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Phenotypic and Genotypic Correlations for Wood Properties of Hybrid Poplar Clones of Southern Quebec [†]

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Abstract: This study aims to understand the phenotypic and genotypic correlations among wood anatomical, physical, and mechanical properties of hybrid poplar clones. Samples were taken from seven clones grown on 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, and radial shrinkage), and mechanical wood properties (flexural modulus of elasticity (MOE), modulus of rupture (MOR), ultimate crushing strength parallel to the grain). The observed phenotypic and genotypic correlations between these wood properties were moderate to strong, except for fiber length and vessel proportion. Genotypic correlations for all wood properties were higher than for 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. Furthermore, results from this study show close genotypic and phenotypic correlations between fiber proportion, fiber wall thickness, and wood density, which consequently affect 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

1. Introduction

Canadian forests are among the most extensive in the world and represent one of Canada's most valuable natural resources. Poplar is one of the most important components of this resource, particularly the stands located in the boreal region of the country. In Québec, the Ministère de l'Énergie et des Ressources naturelles (Quebec's ministry of energy and natural resources) has been actively breeding and selecting hybrid poplar clones for growth, adaptability to climatic conditions, and wood quality [1]. The genetic improvement program for poplars was started in 1969 to produce improved hybridized poplar populations using five main parental species: *Populus balsamifera* L., *Populus deltoides*

Bartr., *Populus maximowiczii* A. Henry, *Populus nigra* L., and *Populus trichocarpa* Terr. & Gray [2]. In 2003, anticipated yields were 14 m³/ha·year on average sites, and 20 m³/ha·year on the best sites in southern Quebec [3]. In the boreal region, they were 12 m³/ha·year on the best sites and 10 m³/ha·year on average sites [3]. In Quebec, approximately 12,000 ha of hybrid poplar plantations are managed commercially, while small private landowners have only planted around 1000 ha [4,5].

Poplars are important species for the forest products industries, particularly as a short-rotation tree species providing fiber for pulp and paper, engineered wood products such as oriented strand board, laminated veneer lumber, and structural composite lumber [6]. 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 [7,8].

The introduction of wood quality trait selection criteria is considered 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 [9]. Poplars show substantial variation in many important wood properties, such as fiber dimensions [10,11], and wood density [12]. 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 [13]. Despite its key importance, density is not the only basic property involved in wood mechanical strength development. Jacobsen et al. [14] stated that high mechanical strength is associated with thick fiber walls. Moreover, the thickness of poplar cell walls is in turn positively correlated with wood density [11,15].

In a breeding program, knowledge of genetic correlation plays a vital role in the prediction of correlated responses and the development of effective selection indices. Several studies have focused on the fiber morphology, density, and growth properties of poplars [10–12,16–20]. 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 as follows: (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.

2. Materials and Methods

The materials used in this study were collected from three hybrid poplar clonal trials established by the *Direction de la recherche forestière, ministère de l'Énergie et des Ressources naturelles du Québec* (Department of forest research at Quebec's ministry of energy and 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 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 1). Trees for clone DNxM-915508 were obtained from a 1995 trial at the Pointe-Platon site (Table 2).

Table 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°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 clay loam soil	Champlain marine deposit with silty clay soil.	Sandy loam soil
Initial spacing	1 m × 3 m	1.2 m × 3.5 m	1.5 m × 3.5 m

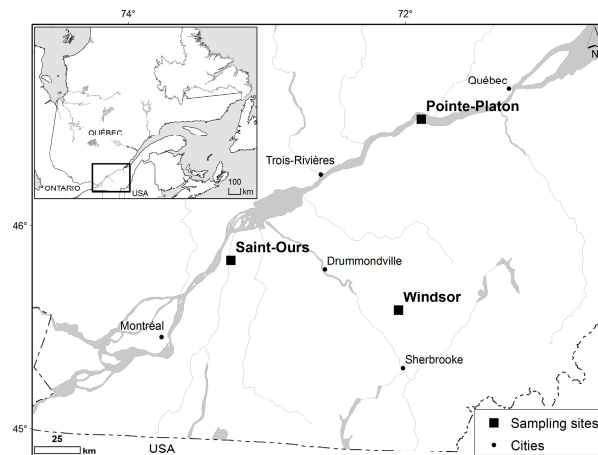


Figure 1. Map of sampling sites located in the south of the Province of Quebec, Canada.

Table 2. Clones of hybrid poplar selected for the study [1,2,21].

Clone	Hybrid *	Female Parent *	Male Parent *	Note
DxN-131	<i>Populus deltoides</i> × <i>P. nigra</i>	<i>P. deltoides</i>	<i>P. nigra</i> 'Italica' as the putative father	A natural hybrid from Montreal, Quebec
TxD-3230	<i>P. trichocarpa</i> × <i>P. deltoides</i> Syn.: <i>P. ×generosa</i> 'Boelare'	<i>P. trichocarpa</i> 'Fritzi Pauley' (from Washington)	<i>P. deltoides</i> (from a cross between <i>P. deltoides</i> from Iowa and from Missouri)	Clone S.910-8 from Belgium. Cultivar 'Boelare'
DxN-3565	<i>P. deltoides</i> × <i>P. nigra</i> Syn.: <i>P. ×canadensis</i>	<i>P. deltoides</i> (from a cross between <i>P. deltoides</i> from Iowa and Illinois)	<i>P. nigra</i> (from a cross between <i>P. nigra</i> from Italy and from Belgium)	Family/tree from Belgium
DxN-3570	<i>P. deltoides</i> × <i>P. nigra</i>	<i>P. deltoides</i>	<i>P. nigra</i> (from a cross between <i>P. nigra</i> from Italy and from Belgium)	Family/tree from Belgium
DxN-3586	<i>P. deltoides</i> × <i>P. nigra</i>	<i>P. deltoides</i>	<i>P. nigra</i> (from a cross between <i>P. nigra</i> from Italy and from Belgium)	Family/tree from Belgium
DxN-4813	<i>P. deltoides</i> × <i>P. nigra</i>	<i>P. deltoides</i> (from Trois-Rivières, Quebec)	<i>P. nigra</i> 'Italica'	A controlled cross from Quebec
DNxM-915508	(<i>P. deltoides</i> × <i>P. nigra</i>) × <i>P. maximowiczii</i>	<i>P. deltoides</i> × <i>P. nigra</i> (from Quebec City, Quebec)	<i>P. maximowiczii</i> (from Japan)	A controlled cross selected from Quebec

* Detailed information on hybrid parents and origin is available from Steenackers [21].

