOE (MPa) and ultimate crushing strength (CS, MPa), and proportional limit (PL, MPa) were recorded by a computer linked to the machine for the parallel and perpendicular tests, respectively.

Table 2.5 Wood properties measured for physical and mechanical properties with units.

Property	Abbreviation	Unit	Method of measurement
Basic Density	BD	kg/m^3	ASTM D143
Volumetric shrinkage	VSH	%	ASTM D143
Longitudinal shrinkage	LSH	%	ASTM D143
Tangential shrinkage	TSH	%	ASTM D143
Radial shrinkage	RSH	%	ASTM D143
Flexural modulus of elasticity	MOEF	MPa	ASTM D143
Flexural modulus of rupture	MORF	MPa	ASTM D143
Compression modulus of elasticity in parallel to grain	MOEC	MPa	ASTM D143
Ultimate crushing strength in parallel to grain	CS	MPa	ASTM D143

2.3 STATISTICAL ANALYSIS

The SAS® statistical package, version 9.3 (SAS 2010) was used for all statistical analyses. Residual normal distribution for each trait was verified by both the Shapiro–Wilks' W test and a normal probability plot using SAS Plot and UNIVARIATE procedures. Homogeneity of variance for each trait was verified graphically by scatterplot of studentized residuals (*stdred*) vs. predicted (*pred*) values. Data transformations were not considered necessary to satisfy the assumptions of the analysis of variance and other analyses. Analyses of variance were performed using PROC GLM with Type III (partial sums of squares) estimates to assess the relative magnitude of each source of variation.

Tukey's Studentized Range (HSD) was used to test the statistical significance (at $p<0.05$) of differences among means of clones for each site (PROC GLM, SAS). The variance components were estimated in the model using VARCOMP with the restricted maximum likelihood method (REML) and expressed as a percentage (VAR). Analyses were performed among and within sites and clones. The variance in properties variables among sites was analyzed using the following mixed linear models all fixed effects except the error terms,

$$X_{ijlm} = \mu + S_i + C_j + (S \times C)_{ij} + A_l + H_m + (A \times H)_{lm} + \varepsilon_{ijlm} \tag{2.8}$$

$$X_{ijk} = \mu + S_i + C_j + (S \times C)_{ij} + \varepsilon_{ijk} \tag{2.9}$$

Where, X_{ijlm} = an observation on the l^{th} cambial age and m^{th} stem height of the j^{th} clone from the i^{th} site; X_{ijk} = an observation on the j^{th} clone from the i^{th} site; μ = the overall mean; A_l = the fixed effects associated with the l^{th} cambial age; H_m = the fixed effects associated with the m^{th} stem height; $(A \times H)_{lm}$ = interaction between cambial and stem height; S_i = the fixed effect due to the i^{th} sites; C_j = the fixed effect due to the j^{th} clones; $(S \times C)_{ij}$ = the interaction between site and clone; and ε_{ijlm} and ε_{ijk} = the random error.

Some F ratios involved more than one mean square in the denominator and were tested with approximate degrees of freedom. Tree effects and the site-clone-age interaction were not considered in the analysis, as preliminary testing showed negligible contribution to the total variance. Furthermore, in many cases, the variance component for these terms could not be estimated or was not significant.

The broad-sense heritability or clonal heritability (H_C^2) was calculated from the variance estimates, as follows (Eq. 2.10) (Becker 1984; Falconer and Mackay1996),

$$H_C^2 = \sigma_C^2 / \sigma_P^2 \tag{2.10}$$

where σ_C^2, and σ_P^2 are the genotypic, and phenotypic variance, respectively. Phenotypic variances (σ_P^2) were calculated as shown in Eq. (2.11),

$$\sigma_P^2 = \sigma_C^2 + \sigma_{(s\,x\,c)}^2 + \sigma_e^2. \quad (2.11)$$

where σ_C^2, $\sigma_{(s\,x\,c)}^2$and σ_e^2 are the variance of clones, interection between site and clones and residuals effects, respectively. The genotypic coefficient of variation (CV_G) and the phenotypic coefficient of variation (CV_P) were calculated from Eqs. 2.12, and 2.13, respectively (Burton 1952; Henderson 1953).

$$CV_G = (\sqrt{\sigma_C^2}/\text{mean})x100 \quad (2.12)$$

$$CV_P = (\sqrt{\sigma_P^2}/\text{mean})x100 \quad (2.13)$$

The mathematical expression for the genetic gain (*G*) is expressed in Eq. 2.14. The potential genetic gain from individual tree selection was computed by selection differential (Eq. 2.15) and 10% selection intensity,

$$G = H^2 * S \quad (2.14)$$

$$S = i * \sigma_P \quad (2.15)$$

where h^2 is the heritability, *S* is the selection differential, *i* is the selection intensity (10%), and σ_P is the phenotypic standard deviation. The estimated selection differential was based on a 10% selection intensity which corresponds to 1.73 for a sample of 100 (here $n = 105$) as suggested by Falconer and Mackay (1996). A more common approach to calculate selection intensity values is to use tabulated values of *i* for various proportions selected Falconer and Mackay (1996) is given in table 2.6,

Table 2.6 Truncation point (x_0) and selection intensity (i) for different proportions selected (p in %) in large samples (Falconer and Mackay 1996).

P (%)	x_0	i	P (%)	x_0	i
5	1.645	2.063	9	1.341	1.804
5.5	1.598	2.023	9.5	1.311	1.779
6	1.555	1.985	10	1.282	1.755
6.5	1.514	1.951	11	1.227	1.709
7	1.476	1.918	12	1.175	1.667
7.5	1.440	1.887	13	1.126	1.627
8	1.405	1.858	14	1.080	1.590
8.5	1.372	1.831	15	1.036	1.554

If we assume that we select the top ten percent from a large population (<500) we would expect a selection intensity of 1.755 (Table 2.6). However, we only have 100 individuals measured and select 10 of those (i.e. 10%) we would only get a selection intensity of 1.73 (Table 2.7) based on the following formula,

$$I_{small\ sample} = l_{large\ sample} - \frac{0.25}{\text{number of individual selected}} \quad (2.16)$$

Table 2.7 Selection intensity (i) for small samples, when n individuals are selected from a total number of N (Falconer and Mackay 1996).

			N		
n	80	100	150	200	250
8	1.724	1.828	2.007	2.127	2.217
10	1.621	1.730	1.916	2.040	2.132
15	1.417	1.536	1.738	1.871	1.970
20	1.257	1.386	1.601	1.742	1.846

The Pearson's correlation coefficients for the phenotypic correlation were computed using the SAS CORR procedure. Significance levels were calculated with respect to the null hypothesis r=0.

The genotypic correlation (r_G) of two traits x and y were obtained with,

$$r_G = \frac{\sigma_{c(xy)}}{\sqrt{\sigma^2_{c(x)} \times \sigma^2_{c(y)}}} \quad (2.17)$$

and

$$\sigma_{c(xy)} = \left(\sigma^2_{c(x+y)} - \sigma^2_{c(x)} - \sigma^2_{c(y)}\right)/2 \quad (2.18)$$

Where $\sigma^2_{c(x)}$ is the clone variance component for the trait x, $\sigma^2_{c(y)}$ is the clone variance component for the trait y and $\sigma_{c(xy)}$ is the clone covariance component. The covariance component was calculated using a dummy variable (x+y) and $\sigma^2_{c(x+y)}$ is the variance for dummy variable (x+y). The method is described in detail by Williams et al. (2002). Because of sampling errors and mathematical approximation, some genotypic correlations may exceeded ±1. In these cases, we considered them equal to ±1, considering the asymptotic nature of distribution of the correlation coefficients. The estimation of genotypic correlation was performed with MANOVA option using the GLM procedure in SAS. Standard errors associated with the genotypic correlations (r_G) were estimated using the method presented by Robertson (1959).

$$\sigma(r_G) = \frac{1-r_G^2}{\sqrt{2}} \text{ x } \sqrt{\left[\frac{\sigma(H_x^2) \text{ x } \sigma(H_y^2)}{H_x^2 \text{ x } H_y^2}\right]} \quad (2.19)$$

Where H_x^2 and H_y^2 are the heritability estimates for traits x and y; $\sigma(H_x^2)$ and $\sigma(H_x^2)$ are the associated standard errors for heritability estimates.

CHAPTER III

ANATOMICAL PROPERTIES OF SELECTED HYBRID POPLAR CLONES GROWN IN SOUTHERN QUEBEC[1]

3.1 ABSTRACT

The anatomical properties of seven hybrid poplar clones grown in three sites in southern Quebec, Canada were investigated. Radial and longitudinal variations in selected anatomical properties of wood were measured by image analysis of transverse sections and by fiber quality analysis. Results indicate that all measured anatomical properties varied significantly across sites. Clonal variation was highly significant for all anatomical properties studied, and broad-sense heritability ranged from 0.10 (average vessel lumen area) to 0.76 (cell wall area percentage). Genetic gain was positive for all anatomical properties. The variation in radial pattern was characterized by a rapid increase in the first few years in fiber length, fiber width, fiber proportion, wall thickness, and percent cell wall area. Ray proportion remained constant, whereas the vessel lumen area and vessel proportion decreased with cambial age.

Keywords: Hybrid poplar, Wood anatomical properties, Site, Clonal variation, Age, Heritability, Genetic gain.

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[1] Reprinted in part with permission from Huda, A. A., Koubaa, A., Cloutier, A., Hernández, R. E., and Périnet, P. (2012). "Anatomical properties of selected hybrid poplar clones grown in Southern Quebec." *Bioresources* 7(3): 3779-3799. Published work.

PROPRIÉTÉS ANATOMIQUE DES CLONES SÉLECTIONNES DE PEUPLIER HYBRIDES CULTIVÉS AU SUD DU QUÉBEC

3.2 RÉSUMÉ

Les propriétés anatomiques de sept clones de peuplier hybride cultivés sur trois sites au sud du Québec, Canada, ont été évaluées. Les variations radiales et longitudinales des propriétés anatomiques sélectionnées ont été mesurées par analyse d'image des sections transversales and par analyse de la qualité de la fibre. Les résultats révèlent que toutes les propriétés anatomiques mesurées ont varié significativement selon les sites. La variation clonale a été hautement significative pour toutes les propriétés anatomiques étudiées, et l'héritabilité au sens large a varié de 0.10 (l'aire moyenne de lumière du vaisseau) à 0.76 (pourcentage d'aire de la paroi cellulaire). Le gain génétique était positif pour toutes les propriétés anatomiques. Le patron de variation radiale était caractérisé par une augmentation rapide au cours des premières années de la longueur, de la largeur et de la proportion de fibres, de l'épaisseur de la paroi cellulaire et du pourcentage d'aire de la paroi cellulaire. La proportion de rayons est demeurée constante alors que l'aire de lumière du vaisseau et la proportion de vaisseaux ont diminué avec l'âge cambial.

Mots-clés: Peuplier hybride, Propriétés anatomiques du bois, Site, Variation clonale, Âge, Héritabilité, Gain génétique.

3.3 INTRODUCTION

Forests are one of Canada's most important natural resources. Poplar species and hybrids are among the most widespread and fastest growing tree species in North America, and along with aspen and mixed wood stands, they make up a substantial part of the natural forest. Poplars are increasingly harvested in Canadian forest industries, and they currently account for over 50% of all hardwoods and 11% of overall timber resources in Canada (Avramidis and Mansfield 2005).

Hybrid poplars are hybridizations of two or more species within the genus *Populus*, which, as one of the fastest growing temperate trees, has considerable commercial value (Zsuffa et al. 1996). Hybrid poplars have been genetically modified through selection and crossbreeding to improve growth rate, trunk form, adaptability, and disease resistance (Hernández et al. 1998; Riemenschneider et al. 2001; Zhang et al. 2003; Pliura et al. 2007). Wood formation is a complex developmental process that includes the differentiation of vascular cambial initials into various xylem tissues, cell elongation, and secondary wall synthesis. As the secondary wall forms, the fiber and vessel cells undergo massive thickening, significantly influencing the wood quality. Wood properties are largely genetically determined (Zobel and Jett 1995), and can show growth variations in width and height depending on site conditions and age. For example, some fast growing tropical tree species consist of juvenile wood only when they are harvested at young age (Zobel and Sprague 1998). For optimum wood utilization, the age effects on wood properties must be determined, including the size and type distribution of cells (Peszlen 1994). In addition, genetic improvements designed to produce harvestable size trees at young age may also produce higher percentages of juvenile wood, which would have significant effects on wood properties and industrial processing applications (Burley and Palmer 1979; Mátyás and Peszlen 1997; Hernández et al. 1998). Accordingly, researchers have analyzed anatomical variations in wood elements within and among clones (*Populus spp., Eucalyptus spp.,* *Dalbergia spp.*) in order to assess wood quality (Phelps et al. 1982; Koubaa et al. 1998a; Rao et al. 2002; Pande and Singh 2005).

Panshin and de Zeeuw (1980) conducted a literature review on longitudinal and radial variations in wood anatomical properties. They found three patterns of radial variation in tracheid and fiber length: 1) a rapid increase followed by constant length from pith to bark; 2) a smooth and continuous increase from pith to bark; and 3) an increase from pith to bark up to a maximum, followed by a smooth decrease. A similar trend was reported for vessel element length and for fiber and vessel diameter, although the increase was moderate. Fiber wall thickness increases from pith to bark in some species and remains constant in others. According to Mátyás and Peszlen (1997), wood properties vary greatly within and among poplar trees. However, the findings on variation in poplar wood properties are inconclusive and in some cases contradictory. More specifically, within-tree variation in anatomical properties in hybrid poplars has not been examined, except for a few studies on fiber length (Holt and Murphey 1978; Murphey et al. 1979; Yanchuk et al. 1984; Bendtsen and Senft 1986; Koubaa et al. 1998a; DeBell et al. 1998). These studies found significant clone and longitudinal variation in fiber length. DeBell et al. (1998) found that the variation in fiber length was affected by age but not by growth rate, whereas Koubaa et al. (1998a) found a slightly negative correlation between fiber length and growth rate.

Peszlen (1994) found a significant effect of age on poplar anatomical features. She reported an increase in fiber and vessel lumen area from pith to bark, with a rapid increase in vessel lumen diameter in the first few years followed by constant increase toward the bark. Lei et al. (1996) found a similar variation pattern in white oak. Mátyás and Peszlen (1997) found only slight changes in the radial distribution of vessel lumen, fiber lumen, and cell walls in poplar clones. Kern et al. (2005) noted that various fiber features, such as narrower fiber lumen area, greater cell wall thickness, change in the cellulose microfibril angle, or biochemical features of the lignin in cell walls, might mitigate potential mechanical weakening caused by greater vessel lumen area. Based on an understanding of the anatomical characteristics that determine wood quality in hybrid poplar clones, better selection criteria could be developed for specific final products.

Little information is available on the genetic parameters for the wood anatomical characteristics of poplar species, such as heritability and genetic gain, except for a few studies on fiber length (Farmer and Wilcox 1968; Koubaa et al. 1998a; Zhang et al. 2012) and fiber width (Wang et al. 1991). Estimating heritability and genetic correlation with traits is particularly important for predicting the genetic gain from cloned material (Foster and Shaw 1988) and for better clonal selection.

Accordingly, knowledge of the variation in fiber anatomy is essential for obtaining improved wood quality, better clonal selection, optimum rotation cycles, and better end uses of hybrid poplar clones. We therefore investigated site, clonal, and within-tree variations in selected anatomical properties of hybrid poplar clones grown in field trials in the southern part of the province of Quebec, Canada. The results will contribute to the selection of superior clones in terms of wood anatomical properties.

3.4 MATERIALS AND METHODS

3.4.1 Study area

Materials for this study were collected from three hybrid poplar clonal trials established by the *Direction de la recherche forestière, Ministère des Ressources naturelles et de la Faune du Québec* (department of forestry research at Quebec's ministry of natural resources and wildlife) between 1991 and 1995. Trees for hybrid clones trials were planted at the Saint-Ours and Windsor sites in 1993, and in 1991 at the Pointe-Platon site (Table 3.1). Trees for clone DNxM-915508 were obtained from a 1995 trial at the Pointe-Platon site (Table 3.2). The trial sites are located in Pointe-Platon (46°40'N 71°51'W), Saint-Ours (45°54'N 73°09'W), and Windsor (45°42'N 71°57'W) in southern Quebec, Canada (Figure 3.1).

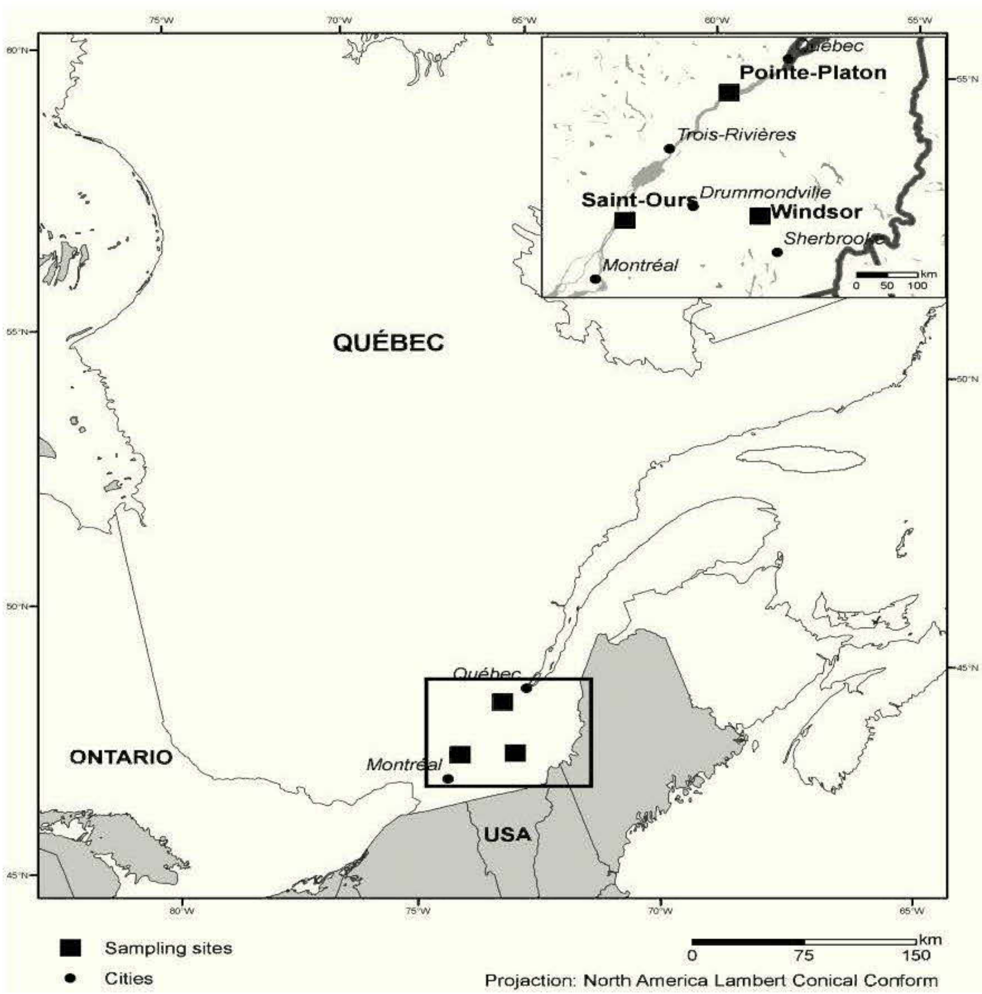

Figure 3.1 Map of sampling sites located in the southern part of the province of Quebec, Canada.

The Saint-Ours site is located in the Champlain marine deposit, where the soil consists of a silty clay deposit (40% clay). The two other sites consist of sandy loam soil (Pliura et al. 2007). All sites were originally used for agriculture, but had been abandoned for several years before the hybrid poplar clones were planted. All tree plantation trial sites had a randomized block design with ten blocks each.

Table 3.1 Site characteristics of hybrid Poplar clonal trials.

	Site		
Characteristics	Pointe-Platon	Saint-Ours	Windsor
Trial number	PLA01791	STO10893	WIN10593
Establishment year	1991	1993	1993
Geographic coordinates	$46^0$40'N, $71^0$51'W	$45^0$54'N, $73^0$09'W	$45^0$42'N, $71^0$57'W
Elevation (m)	60	15	260
Ecological sub-region – bioclimatic domain	Sugar maple – basswood domain	Sugar maple – bitternut hickory domain	Sugar maple – basswood domain
Surface deposit	Sandy loam soil	Champlain marine deposit with silty clay soil.	Sandy loam soil
Initial spacing	1 m x 3 m	1.2 m x 3.5 m	1.5 m x 3.5 m

Table 3.2 Studied hybrid poplar clones.

Clone	Hybrid	Female parent	Male parent	Note
DxN-131	*Populus deltoides* × *P. nigra*	*P. deltoides*	*P. nigra* 'Italica' as the putative father	A natural hybrid selected from the Montréal area, Québec
TxD-3230	*P. trichocarpa* × *P. deltoides* Syn.: *P.* × *generosa* 'Boelare'	*P. trichocarpa* 'Fritzi Pauley' (from Washington)	*P. deltoides* S.1-173 (from a cross between *P. deltoides* V.5 from Iowa and V.9 from Missouri)	Clone S.910-8 from Belgium. Cultivar 'Boelare'
DxN-3565	*P. deltoides* × *P. nigra* Syn.: *P.* × *canadensis*	*P. deltoides* S.513-60 (from a cross between *P. deltoides* V.5 from Iowa and V.12 from Illinois)	*P. nigra* S.157-3 (from a cross between *P. nigra* V.220 from Italy and V.450 from Belgium)	Family/tree from Belgium: 78.017/164
DxN-3570	*P. deltoides* × *P. nigra*	*P. deltoides* S.513-60	*P. nigra* S.157-4 (from a cross between *P. nigra* V.220 from Italy and V.450 from Belgium)	Family/tree from Belgium: 78.018/204
DxN-3586	*P. deltoides* × *P. nigra*	*P. deltoides* S.513-60	*P. nigra* S.132-4 (from a cross between *P. nigra* V.441 from Italy and V.450 from Belgium)	Family/tree from Belgium: 78.016/156
DxN-4813	*P. deltoides* × *P. nigra*	*P. deltoides* 226 (from Trois-Rivières, Québec)	*P. nigra* 'Italica'	A controlled cross selected from Québec
DNxM-915508	(*P. deltoides* × *P. nigra*) × *P. maximowiczii*	*P. deltoides* × *P. nigra* (from Québec City)	*P. maximowiczii* (from Japan)	A controlled cross selected from Québec

* Trees for the clone DNxM-915508 at Pointe-Platon were sampled from another trial PLA16495.

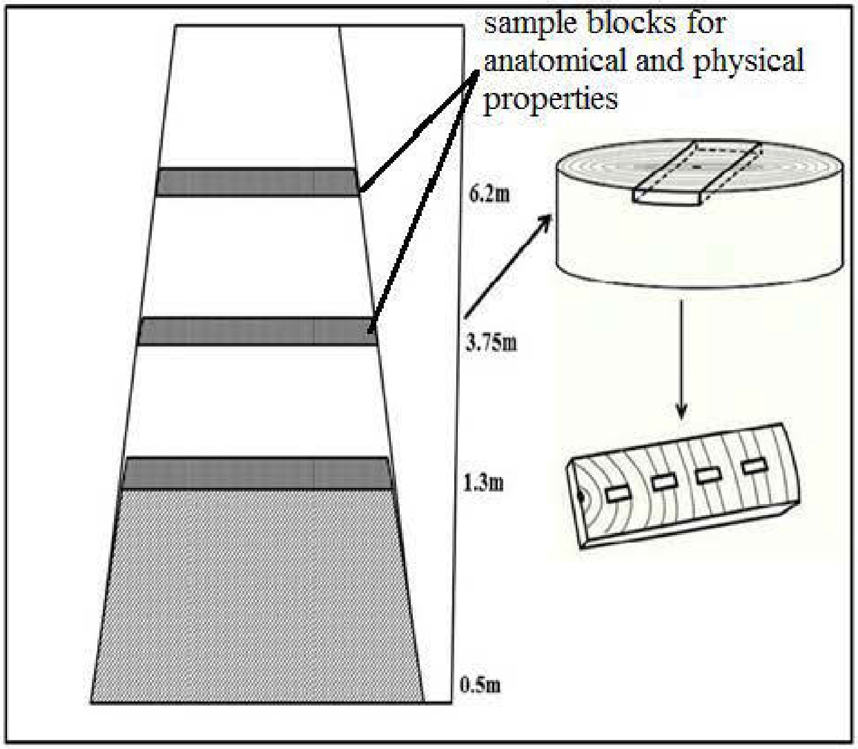

Figure 3.2 Schematic diagram of the sampling procedure for the analysis of hybrid poplar wood anatomical properties.

3.4.2 Sample collection and preparation

Seven hybrid clones (Table 3.2) were selected for this study. Five trees per site were randomly sampled for each clone, for a total of 105 trees. Trees were cut from the St-Ours and Windsor sites after 15 growing seasons. Trees were cut from the Pointe-Platon site after 17 growing seasons, except for clone DNxM-915508, which was felled after 13 growing seasons. Disks 10 cm thick were collected from each tree from breast height upward at 2.5 m intervals (Figure 3.2) and used for anatomical analysis. Wax was applied to the disk edges to limit drying and prevent decay and other environmental alterations. Samples were then transported to the Wood Research Centre, Université Laval, Quebec, Canada and kept frozen until test sample preparation. A 2.5 cm thick slab was cut along a diameter of each disk (bark to bark passing through the pith) and then conditioned at 20 °C and 60% relative humidity for several weeks until reaching 12% moisture content.

A series of radially oriented sample blocks sized 1 (T) x 1 (R) x 2 (L) cm was systematically cut from annual growth rings (3, 6, 9, and 12) using a precision saw and a chisel. At the annual growth ring with a cambial age of 15, there was insufficient wood to prepare samples for properties measurement by WinCELL, an image analysis system specifically designed for wood cells analysis, from Regent Instruments, Québec, Canada. Cross sections of 20 μm were cut using a rotary microtome with a disposable blade positioned at approximately 15 degrees. Sections were then bleached with sodium hypochlorite solution (80 mL water + 5 drops of bleach) for 1 minute and washed in a distilled water bath for 1 minute. Sections were then double stained with 1% safranin stain for 5 minutes and 0.1% astra blue stain for 15 minutes. Excess stain was removed by washing sections successively in 50, 80, and 100% ethanol solution. Thin sections were further dehydrated using toluene and then permanently mounted on microscope slides with coverslips using permount. Samples were left for two weeks to ensure proper drying of the permount.

Samples were photographed at ×50 magnification using a Leica compound microscope (DM 1000) equipped with a PL-A686 high resolution microscopy camera to capture black and white images (tiff electronic file format) at 1200x1600 resolution using a green filter to maximize contrast (Figure 3.3). WinCELL Pro 2004a (Régent Instruments Inc. 2004) was used to measure average fiber wall thickness, fiber lumen area, vessel lumen area, fiber diameter, and vessel diameter. Average fiber diameter accounts for average fiber lumen diameter and the respective two-sided fiber wall thickness. Cell wall area (%) was estimated by subtracting the percent areas of the vessel lumen, ray, and fiber lumen from the image area (Peszlen 1994).

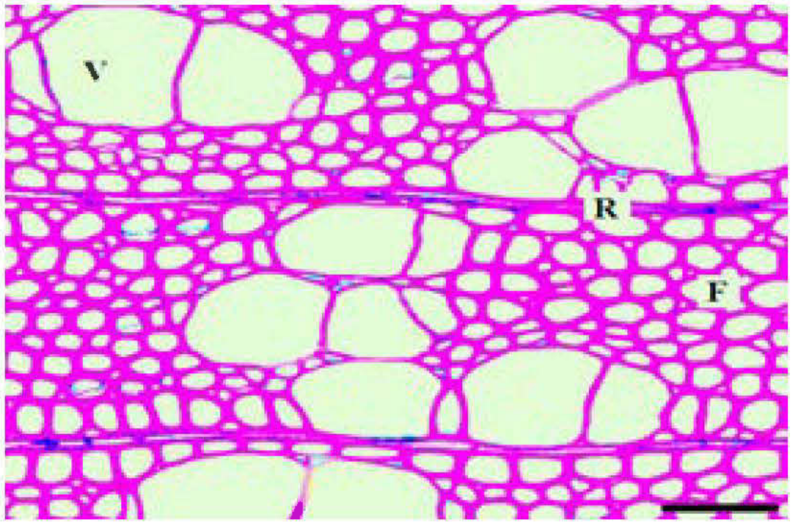

Figure 3.3 Microscopic cross-section of hybrid poplar wood: V = vessel, R = ray, F = fiber, Scale bar = 50 μm.

The proportion of tissue in the different cell types was estimated from two cross-sections of each wood block. Vessel cells were distinguished from fiber and ray by analyzing 570 μm^2 fields (corresponding to four squares of the grid) and noting the tissue types within the field. Fiber proportion was measured using the same method. Ray proportion was obtained by subtracting from unity the vessel and fiber areas.

The same thick slabs used for wood anatomy analysis were used to analyze fiber properties from pith to bark at different tree heights using a Fiber Quality Analyzer (FQA) (OpTest Equipment Inc., LDA02, Ontario, Canada). A series of radially oriented thin tangential sections was systematically cut from annual growth rings 3, 6, 9, 12, and 15 for fiber length and fiber width measurement. Tangential sections were macerated using Franklin's method. Sections were soaked in Franklin solution (1:1, glacial acetic acid: 30% hydrogen peroxide) and heated at 70 °C for approximately 48 hours. The solution was decanted and the remaining fibrous material was washed under vacuum with deionized water until reaching neutral pH. The distribution of fiber length and width was measured automatically using the FQA. A total of 5,000 fibers were measured for each sampled growth ring.

3.4.3 Statistical analysis

The SAS® statistical package, version 9.2 (SAS 2008) was used for all statistical analyses. Normality and homogeneity of variance for residuals were tested using UNIVARIATE statistics. Data transformations were not considered necessary to satisfy the assumptions of the analysis of variance and other analyses. Analyses of variance were performed using PROC GLM with Type III (partial sums of squares) estimates to assess the relative magnitude of each source of variation. Analyses were performed among and within sites and clones. The variance in anatomical properties variables among sites was analyzed using the following mixed linear model (Eq. 3.1),

$$X_{ijlm} = \mu + S_i + C_j + (S \times C)_{ij} + A_l + H_m + (A \times H)_{lm} + \varepsilon_{ijlm} \quad (3.1)$$

where X_{ijlm} is an observation on the l^{th} age and m^{th} height of the j^{th} clone from the i^{th} site; μ is the overall mean; A_l, H_m, and $(A \times H)_{lm}$ are the fixed effects and their interactions, respectively; S_i is the fixed effect due to the i^{th} site; C_j is the fixed effect due to the j^{th} clone; $(S \times C)_{ij}$ is the interaction between site and clone; and ε_{ijlm} is the random error. Some F ratios involved more than one mean square in the denominator and were tested with approximate degrees of freedom. Tree effects and the site-clone-age interaction were not considered in the analysis, as preliminary testing showed negligible contribution to the total variance. Furthermore, in many cases, the variance component for these terms could not be estimated or was not significant.

