

## Genetic influence on components of wood density variation in white spruce

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Conifer breeding programmes are increasingly selecting for wood quality in addition to growth so to ensure a sufficient flow of high-quality fibre from future forest plantations. As wood density is one of the most frequently used indicators of wood quality, there is a growing interest to consider this trait in selection, and thus enhance the properties of end-use products from planted trees. However, wood density varies at different scales within trees, with pith-to-bark patterns and year-to-year fluctuations representing two important sources of variation. From both physiological and end-use points of view, it is desirable to produce stems with limited pith-to-bark and year-to-year wood density variation. In the present study, we assessed patterns of pith-to-bark and year-to-year variation in 2196 wood density patterns and evaluated the genetic control of traits characterizing this variation. The experimental data came from a 15-year-old white spruce genetic trial representing 93 full-sib families replicated in two contrasting environments in Quebec, Canada. To separate pith-to-bark from year-to-year variation, non-linear models were developed to describe pith-to-bark patterns of variation in the mean ring density (MRD) of individual trees as well as for latewood density (LWD) and latewood proportion. We observed that pith-to-bark variation was more under genetic control than year-to-year variation, for which only LWD and proportion of latewood width to overall ring width reached moderate genetic control. Little genotype-by-environment interaction was observed although wood density patterns differed significantly between sites. The present approach could help identify trees or families that tend to have limited pith-to-bark and year-to-year variation in wood density as part of tree genetic improvement programmes to provide future trees with more uniform and desirable wood attributes.

### Introduction

Forest plantations regenerate a large proportion of the forests harvested annually. Some of the advantages of replanting instead of relying on natural regeneration is the control of species composition, the possibility to choose specific genotypes in seedling stock and to consider future feedstock requirements of the forest industry. Through genetic selection programmes, planted trees usually grow faster and can be made more resistant to disturbances, while maintaining desirable wood properties (Beaulieu and Bousquet, 2010). In forestry, genetic improvement consists of selecting trees with traits of interest, to mate and reproduce them and ultimately choose their best progeny as planting material (Zobel *et al.*, 1984). Tree breeding programmes therefore bear fundamental importance to ensure that the forest resource meets the future needs of end-users (Mullin *et al.*, 2011; McLean *et al.*, 2016; Hassegawa *et al.*, 2020).

Until recently, tree breeding efforts were primarily dedicated to increasing wood volume production (Li *et al.*, 1997; Mullin *et al.*, 2011). Past selection efforts together with heritable genetic variation for growth traits have led to significant growth gains for several species. However, the negative genetic correlations usually observed between growth and wood quality traits have raised concerns about wood structural quality in plantations (Beaulieu and Bousquet, 2010; Lenz *et al.*, 2010, 2013; Kennedy *et al.*, 2013; Hong *et al.*, 2014). Conifer breeding programmes have thus started to consider wood quality traits among selection criteria to maintain and improve the end-use properties of commercial lumber from plantations. For example, in eastern Canada, important genetic selection programmes are in place for spruces, such as white spruce (*Picea glauca* (Moench) Voss) (Beaulieu, 2003; Mullin *et al.*, 2011; Lenz *et al.*, 2013). This species bears significant economic importance due to its abundance over a vast geographical area and desirable wood properties

such as high wood density, stiffness and strength compared with other species in the boreal forest of North America (Eyre, 1980; Abrahamson, 2015). In the province of Quebec, two generations of white spruce seed orchards have been established to support the production of improved planting material (Mullin *et al.*, 2011). In recent years, white spruce seedlings all from improved sources have accounted for approximately 20 per cent of the 130 million seedlings planted annually in Quebec's public forest (Villeneuve *et al.*, 2016).

The concept of wood quality is based on the suitability of various wood characteristics for a specific end-use (Briggs and Smith, 1986). White spruce logs are primarily used as feedstock for the dimensional lumber industry, whereas by-products in the form of wood chips, shavings and sawdust are usually processed by pulp and paper mills. Properties that determine lumber quality include both mechanical and physical properties (Zhang and Koubaa, 2008). For pulp and paper, wood quality is more dependent on fibre length, cellulose content and wood density, which is linked to pulp yield (Santos *et al.*, 2012). Beyond those specific traits, wood density is one of the most widely used indicators of wood quality, both because of its relative ease of measurement and because of its positive correlation with other physico-mechanical characteristics of the material (Mckendry, 2002; Macdonald and Hubert, 2002; Alteyrac *et al.*, 2006). Increasingly, studies are investigating the genetic control of wood physical traits such as wood density (Lenz *et al.*, 2010; McLean *et al.*, 2016). Lenz *et al.* (2011) studied the relationships between wood traits including density, microfibril angle, stiffness and radial growth in white spruce. The authors found that the genetic control of traits, as well as the correlations between them varied from ring to ring and followed distinct trends with cambial age.

In addition to its mean value in a stem or piece of lumber, the radial variation of wood density can have an important effect on the suitability of wood for end-use (Gardiner *et al.*, 2011). Such radial variation occurs at two scales, forming both pith-to-bark and year-to-year variation (Nicault *et al.*, 2010). In spruce species, the pith-to-bark pattern of variation is generally characterized by higher wood density near the pith and a decrease to reach a minimum in the early years of growth, followed by a gradual increase as ring width tends to decrease near the bark (Koubaa *et al.*, 2005; Lenz *et al.*, 2010; Chen *et al.*, 2014).

In temperate and boreal species such as white spruce, part of the year-to-year variation of wood density is related to the succession of growing seasons and much variation is also observed within growing seasons (Corriveau *et al.*, 1991). Low-density earlywood is produced in the spring and allows sap conduction in the xylem (Smith, 1985; Schweingruber *et al.*, 1993). The latewood formed at the end of the growing season is characterized by higher wood density. It has mainly a structural function in the tree. Despite the predictable pattern caused by this succession of seasons, both early- and latewood densities are known to vary from year-to-year (Koubaa *et al.*, 2000, 2005; Björklund *et al.*, 2017). Studies have linked the inter-annual variability of wood density with variations in annual environmental conditions (Becker *et al.*, 1995; Huang *et al.*, 2007; Nicault *et al.*, 2010; Zaehle *et al.*, 2014). More specifically, long-term growth analyses have shown a link between yearly wood density values and climate variables, such as the effect of summer temperatures in white

spruce (D'Arrigo *et al.*, 1992) and other species (Franceschini *et al.*, 2013a).

In a recent survey of sawmillers, the uniformity or homogeneity of wood properties was considered as one of the most desirable wood traits (Hasegawa *et al.*, 2020). It is therefore advisable from both biological and end-use points of view to produce wood with reduced pith-to-bark and year-to-year variation of wood density within the stem. However, we are not aware of any studies that have investigated the heritability of year-to-year or pith-to-bark wood density variation, or the genetic influence on such levels of variation.