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 [11]. 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. A thinning operation removed two-thirds of the trees from these sites in early 2006.

Five trees of each clone were randomly sampled at each site, for a total of 105 trees. Trees were cut from the Saint-Ours and Windsor sites after 15 growing seasons and from the Pointe-Platon site after 17 growing seasons. Figure 2 illustrates the sampling used in this study. A log between 0.5 m and 1.3 m in length was collected from each tree stem after felling to extract samples for the measurement of shrinkage and mechanical properties. Discs were taken at 1.3 m, 3.75 m and 6.2 m for the measurement of X-ray densitometry and anatomical properties. 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 les matériaux renouvelables, Université Laval, Quebec, QC, Canada) and were kept frozen until test sample preparation. A 2.5 cm

thick 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. This slab was used to extract wood blocks of 1 cm × 1 cm × 1 cm from annual rings 3, 6, 9 and 12 (Figure 2). The blocks served for the preparation of samples for the measurement of anatomical properties. Cross sections of 20 µm were cut using a sliding microtome with a disposable blade. Sections were then double stained with 1% safranin for 5 min and 0.1% astrablue for 15 min. Excess stain was removed by washing sections successively using 50%, 80%, and 100% ethanol solutions. Safranin stains all tissues, and astrablue replaces safranin in the purely cellulosic G-layers of tension wood. Sections were then permanently mounted on microscope slides with cover slips using a Permount mounting medium. Samples were left for two weeks to allow the mounting medium to dry thoroughly.

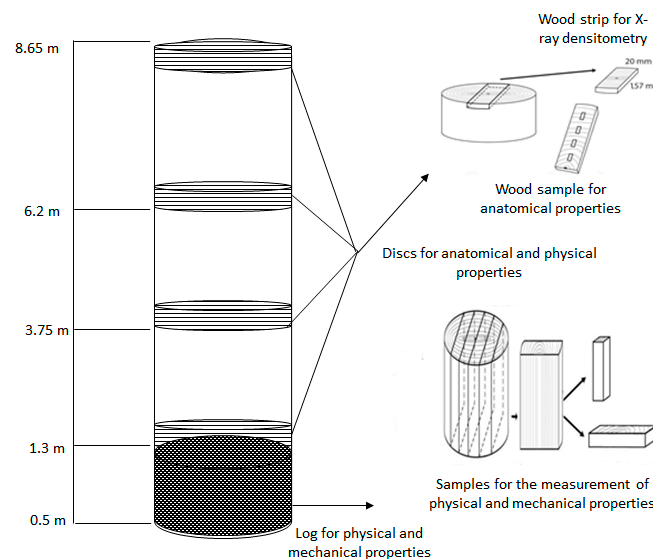


Figure 2. Sampling methods for discs and logs and test samples for the anatomical, physical and mechanical properties of wood.

Twenty-four sample images per tree for a total of 2520 sample images were taken at 50× magnification with a Leica compound microscope (DM 1000, Buffalo Grove, IL, USA) equipped with a PL-A686 high-resolution microscopy camera (Adept Turnkey, Brookvale, Australia). 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., Quebec, QC, Canada), 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 for two sections from each wood sample block. Vessel tissue was distinguished from fiber and ray tissue by defining a 570 µm² 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) (LDA02, OpTest Equipment Inc., Hawkesbury, ON, Canada) was used to measure fiber length.

For physical and mechanical properties, specimens were cut into 20 mm (T, tangential) × 20 mm (R, radial) × 100 mm (L, longitudinal) pieces for basic density, shrinkage, and compression tests, and 20 mm (T) × 20 mm (R) × 330 mm (L) pieces for bending tests. Defect-free samples (315 samples) were carefully selected for these studies. Sample preparation and measurement of physical and mechanical properties were conducted according to the ASTM D143 (standard test methods for small clear specimens of timber) [22]. The physical properties were basic density (oven-dry mass to green volume ratio) and total volumetric, longitudinal, tangential and radial shrinkages. The 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 using an analytical balance and a digital micrometer was used to determine their T, R, and L dimensions. Shrinkage corresponds to the ratio of the variation of dimension to the saturated dimension in each direction. Three-point static bending tests were carried out using a universal testing machine (Zwick/Roell Z20, Zwick Roell, Ulm, Germany) with a span length of 300 mm and maximum load of 20 kN. Compression tests, parallel to the grain, were performed using a universal testing machine (Zwick/Roell Z100) with a maximum load of 100 kN. The load for the mechanical experiments was applied continuously throughout the test at a rate of motion of the movable crosshead of 0.02 mm/mm of nominal specimen length/min.

SAS[®] version 9.4 [23] was used for all statistical analyses. The SAS MIXED procedure with the Restricted Maximum Likelihood estimation method (REML) was used to test the effects of the studied factors [24]. Analyses of variance were performed on mean values of each tree for every variable. The following equation presents the statistical model used for these analyses:

$$Y_{ijk} = \mu + S_i + C_j + (S \times C)_{ij} + \varepsilon_{ijk} \quad (1)$$

where Y_{ijk} is the mean value on the k th tree of the j th clone from the i th site; μ is the overall mean; 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 fixed effect of the interaction between site i and clone j and ε_{ijk} is the random error. The tree nested effect (ramet within clone) was confounded with the error term. Residuals were tested for normality and homogeneity of variance using statistics provided by the SAS UNIVARIATE procedure.

