Forestry *An International Journal of Forest Research*

Institute of Chartered Foresters

Forestry 2022; **95**, 492–503, https://doi.org/10.1093/forestry/cpac006
Advance Access publication 22 March 2022

Multi-trait selection for improved solid wood physical and flexural properties in white spruce

Iman Rashidi-Jouybari[1,2,*], **Patrick Lenz**[2,3], **Jean Beaulieu**[1,2], **Simon Nadeau**[3], **Jean Bousquet**[1,2] and **Alexis Achim**[1]

[1]Département des sciences du bois et de la forêt, Centre de recherche sur les matériaux renouvelables, Université Laval, Québec, 2405 De la Terrasse St, Quebec city, QC G1V 0A6, Canada
[2]Canada Research Chair in Forest Genomics, Forest Research Centre, Université Laval, Québec, 2405 De la Terrasse St, Quebec city, QC G1V 0A6, Canada
[3]Natural Ressources Canada, Canadian Forest Service, Canadian Wood Fibre Center, 1055 rue du P.E.P.S., PO Box 10380, Stn. Sainte-Foy, Québec, QC G1V 4C7, Canada

*Corresponding author Tel: +1-(581)681-8122; E-mail: Iman.RashidiJouybari.1@ulaval.ca

Received 8 November 2021

Commercial production of high-quality lumber for Nordic conifers is negatively impacted by long rotation age and adverse negative correlations between growth and wood quality traits. A prospective solution to ensure sufficient fibre quality from future plantations is to identify key wood traits for desired applications and to consider them in tree breeding programs. In this study, we used the widespread and largely reforested white spruce (*Picea glauca* [Moench] Voss) in Canada to investigate the genetic control of wood flexural properties such as stiffness, i.e. modulus of elasticity (MOE), and strength, i.e. modulus of rupture (MOR). We also looked at their phenotypic and genetic correlations with other wood quality and growth traits to assess the efficiency of indirect methods of selection to improve wood flexural properties in the context of multi-trait selection in tree breeding programs. To achieve this, standardized solid wood samples, growth records and standing tree wood quality traits were collected from 289 trees belonging to 38 white spruce families from a polycross genetic trial established on two different sites in the province of Quebec, Canada. Flexural stiffness and strength, height, diameter at breast height (DBH) and wood density showed moderate to high heritability. Flexural stiffness was also positively correlated at the genetic level with flexural strength, average wood density and acoustic velocity as an indirect measure of dynamic MOE ($r_G = 0.99$, $r_G = 0.78$ and $r_G = 0.78$, respectively). When selecting the top 5 per cent of the trees, the expected genetic gains varied from 3.6 per cent for acoustic velocity to 16.5 per cent for MOE. Selection based on wood density and acoustic velocity would result in considerable genetic gains in flexural stiffness. Several multi-trait selection scenarios were tested to investigate the genetic gains obtained from selecting with different combinations of growth and wood quality traits. The results showed that indirect selection for wood flexural properties by means of acoustic velocity and wood density are efficient methods that can be combined in operational white spruce breeding programs to increase simultaneously genetic gains for growth and wood flexural properties.

Introduction

With the worldwide endeavour to meet an increasing wood demand and protect larger areas of natural forests, plantation-grown fibre is becoming increasingly important. The tendency in forest management towards gradually shorter rotations (i.e. higher proportion of juvenile wood), despite the negative correlation between growth rate and wood traits (Lenz *et al.*, 2011; Chen *et al.*, 2014), leads to important quality sacrifices in plantation-grown wood (Sattler and Stewart, 2016). This loss of quality represents an important concern for forest product industries using spruce and other conifers for their wood supply (Hassegawa *et al.*, 2020).

Among the prospective solutions to ensure sufficient fibre quality from future plantations is the identification of key wood traits for desired applications and to consider those traits in tree breeding programs. This requires an improved knowledge of the magnitude of the genetic control to estimate genetic gain when selecting for wood traits and closely related traits that could be used as indirect methods of assessments of key wood quality indicators (Lenz *et al.*, 2011, 2013; Hayatgheibi *et al.*, 2017, 2019). To enable accurate selection for key traits, it is also necessary to

Handling editor: Dr. Mark Ducey

better understand the relationships between growth and wood quality traits at the genetic level so that both can be considered in tree selection. With this enhanced knowledge, tree breeding may enable multi-trait selection of improved reforestation stocks that will improve the production of high-quality timber per unit land area, which in turn will contribute to optimizing the product value chain (Wu *et al.,* 2007a; Burdon *et al.,* 2008).

Generally, wood density, microfibril angle (MFA) and wood mechanical strength and stiffness are considered as the most important traits for lumber used in structural applications (Chen *et al.,* 2015; Hassegawa *et al.,* 2020). So far, several indirect and non-destructive methods have been developed for assessing these wood quality traits on standing trees (Wessels *et al.,* 2011). Other methods rely on increment cores for the assessment of chemical and mechanical wood properties such as wood density and stiffness (Schimleck *et al.,* 2003; Lenz *et al.,* 2013; Giroud *et al.,* 2017; Franceschini *et al.,* 2019). Nevertheless, few studies have focused on the direct assessment of physico-mechanical wood flexural properties using solid wood samples (but see Chen *et al.,* 2014, 2015). Despite the fact that wood quality traits such as stiffness and bending strength can be predicted indirectly using wood density and/or acoustic velocity (Lenz *et al.,* 2013; Paradis *et al.,* 2013), more direct measurements are required to directly assess the mechanical properties associated with the quality of plantation-grown wood and validate indirect methods of assessment of wood flexural properties (Beaulieu *et al.,* 2006).

White spruce (*Picea glauca* [Moench] Voss) is considered as one of the most important boreal conifer species in North America with its natural transcontinental distribution ranging from Newfoundland to Alaska. As a boreal and sub-boreal species, it is naturally slow growing but benefits from a long life expectancy, relatively high shade-tolerance, low mortality rates and a periodic dispersal of large crops of seed (Gärtner *et al.,* 2011). In addition to its ecological importance, white spruce is a key component of the commercial wood production deriving from the Canadian boreal forest, with significant contributions to the value chain of products such as dimension lumber and pulp and paper (Lenz *et al.,* 2013; Mvolo *et al.,* 2019). Hence, it is also among the most planted tree species and substantial efforts have been dedicated to the development of tree breeding programs across Canada (Mullin *et al.,* 2011). Research in genetics and tree breeding programs for white spruce have been initiated in the 1950s in different parts of Canada and the northern United States. However, breeding programs have been primarily directed towards the improvement of growth productivity and considerably less attention has been given so far to the improvement of wood quality traits (Mullin *et al.,* 2011).

Several studies have been published on the genetic aspects of wood density and other wood properties in white spruce from western (Ivkovich *et al.,* 2002) and eastern Canada (Corriveau *et al.,* 1991; Lenz *et al.,* 2013), including genomic selection applications (Beaulieu *et al.,* 2014; Lenz *et al.,* 2020a). They showed that heritability estimates are moderate to high for wood quality traits related to properties such as wood density, flexural stiffness and strength (Beaulieu *et al.,* 2006; Lenz *et al.,* 2013). These heritability estimates are generally higher than those usually observed for growth productivity traits (Beaulieu and Bousquet, 2010; Beaulieu *et al.,* 2014; Lenz *et al.,* 2020a), which leads to important expected genetic gains in tree selection programs (e.g. Lenz *et al.,* 2020a).