In this study, we evaluated the patterns of pith-to-bark and year-to-year variations of wood density in white spruce and their heritability in wood increment cores from a genetic trial of progeny from controlled crosses, which was repeated in two contrasting environments. The objectives of this study were (1) to compare the general pith-to-bark trends of MRD, LWD and latewood percentage (LWP) in two different environments; (2) to evaluate and compare the year-to-year variation of MRD, LWD and LWP in two different environments; (3) to evaluate the genetic control of pith-to-bark and year-to-year variation of wood density, and determine if genetic selection could help produce more uniform/homogenous wood.

## Material and methods

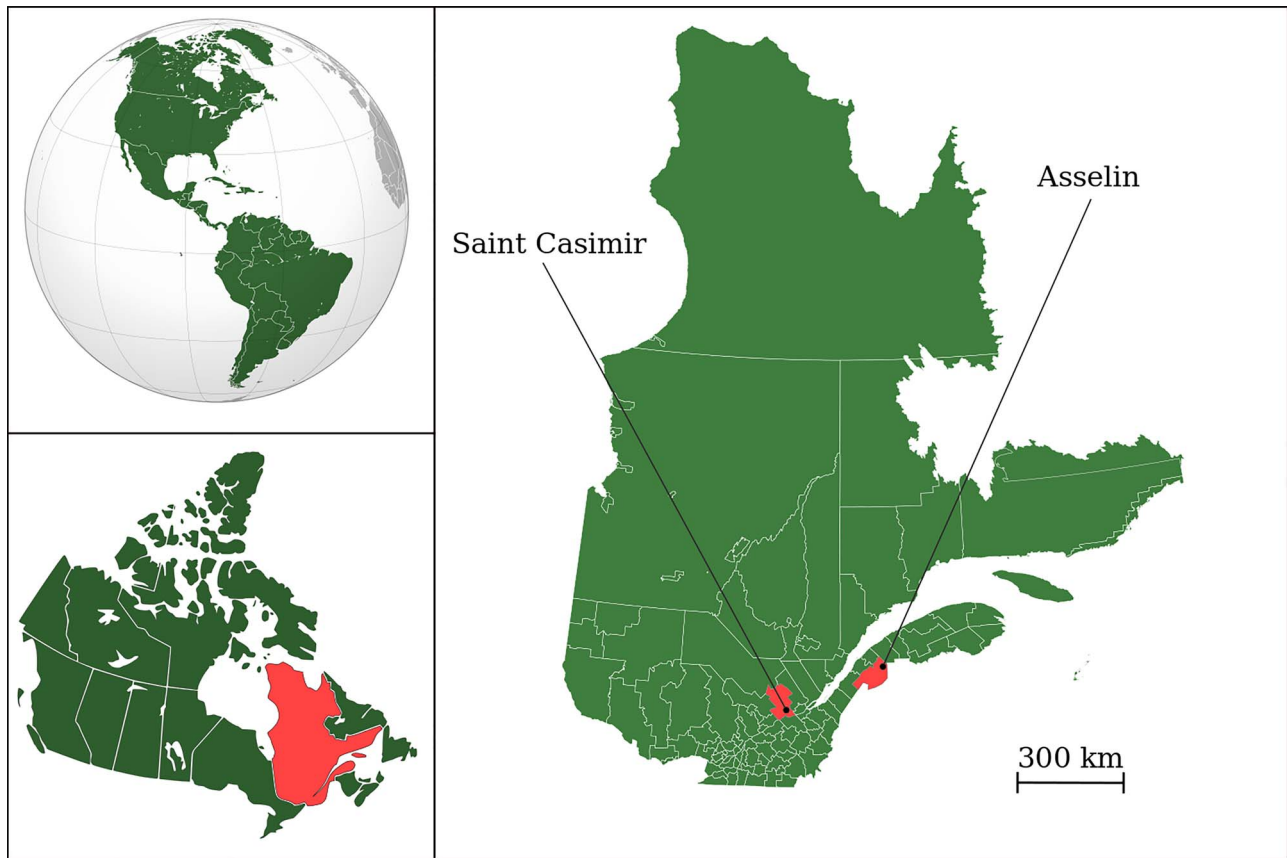
### Sampling

The trees assessed in this study were sampled from two genetic tests designed to assess the genetic merit of first-generation crosses, which had been subdivided into breeding groups and delineated by provenance or geographic region of origin of seed sources. Experimental plantations were planted in 1999 with 2-year-old seedlings in Asselin, in the balsam fir-yellow birch ecological domain, and in Saint-Casimir in the maple-basswood ecological domain in Quebec, Canada (Bailey *et al.*, 1985) (Figure 1). The plantations were laid out as a randomized complete block design to control for any possible impact of within-site heterogeneity such as slope or soil type (Table 1). In each block, each cross was represented by five-tree row-plots (spacing of 2 × 2 m) (Beaulieu *et al.*, 2014).

For this study, we sampled wood increment cores from 93 full-sib families for a total of 2196 white spruce trees. The samples were collected from nine blocks, with each family represented in each block. Around 11 trees per cross were sampled in each site to obtain balanced estimates of genetic variance in each tested environment.

### Sample preparation and scanning

Radial profiles of wood density and ring width were obtained from wood cores taken from the south-facing side and at breast height (1.3 m above ground) of each sampled tree in 2015 when the plantations were 15 years of age. Wood cores were extracted with a Soxhlet apparatus and acetone overnight, then precisely cut to 1.68 mm thickness using a pneumatic twin-blade saw and air-dried to a 7 per cent moisture content before the wood density analysis. Wood density profiles were obtained by scanning increment cores from pith-to-bark along the radial face at a resolution of 25 µm in the QTRS-01X ring analyzer



**Figure 1** Location of the two study sites.

**Table 1** Location and climatic means (over 1981–2010) of the two plantation sites.

Site	Sample number	LAT (°N)	LON (°W)	ELV (m)	MAT (°C)	TAP (mm)	Soil type	Ecological region
Asselin	1035	47.88	−68.44	349	2.4	1042.0	Loamy soils	Balsam fir-yellow birch
Saint-Casimir	1161	46.70	−72.11	53	4.7	1135.7	Sandy-loam soils	Maple-basswood

LAT = latitude; LON = longitude; ELV = elevation; MAT = mean annual temperature; TAP = total annual precipitation.

(Quintek Measurement Systems Inc., Knoxville, TN, USA). From the density profiles, the limits of the annual growth rings were determined together with the ring width and relative proportions of earlywood and latewood in each annual ring. The limit between two annual rings was determined by the internal algorithm of the Quintek software. Due to the pith-to-bark variation in wood density, it was not possible to use a constant threshold to delineate earlywood and latewood within individual rings. The transition between earlywood and latewood was thus defined as the average between the minimum and the maximum wood density values of each ring (Mothe *et al.*, 1998). A series of in-house routines included checks for possible errors such as missing rings and abnormally low or high readings.

To meet the objectives of this study, it was essential to accurately crossdate each ring profile, a process that was achieved using the COFECHA dendrochronology software (Holmes, 1983). As a result of this process, 127 samples, for which dating was

incorrect and could not be corrected, were eliminated. Incomplete or false rings were also excluded from the dataset.

