ANATOMICAL PROPERTIES OF SELECTED HYBRID POPLAR CLONES GROWN IN SOUTHERN QUEBEC

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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, width, and proportion, wall thickness, and percent cell wall area. Ray proportion remained constant, whereas the vessel lumen area and proportion decreased with cambial age.

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

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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.* 1998; 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.* 1998; 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.* (1998) 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 of 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.* 1998; 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.

MATERIALS AND METHODS

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 1). Trees for clone DNxM-915508 were obtained from a 1995 trial at the Pointe-Platon site (Table 2). The trial sites are located in Pointe-Platon ($46^0$40'N $71^0$51'W), Saint-Ours ($45^0$54'N $73^0$09'W), and Windsor ($45^0$42'N $71^0$57'W) in southern Quebec, Canada (Fig. 1). 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 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	2bT Sugar maple – basswood domain	2aT Sugar maple – bitternut hickory domain	2cT 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

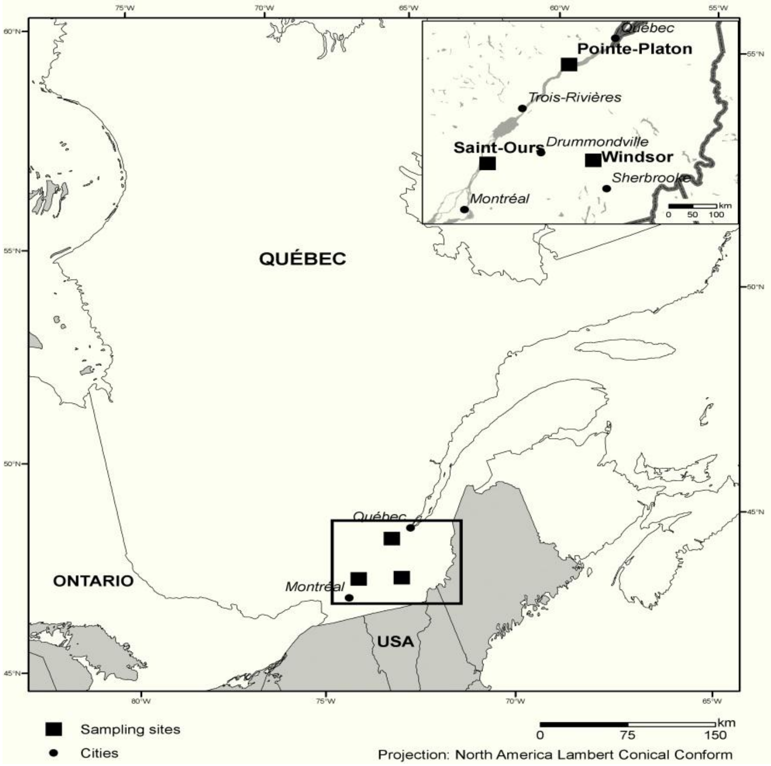

Fig. 1. Map of sampling sites located in the southern part of the province of Quebec, Canada

Sample Collection and Preparation

Seven hybrid clones (Table 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 (Fig. 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.

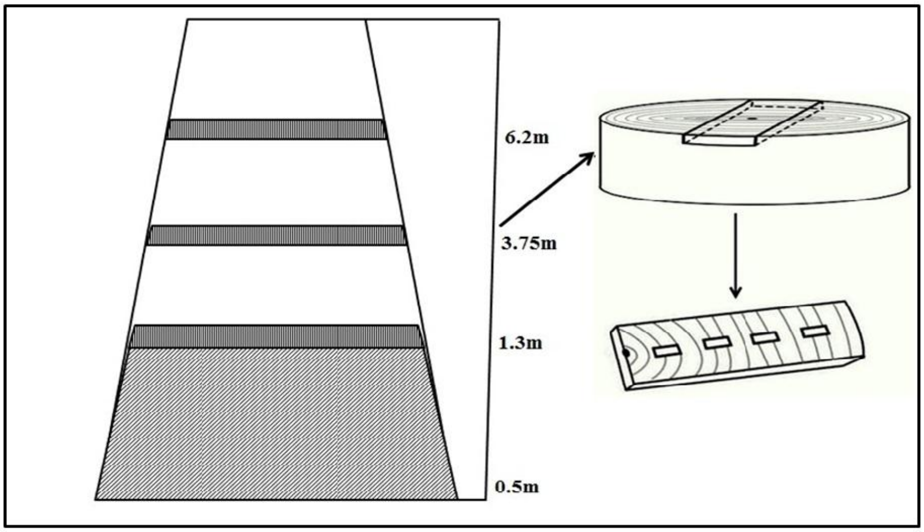

Fig. 2. Schematic diagram of the sampling procedure for the analysis of hybrid poplar wood anatomical properties

Table 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, Qué.)	*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* (Japan)	A controlled cross selected from Québec

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

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 (Fig. 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).