While knowledge about the heritability of wood quality traits is important, knowing the direction and magnitude of the genetic correlations between growth traits, wood density and other wood quality traits such as wood stiffness and other wood flexural properties is essential to develop efficient strategies of multi-trait selection for reforestation stocks with improved wood quality and growth productivity traits. Only a limited number of studies have examined genetic correlations between growth traits and key wood properties in white spruce (Lenz *et al.,* 2011, 2013). These studies have revealed possible adverse effects of higher growth productivity on wood quality traits at the genetic level.

Breeding programs of wind-pollinated conifers have conventionally relied on recurrent selection of superior genotypes (Wheeler *et al.,* 2015), which are then multiplied to produce large numbers of genetically improved seeds. Different approaches of genetic testing including various mating designs have been used to evaluate the genetic merit of trees in a breeding population, estimate their so-called breeding value as well as genetic variance components and the heritability of the traits of interest (Falconer, 1996; White *et al.,* 2007; Zobel and Van Buijtenen, 2012; Lenz *et al.,* 2020b). In comparison to other mating designs, the polycross design offers a cost-effective system to realize fewer crosses while implicating a diverse set of parents (Kumar *et al.,* 2007). Overall, polycross mating offers opportunities in terms of ease of implementation while leading to adequate estimates of breeding values of each female parent, resulting in improved genetic gains due to the evaluation of numerous parental combinations (Lambeth *et al.,* 2001).

Based on such a polycross trial, we present a comprehensive genetic study of solid wood physico-mechanical properties in white spruce and their genetic relationships with growth and other wood quality traits. Our objectives were to (a) determine the heritability of intrinsic solid wood physico-mechanical properties, (b) estimate their genetic correlations with other wood quality and growth productivity variables to identify key traits influencing the properties of solid wood and (c) evaluate multi-trait selection scenarios so to integrate intrinsic solid wood properties in white spruce tree improvement.

Materials and methods

Sampling material

We analysed 20-year-old white spruce trees from a genetic trial located in the province of Quebec, Canada, which was replicated on two sites as part of a polycross progeny trial replicated in different regions of the province. The first study site was located at the Serge-Légaré Arboretum near Valcartier, north of Québec City (Lat. 46° 58′ N, Long. 71° 28′ W, Elev. 212 m, planted in 1996) in the sugar maple basswood bioclimatic domain and the second site was located in Normandin (Lat. 48° 50′ N, Long. 72° 31′ W, Elev. 122 m, planted in 1997) in the northern balsam fir-yellow birch bioclimatic domain. The experimental layout followed a randomized complete block design, with four blocks per site. In each block, four single-tree plots per polycross family were arranged in an interlocking layout to enable systematic thinning operations (Libby and Cockerham, 1980). The spacing between trees was 1.5 m × 1.8 m and 2 m × 2 m at Valcartier and Normandin, respectively.

In total, 38 polycross families were sampled but one family was not represented at NOR. The polycross implicated a balanced pollen mixture of 19 male parents. The resulting progeny represents half-sib families following conventional pedigree selection schemes where the specific father of each tree remains unknown. However, the use of genetic markers enabled to additionally trace the paternal contribution to each tree (Lenz *et al.* 2020a). Phenotypic trait measurements were assessed on four to nine (7.5 on average) trees per family for a total of 289 trees that were felled during a systematic thinning of the genetic trial. Mortality led to slight variation in the number of trees per family and site that were available for the experiment. At both sites, diameter at breast height (DBH, measured 1.3 m from ground level), tree height and acoustic velocity (AV, assessed between 30 cm and 1.3 m from the ground) were measured at age 19 (i.e. measured in 2015 at Valcartier and in 2016 at Normandin). In addition, increment cores were collected from the south facing side of trees at breast height for wood density and ring width (RW) measurements. For the assessment of wood flexural properties, trees were felled and two standardized samples per tree were sawn from a stem section just above breast height (Figure 1). A short log was collected above breast height (1.3 m), transported and stored at Laval University's Renewable Materials Research Centre.

Wood flexural properties

Flexural modulus of rupture (MOR) and modulus of elasticity (MOE) are two commonly used parameters to characterize the static bending properties of wood for structural applications. Specimens were prepared from both sides of a radial slab sawn in the north to south face. Specimens were extracted as close as possible to the bark on each side (Figure 1) and were prepared with final dimensions of 2.54 cm × 2.54 cm × 40.64 cm. They were then stored in a conditioning chamber (60 per cent relative humidity at 20°C) for two months until the stabilization of moisture content. Static bending tests were performed by three-point loading according to ASTM standard D 143-94 (ASTM 1999). The load was applied to the tangential–longitudinal face closest to the pith with a specimen supports set 38.1 cm apart for a 15:1 span to depth ratio and speed ratio of 2.5 mm/min. The specimens were subjected to static bending tests using an Instron universal testing machine with a 50 kN load cell. Each sample was loaded until destruction occurred to determine both the MOR and MOE. The value of MOR, reflecting the maximum load-carrying capacity, was calculated from the maximum loading force as in equation (1):

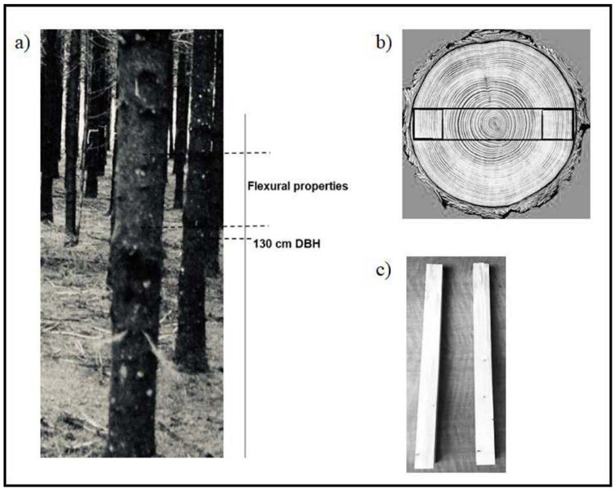

Figure 1 Sample preparation for wood flexural properties, including where the samples were taken from tree stem (a), where the samples were taken from bolt (b), final sample (c).

$$\mathrm{MOR} = 3F_{\max}\frac{l}{2bh^2} \tag{1}$$

where $F_{\max}$ (or force of destruction) is maximum loading force, l is the span of supports, b is the width of cross-section of sample and h is height of the sample.

MOE, which is related to stiffness, was calculated based on the forces measured at an interval of 10 per cent to 40 per cent (linear portion of the load–deflection curve) of the maximum loading force. MOE was obtained using equation (2):

$$\mathrm{MOE} = \frac{l^3\left(F_{40\%} - F_{10\%}\right)}{4bh^3\left(u_{40\%} - u_{10\%}\right)} \tag{2}$$

where l is the span of supports, $F_{40\%}$ and $F_{10\%}$ are the forces at the 40 per cent and 10 per cent level of the maximum force $F_{\max}$, b is the width of the cross-section of sample and h is the height of the sample, and $u_{40\%}$ and $u_{10\%}$ are deflections at forces $F_{40\%}$ and $F_{10\%}$.

Acoustic velocity

Acoustic velocity (AV), which can provide a non-destructive estimate of wood stiffness (Lenz *et al.,* 2011, 2013), was obtained on standing trees at age 19 using the Hitman ST300 device (Fibregen, Christchurch, New Zealand) (Huang, 2005). We used an average value of 24 readings from each tree in the analyses. For each study site, the measurements were taken within a two-week period in June/July 2012 to reduce temperature and moisture content differences that might have influenced the speed of sound waves transiting in stems (Gao *et al.,* 2013). In the Normandin site, only 85 trees were available for testing acoustic velocity.