### Model development

To describe the pith-to-bark wood density variation pattern and to separate it from year-to-year variation, a non-linear model was developed representing the pattern of wood density variation as a function of cambial age density. A first attempt to fit comprehensive non-linear mixed effects models proved unsuccessful because of the complex covariance structures of the random genetic effects in addition to experimental design effects. Consequently, we chose to apply the two-step non-linear modelling approach proposed by Xiang *et al.* (2014). Bontemps and Esper (2011) showed that such an approach produces equivalent results to the detrending method commonly used

in dendrochronology. The first step involved adjusting a non-linear equation describing the pith-to-bark profile of each core separately. To achieve this, we used the 'optim' function of the R software (R Core Team, 2018) that iteratively searched for optimal parameter values of the model. As a result, we obtained a database of different parameter values for each core. Model fit was assessed through a combination of visual analysis of plotted residuals against fitted values as well as statistics such as mean error (E), mean absolute error (|E|), mean absolute percentage error (|E|%) and root mean square error. Our model is therefore an adjustment of Xiang *et al.* (2014) according to our data. The form of the non-linear equation fitted to each profile was as follows:

$$Y_c(t) = b_0 \times \exp\left(\frac{b_1}{t}\right) + \frac{t}{b_2} + e \quad (1)$$

where  $Y_c$  can be either the MRD ( $\text{kg.m}^{-3}$ ), the mean ring LWD ( $\text{kg.m}^{-3}$ ) or the percentage of latewood (%),  $t$  is the cambial age (years),  $b_0$ ,  $b_1$  and  $b_2$  are the adjusted parameter values, and  $e$  is the residual error term. In this model, parameter  $b_0$  is the minimum wood density that tends to be reached in the first few rings from the pith;  $b_1$  represents the rate of decline from the value in ring 1 to the minimum defined by  $b_0$ ;  $b_2$  quantifies the rate of increase with cambial age beyond the age at which the minimum value is reached. The increasing effect of the  $b_2$  parameter is linear. The latter quickly becomes negligible (i.e. after 4 or 5 years) as the value of the exponential term tends towards an asymptotic value of 1. This model only applies to the observed range of cambial age (i.e. the first 11 years) because, in reality, values of wood density should tend towards an asymptote at older cambial ages, which had not been reached in our dataset. Values in the error term were assumed to be normally distributed, with  $N(0, \sigma^2)$ . The developed model follows the above-described type II wood density trend (Panshin and De Zeeuw, 1980). Figure 2 illustrates the effects of the three parameters on the behaviour of equation 1. The values of each of these parameters for our sampled trees were then used as indicators of pith-to-bark variation and were thus used as dependent variables in the quantitative genetic analyses described below.

The models fitted to each wood density, LWD or latewood proportion profiles were deemed to represent the pith-to-bark variation. In the second step, the variation of year-to-year was then obtained by subtracting the predictions from the observed values in each ring.

### Quantifying the level of year-to-year variation

An index was developed to quantify the level of year-to-year variation in each of the pith-to-bark profiles. This index made it possible to determine the amplitude of the year-to-year variation of the dependent variables. It can also be used to identify individuals and families that were less sensitive to year-to-year variation. We first subtracted the observed from the predicted values of the pith-to-bark profiles to obtain a yearly series of residuals for each wood core. As we were interested in quantifying the difference between residuals from consecutive years, no matter

whether they were positive or negative, the absolute value was used in the index, which was expressed as:

$$V_c = \sum |Y_n - Y_{n-1}| \quad (2)$$

where  $V_c$  is the index for  $c$  being either the MRD, the mean LWD or the percentage of latewood,  $Y_n$  is the residual value of year  $n$  and  $Y_{n-1}$  is the residual of the previous year. Once applied to the detrended pith-to-bark profiles, the value of this index was used as an indicator of the year-to-year sensitivity of our three ring density metrics that are mean ring density (MRD), latewood density (LWD) and latewood percentage (LWP) (Parker and Hensch, 1971; D'Arrigo *et al.*, 1992). A  $t$  test was used to compare both sites.

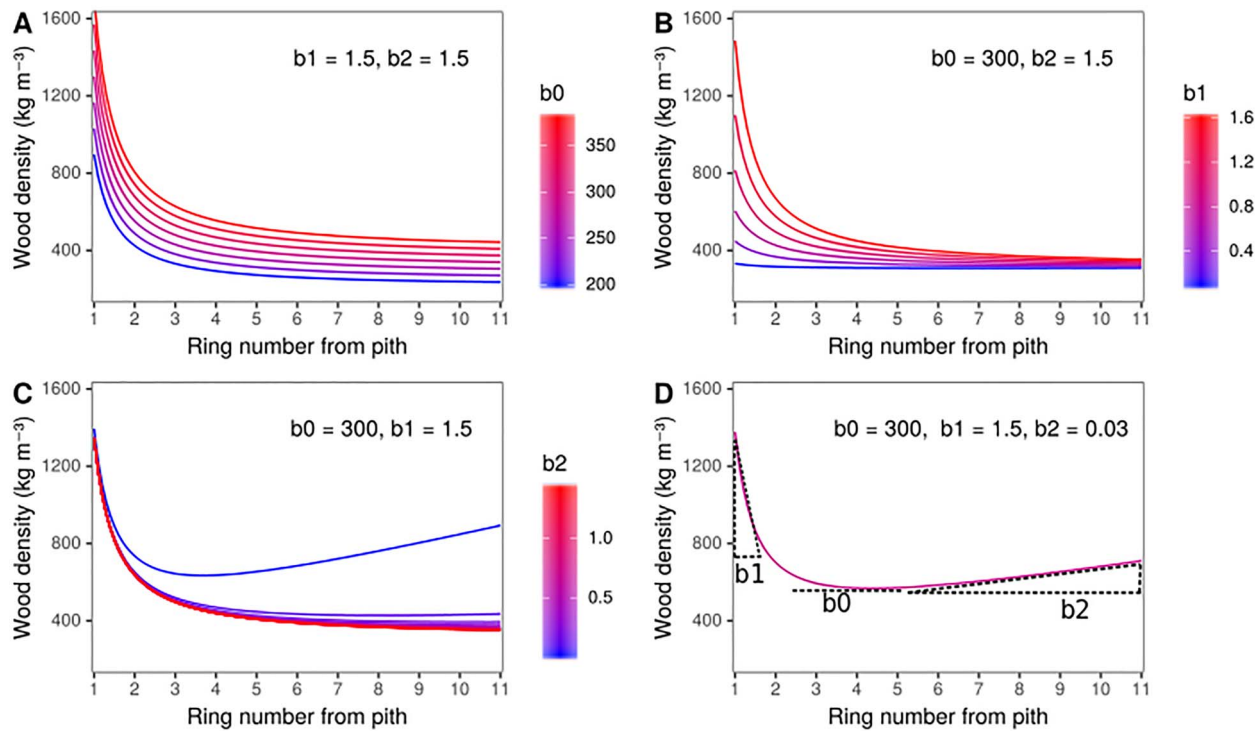
### Quantitative genetic analyses

Variance variables for genetic analysis were estimated for each site separately using the ASReml-R package, version 3.0 (Butler *et al.*, 2017) using an individual tree linear mixed model (the so-called 'animal model'):