Tukey's Studentized Range (HSD) was used to test the statistical significance (at $p<0.05$) of differences among means of clones for each site (PROC GLM, SAS). The variance components were estimated in the model using VARCOMP with the restricted maximum likelihood method (REML) and expressed as a percentage (VAR). The broad-sense or clonal heritability (H_C^2) was calculated from the variance estimates, as follows (Eq. 3.2) (Becker 1984; Falconer and Mackay1996),

$$H_C^2 = \sigma_C^2 / \sigma_P^2 \quad (3.2)$$

where σ_C^2 and σ_P^2 are the genotypic and phenotypic variance, respectively. Phenotypic variance (σ_P^2) was calculated as shown in Eq. (3.3).

$$\sigma_P^2 = \sigma_C^2 + \sigma_{(s\,\mathrm{x}\,c)}^2 + \sigma_e^2. \quad (3.3)$$

where σ_C^2, $\sigma_{(s\,\mathrm{x}\,c)}^2$and σ_e^2 are the variance of clones, interection between site and clones and residuals effects, respectively.

The genotypic coefficient of variation (CV_G) and the phenotypic coefficient of variation (CV_P) were calculated from Eqs. 3.4 and 3.5, respectively (Burton 1952; Henderson 1953).

$$CV_G = (\sqrt{\sigma_C^2}/\mathrm{mean})\mathrm{x}100 \quad (3.4)$$

$$CV_P = (\sqrt{\sigma_P^2}/\mathrm{mean})\mathrm{x}100 \quad (3.5)$$

The mathematical expression for the genetic gain (*G*) is expressed in Eq. 3.6. The potential genetic gain from individual tree selection is computed by selection differential (Eq. 3.7) and 10% selection intensity,

$$G = H_C^2 * S \quad (3.6)$$

$$S = i * \sigma_P \quad (3.7)$$

where H_C^2 is the heritability, S is the selection differential, i is the selection intensity (10%), and σ_P is the phenotypic standard deviation.

3.5 RESULTS AND DISCUSSION

3.5.1 Within- and among-site variation

Growth site variable showed a highly significant effect on all studied wood anatomical properties (Table 3.3). Table 3.4 presents the mean and standard error of the anatomical properties of all studied hybrid poplar clones.

Trees from the Saint-Ours site showed the highest fiber length (0.99 ± 0.17 mm), and trees from Pointe-Platon showed the lowest (0.90 ± 0.19 mm), with a 10% difference between the lowest and highest length (Table 3.4). Highest fiber diameter, vessel lumen area, and vessel diameter were also found in trees from Saint-Ours, with the lowest from Pointe-Platon.

Table 3.3 Results of the analysis of variance of wood anatomical characteristics of hybrid poplar clones (F values and variance components of 11 wood anatomical properties: fiber length (FL), fiber width (FW), fiber wall thickness (FWT), average fiber lumen area (AFLA), average fiber diameter (AFD), average vessel lumen area (AVLA), average vessel diameter (AVD), fiber proportion (FP), vessel proportion (VP), ray proportion (RP), and cell wall area (CWA)).

	Site	Clone	Clone x Site	Height	Cambial age	Height x Cambial age
			F value			
FL	149.16^{**}	44.48^{**}	3.81^{**}	8.95^{**}	1172.21^{**}	0.74^{ns}
FW	16.58^{**}	2.35^{*}	7.72^{**}	1.33^{ns}	41.29^{**}	3.13^{**}
FWT	56.58^{**}	56.74^{**}	15.90^{**}	7.91^{**}	8.47^{**}	2.54^{*}
AFLA	100.93^{**}	269.82^{**}	166.69^{**}	21.46^{**}	32.87^{**}	1.02^{ns}
AFD	93.57^{**}	78.60^{**}	46.60^{**}	4.15^{*}	7.61^{**}	0.96^{ns}
AVLA	748.11^{**}	10.10^{**}	9.00^{**}	0.15^{ns}	0.17^{ns}	0.52^{ns}
AVD	555.47^{**}	327.13^{**}	102.44^{**}	44.81^{**}	61.09^{**}	1.88^{ns}
FP	427.37^{**}	741.61^{**}	333.12^{**}	67.16^{**}	78.70^{**}	2.23^{ns}
VP	106.56^{**}	390.93^{**}	118.55^{**}	54.31^{**}	71.75^{**}	1.91^{ns}
RP	654.15^{**}	94.67^{**}	201.04^{**}	0.48^{ns}	0.47^{ns}	0.46^{ns}
CWA	345.99^{**}	384.46^{**}	15.42^{**}	30.08^{**}	55.62^{**}	0.57^{ns}
			Variance components (%)[a]			
FL	5.30	3.46	0.72	0.29	71.13	0.0
FW	3.65	1.80	5.76	0.0	10.71	1.48
FWT	6.11	14.10	15.90	0.79	1.17	0.92
AFLA	2.65	13.77	57.37	1.13	2.37	0.0
AFD	5.70	7.44	37.87	0.37	1.03	0.0
AVLA	61.28	0.20	4.65	0.0	0.0	0.0
AVD	20.36	24.13	31.52	1.94	3.54	0.16
FP	2.54	25.40	57.52	1.62	2.56	0.12
VP	6.61	30.36	37.20	2.43	4.30	0.17
RP	19.70	14.00	49.11	0.0	0.0	0.0
CWA	18.41	47.87	5.63	1.61	4.01	0.0

*Significant at $P<0.05$ probability level. **Significant at $P<0.01$ probability level. [ns] Non-significant at $P<0.05$ probability level. [a] Variance component as a percentage of the total variance.

For fiber width, the Windsor site showed the highest average and Pointe-Platon the lowest average (Table 3.4). Pointe-Platon trees showed higher fiber wall thickness than trees from the two other sites, with a 12.4% difference between the highest and lowest average (Table 3.4).

Pointe-Platon trees showed the lowest average fiber lumen area, fiber diameter, vessel lumen area, and vessel diameter (Table 3.4). Pointe-Platon trees showed the highest fiber proportion and cell wall area, and the lowest average vessel lumen area and diameter and ray proportion (Table 3.4).

The significant site effect concurs with previous studies (Murphey et al. 1979; Phelps et al. 1982; Yanchuk et al. 1984; Bendtsen and Senft 1986; DeBell et al. 1998; Chauhan et al. 1999; Zhang et al. 2003; Pliura et al. 2007). Several factors may explain this significant site effect on the anatomical properties, including edaphic and climatic conditions (Peszlen 1994; Pliura et al. 2007). Trees from the Saint-Ours site showed higher fiber length, vessel proportion, and vessel dimensions. This could be explained by higher moisture availability and better drainage conditions as well as the soil surface deposition at the Saint-Ours site compared to the two other sites.

3.5.2 Clonal variation in fiber anatomical properties

The clone effect on the examined wood anatomical properties was highly significant (Table 3.3). The variance component analysis indicated that the clone effect varied among the studied properties, ranging from 0.2% to 47.9%. The clone effect on fiber width, although significant at the 0.05 probability level, was low (1.8%). Similarly, the clonal variance component of the vessel lumen area was also negligible (0.2%). In contrast, the variance component for the cell wall area percentage was the highest (47.8%) among all the anatomical properties (Table 3.3).

Table 3.4 Least squares means of clones at different sites and multiple comparison tests of hybrid poplar clones (fiber length (FL), fiber width (FW), fiber wall thickness (FWT), average fiber lumen area (AFLA), average fiber diameter (AFD), average vessel lumen area (AVLA), average vessel diameter (AVD), fiber proportion (FP), vessel proportion (VP), ray proportion (RP), and cell wall area (CWA)).

Point-Platon											
Clone	FL (mm)	FW (μm)	FWT (μm)	AFLA (μm^2)	AFD (μm)	AVLA (μm^2)	AVD (μm)	FP (%)	VP (%)	RP (%)	CWA (%)
DxN-131	0.83^{C}	26.78^{BC}	2.74^{B}	75.86^{B}	21.34^{B}	1429^{A}	40.22^{F}	59.50^{B}	23.66^{F}	16.84^{C}	41.91^{B}
TxD-3230	0.89^{AB}	27.34^{AB}	2.18^{D}	71.84^{C}	20.30^{D}	1382^{B}	50.26^{C}	55.82^{D}	29.57^{C}	14.62^{E}	39.46^{D}
DxN-3565	0.90^{AB}	27.21^{AB}	2.34^{D}	79.05^{A}	22.62^{A}	1438^{A}	36.16^{G}	62.20^{A}	21.27^{G}	16.53^{C}	44.09^{A}
DxN-3570	0.94^{A}	26.19^{CD}	2.24^{D}	71.55^{C}	20.24^{D}	1425^{A}	48.87^{D}	55.65^{D}	28.75^{D}	15.61^{D}	40.40^{C}
DxN-3586	0.95^{A}	27.74^{A}	2.72^{BC}	59.90^{E}	17.17^{F}	1457^{A}	55.06^{A}	47.22^{F}	32.39^{A}	20.39^{A}	37.18^{E}
DxN-4813	0.91^{AB}	26.42^{CD}	2.93^{A}	72.15^{C}	20.60^{C}	1443^{A}	42.80^{E}	56.65^{C}	25.18^{E}	18.18^{B}	44.50^{A}
DNxM-915508	0.85^{BC}	25.99^{D}	2.56^{C}	69.23^{D}	19.70^{E}	1435^{A}	51.35^{B}	54.18^{E}	30.21^{B}	15.62^{D}	39.58^{D}
Average ± SE	0.90 ± 0.19	26.81 ± 2.29	2.53 ± 0.53	71.34 ± 6.14	20.32 ± 1.74	1430 ± 91	46.36 ± 6.98	55.87 ± 4.77	27.27 ± 4.11	16.86 ± 2.45	41.04 ± 2.92

Saint-Ours											
Clone	FL (mm)	FW (μm)	FWT (μm)	AFLA (μm^2)	AFD (μm)	AVLA (μm^2)	AVD (μm)	FP (%)	VP (%)	RP (%)	CWA (%)
DxN-131	0.95^{D}	27.49^{AB}	2.31^{C}	74.93^{C}	22.07^{C}	2114^{A}	56.18^{C}	54.74^{C}	29.57^{C}	15.69^{E}	40.43^{C}
TxD-3230	0.95^{D}	28.10^{A}	2.30^{CD}	72.47^{D}	21.32^{D}	1907^{B}	52.84^{D}	52.88^{D}	27.81^{D}	19.31^{B}	38.70^{D}
DxN-3565	1.01^{BC}	26.74^{C}	2.54^{B}	78.32^{B}	23.27^{B}	1985^{B}	50.19^{E}	57.71^{B}	26.42^{E}	15.87^{E}	43.31^{A}
DxN-3570	1.07^{A}	27.21^{BC}	2.17^{DE}	74.62^{C}	21.96^{C}	2005^{AB}	60.04^{A}	54.45^{C}	31.60^{A}	13.95^{F}	41.44^{B}
DxN-3586	1.02^{AB}	26.90^{BC}	2.16^{ED}	72.59^{D}	21.41^{D}	2012^{AB}	56.22^{C}	53.09^{D}	29.59^{C}	17.33^{D}	37.34^{E}
DxN-4813	0.97^{CD}	27.01^{BC}	2.74^{A}	80.11^{A}	23.60^{A}	1778^{C}	44.32^{F}	58.54^{A}	23.33^{F}	18.13^{C}	42.83^{A}
DNxM-915508	0.96^{CD}	28.05^{A}	2.04^{F}	62.25^{E}	18.25^{E}	1721^{C}	57.80^{B}	45.25^{E}	30.42^{B}	24.33^{A}	39.28^{D}
Average ± SE	0.99 ± 0.17	27.36 ± 2.29	2.32 ± 0.42	73.56 ± 6.00	21.68 ± 1.78	1932 ± 355	54.01 ± 6.25	53.79 ± 4.41	28.43 ± 3.29	17.81 ± 3.50	40.48 ± 2.57

Windsor											
Clone	FL (mm)	FW (μm)	FWT (μm)	AFLA (μm^2)	AFD (μm)	AVLA (μm^2)	AVD (μm)	FP (%)	VP (%)	RP (%)	CWA (%)
DxN-131	0.88^{C}	27.65^{AB}	2.13^{CD}	73.57^{C}	20.45^{BC}	1467^{A}	46.18^{D}	51.89^{E}	25.09^{D}	23.03^{A}	38.23^{C}
TxD-3230	0.95^{A}	26.40^{C}	1.88^{E}	71.92^{D}	22.05^{A}	1420^{B}	57.13^{A}	46.59^{F}	30.57^{A}	22.84^{A}	38.63^{C}
DxN-3565	0.94^{AB}	27.11^{BC}	2.66^{A}	74.40^{BC}	19.72^{C}	1476^{A}	45.14^{D}	58.94^{A}	24.57^{D}	16.49^{D}	39.88^{B}
DxN-3570	0.96^{A}	27.77^{AB}	2.02^{D}	71.36^{D}	20.11^{C}	1464^{A}	54.38^{B}	47.52^{F}	29.61^{B}	22.87^{A}	38.53^{C}
DxN-3586	0.98^{A}	28.39^{A}	2.44^{B}	76.22^{A}	20.45^{BC}	1494^{A}	45.43^{D}	54.64^{C}	24.72^{D}	20.64^{B}	35.49^{E}
DxN-4813	0.93^{AB}	27.88^{A}	2.51^{B}	74.95^{B}	21.06^{B}	1480^{A}	45.75^{D}	55.94^{B}	24.87^{D}	19.19^{C}	41.51^{A}
DNxM-915508	0.89^{BC}	27.65^{AB}	2.16^{C}	73.48^{C}	20.25^{BC}	1469^{A}	49.73^{C}	53.22^{D}	27.63^{C}	19.15^{C}	36.56^{D}
Average ± SE	0.93 ± 0.18	27.55 ± 2.45	2.25 ± 0.42	73.70 ± 3.49	20.61 ± 2.53	1467 ± 91	49.17 ± 5.96	52.54 ± 4.38	26.76 ± 2.97	20.70 ± 2.69	38.36 ± 2.50

						Clonal Average						
Clone	FL (mm)	FW (μm)	FWT (μm)	AFLA (μm^2)	AFD (μm)	AVLA (μm^2)	AVD (μm)	FP (%)	VP (%)	RP (%)	CWA (%)
DxN-131	0.88^{D}	27.30^{AB}	2.39^{C}	74.76^{C}	21.38^{B}	1676^{A}	47.69^{D}	55.28^{C}	26.16^{D}	18.56^{C}	40.15^{B}
TxD-3230	0.93^{BC}	27.28^{AB}	2.12^{E}	72.08^{D}	21.24^{B}	1574^{B}	53.48^{B}	51.67^{E}	29.31^{B}	19.02^{B}	38.92^{C}
DxN-3565	0.95^{B}	27.02^{B}	2.5^{B}	77.46^{A}	22.02^{A}	1644^{A}	43.74^{E}	59.67^{A}	24.05^{F}	16.28^{E}	42.61^{A}
DxN-3570	0.99^{A}	27.06^{B}	2.15^{E}	72.53^{D}	20.78^{D}	1635^{A}	54.43^{A}	52.65^{D}	29.99^{A}	17.35^{D}	40.16^{B}
DxN-3586	0.98^{A}	27.68^{A}	2.45^{BC}	69.50^{E}	19.64^{D}	1646^{A}	52.15^{C}	51.62^{E}	28.88^{D}	19.50^{A}	36.66^{E}
DxN-4813	0.94^{B}	27.10^{B}	2.72^{A}	75.64^{B}	21.71^{A}	1563^{B}	44.29^{E}	57.01^{B}	24.49^{E}	18.51^{C}	42.95^{A}
DNxM-915508	0.90^{CD}	27.23^{B}	2.25^{D}	68.30^{F}	19.39^{D}	1544^{B}	53.00^{B}	50.81^{F}	29.40^{B}	19.79^{A}	38.45^{D}
Overall Average ± SE	0.94 ± 0.19	27.24 ± 2.36	2.37 ± 0.47	72.87 ± 5.46	20.87 ± 2.13	1611 ± 317	49.86 ± 7.15	54.06 ± 4.72	27.49 ± 3.56	18.45 ± 3.34	39.37 ± 2.91

*Means within a column followed by the same letter are not statistically different at p=0.05 for each site separately.

Differences among clones were also significant for wood element proportions (fiber, vessel, and ray), as shown in Table 3.3. The highest interclonal variation was observed for vessel proportion, whereas ray proportion showed a significant clone effect but a low variance component (Table 3.3).

The clone effect was reflected in the differences in means among clones for all studied properties. For example, clone DxN-4813 showed the highest fiber wall thickness, whereas clone DxN-3565 showed the highest fiber lumen area and average fiber diameter. Clone DxN-131 showed the highest vessel lumen area, and clone DxN-3570 showed the highest average vessel diameter (Table 3.4).

The highest fiber proportion was found for clone DxN-3565 and the lowest for clone DNxM-915508, for a 17.4% difference (Table 3.4). The highest vessel proportion percentage was found for clone DxN-3570 and the lowest for clone DxN-3565, for a 27.4% difference. The highest and lowest ray proportions were found for clone DNxM-915508 and DxN-3565, respectively.

The effect of site x clonal interaction was also highly significant (Table 3.3). This indicates that clonal variation varied across the sites. The variance components of the site x clone interaction for fiber lumen area and fiber proportion were higher than for the other anatomical properties (Table 3.3). This variation was probably caused by the low number of clones involved (7) and the fact that the trees were sampled from small clonal test plots rather than a commercial plantation with large monoclonal blocks. Clonal tests are subject to effects from neighboring plots due to competition among clones. However, these environmental effects, although significant, are negligible compared to the clonal and within-tree variation.

According to Monteoliva et al. (2005), fiber anatomical properties have a major influence on the quality of pulp and paper products as well as solid wood products.

Pliura et al. (2007) and Huda et al. (2011a) found that fiber wall thickness was positively correlated to wood density in poplar hybrids. At the cellular level, increased cavitation resistance and stem mechanical strength were associated with thicker cell walls (Jacobsen et al. 2005). Greater fiber length is preferred for pulp and paper production because a better fiber network is achieved, resulting in higher paper strength. Karlsson (2006) also argued that narrow fiber width is desirable for pulp and paper applications because it results in smoother paper and more uniform formation.

Based on the results of the present study, clone DxN-3570, which showed high fiber length and narrow fiber width, would be promising for pulp and paper manufacturing. Similarly, clones DxN-4813 and DxN-3565, which showed the highest cell wall thickness, would have good density and mechanical properties, resulting in higher yield for fiber-based products (Huda et al. 2011a). In fact, of the seven studied hybrid poplar clones, these two presented the highest wood density (Huda et al. 2011a; Hernández et al. 2011).

Although only seven hybrid poplar clones were included in this study, the significant variation in morphological properties within sites and clones indicates good opportunities for selecting the most performing clones in terms of anatomical properties, both for breeding and for processing for specific end uses.

Table 3.5 Anatomical properties of various *Populus* clones and their hybrids (fiber length (FL), fiber width (FW), fiber wall thickness (FWT), average fiber lumen area (AFLA), average fiber diameter (AFD), average vessel lumen area (AVLA), average vessel diameter (AVD), fiber proportion (FP), vessel proportion (VP), ray proportion (RP), and cell wall area (CWA)).

References	Species or hybrid	FL (mm)	FW (μm)	FWT (μm)	AFLA (μm^2)	AFD (μm)	AVLA (μm^2)	AVD (μm)	FP (%)	VP (%)	RP (%)	CWA (%)
Present study	Hybrid poplar	0.94	27.2	2.4	72.9	20.9	1611	49.9	54.1	27.5	18.5	39.4
Koubaa *et al.* (1998a)	*P. x euramericana*	1.02	-	-	-	-	-	-	-	-	-	-
Fang and Yang (2003)	Poplar clones	1.10	24.8	-	-	-	-	-	-	-	-	-
Fang *et al.* (2004)	Poplar clones	0.83-1.27	23-26	-	-	-	-	-	-	-	-	-
Rydholm (1965)	Hybrid poplar	0.92	20	1.2	-	-	-	-	-	-	-	-
Peszlen (1994)	*P. x euramericana*	0.62-0.71	-	-	-	9.7-12.5	-	43.9-49.5	-	-	-	37.1-45.9
Mátyás and Peszlen (1997)	*P. x euramericana*	0.62-0.71	-	-	-	9.7-12.5	-	43.9-49.5	-	-	-	37.1-45.9
Panshin and de Zeeuw (1980)	Poplar spp.	1.32-1.38	-	-	-	-	-	-	53-60	28-34	11-14	-
Cheng and Bensend (1979)	*Populus* clones	0.68-0.83	-	-	-	-	-	-	57.1-68.5	25.9-31.4	8.4-11.6	-
Sutton and Tardif (2005)	*P. tremuloides*	-	-	2.3-2.4	66-83	15.3-16.5	-	-	-	-	-	41.9-42.2

Except for fiber length, few data on anatomical properties of poplar species have been reported in the literature (Table 3.5). The results on anatomical properties obtained in this study are generally in good agreement with previously reported data except for fiber width, average fiber diameter and ray proportion (Table 3.5) which showed higher values than previously reported data.

Moreover, the literature contains little data on genetic parameters such as heritability and genetic gain for the wood anatomical characteristics of poplar species, aside from a few studies on fiber length, which can be compared with the present study. Genetic parameters such as heritability and genetic gain for particular properties are important tools for predicting genetic gains (Foster and Shaw 1988).

Based on these variations, hybrid poplar clones could be better selected for higher heritability and genetic gain, even with simple selection procedures. The high heritability and genetic gain for fiber length, fiber wall thickness, fiber proportion, vessel proportion, and cell wall area percentage indicate that these properties are primarily genetically determined in hybrid poplars, and can be selected through phenotypic performance.

The clonal and environmental variations (Table 3.3) were used to estimate various genetic parameters, including heritability and genetic gain for anatomical properties (Table 3.6). The phenotypic coefficient of variation was higher than the genotypic coefficient of variation for all studied properties (Table 3.6). This indicates that the apparent variation in clones was not only genotypic, it was also due to environmental factors. The extent of the environmental influence on a given property is indicated by the difference between the phenotypic and genotypic coefficient of variation. A small difference indicates a low environmental effect (Saifullah and Rabbani 2009).

Broad-sense heritability for anatomical properties ranged from 0.10 to 0.76, with high heritability for fiber wall thickness and cell wall area (Table 3.6). The heritability for fiber length was 0.59, which is comparable to that reported for hybrid poplars (H^2=0.41) by Koubaa et al. (1998a). However, heritability for fiber length in different species of *Populus tremuloides* was reported at 0.43 by Yanchuk et al. (1984), and at 0.61 by Klasnja et al. (2003) and at 0.36 by Farmer and Wilcox (1968) for *Populus deltoides*. These results confirm that fiber length in hybrid poplar is only moderately genetically determined, as suggested by Koubaa et al. (1998a).

Table 3.6 Estimates of genetic parameters of 7 hybrid poplar clones (fiber length (FL), fiber width (FW), fiber wall thickness (FWT), average fiber lumen area (AFLA), average fiber diameter (AFD), average vessel lumen area (AVLA), average vessel diameter (AVD), fiber proportion (FP), vessel proportion (VP), ray proportion (RP), and cell wall area (CWA)).

	Broad-sense heritability	Genotypic coefficient of variation	Phenotypic coefficient of variation	Genetic gain
FL	0.59	11.11	24.29	5.11
FW	0.28	2.07	6.94	1.20
FWT	0.73	13.95	22.07	6.02
AFLA	0.57	2.84	7.66	2.77
AFD	0.23	2.85	10.44	1.31
AVLA	0.10	2.19	22.13	0.83
AVD	0.59	7.55	15.36	4.04
FP	0.62	4.61	9.14	5.11
VP	0.58	7.72	14.01	3.82
RP	0.37	7.47	20.47	2.92
CWA	0.76	5.42	7.83	4.67

Heritability for fiber width was 0.28, in good agreement with the heredity for hybrid poplar (H^2=0.33) found by Wang et al. (1991). The highest heritability was obtained for cell wall area (0.76), followed by fiber wall thickness (0.73), fiber proportion (0.62), and vessel proportion (0.58). Genetic gain for anatomical properties of hybrid poplar clones ranged from 0.83 to 6.02. The highest genetic gain was obtained for fiber wall thickness (6.02), followed by fiber length (5.11), fiber proportion (5.11), and cell wall area (4.67). The genetic gain for vessel proportion was 3.82 (Table 3.6).

3.5.3 Within-tree variation

The effects of tree height and cambial age were highly significant on most of the examined properties, except for vessel area and ray proportion (Table 3.3). The patterns for radial and longitudinal variation in fiber properties, vessel properties, and element proportions are shown in Figures 3.4 to 3.10, respectively.

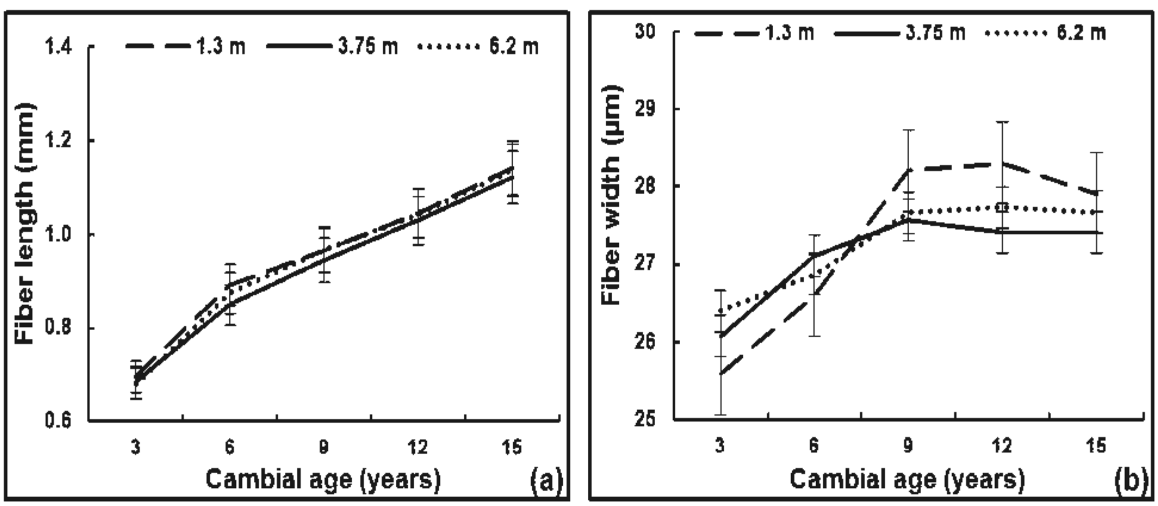

Figure 3.4 Variation and standard error for (a) fiber length and (b) fiber width with cambial age and tree height in hybrid poplar clones.

The variation in fiber length with cambial age at each of the three sampled heights is illustrated in Figure 3.4a. At all heights, fiber length was short near the pith, increased rapidly during the early years, and then continued to increase at a lower rate towards the bark (Figure 3.4a). This variation pattern concurs with previous studies (Peszlen 1994; Mátyás and Peszlen 1997; DeBell et al. 1998; Koubaa et al. 1998a). The increase in fiber length from pith to bark could be explained by the increase in length of cambial initials with increasing cambial age, as discussed in previous studies (Peszlen 1994; Koubaa et al. 1998a; DeBell et al. 1998; Jorge et al. 2000; Fang and Yang 2003; Fang et al. 2004). The fiber length of hybrid poplar is shorter near the pith due to a high proportion of juvenile wood. The general pattern of fiber length found in this study did not allow a clear differentiation between juvenile and mature wood.

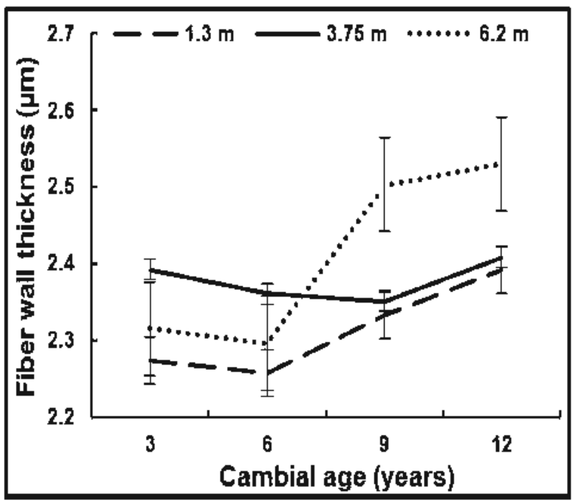

Figure 3.5 Variation and standard error for fiber wall thickness with cambial age and tree height in hybrid poplar clones.

Maturation age is defined as the age at which the size of wood elements stabilizes. The radial variation pattern for the studied anatomical properties showed no evidence of a transition from juvenile to mature wood at any cambial age. Thus, the radial variation in anatomical properties indicated that the wood in the studied hybrid poplar clones was still juvenile.

The radial variation in fiber length was the main source of variation, accounting for 71.1% of the total variation (Table 3.3). This result concurs with a previous study on *P. x euramericana* clones (Koubaa et al. 1998a), where cambial age accounted for 80.5% of the total variation.

The radial variation in fiber width accounted for 10.7% of the total variation, and was characterized by an increase from pith to bark to reach a maximum at cambial age 9, followed by a slight decrease in the outer rings (Figure 3.4b). The same variation pattern was obtained for the three sampled heights.

Fiber wall thickness tended to increase from the pith outwards from cambial age 6. This trend is clearly shown at heights 1.3 m and 6.2 m (Figure 3.5). However, at height 3.75 m, a slight decrease from pith to bark is shown. The radial variation in fiber wall thickness accounted for 1.2% of the total variation (Table 3.3).

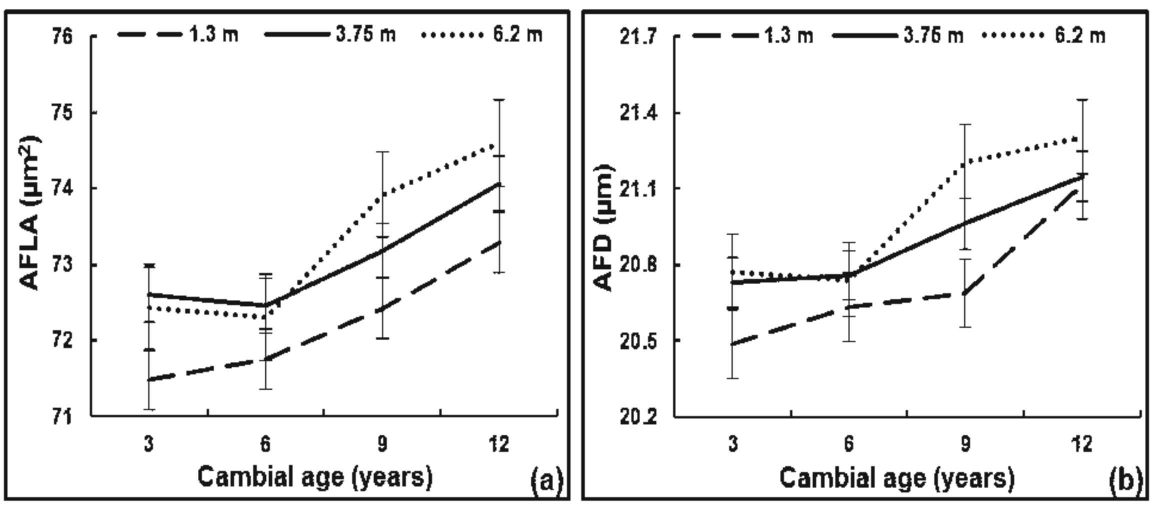

Figure 3.6 Variation and standard error for (a) average fiber lumen area (AFLA) and (b) average fiber diameter (AFD) with cambial age and tree height in hybrid poplar clones.