Wood density

Increment cores were cut to a thickness of 1.68 mm with a twin-blade pneumatic saw. Further, they were Soxhlet extracted overnight using acetone, and conditioned to approximately 8 per cent moisture content before further analysis (Ukrainetz *et al.,* 2008). Wood density profiles were determined by *x*-ray densitometry at a resolution of 25 μm with a QTRS-01X Tree Ring Analyzer (Quintek Measurement Systems Inc., Knoxville, TN, USA). Tree ring boundaries were determined with the internal algorithm of the Quintek software. In the current work, area-weighted means of wood density and ring width were calculated for each increment core.

Statistical analyses

In order to estimate genetic parameters, such as genetic control, gain or correlated gain, variance components were estimated with an individual-tree mixed model (the so-called animal model) using ASReml-R v.3.0 in R (Wolak, 2019). The following model was fitted for each trait as:

$$\boldsymbol{y} = \boldsymbol{X\beta} + \boldsymbol{Z_1 a} + \boldsymbol{Z_2 sa} + \boldsymbol{e} \tag{3}$$

where $\boldsymbol{y}$ is the phenotypic value of analysed wood and growth traits; $\boldsymbol{\beta}$ is the vector of fixed effects, including the overall mean, the site and the block within site effect; $\boldsymbol{a}$ is the random additive genetic effect, with $\boldsymbol{a} \sim N(\boldsymbol{0}, \sigma^2{}_a\, \boldsymbol{A})$; $\boldsymbol{sa}$ is the random interaction of site with additive genetic effects, with $\boldsymbol{sa} \sim N(\boldsymbol{0}, \sigma^2{}_{sa}\, \boldsymbol{I}_s \otimes \boldsymbol{A})$; and $\boldsymbol{e}$ is the residual term, with $\boldsymbol{e} \sim N(\boldsymbol{0}, \sigma^2{}_e\, \boldsymbol{I}_e)$. The $\boldsymbol{X}$ and $\boldsymbol{Z}$ matrices are incidence matrices linking observations to their corresponding effects, and $\boldsymbol{I}_x$ is an identity matrix. The symbol $\otimes$ refers to the Kronecker product. The matrix $\boldsymbol{A}$ reflects the genetic relationships between trees, which is computed from the full pedigree with known mothers from the polycross and retrieved fathers from paternity assignment using genome-wide single nucleotide polymorphism (SNP) markers as described previously (Lenz *et al.*, 2020a).

To successfully breed for a given trait, it needs to be under some degree of genetic control instead of being completely influenced by the environment or random effects. Genetic control was estimated as the individual narrow-sense heritability $\hat{h}_i^2$ according to the following equation:

$$\hat{h}_i^2 = \hat{\sigma}_a^2 / \left(\hat{\sigma}_a^2 + \hat{\sigma}_{sa}^2 + \hat{\sigma}_e^2\right) \tag{4}$$

where $\hat{\sigma}_a^2$ is the additive genetic variance estimated with the above model, $\hat{\sigma}_{sa}^2$ is the variance of the interaction between site and additive genetic effects, and $\hat{\sigma}_e^2$ is the residual variance. To evaluate the success of selection, genetic gain (G_A) was calculated as:

$$\mathrm{G}_A = i \times \mathrm{CV}_p \times \hat{h}_i^2 \tag{5}$$

where CV_p is the coefficient of variation (calculated as the phenotypic standard deviation divided by the mean of a specific trait) and $\hat{h}_i^2$ is the individual narrow-sense heritability from equation (4). A selection differential of $i = 2.06$ that corresponds to a selection intensity of $\alpha = 0.05$ was assumed. This means that 5 per cent of most superior trees are retained for breeding in the next generation.

Another important information is if superior trees will perform similarly across different environments. Hence, the amplitude of genotype-by-environment interaction ($G \times E$), or type-B correlation $\hat{r}_{\mathrm{B}}$, was estimated as:

$$\hat{r}_{\mathrm{B}} = \hat{\sigma}_a^2 / \left(\hat{\sigma}_a^2 + \hat{\sigma}_{sa}^2\right) \tag{6}$$

using the variance components of equation (3).

Performing selection on a specific trait of interest will often alter other traits. To evaluate the extent of relationship among traits and if relationships are positive or negative, phenotypic and genetic correlations are estimated. Bivariate models were run for all pairs of traits. The following model was fitted:

$$\begin{bmatrix} \boldsymbol{y_i} \\ \boldsymbol{y_j} \end{bmatrix} = \boldsymbol{Xt} + \boldsymbol{Z_1 a}\,(\boldsymbol{t}) + \boldsymbol{e} \tag{7}$$

where $\boldsymbol{y_i}$ and $\boldsymbol{y_j}$ are the stacked vectors of phenotypic observations for trait i and trait j, respectively; t is the vector of fixed effects of traits (i.e. the overall mean, the site and the block effect for each trait); $\boldsymbol{a}(\boldsymbol{t})$ is the random additive genetic effect within trait, with $\boldsymbol{a}(\boldsymbol{t}) \sim N(0, \boldsymbol{V_A} \otimes \boldsymbol{A})$; and $\boldsymbol{e}$ is the residual error, with $\boldsymbol{e} \sim N(0, \boldsymbol{I_e} \otimes \boldsymbol{V_R})$. The matrices $\boldsymbol{V_A}$, and $\boldsymbol{V_R}$ are 2×2 variance–covariance matrices defining unique variances for each trait and correlations between traits (r_a and r_e, respectively).

Finally, to evaluate the effect of selection for one trait on genetic gain for another trait, we calculated an estimate of the indirect selection efficiency as:

$$\hat{E}_{\mathrm{ind}} = \frac{\hat{h}_x}{\hat{h}_y} \times \hat{r}_{G(x,y)} \tag{8}$$

where $\hat{h}_x$ and $\hat{h}_y$ are, respectively, the square roots of heritability of the selected trait x, and the related trait y, and $\hat{r}_{G(x,y)}$ is the additive genetic correlation between both traits. Equal selection differentials were assumed for both traits ($i_x = i_y$).

Multi-trait selection indices

Tree breeders increasingly need to consider many different traits related to growth, quality or even resistance and adaptive capacity. Index selection presents a suitable tool to optimize genetic gain for most important traits and to handle adverse correlations among selection traits. To estimate genetic gains in a multi-trait selection scenario, four traits of economic interest were combined into a selection index (SI) as follows:

$$\mathrm{SI} = w_1 \mathrm{MOE}_{\mathrm{BV}} + w_2 \mathrm{Height}_{\mathrm{BV}} + w_3 \mathrm{DBH}_{\mathrm{BV}} + w_4 \mathrm{Density}_{\mathrm{BV}} \tag{9}$$

where $\mathrm{MOE}_{\mathrm{BV}}$, $\mathrm{Height}_{\mathrm{BV}}$, $\mathrm{DBH}_{\mathrm{BV}}$ and $\mathrm{Density}_{\mathrm{BV}}$ are the breeding values from the single-trait analyses. Breeding values describe the additive genetic merit of each tree and are free of environmental and experimental design effects. Mathematically, they are the best linear unbiased prediction (BLUP) of the random genetic effect of the mixed model (equation (3)) fitted for each trait, and w_i is the relative weight given to each trait, with the restrictions:

$$0 \le wi \le 1 \text{ for all traits, and}$$

$$w1 + w2 + w3 + w4 = 1$$

Breeding values for each trait were scaled to unit variance. For each SI, trees were ranked according to decreasing values of the

Table 1 Trait means and variation among 289 trees representative of 38 polycross families tested on two sites (SD are standard deviations).