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

To determine the genotypic correlations, the clone effect was considered random in the previous model (Equation (1)), as well as the $(S \times C)$ interaction, to evaluate the variance components. The type A genotypic correlation (r_A) of traits x and y (Equation (2)) and their standard error were obtained using the SAS MIXED and IML procedures (REML method) according to the approach proposed by Holland [24].

$$r_A = \frac{\sigma_{c(xy)}}{\sqrt{\sigma_{c(x)}^2 \times \sigma_{c(y)}^2}} \quad (2)$$

where $\sigma_{c(x)}^2$ is the clonal variance of trait x , $\sigma_{c(y)}^2$ is the clonal variance of trait y and $\sigma_{c(xy)}$ is the genetic covariance between traits x and y .

Approximate standard errors for the genotypic correlation estimates were obtained with the delta method, on the basis of a Taylor series expansion [25]. Some genotypic correlations exceeded ± 1 because of sampling errors and mathematical approximations. In these cases, we considered them equal to ± 1 , and their standard error was assumed equal to 0.

3. Results and Discussion

3.1. General Descriptive Statistics

The mean values, standard errors, range, and coefficients of variation of all studied properties in each of the three sites are presented in Table 3. Trees from the Saint-Ours site had the highest fiber length while those from the Pointe-Platon site had the highest fiber proportion and fiber wall thickness. Huda et al. [26] reported that the site and clone effects on these wood anatomical properties were significant. Saint-Ours trees showed the highest density, average flexural MOE, and crushing strength parallel to the 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.

Table 3. Descriptive statistics of wood properties of hybrid poplar clones at the three sites.

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

3.2. Effect of Site, Clone and Site \times Clone Interaction

The results of the analysis of variance are shown in Table 4. As discussed in previous reports [26–28], the clone effect was highly significant for anatomical, physical and mechanical properties. A clone effect is indicative of the genetic control of the studied properties, which were under weak to moderate genetic control [15,26–28]. Site effect was also highly significant for most of the examined traits. Several factors explain the significant site effect on the studied properties, including edaphic and climatic conditions [20,29].

Table 4. Analysis of variance on selected wood properties of hybrid poplars.

	Site			Clone			Clone \times Site		
Property	df _n	df _d MS	F Value	df _n	df _d	F Value	df _n	df _d	F Value
FL	2	84	39.3 **	6	84	11.7 **	12	84	1.0 ^{ns}
FP	2	84	59.8 **	6	84	105.6 **	12	84	45.4 **
VP	2	84	18.7 **	6	84	69.1 **	12	84	20.5 **
FWT	2	84	26.8 **	6	84	26.7 **	12	84	7.5 **
TW	2	84	0.1 ^{ns}	6	84	13.3 **	12	84	1.7 ^{ns}
BD	2	73	4.2 *	6	73	19.4 **	12	73	1.5 ^{ns}
VSH	2	83	6.2 **	6	83	7.8 **	12	83	3.6 **
LSH	2	83	8.7 **	6	83	7.8 **	12	83	0.7 ^{ns}
RSH	2	82	1.6 ^{ns}	6	82	2.7 *	12	82	2.1 *
TSH	2	83	3.5 *	6	83	4.9 **	12	83	1.6 ^{ns}
MOE	2	83	21.5 **	6	83	3.9 **	12	83	1.1 ^{ns}
MOR	2	83	7.1 **	6	83	26.9 **	12	83	1.5 ^{ns}
CS	2	76	9.4 **	6	76	21.8 **	12	75	0.3 ^{ns}

df_n: numerator degrees of freedom, df_d: denominator degrees of freedom, 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, CS: ultimate crushing strength parallel to the grain * Significant at $p < 0.05$ probability level; ** Significant at $p < 0.01$ probability level; ns not-significant at $p < 0.05$ probability level.

The effect of site \times clone interaction ($S \times C$) was significant for most of the anatomical (FP (fiber proportion), VP (vessel proportion), FWT (fiber wall thickness)) and shrinkage (VSH (volumetric shrinkage), RSH (radial shrinkage)) properties (Table 4). For these properties, the ranking of the clones changes from one site to another [30]. For the wood density and mechanical properties, the $S \times C$ interaction was not significant and the ranking of clones does not change across sites. This result is expected for clonal trials and is in a good agreement with previous findings [10–12,16–20,30]. Zobel and Jett [30] reported that for wood properties, especially wood density, the $G \times E$ interaction (Genotype \times Environment) is very small. However, considering the relatively low number of studied sites (three sites) and the number of replicates within each site (seven clones and five trees per clone), the results are indicative and a larger population should be sampled for more precise estimation of the various genetic and phenotypic parameters.

3.3. Phenotypic Correlations between Wood Properties

The results of the correlation analysis between the studied properties are presented in Table 5. The correlations between fiber length and all other wood properties were not significant at both tree and clone levels. The non-significant correlation between fiber length and wood density is in good agreement with previous findings for hybrid poplar clones [10] and for *P. trichocarpa* [31]. For both tree and clone levels, a close negative relationship was found between fiber and vessel proportions. 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 [15,32] and other hardwoods [29,33–36].

A positive relationship between fiber proportion and fiber wall thickness was also observed (Table 5). 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. Wood density was correlated to all anatomical features, except fiber length, at both the clone and tree levels. Indeed, the fiber morphological properties of wood largely determine its density [37]. Higher fiber proportion and fiber wall thickness are associated with higher wood density [38,39]. On the other hand, a high percentage of vessel proportion will yield hydraulic conductivity, which could cause higher shrinkage, and a disruption in wood structure. Joon [40] reported that the large number of vessel elements present in poplar wood is mainly responsible for the disruption of its structure.

Positive and significant correlations between tension wood proportion and fiber wall thickness were found (Table 5). 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 to tension wood proportion. These findings are in good agreement with previous findings for eastern cottonwood [41].

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. [42] suggested that increased wall thickness for tension wood fibers was mainly due to an increased thickness of the unlignified cellulosic G-layer of the secondary wood layer. The correlation between tension wood proportion and wood density at the clone level (0.78) was much higher than that at the tree level (0.35). Indeed, the clone is the only factor that showed a significant effect on the tension wood proportion (Table 4). In addition, the high variance component for the error terms suggests a high dispersion of the data at the tree level.