Average fiber lumen area (Figure 3.6a), average fiber diameter (Figure 3.6b), and cell wall area (Figure 3.7) increased from pith outwards. Although the age effect on these properties was significant, it contributed little to the total variation. It accounted for only 2.4%, 1.0%, and 4.0% for the lumen area, fiber diameter and cell wall area, respectively (Table 3.3).

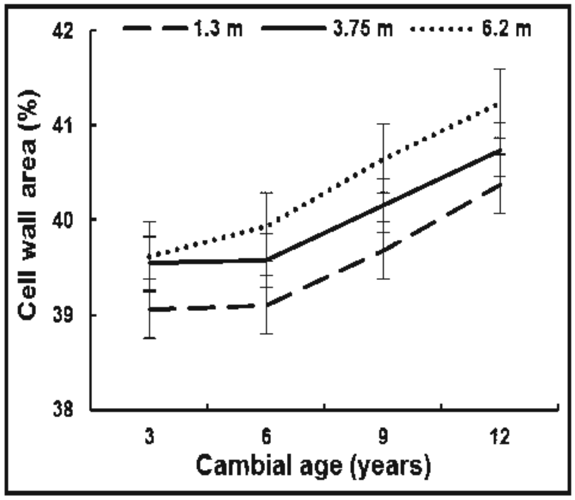

Figure 3.7 Variation in cell wall area percentage with cambial age and tree height in hybrid poplar clones.

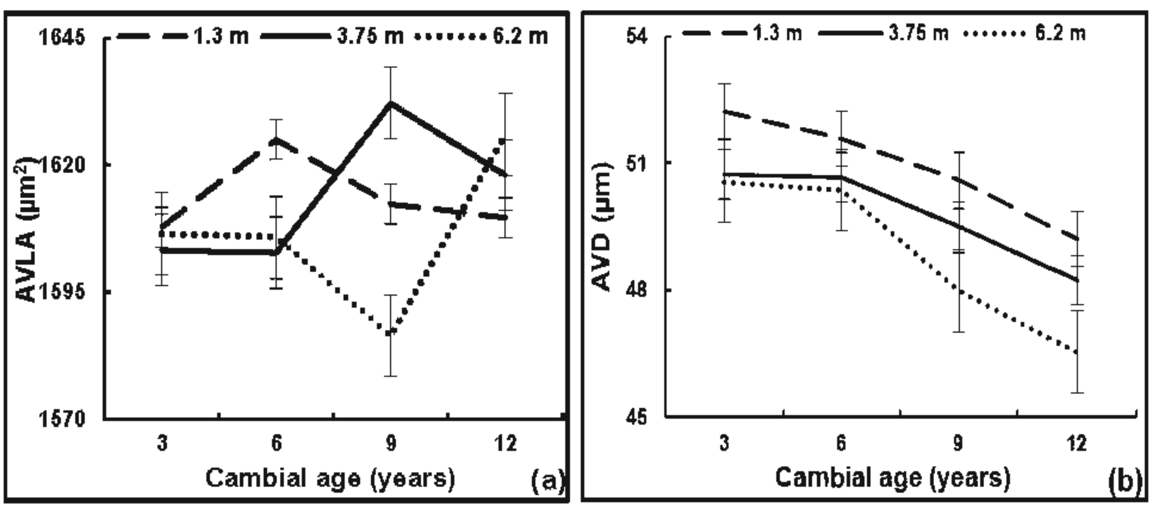

Figure 3.8 Variation and standard error for (a) average vessel lumen area (AVLA) and (b) average vessel diameter (AVD) with cambial age and tree height for hybrid poplar clones.

The average vessel lumen area (Figure 3.8a) remained relatively constant. This result is supported by the non-significant effect of age and height on vessel area (Table 3.3). The average vessel diameter showed a decreasing trend with increasing cambial age (Figure 3.8b). However, despite the significant effect of age on vessel diameter, it accounted for only 3.5% of the total variation (Table 3.3). The radial variation pattern from pith to bark for the fiber lumen and vessel lumen area confirms the results of other studies in poplar clones. For example, although the fiber lumen area increased slightly with age, the vessel lumen area remained relatively constant in poplar clones (Mátyás and Peszlen 1997).

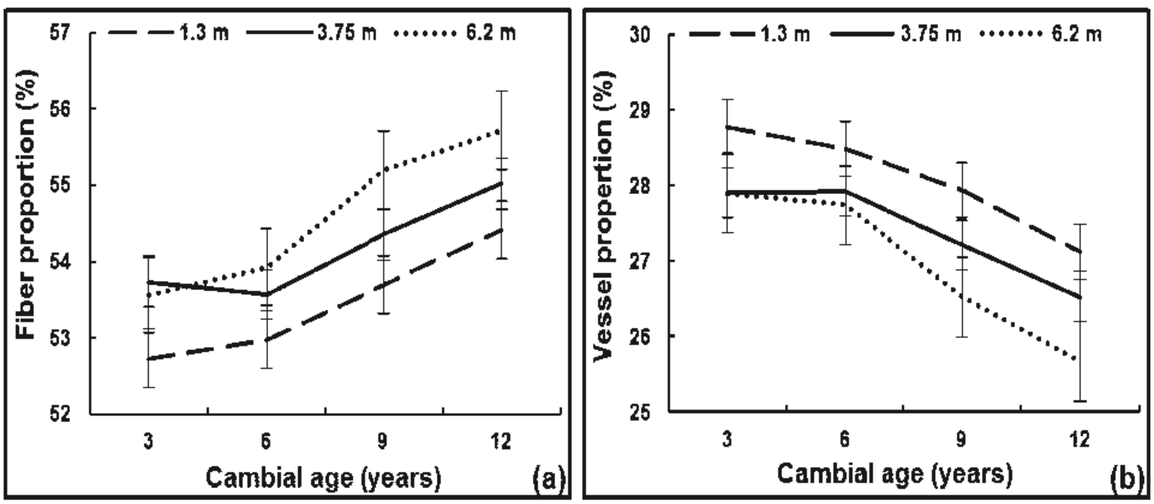

Figure 3.9 Variation and standard error for (a) fiber and (b) vessel proportions with cambial age and tree height in hybrid poplar clones.

Figures 3.9 and 3.10 present the radial variation in wood element proportions. Fiber proportion showed a significant increase from pith to bark for the three sampled heights (Figure 3.9a), whereas vessel proportion showed the inverse trend (Figure 3.9b). Cambial age showed significant variation in both properties, accounting for 2.6% and 4.3% of the total variation in fiber and vessel proportion, respectively (Table 3.3). However, no particular radial pattern of ray proportion was observed. In fact, the age effect on ray proportion was non-significant (Table 3.3). These results contradict those of Isebrands (1972), who found that wood formed in the juvenile crown of eastern cottonwood usually had a lower percentage of vessels than wood in more mature crowns. He also reported a noticeable decrease in the percentage of fibers with increasing distance from the pith and tree height.

Fiber length at all cambial ages increased with increasing tree height (Figure 3.4a). Although significant (α= 5%), the variation in fiber length with tree height was marginal, accounting for less than 0.5% of the total variation (Table 3.3). Fiber width tended to increase with increasing height near the pith but in the outer rings, the opposite trend was observed (Figure 3.4b). The longitudinal variation in fiber width was also marginal. It accounted for less than 2% of the total variation (Table 3.3).

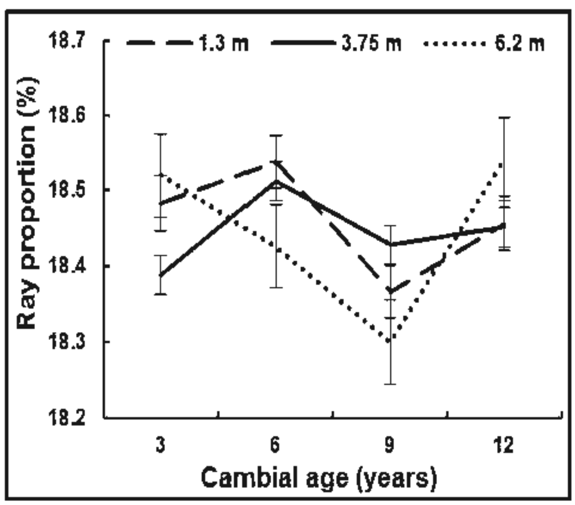

Figure 3.10 Variation and standard error for ray proportion with cambial age and tree height in hybrid poplar clones.

Fiber wall thickness (Figure 3.5), average fiber lumen area (Figure 3.6a), average fiber diameter (Figure 3.6b), and cell wall area (Figure 3.7) increased with increasing tree height. Despite the significant effect of tree height on these properties, the longitudinal variation was marginal, accounting for less than 1.6% of the total variation

(Table 3.3). Panshin and de Zeeuw (1980) found that fiber diameter and wall thickness in hardwoods decreased from the base of the stem to the crown. In the present study, three heights were sampled at 1.3 m, 3.75 m, and 6.2 m, well above the base of the tree crown (data not shown).

The effect of tree height was non-significant on vessel lumen area, and no particular longitudinal variation pattern was found (Figure 3.8a). However, the average vessel diameter decreased with increasing tree height (Figure 3.8b). Although significant, the variation in height accounted for only 1.9% of the variation (Table 3.3).

The longitudinal variation in the fiber, vessel, and ray proportion are shown in Figures. 3.9a, 3.9b, and 3.10, respectively. Ray proportion did not vary with tree height (Figure 3.10). However, fiber proportion increased with increasing tree height, whereas vessel proportion showed the opposite trend. Although statistically significant (α= 5%), these variations accounted for less than 2.5% (Table 3.3) of the total variation, and were also considered marginal. The longitudinal pattern of fiber proportion runs contrary to the study by Isebrands (1972), who found a noticeable decrease in fiber proportion with increasing tree height.

The results on the longitudinal variation in the anatomical properties of hybrid poplar concur with previous studies in poplar clones (Fang and Yang 2003), red alder (Gartner et al. 1997), and several other hardwoods (Panshin and de Zeuuw 1980; Kellison 1981; Zobel and van Buijtenen 1989). Although the variations in some wood anatomical properties with tree height were statistically significant, they were relatively small and considered marginal.

3.6 CONCLUSIONS

This study examined site, clone, and within-tree variations in selected anatomical properties of hybrid poplar clones grown in southern Quebec, Canada. The effect of site on the studied properties was highly significant, and was explained by environmental conditions and site quality. The highly significant clone effect indicated genetic variation in the examined properties. Thus, broad-sense heritability ranged from 0.10 (for average vessel area) to 0.76 (for cell wall area). It would therefore be possible to select superior hybrid poplar clones in terms of desired anatomical properties. Similarly, up to 6.02% genetic gain could be obtained for fiber wall thickness.

The within-tree variation indicated highly significant radial variation in most studied trends. However, the longitudinal variation, although significant in most cases, was marginal and had no practical implications.

3.7 ACKNOWLEDGEMENTS

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CHAPTER IV

VARIATION IN WOOD DENSITY AND RADIAL GROWTH WITH CAMBIAL AGE IN HYBRID POPLAR CLONES[2]

4.1 ABSTRACT

The main objective of this study was to investigate the radial variations in selected wood quality parameters of hybrid poplar clones from Southern Quebec. Wood samples from seven clones of three sites were obtained. Wood density and ring width of cross sections were measured systematically from pith to bark using X-ray densitometry. The analysed traits examined were annual ring density, earlywood density, latewood density, transition density, annual ring width, earlywood width, latewood width, and latewood percentage. Except for latewood percentage, all measured wood traits varied significantly among clones and across sites. The radial pattern of variation of the density traits was characterized by an increase with increasing stem height. Ring width traits gradually decreased with cambial age, whereas latewood percentage remained constant. The heritability values of radial profiles of these traits were more irregular from one ring to the next with a gradual increase towards the older rings.

Keywords: Hybrid poplar, ring density, ring width components, radial variation, heritability.

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[2] Huda, A. A., Koubaa, A., and Cloutier, A. “Variation in wood density and radial growth with cambial age in hybrid poplar clones.” Working paper.

VARIATION DE LA MASSE VOLUMIQUE ET DE LA CROISSANCE RADIALE AVEC L'ÂGE CAMBIAL CHEZ DES CLONES DE PEUPLIER HYBRIDE

4.2 RÉSUMÉ

L'objectif principal de cette étude a été d'examiner les variations radiales avec l'âge cambial de quelques paramètres de la qualité du bois des clones de peuplier hybride du Sud du Québec. Des échantillons de bois de sept clones issus de trois sites expérimentaux ont été prélevés. La masse volumique du bois et la largeur du cerne des sections transversales ont été mesurées systématiquement de la moelle à l'écorce à l'aide du densitomètre à rayon-X. Les caractères analysés ont été les masses volumiques du cerne annuel, l du bois initial, du bois final, au point de transition, les largeurs du cerne annuel, du bois initial et du bois final, et la proportion de bois final. Les résultats indiquent que tous les caractères mesurés ont varié significativement entre les clones à l'exception de la proportion de bois final, et selon les sites. Le patron de variation radiale des masses volumiques étudiées a été caractérisé par une augmentation de la base vers le sommet des tiges. La largeur du cerne annuel et de ses composantes ont progressivement diminué avec l'âge cambial alors que la proportion de bois final est demeurée constante. Les profils d'héritabilité de ces caractères ont été plus irréguliers d'un cerne à l'autre avec une augmentation graduelle en allant vers les cernes plus âgés.

Mots-clés: Peuplier hybride, masse volumique, variation radiale, héritabilité.

4.3 INTRODUCTION

Hybrid poplars are progeny from crosses between trees of two or more species within the genus *Populus*. Hybrid poplars are genetically predisposed to grow faster and have wider adaptability than either parent species. Hybrid crosses also create heterosis (hybrid vigor) in which the progeny has increased performance of traits beyond what is capable by either parents. The majority of hybrid poplar breeding in Canada utilizes three native species: *Populus deltoides* (Eastern cottonwood), *Populus balsamifera* (balsam poplar) and *Populus trichocarpa* (western black cottonwood) and two non-native species: *Populus maximowiczii* (Asian black poplar) and *Populus nigra* (European black poplar) (Demchik et al. 2002).

In Canada, hybrid poplar plantations are of particular interest because short rotation forestry can contribute to a stronger, more stable and renewable supply of fiber. It can also help relieve the harvesting pressure on natural forests. Moreover, on good sites, hybrid poplars grow faster than any other northern temperate region tree. In the past, small industrial plantations of hybrid poplar were established in Canada, from Quebec to British Columbia. According to Messier et al. (2003), the anticipated yields were 14 m^3/ ha.yr on average sites, and 20 m^3/ ha.yr on the best sites of southern Québec in 2003. On the other hand, in the boreal region, the yields were 12 m^3/ ha.yr on the best sites and 10 m^3/ ha.yr on average sites (Messier et al. 2003). Attractive potential yields of hybrid poplar, motivate forest industries to plant hybrid poplar for fiber production in Quebec. As a result, approximately 12 000 ha of fast-growing poplar plantations are managed by industrials, whereas only 1 000 ha were planted by small private landowners in the Province of Quebec (Fortier et al. 2012).

Wood density is considered as the most important property of the wood defining its quality (Bendtsend 1978). Besides, wood density is relatively easy to measure and it influences both the yield and quality of wood fiber products and solid wood products, including the pulp industry (Zobel and Jett 1995). This makes wood density an excellent trait to predict end-use characteristics of wood (Jozca and Middleton 1995; Pot et al. 2002). Previous research found that the density increases with cambial age (Debell et al. 2002; Pliura et al. 2006; Park et al. 2009), whereas others found a decrease value with an increase of age (Yanchik et al. 1983). On the other hand, short rotation plantations for industry produce a large proportion of juvenile wood, characterized by short fiber length and low wood density (Zobel 1984; Balatinecz and Kretschmann 2001).

Most wood property assessments are time consuming and expensive. As a result, tree breeding programs efforts have focused on improving easily measurable traits such as fiber properties and wood density. Knowledge of the variation in wood density and ring width traits is essential for improving wood quality as one of the selection criteria in poplar breeding programs. Previous research showed the existence of wood density variation of hybrid poplar clones mostly at young cambial age (DeBell et al. 2002; Pliura et al. 2006). Since 15 years old trees were available to us, the objectives of this study were to: 1) investigate site and clonal variations of specific wood traits; 2) examine radial patterns of specific wood traits of hybrid poplar clones grown in southern Quebec. The information obtained from this study on wood density and its variation by clone, and cambial age will be important to tree breeders to improve the wood quality for different end uses.

4.4 MATERIALS AND METHODS

4.4.1 Study area

The materials used in this study were collected from three hybrid poplar clonal trials established by the *Direction de la recherche forestière, Ministère des Ressources naturelles du Québec* (Research branch at Quebec's ministry of natural resources) between 1991 and 1995 (Table 4.1). The trial sites are located in Pointe-Platon

(46°40'N 71°51'W), Saint-Ours (45°54'N 73°09'W), and Windsor (45°42'N 71°57'W) in southern Quebec, Canada (Figure 4.1). Trees for hybrid clone trials were planted at the Saint-Ours and Windsor sites in 1993, and in 1991 at the Pointe-Platon site (Table 4.2). Trees for clone DNxM-915508 were obtained from a 1995 trial at the Pointe-Platon site (Table 4.2).

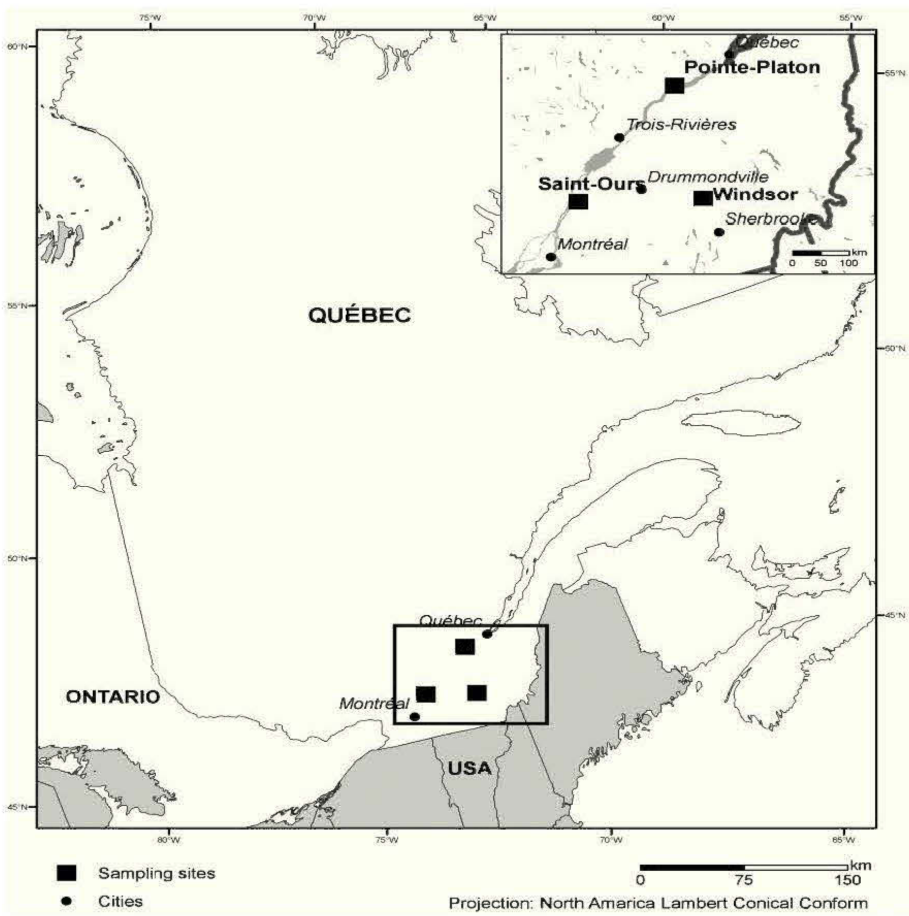

Figure 4.1 Map of sampling sites located in the southern part of the province of Quebec, Canada.

Table 4.1 Studied hybrid poplar clones.

Clone	Hybrid	Female parent	Male parent	Note
DxN-131	*Populus deltoides* × *P. nigra*	*P. deltoides*	*P. nigra* 'Italica' as the putative father	A natural hybrid selected from the Montréal area, Québec
TxD-3230	*P. trichocarpa* × *P. deltoides* Syn.: *P.* × *generosa* 'Boelare'	*P. trichocarpa* 'Fritzi Pauley' (from Washington)	*P. deltoides* S.1-173 (from a cross between *P. deltoides* V.5 from Iowa and V.9 from Missouri)	Clone S.910-8 from Belgium. Cultivar 'Boelare'
DxN-3565	*P. deltoides* × *P. nigra* Syn.: *P.* × *canadensis*	*P. deltoides* S.513-60 (from a cross between *P. deltoides* V.5 from Iowa and V.12 from Illinois)	*P. nigra* S.157-3 (from a cross between *P. nigra* V.220 from Italy and V.450 from Belgium)	Family/tree from Belgium: 78.017/164
DxN-3570	*P. deltoides* × *P. nigra*	*P. deltoides* S.513-60	*P. nigra* S.157-4 (from a cross between *P. nigra* V.220 from Italy and V.450 from Belgium)	Family/tree from Belgium: 78.018/204
DxN-3586	*P. deltoides* × *P. nigra*	*P. deltoides* S.513-60	*P. nigra* S.132-4 (from a cross between *P. nigra* V.441 from Italy and V.450 from Belgium)	Family/tree from Belgium: 78.016/156
DxN-4813	*P. deltoides* × *P. nigra*	*P. deltoides* 226 (from Trois-Rivières, Québec)	*P. nigra* 'Italica'	A controlled cross selected from Québec
DNxM-915508	(*P. deltoides* × *P. nigra*) × *P. maximowiczii*	*P. deltoides* × *P. nigra* (from Québec City)	*P. maximowiczii* (from Japan)	A controlled cross selected from Québec

* Trees for the clone DNxM-915508 at Pointe-Platon were sampled from another trial PLA16495.

The Saint-Ours site is located in the Champlain marine deposit, where the soil consists of a silty clay deposit (40% clay). The two other sites consist of sandy loam soil (Pliura et al. 2007). All sites were originally used for agriculture, but had been abandoned for several years before the hybrid poplar clones were planted. All tree plantation trial sites had a randomized block design with ten blocks each. A systematic thinning was carried out in 1995 at the Pointe-Platon site and in 1996 at Windsor and Saint-Ours sites. Early in 2006, a thinning operation was carried out removing two-third of the trees from these plantation sites.

Table 4.2 Site characteristics of hybrid poplar clonal trials.

	Site		
Characteristics	Pointe-Platon	Saint-Ours	Windsor
Trial number	PLA01791	STO10893	WIN10593
Establishment year	1991*	1993	1993
Geographic coordinates	$46^0$40'N, $71^0$51'W	$45^0$54'N, $73^0$09'W	$45^0$42'N, $71^0$57'W
Elevation (m)	60	15	260
Surface deposit	Sandy loam soil	Champlain marine deposit with silty clay soil.	Sandy loam soil
Initial spacing	1 m x 3 m	1.2 m x 3.5 m	1.5 m x 3.5 m
Spacing after 1st Thinning	2 m x 3 m	2.4 m x 3.5 m	3 m x 3.5 m

* DNxM-915508 – 1995.

4.4.2 Sample collection and preparation

Five trees of each clone were randomly sampled at each site, for a total of 105 trees. Disks 10 cm thick were collected from each tree from breast height upward at 2.5 m intervals and used for anatomical analysis (Figure 4.2). Disc edges were coated with wax to maintain wood moisture content and to prevent decay and other environmental alterations. Samples were then transported to the Renewable Materials Research Centre (Centre de recherche sur les matériaux renouvelables, Université Laval, Quebec, Canada) and kept frozen until test samples preparation. A 2.5 cm wide slab was cut horizontally along the diameter of each disc (bark to bark passing through the pith) and then conditioned at 20°C and 60% relative humidity for several weeks until an equilibrium moisture content of 12% was reached.

To determine wood density by X-ray densitometry, thin strips approximately 20 mm wide and 1.57 mm thick (Figure 4.2) were sawn from each disk (bark to bark passing through the pith). Samples were then conditioned to 12% equilibrium moisture content (EMC) before measurement.

Ring and wood density components were measured using a QTRS-01X Tree-Ring X-Ray Scanner (QMC, Knoxville, Tennessee). A linear resolution step size of 20 μm was used for X-ray densitometry. The density calculation required knowledge of the mass attenuation coefficient (cm^2/g) of the wood. Calibration to the appropriate mass attenuation coefficient was conducted using a set of 25 radial strips from cores. The 25 mass attenuation coefficients were averaged to provide the final value used to calculate wood density. In order to run the QMS X-ray densitometer, some values need to be known such as wood moisture content, wood sample dimensions and age, and target density. Target density was measured at 10.20% moisture content. After conditioning, rings from pith to bark were scanned in air-dried condition.

From the wood density profiles, annaul ring density (ARD), earlywood density (EWD), and latewood density (LWD) were calculated for each annual ring. Demarcation between earlywood and latewood was determined for each annual ring by the maximum derivative method using a six-degree polynomial (Koubaa et al. 2002). The density at the demarcation point on the polynomial curve was defined as the transition density (TD). From the same density profiles, annual ring width (ARW), earlywood width (EWW), and latewood width (LWW) were determined. Latewood proportion (LWP) was calculated as the ratio of latewood width to annual ring width. During scanning, precautions were taken to eliminate incomplete or false rings and rings with compression wood or branch tracers. False and missing rings were detected by visually cross-dating ring width chronologies and numerically verified using COFECHA software (Holmes 1983). A total of 315 strips were analyzed by X-ray densitometry.

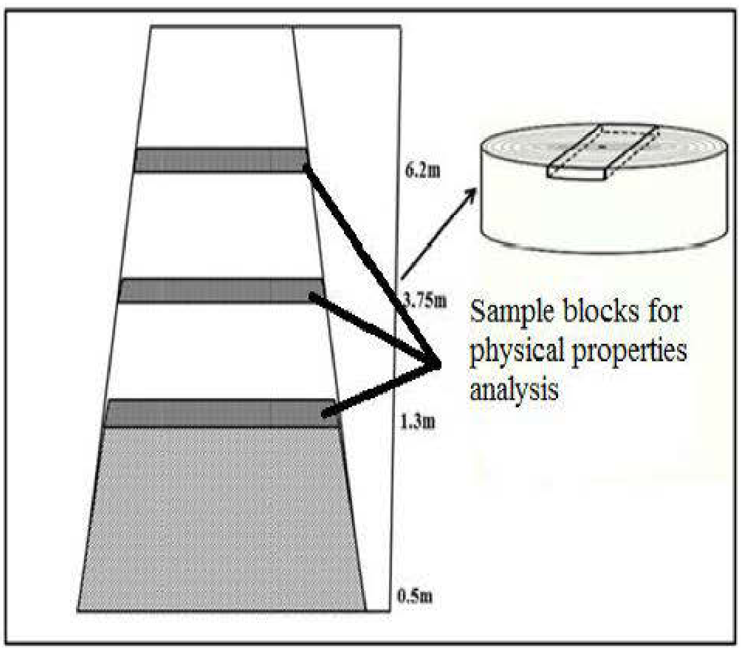

Figure 4.2 Schematic diagram of the sampling procedure for the analysis of hybrid poplar wood anatomical properties.

4.4.3 Statistical analysis

The SAS® statistical package, version 9.3 (SAS 2010) was used for all statistical analyses. Normality and homogeneity of variance for residuals were tested using UNIVARIATE procedure. Data transformations were not considered necessary to satisfy the assumptions of the analysis of variance and other analyses. Analyses of variance were performed using PROC GLM with Type III (partial sums of squares) estimates to assess the relative effect of each source of variation. Analyses were performed among and within sites and clones. The variance in anatomical properties variables among sites was analyzed using the following mixed linear model (Eq. 4.1),

$$X_{ijlmn} = \mu + S_i + C_j + (S \times C)_{ij} + A_l + H_m + (A \times H)_{lm} + \varepsilon_{ijlmn} \quad (4.1)$$

where X_{ijlm} is an observation on the l^{th} age and m^{th} height of the j^{th} clone from the i^{th} site; μ is the overall mean; A_l, H_m, and $(A \times H)_{lm}$ are the fixed effects and their interactions, respectively; S_i is the fixed effect due to the i^{th} site; C_j is the fixed effect due to the j^{th} clone; $(S \times C)_{ij}$ is the interaction between site and clone; and ε_{ijlm} is the random error. Some F ratios involved more than one mean square in the denominator and were tested with approximate degrees of freedom. Tree effects and the site-clone-age interaction were not considered in the analysis, as preliminary testing showed negligible contribution to the total variance. Furthermore, in many cases, the variance component for these terms could not be estimated or was not significant.

Tukey's Studentized Range (HSD) was used to test the statistical significance (at $p<0.05$) of differences among means of clones for each site (PROC GLM, SAS). The variance components were estimated in the model using VARCOMP with the restricted maximum likelihood method (REML) and expressed as a percentage (VAR).

The broad-sense heritability or clonal heritability (H_C^2) was calculated from the variance estimates, as follows (Eq. 4.2) (Becker 1984; Falconer and Mackay 1996):

$$H_C^2 = \sigma_C^2 / \sigma_P^2 \quad (4.2)$$

where σ_C^2 and σ_P^2 are the genotypic and phenotypic variance, respectively. Phenotypic variance (σ_P^2) was calculated as shown in Eq. (4.3).

$$\sigma_P^2 = \sigma_C^2 + \sigma_{(s \text{ x } c)}^2 + \sigma_e^2. \quad (4.3)$$

where σ_C^2, $\sigma_{(s \text{ x } c)}^2$ and σ_e^2 are the variance of clones, interection between site and clones and residuals effects, respectively.

4.5 RESULTS AND DISCUSSION

4.5.1 Analysis of variance

F values for variance components from the analysis of variance are presented in Table 4.3. The results show that site effects were statistically significant for all properties (Table 4.3). The site effect accounted for 2.5% to 6.8% of the total variation, depending on the examined property (Table 4.3). These results are in good agreement with Pliura et al. (2005; 2006) and Zhang et al. (2003) results reported for wood density. They reported significant site effects on wood properties, whereas Peszlen (1998) did not find any site effect on wood density. Among all examined properties, site effect on latewood width was low (2.5%), but high on latewood density (6.8%). This effect indicates that site has significant effects with low variance components. Similarly, low variance of wood density traits and growth ring traits were found in studies of coniferous species (Hylen 1999; Koubaa et al. 2005; Park et al. 2009).

Table 4.3 Results of the analysis of variance of wood density component and fiber characteristics of hybrid poplar clones (F values and variance components).