Trait*	Units	Valcartier ($n = 144$ trees)			Normandin ($n = 145$ trees)		
		Age	Mean	SD	Age	Mean	SD
MOE	MPa	20	8510.0	1728.2	20	8271.2	1846.9
MOR	MPa	20	55.3	8.9	20	58.1	9.3
DBH	mm	19	113.5	20.4	19	135.9	27.2
Height	cm	19	957.2	136.7	19	842.4	175.2
AV	km/s	19	368.7	32.8	19	352.5	24.1
Density	kg/m^3	18	387.3	25.3	18	384.1	30.7
RW	mm	18	3.2	0.6	18	4.1	0.7

Measured traits in descending order are modulus of elasticity (MOE), modulus of rupture (MOR), diameter at breast height (DBH), tree height (Height), acoustic velocity (AV), average wood density (Density) and average ring width (RW).

index and the top 5 per cent trees were selected to calculate the expected genetic gain for each trait.

Results

From a total of 289 trees representative of 38 polycross families tested on two experimental sites, we obtained two wood flexural measurements and an average per tree was used for the following analyses. Table 1 provides an overview of wood trait means and standard deviations (SD) at both study sites. Wood quality traits had higher values in Valcartier, while radial growth was higher at Normandin. On average, radial growth in terms of DBH and ring width was 17 per cent and 22 per cent higher at Normandin than at Valcartier, respectively. The opposite trend was observed for height growth and wood density with values being 12 per cent and 1 per cent higher, respectively, at Valcartier than at Normandin. In fact, trees in the Valcartier site were planted at a narrower spacing, resulting in higher height to diameter ratio. In addition, static MOE was around 3 per cent higher at Valcartier, while MOR was about 5 per cent higher at Normandin.

In the analyses across both sites, trait heritability ranged from 0.24 to 0.46 using the animal model (Table 2). Wood traits tended to show higher heritability than growth traits. For instance, wood density and MOE were found to be under moderate genetic control ($\hat{h}_i^2 = 0.46$, $\hat{h}_i^2 = 0.38$, respectively), while MOR was under low to moderate genetic control ($\hat{h}_i^2 = 0.26$). Heritability estimates for growth and other traits such as height, DBH, AV and RW were low to moderate ($\hat{h}_i^2 = 0.17$ to $\hat{h}_i^2 = 0.29$). Type-B genetic correlations were calculated as a surrogate for genotype-by-environment interaction between trial sites. Wood flexural traits and average wood density showed very high type-B genetic correlations ($\hat{r}_B = 0.99$) and hence, little genotype-by-environment interaction. Slightly lower but still high type-B correlations were estimated for acoustic velocity and growth traits (from $\hat{r}_B = 0.86$ to $\hat{r}_B = 0.95$).

To evaluate the genetic relationships between the different traits, we estimated genetic and phenotypic correlations using a bivariate modelling approach (Table 3). Moderate to high genetic correlations were found between wood flexural properties and other wood quality traits. Moderate to strong negative genetic correlations were obtained between wood flexural properties and tree growth traits, while phenotypic correlations were low to moderate. For example, low to moderate negative genetic correlations were observed between wood flexural properties and tree height, but the correlation was positive at the phenotypic level. Overall, these results confirm that higher wood quality could be obtained by higher wood flexural properties as assessed indirectly by acoustic velocity and wood density.

Significant genetic gains from single-trait selection were estimated for wood flexural properties when selecting the top 5 per cent trees for each trait (Table 4). Expected genetic gains varied between 3.6 per cent for acoustic velocity and 16.5 per cent for MOE. Similar gains were estimated for MOR, height and wood density. It should be noted that the smaller genetic gain estimated for acoustic velocity is probably due to a lower heritability, while heritability was higher for most other traits. The indirect selection efficiency allows estimating the effect of selection for a particular trait on different other traits (Table 4). Selection for a growth trait would also enhance other traits of the same category. A selection strategy aiming to improve DBH or tree height could at the same time increase gain ratio in ring width ($E = 0.51$ and $E = 0.89$, respectively) but would largely reduce gains in wood quality traits. Selection based on wood density would still indirectly decrease DBH ($E_{\text{ind}} = -0.46$) but would indirectly improve and virtually realize all genetic gain for wood flexural properties. Selection for MOE would also result in virtually realizing all gain for MOR and acoustic velocity, while its indirect effect on height and MFA would be much smaller. In contrast, selection based on acoustic velocity had rather little effect on tree growth traits, while it would allow realizing 62 per cent and 49 per cent of the genetic gains in MOE and MOR, respectively.

In practice, tree breeders do not only consider the correlated response between a pair of traits but also seek to balance genetic gains for several selection objectives. We hence evaluated five multi-trait selection scenarios based on different combinations of selection traits (MOE, MOR, wood density, acoustic velocity, DBH and tree height) and evaluated their effect on genetic gain (Table 5). Based on scenario #1, targeting tree height and volume at the same time appeared to be detrimental to gains in wood flexural properties. Considering wood density as a surrogate decreased the gains in wood flexural properties significantly too (scenario #2). Most promising was the combination of selection

Table 2 Estimates of genetic control (narrow-sense heritability, $\hat{h}_i^2$) for growth and wood quality properties as well as type-B correlations ($\hat{r}_B$) (SE are standard errors).

	$\hat{h}_i^2$	SE	$\hat{r}_B$	SE
MOE	0.38	0.17	0.99	0.49
MOR	0.26	0.16	0.99	0.59
Height	0.29	0.16	0.86	0.50
DBH	0.28	0.17	0.95	0.63
AV	0.24	0.21	0.90	0.52
Density	0.46	0.17	0.99	0.34
RW	0.24	0.17	0.98	0.69

See Table 1 for trait definitions.

Table 3 Pairwise correlations between traits.

	MOE	MOR	Height	AV	DBH	Density	RW
MOE		0.99 (0.01)	−0.24 (0.34)	0.78 (0.23)	−0.40 (0.30)	0.78 (0.16)	−0.43 (0.30)
MOR	0.85 (0.02)		−0.34 (0.41)	0.51 (0.34)	−0.33 (0.35)	0.85 (0.17)	−0.34 (0.35)
Height	0.26 (0.06)	0.15 (0.06)		−0.15 (0.41)	0.70 (0.17)	0.13 (0.30)	0.47 (0.28)
AV	0.42 (0.06)	0.33 (0.08)	0.01 (0.07)		−0.09 (0.42)	0.16 (0.33)	−0.35 (0.37)
DBH	0.08 (0.06)	−0.07 (0.06)	0.70 (0.03)	−0.19 (0.07)		−0.36 (0.27)	0.83 (0.11)
Density	0.23 (0.06)	0.32 (0.05)	−0.16 (0.06)	0.20 (0.07)	−0.40 (0.06)		−0.30 (0.29)
RW	0.05 (0.06)	−0.06 (0.06)	0.60 (0.04)	−0.19 (0.07)	0.86 (0.01)	−0.39 (0.05)	

Genetic correlations are above, and phenotypic correlations are below the diagonal. Standard errors associated to estimates are in parentheses. See Table 1 for trait definitions.