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.

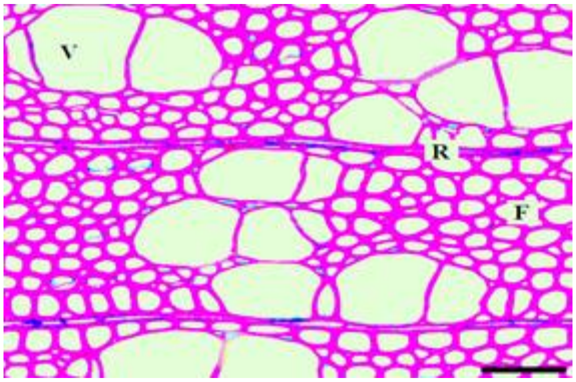

Fig. 3. Microscopic cross-section of hybrid poplar wood: V = vessel, R = ray, F = fiber, Scale bar = 50 *μ*m

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.

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. 1),

$$X_{ijlm} = \mu + S_i + C_j + (S \text{ x } C)_{ij} + A_l + H_m + (A \text{ x } H)_{lm} + \varepsilon_{ijlm} \quad (1)$$

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 $(A \text{ x } H)_{lm}$ 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; $(S \text{ x } C)_{ij}$ 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 individual broad-sense heritability (H^2) was calculated from the variance estimates, as follows (Eq. 2) (Becker 1984; Falconer and Mackay1996),

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

where σ_G^2 and σ_P^2 are the genotypic and phenotypic variance, respectively. Phenotypic variance (σ_P^2) was calculated as shown in Eq. (3).

$$\sigma_P^2 = \sigma_s^2 + \sigma_c^2 + \sigma_h^2 + \sigma_a^2 + \sigma_e^2. \quad (3)$$

The genotypic coefficient of variation (CV_G) and the phenotypic coefficient of variation (CV_p) were calculated from Eqs. 4 and 5, respectively (Burton 1952; Henderson 1953).

$$CV_G = (\sqrt{\sigma_G^2/\text{mean}})\text{x}100 \quad (4)$$

$$CV_p = (\sqrt{\sigma_P^2/\text{mean}})\text{x}100 \quad (5)$$

The mathematical expression for the genetic gain (G) is expressed in Eq. 6. The potential genetic gain from individual tree selection is computed by selection differential (Eq. 7) and 10% selection intensity,

$$G = h^2 * S \quad (6)$$

$$S = i * \sigma_P \quad (7)$$

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.

RESULTS AND DISCUSSION

Within- and Among-Site Variation

Growth site variable showed a highly significant effect on all studied wood anatomical properties (Table 3). Table 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 4). Highest fiber diameter, vessel lumen area, and vessel diameter were also found in trees from Saint-Ours, with the lowest from Pointe-Platon.

For fiber width, the Windsor site showed the highest average and Pointe-Platon the lowest average (Table 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 4).

Pointe-Platon trees showed the lowest average fiber lumen area, fiber diameter, vessel lumen area, and vessel diameter (Table 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 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.

Clonal Variation in Fiber Anatomical Properties

The clone effect on the examined wood anatomical properties was highly significant (Table 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).

Differences among clones were also significant for wood element proportions (fiber, vessel, and ray), as shown in Table 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).

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 4).

Table 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*Site	Height	Cambial Age	Height*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.

Table 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)).

Clone	FL (mm)	FW (μm)	FWT (μm)	AFLA (μm^2)	AFD (μm)	AVLA (μm^2)	AVD (μm)	FP (%)	VP (%)	RP (%)	CWA (%)
	Pointe-Platon										
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										
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										
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										
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.