Source of variation	Site	Clone	Clone x site	Height	Cambial age	Height x Cambial age
Characteristic	F value					
Annual ring density (kg/m³)	105.6**	46.0**	3.9**	22.7**	50.8**	1.7**
Earlywood density (kg/m³)	63.5**	42.7**	3.1**	18.4**	50.8**	2.2**
Latewood density (kg/m³)	125.0**	19.3**	6.8**	8.7*	11.5**	0.5ns
Transition density (kg/m³)	109.1**	23.7**	4.01**	8.5**	20.9**	1.0ns
Annual ring width (mm)	45.6**	22.9**	2.4**	37.2**	13.2**	1.0ns
Earlywood width (mm)	46.5**	16.4**	1.7ns	32.2**	14.9**	1.4ns
Latewood width (mm)	9.7**	8.4**	2.1*	8.4**	2.0**	1.1ns
Latewood percentage (%)	7.5**	0.5ns	1.5ns	1.2ns	3.1**	1.7*
	Variance components (%)[a]					
Annual ring density (kg/m³)	5.3	7.4	1.0	1.1	12.6	0.6
Earlywood density (kg/m³)	3.3	5.0	0.8	0.9	13.1	1.0
Latewood density (kg/m³)	6.8	7.4	2.2	0.5	3.0	0.0
Transition density (kg/m³)	5.9	9.2	1.2	0.4	5.5	0.0
Annual ring width (mm)	2.8	3.0	0.6	2.2	3.9	0.0
Earlywood width (mm)	2.9	2.1	0.3	1.9	4.4	0.3
Latewood width (mm)	2.5	4.6	2.5	2.1	1.6	0.3
Latewood percentage (%)	3.7	5.2	0.7	3.2	4.5	6.1

*Significant at $P<0.05$ probability level. **Significant at $P<0.01$ probability level. [ns] Non-significant at $P<0.05$ probability level. [a] Variance component as a percentage of the total variance.

The analysis of variance (Table 4.3) indicated significant clonal variation in the wood density and ring width traits of hybrid poplar clones wood except for latewood percentage. The significant differences observed among clones for the studied properties are an indication of a clonal effect on wood properties. As indicated by the variance component results, the clone effect were either low or medium, ranging from 2.1% to 9.2%, depending on the examined property (Table 4.3). With respect to wood densities, clonal variation accounted for 9.2% of the total variance in transition density followed by annual ring density (Table 4.3).

Differences among clones were also significant for ring width components, as shown in Table 4.3. The highest interclonal variation was observed for latewood percentage (5.2%), whereas earlywood width (2.1%) showed significant clone effects but low variation (Table 4.3). These interclonal low variations are in good agreement with what was reported by Beaudoin et al. (1992). The clonal variation in wood density was in good agreement with previous reports on poplar species (Zhang et al. 2003; Pliura et al. 2006).

In this study, statistically significant G x E interaction corresponding to clone x site effects were observed for most wood density and ring component properties studied expect earlywood width and latewood percentage. Although this effect was significant for most properties, it accounted for a relatively small percentage of the total variation (0.3% to 2.4%). In other study of poplar species, significant clone x site interaction for wood density were not observed (Farmer and Wilcox 1968; Nepveu et al. 1985). This small effect of the G x E interaction was probably due to the small differences in growth conditions or due to the low number of clones used in this study, and to large residual variance for studied properties; therefore, site x clone interaction observed in this study might have a certain limit.

Table 4.4 Least squares mean for selected cambial age for each tree height and multiple comparison tests.

Height (m)	Wood density components							Ring width components						
	Cambial age 1*	Cambial age 3	Cambial age 6	Cambial age 9	Cambial age 12	Cambial age 15	Overall average	Cambial age 1	Cambial age 3	Cambial age 6	Cambial age 9	Cambial age 12	Cambial age 15	Overall average
	Annual ring density (kg/m^3)							Annual ring width (mm)						
1.3	421^{a}	400^{b}	413^{b}	435^{b}	468^{a}	458^{a}	433	9.5^{a}	7.4^{a}	7.0^{a}	8.3^{a}	7.1^{a}	6.7^{a}	7.9
3.75	421^{a}	399^{b}	423^{ab}	442^{ab}	470^{a}	449^{a}	436	8.2^{b}	7.4^{a}	7.6^{b}	7.2^{b}	5.9^{b}	6.1^{a}	7.2
6.2	436^{a}	414^{a}	440^{a}	459^{a}	458^{a}	453^{a}	446	8.1^{b}	7.3^{b}	7.3^{b}	7.0^{bc}	6.3^{ab}	6.3^{a}	7.0
	Earlywood density (kg/m^3)							Earlywood width (mm)						
1.3	391^{a}	377^{b}	393^{b}	418^{b}	453^{a}	437^{a}	414	6.2^{a}	4.9^{a}	6.0^{a}	5.6^{a}	4.7^{a}	4.2^{a}	5.3
3.75	396^{a}	377^{b}	403^{ab}	423^{b}	450^{a}	428^{a}	417	5.3^{ab}	5.2^{a}	5.2^{b}	4.7^{b}	3.7^{b}	3.8^{a}	4.8
6.2	416^{a}	395^{a}	422^{a}	442^{a}	433^{ab}	433^{a}	427	5.9^{ab}	4.9^{a}	4.7^{c}	4.4^{b}	4.1^{ab}	4.1^{a}	4.6
	Latewood density (kg/m^3)							Latewood width (mm)						
1.3	506^{a}	456^{a}	470^{a}	482^{a}	500^{a}	495^{a}	481	3.3^{a}	2.5^{a}	3.0^{a}	2.7^{a}	2.4^{a}	2.5^{a}	2.7
3.75	495^{a}	457^{a}	477^{a}	482^{a}	506^{a}	489^{a}	482	2.9^{ab}	2.2^{a}	2.4^{ab}	2.5^{a}	2.3^{a}	2.3^{ab}	2.4
6.2	519^{a}	465^{a}	481^{a}	493^{a}	504^{a}	490^{a}	491	2.3^{b}	2.4^{a}	2.6^{ab}	2.6^{a}	2.3^{a}	2.4^{a}	2.4
	Transition density (kg/m^3)							Latewood percentage (%)						
1.3	471^{ab}	419^{ab}	435^{a}	455^{a}	479^{ab}	466^{a}	452	34.8^{a}	32.7^{a}	33.0^{a}	32.2^{a}	35.1^{a}	36.7^{a}	33.3
3.75	462^{ab}	423^{a}	443^{a}	453^{a}	495^{a}	458^{a}	455	34.4^{a}	30.0^{a}	33.1^{a}	35.8^{a}	37.9^{a}	36.2^{a}	33.9
6.2	492^{a}	436^{a}	452^{a}	470^{a}	468^{b}	459^{a}	463	26.6^{b}	32.3^{a}	35.6^{a}	36.8^{a}	34.6^{a}	37.7^{a}	34.4

* Cambial age is selected to maintain synchronisation with other properties measures in this research

F value and variance components from the analysis of variance for the height, cambial age, and height x cambial age interaction of percentage of ring densities and ring width components are presented in Table 4.3. The results show that height effects were statistically significant for all properties except latewood percentage (Table 4.3). The height effect accounted for 0.4% to 3.2% of the total variation, depending on the examined property (Table 4.3). On the other hand, cambial age effects were statistically significant for all properties with a variation range of 1.6% to 12.6% of the total variation of examined properties. Most of the properties of height x cambial age interaction were not significant and contributed minimally to the total variation except latewood percentage.

4.5.2 Radial variation in ring density components

Previous studies on radial variation in wood density components were generally based on samples taken at breast height. In this study, we investigated the variation in wood density components at three different commercial heights from pith to bark at a tree age of 15 years.

At selected cambial age, most of the properties were not statistically significant for each tree height (Table 4.4). All ring density components decrease from the pith to age 4, then increase to age 14 (Figures 4.3, 4.4, 4.5, 4.6). This variation pattern is in good agreement with previous reports on trembling aspen (Yanchuk et al. 1983), hybrid poplar clones (Beaudoin et al. 1992; DeBell et al. 2002).

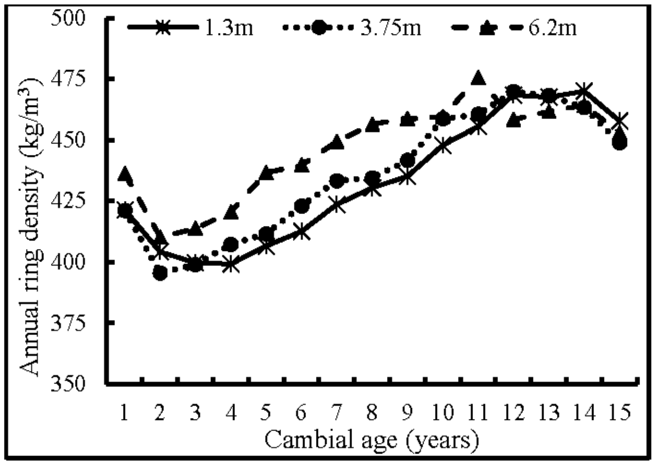

Figure 4.3 Radial pattern of annual ring density for selected stem height with cambial age.

Annual ring density (ARD) decreased first from the pith to age 3, then increased towards the age 15 (Figure 4.3; Table 4.4). Similar variation patterns were shown at the three height positions. ARD at all cambial ages increased with increasing tree height (Figure 4.3). This variation pattern is in good agreement with previous reports on poplar species (Yanchuk et al. 1983; DeBell et al. 2002). However, at all height positions, ARD showed highest density at age 12. The variation in ARD with cambial age accounted for 12.6% of the total variation (Table 4.3).

Earlywood density (EWD) followed a similar variation pattern (Figure 4.4). EWD was about 19 kg/m^3 lower than ARD at 1.3 m, 3.75 m and 6.2 m height. Analysis of variance confirmed that the effect of cambial age on EWD was significant, accounting for 13.2% of the total variation. On the other hand, analysis of variance for the effects of height was significant for both ARD and EWD, but variations are marginal (Table 4.3).

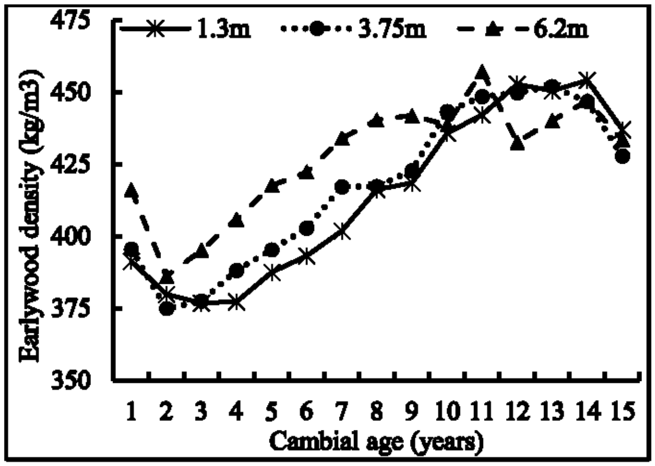

Figure 4.4 Radial pattern of earlywood density for selected stem height with cambial age.

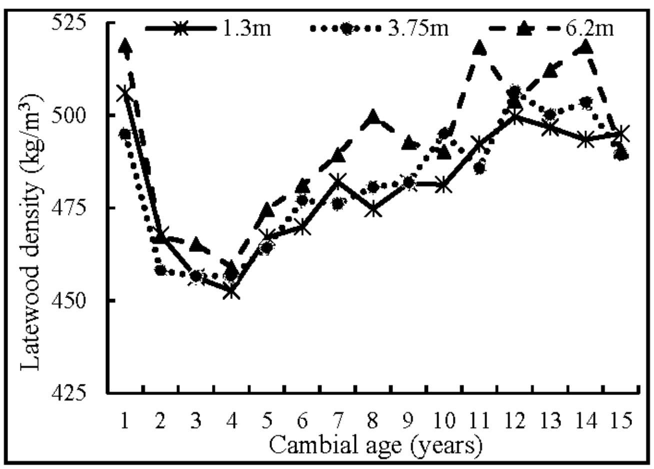

Figure 4.5 Radial pattern of latewood density for selected stem height with cambial age.

The radial variation in latewood density (LWD) accounted for 3% of the total variation, and was characterized by a rapid decrease from pith to age 4, then increasing outwards (Figure 4.5). The same pattern was obtained for the three sampled heights.

Tree height of 6.2 m showed the highest LWD for all cambial ages (Figure 4.5). LWD was about 48 kg/m^3, 46 kg/m^3, and 45 kg/m^3 higher than ARD at 1.3 m, 3.75 m and 6.2 m height, respectively. Like other wood densities, transition density (TD) followed a similar pattern (Figure 4.6). Analysis of variance confirmed that the effect of cambial age on TD was significant accounting for 5.5% of the total variation, whereas, height effect was marginal (Table 4.3). At selected cambial ages the TD did not show any significant difference at the three different heights (Table 4.4).

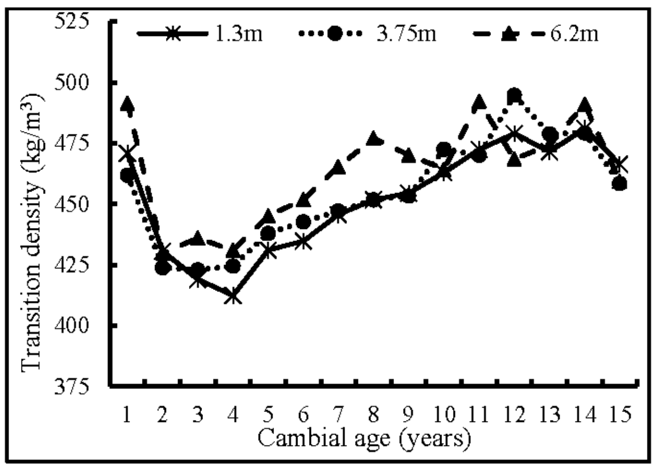

Figure 4.6 Radial pattern of transition density for selected stem height with cambial age.

The variation at different stem heights largely explained the significant interaction between height and cambial age for all studied ring density traits. Initial decrease in ring density is associated with the presence of live branches, which remain photosynthetically active (Koubaa et al. 2005). Effects of this phenomenon result in extended earlywood production. Beaudoin et al. (1992) found that wood density of hybrid poplar clones tended to be high at the bottom of the tree, decreased at its minimum at mid-height and then increase near the merchantable stem height. Whereas, Karki (2001) found that the wood density of aspen was high at the top of the crown and in the outer rings near the bark. Many researchers also reported that wood density increased with cambial age (Boyce and Kaiser 1961; Yanchuk et al. 1983; DeBell et al. 2002). However, wood near the pith contains juvenile wood known to be of lower density than mature wood (Dadswell 1958; Zobel and Buijtenen 1989). Ring density changes observed in the present study may have been due to the fact that the trees sampled were still in the juvenile stage (Huda et al. 2011a, 2012, 2014). Besides, ring density followed a trend similar to that of anatomical properties of the same hybrid poplar clones reported by Huda et al. (2012). This is consistent with the fact that density is mainly determined by the fiber wall thickness, fiber proportion and cell wall percentage. Moreover, aging of the cambium also plays an important role in the radial variation of ring density (Panshin and de Zeeuw 1980). On the other hand, the percentage and size of fibers and vessels, as well as the distribution of tension wood maybe the major underlying causes of wood density variation with height (Beaudoin et al. 1992), as wood density varies with fiber and vessel proportion and tension wood (Huda et al. 2011a, b, 2014).

At selected cambial ages, most of the ring width traits were not statistically significant for each tree height (Table 4.4). Ring width components showed a decreasing trend with increasing cambial age (Figures 4.7, 4.8, 4.9). This variation pattern is in good agreement with previous reports on trembling aspen (Yanchuk et al. 1983), poplar (DeBell et al. 2002), and with other conifer tree species such as jack pine (Park et al. 2009).

Annual ring width (ARW) decreased first from the pith to age 3, and then increased until age 7 and then decreased with increasing cambial age. (Figure 4.7; Table 4.4). Similar variation patterns occurred at the three height positions. Average ring width at all cambial ages decrease with increasing tree height (Figure 4.7). At height 1.3m, ARW showed higher values for all cambial ages. The variation in ARW with cambial age accounted for 3.9% of the total variation (Table 4.3).

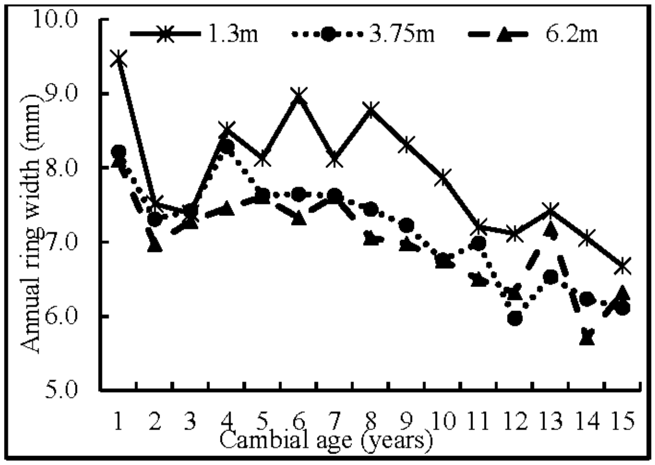

Figure 4.7 Radial pattern of annual ring width for selected stem height with cambial age.

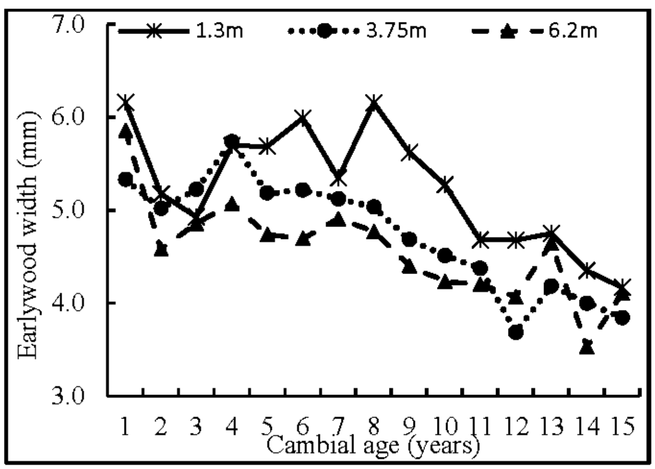

Figure 4.8 Radial pattern of earlywood width for selected stem height with cambial age.

Earlywood width (EWW) followed a variation pattern similar to ARW (Figure 4.8). Analysis of variance confirmed that the effect of cambial age on EWW was significant, accounting for 4.4% of the total variation. On the other hand, analysis of variance for the effects of height was significant for both ARW and EWW, but variations were low (Table 4.3). These variation patterns (Figures 4.7, 4.8) are in good agreement with previous reports on poplars (Yanchuk et al. 1983; Beaudoin et al. 1992; DeBell et al. 2002).

Latewood width (LWW) decreases rapidly from pith until the third ring and then increases between cambial age four to seven, and finally decreases slowly but almost constantly towards bark at 1.3 m and 3.75 m height (Figure 4.9). Latewood width showed highest value near the pith. On the other hand, at 6.2 m height LWW increased slowly until cambial age 6 and then showed a slow decrease outwards. The radial variation in LWW accounted for 2.1% and 1.6% of the total variation for height and cambial age, respectively (Table 4.3).

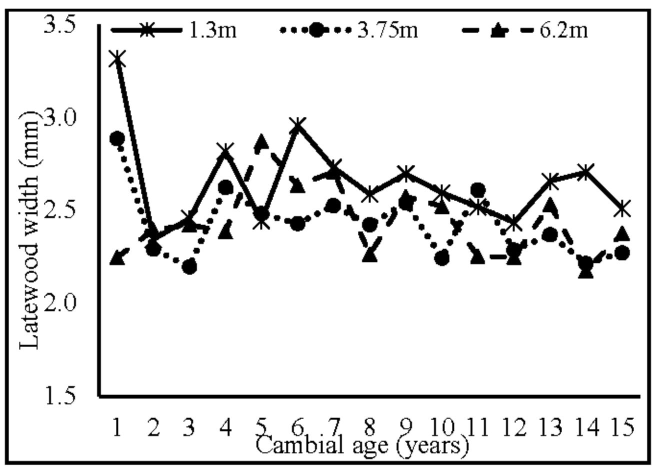

Figure 4.9 Radial pattern of latewood width for selected stem height with cambial age.

The radial variation of latewood proportion (LWP) showed an increasing trend with cambial age at all heights (Figure 4.10). As hybrid poplar is a fast growing species, this pattern of variation of LWP is due to its high proportion of juvenile wood at early age. There was no significant variation among selected cambial ages at three heights for LWP (Table 4.4).

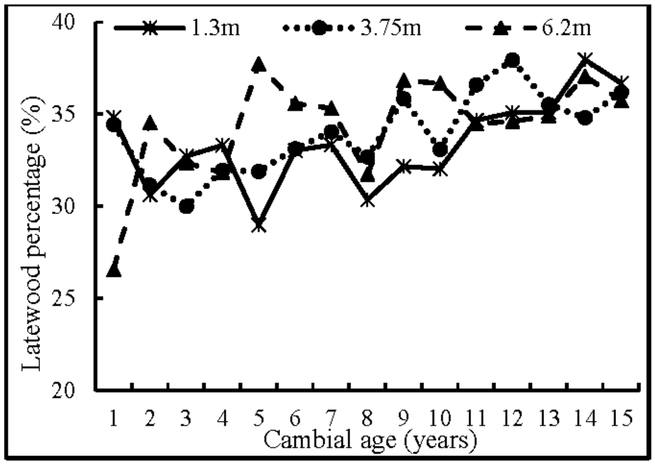

Figure 4.10 Radial pattern of latewood percentage for selected stem height with cambial age.

Hybrid poplar clones are known to be among the fastest growing trees in North America. Fast growth wood formation causes the production of fibers with thin cell walls and of large diameters. Besides, cambial age plays an important role in the radial variation of ring width and latewood formation (Panshin and de Zeeuw 1980). As tree age increases, fiber cell wall thickness increases (Huda et al. 2012) and cell diameter decreases (Larson 1960). As a result, earlywood production is greater in the initial stages of the tree growth. This results in a decrease in ring width and increase in latewood percentage with cambial age, and this explains the patterns of annual ring width, earlywood width, latewood width, and latewood percentage found in the present study.

4.5.3 Age trend of heritability in ring density components

Heritability estimates for ring densities showed less fluctuation with cambial age except transition density (Figure 4.11). The heritability of annual ring density diminished from pith to cambial age 2 (0.42), and increased from cambial age 3 to 15 (Figure 4.11). The highest heritability estimate was recorded at cambial age 11 (0.81).

Heritability for earlywood density also showed similar trend as annual ring density (Figure 4.11). EWD decreased from pith to ring 3, and increased from ring 4 to ring 12 (0.72), where it reached the highest value. Heritability for latewood density also had a similar radial trend with cambial age. Zobel and Jett (1995) found in loblolly pine that heritability has a clear tendency to increase with cambial age. There was a large decrease of heritability from pith (0.75) to ring 3 (0.51), followed by an increase to reached the highest value at cambial age 11 (0.84). In contrast, heritability for transition density showed a high fluctuation with cambial age (Figure 4.11).

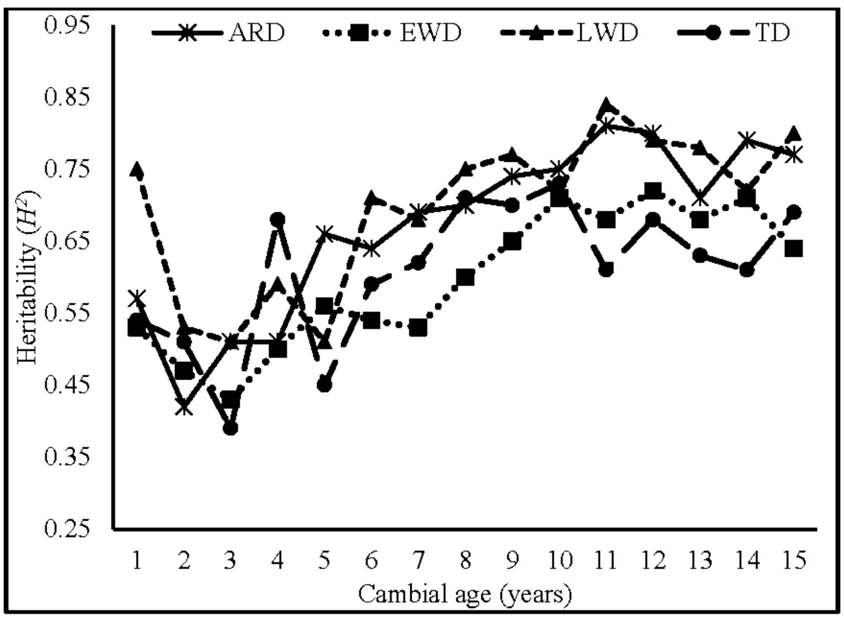

Figure 4.11 Radial pattern of heritability (H^2) for annual ring density (ARD), earlywood density (EWD), latewood density (LWD) and transition density (TD) with cambial age.

Heritability estimates for ring width components showed high fluctuation with cambial age except for latewood proportion (Figure 4.12). The heritability of ARW increased from pith to cambial age 3 (0.41), and showed the highest value at ring 10 (0.50) (Figure 4.12). Heritability for EWW showed a trend similar to EWD, although the heritability value was much lower in EWW (Figure 4.12). Latewood width showed the lowest value at ring 8 (0.18) and then increased towards the bark (Figure 4.12). Latewood percentage showed a very slow and constant increase towards the bark. Among all the ring density traits, LWP showed a lowest heritability. This is likely due to the large environmental impact on LWP (Louzada and Fonseca 2002).

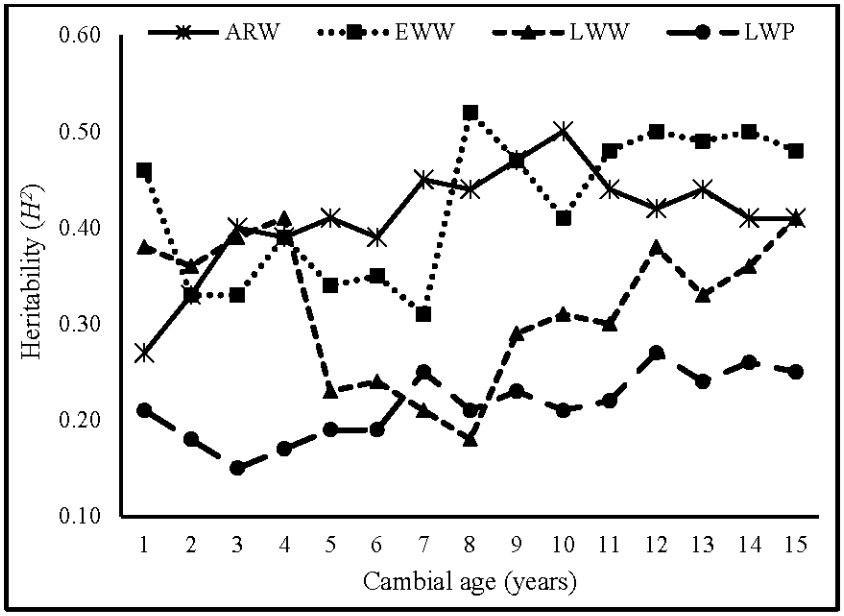

Figure 4.12 Radial pattern of heritability (H^2) for annual ring width (ARW), earlywood width (EWW), latewood width (LWW) and latewood percentage (LWP) with cambial age.

There is no research on age trend of heritability for poplar wood. Although there have been few studies published on age trend of heritability for wood density in conifers (Nicholls 1967a, 1967b; Zobel and Jett 1995; Kumar and Lee 2002; Zamudio et al. 2002). Nicholls (1967a) found a systematic change in heritability with cambial age for wood density. In this study, the trends we observed in heritability with cambial age are consistent with previous findings (Kumar and Lee 2002; Zamudio et al. 2002). Low genetic control for ring width traits has been observed in our study. A similar finding was also reported for pine species by Zamudio et al. (2005). However, our results show higher heritability values for both ring density and ring width traits than those reported for conifers. Moreover, results in our study appear to be more uniform because of multiple sample sites. This information is important because it is not possible to delay the tests till rotation age, so the efficiency of the tree breeding programmes really depends on the capacity to be able to predict mature wood characteristics at a young age

4.6 CONCLUSIONS

This study examined radial variation in ring density traits of hybrid poplar clones grown in southern Quebec. Significant variation was observed for sites and clones. Variation in radial pattern were mostly systematic for all ring density traits. Ring density has an increasing trend with cambial age at all tree heights while ring width traits showed decreasing trends. Ring density traits were under low to moderate genetic control near the pith, and moderate to high with increasing cambial age. Variation of heritability with cambial age clearly showed the potential impact of time for selection efficiency for end uses. However, a better experimental design and further analyses are needed to define the maximum point of selection efficiency.

4.7 ACKNOWLEDGEMENTS

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CHAPTER V

VARIATION OF THE PHYSICAL AND MECHANICAL PROPERTIES OF HYBRID POPLAR CLONES[3]

5.1 ABSTRACT

The physical and mechanical properties of poplar clones largely determine their suitability for various end uses, especially for high value-added applications. The main objective of this study was to determine the clonal variations of selected physical and mechanical properties of seven hybrid poplar clones grown at three sites in southern Quebec, Canada. Five trees per clone were randomly sampled from each site for wood properties measurements. Site had a significant effect on all measured properties except radial shrinkage. All properties of hybrid poplar wood showed significant interclonal variation, indicating the possibility of identifying clones with superior wood properties, especially for density, flexural modulus of rupture, and ultimate crushing strength. High heritability values for the studied properties indicated that these properties are under moderate to high genetic control. The genetic gain for these wood properties ranged from 2.0% to 13.5%.

Keywords: Hybrid poplar clones, Clonal variation, Physical properties, Mechanical properties, Heritability, Genetic gain.

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5.2 RÉSUMÉ

Les propriétés physiques et mécaniques de clones de peuplier hybride déterminent en grande partie leur aptitude à diverses utilisations finales, spécialement pour des applications à haute valeur ajoutée. L'objectif principal de cette étude était d'évaluer la variation clonale des propriétés physico-mécaniques sélectionnées de sept clones de peuplier hybride cultivés en trois sites au sud du Québec, Canada. Cinq arbres par clone ont été échantillonnés aléatoirement dans chaque site pour les mesures des propriétés du bois. Le site a eu un effet significatif sur toutes les propriétés mesurées à l'exception du retrait radial. Toutes les propriétés du bois de peuplier hybride ont montré une variation inter-clonale significative indiquant la possibilité de mettre en évidence les clones avec des propriétés du bois améliorées, spécialement pour la masse volumique, le module de rupture en flexion et la résistance à l'écrasement. Les valeurs élevées d'héritabilité pour les propriétés étudiées indiquent que ces propriétés sont sous contrôle génétique modéré à élevé. Le gain génétique pour toutes les propriétés du bois a varié de 2.0% à 13.5%.

Mots-clés: Peuplier hybride, Variation clonal, Propriétés physiques, Propriétés mécaniques, Héritabilité, Gain génétique.

5.3 INTRODUCTION

Hybrid poplar has received considerable attention for its high productivity compared to other Canadian hardwood and softwood species. It has been widely planted throughout North America due to its fast growth rate and easy hybridization. Hybrid poplar yield reaches up to 15 m^3/ha·yr, much higher than the 1.7 m^3/ha·yr current average yield in Canadian natural forests (Arseneau and Chui 2003). Perinet (1999) reported yields ranging from 8 to 12 m^3/ha·yr in Quebec. The maximum yield observed is 40 m^3/ha·year in Southern Quebec, with 2222 stems/ha (Fortier et al. 2010). Mean annual increment in hybrid poplar plantations at age 7 to 15 years has also been reported to be over 2.6 times higher than that of unmanaged natural stands at age 55 years in southern Ontario (Zsuffa 1973).

Hybrid poplars are hybridizations of two or more species within the genus *Populus*, which, as one of the fastest growing temperate trees, has considerable commercial value (Zsuffa et al. 1996). Hybrid poplars have been genetically improved through selection and crossbreeding to improve growth rate, trunk form, adaptability, and disease resistance (Hernández et al. 1998; Riemenschneider et al. 2001; Zhang et al. 2003; Pliura et al. 2007).