Table 4 Efficiency of indirect selection between different growth and wood traits as expressed in terms of genetic gains.

		Indirect effect on						
		MOE	MOR	Height	DBH	AV	Density	RW
Selection trait	MOE	**16.50**	1.19	-0.28	-0.46	0.98	0.71	-0.54
	MOR	0.82	**9.18**	-0.33	-0.32	0.53	0.64	-0.25
	Height	-0.21	-0.37	**8.56**	0.62	-0.16	0.10	0.51
	DBH	-0.34	-0.34	0.70	**11.56**	-0.10	-0.28	0.89
	AV	0.62	0.49	-0.14	-0.08	**3.56**	0.11	-0.30
	Density	1.09	1.13	0.16	-0.46	0.22	**6.93**	-0.41
	RW	-0.34	-0.33	0.43	0.77	-0.36	-0.22	**11.70**

Estimates of genetic gains are in percent from selecting the top 5% of trees. Gains from single-trait selection are in bold on the diagonal. See Table 1 for trait definitions.

for acoustic velocity and tree height (scenario #3), a possibility for early selection that resulted in important genetic gains in wood flexural properties while increasing growth as well. Gains were almost positive for all traits, yet there was still a potential to get higher gains in wood flexural properties. Indeed, including wood flexural properties in selected traits allowed to obtain significant gains for these traits (scenario #4: 14.1 per cent and 7.7 per cent for MOE and MOR, respectively). Including DBH among the selected traits did secure gains in volume, but it decreased gains in MOR and wood density, two important wood quality traits (scenario #1). Overall, scenarios including DBH were not advantageous for improvement of flexural traits and concentration on height selection for improving growth led to the best gain in wood quality.

Discussion

Wood flexural properties are key wood quality drivers for wood in structural applications. Despite their importance, those traits are rarely assessed in tree breeding programs and even less from solid wood samples, and reports on genetic parameter estimates are scarce. Our assessment of wood flexural properties from solid wood samples collected from a genetic trial established on

Table 5 Genetic gains for each trait when selecting the top 5% of trees in five selection index scenarios.

	Selection index scenario[1]	MOE (%)	MOR (%)	Height (%)	DBH (%)	AV (%)	Density (%)	RW (%)
S_1	3/4H + 1/4DBH	0.1	-0.8	8.5	10.3	0.4	-0.5	8.3
S_2	2/3H + 1/3D	4.5	2.2	7.5	6.4	1.17	4.0	5.4
S_3	2/3H + 1/3AV	7.7	2.8	7.3	8.0	3.0	1.4	5.4
S_4	1/4MOE + 1/4MOR + 1/2H	14.2	7.7	5.2	3.7	1.3	2.9	3.3
S_5	1/4H + 1/4DBH + 1/4D + 1/4AV	5.7	2.2	7.5	8.0	2.2	2.9	5.6

See Table 1 for trait definitions. H = tree height; D = average wood density.

two environmentally contrasted sites participated in elucidating the genetic underpinnings of wood flexural traits and proposes original approaches for their consideration in selection decisions in tree breeding.

Significant differences for both wood flexural properties, MOE and MOR, were observed between the two study sites. Higher MOE and height values were obtained in the southernmost site in Valcartier, while higher MOR and DBH were obtained in the Normandin site located further north. At the same time, the radial growth rate in Valcartier was lower, leading to trees with less taper than in Normandin. Besides the somewhat warmer climatic conditions in Valcartier, those differences were mostly attributable to the planting density, which was higher in Valcartier resulting in quicker crown closure and ascent of the live crown. Also, no significant genotype-by-environment interaction ($G \times E$) was noted for wood flexural properties between the two study sites.

For wood structural applications, MOE is generally considered as the most important property among lumber quality traits, even when compared with mechanical strength (MOR) (Johansson and Kliger, 2000). In this study, the overall mean of MOE value was about 23 per cent lower than that of white spruce grown in natural forests (Jessome, 1977) and 28 per cent lower than lumber from SPF group in Canada (Spruce-Pine-Fir group, according to standard CAN/CSA-086.1-M89, CWC 2001). In conifers, wood flexural properties are known to be lower in the juvenile wood (Barrett and Kellogg, 1991) where the microfibril angle is larger (Cave and Walker, 1994; Megraw *et al.*, 1999). It is generally assumed that white spruce does not initiate mature wood formation before the 15th ring (Corriveau *et al.*, 1991; Zhou and Smith, 1991). In this study, the samples were taken at average age of 20 years; thus, we can assume that the tested specimens included a high proportion of juvenile wood. The gradual transition from juvenile to mature wood leads to a typical radial pattern of MOE variation whereby values increase rapidly from the pith outwards before reaching an asymptote in mature wood. This pattern can be altered by environmental conditions (Lachenbruch *et al.*, 2011). The higher competition at the Valcartier site is likely to have accelerated the transition to mature wood, which would explain the higher MOE values observed at this site.

Moderate heritability allows for sizeable genetic gains in wood flexural properties

In our study, narrow-sense heritability estimates for wood quality traits were higher than for tree growth traits, and the highest values were obtained for wood density. The moderate to high heritability as well as expected genetic gains for wood density is in accordance with estimates reported in previous studies on white spruce (Corriveau *et al.*, 1991; Ivkovich *et al.*, 2002; Beaulieu *et al.*, 2006; Lenz *et al.*, 2011). This underlines the potential for considering this wood trait in white spruce tree improvement. On the other hand, the heritability estimates for MOE and MOR were moderate. In other studies, heritability estimates for MOE and MOR were respectively reported as moderate or low in white spruce (Beaulieu *et al.*, 2006), whereas they were moderate to high for both traits in *Pinus radiata* (Wu *et al.*, 2007b). The moderate heritability observed here for acoustic velocity was observed previously and makes it a promising fast-assessment trait for improving wood stiffness and product quality without direct assessment with solid wood samples (Lenz *et al.*, 2013; Beaulieu *et al.*, 2014). Overall, the moderate to strong genetic control of wood traits suggests that satisfactory genetic gains could be achieved when they are considered for selection in white spruce.

The $G \times E$ interaction, which is an important indicator of the degree to which the genetic performance of families is likely to differ among sites, was rather low for all traits. This result indicates that little rank changes can be expected across environments. The lowest $G \times E$ interaction was found for wood flexural properties and wood density, while somewhat higher $G \times E$ interaction was observed for growth traits, which is consistent with previous studies on spruce species (Beaulieu *et al.*, 2014; Chen *et al.*, 2017). In their study, Chen *et al.* (2017) reported average type-B correlations from 0.60 to 0.89 for tree height in six Norway spruce (*Picea abies)* test series from southern and central Sweden. Their type-B correlations were hence lower than those observed in the present study. As our test sites were located in contrasted environments representative of the two main white spruce breeding zones in the province of Quebec (Li *et al.*, 1997), we can expect that our results should be applicable over different zones in eastern Canada. As a result, among the wood traits tested, flexural properties and wood density had higher heritability estimates and lower $G \times E$ interaction.