The highest fiber proportion was found for clone DxN-3565 and the lowest for clone DNxM-915508, for a 17.4% difference (Table 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). 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). 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.* (2011) 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.* 2011). In fact, of the seven studied hybrid poplar clones, these two presented the highest wood density (Huda *et al.* 2011; 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.

Except for fiber length, few data on anatomical properties of poplar species have been reported in the literature (Table 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 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 variations such as heritability and genetic gain for particular properties are important tools for predicting genetic gains (Foster and Shaw 1988).

Table 5. Anatomical Properties of Various *Populus* Clones and 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)**	**AVD (μm)**	**FP (%)**	**VP (%)**	**RP (%)**	**CWA (%)**
Present study	Hybrid poplar	0.94	27.2	2.4	72.9	20.9	49.9	54.1	27.5	18.5	39.4
Koubaa *et al.* (1998)	*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

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.

Table 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

The clonal and environmental variations (Table 3) were used to estimate various genetic parameters, including heritability and genetic gain for anatomical properties (Table 6). The phenotypic coefficient of variation was higher than the genotypic coefficient of variation for all studied properties (Table 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 6). The heritability for fiber length was 0.59, which is comparable to that reported for hybrid poplar (H^2=0.41) by Koubaa *et al.* (1998). 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.* (1998).

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.

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). The patterns for radial and longitudinal variation in fiber properties, vessel properties, and element proportions are shown in Figures 4 to 10, respectively.

The variation in fiber length with cambial age at each of the three sampled heights is illustrated in Fig. 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 (Fig. 4a). This variation pattern concurs with previous studies (Peszlen 1994; Mátyás and Peszlen 1997; DeBell *et al.* 1998; Koubaa *et al.* 1998). 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.* 1998, 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 (Fig. 4a).

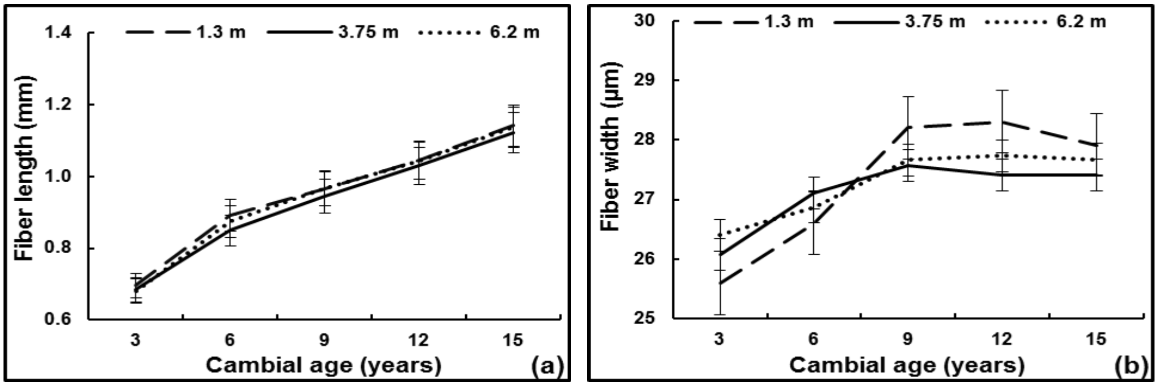

Fig. 4. Variation and standard error for (a) fiber length and (b) fiber width with cambial age and tree height in hybrid poplar clones

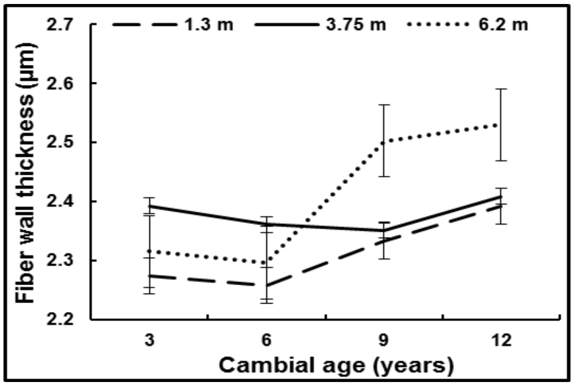

Fig. 5. Variation and standard error for fiber wall thickness with cambial age and tree height in hybrid poplar clones

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). This result concurs with a previous study on *P. x euramericana* clones (Koubaa *et al.* 1998), 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 (Fig. 4b). The same variation pattern was obtained for the three sampled heights.