For many years the selection criteria were mainly good tree and growth characteristics, resistance to pest and disease, adaptability, and low levels of growth stress. Despite the need to include wood properties in breeding programs, basic wood properties were not seriously considered so far. Since timber is the final objective of genetic tree improvement program, studies on wood properties of clones appear to be of far greater interest (Nocetti 2008). This increase has revealed a need for the selection and improvement of planting materials, to be used in the production of high quality timber. Thus, wood properties of hybrid poplar clones and their end-use potential have been taken into account in breeding programs (Zhang et al. 2003).

The fast growth of hybrid poplar is generally associated with low wood properties, especially wood density and mechanical properties (Beaudoin et al. 1992; Hernández et al. 1998). Wood basic density of hybrid poplar in North America ranges from 300 to 390 kg/m^3, and standing trees have high moisture content, typically almost 100%, with only minor differences between sapwood and heartwood (Balatinecz et al. 2001). Currently, poplar wood is primarily used to supply fiber for pulp and paper production and engineered wood products such as oriented strand board (OSB), laminated veneer lumber (LVL), and structural composite lumber (Balatinecz et al. 2001). Hybrid poplar wood is particularly well suited for these uses (Mansfield 2007).

Mechanical properties are controlled by physical and anatomical characteristics such as wood density, grain angle, fiber length, and microfibril angle of the S2 layer in the cell wall (Tokumoto et al. 1997). Wood density is a commonly used quality indicator that is related to other wood properties such as mechanical strength and shrinkage as well as pulp yield and properties (Panshin and de Zeeuw 1980). Wood density is influenced mainly by genotype (Zhang 1998). Flexural stiffness and strength are strongly influenced by wood density (Huang et al. 2003; De Boever et al. 2007; Innes 2007) and cellular structure.

A number of studies have been conducted on inter- and intra-clonal variation of wood density and shrinkage in poplar species (Nepveu et al. 1978; Olson et al. 1985; Ivkovich 1996; Koubaa et al. 1998b; Pliura et al. 2007). Only few investigations concerning variations in fiber characteristics, density, and mechanical properties of different poplar clones can be found in the literature (Hernández et al. 1998; Koubaa et al. 1998a; Pliura et al. 2007, Huda et al. 2011a, 2012). However, little is known about the clonal variation influencing physical and mechanical properties of hybrid poplar clones. Besides, little information is available on the genetic parameters of the physical and mechanical properties of poplar clones, such as heritability and genetic gain, except for a few studies on density and shrinkage (Hernández et al. 1998; Koubaa et al. 1998b;

Zhang et al. 2003). Therefore, the main objective of this study was to investigate the clonal variation in the physical and mechanical properties of selected hybrid poplar clones grown at three sites in southern Quebec, Canada. The heritability and genetic gain in selected properties of these clones were also studied.

5.4 MATERIAL AND METHODS

5.4.1 Sample collection and preparation

Seven hybrid clones from three sites (Saint-Ours, Pointe-Platon, and Windsor) in southern Quebec, Canada were selected for this study (Figure 5.1, Table 5.1). Trees for hybrid clones trials grown at Saint-Ours and Windsor were planted in 1993. Trees for the trials at Pointe-Platon site were planted in 1991. For the clone DNxM-915508 at Pointe-Platon site, trees were obtained from a 1995 trial (Table 5.2).

Table 5.1 Clones of hybrid poplar selected for the study.

Clone	Hybrid	Female parent	Male parent	Note
DxN-131	*Populus deltoides* × *P. nigra*	*P. deltoides*	*P. nigra* 'Italica' as the putative father	A natural hybrid selected from the Montreal area, Québec
TxD-3230	*P. trichocarpa* × *P. deltoides* Syn.: *P.×generosa* 'Boelare'	*P. trichocarpa* 'Fritzi Pauley' (from Washington)	*P. deltoides* S.1-173 (from a cross between *P. deltoides* V.5 from Iowa and V.9 from Missouri)	Clone S.910-8 from Belgium. Cultivar 'Boelare'
DxN-3565	*P. deltoides* × *P. nigra* Syn.: *P.×canadensis*	*P. deltoides* S.513-60 (from a cross between *P. deltoides* V.5 from Iowa and V.12 from Illinois)	*P. nigra* S.157-3 (from a cross between *P. nigra* V.220 from Italy and V.450 from Belgium)	Family/tree from Belgium: 78.017/164
DxN-3570	*P. deltoides* × *P. nigra*	*P. deltoides* S.513-60	*P. nigra* S.157-4 (from a cross between *P. nigra* V.220 from Italy and V.450 from Belgium)	Family/tree from Belgium: 78.018/204
DxN-3586	*P. deltoides* × *P. nigra*	*P. deltoides* S.513-60	*P. nigra* S.132-4 (from a cross between *P. nigra* V.441 from Italy and V.450 from Belgium)	Family/tree from Belgium: 78.016/156
DxN-4813	*P. deltoides* × *P. nigra*	*P. deltoides* 226 (from Trois-Rivieres, Quebec)	*P. nigra* 'Italica'	A controlled cross selected from Quebec
DNxM-915508	(*P. deltoides* × *P. nigra*) × *P. maximowiczii*	*P. deltoides* × *P. nigra* (from Quebec City)	*P. maximowiczii* (from Japan)	A controlled cross selected from Quebec

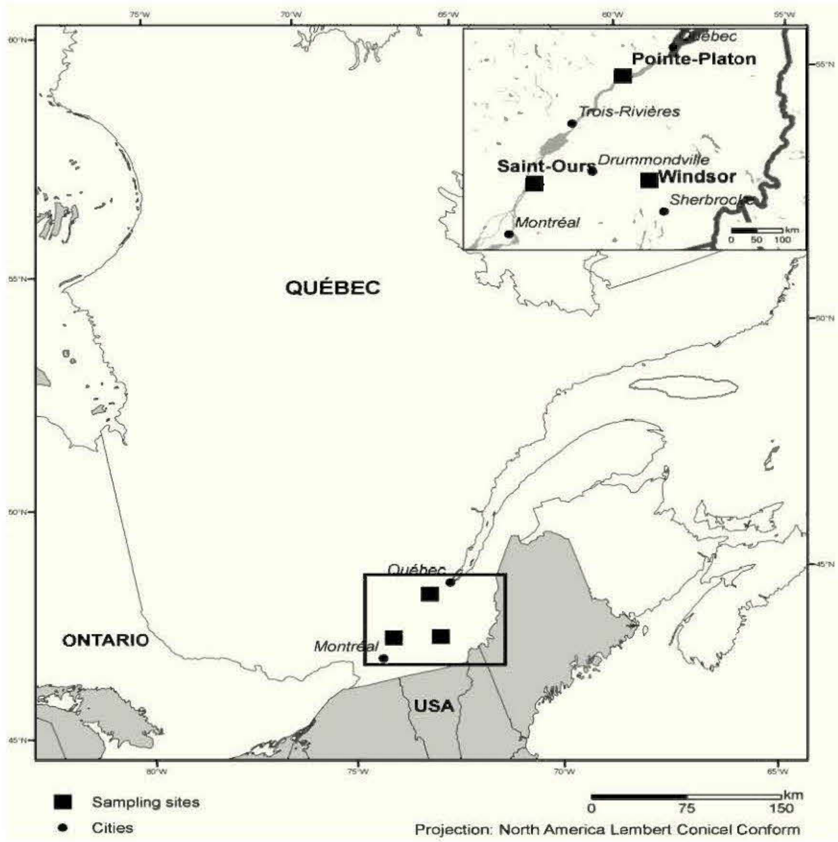

Figure 5.1 Map of sampling sites located in the south of the Province of Quebec, Canada.

The Saint-Ours site is located in the Champlain marine deposit, where the soil consists of a silty clay deposit with 40% clay (Table 5.2). The two other sites consist of sandy loam soil (Pliura et al. 2007). The Windsor site is located in a slightly more elevated geographical area with cooler climatic conditions. All tree plantation trial sites had a randomized block design with ten blocks each. One systematic thinning was carried out in 1995 at the Pointe-Platon site and in 1996 at the Windsor and Saint-Ours sites. Early in 2006, a thinning operation was carried out, removing two-thirds of the trees from these plantation sites.

Table 5.2 Site characteristics of hybrid poplar clonal trials.

	Site		
Characteristics	Pointe-Platon	Saint-Ours	Windsor
Trial number	PLA01791	STO10893	WIN10593
Establishment year	1991	1993	1993
Geographic coordinates	46°40'N, 71°51'W	45°54'N, 73°09'W	45°42'N, 71°57'W
Elevation (m)	60	15	260
Ecological sub-region–bioclimatic domain	Sugar maple – basswood domain	Sugar maple – bitternut hickory domain	Sugar maple – basswood domain
Surface deposit	Sandy loam soil	Champlain marine deposit with silty clay soil.	Sandy loam soil
Initial spacing	1 m x 3 m	1.2 m x 3.5 m	1.5 m x 3.5 m

Five trees of each clone were randomly sampled at each site, for a total of 105 trees. Samples were collected in July, August, and early September 2007. A log of 800 mm in length with its base at a height of 0.5 m above the ground was collected for physical and mechanical property measurements from each tree stem after felling. Disc edges were coated with wax to maintain wood moisture content and to prevent decay and other environmental alterations. Samples were then transported to the Wood Research Centre (Centre de recherche sur le bois, Université Laval, Quebec, Canada), and were kept frozen until the test samples preparation. A 2.5 cm-wide slab was cut along the diameter of each disc (bark to bark passing through the pith) and then conditioned at 20 °C and 60% relative humidity for several weeks until an equilibrium moisture content of 12% was reached.

For physical and mechanical properties, specimens were cut into 20 mm (T) x 20 mm (R) x 100 mm (L) pieces for density, shrinkage, and compression tests, and 20 mm (T) x 20 mm (R) x 330 mm (L) pieces for bending tests. Sample preparation and measurement of physical and mechanical properties were conducted according to ASTM D143 (ASTM 2007), except for dimension of samples. Physical properties measured were basic density (oven-dry mass to green volume ratio), total volumetric, longitudinal, tangential, and radial shrinkage. Mechanical properties measured were modulus of elasticity (MOE) and modulus of rupture (MOR) in static bending, and the ultimate crushing strength (CS) parallel to the grain in compression. Basic density was calculated as the oven-dry mass to green volume ratio just after the sample preparation. The specimens were weighed in an analytical balance and a digital micrometer was used to determine their T, R, and L dimensions. Longitudinal, radial, and tangential shrinkages were calculated as the ratio of the dimensional variation in each direction between saturated and oven-dry states on the dimension in the saturated state. Volumetric shrinkages were calculated from direct volume measurement. Three-point static bending tests were carried out using a universal testing machine (Zwick/Roell Z020) with a span length of 300 mm and maximum load of 20 kN. Compression parallel to the grain tests were performed on a universal testing machine (Zwick/Roell Z100) with a maximum load of 100 kN.

5.4.2 Statistical analysis

SAS® version 9.3 (SAS Institute Inc. 2010) was used for all statistical analyses. Residuals were tested for normality and homogeneity of variance using statistics provided by the UNIVARIATE procedure. Data transformations were not necessary to satisfy the assumptions of analysis of variance and other analyses. Analyses of variance were performed with the GLM procedure using Type III (partial sums of squares) estimation to assess the relative magnitude of each variation source. The tree effect was confounded with the error term since it was not statistically significant for all studied properties. The mixed linear model was used for the univariate analysis,

$$X_{ijk} = \mu + S_i + C_j + (S \text{ x } C)_{ij} + \varepsilon_{ijk} \quad (5.1)$$

where X_{ijk} is an observation on the the jth clone from the ith site; μ is the overall mean; S_i is the fixed effect due to the ith site; C_j is the fixed effect due to the jth clone; $(S \text{ x } C)_{ij}$ is the interaction between site and clone and ε_{ijk} is the random error. Some *F*-ratios involved more than one means square in the denominator and were tested with approximate degrees of freedom.

Tukey's Studentized range (HSD) was used to test the statistical significance (at $p<0.05$) of differences among means of clones for each site (PROC GLM, SAS). The variance components were estimated in the model using VARCOMP with the restricted maximum likelihood method (REML) and expressed as a percentage (VAR).

The broad-sense heritability or clonal heritability (H_C^2) was calculated from the variance estimates, as follows (Eq. 5.2) (Becker 1984; Falconer and Mackay1996),

$$H_C^2 = \sigma_C^2 / \sigma_P^2 \quad (5.2)$$

where σ_C^2, and σ_P^2 are the genotypic and phenotypic variance, respectively. Phenotypic variance (σ_P^2) was calculated as shown in Eq. (5.3),

$$\sigma_P^2 = \sigma_C^2 + \sigma_{(S \text{ x } C)}^2 + \sigma_e^2. \quad (5.3)$$

where σ_C^2, $\sigma_{(S \text{ x } C)}^2$and σ_e^2 are the variance of clones, interection between site and clones and residuals effects, respectively.

The genotypic coefficient of variation (CV_G) and the phenotypic coefficient of variation (CV_P) were calculated from Eqs. 5.4, and 5.5, respectively (Burton 1952; Henderson 1953).

$$CV_G = (\sqrt{\sigma_C^2}/\mathrm{mean})\mathrm{x}100 \quad (5.4)$$

$$CV_P = (\sqrt{\sigma_P^2}/\mathrm{mean})\mathrm{x}100 \quad (5.5)$$

The mathematical expression for the genetic gain (G) is expressed in Eq. 5.6. The potential genetic gain from individual tree selection is computed by selection differential (Eq. 5.7) and 10% selection intensity,

$$G = H_C^2 * S \quad (5.6)$$

$$S = i * \sigma_P \quad (5.7)$$

where $H_C^{2\,2}$ is the heritability, S is the selection differential, i is the selection intensity (10%), and σ_P is the phenotypic standard deviation. The estimated selection differential was based on a 10% selection intensity which corresponds to 1.73 for a sample of 100 (here n = 105) as suggested by Falconer and Mackay (1996).

5.5 RESULTS AND DISCUSSION

5.5.1 Site variation

In this study, the physical and mechanical properties of selected hybrid poplar clones wood in three sites were determined. Site had a significant effect on all studied properties except for radial shrinkage (Table 5.3). This exception was probably due to edaphic effects and climatic conditions such as variation in drainage, elevations of the sites, temperature, and precipitation amounts. Site effect accounted for 2.3% to 15.9% of the total variation, depending on the examined property (Table 5.3). These results are in good agreement with Pliura et al. (2005; 2007) and Zhang et al. (2003), who reported significant site effects on wood physical and mechanical properties of hybrid poplar clones.

Table 5.3 Results of the analysis of variance of wood physical and mechanical properties of hybrid poplar clones (basic density (BD), volumetric shrinkage (VSH), longitudinal shrinkage (LSH), radial shrinkage (RSH), and tangential shrinkage (TSH)).

Physical Properties											
		BD (kg/m^3)		VSH (%)		LSH (%)		RSH (%)		TSH (%)	
	DF[b]	P>F-value	VAR[a]	P>F-value	VAR	P>F-value	VAR	P>F-value	VAR	P>F-value	VAR
Site	2	6.8^{**}	8.4	6.2^{**}	4.8	8.9^{**}	15.9	2.6^{ns}	2.3	3.7^{*}	2.5
Clone	6	13.4^{**}	42.3	4.0^{**}	2.7	4.3^{**}	15.6	2.4^{*}	4	4.6^{**}	10
Site x Clone	12	0.8^{ns}	-	3.4^{**}	29.0	0.9^{ns}	-	1.7^{ns}	11.1	2.4^{**}	19.7
Error	83		49.4		62.5		68.5		82.6		67.8

Mechanical Properties							
		Flexural MOE (MPa)		Flexural MOR (MPa)		Ultimate crushing strength || to grain (MPa)	
	DF[b]	P>F-value	VAR[a]	P>F-value	VAR	P>F-value	VAR
Site	2	10.5^{**}	11.3	6.3^{**}	6.6	9.9^{**}	14.8
Clone	6	4.5^{**}	4.5	18.6^{**}	50.4	11.5^{**}	38.4
Site x Clone	12	2.5^{**}	20.7	1.0^{ns}	0.2	0.4^{ns}	-
Error	83		68.0		42.8		46.8

*Significant at $P < 0.05$ probability level; **Significant at $P < 0.01$ probability level; [ns] Non-significant at $P < 0.05$ probability level;

[a] Variance component as a percentage of the total variance

[b] Degrees of freedom

The effect of site on density was statistically significant. This effect showed that site differ considerably in environmental condition through different growth rate, development of trees at different sites and heterogeneous competition effects. Significant site effects for wood density have been reported by Zhang et al. (2003) and Pliura et al. (2005). By contrast, Peszlen (1998) did not find any density difference among the three clones of *Populus* planted in two sites in Hungary.

Based on multiple comparisons, Windsor differed significantly in average density from other sites at the 0.05 level (Table 5.4). Trees from the Saint-Ours site showed the highest density values, and trees from Windsor showed the lowest. These results differ from the findings of Pliura et al. (2005), who reported higher wood density at the Windsor site than at the Saint-Ours site. However, the trees they used were younger than those of the present study.

Based on multiple comparisons of means, trees from the Pointe-Platon site differed significantly in volumetric and tangential shrinkage from other sites at the 0.05 level. The shrinkage values appeared to be lower in Pointe-Platon site compared to Saint-Ours and Windsor sites (Table 5.4). Therefore, dimensional stability of trees coming from this site should be better. Trees from Windsor and Saint-Ours showed similar values of volumetric, tangential, and radial shrinkages. These results concur with the previous study on hybrid poplar clones collected from Saint-Ours and Windsor sites by Pliura et al. (2005). Nepveu et al. (1985) have reported significant site effect for tangential shrinkage of poplar clones. The Windsor site showed significant difference with other sites for longitudinal shrinkage (Table 5.4). However, no significant difference was found for radial shrinkage among the sites.

Table 5.4 Least squares means of clones and multiple comparison tests of hybrid poplar clones (basic density (BD), volumetric shrinkage (VSH), longitudinal shrinkage (LSH), radial shrinkage (RSH), tangential shrinkage (TSH), flexural modulus of elasticity (MOEF), flexural modulus of rupture (MORF), and ultimate crushing strength parallel to the grain (CS)).

Clone	Physical properties					Mechanical properties		
	BD (kg/m^3)	VSH (%)	LSH (%)	RSH (%)	TSH (%)	MOEF (MPa)	MORF (MPa)	CS (MPa)
				Site Average				
Pointe-Platon	350^{A}	7.53^{B}	0.41^{B}	2.71^{A}	4.64^{B}	7330^{A}	77.2^{A}	44.4^{AB}
Saint-Ours	353^{A}	8.11^{A}	0.40^{B}	2.61^{A}	5.13^{A}	7500^{A}	75.8^{A}	45.6^{A}
Windsor	340^{B}	8.19^{A}	0.48^{A}	2.45^{A}	5.19^{A}	6560^{B}	73.2^{B}	42.9^{B}
				Clonal Average				
DxN-131	341^{B}	8.33^{AB}	0.37^{BC}	2.75^{AB}	4.85^{BC}	7010^{AB}	72.4^{B}	41.9^{CD}
TxD-3230	339^{B}	8.30^{AB}	0.46^{AB}	2.41^{AB}	5.53^{AB}	7020^{AB}	73.1^{B}	42.5^{CD}
DxN-3565	369^{A}	7.93^{BC}	0.45^{AB}	2.87^{A}	5.22^{BC}	7480^{A}	82.2^{A}	46.8^{B}
DxN-3570	343^{B}	7.37^{C}	0.35^{C}	2.33^{B}	4.54^{C}	6970^{AB}	74.7^{B}	43.0^{CD}
DxN-3586	327^{B}	7.56^{BC}	0.40^{BC}	2.62^{AB}	4.56^{C}	6600^{B}	69.9^{B}	40.8^{D}
DxN-4813	380^{A}	8.92^{A}	0.54^{A}	2.85^{A}	5.80^{A}	7520^{A}	84.9^{A}	49.9^{A}
DNxM-915508	334^{B}	7.25^{C}	0.44^{BC}	2.27^{B}	4.45^{C}	7290^{AB}	70.3^{B}	44.6^{BC}
Overall Average ± SE	348 ± 25	7.95 ± 1.12	0.43 ± 0.09	2.59 ± 0.65	4.99 ± 1.06	7130 ± 804	75.4 ± 7.16	44.3 ± 4.03

*Means within a column followed by the same letter are not statistically different at $p = 0.05$`.

Differences among sites were also significant for wood mechanical properties, as shown in Table 5.3. The variance component analysis indicates that the site effect varied among the studied mechanical properties ranging from 6.6% to 14.8%. Based on multiple comparisons, the overall mechanical properties were more homogenous between the Pointe-Platon and Saint-Ours sites (Table 5.4). A similar observation was reported for mechanical properties of 10-year-old hybrid poplar clones for these two sites by Yu et al. (2008). Mátyás and Peszlen (1997) also reported that site did not affect MOE and MOR of three *euramericana* poplar hybrid clones. They concluded that the lack of difference was probably due to narrow range of density in their study. However, the Windsor site differed significantly from the two other sites at the 0.05 level, wood produced there having lower strength properties. This site has a very high elevation compared to the other two sites which might explain the lower mechanical properties of wood grown in this site. Cown et al. (2006) observed strong and negative effects between structural wood properties of radiata pine and elevation. Saint-Ours trees showed the highest average flexural MOE and crushing strength parallel to grain. Pointe-Platon trees showed the highest flexural MOR.

It is generally believed that rapid growth rate results in low density and low mechanical properties. Variations in wood quality with tree growth are strongly related to physical and chemical characteristics of soil. Sites with favorable soil properties for stand growth may produce low density wood (Grekin and Verkasalo 2010). Numerous authors have shown the importance of environmental effects on wood properties (Zobel and Van Buijtenen 1989). One of the most difficult environmental factors to relate to wood quality is the overall effect of soil and climate, known as site quality (Zobel and Jett 1995). Also, the success of timber production is primarily governed by genotype, site quality, and silvicultural practices (Malan 1995). According to our results, the variations in the mechanical properties in clones could be based on different factors, such as site and growth conditions. In particular, altitude, soil, climatic conditions, spacing, and elevation can affect the physical and mechanical properties, as reported by Macdonald and Hubert (2002). The difference observed among sites for these wood properties emphasize the importance of proper site selection.

5.5.2 Clonal variation

The analysis of variance (Table 5.3) indicated significant clonal variation in the physical and mechanical properties of hybrid poplar clones wood. The significant differences observed among clones for the studied properties are an indication of a clonal effect on wood properties. As indicated by the variance component results, the clone is either low or high, ranging from 2.7% to 50.4%, depending on the examined property (Table 5.3).

With respect to physical properties, clonal variation accounted for 42.3% of the total variance in wood density (Table 5.3). The high clonal variation in wood density is in good agreement with previous works (Yanchuk et al. 1983; Beaudoin et al. 1992; Zhang et al. 2003; Pliura et al. 2005; 2007). Clone DxN-4813 showed the highest wood density (380 kg/m^3), whereas clone DxN-3586 showed the lowest (327 kg/m^3). Similar results were obtained with samples taken at greater heights within the same trees in a wood machining experiment (Hernández et al. 2011).

On the other hand, the clonal variation accounted for only 2.7% of the total variance in volumetric shrinkage. This result is in good agreement with previous reports (Nepveu et al. 1978; Koubaa et al. 1998b; Pliura et al. 2005). Clone DxN-4813 showed the highest volumetric shrinkage (Table 5.4). The clonal variation accounted for 16%, 4%, and 10% of the total variance in longitudinal, radial, and tangential shrinkages, respectively. Overall means for longitudinal, radial, and tangential shrinkages were 0.43%, 2.6%, and 5%, respectively (Table 5.4). These values are slightly lower than those reported in previous studies (Alden 1995; Koubaa et al. 1998b; Pliura et al. 2005). These lower shrinkage values indicate higher dimensional stability of these clones.

The difference in the physical properties may be attributed to factors such as age, origin, and juvenile wood proportion of the trees. The range of clonal means for density and shrinkage suggests that there was sufficient variation among clones to justify clonal selection to improve wood physical properties.

The interclonal variation in mechanical strength (flexural MOE, flexural MOR, and ultimate crushing strength parallel to the grain) was significant (Table 5.3). Clones with denser wood generally showed higher mechanical properties (Table 5.4). This result is in good agreement with previous reports (Bendtsen et al. 1981; Hernández et al. 1998; Kretschmann et al. 1999; De Boever et al. 2007). In contrast, Mátyás and Peszlen (1997) did not detect significant clonal effects for strength properties of poplar clones. Based on multiple comparison of means, differences among clones were found for mechanical properties at the 0.05 percent level, which helps to select clones with high yield mechanical properties.

The interclonal variation accounted for 4.5% and 50.4% of the variance in flexural MOE and flexural MOR, respectively (Table 5.3). The overall MOE of the clones studied was comparable to or higher than previous results (Mátyás and Peszlen 1997; Kretschmann et al. 1999; De Boever et al. 2007). On the other hand, the overall MOR of clones was higher than previous results (Kretschmann et al. 1999; De Boever et al. 2007). Based on multiple comparison of means, clone-4813 and clone-3565 showed higher flexural strength properties among all studied clones (Table 5.4).

The interclonal variation accounted for 38% of the variance in ultimate crushing strength parallel to the grain (Table 5.3). The overall ultimate crushing strength parallel to the grain for the clones was 44.3 MPa, with large standard errors (Table 5.4). Ultimate crushing strength parallel to the grain of clones in our study was compared with those from previous studies. The results showed higher values than those reported by Bendtsen et al. (1981) and Mátyás and Peszlen (1997) and lower than the results of Hernández et al. (1998). The lower values obtained in the current study could be explained by several factors including the fact that the material of this study was still juvenile (Table 5.2). The radial variation of the anatomical properties of the same material also confirmed that the wood of the studied clones was juvenile (Huda et al. 2012).

The higher values obtained for mechanical properties of hybrid poplar compared to other poplar species might indicate that wood strength properties of these clones could be improved by clonal selection. The level of variation among clones appeared to indicate a genetic control of these properties.

Direct comparison to data from similar investigations could not be made for the mechanical properties measurement due to the different test conditions, such as moisture condition during testing, portion of tree for sampling, sample dimensions, and sampling methods. The age and site effect could also explain the higher values. Hernández et al. (1998) stated that samples from juvenile wood showed lower mechanical strength, but could develop higher properties at maturity.

The site x clone interaction of all variables was not significant (Table 5.3), except for wood volumetric shrinkage, tangential shrinkage, and flexural MOE properties. The non-significant site x clone interaction for wood density and strength properties indicates that, for these properties, the studied clones behaved similarly in the three sites.

5.5.3 Genetic parameters of wood properties

For many wood quality traits, there is little or no information available about the degree of genetic variation or the heritability of the properties. Most data are available for properties that are easier to measure, such as basic density. In this study, the clonal and environmental variations were used to estimate various genetic parameters, including heritability and genetic gain for physical and mechanical properties of selected hybrid poplar clones. The overall mean values of genetic variation for wood properties are presented in Table 5.5.

Table 5.5 Estimates of genetic parameters of wood properties for 7 hybrid poplar clones.

Traits*	Broad-sense heritability	Genotypic coefficient of variation	Phenotypic coefficient of variation	Genetic gain
BD (kg/m^3)	0.72	5.36	7.41	6.65
VSH (%)	0.39	5.61	14.36	4.77
LSH (%)	0.53	13.62	25.74	13.53
RSH (%)	0.19	4.74	25.44	2.02
TSH (%)	0.40	8.73	21.73	6.52
MOEF (MPa)	0.37	4.58	12.26	2.07
MORF (MPa)	0.76	7.54	9.97	9.52
CS (MPa)	0.74	7.12	9.59	9.43

* BD: Basic density; VSH: volumetric shrinkage, LSH: longitudinal shrinkage, RSH: radial shrinkage, TSH: tangential shrinkage, MOEF: flexural modulus of elasticity, MORF: flexural modulus of rupture, CS: ultimate crushing strength parallel to the grain

The genetic and phenotypic coefficients of variation values for wood density in the present study were lower than the values reported by Pliura et al. (2007). However, our study showed lower difference between the genotypic (5.36) and phenotypic (7.41) coefficients of variation.

This low difference indicates that the environmental influence on wood density of the studied clones was low. The heritability for wood density was 0.72, which is comparable to or higher than previous results. Heritability for wood density of *Populus* clones was reported at 0.51 by Peszlen (1998), and at 0.35 by Yanchuk et al. (1983) for *Populus tremuloides*, and at 0.69 by Farmer and Wilcox (1968) and Beaudoin et al.

(1992) for *P. euramericana* clones, and at 0.22 to 0.52 by Pliura et al. (2007) for hybrid poplar clones.

The reasons for high heritability for wood density could be related to a lower contribution for nonadditive genetic variance and substantial genome by environment (G x E) interactions (Saifullah and Rabbani 2009). The site x clone interaction for wood density was non-significant and accounted for less than 1% of the total variation (Table 5.3). There is also evidence that the properties that are highly responsive to environmental variation are well known to have low heritability (Price and Schluter 1991). The genetic gain for wood density obtained in the present study is comparable to that reported by Zhang et al. (2003).

The difference between genotypic and phenotypic coefficients of variation of shrinkage properties were high, indicating high environmental influence on such properties. These properties showed moderate heritability except for radial shrinkage. The heritability values of shrinkage were in agreement with those of Koubaa et al. (1998b) and Nepveu et al. (1978) for *P. x euramericana* hybrid. The genetic gain values for shrinkage properties ranged from 2.0 to 13.5. The highest genetic gain was observed for longitudinal shrinkage (13.5), followed by tangential shrinkage (6.5).

There are even fewer works for genetic parameter of hybrid poplar clones in the literature on mechanical properties. Hernández et al. (1998) observed a broad-sense heritability of 0.34 for MOE and 0.47 for crushing strength, which are comparable with the values found in the present study. The flexural MOR and crushing strength showed high heritability values of 0.76 and 0.74, respectively. The genetic gain for flexural MOE was low. However, flexural MOR and ultimate crushing strength parallel to the grain showed high genetic gains (Table 5.5).

5.5.4 Practical implications

Seven hybrid poplar clones investigated in this study showed significant variation in physical and mechanical properties among sites and clones, indicating good opportunities for selecting the best performing clones both for breeding and for desired end-products. The differences observed among sites and clones for these wood properties emphasize the importance of proper site and genotype selection along with proper silvicultural practices, which govern the success of timber production (Malan 1995).

Wood dimensional stability is one of the most significant physical property for the manufacture of solid wood products, where drying and seasoning are mandatory. The dimensional stability of all the studied poplar clones indicates their potential to be used for manufacturing of solid wood products for indoor applications and building materials.

Several economic studies have shown that wood density has a major impact on wood product industry profits because of its impact on harvesting, transportation, and milling costs (Lowe et al. 1999). In addition, wood density has an impact on pulp and paper products; even a slight modification of these properties could be of commercial importance. Wood from the studied hybrid poplar clones is well suited for particle-, flake-, and strand-based composite boards due to its low density, ease of flaking, low processing cost and availability (Geimer 1986; Semple et al. 2007).