The correlation between tension wood proportion and volumetric shrinkage was not significant (Table 5). The volumetric shrinkage of wood is influenced by the tension wood content. The samples from the present study might have variable tension wood contents, which thereby explains the insignificant variation of volumetric shrinkage values among the tested clones, although this result is difficult to explain. However, Gorisek and Straze [43] reported that chemical composition and cell wall organization such as high crystallinity of cellulose in the G-layer, small amounts of matrix substance, and smaller micro voids in cell walls, are probable reasons for the non-significant relationship between wood shrinkage and tension wood. On the other hand, the presence of tension wood was positively correlated to longitudinal, radial, and tangential shrinkages. Ollinmaa [44] found significant positive correlations between longitudinal shrinkage and tension wood proportions for aspen and alder. Many authors also confirmed the existence of a positive correlation between tension wood and longitudinal shrinkage in poplar wood [45] and other hardwoods [46,47]. Sassus [48] described that axial shrinkage of tension wood is often more than five times higher than that of normal wood for beech and poplar.

The correlation coefficients between tension wood and mechanical properties were also significant (Table 5). This result is in good agreement with Pilate et al. [49], who suggested that the presence of the G-layer contributes in a significant way to the 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, Hernández et al. [50] found that tension wood did not affect the machining properties of these same hybrid poplar clones. Clair et al. [51] also found similar results for chestnut. For poplar, the secondary wall of the tension wood is replaced by a poorly lignified or purely cellulosic layer that is generally thick [42]. Besides, tension wood is characterized by a higher proportion of fibers and a lower proportion of vessels [52]. As a result, the increase in fiber proportion implies more walls by volume of wood tissue, thus, a higher density and higher mechanical properties [15].

Table 5. Pearson correlation coefficients among the anatomical, physical, and mechanical properties of hybrid poplar clones. The upper right part (*in italic*) of the table presents the correlations among trees ($n = 105$) and the lower left part indicates the correlations among clones 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	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	-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	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^{**}
RSH	-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^{**}
TSH	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	-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	-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	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; 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 phenotypic correlation 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 *Populus × canadensis* hybrid clones [18]. However, Koubaa et al. [18] recommended the 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 are affected by several wood properties, such as the heartwood to sapwood ratio and the microfibril angle in the S2 layer [53]. Our results showed that, among the properties studied, wood density has the greatest effect on wood shrinkage but the correlations were only moderate or non-significant (Table 5). 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 [54]. This study showed that mechanical properties improved with increased fiber proportion, although no significant relationship with other anatomical properties was found, except for tension wood (Table 5). Bendtsen et al. [55] studied the mechanical properties of cottonwood and hybrid poplar 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 only moderately significant. Previous studies have found highly significant relationships between density and mechanical properties in hybrid poplar clones [56,57]. At the individual tree level, density showed a highly significant correlation with flexural MOR and ultimate crushing strength and a moderate but significant correlation with flexural MOE. On the other hand, density highly affected all mechanical properties at the clonal level. Similarly, all mechanical properties were moderately to highly correlated to wood density. Using the overall tree density instead of the density of the tested sample for the correlation analysis explains the moderate relationships. 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.

The correlation analysis showed that test sample density had a strong correlation with flexural MOE (Figure 3) and MOR (Figure 4) and the ultimate crushing strength (Figure 5). This result is in good agreement with previous findings [58,59].

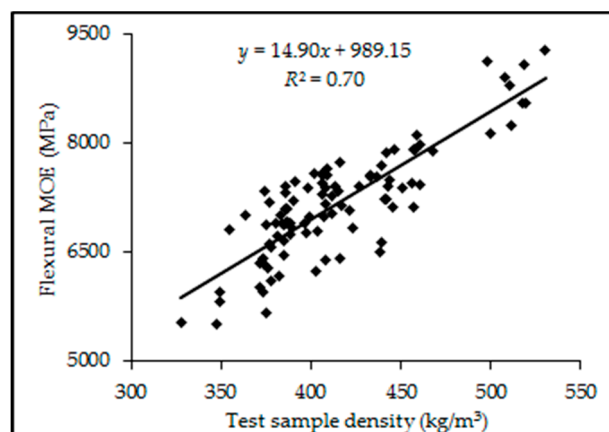


Figure 3. Relationship between test sample density and flexural modulus of elasticity.

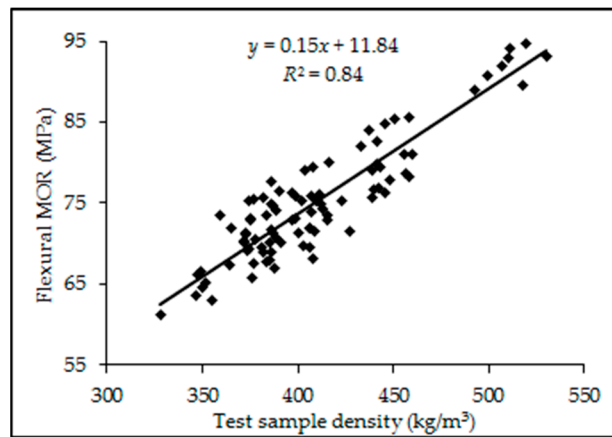


Figure 4. Relationship between test sample density and flexural modulus of rupture.

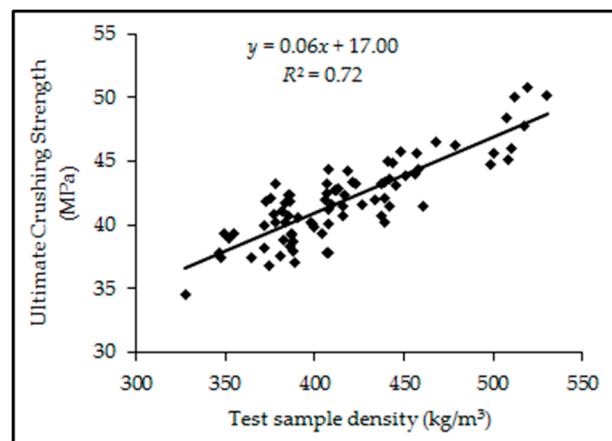


Figure 5. Relationship between test sample density and ultimate crushing strength parallel to the grain.