Fiber wall thickness tended to increase from the pith outwards. This trend is clearly shown at heights 1.3 m and 6.2 m (Fig. 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).

Average fiber lumen area (Fig. 6a), average fiber diameter (Fig. 6b), and cell wall area (Fig. 7) increased from the 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). The average vessel lumen area (Fig. 8a) remained relatively constant. This result is supported by the non-significant effect of age on vessel area (Table 3). The average vessel diameter showed a decreasing trend with increasing cambial age (Fig. 8b). However, despite the significant effect of age on vessel diameter, it accounted for only 3.5% of the total variation (Table 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).

Figures 9 and 10 present the radial variation in wood element proportions. Fiber proportion showed a significant increase from pith to bark for the three sampled heights (Fig. 9a), whereas vessel proportion showed the inverse trend (Fig. 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). However, no particular radial pattern of ray proportion was observed. In fact, the age effect on ray proportion was non-significant (Table 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 (Fig. 4a). Although significant ($\alpha = 5\%$), the variation in fiber length with tree height was marginal, accounting for less than 0.5% of the total variation (Table 3). Fiber width tended to increase with increasing height near the pith but in the outer rings, the opposite trend was observed (Fig. 4b). The longitudinal variation in fiber width was also marginal. It accounted for less than 2% of the total variation (Table 3).

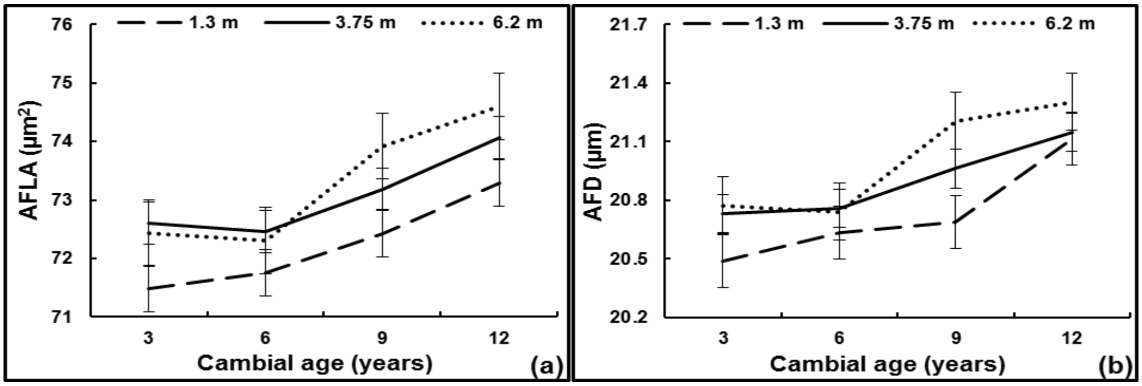

Fig. 6. Variation and standard error for (a) average fiber lumen area (AFLA) and (b) average fiber diameter (AFD) with cambial age and tree height in hybrid poplar clones

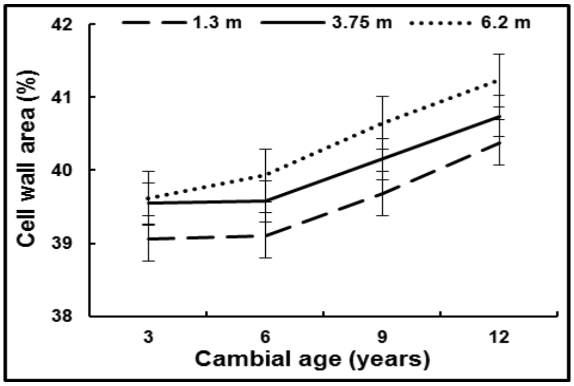

Fig. 7. Variation in cell wall area percentage with cambial age and tree height in hybrid poplar clones