$$y = X\beta + Z_1a + Z_2d + e \quad (3)$$

where  $y$  is the phenotype that represents our different traits here, i.e. MRD, the model parameters ( $b_0$ ,  $b_1$  and  $b_2$ ) and the year-to-year variation index ( $V_c$ );  $\beta$  represents the vector of fixed effects (block) including the overall mean,  $a$  is the random additive genetic effect, with  $a \sim N(0, \sigma_a^2 A)$ ;  $d$  is the random family effect, which is equivalent to the genetic dominance effect, with  $d \sim N(0, \sigma_d^2 I_D)$ ; and  $e$  is the residual term, with  $e \sim N(0, \sigma_e^2 I_e)$ .  $A$  is the pedigree-based relationship matrix identifying common parents of trees.  $I_D$  and  $I_e$  are identity matrices of their proper dimension. The matrices  $Z_1$  and  $Z_2$  are incidence matrices of their corresponding effects.

Additive and dominance genetic effects inform on the genetic architecture of a given trait and describe how alleles at a given locus contribute to the genetic variation in trait value (i.e. both alleles add up or one dominates over the other, respectively). Knowing the size of additive and dominance effects allows tree breeders to estimate the possibility to improve a trait through selection of superior trees and breeding, and further to determine genetic gains and the appropriate propagation methods for seed stock production. Genetic control or heritability is one of the key parameters for estimating the potential for breeding success. Heritability represents the proportion of variation in a trait that is due to genetic variation, and which can be in turn transmitted to next generations (i.e. that the offspring of selected trees has similar superior properties). Individual narrow-sense heritability that estimates the proportion of genetic variance in the phenotypic variance of trees was hence calculated as:



**Figure 2** Visual representation of parameter effects in the retained non-linear model for wood density in (A–C). D is an illustration of the type II density profile of Panshin and De Zeeuw (1980).

$$h_{\text{ind}}^2 = \frac{\sigma_a^2}{(\sigma_a^2 + \sigma_d^2 + \sigma_e^2)} \quad (4)$$

where  $h_{\text{ind}}^2$  is individual narrow-sense heritability,  $\sigma_a^2$  is the additive genetic variance,  $\sigma_d^2$  is the random dominance genetic and  $\sigma_e^2$  is the residual variance. The individual broad-sense heritability that estimates the proportion of both additive and dominance genetic variances in the phenotypic variance of trees was calculated as:

$$H_{\text{ind}}^2 = \frac{(\sigma_a^2 + \sigma_d^2)}{(\sigma_a^2 + \sigma_d^2 + \sigma_e^2)} \quad (5)$$

where  $H_{\text{ind}}^2$  is the individual broad-sense heritability,  $\sigma_a^2$  is the additive genetic variance,  $\sigma_d^2$  is the random dominance genetic and  $\sigma_e^2$  is the residual variance. Standard errors of heritability estimates were obtained using the delta method (vpredict function from the Asreml, version 3.0; Wolak, 2012).

### Spearman's rank correlations (Spearman's $\rho$ )

To assess the interaction between the two tested environments and the genetic ranking, we calculated Spearman's rank correlation coefficients of the family means between the two study sites. Correlation coefficients were calculated for the variation index ( $V_c$ ) as well as the three parameters used to summarize pith-to-bark trends ( $b_{0j}$ ,  $b_{1j}$  and  $b_{2j}$ ) for each of the three ring density

metrics. The *cor.test* function from 'stats' package in R was used to calculate Spearman's  $\rho$ .