3.4. Genotypic Correlations between Wood Properties

Genotypic correlations among traits were moderate to strong, depending on traits (Table 6). A significant negative genetic or genotypic correlation has been found between density and growth properties in many studies involving poplar and its hybrids [11,16–19,56]. However, no study has addressed the genotypic correlations among different wood properties in hybrid poplar clones.

Table 6. Estimated genotypic correlations (below diagonal) and standard errors (above diagonal, *in Italic*) for the anatomical, physical, and mechanical properties of hybrid poplar clones.

	FL	FP	VP	FWT	TW	BD	VSH	LSH	TSH	RSH	MOE	MOR	CS
FL	1	<i>0.57</i>	<i>0.48</i>	<i>0.50</i>	<i>0.46</i>	<i>0.44</i>	<i>0.51</i>	<i>0.44</i>	<i>0.51</i>	<i>0.96</i>	<i>0.43</i>	<i>0.44</i>	<i>0.43</i>
FP	−0.07 ^{ns}	1	<i>0</i>	<i>0.33</i>	<i>0</i>	<i>0</i>	<i>0.49</i>	<i>0.49</i>	<i>0</i>	<i>0</i>	<i>0.35</i>	<i>0</i>	<i>0.31</i>
VP	0.21 ^{ns}	−1.00 ^{**}	1	<i>0</i>	<i>0</i>	<i>0</i>	<i>0</i>	<i>0.36</i>	<i>0</i>	<i>0</i>	<i>0.30</i>	<i>0.17</i>	<i>0.23</i>
FWT	−0.06 ^{ns}	0.99 ^{**}	−1.00 ^{**}	1	<i>0.13</i>	<i>0.24</i>	<i>0.42</i>	<i>0.34</i>	<i>0.44</i>	<i>0</i>	<i>0.46</i>	<i>0.25</i>	<i>0</i>
TW	−0.09 ^{ns}	1.00 ^{**}	−1.00 ^{**}	0.88 ^{**}	1	<i>0</i>	<i>0</i>	<i>0.13</i>	<i>0.17</i>	<i>0</i>	<i>0.16</i>	<i>0</i>	<i>0</i>
BD	−0.03 ^{ns}	1.00 ^{**}	−1.00 ^{**}	0.90 ^{**}	1.00 ^{**}	1	<i>0.32</i>	<i>0.23</i>	<i>0.23</i>	<i>0</i>	<i>0.13</i>	<i>0</i>	<i>0.08</i>
VSH	−0.39 ^{ns}	0.70 ^{ns}	−1.00 ^{**}	0.64 ^{ns}	1.00 ^{**}	0.82 [*]	1	<i>0.36</i>	<i>0</i>	<i>0</i>	<i>0.54</i>	<i>0.34</i>	<i>0.42</i>
LSH	−0.21 ^{ns}	0.49 ^{ns}	−0.62 ^{ns}	0.63 ^{ns}	0.89 ^{**}	0.74 ^{**}	0.72 [*]	1	<i>0</i>	<i>0</i>	<i>0.26</i>	<i>0.23</i>	<i>0.15</i>
TSH	−0.28 ^{ns}	1.00 ^{**}	−1.00 ^{**}	0.63 ^{ns}	0.95 ^{**}	0.99 ^{**}	1.00 ^{**}	1.00 ^{**}	1	<i>0</i>	<i>0.40</i>	<i>0.23</i>	<i>0</i>
RSH	−0.17 ^{ns}	1.00 ^{**}	−1.00 ^{**}	1.00 ^{**}	1.00 ^{**}	1.00 ^{**}	1.00 ^{**}	1.00 ^{**}	1.00 ^{**}	1	<i>1.17</i>	<i>0</i>	<i>0</i>
MOE	−0.42 ^{ns}	0.88 ^{**}	−0.79 ^{**}	0.77 ^{ns}	0.95 ^{**}	0.96 ^{**}	0.60 ^{ns}	0.96 ^{**}	0.91 [*]	0.71 ^{ns}	1	<i>0.19</i>	<i>0</i>
MOR	0.12 ^{ns}	1.00 ^{**}	−0.95 ^{**}	0.88 ^{**}	1.00 ^{**}	1.00 ^{**}	0.86 [*]	0.75 ^{**}	0.99 ^{**}	1.00 ^{**}	0.81 ^{**}	1	<i>0.08</i>
CS	−0.12 ^{ns}	0.87 ^{**}	−0.83 ^{**}	1.00 ^{**}	1.00 ^{**}	0.92 ^{**}	0.65 ^{ns}	0.85 ^{**}	1.00 ^{**}	1.00 ^{**}	1.00 ^{**}	0.91 ^{**}	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 $p = 0.01$.

Genotypic correlations between fiber length and other wood properties were negative (except for vessel proportion and flexural MOR) but weak and non-significant. The genotypic correlation between fiber length and density in the present study is in good agreement with a previous report [31] 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 strategies. However, weak correlations among these properties could be an indication that the properties are functionally or developmentally less related, and are therefore less integrated, phenotypically and genetically speaking. 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 a predictor for wood quality for hybrid poplar breeding programs.

The genotypic correlations among fiber proportion and other wood properties were strong and positive, while the genotypic correlation with vessel proportion was negative. Hence, this result indicates the greater importance of fiber proportion for end-uses. As expected, the genotypic correlations were strong and negative between vessel proportion and other properties (Table 6). Additionally, fiber proportion and vessel proportion always showed the 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 correlation. At the genetic level, fiber wall thickness was associated with higher fiber proportion, indicating a tendency for higher mechanical properties. Indeed, the thicker fiber wall corresponds to a higher fiber proportion or smaller vessel diameter, which induces higher wood density and mechanical properties. All correlations with tension wood were positive and high, with the exception of vessel proportion, where a strong negative genotypic correlation was detected. The gelatinous fiber layer in tension wood has narrower vessels and a lower vessel area [15]. In tension wood, the S3 layer of the secondary wall is replaced by the thick cellulosic layer known as the gelatinous fiber layer inside the lumen of the fiber. Kaeiser and Boyce [41] reported that gravitational stimulus generally induces the formation of gelatinous fibers, which modify the anatomical characteristics of other elements of wood, such as modifications in 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 a hydrophilic substance within the G-layers [60]. As a result, when tension wood is dried and water removed rapidly, it causes a greater level of shrinkage and it impacts 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. [10] reported a similar result 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 reductions 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 [11,56]. The genotypic correlations among density and the various shrinkage properties were moderate. Moreover, the genotypic correlation between wood density and mechanical properties was positive and strong (Table 6).