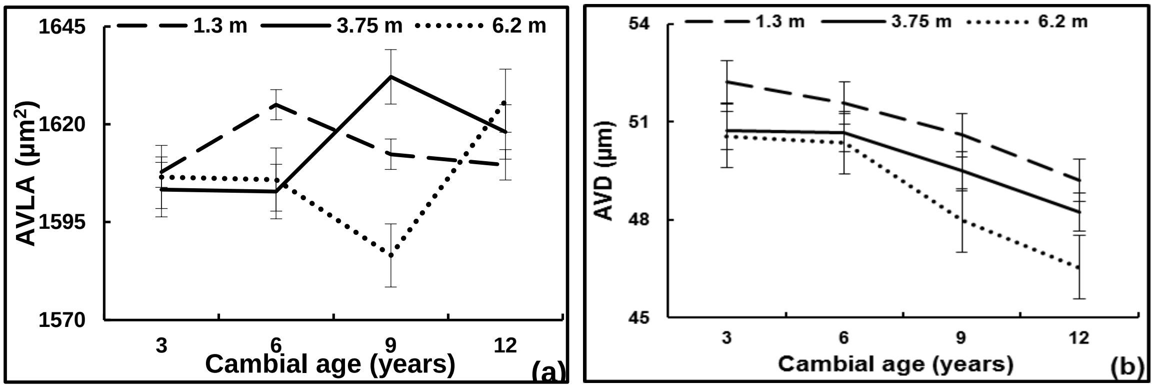

Fig. 8. Variation and standard error for (a) average vessel lumen area (AVLA) and (b) average vessel diameter (AVD) with cambial age and tree height for hybrid poplar clones

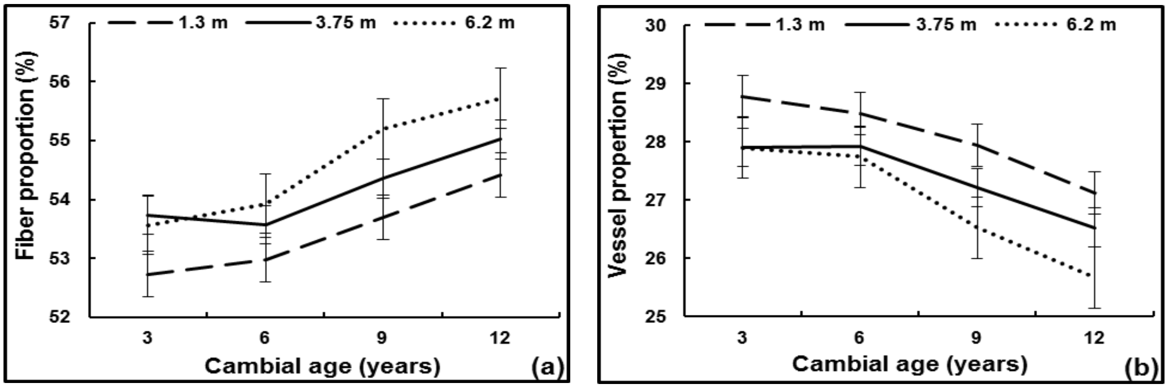

Fig. 9. Variation and standard error for (a) fiber and (b) vessel proportions with cambial age and tree height in hybrid poplar clones

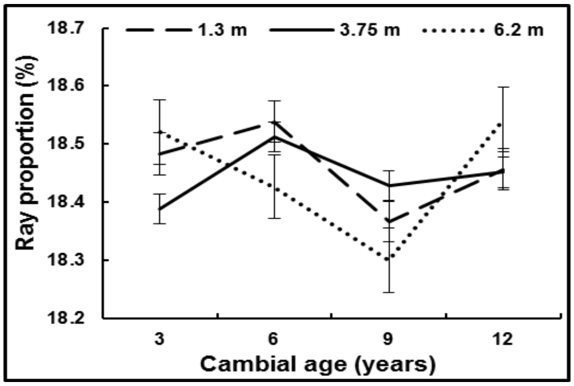

Fig. 10. Variation and standard error for ray proportion with cambial age and tree height in hybrid poplar clones

Fiber wall thickness (Fig. 5), average fiber lumen area (Fig. 6a), average fiber diameter (Fig. 6b), and cell wall area (Fig. 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). 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 (Fig. 8a). However, the average vessel diameter decreased with increasing tree height (Fig. 8b). Although significant, the variation in height accounted for only 1.9% of the variation (Table 3).

The longitudinal variation in the fiber, vessel, and ray proportion are shown in Figs. 9a, 9b, and 10, respectively. Ray proportion did not vary with tree height (Fig. 9). However, fiber proportion increased with increasing tree height, whereas vessel proportion showed the opposite trend. Although statistically significant ($\alpha = 5\%$), these variations accounted for less than 2.5% (Table 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 Zeeuw 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.

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.

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