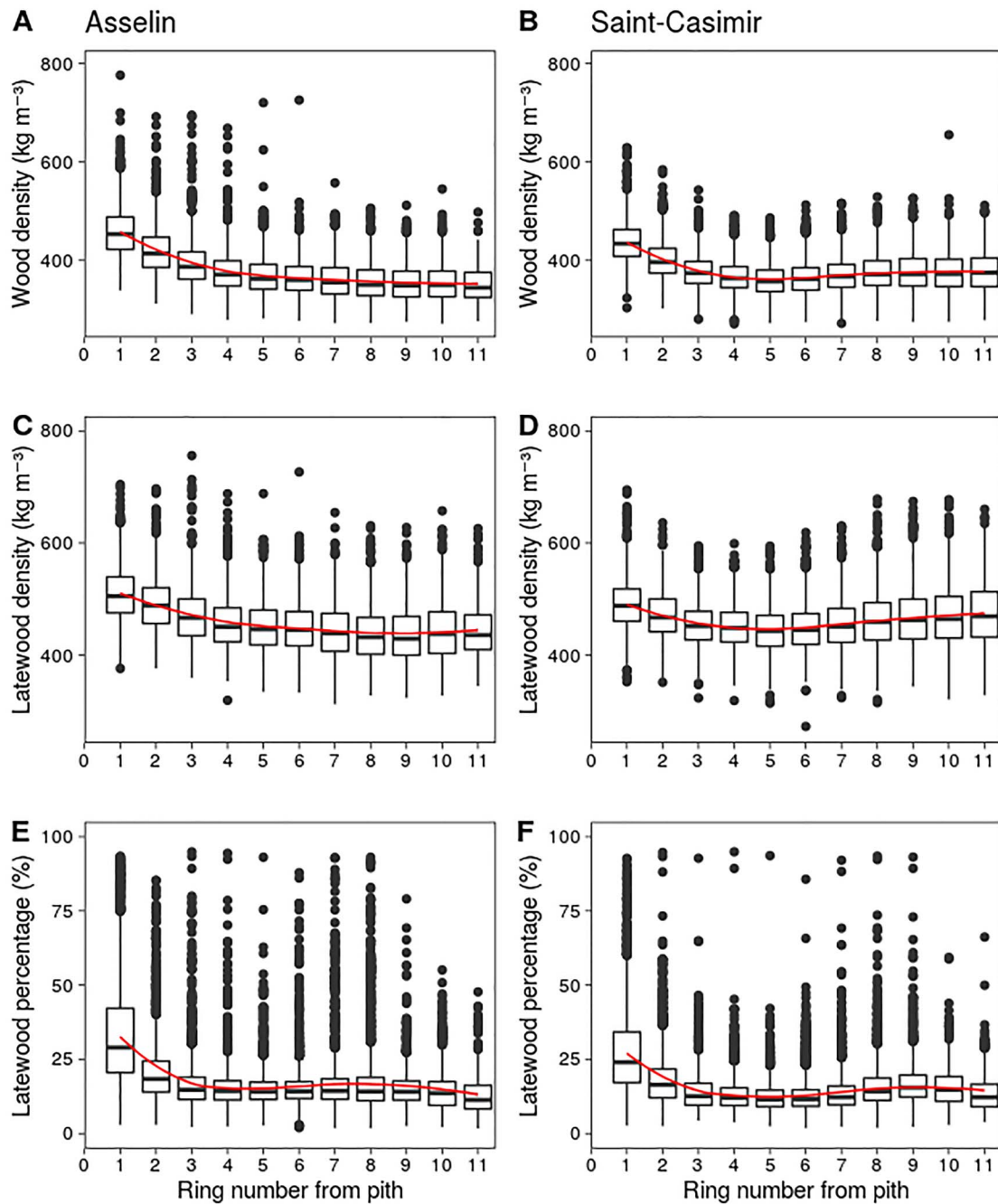
## Results

### Pith-to-bark variation of wood density

We analysed 2196 wood density profiles obtained from a genetic trial repeated in two contrasting environments. The initial patterns of wood density variation from pith-to-bark were similar in both study sites until year 5 (Figure 3). The rapid decline observed near the pith corresponded to the type II wood density radial profile described by Panshin and De Zeeuw (1980). On average, ring density metrics decreased rapidly in the first five growth rings for both sites. From the sixth year onward, the average wood density metrics stabilized at Asselin (Figure 3A, C and E), whereas they increased slightly at Saint-Casimir (Figure 3B, D and F) towards a plateau at year 8, approximately.

Equation 1 allowed us to obtain the general patterns of variation of each of the ring density metrics. Table 2 presents the fit indices and the error statistics of the final models. Overall, the proportion of variance explained by the models was about 50 per cent for MRD variation and its metrics. Still, there was significant variation around the predicted mean variation pattern, as indicated by the absolute mean error.

A summary of parameter estimates for the models fitted to the profiles of individual parameter trees is presented in Table 3. Student



**Figure 3** Pith-to-bark patterns of wood density variation from increment cores taken at breast height. The trend lines were obtained by applying a LOESS spline to predictions from the non-linear models adjusted to all trees.

*t* tests performed on model parameters showed no statistical differences between sites ( $P > 0.05$ ).

We estimated phenotypic correlations between the parameters  $b_0$ ,  $b_1$  and  $b_2$  to evaluate the links and better interpret the pith-to-bark wood density variations (Table 4). We observed a negative correlation  $>0.5$  between  $b_0$  and  $b_1$ . However, correlations between  $b_0$  and  $b_2$  and between  $b_1$  and  $b_2$  were low.

#### Year-to-year variation of density, LWD and LWP

Figure 4 illustrates the variation index  $V_c$  for each of the three ring density metrics, MRD, LWP and LWD, respectively. Trees with a low  $V_{MRD}$  index consequently showed low year-to-year variation and more homogenous wood. The average value and the standard errors of  $V_{MRD}$  was significantly higher in Asselin than in Saint-Casimir (*t* test,  $P < 0.001$ ), and so was value of  $V_{LWP}$

**Table 2** Fit indices and error statistics of the models fitted to each core.

Wood property	Site	Sample number	Adjusted $R^2$	E	E	E %	RMSE
Wood density ( $\text{kg}\cdot\text{m}^{-3}$ )	Asselin	1035	0.49 (0.18)	$8.10^{-6}$ ( $2.10^{-2}$ )	58.61 (0.10)	0.15 (0.70)	76.28 (14.33)
	Saint-Casimir	1161	0.49 (0.12)	$7.10^{-5}$ ( $1.10^{-1}$ )	48.15 (4.00)	0.13 (0.20)	65.35 (10.11)
Latewood density ( $\text{kg}\cdot\text{m}^{-3}$ )	Asselin	1035	0.50 (0.21)	$9.10^{-5}$ ( $4.10^{-1}$ )	63.31 (5.00)	0.20 (0.80)	88.30 (16.65)
	Saint-Casimir	1161	0.51 (0.05)	$8.10^{-5}$ ( $5.10^{-1}$ )	55.78 (0.20)	0.19 (0.20)	82.60 (13.45)
Latewood proportion (%)	Asselin	1035	0.48 (0.33)	$1.10^{-6}$ ( $6.10^{-3}$ )	2.31 (0.10)	0.17 (0.90)	0.08 (0.02)
	Saint-Casimir	1161	0.48 (0.29)	$1.10^{-6}$ ( $1.10^{-2}$ )	2.60 (0.90)	0.17 (0.60)	0.06 (0.01)

Mean error (E), mean absolute error (|E|), mean absolute percentage error (|E|%) and root mean squared error (RMSE) were calculated from the model predictions. Standard errors are in parentheses.

**Table 3** Comparison of non-linear model parameters ( $b_0$ ,  $b_1$  and  $b_2$ , see equation 1) from the two study sites.

Wood traits	Parameters	Site Asselin	Site Saint-Casimir
Mean ring density	$b_{0\text{MRD}}$	302.78 (55.90)	304.40 (41.90)
	$b_{1\text{MRD}}$	0.97 (0.16)	1.09 (0.15)
	$b_{2\text{MRD}}$	17.02 (2.20)	14.87 (2.00)
Latewood density	$b_{0\text{LWD}}$	568.02 (70.30)	443.30 (53.00)
	$b_{1\text{LWD}}$	-0.04 (0.19)	0.10 (0.10)
	$b_{2\text{LWD}}$	-299.10 (30.31)	-268.40 (200.00)
Latewood percentage	$b_{0\text{LWP}}$	68.82 (30.30)	85.80 (30.80)
	$b_{1\text{LWP}}$	-104.60 (33.04)	-133.40 (21.80)
	$b_{2\text{LWP}}$	79.69 (20.77)	18.30 (2.46)

Average values and standard error for the 2196 wood cores are given. MRD is mean ring density, LWD is latewood density and LWP is latewood percentage. Standard errors of estimates are in parentheses.

( $t$  test,  $P < 0.001$ ). However, the average values of  $V_{\text{LWD}}$  were not significantly different for the two study sites.

### Genetic control of wood density variation

Individual tree heritability of pith-to-bark and year-to-year variation of ring density traits and their derived indices are shown in Table 5. Broad- and narrow-sense heritability estimates showed no marked differences between sites for all individual traits. They ranged between  $0.01 \pm 0.001$  and  $0.70 \pm 0.12$  for Asselin, and between  $0.03 \pm 0.01$  and  $0.82 \pm 0.15$  for Saint-Casimir. In contrast, when the sources of variation and their associated parameters were considered for each metric of wood density (mean density, LWD and LWP), differences were observed in the heritability values.