This study further found strong genotypic correlations between wood mechanical properties and anatomical properties, except for fiber length, which does not play an important role in mechanical properties. On the other hand, the strong positive relationships between mechanical properties and anatomical properties (fiber proportion and fiber wall thickness) at the genetic level present a possible strategy for wood quality improvement. Breeding strategies that 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 in tree breeding programs could lead to an improvement

in mechanical strength properties. Moreover, these high genotypic correlations with MOE and MOR make density a strong candidate for the direct genetic improvement of general wood quality. The use of this property could 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 the value of solid wood products, and decrease production costs. However, the choice of the properties to be included in the improvement program 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 as a selection strategy for the improvement of mechanical wood properties.

Broad literature surveys suggested that genetic and phenotypic correlations for wood properties have the same sign and magnitude [59–61]. Our findings 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 (Tables 5 and 6). However, stronger genotypic correlations were found compared to phenotypic correlations for all wood properties. These results may be explained by the environmental influences that weaken the phenotypic correlation between wood properties in comparison to the genotypic correlation. This is consistent with findings from an earlier study showing environmental influence on the phenotypic and genotypic coefficients of variation for wood anatomical properties [26].

Some of the genetic correlations, showed a relatively high standard error. This result could be explained by the relatively small sample investigated in this study. Thus, a larger sampling is needed for more precise estimation of the various genetic parameters.

4. Conclusions

The 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 clone attributes could be involved in mechanical performance. Therefore, caution is recommended when selecting clones for mechanical properties 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.

The genotypic correlations for all wood components were higher and more stable than the corresponding phenotypic correlations. Several strong genotypic relationships were presented in this study, which are good indicators for the detection of genetic effects, thus leading to significant improvement in the selection process for these properties. Considerable variation in wood properties within trees and clones was of sufficient magnitude and could provide an opportunity to select clones for utilization in different applications. However, a future challenge will be to determine whether breeding objectives are compatible with industrial objectives by improving wood properties.

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References

1. Périnet, P.; Caron, F.; Fauchon, A. *Liste des Clones Recommandés de Peuplier Hybride selon les Sous-Régions Écologiques au Québec*; Direction de la Recherche Forestière, MRNQ: Québec, QC, Canada, 2012; p. 1.
2. Périnet, P. The Poplar breeding program in Québec. In *Proceedings of the Poplar Culture: A Collaborative Effort from Clone to Mill, Annual Meeting of the Poplar Council of Canada*, Québec, QC, Canada, 16–21 September 2007; CPC/PCC 2007 Field Trip Guide. Périnet, P., Perron, M., Bélanger, P., Eds.; MRNF-DRF: Québec, QC, Canada, 2007; pp. 11–12.
3. Messier, C.; Bigué, B.; Bernier, L. Using fast-growing plantations to promote forest ecosystem protection in Canada. *Unasylva* **2003**, *54*, 59–63.
4. Fortier, J.; Bigué, B.; Morissette, S.; Couture, J. *Le Guide de Populiculture au Québec: Guide Pratique sur la Culture du Peuplier Hybride au Québec*; Réseau Ligniculture Québec: Québec, QC, Canada, 2011; p. 124.
5. Morissette, S. *Superficies de Peuplier Hybride en Production au Québec*; Lignes et Cultures, Bulletin du Réseau Ligniculture Québec: Québec, QC, Canada, 2012; Volume 11, p. 8.
6. Balatincez, J.J.; Kretschmann, D.E.; Leclercq, A. Achievements in the utilization of poplar wood—Guide posts for the future. *For. Chron.* **2001**, *77*, 265–269. [[CrossRef](#)]
7. Geimer, R.L. Properties of structural flakeboard manufactured from 7-year-old intensively cultured poplar, tamarack, and pine. *For. Prod. J.* **1986**, *36*, 42–48.
8. Semple, K.E.; Vaillant, M.H.; Kang, K.Y.; Oh, S.W.; Smith, G.D.; Mansfield, S.D. Evaluating the suitability of hybrid poplar clones for the manufacture of oriented strand boards. *Holzforschung* **2007**, *61*, 430–438. [[CrossRef](#)]
9. Downes, G.M.; Hudson, I.; Raymond, C.A.; Dean, G.H.; Michell, A.J.; Schimleck, L.R.; Evans, R.; Muneri, A. *Sampling Plantation Eucalypts for Wood and Fibre Properties*; CSIRO Publishing: Collingwood, New Zealand, 1997; p. 132. ISBN 0-6430-6284X.
10. Zhang, S.Y.; Yu, Q.; Chauret, G.; Koubaa, A. Selection for both growth and wood properties in hybrid poplar clones. *For. Sci.* **2003**, *49*, 901–908.
11. Pliura, A.; Zhang, S.Y.; Mackay, J.; Bousquet, J. Genotypic variation in wood density and growth traits of poplar hybrids at four clonal trials. *For. Ecol. Manag.* **2007**, *238*, 92–106. [[CrossRef](#)]
12. Zhang, P.; Wu, F.; Kang, X. Genotypic variation in wood properties and growth traits of triploid hybrid clones of *Populus tomentosa* at three clonal trials. *Tree Genet. Genom.* **2012**, *8*, 1041–1050. [[CrossRef](#)]
13. Panshin, A.J.; de Zeeuw, C. *Textbook of Wood Technology*; McGraw-Hill Book Co.: New York, NY, USA, 1980; p. 732. ISBN 13: 978-0070484405.
14. Jacobsen, A.L.; Ewers, F.W.; Pratt, R.B.; Paddock, W.A.; Davis, S.D. Do xylem fibers affects vessel cavitation resistance? *Plant Physiol.* **2005**, *139*, 546–556. [[CrossRef](#)] [[PubMed](#)]
15. Huda, A.; Koubaa, A.; Cloutier, A.; Hernández, R.E.; Fortin, Y. Wood Quality of hybrid poplar clones: Clonal variation and property interrelationships. In *Proceedings of the 3rd International Scientific Conference on Hardwood Processing*, Virginia Tech, Blacksburg, VA, USA, 16–18 October 2011; pp. 281–289.
16. Yanchuk, A.; Dancik, B.; Micko, M. Variation and heritability of wood density and fiber length of trembling aspen in Alberta, Canada. *Silv. Genet.* **1984**, *33*, 11–16.
17. Beaudoin, M.; Hernández, R.E.; Koubaa, A.; Poliquin, J. Interclonal, intraclonal, and within-tree variation in wood density of poplar hybrid clones. *Wood Fiber Sci.* **1992**, *24*, 147–153.
18. Koubaa, A.; Hernández, R.E.; Beaudoin, M. Shrinkage of fast-growing poplar hybrid clones. *For. Prod. J.* **1998**, *48*, 82–87.
19. Koubaa, A.; Hernández, R.E.; Beaudoin, M.; Poliquin, J. Interclonal, intraclonal, and within-tree variation in fiber length of poplar hybrid clones. *Wood Fiber Sci.* **1998**, *30*, 40–47.