Adverse genetic correlations between growth and wood quality traits

Before including candidate traits in operational tree breeding programs, interactions between traits need to be well understood. Generally, genetic correlations were slightly higher than their phenotypic counter parts, as environmental effects not controlled by the experimental design also influenced the phenotypic correlations. Moderate phenotypic correlations were observed between wood flexural properties and wood density, while the corresponding genetic correlations were higher. The lower phenotypic correlations can be attributed to the fact that wood density is affected to some degree by environmental factors. In addition, the presence of so-called flexure wood (Telewski, 1989) in the juvenile zone, characterized by a high lignin content, large microfibril angle and high wood density, but low strength and stiffness (Beaulieu *et al.,* 2006; Sattler and Stewart, 2016) can explain the weak correlation between wood density and flexural properties, especially at an early age (Beaulieu *et al.,* 2006). The genetic relationships observed between wood density and growth-related traits, such as DBH, tree height, ring width, as well as earlywood width and its proportion (results not shown), were generally negative except for tree height. Similar negative genetic correlations were observed between growth traits and the flexural properties of solid wood samples. Such adverse genetic correlations between growth and wood quality traits have been frequently reported (Lenz *et al.,* 2013; Hong *et al.,* 2014; Giroud *et al.,* 2017). In tree breeding, genetic correlations are usually estimated from replicated field tests of relatively young trees compared with those at rotation age. Thus, wood samples such as those used in this study contain a high proportion of juvenile wood, which leads to inferior bending properties and lower genetic correlations between wood quality and growth traits (Koubaa *et al.,* 2005). Other studies have confirmed the importance of environmental effects on wood properties and correlations between traits, especially at low cambial ages (Beaulieu *et al.,* 2006; Lenz *et al.,* 2011), while genetic effects appear to have a stronger influence as trees progress towards the stage of mature wood production (Lenz *et al.,* 2010). Generally, growth traits have also been shown to be negatively correlated with wood density at the phenotypic level in numerous conifer species (Macdonald and Hubert, 2002). In fact, higher growth rates in conifers are generally associated with higher earlywood proportions in growth rings, which consequently harbour a lower average wood density (Lenz *et al.,* 2010; Franceschini *et al.,* 2013).

Tree height and DBH were under strong and positive genetic and phenotypic correlations, which are consistent with previous results in white spruce (Lenz *et al.,* 2013). Since negative genetic correlations exist between wood flexural properties and tree volume–related traits, such as DBH and ring width, it appears that any improvement in growth would negatively affect flexural properties. A higher juvenile wood proportion associated with large ring widths at the Normandin site is likely the main factor explaining the lower wood stiffness observed at this site. The negative effect of tree growth rate on wood flexural properties has also been reported for white spruce, both at the genetic (Beaulieu *et al.,* 2006) and phenotypic (Sattler and Stewart, 2016) levels, as well as for other conifers, such as Scots pine (Mattsson, 2003), loblolly pine (Biblis, 1997), radiata pine (Grant *et al.,* 1984) and Norway and Sitka spruces (Danborg, 1996). Such a relationship can be explained by extended juvenile wood production and a decrease in wood density with increasing growth rate (Watt *et al.,* 2011; Sattler *et al.,* 2014). For tree breeders, the adverse correlations between growth and wood quality traits imply a need to understand how selection for a specific trait would affect other traits.

Relationships between direct and indirect assessment of wood flexural properties

While the phenotypic and genetic correlations between MOE and MOR were high, genetic correlations with acoustic velocity for both traits were much higher than phenotypic correlations, with MOE having highest genetic correlations with acoustic velocity and wood density with a value of 0.78 (Table 3). For MOR, the genetic correlation was even higher with wood density but much lower with acoustic velocity. Thus, solid wood assessments indicate that acoustic velocity represents a useful indirect method to assess wood flexural properties at the genetic level, in particular for MOE, which is encouraging for tree breeders who want to assess more conveniently hundreds to thousands of candidate trees for selection regarding wood flexural properties (Lenz *et al.,* 2013). The genetic correlation between acoustic velocity and wood density was much lower than those reported above, thus indicating that acoustic velocity is complementary to wood density in describing different aspects of wood quality. In addition, the negative genetic correlations between acoustic velocity and growth traits were less pronounced than those between growth traits and MOE or MOR. This may be attributable to the fact that acoustic velocity is not only related to the MOE of the material, but also to its fresh-cut density (Paradis *et al.,* 2013). Despite being a useful indirect method to assess wood flexural properties at the genetic level, our results suggest that acoustic velocity is not as accurate as the direct assessment using solid wood samples in describing the adverse genetic correlations between growth and wood quality traits. Relying on acoustic velocity for such a purpose could lead to an underestimation of the general pattern of adverse relationship between growth and wood quality traits.

As an indirect method of assessing MOE, acoustic velocity was more affected by non-genetic factors than solid wood assessments, as indicated by the lower phenotypic correlation between MOE and acoustic velocity (0.42) compared with the corresponding genetic correlation. This is confirmed by heritability estimates, where the direct assessment of MOE using solid wood samples had a much higher heritability value and smaller standard error than that for acoustic velocity. Non-genetic factors that might affect the ability of acoustic velocity to assess accurately the genetic value of trees include the presence of stem defects and knots (Lenz *et al.,* 2013). The abundance and size of knots may vary from tree to tree, which may be linked to genetic differences, but also the age of the trees, the initial spacing of the test plantations, the thinning schedule and the age at which crown closure has been reached. All these factors could have induced non-genetic variation in acoustic velocity measurements. As described previously, marginally different spacing was used at establishment for the two test sites, and the Valcartier test site had reached crown closure more rapidly than Normandin. While our statistical model accounted for site differences, acoustic velocity was indeed marginally more affected by $G \times E$ interaction than MOE or MOR estimated from solid wood samples, which indicates underlying site-specific effects generating more variation in acoustic velocity measurements than in MOE assessed directly from solid wood samples.

Improving wood flexural properties through indirect selection

To enhance wood quality in future plantations, direct selection for wood flexural properties appears attractive given the significant genetic gain estimated in this study for both MOE and MOR. Nevertheless, the direct and destructive assessment of wood flexural properties using solid wood samples in breeding trials is very costly and operationally difficult to implement. Hence, indirect selection of wood flexural properties is needed and selection based on acoustic velocity or wood density has been suggested as a potential strategy for wood quality improvement (Wielinga *et al.,* 2009; El-Kassaby *et al.,* 2011; Lenz *et al.,* 2013).

As indicated by indirect selection efficiencies (Table 4) and the strong positive relationship with wood flexural properties, selection for acoustic velocity and wood density could help realize a significant proportion of the gains associated with wood flexural traits. For both MOE and MOR, a higher efficiency of indirect selection was found for wood density than for acoustic velocity, and acoustic velocity had its highest efficiency with MOE. Despite a comparably small expected genetic gain for acoustic velocity, considering wood density as a single early selection trait for MOE and MOR may require caution, due to the fact that its selection efficiency at a very early age has been found to be reduced given the high proportion of juvenile wood near the pith (Lenz *et al.,* 2011). The rather small correlation in this study between wood density and acoustic velocity is also consistent with previous findings (Lenz *et al.,* 2013), and it indicates that there is limited overlap in the patterns of genetic variation between the two traits. Then, it is likely that combining these two traits for indirect selection would result in higher gains in MOE and MOR than using only one trait. Thus, our results support the idea that both variables could be used in conjunction to provide a non-destructive, indirect assessment of wood flexural properties, as tested in multi-trait selection scenario #5.