Overall, heritability estimates tended to decrease as the level of variation increased, i.e. heritability was higher for pith-to-bark variation than for year-to-year variation. Heritability of LWP was lower than that of MRD and latewood for the mean and model parameters except for parameter  $b_2$ . For parameter  $b_2$ , which is linked with wood density at a more mature age, heritability was higher in LWP than for LWD and MRD. Heritability was high for the mean values of MRD, LWD and LWP and moderate for parameter  $b_0$ , which is closely related to the mean (Table 5). At a finer scale, parameter  $b_1$ , which is indicative of the magnitude of the value

**Table 4** Phenotypic Pearson correlations between the parameters of the non-linear models.

Wood traits	Parameters	Site Asselin	Site Saint-Casimir
Mean ring density	$b_{0\text{MRD}}$ vs $b_{1\text{MRD}}$	-0.61	-0.72
	$b_{0\text{MRD}}$ vs $b_{2\text{MRD}}$	-0.03	-0.12
	$b_{1\text{MRD}}$ vs $b_{2\text{MRD}}$	0.24	0.13
Latewood density	$b_{0\text{LWD}}$ vs $b_{1\text{LWD}}$	-0.55	-0.7
	$b_{0\text{LWD}}$ vs $b_{2\text{LWD}}$	-0.05	-0.15
	$b_{1\text{LWD}}$ vs $b_{2\text{LWD}}$	0.17	0.11
Latewood percentage	$b_{0\text{LWD}}$ vs $b_{1\text{LWD}}$	-0.65	-0.68
	$b_{0\text{LWD}}$ vs $b_{2\text{LWD}}$	-0.01	-0.08
	$b_{1\text{LWD}}$ vs $b_{2\text{LWD}}$	0.22	0.18

of each ring density metric near the pith, showed low heritability values, as did parameter  $b_2$ .

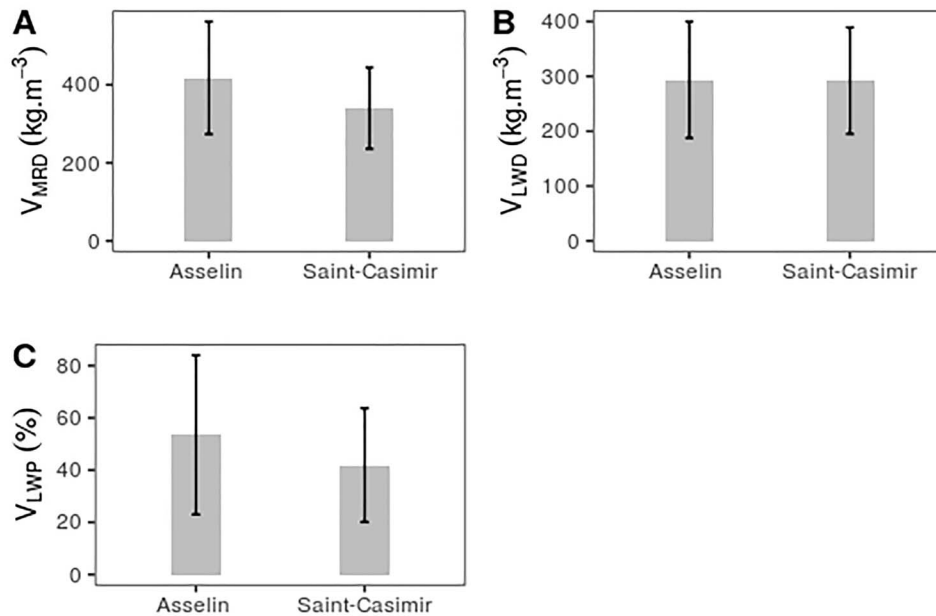
Broad-sense heritability was slightly higher than the narrow-sense heritability and followed the same pattern for all traits. Finally, at the finest scale, heritability values for the  $V$  indices indicative of year-to-year variation of ring density metrics were also low. In this case, heritability estimates close to 0.1 were observed for the latewood variables, whereas virtually no genetic control was found for MRD variation.

Having observed significant difference in wood density variation metrics among individual trees and growing environments, we aimed to elucidate the genetic control of those traits. Family rank correlations among experimental sites were moderate to high ( $\rho > 0.5$ , Figure 5) for the tree ring density traits, and similarly for all model parameters serving as indicators of pith-to-bark variation. This trend indicates a rather similar performance of progeny across environments, that is low genotype  $\times$  environment ( $G \times E$ ) interactions. High correlation values were also observed for year-to-year variation indices of LWD and LWP ( $V_{\text{LWD}}$  and  $V_{\text{LWP}}$ , respectively).

## Discussion

### Deciphering sources of variation in wood density

In the present study, we evaluated and modelled the non-linear patterns of pith-to-bark and year-to-year variations of wood density and its metrics. We estimated the genetic control of those traits in two experimental sites characterized by different climate and site conditions.



**Figure 4** Average of year-to-year variation of (A) mean ring density ( $V_{MRD}$ ), (B) LWD ( $V_{LWD}$ ) and (C) LWP ( $V_{LWP}$ ) with standard errors of mean values.

**Table 5** Individual tree heritability of mean ring density (MRD), latewood density (LWD), latewood percentage (LWP), model parameters  $b_0$ ,  $b_1$  and  $b_2$  and the index of year-to-year variation ( $V$ ).

Wood traits	Variables	Site Asselin		Site Saint-Casimir	
		$h^2$	$H^2$	$h^2$	$H^2$
Mean ring density	MRD	0.58 (0.10)	0.69 (0.12)	0.71 (0.10)	0.82 (0.15)
	LWD	0.27 (0.07)	0.36 (0.01)	0.30 (0.07)	0.41 (0.12)
	LWP	0.08 (0.04)	0.12 (0.05)	0.03 (0.02)	0.08 (0.03)
	$b_{0MRD}$	0.20 (0.06)	0.26 (0.09)	0.30 (0.07)	0.34 (0.10)
	$b_{1MRD}$	0.10 (0.04)	0.18 (0.05)	0.06 (0.03)	0.06 (0.04)
	$b_{2MRD}$	0.10 (0.04)	0.19 (0.12)	0.03 (0.02)	0.03 (0.02)
	$V_{MRD}$	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Latewood density	$b_{0LWD}$	0.25 (0.07)	0.33 (0.07)	0.33 (0.07)	0.38 (0.01)
	$b_{1LWD}$	0.07 (0.03)	0.10 (0.03)	0.10 (0.04)	0.15 (0.06)
	$b_{2LWD}$	0.01 (0.00)	0.02 (0.00)	0.02 (0.00)	0.03 (0.02)
	$V_{LWD}$	0.13 (0.05)	0.25 (0.09)	0.08 (0.03)	0.12 (0.05)
	$V_{LWP}$	0.10 (0.01)	0.17 (0.00)	0.11 (0.00)	0.20 (0.01)
Latewood percentage	$b_{0LWP}$	0.02 (0.00)	0.02 (0.00)	0.02 (0.00)	0.02 (0.00)
	$b_{1LWP}$	0.03 (0.01)	0.03 (0.01)	0.04 (0.02)	0.05 (0.00)
	$b_{2LWP}$	0.09 (0.01)	0.13 (0.01)	0.10 (0.04)	0.17 (0.01)
	$V_{LWP}$	0.10 (0.01)	0.17 (0.00)	0.11 (0.00)	0.20 (0.01)