20. Pliura, A.; Yu, Q.; Zhang, S.Y.; MacKay, J.; Périnet, P.; Bousquet, J. Variation in wood density and shrinkage and their relationship to growth of selected young poplar hybrid crosses. *For. Sci.* **2005**, *51*, 472–482.
21. Steenackers, V. The collection and distribution of seeds and cuttings of poplar species, hybrids and clones which are of importance for biomass production in energy plantations—Progress report CPB-13 (*Populus nigra*, *Populus trichocarpa*, *Populus yunnanensis*). In Proceedings of the IEA/FAO Workshop, Rungstedgaard, Denmark, 28–30 October 1985; Mitchell, C.P., Nilsson, P.O., Zsuffa, L., Eds.; Research in Forestry for Energy: Garpenberg, Sweden, 1986; Volume 1, pp. 107–110.
22. ASTM. *Standard Test Methods for Small Clear Specimens of Timber*; D 143-94 (Reapproved 2007); ASTM International: Philadelphia, PA, USA, 2007; p. 32.
23. *User's Guide*, version 9.4; SAS Institute Inc.: Cary, NC, USA, 2013.
24. Holland, J.B. Estimating Genotypic Correlations and Their Standard Errors Using Multivariate Restricted Maximum Likelihood Estimation with SAS Proc MIXED. *Crop Sci.* **2006**, *46*, 642–654. [[CrossRef](#)]
25. Lynch, M.; Walsh, B. *Genetics and Analysis of Quantitative Traits*; Sinauer Associates, Inc.: Sunderland, MA, USA, 1998; p. 980.
26. Huda, A.; Koubaa, A.; Cloutier, A.; Hernández, R.E.; Périnet, P. Anatomical properties of selected hybrid poplar clones grown in Southern Quebec. *BioResources* **2012**, *7*, 3779–3799.
27. Huda, A.; Koubaa, A.; Cloutier, A.; Hernández, R.E.; Fortin, Y. Qualité du bois de peuplier hybride: Effet du site, du clone et de l'âge sur les propriétés anatomiques, physiques et mécaniques de l'arbre. *Info-RLQ* **2011**, *8*, 1–5.
28. Huda, A.; Koubaa, A.; Cloutier, A.; Hernández, R.E.; Fortin, Y. Variation of the physical and mechanical properties of hybrid poplar clones. *BioResources* **2014**, *9*, 1456–1471. [[CrossRef](#)]
29. Peszlen, I. Influence of age on selected anatomical properties of *Populus* clones. *IAWA J.* **1994**, *15*, 311–321. [[CrossRef](#)]
30. Zobel, B.J.; Jett, J.J. *Genetics of Wood Production*; Springer Series in Wood Science; Springer: New York, NY, USA, 1995; p. 338.
31. Porth, I.; Klápšte, J.; Lai, B.S.K.; Geraldès, A.; Muchero, W.; Tuskan, G.A.; Douglas, C.J.; El-Kassaby, Y.A.; Manfield, S.D. *Populus trichocarpa* cell wall chemistry and ultrastructure trait variation, genetic control and genetic correlations. *New Phytol.* **2013**, *197*, 777–790. [[CrossRef](#)] [[PubMed](#)]
32. Eckstein, D.; Liese, W.; Shigo, A.L. Relationship of wood structure to compartmentalization of discoloured wood in hybrid poplar. *Can. J. For. Res.* **1979**, *9*, 205–210. [[CrossRef](#)]
33. Taylor, F.W.; Wooten, T.E. Wood property variation of Mississippi delta hardwoods. *Wood Fiber Sci.* **1973**, *5*, 2–13.
34. Cheng, W.W.; Benseid, D.W. Anatomical properties of selected *Populus* clones grown under intensive culture. *Wood Sci.* **1979**, *11*, 182–187.
35. Mátyás, C.; Peszlen, I. Effect of age on selected wood quality traits of poplar clones. *Silv. Genet.* **1997**, *46*, 64–72.
36. Pande, P.K.; Singh, M. Intraclonal, inter-clonal and single tree variations of wood anatomical properties and specific gravity of clonal ramets of *Dalbergia sissoo* Roxb. *Wood Sci. Technol.* **2005**, *39*, 351–366. [[CrossRef](#)]
37. Pot, D.; Chantre, G.; Rozenberg, P.; Rodrigues, J.C.; Jones, G.L.; Pereira, H.; Hannrup, B.; Cahalan, C.; Plomion, C. Genetic control of pulp and timber properties in maritime pine (*Pinus pinaster* Ait.). *Ann. For. Sci.* **2002**, *59*, 563–575. [[CrossRef](#)]
38. Fujiwara, S.; Sameshima, K.; Kuroda, K.; Takamura, N. Anatomy and properties of Japanese hardwoods. I. Variation of fibre dimensions and tissue proportions and their relation to basic density. *IAWA J.* **1991**, *12*, 419–424. [[CrossRef](#)]
39. Ziemińska, K.; Butler, D.W.; Gleason, S.M.; Wright, I.J.; Westoby, M. Fibre wall and lumen fractions drive wood density variation across 24 Australian angiosperms. *AoB Plants* **2013**, *5*, plt046. [[CrossRef](#)]
40. Joon, A. High Yield Pulp of Hybrid Poplar Wood by Integrating Steam Explosion Process as a Pre-Stage to Alkali Pulp. Master's Thesis, University of Toronto, Toronto, ON, Canada, 2000.
41. Kaeiser, M.; Boyce, S.G. The relationship of gelatinous fibers to wood structure in Eastern cottonwood (*Populus deltoides*). *Am. J. Bot.* **1965**, *52*, 711–715. [[CrossRef](#)]
42. Okumura, S.; Harada, H.; Saiki, H. Thickness variation of the G-layer along a mature and a differentiating tension wood fiber in *Populus euramericana*. *Wood Sci. Technol.* **1977**, *11*, 23–32. [[CrossRef](#)]