Knowledge of the wood mechanical properties is required to define the utilization in applications such as furniture and building material. Despite this requirement, characteristics related to the strength and elasticity of wood are also fundamental, both to the structural stability of trees and safety of manufactured wood products (Lima et al. 1999). Clones with higher density and mechanical properties, such as DxN-4813 and DxN-3565, would result in higher fiber yield for the pulp industry and stronger wood for the lumber industry. Such clones also performed the best for most of the wood machining processes studied in a parallel study (Hernández et al. 2011). DxN-4813, together with DxN-3570, had the best response to steam bending process (Kuljich et al. 2013). Clones DxN-4813 and DxN-3565 could be potential raw material for the pallet industry in the Quebec region, as both have better density and mechanical properties.

The increase of hybrid poplar clones production as a raw material for pulp and paper, and wood industries requires a deeper knowledge of their genetics. Moderate to high heritabilities in these properties suggest that satisfactory genetic gains could be obtained through proper clones selection.

5.6 CONCLUSIONS

The significant effects of site on the physical and mechanical properties of hybrid poplar clones show that Saint-Ours site is the best site followed by Pointe-Platon and Windsor sites, respectively.

The clone effect is highly significant and more important than site effects for most studied properties, indicating the possibility of selecting clones with desirable attributes.

With the exception of radial shrinkage, for which broad-sense heritability is low, all other wood properties investigated are under moderate to high genetic control. The heritability, and genetic and phenotypic coefficients of variation observed for physical and mechanical properties, suggests that high genetic control could be expected from independent selection for each of these properties.

The clonal variation, heritability, and genetic gain values for the properties investigated in this study should help poplar breeding programs that aim to optimize poplar hybrid clones for solid wood and fiber-based products.

5.7 ACKNOWLEDGEMENTS

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CHAPTER VI

PHENOTYPIC AND GENOTYPIC CORRELATIONS FOR WOOD PROPERTIES OF HYBRID POPLAR CLONES OF SOUTHERN QUEBEC[4]

6.1 ABSTRACT

This study aimed at understanding the phenotypic and genotypic correlations among wood anatomical, physical, and mechanical properties of hybrid poplar clones. Samples were taken from seven clones grown in three sites in Southern Quebec, Canada. Five trees per clone were randomly sampled from each site to measure anatomical (fiber length, fiber proportion, vessel proportion, fiber wall thickness, tension wood), physical (basic density, volumetric, longitudinal, tangential, radial shrinkage), and mechanical wood properties (flexural MOE, MOR, ultimate crushing strength parallel to the grain). The observed phenotypic and genotypic correlations between these wood properties were moderate to strong for all properties, except fiber length and vessel proportion. Genotypic correlations for all wood properties were higher than corresponding phenotypic correlations. Furthermore, fiber length showed weak correlations, whereas, vessel proportion showed strongly negative correlations with all other properties. Strong correlations were also found among fiber proportion, fiber wall thickness, basic density, and mechanical properties. Results from this study further showed close genotypic and phenotypic correlations between fiber proportion, fiber wall thickness, and wood density and consequently on the mechanical performance of wood products. These findings indicate that there is a substantial opportunity to improve wood quality by selecting several wood properties for different end uses.

Keywords: Hybrid poplar, Phenotypic correlations, Genotypic correlations, Wood anatomical, Physical and mechanical properties.

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[4] Huda, A. A., Koubaa, A., Cloutier, A., Hernández, R. E., Périnet, P., and Fortin, Y. "Phenotypic and genotypic correlations for wood properties of hybrid poplar clones of Southern Quebec." Working paper.

CORRÉLATIONS PHÉNOTYPIQUE ET GÉNOTYPIQUE POUR LES PROPRIÉTÉS DU BOIS DES CLONES DE PEUPLIER HYBRIDE DU SUD DU QUÉBEC

6.2 RÉSUMÉ

Cette étude a pour but de comprendre les corrélations phénotypique et génotypique parmi les propriétés anatomiques, physiques et mécaniques du bois de clones de peuplier hybrides. Des échantillons ont été prélevés de sept clones cultivés en trois sites au sud du Québec, Canada. Cinq arbres par clone ont été échantillonnés aléatoirement dans chaque site pour mesurer les propriétés anatomiques (longueur des fibres, proportion de fibres, proportion de vaisseaux, épaisseur de la paroi des fibres, bois de tension), physiques (densité basale, retrait radial, tangentiel, longitudinal et volumétrique) et mécaniques (MOE en flexion, MOR, résistance à l'écrasement parallèle au fil du bois). Les corrélations phénotypique et génotypique observées avec les propriétés du bois étaient modérées à fortes, à l'exception de celles avec la longueur des fibres et de la proportion de vaisseaux. Les corrélations génotypiques pour toutes les propriétés du bois étaient plus élevées que les corrélations phénotypiques correspondantes. Par ailleurs, il y avait une faible la longueur des fibres a montré une faible corrélation négative et proportion de vaisseaux a montré une forte corrélation négative avec toutes les autres propriétés. De fortes corrélations ont également été trouvées entre la proportion de fibres, l'épaisseur de la paroi des fibres, la densité basale et les propriétés mécaniques. Les résultats pour les corrélations génotypique et phénotypique indiquent que la sélection pour une proportion plus élevée de fibres, l'épaisseur de la paroi des fibres pourrait augmenter la densité du bois, et donc avoir un impact positif sur la performance des produits du bois. Ces constations indiquent la présence d'un fort potentiel d'améliorer la qualité du bois par la sélection de plusieurs propriétés du matériau pour différentes applications finales.

Mots-clés: Peuplier hybride, Corrélations phénotypes, Corrélations génotypes, Propriétés anatomiques, physiques et mécaniques du bois.

6.3 INTRODUCTION

The Canadian forests are among the most extensive in the world and represent one of Canada's most valuable natural resources. Poplars is one of the top components of this resource, particularly the stands located in the boreal region of the country. In Québec, the *Ministère des Ressources Naturelles* (Quebec's Ministry of Natural Resources) has been actively breeding and selecting hybrid poplar clones for growth, adaptability to the climatic conditions, and wood quality (Périnet et al. 2012). The genetic improvement program of poplars started in 1969 to produce improved hybridized poplar populations using five main parental species: *Populus balsamifera*, *P. deltoides*, *P. maximowiczii*, *P. nigra*, and *P. trichocarpa* (Périnet et al. 2007). In 2003, the anticipated yields were 14 m^3/ha·yr on average sites, and 20 m^3/ha·yr on the best sites of southern Quebec (Messier et al. 2003). In the boreal region, they were 12 m^3/ha·yr on the best sites and 10 m^3/ha·yr on average sites (Messier et al. 2003). In Québec, approximately 12 000 ha of hybrid poplar plantations are managed by industrials, while small private landowners have only planted around 1 000 ha (Fortier et al. 2011, Morissette 2012).

Poplars are becoming increasingly important species for forest product industries, particularly as a short-rotation tree species for the establishment of fiber for pulp and paper, engineered wood products such as oriented strand board, laminated veneer lumber, and structural composite lumber (Balatinecz et al. 2001). Poplar wood is well suited for particle, flake, and strand-based composite boards due to its low density, ease of cutting, low processing cost and availability (Geimer 1986; Semple et al. 2007).

The introduction of wood quality traits selection criteria is considered as an important objective for the breeding program. However, wood quality can only be defined in terms of specific end-uses and may involve several wood properties, such as fiber morphology, and wood density (Downes et al. 1997). Poplars show substantial variation in many important wood properties, such as fiber dimensions (Zhang et al. 2003; Pliura et al. 2007), and wood density (Zhang et al. 2012). Wood density is a commonly used quality indicator that is related to other wood properties such as mechanical strength and shrinkage as well as pulp yield and properties (Panshin and de Zeeuw 1980). Despite its key importance, density is not the only basic property involved in wood mechanical strength development. Jacobsen et al. (2005) stated that high mechanical strength is associated with thick fiber walls. Moreover, the thickness of poplar cell walls in turn is positively correlated with wood density (Pliura et al. 2007, Huda et al. 2011a).

Knowledge of genetic correlation plays a vital role in the prediction of correlated responses and the development of effective selection indexes in a breeding program. Several studies have focused on the fiber morphology, density, and growth properties of poplars (Yanchuk et al. 1984; Beaudoin et al. 1992; Koubaa et al. 1998 a, b; Zhang et al. 2003; Pliura et al. 2005; Pliura et al. 2007; Zhang et al. 2012). However, there is no available study on the phenotypic and genotypic correlations among anatomical, physical, and mechanical properties of hybrid poplar clones. Therefore, the main objectives of this study were: 1) to estimate the genotypic and the phenotypic correlations among wood anatomical, physical, and mechanical properties, and 2) to evaluate the implication of these relationships in hybrid poplar breeding programs for wood quality.

6.4 MATERIALS AND METHODS

6.4.1 Plant material

The materials used in this study were collected from three hybrid poplar clonal trials established by the *Direction de la recherche forestière, Ministère des Ressources*

Naturelles du Québec (Research Branch at Quebec's Ministry of Natural Resources) between 1991 and 1995. The trial sites are located in Pointe-Platon (46°40'N 71°51'W), Saint-Ours (45°54'N 73°09'W), and Windsor (45°42'N 71°57'W) in southern Quebec, Canada (Figure 6.1). Trees for hybrid clones trials were planted at the Saint-Ours and Windsor sites in 1993, and in 1991 at the Pointe-Platon site (Table 6.1). Trees for clone DNxM-915508 were obtained from a 1995 trial at the Pointe-Platon site (Table 6.2).

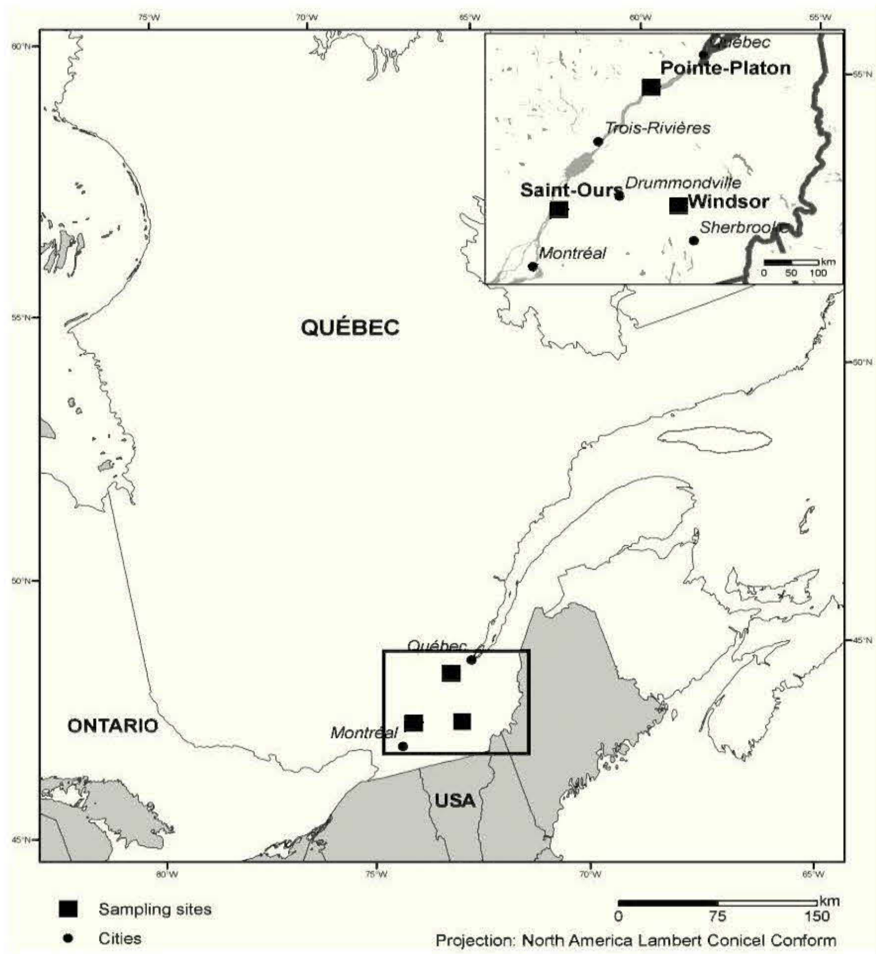

Figure 6.1 Map of sampling sites located in the south of the Province of Quebec, Canada.

The Saint-Ours site is located in the Champlain marine deposit, where the soil consists of a silty clay deposit (40% clay). The two other sites consist of sandy loam soil (Pliura et al. 2007). All sites were originally used for agriculture, but had been abandoned for several years before the hybrid poplar clones were planted. All tree plantation trial sites had a randomized block design with ten blocks each. A systematic thinning was carried out in 1995 at the Platon site and in 1996 at Windsor and Saint-Ours sites. Early in 2006, a thinning operation was carried out removing two-third of the trees from these plantation sites.

Table 6.1 Site Characteristics of Hybrid Poplar Clonal Trials.

Characteristics	Site		
	Pointe-Platon	Saint-Ours	Windsor
Trial number	PLA01791	STO10893	WIN10593
Establishment year	1991	1993	1993
Geographic coordinates	$46^{0}40'N, 71^{0}51'W$	$45^{0}54'N, 73^{0}09'W$	$45^{0}42'N, 71^{0}57'W$
Elevation (m)	60	15	260
Ecological sub-region –bioclimatic domain	Sugar maple – basswood domain	Sugar maple – bitternut hickory domain	Sugar maple – basswood domain
Surface deposit	Sandy clay loam soil	Champlain marine deposit with silty clay soil.	Sandy loam soil
Initial spacing	1 m x 3 m	1.2 m x 3.5 m	1.5 m x 3.5 m

Table 6.2 Clones of hybrid poplar selected for the study.

Clone	Hybrid	Female parent	Male parent	Note
DxN-131	*Populus deltoides* × *P. nigra*	*P. deltoides*	*P. nigra* 'Italica' as the putative father	A natural hybrid selected from the Montreal area, Quebec
TxD-3230	*P. trichocarpa* × *P. deltoides* Syn.: *P.×generosa* 'Boelare'	*P. trichocarpa* 'Fritzi Pauley' (from Washington)	*P. deltoides* S.1-173 (from a cross between *P. deltoides* V.5 from Iowa and V.9 from Missouri)	Clone S.910-8 from Belgium. Cultivar 'Boelare'
DxN-3565	*P. deltoides* × *P. nigra* Syn.: *P.×canadensis*	*P. deltoides* S.513-60 (from a cross between *P. deltoides* V.5 from Iowa and V.12 from Illinois)	*P. nigra* S.157-3 (from a cross between *P. nigra* V.220 from Italy and V.450 from Belgium)	Family/tree from Belgium: 78.017/164
DxN-3570	*P. deltoides* × *P. nigra*	*P. deltoides* S.513-60	*P. nigra* S.157-4 (from a cross between *P. nigra* V.220 from Italy and V.450 from Belgium)	Family/tree from Belgium: 78.018/204
DxN-3586	*P. deltoides* × *P. nigra*	*P. deltoides* S.513-60	*P. nigra* S.132-4 (from a cross between *P. nigra* V.441 from Italy and V.450 from Belgium)	Family/tree from Belgium: 78.016/156
DxN-4813	*P. deltoides* × *P. nigra*	*P. deltoides* 226 (from Trois-Rivières, Quebec)	*P. nigra* 'Italica'	A controlled cross selected from Quebec
DNxM-915508	(*P. deltoides* × *P. nigra*) × *P. maximowiczii*	*P. deltoides* × *P. nigra* (from Quebec City)	*P. maximowiczii* (from Japan)	A controlled cross selected from Quebec

6.4.2 Sampling and measurement

Five trees of each clone were randomly sampled at each site, for a total of 105 trees. Samples were collected in July, August, and early September 2007. A disc of 800 mm in length with its base at a height of 0.5 m above the ground was collected from each tree stem after felling for physical and mechanical properties measurements. Disc edges were coated with wax to maintain wood moisture content and to prevent decay and other environmental alterations. Samples were then transported to the Wood Research Centre (Centre de recherche sur le bois, Université Laval, Quebec, Canada) and were kept frozen until test samples preparation. A 2.5 cm wide slab was cut horizontally along the diameter of each disc (bark to bark passing through the pith) and then conditioned at 20°C and 60% relative humidity for several weeks until an equilibrium moisture content of 12% was reached.

For the anatomical analysis, cross sections of 20 μm were cut using a sliding microtome with a disposable blade. Sections were then double stained with 1% safranin stain for 5 minutes and 0.1% astrablue stain for 15 minutes. Stain in excess was removed by washing sections successively using 50, 80, and 100% ethanol solutions. Safranin stains all tissues, and astrablue replaces safranin in purely cellulosic G-layers of tension wood. Sections were then permanently mounted on microscope slides with cover slips using Permount mounting medium. Samples were left for two weeks to allow the mounting medium to dry thoroughly.

Sample images were taken at ×50 magnification with a Leica compound microscope (DM 1000) equipped with a PL-A686 high-resolution microscopy camera. Black and white images (.tiff format) at 1200 × 1600 resolution were captured using a green filter to maximize contrast. The WinCELL Pro 2004a program (Regent Instruments Inc.), an image analysis system specifically designed for wood cell analysis, was used to measure fiber wall thickness and tension wood proportion. Tissue proportion in different cell types was estimated from 2 sections from each block. Vessel tissue was distinguished from fiber and ray tissue by defining a 570 μm^2 four-square area for every grid examined, and tissue types that fell within this area were noted. Fiber proportion was measured by the same method. A Fiber Quality Analyzer (FQA) (OpTest Equipment Inc., LDA02) was used to measure fiber length (weight-weighted fiber length).

For physical and mechanical properties, specimens were cut into 20 mm (T) x 20 mm (R) x 100 mm (L) pieces for basic density, shrinkage, and compression tests, and 20 mm (T) x 20 mm (R) x 330 mm (L) pieces for bending tests. Sample preparation and measurement of physical and mechanical properties were conducted according to ASTM D 143 (ASTM 2007) except for dimension of samples. Physical properties measured were basic density (oven-dry mass to green volume ratio), total volumetric, longitudinal, tangential and radial shrinkages. Mechanical properties were modulus of elasticity (MOE) and modulus of rupture (MOR) in static bending, and the ultimate crushing strength (CS) parallel to the grain. The specimens were weighed in an analytical balance and a digital micrometer was used to determine their T, R, and L dimensions. Longitudinal, radial, and tangential shrinkages were calculated as the ratio of the dimensional variation in each direction between saturated and oven-dry states on the dimension in the saturated state. Volumetric shrinkage was calculated from direct volume measurement. Three-point static bending tests were carried out using a universal testing machine (Zwick/Roell Z020) with a span length of 300 mm and maximum load of 20 kN. Compression parallel to the grain tests were performed on a universal testing machine (Zwick/Roell Z100) with a maximum load of 100 kN.

6.4.3 Statistical analysis

SAS® version 9.3 (SAS 2010) was used for all statistical analyses. Residuals were tested for normality and homogeneity of variance using statistics provided by the UNIVARIATE procedure. Tree effects were not considered in the analysis, as preliminary testing showed negligible contribution to the total variance. Furthermore, in many cases, the variance component for these terms could not be estimated or was not significant. The mixed linear model was used to estimate variance components for the present study:

$$X_{ijk} = \mu + S_i + C_j + (S \times C)_{ij} + \varepsilon_{ijk} \tag{6.1}$$

where X_{ijk} is an observation on the the *jth* clone from the *ith* site; μ is the overall mean; S_i is the fixed effect due to the *ith* site; C_j is the random effect due to the *jth* clone; $(S \times C)_{ij}$ is the interaction between site and clone and ε_{ijk} is the random error. A limited number of clones are used in this study. Therefore, instead of considering clones as random effect the analysis was carried out with fixed effects. These shortcomings in experimental design does not allow for a precise estimation of genetic parameters, making far reaching generalization or for unambiguous reasoning of observed patterns of variation. However, our estimates are first approximations for studied properties of hybrid poplar clones.

The Pearson's correlation coefficients for the phenotypic interrelationships were computed using the SAS CORR procedure. Significance levels were calculated with respect to the null hypothesis r=0.

The genotypic correlation (r_G) of two traits x and y were obtained with,

$$r_G = \frac{\sigma_{c(xy)}}{\sqrt{\sigma^2_{c(x)} \times \sigma^2_{c(y)}}} \tag{6.2}$$

and

$$\sigma_{c(xy)} = \left(\sigma^2_{c(x+y)} - \sigma^2_{c(x)} - \sigma^2_{c(y)}\right)/2 \tag{6.3}$$

Where $\sigma^2_{c(x)}$ is the clone variance component for the trait x, $\sigma^2_{c(y)}$ is the clone variance component for the trait y, $\sigma^2_{c(x+y)}$ is the variance for dummy variable (x+y). and $\sigma_{c(xy)}$ is the clone covariance component. The method is described in detail by Williams et al. (2002). Because of sampling errors and mathematical approximation, some genotypic correlations may exceeded ±1. In these cases, we considered them equal to ±1, considering the asymptotic nature of distribution of the correlation coefficients. Standard errors associated with the genotypic correlations were estimated using the method presented by Robertson (1959).

$$\sigma_{(r_G)} = \frac{1-r_G^2}{\sqrt{2}} \text{ x } \sqrt{\left[\frac{\sigma(H_x^2) \text{ x } \sigma(H_y^2)}{H_x^2 \text{ x } H_y^2}\right]} \tag{6.4}$$

Where H_x^2 and H_y^2 are the heritability estimates for traits x and y; $\sigma(H_x^2)$ and $\sigma(H_x^2)$ are the associated standard errors for heritability estimates.

6.5 RESULTS AND DISCUSSION

6.5.1 General descriptive statistics

The mean values, standard errors, range, and coefficient of variation of all studied properties in each of the three sites are presented in Table 6.3. Trees from Saint-Ours site had the highest fiber length while Pointe-Platon had the highest fiber proportion and fiber wall thickness. Huda et al. (2012) reported that the site and clone effect on these wood anatomical properties were significant. Saint-Ours trees showed the highest density, average flexural MOE, and crushing strength parallel to grain. Pointe-Platon trees showed the highest flexural MOR. The coefficient of variation (CV) of the measured properties ranged between 4.1% and 23.3% indicating an acceptable level of variability. In previous reports on the same material, we discussed the variance component analysis and their significance at different probability levels of these wood properties (Huda et al. 2011a, b; 2012; 2014).

Table 6.3 Descriptive statistics of wood properties of hybrid poplar clones at the three sites.

	Pointe-Platon			Saint-Ours			Windsor		
	Mean ± SE	Range (Min-Max)	CV (%)	Mean ± SE	Range (Min-Max)	CV (%)	Mean ± SE	Range (Min-Max)	CV (%)
FL (mm)	0.90 ± 0.04	0.83-0.95	5.6	0.99 ± 0.05	0.95-1.07	7.0	0.93 ± 0.04	0.88-0.98	8.8
FP (%)	55.89 ± 4.69	47.22-62.20	8.2	53.82 ± 4.38	45.25-58.67	7.9	52.68 ± 4.43	46.59-58.93	8.1
VP (%)	27.26 ± 3.97	21.27-32.39	14.6	28.38 ± 2.79	23.37-31.60	9.8	26.71 ± 2.55	24.48-30.57	9.6
FWT (μm)	2.53 ± 0.28	2.18-2.93	11.2	2.32 ± 0.25	2.04-2.75	10.6	2.25 ± 0.29	1.88-2.65	12.7
TW (%)	38.57 ± 5.08	32.39-46.79	13.2	38.73 ± 4.28	34.71-46.39	11.1	39.20 ± 7.12	31.97-50.25	18.2
BD (kg/m^3)	349± 21	332-380	5.9	353 ± 23	321-388	6.7	341 ± 19	328-382	5.6
VSH (%)	7.54 ± 0.55	6.77-8.30	7.3	8.11 ± 1.27	6.54-9.65	15.6	8.19 ± 0.42	7.48-8.82	5.1
LSH (%)	0.41 ± 0.06	0.36-0.52	13.9	0.40 ± 0.08	0.30-0.53	18.6	0.48 ± 0.07	0.38-0.56	14.2
RSH (%)	2.70 ± 0.30	2.31-3.13	11.2	2.61 ± 0.26	2.33-2.96	9.8	2.45 ± 0.57	1.81-3.39	23.3
TSH (%)	4.65 ± 0.60	3.95-5.67	12.9	5.13 ± 0.43	4.59-5.78	8.4	5.19 ± 0.91	4.23-6.12	17.5
MOE (MPa)	7332 ± 334	6765-7907	4.6	7499 ± 481	7074-8274	6.4	6558 ± 396	5954-7042	6.0
MOR (MPa)	77.1 ± 5.9	71.0-86.6	7.7	75.8 ± 7.2	68.2-88.5	9.5	73.2 ± 5.3	65.9-82.5	7.2
CS (MPa)	44.3 ± 3.3	41.2-49.6	7.3	45.6 ± 3.4	41.5-51.7	7.4	42.7 ± 3.2	39.5-48.6	7.5

FL fiber length, FP fiber proportion, VP vessel proportion, FWT fiber wall thickness, TW tension wood proportion, BD basic density, VSH volumetric shrinkage, LSH longitudinal shrinkage, RSH radial shrinkage, TSH tangential shrinkage, MOE flexural modulus of elasticity, MOR flexural modulus of rupture, and CS ultimate crushing strength parallel to the grain.

6.5.2 Phenotypic correlations between wood properties

The results of the analysis of correlations between the studied properties are presented in Table 6.4. The correlations between fiber length and all other wood properties were not significant for both tree and clone levels. The non-significant correlation between this property and wood density is in good agreement with previous results for different hybrid poplar clones (Zhang et al. 2003) and for *Populus trichocarpa* (Porth et al. 2013). For both tree and clone levels, a close negative relationship was found between fiber and vessel proportions. This result was expected, because most of the lignocellulosic material in hardwoods consists of vessels and fibers. Increasing the proportion of one element will lead to a decrease in the other. This result is in good agreement with previous reports on hybrid poplar (Eckstein et al. 1979; Huda et al. 2011a) and other hardwoods (Taylor and Wooten 1973; Cheng and Bensend 1979; Peszlen 1994; Mátyás and Peszlen 1997; Pande and Singh 2005).

A positive relationship between fiber proportion and fiber wall thickness was also observed (Table 6.4). Thus, clones with higher fiber proportion tend to develop thicker cell walls. Similarly, the negative relationship between fiber wall thickness and vessel proportion suggests that clones with higher vessel proportions have thinner cell walls. These findings explain the positive correlation between wood density and fiber wall thickness and the negative correlation between vessel proportion and wood density. Wood density was correlated to all anatomical features, except fiber length, at both the clone and tree levels. These results are explained by the fact that the fiber morphological properties of wood largely determine its density (Pot et al. 2002). Greater fiber proportion and fiber wall thickness are associated with higher wood density (Fujiwara et al. 1991; Ziemińska et al. 2013). On the other hand, high percentage of vessel proportion will yield hydraulic conductivity, which could cause higher shrinkage, and disruption in wood structure. Joon (2000) reported that the large number of vessel elements present in poplar wood was mainly responsible for the disruption of its structure.

Positive and significant correlations between tension wood proportion and fiber wall thickness were found (Table 6.4). This means that higher tension wood proportion is associated with smaller fiber lumen area and thicker walls. On the other hand, vessel proportion was negatively correlated with tension wood proportion. These findings are in good agreement with previous findings for eastern cottonwood (Kaeiser and Boyce 1965).

The correlation between wood density and tension wood proportion was positive and significant at both the tree and clone levels. This result could be explained by the higher fiber proportion and greater fiber wall thickness of tension wood. In addition, the formation of tension wood was associated with the presence of a gelatinous layer that increases the amount of cellulosic material in the fiber. Okumura et al. (1977) suggested that increased wall thickness for tension wood fibers was mainly due to increased thickness of the unlignified cellulosic G-layer of the secondary wood layer.

Table 6.4 Pearson coefficients of correlation between the anatomical, physical, and mechanical properties of hybrid poplar clones. Upper right part (in italic) of the table presents the correlations between tree averages (n=105) and the lower left part indicates the correlations between clone averages within sites (n=21)

	FL (mm)	FP (%)	VP (%)	FWT (μm)	TW (%)	BD (kg/m^3)	VSH (%)	LSH (%)	TSH (%)	RSH (%)	MOE (MPa)	MOR (MPa)	CS (MPa)
FL (mm)	1	*-0.16^{ns}*	*0.29^{**}*	*-0.15^{ns}*	*-0.02^{ns}*	*0.07^{ns}*	*-0.04^{ns}*	*-0.14^{ns}*	*0.16^{ns}*	*-0.12^{ns}*	*0.06^{ns}*	*0.08^{ns}*	*0.05^{ns}*
FP (%)	-0.21^{ns}	1	*-0.70^{**}*	*0.53^{**}*	*0.30^{**}*	*0.44^{**}*	*0.19^{ns}*	*0.04^{ns}*	*-0.03^{ns}*	*0.35^{**}*	*0.31^{**}*	*0.53^{**}*	*0.41^{**}*
VP (%)	0.36^{ns}	-0.75^{**}	1	*-0.38^{**}*	*-0.39^{**}*	*-0.41^{**}*	*-0.27^{**}*	*-0.26^{**}*	*-0.08^{ns}*	*-0.27^{**}*	*-0.17^{ns}*	*-0.47^{**}*	*-0.38^{**}*
FWT (μm)	-0.24^{ns}	0.55^{**}	-0.47^{*}	1	*0.30^{**}*	*0.34^{**}*	*0.17^{ns}*	*0.04^{ns}*	*0.06^{ns}*	*0.21^{*}*	*0.15^{ns}*	*0.37^{**}*	*0.33^{*}*
TW (%)	0.04^{ns}	0.43^{ns}	-0.51^{*}	0.47^{*}	1	*0.35^{**}*	*0.19^{ns}*	*0.56^{**}*	*0.41^{**}*	*0.30^{*}*	*0.23^{*}*	*0.53^{**}*	*0.38^{**}*
BD (kg/m^3)	0.08^{ns}	0.57^{**}	-0.52^{*}	0.48^{*}	0.78^{**}	1	*0.36^{**}*	*0.19^{ns}*	*0.12^{ns}*	*0.24^{*}*	*0.42^{**}*	*0.61^{**}*	*0.80^{**}*
VSH (%)	-0.02^{ns}	0.32^{ns}	-0.39^{ns}	0.33^{ns}	0.41^{ns}	0.45^{*}	1	*0.25^{*}*	*0.44^{*}*	*0.09^{ns}*	*-0.08^{ns}*	*0.24^{**}*	*0.30^{**}*
LSH (%)	-0.19^{ns}	0.06^{ns}	-0.37^{ns}	0.12^{ns}	0.56^{**}	0.38^{ns}	0.51^{*}	1	*0.35^{**}*	*0.04^{ns}*	*-0.08^{ns}*	*0.21^{ns}*	*0.27^{**}*
TSH (%)	-0.09^{ns}	0.63^{**}	-0.44^{*}	0.43^{*}	0.44^{*}	0.39^{ns}	0.10^{ns}	-0.19^{ns}	1	*0.03^{ns}*	*0.27^{**}*	*0.28^{**}*	*0.32^{**}*
RSH (%)	0.18^{ns}	-0.03^{ns}	-0.08^{ns}	0.18^{ns}	0.51^{*}	0.43^{*}	0.57^{**}	0.39^{ns}	0.16^{ns}	1	*0.10^{ns}*	*0.24^{**}*	*0.15^{ns}*
MOE (MPa)	-0.02^{ns}	0.52^{**}	-0.29^{ns}	0.30^{ns}	0.44^{*}	0.71^{**}	0.06^{ns}	-0.12^{ns}	0.42^{ns}	-0.03^{ns}	1	0.73^{**}	*0.51^{**}*
MOR (MPa)	-0.01^{ns}	0.66^{**}	-0.57^{**}	0.49^{*}	0.75^{**}	0.90^{**}	0.34^{ns}	0.36^{ns}	0.45^{*}	0.38^{ns}	0.78^{**}	1	*0.69^{**}*
CS (MPa)	0.05^{ns}	0.57^{**}	-0.43^{*}	0.47^{*}	0.73^{**}	0.88^{**}	0.31^{ns}	0.42^{*}	0.30^{ns}	0.35^{ns}	0.83^{**}	0.90^{**}	1

FL fiber length, FP fiber proportion, VP vessel proportion, FWT fiber wall thickness, TW tension wood proportion, BD basic density, VSH volumetric shrinkage, LSH longitudinal shrinkage, RSH radial shrinkage, TSH tangential shrinkage, MOE flexural modulus of elasticity, MOR flexural modulus of rupture, and CS ultimate crushing strength parallel to the grain.