An important challenge of conifer breeding is to overcome the negative relationship between wood quality and growth traits. The critical role of wood density on mechanical traits such as MOE and MOR has long been recognized as well as the reduction in wood density that is resulting from enhanced growth (Zobel and Jett, 2012). Yet, only a handful of conifer breeding programs consider wood density or any other indirect assessment traits to measure and to improve wood quality (Mullin *et al.,* 2011). In forest management, other attempts are made to manage this adverse relationship through enhanced inventory of the natural variability of wood properties, carefully chosen stocking densities or thinning interventions to manage for adequate wood density while preserving growth productivity (Watt *et al.,* 2011; Zobel and Jett, 2012; Xiang *et al.,* 2014; Giroud *et al.,* 2017; Pretzsch, 2020).

So far, the positive relationships between wood traits hint towards good possibilities for indirect selection of wood flexural properties. Negative genetic correlations between wood and growth traits may appear challenging, but they only reach low to moderate strength. This makes it likely that (1) 'correlation breakers' (i.e. trees that combine superior growth and quality traits) can be found and (2) gains can be maximized through multi-trait selection (Lenz *et al.,* 2020b).

Multi-trait selection for gains in wood flexural properties and height growth

To develop a strategy for wood quality improvement in the context of spruce breeding, we combined traits from all categories of variables into selection indices. Targeting higher volume in selection will not result in improved wood flexural properties and will rather result in lower values for wood quality traits in future breeding cycles. Allowing a higher weight on height growth (S_1) may balance some of the negative effects of radial growth (DBH) on wood quality and only lead to a slight decrease of wood density, MOE and MOR. Interestingly, the inclusion of MOE and MOR besides height (S_4) could realize most of the maximum gain for wood flexural traits, albeit to the expense of growth. Economic studies would be needed to determine if the cost for trait assessment and the lower gains in growth productivity could be balanced by the improved wood properties of the product basket (Ivković *et al.,* 2006). For now, the inclusion of indirect selection traits for wood quality, in conjunction with height (S_2 and S_3), could provide some improvement of wood quality traits, while almost maximizing gain for growth. This is especially true for the combination of height and acoustic velocity, given that the negative genetic correlation between these traits was low, thus leading to a promising avenue to concurrently improve growth and wood flexural properties.

Conclusion

This study investigated the genetic parameters of wood flexural properties estimated from solid wood in white spruce, and their phenotypic and genetic relationships with growth traits and other wood quality traits. Based on our findings, it appears that low wood density and most likely high ring width possibly associated with a higher proportion of juvenile wood are the main factors contributing to the low stiffness and strength of wood in these young trees. Hereby, future studies should analyse pith to bark changes to understand the effect of juvenile wood and environment effect on wood strength and stiffness. The negative genetic correlations between MOE/MOR and DBH and ring width suggest that a selection strategy based on volume improvement alone will result in low wood flexural properties in white spruce for the next generation. Moreover, it appears possible to take advantage of early selection since flexural wood properties were moderately to highly heritable and they were genetically correlated with wood density, height and acoustic velocity. Finally, benefitting from the existing genetic relationships, multi-trait selection indices can balance genetic gains and mutually improve tree growth and wood quality traits despite adverse correlations. The integration of indirect wood quality assessment traits into selection indices successfully prevented loss in wood flexural quality although genetic gains for those traits were reduced compared with their direct assessment. Including acoustic velocity and/or wood density besides main selection for tree height corresponded best to the priorities of tree breeders. We conclude that multi-trait index selection is an efficient selection method that can be included into operational spruce breeding programs to facilitate the estimation of the genetic gains for most growth productivity and wood quality traits of interest.

Data availability

In order to comply with Intellectual Property Policies (IPP) of participating governmental institutions in this work, the supporting phenotyping data are not deposited into a public domain. The original data were collected in plantations that are part of operational white spruce breeding programs and are stored in our databases at the Canadian Wood Fibre Centre. It may be shared upon request to the corresponding author and P.L. according to our IPP. The SNP genotyping chip and the reconstructed pedigree used in this study are provided in Lenz *et al.* (2020a).

Acknowledgements

We thank Gaëtan Daoust, René Paquet, Daniel Plourde, the late Serge Légaré (Natural Resources Canada) and all staff of the Ministère des Forêts, de la Faune et des Parcs du Québec, who participated in trial establishment and data collections over the years, in particular Martin Perron, André Rainville and Guildo Gagnon, as well as many collaborators and students. Thanks to Éric Dussault, Philippe Labrie, Marie Deslauriers, Esther Pouliot, Jean-François Légaré (Natural Resources Canada) and François Beaulieu (Canada Research Chair in Forest Genomics, Univ. Laval) for help with wood sampling and phenotypic assessments of test trees. We are grateful to staff at Laval University, including Benoît St-Pierre, Daniel Bourgault, Luc Germain for wood sample preparation according to the testing standards as well as Normand Paradis for their crucial help with the analyses of wood flexural properties. Our thanks go to Sébastien Clément and Jason Miccocci (Natural Resources Canada) for help with databasing and statistical analyses of quantitative trait data.

Conflict of interest statement

Not declared.

Funding

Spruce-Up project (243FOR) funding by Genome Canada, Génome Québec and Genome BC through the Large-Scale Applied Research Program (LSARP); the Renewable Materials Research Center (CRMR); the Canada Research Chair in Forest Genomics of Université Laval; the Ministère des Forêts, de la Faune et des Parcs du Québec; the Canadian Wood Fibre Centre and the Laurentian Forestry Centre of Natural Resources Canada.

References

American Society for Testing and Materials – ASTM. *Annual book of ASTM standards*. Denvers, (D 143-94 - Standard methods of testing small, clear specimens of timber). Philadelphia: ASTM; 1997, p. 23–53.

Barrett, J. and Kellogg, R. 1991 Bending strength and stiffness of second-growth Douglas-fir dimension lumber. *For. Prod. J. (USA)*. **41**, 35–43.

Beaulieu, J. and Bousquet, J. 2010 Facteurs génétiques affectant la variabilité des cernes annuels chez les espèces arborescentes nordiques. In *La dendroécologie: principes, méthodes et applications*, Presses de l'Université Laval, pp. 137–167.

Beaulieu, J., Doerksen, T.K., MacKay, J., Rainville, A. and Bousquet, J. 2014 Genomic selection accuracies within and between environments and small breeding groups in white spruce. *BMC Genomics* **15**, 1048 (16p.).

Beaulieu, J., Zhang, S., Yu, Q. and Rainville, A. 2006 Comparison between genetic and environmental influences on lumber bending properties in young white spruce. *Wood Fiber Sci.* **38**, 553–564.

Biblis, EJ. 1997 Effect of stand age and density on the quality of lumber from 25 to 40 year old loblolly pine plantations. Paper to Topic 12, this Congress.

Burdon, R., Carson, M. and Shelbourne, C. 2008 Achievements in forest tree genetic improvement in Australia and New Zealand 10: *Pinus radiata* in New Zealand. *Aust. For.* **71**, 263–279.

Canadian Council of Forest Ministers (CCFM). 2003 National Forestry Database Program. *Canadian Wood Council (CWC). 2001*. Wood Design Manual 2001. Ottawa, ON. 900 pp.

Cave, I. and Walker, J. 1994 Stiffness of wood in fast-grown plantation softwoods: the influence of microfibril angle. *For. Prod. J.* **44**, 43.

Chen, Z.-Q., Gil, M.R.G., Karlsson, B., Lundqvist, S.-O., Olsson, L. and Wu, H.X. 2014 Inheritance of growth and solid wood quality traits in a large Norway spruce population tested at two locations in southern Sweden. *Tree Genet. Genomes* **10**, 1291–1303.