43. Gorisek, Z.; Straze, A. Sorption and swelling characteristics of normal and tension beech wood (*Fagus sylvatica* L.). In *Wood Structure and Properties'06*; Kurjatko, S., Kudela, J., Lagana, R., Eds.; Arbora Publishers: Zvolen, Slovakia, 2006; pp. 227–231. ISBN 80-968869-4-3.
44. Ollinmaa, P.J. Study on reaction wood. *Acta For. Fen.* **1961**, *72*, 52–54, (In Finnish with English Summary).
45. Clair, B.; Thibaut, B. Shrinkage of the gelatinous layer of poplar and beech tension wood. *IAWA J.* **2001**, *22*, 121–131. [[CrossRef](#)]
46. Polge, H. Essais de caractérisation de la veine verte du merisier. *Ann. Sci. For.* **1984**, *41*, 45–58. [[CrossRef](#)]
47. Nepveu, G. Variabilité. In *Le Bois Matériau d'Ingénierie*; Jodin, P., Ed.; Association pour le Recherche sur le Bois en Lorraine (ARBOLOR): Nancy, France, 1994; pp. 128–182. ISBN 13: 978-2907086073.
48. Sassus, F. Deformations de Maturation et Propriétés du Bois de Tension chez le Hêtre et le Peuplier: Mesures et Modèles. Ph.D. Thesis, ENGREF, Montpellier, France, 1998; p. 170. (in French).
49. Pilate, G.; Dejardin, A.; Laurans, F.; Leple, J.C. Tension wood as a model for functional genomics of wood formation. *New Phytol.* **2004**, *164*, 63–72. [[CrossRef](#)]
50. Hernández, R.E.; Constantineau, S.; Fortin, Y. Wood machining properties of poplar hybrid clones from different sites following various drying treatments. *Wood Fiber Sci.* **2011**, *43*, 394–411.
51. Clair, B.; Ruelle, J.; Thibaut, B. Relationship between growth stresses, mechano-physical properties and proportion of fibre with gelatinous layer in chestnut (*Castanea Sativa* Mill.). *Holzforschung* **2003**, *57*, 189–195. [[CrossRef](#)]
52. Jourez, B.; Riboux, A.; Leclercq, A. Anatomical characteristics of tension wood and opposite wood in young inclined stems of poplar (*Populus euramericana* cv 'Ghoy'). *IAWA J.* **2001**, *22*, 133–157. [[CrossRef](#)]
53. Bektaş, İ.; Güler, C. The determination of some physical properties of beech wood (*Fagus orientalis* Lipsky) in the Andırın region. *Turk. Agric. For. J.* **2001**, *25*, 209–215.
54. Niklas, K.J. *Plant Biomechanics: An Engineering Approach to Plant form and Function*; University of Chicago Press: Chicago, IL, USA, 1992.
55. Bendtsen, B.A.; Maeglin, R.R.; Deneke, F. Comparison of mechanical and anatomical properties of eastern cottonwood and *Populus* hybrid NE-237. *Wood Sci.* **1981**, *14*, 1–14.
56. Hernández, R.E.; Koubaa, A.; Beaudoin, M.; Fortin, Y. Selected mechanical properties of fast-growing poplar hybrid clones. *Wood Fiber Sci.* **1998**, *30*, 138–147.
57. De Boever, L.; Vansteenkiste, D.; Van Acker, J.; Stevens, M. End-use related physical and mechanical properties of selected fast-growing poplar hybrids (*P. trichocarpa* x *P. deltoides*). *Ann. For. Sci.* **2007**, *64*, 621–630. [[CrossRef](#)]
58. Zhang, S.Y. Wood specific gravity–mechanical property relationship at species level. *Wood Sci. Technol.* **1997**, *31*, 181–191. [[CrossRef](#)]
59. Falconer, D.S.; Mackay, T.F. *Introduction to Quantitative Genetics*, 4th ed.; Pearson Education: Harlow, UK, 1996; p. 480. ISBN 13: 978-0582243026.
60. Mellerowicz, E.J.; Gorshkova, T.A. Tensional stress generation in gelatinous fibers: A review and possible mechanism based on cell-wall structure and composition. *J. Exp. Bot.* **2012**, *63*, 551–565. [[CrossRef](#)] [[PubMed](#)]
61. Lynch, M.; Walsh, J.B. *Genetics and Analysis of Quantitative Traits*, 1st ed.; Sinauer Associates, Oxford University Press: Sunderland, MA, USA, 1998; p. 980. ISBN 13: 978-0878934812.



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