^{ns}: Non-significant at p=0.05; *: significant at p=0.05; **: Significant at p=0.01.

The correlation between tension wood proportion and volumetric shrinkage was not significant (Table 6.4). The volumetric shrinkage of wood is influenced by the higher content of tension wood (Chauhan and Walker 2011). The samples of the present study might had variable contents of tension wood, which hereby explains the non-significant variation of volumetric shrinkage values among the tested clones, although, this result is difficult to explain. Gorisek and Straze (2006) reported that the chemical composition and cell wall organization such as high crystallinity of cellulose in G-layer, small amount of matrix substance, smaller micro voids in cell walls, are probable reasons of non-significant relationships between wood shrinkage and tension wood. On the other hand, the presence of tension wood was positively correlated to the longitudinal, radial, and tangential shrinkages. Ollinmaa (1961) also found significant positive correlation between longitudinal shrinkage and tension wood proportions for aspen and alder. Many authors also confirmed the existence of this positive correlation between tension wood and longitudinal shrinkage in poplar wood (Clair and Thibaut 2001) and other hardwoods (Polge 1984; Nepveu 1994). Sassus (1998) described that axial shrinkage of tension wood is often more than 5 times greater than that of normal wood for beech or poplar.

The correlations between tension wood and mechanical properties were also significant (Table 6.4). This result is in good agreement with Pilate et al. (2004), which suggested that the presence of the G-layer contributes, in a significant way, to specific mechanical properties of wood. The results of the present study indicate that tension wood will not negatively affect the mechanical performance of the wood. Similarly, in a parallel study Hernández et al. (2011) found that tension wood did not affect the machining properties of these hybrid poplar clones. Clair et al. (2003) also found similar results for chestnut. In tension wood of poplar, the secondary wall is replaced by a poorly lignified or purely cellulosic layer that is generally thick (Okumura et al. 1977). Besides, tension wood is characterized by a higher proportion of fibers and a lower proportion of vessels (Jourez et al. 2001). As a result, the increase of fiber proportion implies more walls by volume of wood tissue, thus, a higher density and better mechanical properties (Huda et al. 2011a, b).

The correlations between volumetric shrinkage and wood density was positive and significant at the clone and tree levels. For radial shrinkage, the correlation with wood density was significant but those of longitudinal and tangential shrinkage were not. A similar result was reported in *P.* x *euramericana* hybrid clones by Koubaa et al. (1998b). However, Koubaa et al. (1998b) recommended direct measurement of shrinkage values for poplar since several anatomical features, such as growth ring angle, fibril angle or lumen diameter, might significantly influence the shrinkage of juvenile poplar wood. Volumetric shrinkage had no significant relationship with anatomical or mechanical properties in the present study. Volumetric shrinkage and swelling properties are affected by several wood properties, such as the heartwood to sapwood ratio and the microfibril angle in the S_2 layer (Bektaş and Güler 2001). However, our results showed that among the studied properties, wood density had the greatest effect on wood shrinkage. Hence, the direct measurement of shrinkage values of tested poplar clones gives some degree of confidence on their dimensional stability.

A number of anatomical features are known to influence plant mechanical properties (Niklas 1992). The present study showed that mechanical properties improved with increased fiber proportion, although no significant relationship with other anatomical properties was found except tension wood (Table 6.4). Bendtsen et al. (1981) studied the mechanical properties of cottonwood and *Populus* hybrid NE-237 and found that anatomical properties and wood density had an effect on compression strength.

This study also found a positive relationship between wood mechanical properties and density. Although this relationship was significant, it was only moderate. Previous studies have found highly significant relationships between density and mechanical properties in hybrid poplar clones (Hernández et al. 1998; De Boever et al. 2007). At the individual tree level, density showed a highly significant correlation with flexural MOR and ultimate crushing strength and moderate but significant correlation with flexural MOE. On the other hand, at the clonal level, density highly affected all mechanical properties. Similarly, all mechanical properties were moderately to highly correlated to wood density. These moderate relationships could be explained by the fact that the density used for the correlation analysis was the overall tree density of clones and not the density of the tested sample for mechanical properties. In addition, the tested poplar clones were only 15 years of age. Thus, the wood was mainly juvenile and could partially explain the weaker relationship between density and mechanical properties.

On the other hand, correlation analysis showed that test sample density had a strong correlation with flexural MOE (Figure 6.2a) and MOR (Figure 6.2b) and the ultimate crushing strength (Figure 6.2c). This result is in good agreement with Zhang (1997) and Hernández et al. (1998).

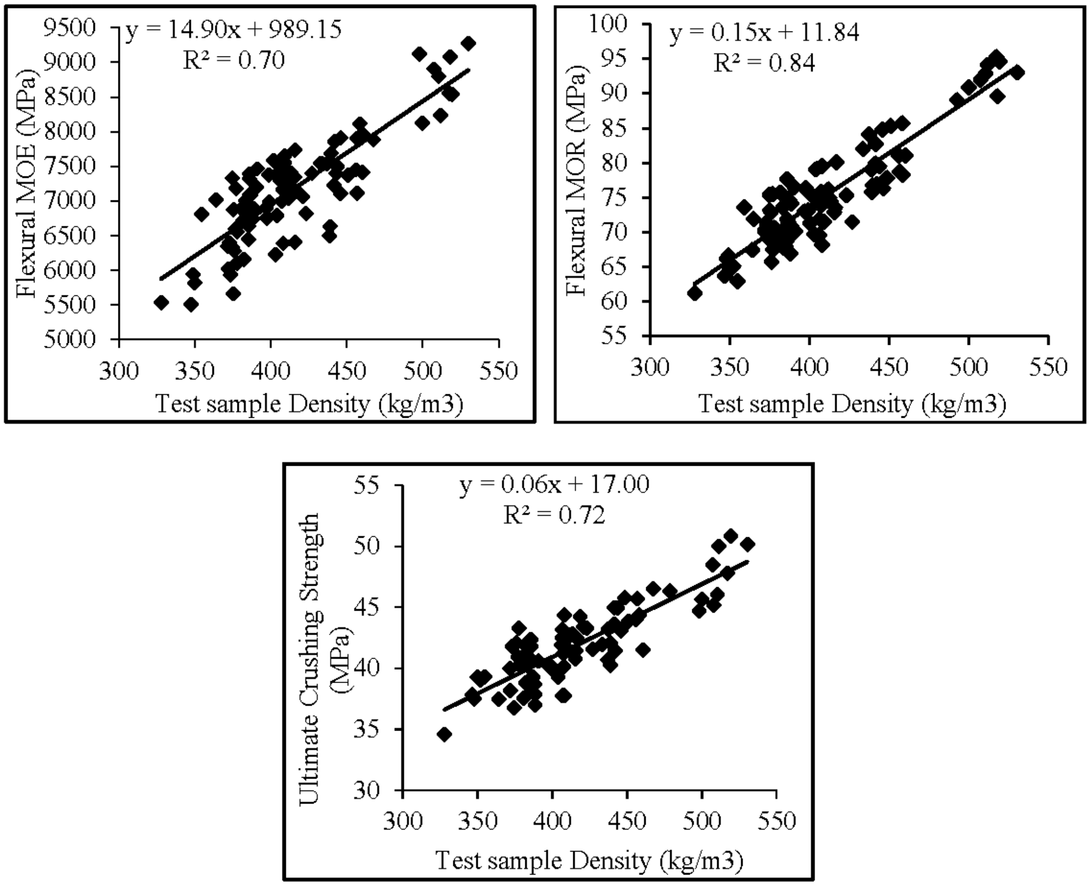

Figure 6.2 Relationship between test samples' density and (a) flexural modulus of elasticity, (b) flexural modulus of rupture, and (c) ultimate crushing strength in parallel to the grain.

6.5.3 Genotypic correlations between wood properties

Genotypic correlations among traits were moderate to strong, depending on traits at individual sites (Table 6.5). Significant negative genetic or genotypic correlation had been found between density and growth properties in many studies involving poplar and its hybrids (Yanchuk et al. 1984; Beaudoin et al. 1992; Hernández et al. 1998;

Pliura et al. 2007). However, no study has addressed the genotypic correlations among different wood properties in hybrid poplar clones.

Genotypic correlation between fiber length and other wood properties were weak and negative, except for vessel proportion and flexural MOR. The genotypic correlation between fiber length and density of the present study are in good agreement with the study of Porth et al. (2013) on *Populus trichocarpa.* In both phenotypic and genotypic correlations, we observed weak relationships among fiber length and other wood properties, which makes fiber length an independent trait for wood breeding strategy. However, weak correlations among these properties could be an indication of properties that are functionally or developmentally less related, and are therefore phenotypically and genetically less integrated. For example, this result suggests that it is difficult to improve both fiber length and basic density simultaneously. As a result, this weak genotypic correlation will have to be considered if density is used alone as predictor for wood quality for hybrid poplar breeding programs.

The genotypic correlations between fiber proportion and other wood properties were strong and positive, while the genotypic correlation with vessel proportion was negative (r = -0.97). Hence, this result indicates the greater importance of fiber proportion for the end-uses. As expected, the genotypic correlations were strong and negative for vessel proportion and other properties (Table 6.5). Additionally, fiber proportion and vessel proportion always showed opposite correlation with the other wood properties especially at the genetic level. The relationship among fiber wall thickness and other wood properties showed strong genotypic correlations. At the genetic level, fiber wall thickness was associated with higher fiber proportion, indicating a tendency for better mechanical properties.

Table 6.5 Estimated genotypic correlations (below diagonal) and standard errors (above diagonals, in Italic) for the anatomical, physical, and mechanical properties of hybrid poplar clones.

	FL (mm)	FP (%)	VP (%)	FWT (μm)	TW (%)	BD (kg/m^3)	VSH (%)	LSH (%)	TSH (%)	RSH (%)	MOE (MPa)	MOR (MPa)	CS (MPa)
FL (mm)	1	*0.15*	*0.23*	*0.14*	*0.15*	*0.18*	*0.24*	*0.25*	*0.24*	*0.27*	*0.12*	*0.15*	*0.22*
FP (%)	-0.10	1	*0.18*	*0.07*	*0.23*	*0.01*	*0.05*	*0.06*	*0.01*	*0.05*	*0.04*	*0.16*	*0.04*
VP (%)	0.24	-0.97	1	*0.18*	*0.15*	*0.01*	*0.36*	*0.26*	*0.10*	*0.19*	*0.23*	*0.13*	*0.20*
FWT	-0.07	0.74	-0.90	1	*0.18*	*0.14*	*0.39*	*0.36*	*0.18*	*0.26*	*0.12*	*0.07*	*0.06*
TW (%)	-0.04	0.87	-0.91	0.88	1	*0.07*	*0.14*	*0.17*	*0.15*	*0.13*	*0.08*	*0.01*	*0.03*
BD	-0.02	0.90	-0.92	0.84	0.86	1	*0.21*	*0.26*	*0.01*	*0.17*	*0.12*	*0.17*	*0.10*
VSH (%)	-0.30	0.62	-0.76	0.69	0.73	0.53	1	*0.22*	*0.01*	*0.01*	*0.36*	*0.21*	*0.28*
LSH (%)	-0.19	0.42	-0.58	0.66	0.77	0.56	0.72	1	*0.38*	*0.14*	*0.04*	*0.10*	*0.11*
TSH (%)	-0.18	0.67	-0.74	0.60	0.82	0.69	1.00	0.93	1	*0.46*	*0.32*	*0.33*	*0.37*
RSH (%)	-0.08	1.00	-0.98	1.00	0.94	1.00	0.99	0.49	0.86	1	*0.24*	*0.11*	*0.12*
MOE (MPa)	-0.23	0.78	-0.77	0.72	0.88	0.97	0.46	0.93	0.72	0.42	1	*0.28*	*0.01*
MOR (MPa)	0.07	0.90	-0.84	0.77	0.76	0.97	0.73	0.64	0.83	0.98	0.68	1	*0.14*
CS (MPa)	-0.01	0.64	-0.74	0.73	0.81	0.93	0.53	0.86	0.67	0.62	1.00	0.83	1

FL fiber length, FP fiber proportion, VP vessel proportion, FWT fiber wall thickness, TW tension wood proportion, BD basic density, VSH volumetric shrinkage, LSH longitudinal shrinkage, RSH radial shrinkage, TSH tangential shrinkage, MOE flexural modulus of elasticity, MOR flexural modulus of rupture, and CS ultimate crushing strength parallel to the grain.

All correlations with tension wood were positive and high, with the exception of vessel proportion where strong negative genotypic correlation was detected, due to the fact that the gelatinous fiber layer formed in tension wood has narrower vessels and a lower vessel area. This result could be explained by the fact that the S_3 layer of secondary wall was replaced by the thick cellulosic layer known as gelatinous fiber layer inside the lumen of the fiber. Kaeiser and Boyce (1965) described that gravitational stimulus generally induce the formation of gelatinous fibers, which modify the anatomical characteristics of other elements of wood, such as modifications of the size of rays, vessels, and fibers in *Populus deltoides*.

Strong genotypic correlations were observed between tension wood and shrinkage properties. Tension wood consists of hydrophilic substance within the G-layers (Mellerowicz and Gorshkova 2012). As a result, when tension wood is dried and water removed rapidly, it causes a greater level of shrinkage and it impacts on wood mechanical properties and, consequently, wood quality.

Density showed strong positive genotypic correlations with all anatomical and mechanical properties except fiber length and vessel proportion. Zhang et al. (2003) reported a similar conclusion for fiber length and wood density in hybrid poplar. The strong genotypic correlations observed between density and these properties indicated that selection of any one of these properties would result in a highly correlated response to selection in the others. However, a breeding program based on density may lead to severe reduction in fiber length, as fiber length had a strong genotypic correlation with growth properties whereas significant negative genetic correlations were found between density and growth properties (Hernández et al. 1998; Pliura et al. 2007). The genotypic correlations among density and different shrinkage properties were moderate. Moreover, the genotypic correlation between wood density and mechanical properties were positive and strong (Table 6.5).

This study further found strong genotypic correlations between the wood mechanical properties and wood anatomical properties except for fiber length that do not play any important role for mechanical properties. On the other hand, the strong positive relationships between mechanical properties and anatomical properties (fiber proportion and fiber wall thickness) at genetic level present a possible strategy for wood quality improvement. Breeding strategies that would aim to improve fiber proportion and fiber wall thickness, and thus increase mechanical wood properties would have negligible influence on fiber length. The genotypic correlations among mechanical properties and density were very strong. As a result, the inclusion of wood density into tree breeding programs can lead to an improvement of mechanical strength properties. Moreover, these high genotypic correlations with MOE and MOR make density a strong candidate for direct genetic improvement of general wood quality. The use of this property can also ultimately benefit solid wood and fiber-based wood products. For example, selection for increased wood density for industrial implications would at the same time increase pulp yield and solid wood product value, and decrease production costs. However, the choice of the properties to be included in improvement programs often depends on their ease of assessment or determination. Therefore, wood properties such as fiber proportion, fiber wall thickness and easily measurable wood density can be used for the improvement of mechanical wood properties as a selection strategy.

Broad literature surveys suggested that genetic and phenotypic correlations had the same sign and even the magnitude (Falconer and Mackey 1996; Lynch and Walsh 1998). Our finding also confirmed the relationships of phenotypic and genetic correlations reported in the literature. For example, phenotypic and genetic correlations of vessel proportion with all properties were all negative. However, in the present study, the genotypic correlations were found stronger than phenotypic correlations for all wood properties. These results might be explained by the environmental influences that weaken phenotypic correlations between wood properties in comparison to genotypic correlations. This is consistent with findings from an earlier study showing environmental influence on phenotypic coefficient of variation and genotypic coefficient of variation of wood anatomical properties (Huda et al. 2012).

6.6 CONCLUSIONS

Anatomical, physical, and mechanical properties of hybrid poplar clones were measured and the results were analyzed for phenotypic and genotypic variations. The variation in anatomical properties largely explained that observed in wood density. This study showed that the correlations of fiber properties together with basic density and strength properties were strong and significant at both phenotypic and genetic levels. Similarly, tension wood proportion was positively correlated to fiber proportion and cell wall thickness. Only the correlations between fiber length and other properties did not follow this trend. The correlations between wood density and mechanical properties were moderate at the phenotypic level and strong at the genotypic level. It is therefore apparent that, apart from wood density, other attributes of clones could be involved in mechanical performance. Therefore, caution should be taken when selecting clones for mechanical properties only based on density data, and the within-tree variation of wood density should also be considered. The total volumetric shrinkage was only correlated to wood density.

Several strong genotypic relationships were presented in this study, which indicates a good indicator for detection of genetic effects, thus, lead to significant improvement in selection process of these properties. Considerable variation in wood properties within trees and clones were of sufficient magnitude and could provide an opportunity to select clones for utilization in different applications. However, a future challenge will determine whether breeding objectives will be compatible with industrial objectives by improving wood properties.

6.7 ACKNOWLEDGMENTS

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CHAPTER VII

GENERAL CONCLUSIONS

Hybrid poplar plantations is of particular interest because short rotation forestry can contribute to a stronger, more stable and renewable supply of fiber. These hybrids are valued for both lumber and pulpwood production. Therefore, the use of fast-growing trees such as the species of the *Populus* genus and their clones in conjunction with intensive silvicultural practices has been postulated as a mean to meet the increasing demand for wood products. Besides, forest products companies are interested in hybrid poplar clones for manufacturing a variety of products, such as pulp and paper, panels, veneers, and solid wood products. Thus, this thesis is concerned with the assessment of hybrid poplar wood properties, and their utilization by the forest industry. Fast growth tree species are known to lead to a significant loss of wood quality, namely in wood density and mechanical properties. Therefore, along with growth rate, health and adaptability, wood quality should be included into selection criteria of hybrid poplar breeding programs. This research was undertaken to improve the understanding of the wood quality variation in hybrid poplar clones grown in Southern Quebec, for optimum use of this wood for fiber-based and timber-based products manufacturing.

Wood properties of seven hybrid poplar clones from three different sites were analyzed, in order to study site and clonal variation of anatomical, physical, and mechanical properties, and to study the within tree variations of various anatomical and physical properties. Additionally, correlations between wood properties were calculated, and genetic parameters of these properties were evaluated. These results and relationships led to a better understanding of the variability inwood quality traits between clones, within trees, and the variability due to other environmental factors. These results also demonstrated the potential of hybrid poplar clones to fulfil the demand for fiber and solid wood of Quebec's and Canada's industry.

SITE AND CLONAL VARIATIONS

Site effects reflect the reaction of trees to the combined effects of edaphic and climatic condition. On the other hand, clonal variations for selected wood properties could be based the progenitor's characteristics of hybrid crossess as well as other factors like site in growth and tree development. In particular, altitude, soil, climatic conditions, elevation, spacing, fertilization, thinning and pruning can affect the physical and mechanical properties.

The analysis of variance and multiple comparison tests demonstrated that, anatomical, physical, and mechanical properties of hybrid poplar clones vary with site quality in southern Quebec plantations. Trees from the Saint-Ours site showed higher fiber length, vessel proportion, and vessel dimensions. Whereas, Pointe-Platon trees showed the highest fiber proportion, fiber wall thickness and cell wall area. This could be explained by higher moisture availability and better drainage conditions as well as the soil surface deposition at the Saint-Ours site compared to the two other sites. Clones from the Saint-Ours site showed the highest density values, and the shrinkage values appeared to be lower in Pointe-Platon site, leading to a better dimensional stability. Saint-Ours site revealed higher strength properties followed by Pointe-Platon site. Favorable conditions of site in growth facilitated the revelation of clonal difference in different wood properties. Although, the presence of site x clone interaction for most wood properties, the clonal variance component for most wood properties were higher or similar to site. This calls for selecting clones suitable for each site, although end-uses of the clones should be considered in order to achieve optimal clonal deployment.

The difference observed among sites for these wood properties emphasizes the importance of proper site selection.

Because of a limited representation of sites, results for the present study do not allow generalization of sites as a whole, but are valid for plantation in degraded and abandoned agricultural land of southern part of Canada especially in Quebec with proper site preparation. For plantation of hybrid clones in boreal regions, further study should require; as well as more hybrid poplar clones should be considered in future study for the generalization of genotypic effect for poplar breeding programs.

RADIAL VARIATIONS OF WOOD PROPERTIES

The study of pith to bark profiles of variation in anatomical, and ring density properties enables a new level of understanding of the relationship between anatomical properties and wood densities properties to be gained. All anatomical properties and ring densities showed variations with increasing cambial age. The radial variation of anatomical properties was characterized by a rapid increase in the first few years in fiber length, fiber width, fiber proportion, wall thickness, and percent cell wall area, whereas the vessel lumen area and vessel proportion decreased with cambial age. An increased rate of growth resulted in an increase in fiber length, fiber width, thinner fiber wall thickness, vessel proportion, and due to a combination of these factors a lower wood density. Similarly, results obtained from ring density properties, showed that increasing pattern with increasing cambial age. The ring width properties were largest in the growth rings adjacent to the pith, with a decreasing rate of change with increasing cambial age. The patterns of radial variation of the examined wood properties did not show any evidence of juvenile to mature wood transition. These patterns of variation indicated that the wood in the studied hybrid poplar clones was still juvenile.

GENETIC PARAMETERS OF WOOD PROPERTIES

Genotypic correlations for all studied properties were higher than corresponding phenotypic correlations. High Genotypic correlations between ring density components were found. Earlywood density had higher genetic and phenotypic correlation with annual ring density than latewood density.

The phenotypic and Genotypic correlations between growth properties and ring density components were negative from moderate to high, suggesting that selection for one property would negatively affect the other one. Close genotypic and phenotypic correlations between fiber proportion, fiber wall thickness, and wood density were found. In both phenotypic and genotypic correlations, weak relationships among fiber length and other wood properties were observed. These results suggest that fiber length is an independent trait for wood breeding strategy.

Among the properties studied, wood density had the greatest effect on wood shrinkage. Hence, the direct measurement of shrinkage values of tested poplar clones gives some degree of confidence on their dimensional stability. The genotypic correlations among mechanical properties and density were very strong. As a result, the inclusion of wood density into tree breeding programs can lead to an improvement of mechanical strength properties of selected materials. Moreover, the high genotypic correlations of density with MOE and MOR make it a strong candidate for direct genetic improvement of general wood quality.

In breeding programs, reliable qualitative genetic estimates, such as traits heritability, is needed in order to precisely evaluate the expected genetic gain. Besides, genetic control of wood properties strongly influences the genetic gain that can be obtained from one generation to another.

This study further evaluated the evolution of the heritability with cambial age. The heritability of ring densities components were small near the pith, probably caused by the environmental influence and the photosynthetic behavior at early age. Moderate to high heritability values were found for fiber length, fiber wall thickness, fiber proportion, cell wall thickness, basic density, and for wood mechanical properties.

From the genetic parameters estimations, it was possible to estimate the genetic gain by selecting the best clones in terms of wood quality. For example, genetic gains of 5% for fiber length and fiber proportion, 6% for fiber wall thickness, 7% for density, and 9% for mechanical properties. Thus, there is potential to increase wood quality based on the clonal performance by estimating the gain of hybrid poplar clones wood properties. However, it is necessary to analyze and adding more economic information on the several properties studied to obtain a more accurate estimation of the possible genetic gain.

PRACTICAL IMPLICATIONS

The significant variations in physical and mechanical properties among sites and clones, indicates good opportunities for selecting the best performing clones both for breeding and for desired end-products. The differences observed among sites and clones for these wood properties emphasize the importance of proper site and genotype selection along with proper silvicultural practices, which govern the success of timber production. Moreover, the quantity and quality of wood and fiber properties of trees affect the suitability of genotypes as raw material for pulp and paper, and for wood processing.

Poplar fibers are shorter and finer than those of softwoods grown in Canada, which offer excellent optical properties of paper. However, blending of poplar fibers with softwood pulp is recommended for overall sheet strength. On the other hand, increased fiber length generally improves coherence between fibers, thus improving the physical properties of the ensuing paper. However, selection for density would have negative impact on fiber diameter and thus have an impact on pulp and paper properties such as smoothness and opacity. Nevertheless, the vessel elements of poplar significantly enhance the smoothness and opacity of sheets, making poplars well suited for printing papers. Clones with higher vessel proportion and thinner fiber walls would be suitable for tissue paper, where smoothness is a desirable quality.

Wood dimensional stability is one of the most significant physical property for the manufacture of solid wood products, where drying and seasoning are mandatory. The dimensional stability of all the studied hybrid poplar clones indicates their potential to be used for manufacturing of solid wood products for indoor applications and building materials. In addition, wood density has an impact on pulp and paper products; even slight modification of these properties could be of commercial value. Wood from the studied hybrid poplar clones is well suited for particle-, flake-, strand-based composite boards, and packaging industries due to its low density, ease of flaking, low processing cost and availability.

Knowledge of the wood mechanical properties is required to define the utilization in applications such as furniture and building material. Despite this requirement, characteristics related to the strength and elasticity of wood are also fundamental, both to the structural stability of trees and safety of manufactured wood products. Clones with higher density and mechanical properties, such as DxN-4813 and DxN-3565, would result in higher fiber yield for the pulp industry and stronger wood for the lumber industry. Clones DxN-4813 and DxN-3565 could be potential raw material for the pallet industry in the Quebec region, as both have better density and mechanical properties.

The increase of hybrid poplar clones production as a raw material for pulp and paper, and wood industries requires a deeper knowledge of their genetics. From a breeding point of view, the simultaneous consideration of multiple wood properties in breeding programs seems difficult due to high cost, difficult to measure and adverse correlations. The results of this study showed that easily measureable properties like fiber length and wood density would allow for effective improvement of wood quality. Moreover, moderate to high heritability values in these properties suggest that satisfactory genetic gains could be obtained through proper clonal selection.

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APPENDIX A

WOOD QUALITY OF HYBRID POPLAR CLONES IN SOUTHERN QUÉBEC: CLONAL VARIATION AND PROPERTY INTERRELATIONSHIPS[5]

A.1 ABSTRACT

To meet the growing demand for wood fiber, interest has turned toward productive short-rotation species. Hybrid poplar clones have higher productivity than most eastern Canadian hardwood and softwood species. The physical, mechanical, and morphological properties of hybrid poplar wood largely determine its suitability for various uses, especially for high-value-added applications. The main objective of this study was to determine clonal variations and property interrelationships for anatomical, physical, and mechanical properties of seven hybrid poplar clones grown at three sites in southern Quebec, Canada. Five trees per clone were randomly sampled from each site to measure anatomical (fiber proportion, vessel proportion, fiber wall thickness, tension wood), physical (basic density, volumetric shrinkage), and mechanical wood properties (compression and bending). Relationships among anatomical, physical, and mechanical properties were determined. All anatomical, physical, and mechanical properties of hybrid poplar wood showed significant clonal variation, indicating the possibility of identifying clones with superior wood properties. Results also revealed close relationships between anatomical, physical, and mechanical properties. Increasing tension wood proportion was associated with increasing fiber wall thickness and fiber proportion and decreasing vessel proportion. Strong correlations also were found between fiber proportion, basic density, and mechanical properties. Practical implications for breeding and end uses are discussed.

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QUALITÉ DU BOIS DE CLONES DE PEUPLIERS HYBRIDES DANS LE QUÉBEC MÉRIDIONAL: VARIATION INTER-CLONES ET CORRÉLATIONS ENTRE LES PROPRIÉTÉS DU BOIS

A.2 RÉSUMÉ

Pour répondre à la demande croissante de la fibre du bois, une des alternatives est d'avoir recours à la production d'espèces à croissance rapide et courte rotation. Les clones de peupliers hybrides ont la productivité plus élevée que la plupart des autres espèces (feuillues et résineuses) de l'est canadien. Les propriétés physiques, mécaniques et morphologiques du bois de peuplier hybride déterminent, en grande partie, son aptitude à satisfaire les exigences de diverses utilisations, notamment pour des applications à haute valeur ajoutée. L'objectif principal de cette étude est d'investiguer les variations inter-clones des propriétés anatomiques, physiques et mécaniques, ainsi que de déterminer les corrélations de ces propriétés entre elle. Un total de sept clones de peupliers hybrides, cultivés sur trois sites dans le sud du Québec, Canada sont étudiés. Cinq arbres par clone ont été échantillonnés de façon aléatoire pour chaque site pour mesurer les propriétés anatomiques (proportion de fibres, proportion de vaisseaux, épaisseur de la paroi de la fibre et proportion du bois de tension), physiques (densité et retrait) et mécaniques (compression et flexion). Les relations entre les caractéristiques anatomiques, physiques et mécaniques ont été également déterminées. Toutes les propriétés étudiées ont montré une variation inter-clone significative, permettant l'identification des clones avec des propriétés du bois de qualité supérieure. Les résultats ont également révélé des corrélations fortes entre les différentes propriétés étudiées. L'augmentation de la proportion du bois de tension était associée à une augmentation de l'épaisseur de la paroi et la proportion de la fibre, et la diminution de la proportion de vaisseaux. De fortes corrélations ont également été trouvées entre la proportion de la fibre, la densité du bois, et les propriétés mécaniques. Des implications pratiques pour des utilisations sont discutées.

A.3 INTRODUCTION

As the consumption of wood and wood-based materials increases, there is a need to develop alternative wood sources such as short-rotation and fast-growing species. Hybrid poplars have received considerable attention for their high productivity compared to native Canadian hardwood and softwood species. It has been widely planted throughout North America due to fast growth rate and easy hybridization. Hybrid poplars yield reach up to 15 m^3/ha.year, much higher than the current average yield in Canadian natural forests, at 1.7 m^3/ha.year (Arseneau and Chiu 2003). Mean annual increment in hybrid poplar plantations at age 7 to 15 years also has been reported at over 2.6 times that of unmanaged natural stands at age 55 years in southern Ontario (Zsuffa 1973). The fast growth of hybrid poplar is generally associated with quite weaker wood properties, especially wood density and mechanical properties (Beaudoin et al. 1992; Hernández et al. 1998). Wood basic density of hybrid poplars in North America ranges from 300 to 390 kg/m^3, and standing trees have high moisture content, typically almost 100%, with only minor differences between sapwood and heartwood (Balatinecz et al. 2001). Currently, poplar wood is used primarily to supply fiber for pulp and paper production and engineered wood products such as oriented strand board (OSB), laminated veneer lumber (LVL), and structural composite lumber (Balatinecz et al. 2001; Heräjärvi 2009; Castro and Fragnelli 2006). Hybrid poplar wood is particularly well suited for these uses (Mansfield 2007) due to its good compressibility and wood uniformity.