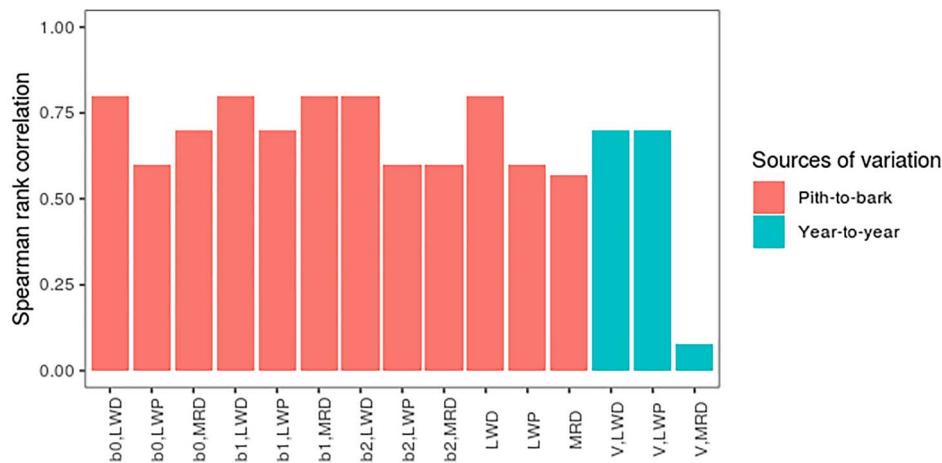
$H^2$  is the broad-sense heritability and  $h^2$  is the narrow-sense heritability. Standard errors of estimates are in parentheses.

The non-linear models allowed us to describe the individual pith-to-bark wood density trends of our young white spruce samples. An equation composed of only two terms was sufficient to describe the observed wood density profiles in our data. This is likely due to the fact that the trees analysed were young compared with previous studies in which more terms had to be used (Xiang *et al.*, 2014). Our equation allowed to describe a type

II density pattern as named by Panshin and De Zeeuw (1980), which is often observed in spruce species (Koubaa *et al.*, 2005; Alteyrac *et al.*, 2006; Lenz *et al.*, 2010; Gardiner *et al.*, 2011; Xiang *et al.*, 2014).

Despite its common use as a wood quality indicator, caution must be used when linking wood density to suitability for end-use. The zone of high wood density near the pith, which was





**Figure 5** Spearman rank correlation coefficients of family means between the two study sites (Asselin and Saint-Casimir). MRD is mean ring density, LWD is latewood density, LWP is latewood percentage,  $b_0$ ,  $b_1$  and  $b_2$  are the parameters of the model and V is the index of year-to-year variation. Correlations were significant for all traits indicating little  $G \times E$  interaction except for  $V_{MRD}$ .

quantified by the value of the  $b_1$  parameter, can be referred to as flexure wood and has properties analogous to compression wood with high microfibril angle, high lignin content and consequently low stiffness (Telewski, 1989; Meinzer *et al.*, 2011). From an end-use perspective, such wood will generally not be considered of high quality despite the higher wood density. Ideally, selection efforts should aim at identifying trees in which the characteristics of flexure wood are attenuated, i.e. where the lower severity of flexure wood would lead to a lower pith-to-bark variation of wood density. More generally, selection for more uniform wood should result in higher quality and value of wood products (Koubaa *et al.*, 2005; Hasegawa *et al.*, 2020).

Conversely, an increase in wood density in rings close to the bark is generally related to the proportion of latewood that tends to increase as rings tend to become narrower at older cambial ages (Moore, 2011). Such a negative correlation between wood density and radial growth rate has highlighted the need for selecting trees and families that exhibit fast growth as well as high wood density (Lenz *et al.*, 2011). Using our non-linear modelling approach, such trees could be characterized as exhibiting rapid radial growth as well as a low value of the  $b_2$  parameter (Figure 2).

The used non-linear models were not only suitable to model MRD, but also LWD and latewood proportion. Taking into account the patterns of pith-to-bark variation in these ring density metrics allowed a finer characterization of their year-to-year variation pattern. This approach can facilitate the study of the effects of annual climate variation, which is known to influence latewood characteristics as well as MRD (Parker and Henoeh, 1971; D'Arrigo *et al.*, 1992). Low year-to-year variation in radial growth has been linked to higher vigour, and resilience to climatic variation in several species (Franceschini *et al.*, 2013a,b). Suarez *et al.* (2004) found that individuals with highly variable growth from year to year were more prone to die from the effects of drought than trees growing more regularly. Recent studies have also shown a link between

annual tree growth and climate sensitivity of different genetic origins of seed sources within trees species (Housset *et al.*, 2018; Sebastian-Azcona *et al.*, 2018; Depardieu *et al.*, 2020). Due to the negative correlation between wood density and growth response traits to drought (growth resilience and recovery) (Depardieu *et al.*, 2021), it is possible that lower year-to-year variation in wood density is also desirable in the context of climate change.

From a wood quality standpoint, large variation of wood density can affect the performance of sawn timber. For example, a large variation in the wood properties within a sawnwood piece may lead to dimensional changes after processing (Macdonald and Hubert, 2002) and non-homogeneous machining properties. Therefore, wood uniformity is a desirable attribute for sawmillers as found by Hasegawa *et al.* (2020).

### Individual tree heritability

In addition to trait variation, heritability is the key parameter to evaluate whether important genetic gains can be expected for a selection trait (Zobel and Talbert, 1984). In this study, significant heritability estimates were obtained for wood density variation indices, which is encouraging for their inclusion in operational breeding. The genetic control of MRD was high for both sites. This result is in line with previous results in white spruce (Corriveau *et al.*, 1991; Yanchuk and Kiss, 1993; Ivkovich *et al.*, 2002a,b; Beaulieu *et al.*, 2006), which reported narrow-sense heritability values ranging from 0.36 to 0.80. These studies have shown that the mean wood density in a stem or in the cross-section of a lumber piece is a trait under moderate to strong genetic control, and that genetic selection for this trait would result in considerable gain. In contrast to MRD, LWD and LWP had low to moderate heritability in each site, which is also in agreement with previous studies (Louzada and Fonseca, 2002; Lenz *et al.*, 2010).

Model parameters  $b_0$ ,  $b_1$ ,  $b_2$  had low to moderate heritability and values were similar between sites. Parameter  $b_0$  had moderate heritability, whereas parameters  $b_1$  and  $b_2$  had low heritability. Breeding programmes are beginning to include MRD in

selection criteria, but it seems relevant to distinguish the different sources of within-tree variation in wood density. Overall, pith-to-bark sources of variation in wood density (MRD,  $b_0$ ,  $b_1$ ,  $b_2$ ) had heritability values that could allow them to be considered in genetic improvement programmes. Although  $b_1$  and  $b_2$  had low heritability with values below 0.2, growth in height and diameter are under similar levels of genetic control and much improvement in productivity has been achieved over the years in various conifers (Zobel and Talbert, 1984). It should be emphasized that heritability is not the only criterion for considering a trait as a potential selection criterion. Genetic gain also depends on sizeable trait variation and selection intensity, which is dependent upon the effective size of the breeding populations. Relationships among traits and operational constraints can also influence breeding objectives. The importance of wood uniformity for the wood processing industry (Hasegawa *et al.*, 2020) suggests that the inclusion of these metrics into operational tree breeding programmes would be of interest. However, one limitation of our approach was that we assessed the heritability of model parameters ( $b_0$ ,  $b_1$ ,  $b_2$ ) that were not intrinsic to trees but rather estimated from a model adjusted to radial ring measurements made on them. Yet, these parameters do provide complementary information on pith-to-bark variation of wood density metrics. Our results showed that pith-to-bark trends characterized by high  $b_0$  values tend to have a lower rate of decrease of wood density metrics near the pith because of the negative correlation with  $b_1$ . Both parameters were not strongly correlated with  $b_2$ .

The heritability estimates for the year-to-year variation indices related to LWD ( $V_{LWD}$ ) differed between sites, suggesting different strength of environmental conditions on the expression of these traits. However, family ranks among families between sites were reasonably conserved, indicating non-significant  $G \times E$  interactions and little performance shifts among families. This result suggests that if trees are to be selected for reforestation as a result of this study, they could be deployed on different sites with limited risk of maladjustment even in the absence of site-specific selection (Beaulieu *et al.*, 1989). However, the level of genetic control of  $V_{LWD}$  appeared to be different between sites, notwithstanding the families selected, which would suggest more in-depth analysis of environmental factors most affecting this year-to-year variation trait. As for the heritability of the year-to-year variation related to LWP ( $V_{LWP}$ ), it did not differ much between sites, suggesting that the amplitude of potentially different environmental effects was less for this trait than for  $V_{LWD}$ .

The amplitude of phenotypic variation related to latewood indices ( $V_{LWD}$ ,  $V_{LWP}$ ) was higher than that of the MRD ( $V_{MRD}$ ), which heritability estimates were null. In the context of genetic selection for reforestation, the amplitude of variation linked to latewood variables could therefore be prioritized. Multi-trait selection schemes addressing simultaneously several wood traits should also be considered by simulating various scenarios where realistic economical weights among traits studied or targeted should be determined.

The estimates of broad-sense heritability comprise dominance effects in addition to the basic additive genetic effects. They were slightly higher for all variables related to pith-to-bark variation and to year-to-year variation compared with their narrow-sense counterparts. We can hence conclude that wood density variation indices are mainly under additive genetic

control with only minor contributions from dominance effects. In a deployment context, seed production from standard open-pollinated orchards would then be sufficient to capture much of the observed genetic variance in these wood density traits, whereas the selection of superior families and mass propagating their offspring from direct crosses or vegetative reproduction would be necessary for capturing the dominance variance and other possible non-additive genetic effects not assessed in the current study.

In general, our results showed that heritability was lower for year-to-year related traits compared with traits describing the pith-to-bark variation. This is in agreement with those of Nicault *et al.*, (2010), who showed the pith-to-bark variation being related to cambial age and, therefore, being more regulated by internal processes than year-to-year variation, which was mainly related to environmental conditions. We can therefore infer that individual tree heritability of wood density metrics is lower at the finer scale of observation, i.e. variation from ring to ring, compared with variation trends spanning several years. Besides being a trait that is sought after by the wood industry, high LWD and high latewood proportion could render trees more resilient to environmental stresses such as drought episodes. Indeed, a low year-to-year LWD variation has been linked to a higher vigour and resilience to environment variation (Franceschini *et al.*, 2013a,b). Thus, heritability of year-to-year variation in LWD ( $V_{LWD}$ ,  $V_{LWP}$ ) should be considered in tree selection, whether as a positive selection criterion or as a minimum threshold when selection priority is on other traits. Consequently, these trees should harbour better suitability for end-use and be less sensitive to environmental variation.

### Variable wood density patterns between study sites

General trends of wood density and its metrics were similar in both sites. The Asselin plantation was established in a more heterogeneous environment, which was reflected in slower height and diameter growth and slightly higher overall variation compared with the trees from Saint-Casimir (Lenz *et al.*, 2013). In Saint-Casimir, the mean wood density decreased from the pith, followed by a stabilization and a slight increase to reach a plateau in the eighth year. This represents the transition to mature wood, probably caused by crown closure starting earlier than in Asselin. In Asselin, wood density decreased from the pith outwards and levelled off after year 8 without showing any sign of beginning mature wood formation.

Aside from pith-to-bark variation, differences in environmental conditions between sites also led to differences in year-to-year variation, thus suggesting that different reforestation sites may lead to significant variation in some wood density metrics.  $t$  tests also showed that the year-to-year variation was significantly different between the two study sites in terms of MRD ( $V_{MRD}$ ) and LWD ( $V_{LWD}$ ). The mean year-to-year variation could be reflecting the effect of climatic variation or site conditions on physiological processes (Nicault *et al.*, 2010). Differences between site conditions, climatic conditions might thus explain the significant differences observed in  $V_{MRD}$  and  $V_{LWD}$  between both sites (Vaganov and Shashkin, 2000; Briffa *et al.*, 2001). With radial growth being controlled mainly by the environment (Corriveau *et al.*, 1991; Ivkovich *et al.*, 2002a, Beaulieu and

Bousquet, 2010), it is likely that much of the observed differences in wood density are a consequence of differences in ring width patterns (Koubaa *et al.*, 2005). Knowing that increasing variation in climatic conditions is projected in years to come (Shukla *et al.*, 2019), genetic selection based on these traits may prove to be relevant in the long term, both for tree vigour and wood quality considerations. In contrast to the previous two metrics,  $V_{LWP}$  was not statistically different between the two sites and it was more heritable than LWP.

## Conclusion

The approach used in this study allowed us to separate and better understand the pith-to-bark and year-to-year variations of wood density and its variables. Our approach allows the identification of trees or families with low pith-to-bark variation in wood properties and trees or families with a low year-to-year variation. The pith-to-bark variation signal was much more under genetic control than the year-to-year variation. Among the latter, only latewood traits were under moderate genetic control. Although variation was observed between the two study sites, family rank correlations for inter-annual variation in latewood characteristics remained high between them. This suggests a low genotype–environment interaction, which would indicate that the deployment of selected material could encompass a range of reforestation site conditions. Together with the reported phenotypic variability, the estimated significant genetic control of wood density variation traits in this study makes them strong candidates for consideration in breeding programmes targeting more wood uniformity. Despite a non-negligible dominance-effect component, wood density variation was mainly under additive genetic control. Hence, breeding and deployment could focus on the additive genetic variance component, such that deployment through open-pollinated seed orchards could represent a reasonable option. Considering genotypes with favourable metrics of wood density variation in genetic improvement programmes should lead to higher wood uniformity from future plantations and allow for the production of high-valued wood products. Nevertheless, future studies should validate the genetic parameters and gains for wood density variation traits in other genetic trials and evaluate their relationship with growth and wood quality for consideration in multi-trait selection schemes. Another focus should be on the biological importance of wood density variation traits and their relationships with tree resilience, such as that associated with sporadic events like severe droughts. Finally, the follow-up of the trends identified in this study should also be pursued with older trees and for various conifer species.

## Data Availability Statement

The data underlying this article were provided by Canadian Forest Service by permission. Data will be shared on request to the corresponding author with permission of Canadian Forest Service.

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## Conflict of interest statement

None declared.

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