Only a few studies have investigated hybrid poplar wood properties and their variation (Avramidis and Mansfield 2005; Hernández et al. 1998; Koubaa et al. 1998 a, b; Lehto 1995) as well as their suitability for different end uses (Avramidis and Mansfield 2005; Mansfield 2007). Results show that age, cloning, and growth conditions are the main sources of this variation (Hernández et al. 1998; Koubaa et al. 1998a, b; Pliura et al. 2007).

It is widely assumed that wood properties in fast-growing species are inferior to those in natural forest species. Moreover, advances in genetic manipulations to obtain harvestable size at a young age may produce a higher percentage of juvenile wood, which has significant effects on wood properties and processing (Hernández et al. 1998; Mátyás and Peszlen 1997). Accordingly, researchers have investigated anatomical variation in wood elements within and among clones (*Populus spp., Eucalyptus spp., Dalbergia spp.*; Koubaa *et al.* 1998a; Pande and Singh 2005; Phelps et al. 1982; Rao et al. 2002). Kern et al. (2005) argued that various fiber features, such as smaller fiber lumen area, greater cell wall thickness, a change in microfibril angle, or biochemical features of the lignin in cell walls, might override potential mechanical weakening caused by greater vessel lumen area. Knowledge of the variation in anatomical properties in hybrid poplar clones would be useful for selecting hybrid poplar clones. This variation largely determines the lignocellulosic yield of the wood, its impact on physical and mechanical properties, and consequently the suitability of the wood for various end uses (Burley and Palmer 1979).

Mechanical properties are controlled by physical and anatomical characteristics such as wood density, grain angle, fiber length, and microfibril angle (Tokumoto et al. 1997). Wood density is a commonly used quality indicator that is related to other wood properties such as mechanical strength and shrinkage as well as pulp yield and properties (Panshin and de Zeeuw 1980). Wood density is influenced mainly by genotype, ageing of the cambium and growth rate (Zhang 1998). Stiffness and strength are strongly influenced by wood density (De Boever et al. 2007; Huang et al. 2003; Innes 2007) and cellular structure (Huang et al. 2003). Stem mechanical strength was associated with thick fiber walls (Jacobsen et al. 2005). A study on wood property variation in hybrid poplar clones found that fiber wall thickness positively correlated with wood density (Pliura et al. 2007).

Previous studies on hybrid poplar wood have found significant differences in wood properties and growth rates among clones and within trees, mainly at different ages and heights (Hernández et al. 1998; Koubaa et al. 1998a; Pliura et al. 2007). No studies have been published on clonal variation or interrelationships among anatomical, physical, and mechanical properties of hybrid poplar clones. The main objective of this study was therefore to investigate clonal variation in the anatomical, physical, and mechanical properties of selected hybrid poplar clones grown at three sites in southern Quebec, Canada. A second objective was to assess the interrelationships among wood's anatomical, physical, and mechanical properties.

A.4 MATERIAL AND METHODS

Seven hybrid clones from three sites (Saint-Ours, Pointe-Platon, and Windsor) were selected for this study (Figure A.1, Table A.1). The Saint-Ours site is part of the Champlain marine deposit with rich salty-clay soil (40% clay), whereas other sites belong to the sandy loam soil type. Five trees for each clone were randomly sampled at each site, for a total of 105 trees; all trees were 15 years old. Samples were collected in July, August, and early September 2007. From each tree, 10cm wide discs were collected at 2.5 m intervals above breast height for the anatomical investigation. Disc edges were coated with wax to maintain wood moisture content and to prevent decay and other environmental alterations. A log 800 mm in length with its base at a height of 0.5m above the ground was collected from each tree stem after felling for physical and mechanical property measurements. Samples were then transported to the Wood Research Centre (Centre de recherche sur le bois, Université Laval, Quebec, Canada) and kept frozen (-5°C) until test sample preparation. A 2.5 cm wide slab was cut along the diameter of each disk (bark to bark passing through the pith) and then conditioned at 20°C and 60% relative humidity for several weeks until an equilibrium moisture content of 12% was reached.

Table A.1 List of hybrid poplar clones collected from three sites in southern Quebec, Canada.

Clone	Hybrid
131	DxN: *Populus deltoides* x *P. nigra*
3230	TxD: *P. trichocarpa* x *P. deltoides*
3565	DxN: *P. deltoides* x *P. nigra*
3570	DxN: *P. deltoides* x *P. nigra*
3586	DxN: *P. deltoides* x *P. nigra*
4813	DxN: *P. deltoides* x *P. nigra*
915508	DNxM: (*P. deltoides* x *P. nigra)* x *P. maximowiczii*

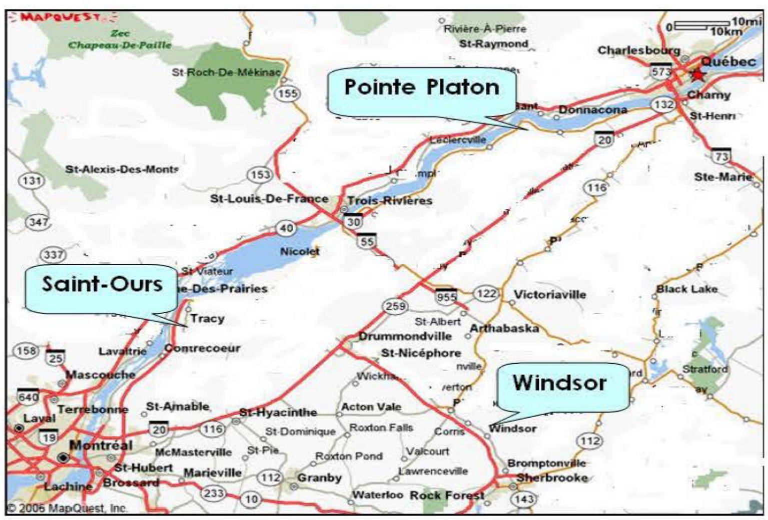


Figure A.1 Map of southern Quebec showing sampling sites.

A series of radial sample blocks of 1 cm x 1 cm x 2 cm were cut from systematic annual growth rings (3, 6, 9, 12) from slabs using a precision saw and a chisel. For the anatomical analysis, thin cross-sections of 20 μm thickness were cut using a rotary microtome with disposable blades inclined at an approximately 15° angle. Sections were then double-stained with 1% safranin stain for 5 minutes and 0.1% astrablue stain for 15 minutes. Sections were then washed in successive ethanol baths (50 %, 80 %, and 100 %) to remove excess stain. Safranin stains all tissues, and astrablue replaces safranin in purely cellulosic G-layers of tension wood. Double-staining is used to detect and confirm tension wood. Sections were then permanently mounted on microscope slides with cover slips using permount. Samples were left for 2 weeks to allow the permount to dry thoroughly. Sample images were taken at ×50 magnification with a Leica compound microscope (DM 1000) equipped with a PL-A686 high-resolution microscopy camera. Black and white images (.tiff format) at 1200 x 1600 resolution were captured using a green filter to maximize contrast. The WinCELL Pro 2004a program (Régent Instruments Inc. 2004) was used to measure fiber wall thickness and tension wood proportion. Tissue proportion in different cell types was estimated from 2 sections from each block. Vessel tissue was distinguished from fiber and ray tissue by defining a 570 μm^2 four-square area for every grid examined, and tissue type that fell within this area was measured. Fiber proportion was measured by the same method.

For physical and mechanical properties, specimens were cut into 20 mm x 20 mm x 100 mm pieces from slab for density, shrinkage, and compression tests, and 20 mm x 20 mm x 330 mm pieces for the bending test. Sample preparation and measurement of physical and mechanical properties were conducted according to ASTM D 143 (ASTM 2007). Properties measured were the basic density (oven-dry mass to green volume ratio), total volumetric shrinkage, and modulus of elasticity (MOE) in static bending and in parallel-to-the-grain compression. For each test, 3 specimens per tree were measured.

SAS® version 8 (SAS Institute Inc. 2008) was used for all statistical analyses. Residuals were tested for normality and homogeneity of variance using statistics provided by the UNIVARIATE procedure. Data transformations were not considered necessary to satisfy the assumptions of analysis of variance and other analyses. Analyses of variance were performed with the GLM procedure using Type III (partial sums of squares) estimation to assess the relative magnitude of each variation source. For all properties studied, the tree effect was not significant, and consequently this factor was removed from the analysis. The mixed linear model was used for the univariate analysis:

$$X_{ijk} = \mu + S_i + C_j + (S \times C)_{ij} + \varepsilon_{ijk} \qquad \text{(A.1)}$$

where $Xijk$ is an observation on the the jth clone from the ith site; μ is the overall mean; Si is the fixed effect due to the ith site; Cj is the fixed effect due to the jth clone; $(S \times C)_{ij}$ is the interaction between site and clone; and εijk is the random error. Some F-ratios involved more than one means square in the denominator and were tested with approximate degrees of freedom. Duncan's multiple range test was used to test the statistical significance (at $p<0.05$) of differences between means for clones at each site (SAS GLM procedure). Variance components were estimated using the VARCOMP procedure (restricted maximum likelihood option) and expressed as a percentage (VAR). The Pearson's correlation coefficients for the interrelationships were computed using the SAS CORR procedure.

A.5 RESULT AND DISCUSSION

A.5.1 Site and clonal variation

Site had a significant effect on all studied properties except on tension wood proportions (Table A.2). The site effect accounted for 2.9 to 20.4% of the total variation, depending on the property examined (Table A.2). These results are in good agreement with Pliura et al. (2007) and Zhang et al. (2003) who reported significant site effects on wood anatomical, physical, and mechanical properties of hybrid poplar clones.

Table A.2 Analysis of variance in wood anatomical, physical, and mechanical properties of hybrid poplar clones.

	DF[b]	F-value	VAR[a]	F-value	VAR	F-value	VAR	F-value	VAR
	Anatomical properties								
		FP (%)		VP (%)		FWT (μm)		TW (%)	
Site	2	59.9**	2.9	18.7*	-	26.7**	13.3	2.1[NS]	20.1
Clones	3	105.6**	28.0	69.2**	40.3	26.8**	31.3	9.5**	21.0
Site x Clones	12	45.3**	62.1	20.5**	47.4	7.4**	31.2	1.3[NS]	-
Error	83		7.0		12.3		24.2		58.9
	Physical properties					Mechanical properties			
		Density (g/m^3)		VSH (%)		Flexural MOE		Compression || MOE	
Site	2	6.8**	8.4	6.2**	4.8	10.5**	11.3	10.9**	20.4
Clones	3	13.4**	42.3	4.0**	2.7	2.49*	4.5	5.5**	20.0
Site x Clones	12	0.8[NS]	-	3.4**	29.0	2.53**	20.7	0.8[NS]	-
Error	83		49.4		62.5		68.0		59.6

Fiber proportion (FP), vessel proportion (VP), fiber wall thickness (FWT), tension wood proportion (TW), density, volumetric shrinkage (VSH), flexural MOE, and MOE in compression parallel to grain at $P<0.05$ significance level.

Level of significance of effects is denoted by *P<0.05, **P<0.01, and [NS] not significant.

[a] Variance of a source as a percentage of the total variance of each variable.

[b] Degree of freedom.

The analysis of variance (Table A.2) indicated significant clonal variation in wood anatomical, physical, and mechanical properties of hybrid poplar clones. The variance component for the clone effect ranged from 2.7 to 42.3%, depending on the examined property. Clonal variance components for the anatomical properties were 28.0% for fiber proportion, 40.3% for vessel proportion, 31.3% for fiber wall thickness, and 21.0% for tension wood. The highest fiber proportion percentage was found for clone DxN-3565 and the lowest for clone DNxM-915508, for a 17.4% difference (Table A.3). The highest vessel proportion percentage was found for clone DxN-3570 and the lowest for clone DxN-3565, for a 27.4% difference. The highest and lowest fiber wall thickness was found for clone DxN-4813 and TxD-3230, respectively. The highest and lowest tension wood was found for clone DxN-4813 and DxN-3570, respectively (Table A.3).

With respect to physical properties, clonal variation accounted for 42.3% of the total variance in wood density. The high clonal variation in wood density is in good agreement with previous works (Beaudoin et al. 1992; Pliura et al. 2007; Zhang et al. 2003). On the other hand, the clonal variation accounted for only 2.7% of the total variance in volumetric shrinkage. This result is in good agreement with previous reports (Koubaa et al. 1998b; Pliura et al. 2007). Clone DxN-4813 showed the highest wood density and volumetric shrinkage. Overall means for density and shrinkage were 0.35 g/cm^3 and 7.8%, respectively (Table A.3). The range of clonal means for density and shrinkage suggests that there was sufficient variation among clones to justify clonal selection to improve wood physical properties.

The clonal variation in mechanical strength (flexural MOE and MOE in compression parallel to grain) was significant (Table A.2). Clonal variation accounted for 4.5% of the variance in flexural MOE and 20% of the variance in compression MOE. Clones with denser wood generally showed higher flexural and compression MOE (Table A.3). The overall means for flexural and compression MOE for clones were 7,131 MPa and 4,441 MPa, respectively, with large standard errors (Table A.3). The site x clone interaction of all variables also was significant (Table A.2), except for wood density, indicating that the clone effect on the studied properties varies across sites. Clones that perform well in one site do not necessarily perform well in another site. The non-significant interaction site x clone for wood density indicates that the density of the studied clones is the same for all three sites.

Table A.3 Least square means of clones and multiple comparison (Duncan's) tests of hybrid poplar clones.

Clone	Anatomical properties				Physical properties		Mechanical properties	
	FP (%)	VP (%)	FWT (μm)	TW (%)	Density (kg/m³)	VSH (%)	Flexural MOE (MPa)	Parallel compression MOE (MPa)
DxN-131	55.3^{C}	26.2^{D}	2.4^{C}	36.2^{C}	340^{B}	8.3^{B}	7007^{AB}	4352^{C}
TxD-3230	51.7^{E}	29.3^{B}	2.1^{E}	37.1^{C}	338^{B}	8.3^{B}	7023^{AB}	4205^{D}
DxN-3565	59.7^{A}	24.1^{F}	2.5^{B}	44.1^{B}	368^{A}	7.9^{BC}	7483^{A}	4754^{A}
DxN-3570	52.7^{D}	$30,0^{A}$	2.2^{E}	35.1^{C}	344^{B}	7.4^{CD}	6965^{AB}	4458^{B}
DxN-3586	51.6^{E}	28.9^{D}	2.5^{BC}	35.7^{C}	329^{B}	7.6^{CD}	6597^{B}	4327^{C}
DxN-4813	57.0^{B}	24.5^{E}	2.7^{A}	47.8^{A}	378^{A}	8.9^{A}	7523^{A}	4692^{A}
DNxM-915508	50.8^{F}	29.4^{B}	2.3^{D}	35.8^{C}	332^{B}	7.2^{D}	7289^{AB}	4273^{CD}
Average ± SE	55.9 ± 4.8	27.3 ± 4.1	2.5 ± 0.5	38.8 ± 7.1	347 ± 26	7.8 ± 0.8	7131 ± 817	4441 ± 530

Averages followed by the same letter are not statistically different at p=0.05.

A.5.2 Interrelationships between wood properties

Table A.4 summarizes the results of the analysis of correlations between the properties studied. At both the tree and clone level, a close negative relationship was found between fiber and vessel proportions (Table A.4). This result was expected because most of the lignocellulosic material in hardwoods consists of vessels and fibers. Increasing the proportion of one element leads to a decrease in the other. This result is in good agreement with previous studies on hybrid poplar and other hardwoods

(Cheng and Bensend 1979; Mátyás and Peszlen 1997; Pande and Singh 2005; Peszlen 1994; Taylor and Wooten 1973).

Table A.4 Correlation coefficients of Pearson among the anatomical, physical, and mechanical properties of hybrid poplar clones. Upper right part (in italic) of the table presents the correlations between tree averages (n=105) and the lower left part of the table indicates the correlations between clone averages within sites (n=21).

	FP	VP	FWT	TW	Density	VSH	MOEF	MOEC
Fiber Proportion (FP)	1	-0.70^{**}	0.53^{**}	0.30^{**}	0.44^{**}	0.19^{ns}	0.33^{**}	0.36^{**}
Vessel Proportion (VP)	-0.75^{**}	1	-0.38^{**}	-0.39^{**}	-0.41^{**}	-0.27^{**}	-0.132^{ns}	-0.17^{ns}
Fiber Wall Thickness (FWT)	0.55^{**}	-0.47^{*}	1	0.30^{**}	0.34^{**}	0.17^{ns}	0.16^{ns}	0.06^{ns}
Tension Wood Proportion (TW)	0.43^{ns}	-0.51^{*}	0.47^{*}	1	0.35^{**}	0.19^{ns}	0.14^{ns}	0.19^{ns}
Density	0.57^{**}	-0.52^{*}	0.48^{*}	0.78^{**}	1	0.37^{**}	0.34^{**}	0.36^{**}
Volumetric Shrinkage (VSH)	0.32^{ns}	-0.39^{ns}	0.34^{ns}	0.40^{ns}	0.47^{*}	1	-0.07^{ns}	-0.04^{ns}
Flexural MOE (MOEF)	0.54^{**}	-0.28^{ns}	0.35^{ns}	0.47^{*}	0.63^{**}	0.03^{ns}	1	0.37^{**}
Compression // MOE (MOEC)	0.55^{**}	-0.24^{ns}	0.27^{ns}	0.39^{ns}	0.60^{**}	0.06^{ns}	0.74^{**}	1

^{ns}: Non-significant; *: significant at p=0.05; **: Significant at p=0.01.

We noted a positive relationship between fiber proportion and fiber wall thickness (Table A.4). Thus, clones with higher fiber proportion tend to develop thicker cell walls. Similarly, the negative relationship between fiber wall thickness and vessel proportion suggests that clones with higher vessel proportion have thinner cell walls. These findings explain the positive correlation between wood density and fiber wall thickness and the negative correlation between vessel proportion and wood density. Indeed, wood density was correlated to all anatomical features at both the clone and tree level. These results are explained by the morphological properties of wood which largely determine its density and higher fiber proportion and fiber wall thickness that are associated with higher wood density.

Positive and significant correlations between tension wood proportion and fiber wall thickness were found (Table A.4). This meant that higher tension wood proportion is associated with smaller fiber lumen area and thicker walls. On the other hand, vessel proportion was negatively correlated to tension wood proportion. These findings are in good agreement with previous results (Kaeiser and Boyce 1995).

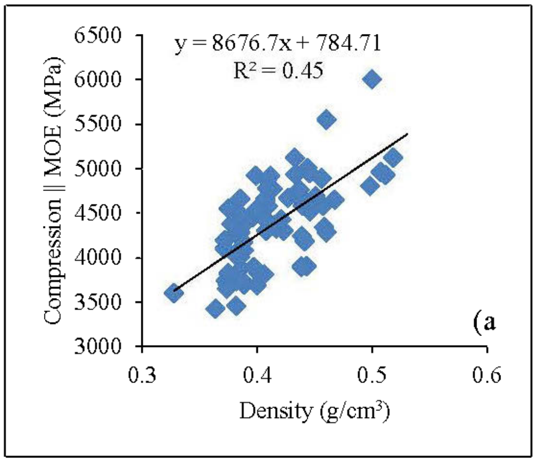
The correlation between wood density and tension wood proportion was positive and significant at both the tree and clone levels. This result could be explained by the higher fiber proportion and greater fiber wall thickness of tension wood. In addition, the formation of tension wood was associated with the presence of a gelatinous layer that increases the amount of cellulosic material in the fiber. Okumura et al. (1977) suggest that increased wall thickness for tension wood fiber was due to increased thickness of the unlignified cellulosic G-layer of the secondary wood layer.

The correlation between tension wood proportion and volumetric shrinkage was not significant. Clair and Thibaut (2001) reported that tension wood shows higher longitudinal and transverse shrinkage in poplar wood. The correlation between tension wood and either flexural or compression MOEs also were not significant. This result is contrary to that of Pilate et al. (2004) who suggested that the presence of the G-layer affects the mechanical properties of wood. The results of the present study indicate that tension wood will not negatively affect either the mechanical performance or the dimensional stability of the wood in service. Similarly, Constantineau (2010) also found that tension wood did not affect the machining properties of these poplar hybrid clones.

Volumetric shrinkage showed positive and significant correlation with wood density. A similar result was reported in *P. euramericana* by Koubaa et al. (1998b). Volumetric shrinkage had no significant relationship with anatomical or mechanical properties in the present study. Volumetric shrinkage and swelling properties are affected by several wood factors, such as the heartwood to sapwood ratio and the microfibril angle in the S2 layer (Bektaş and Güler 2001). However, our results showed that the parameter that exerts the greatest effect on wood shrinkage is wood density.

The relationship between the anatomical and mechanical properties of plants has received considerable attention for its sophisticated multifunctionality (Speck 1994). A number of anatomical features are known to influence plant mechanical properties (Niklas 1992). The present study showed that mechanical properties improved with increased fiber proportion, although no significant relationship with other anatomical properties was found (Table A.4).

This study also found a positive relationship between mechanical properties and wood density. Although this relationship was significant, it was only moderate. Previous studies have found highly significant relationships between density and mechanical properties in hybrid poplar clones (Hernández et al. 1998; De Boever et al. 2007). The moderate relationship found in our study could be explained by the fact that the density used for the correlation analysis was the tree density and not the density of the sample tested. In addition, the test poplar clones were only 15 years of age. Thus, the wood was mainly juvenile and could partially explain for the weaker density mechanical properties relationship. However, the correlation between mechanical properties and test sample density was strong and highly significant (Figure A.2). This result is in good agreement with Zhang (1997) and Hernández et al. (1998). The apparent MOE in static bending was more dependent on wood density than was the MOE in parallel compression.



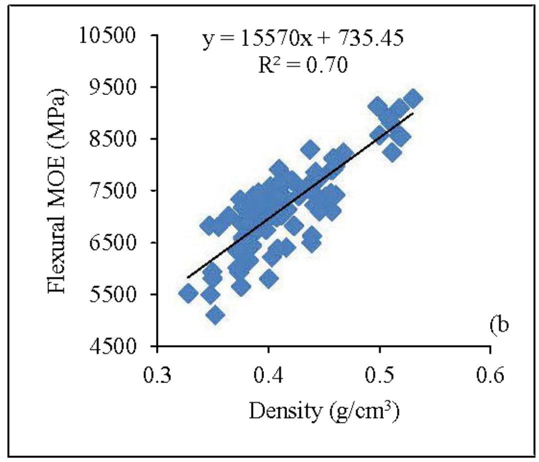


Figure A.2 Relationship between wood density of test samples and (a) parallel compression MOE and (b) flexural MOE.

A.5.3 Practical Implications

The significant effect of clones on the studied properties suggests that clones can be selected for desirable properties. For example, clones with higher vessel proportion and thinner fiber walls, such as DxN-3570, would be suitable for tissue paper, where smoothness is a desirable quality. Vessel elements enhances the smoothness and opacity and is suitable for printing papers (Koubaa 2003). Thus, clone DxN-3570 would be suitable for printing papers. Similarly, clones with higher density and mechanical properties, such as DxN-4813 and DxN-3565, would result in higher fiber yield for the pulp industry and stronger wood for the lumber industry. Such clones also performed the best for most of the wood machining processes studied in a parallel study (Constantineau 2010). Clones DxN-4813 and DxN-3565 would be potential raw material for the pallet industry in the Quebec region as both have better density and mechanical properties.

The moderate correlation between wood density and mechanical properties was unexpected and indicates that density should be used with caution as the sole criteria for clone selection. Selecting for strength based on wood density alone might lead to discarding good clones or selecting low-strength clones.

A.6 CONCLUSIONS

The anatomical, physical, and mechanical properties of hybrid poplar clones were measured and the results were analyzed for clonal and interrelationship variation. The clone effect was highly significant for most studied clones indicating the possibility of selecting clones with desirable attributes. All anatomical properties were interrelated. In general, clones with higher fiber proportion showed thicker cell walls and lower vessel proportion. The variation in anatomical properties largely explained that of wood density. Clones with higher density had higher fiber proportion, thicker cell walls, and lower vessel proportion. Tension wood proportion was positively correlated to fiber proportion and cell wall thickness. The total volumetric shrinkage was correlated to wood density only. Wood density was highly correlated to all studied traits. The correlation between wood density and mechanical properties was moderate. It is therefore apparent that, apart from wood density, other attributes of clones could be involved in mechanical performance. Therefore, caution should be taken when selecting clones for mechanical properties based on density data and the within-tree variation of wood density should be considered.

A.7 ACKNOWLEDGEMENTS

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APPENDIX B

Table B.1 Growth properties of Pointe-Platon site.

	Mean growth data PLA01791 (after 5, 10 & 15 years)								
	1995			2000			2005		
Clone	n	Ht (cm)	DBH (mm)	n	Ht (cm)	DBH (mm)	n	Ht (cm)	DBH (mm)
DxN-131	18	544	40	17	1241	127	16	1704	215
TxD-3230	17	569	48	17	1196	144	18	1766	240
DxN-3565	20	508	38	20	1120	110	19	1556	178
DxN-3570	20	622	51	20	1271	148	20	1747	233
DxN-3586	14	419	31	11	1143	139	11	1591	223
DxN-4813	18	427	29	18	1066	102	17	1591	183
Average		515	40		1173	128		1659	212

Table B.2 Growth properties of Saint-Ours site.

	Mean growth data STO10893 (after 3, 5, 10 & 15 years)											
	1995			1997			2002			2007		
Clone	n	Ht (cm)	DBH (mm)	n	Ht (cm)	DBH (mm)	n	Ht (cm)	DBH (mm)	n	Ht (cm)	DBH (mm)
DxN-131	18	565	51	17	864	96	17	1618	185	12	2170	230
TxD-3230	19	708	66	18	1083	130	18	1834	264	15	2373	360
DxN-3565	19	624	56	20	967	110	20	1615	209	15	2206	288
DxN-3570	20	619	57	17	1014	113	17	1741	225	8	2199	309
DxN-3586	20	633	65	18	979	127	18	1706	247	13	2342	344
DxN-4813	20	553	47	12	868	92	11	1575	188	7	2010	209
DNxM-915508	20	652	63	16	1043	119	16	1702	214	11	2267	309

Mean-Test		622	58		974	112		1684	219		2224	293

Table B.3 Growth properties of Windsor site.

	Mean growth data WIN10593 (after 3, 5, 10 & 15 years)											
	1995			1997			2002			2007		
Clone	n	Ht (cm)	DBH (mm)	n	Ht (cm)	DBH (mm)	n	Ht (cm)	DBH (mm)	n	Ht (cm)	DBH (mm)
DxN-131	20	308	17	20	492	50	19	1278	154	14	1949	250
TxD-3230	20	418	32	20	677	80	20	1576	222	18	2178	330
DxN-3565	19	381	28	19	587	67	19	1351	172	14	1959	264
DxN-3570	19	358	23	19	594	61	19	1393	187	13	2004	291
DxN-3586	20	275	17	19	451	51	19	1088	143	14	1699	215
DxN-4813	20	332	21	20	545	59	20	1377	174	15	2090	267
DNxM-915508	20	320	23	20	548	64	20	1275	166	15	1967	263
Mean-Test		342	23		556	62		1334	174		1978	269

Table B.4 Descriptive statistics, heritability and genetic gain table for different ring density traits.

Properties	Mean ± SE	Coeff. Var.	Heritability (H^2)	Genetic gain
Annual ring density (kg/m^3)	438 ±29	12.5	0.69	18.63
Earlywood density (kg/m^3)	419± 28	14.7	0.58	14.55
Latewood density (kg/m^3)	485±36	13.4	0.71	21.23
Transition density (kg/m^3)	456±32	14.4	0.61	19.08
Annual ring width (mm)	7.4±1.0	40.5	0.56	7.61
Earlywood width (mm)	4.9±0.7	30.7	0.45	2.97

Latewood width (mm)	2.5±0.4	24.0	0.39		1.46

Table B.5 Dynamic MOE (MPa) of studied hybrid poplar clones.

Clones	Pointe-Platon	St-Ours	Windsor
DxN-131	8719	8329	7599
TxD-3230	8711	8799	7598
DxN-3565	9939	10811	7409
DxN-3570	8650	8535	7040
DxN-3586	7849	8115	6678
DxN-4813	8833	10944	8471
DNxM-915508	9038	9220	8534

Table B.6 Descriptive statistics table of growth properties

Properties	Mean ± SE	Coeff. Var.	Heritability (H^2)
DBH, age 10 (mm)	174.5±9.5	16.81	0.18
DBH, age 15(mm)	261.3±12.1	10.3	0.30
Height, age 10(m)	14.1±0.8	24.7	0.27
Height, age 15(m)	19.8±1.0	25.9	0.23

Table B.7 Phenotypic (above diagonal, *in Italic*) and genetic correlation (below diagonal, with standard error given in brackets) coefficient between all ring properties.

	ARD	EWD	LWD	TD	ARW	EWW	LWW
Annual ring density (ARD)	1	*0.92***	*0.70***	*0.81***	*-0.17***	*-0.15***	*-0.10***
Earlywood density (EWD)	0.97 (0.17)	1	*0.47***	*0.68***	*-0.11***	*-0.07***	*-0.11***
Latewood density (LWD)	0.82 (0.22)	0.71 (0.19)	1	*0.91***	*-0.22***	*-0.07***	*-0.30***
Transition density (TD)	0.96 (0.09)	0.88 (0.15)	1.02 (0.10)	1	*-0.21***	*-0.07***	*-0.29***
Annual ring width (ARW)	-0.48 (0.35)	-0.37 (0.33)	-0.48 (0.21)	-0.45 (0.22)	1	*0.84***	*0.64***
Earlywood width (EWW)	-0.39 (0.28)	-0.26 (0.39)	-0.29 (0.36)	-0.38 (0.30)	1.00 (0.11)	1	*0.14***
Latewood width (LWW)	0.39 (0.22)	0.35 (0.26)	-0.49 (0.17)	-0.43 (0.29)	0.86 (0.10)	0.57 (0.16)	1

^{ns}: Non-significant at p=0.05; *: significant at p=0.05; **: Significant at p=0.01.

Table B.8 Phenotypic (r_P) and genetic (r_G) correlation between growth properties and ring densities components

	DBH				Height			
	Age 10		Age 15		Age 10		Age 15	
	r_P	r_G	r_P	r_G	r_P	r_G	r_P	r_G
Annual ring density	-0.50^{ns}	-0.63	-0.59^{ns}	-0.71	-0.60^{ns}	-0.73	-0.71^{*}	-0.78
Earlywood density	-0.39^{ns}	-0.51	-0.55^{ns}	-0.64	-0.53^{ns}	-0.65	-0.67^{*}	-0.76
Latewood density	-0.37^{ns}	-0.47	-0.25^{ns}	-0.49	-0.29^{ns}	-0.38	-0.43^{ns}	-0.53
Transition density	-0.51^{ns}	-0.67	-0.51^{ns}	-0.68	-0.49^{ns}	-0.55	-0.68^{*}	-0.69
Annual ring width	0.89^{**}	0.97	0.76^{**}	0.84	0.78^{**}	1.01	0.56^{ns}	0.70
Earlywood width	0.82^{*}	0.93	0.73^{**}	0.82	0.70^{*}	0.80	0.47^{ns}	0.68
Latewood width	0.92^{**}	1.07	0.78^{**}	0.89	0.89^{**}	0.97	0.68^{*}	0.73

^{ns}: Non-significant at p=0.05; *: significant at p=0.05; **: Significant at p=0.01.