Chen, Z.-Q., Karlsson, B., Lundqvist, S.-O., García Gil, M.R., Olsson, L. and Wu, H.X. 2015 Estimating solid wood properties using Pilodyn and acoustic velocity on standing trees of Norway spruce. *Ann. For. Sci.* **72**, 499–508.

Chen, Z.-Q., Karlsson, B. and Wu, H.X. 2017 Patterns of additive genotype-by-environment interaction in tree height of Norway spruce in southern and Central Sweden. *Tree Genet. Genomes* **13**, 25.

Corriveau, A., Beaulieu, J. and Daoust, G. 1991 Heritability and genetic correlations of wood characters of upper Ottawa Valley white spruce populations grown in Quebec. *For. Chron.* **67**, 698–705.

Danborg, F. 1996 *Research Series, 18: Juvenile Wood in Norway and Sitka Spruce: Anatomy, Density, Drying Properties, Visual Grading and Strength Properties [Based on 4 Articles]*. KVL, DSR.

El-Kassaby, Y.A., Cappa, E.P., Liewlaksaneeyanawin, C., Klápště, J. and Lstibůrek, M. 2011 Breeding without breeding: is a complete pedigree necessary for efficient breeding? *PLoS One* **6**, e25737.

Falconer, D.S. 1996 *Introduction to Quantitative Genetics*. Pearson Education India.

Franceschini, T., Ferraille, T., Giroud, G., Barrette, J. and Schneider, R. 2019 Modelling wood density and modulus of elasticity in white spruce plantations in eastern Québec. *For. Chron.* **95**, 196–206.

Franceschini, T., Longuetaud, F., Bontemps, J.-D., Bouriaud, O., Caritey, B.-D. and Leban, J.-M. 2013 Effect of ring width, cambial age, and climatic variables on the within-ring wood density profile of Norway spruce *Picea abies* (L.) karst. *Trees* **27**, 913–925.

Gao, S., Wang, X., Wang, L. and Allison, R.B. 2013 Effect of temperature on acoustic evaluation of standing trees and logs: part 2: field investigation. *Wood Fiber Sci.* **45**, 15–25.

Gärtner, S.M., Lieffers, V.J. and Macdonald, S.E. 2011 Ecology and management of natural regeneration of white spruce in the boreal forest. *Environ. Rev.* **19**, 461–478.

Giroud, G., Bégin, J., Defo, M. and Ung, C.-H. 2017 Regional variation in wood density and modulus of elasticity of Quebec's main boreal tree species. *For. Ecol. Manag.* **400**, 289–299.

Grant, D., Anton, A. and Lind, P. 1984 Bending strength, stiffness, and stress-grade of structural Pinus radiata: effect of knots and timber density. *N. Z. J. For. Sci.* **14**, 331–348.

Hassegawa, M., Savard, M., Lenz, P.R., Duchateau, E., Gélinas, N., Bousquet, J. *et al.* 2020 White spruce wood quality for lumber products: priority traits and their enhancement through tree improvement. *Forestry Res.* **93**, 16–37.

Hayatgheibi, H., Fries, A., Kroon, J. and Wu, H.X. 2017 Genetic analysis of lodgepole pine (*Pinus contorta*) solid-wood quality traits. *Can. J. For. Res.* **47**, 1303–1313.

Hayatgheibi, H., Fries, A., Kroon, J. and Wu, H.X. 2019 Genetic analysis of fiber-dimension traits and combined selection for simultaneous improvement of growth and stiffness in lodgepole pine (*Pinus contorta*). *Can. J. For. Res.* **49**, 500–509.

Hong, Z., Fries, A. and Wu, H.X. 2014 High negative genetic correlations between growth traits and wood properties suggest incorporating multiple traits selection including economic weights for the future scots pine breeding programs. *Ann. For. Sci.* **71**, 463–472.

Huang, C.-L. 2005 *System and Method for Measuring Stiffness in Standing Trees*. Google Patents.

Ivković, M., Wu, H.X., McRae, T.A. and Powell, M.B. 2006 Developing breeding objectives for radiata pine structural wood production. I. Bioeconomic model and economic weights. *Can. J. For. Res.* **36**, 2920–2931.

Ivkovich, M., Namkoong, G. and Koshy, M. 2002 Genetic variation in wood properties of interior spruce. II. Tracheid characteristics. *Can. J. For. Res.* **32**, 2128–2139.

Jessome, A. 1977 *Strength and Related Properties of the Wood Grown in Canada. Rpt. 21. Eastern Forest Product Lab*. Forestry Tech.

Johansson, M. and Kliger, R. 2000 Variability in strength and stiffness of structural Norway spruce timber: Influence of raw material parameters. In *Proceedings of the World Conference on Timber Engineering*; Barrett, J.D., Ed.; WCTE: Whistler, BC, Canada; Volume 9.

Koubaa, A., Isabel, N., Zhang, S.Y., Beaulieu, J. and Bousquet, J. 2005 Transition from juvenile to mature wood in black spruce (Picea mariana [Mill.] B.S.P.). *Wood Fiber Sci.* **37**, 445–455.

Kumar, S., Gerber, S., Richardson, T. and Gea, L. 2007 Testing for unequal paternal contributions using nuclear and chloroplast SSR markers in polycross families of radiata pine. *Tree Genet. Genomes* **3**, 207–214.

Lachenbruch, B., Moore, J.R. and Evans, R. 2011 Radial Variation in Wood Structure and Function in Woody Plants, and Hypotheses for its Occurrence. *In Size-and age-related changes in tree structure and function*, Springer, pp. 121–164.

Lambeth, C., Lee, B.-C., O'Malley, D. and Wheeler, N. 2001 Polymix breeding with parental analysis of progeny: an alternative to full-sib breeding and testing. *Theor. Appl. Genet.* **103**, 930–943.

Lenz, P., Auty, D., Achim, A., Beaulieu, J. and Mackay, J. 2013 Genetic improvement of white spruce mechanical wood traits – early screening by means of acoustic velocity. *Forests* **4**, 575–594.

Lenz, P., Cloutier, A., MacKay, J. and Beaulieu, J. 2010 Genetic control of wood properties in *Picea glauca* – an analysis of trends with cambial age. *Can. J. For. Res.* **40**, 703–715.

Lenz, P., MacKay, J., Rainville, A., Cloutier, A. and Beaulieu, J. 2011 The influence of cambial age on breeding for wood properties in *Picea glauca*. *Tree Genet. Genomes* **7**, 641–653.

Lenz, P.R., Nadeau, S., Azaiez, A., Gérardi, S., Deslauriers, M., Perron, M. *et al.* 2020a Genomic prediction for hastening and improving efficiency of forward selection in conifer polycross mating designs: an example from white spruce. *Heredity* **124**, 562–578.

Lenz, P.R., Nadeau, S., Mottet, M.J., Perron, M., Isabel, N., Beaulieu, J. *et al.* 2020b Multi-trait genomic selection for weevil resistance, growth, and wood quality in Norway spruce. *Evol. Appl.* **13**, 76–94.

Li, P., Beaulieu, J. and Bousquet, J. 1997 Genetic structure and patterns of genetic variation among population in eastern white spruce (Picea glauca). *Can J. For. Res.* **27**, 189–198.

Libby, W. and Cockerham, C. 1980 Random non-contiguous plots in interlocking field layouts. *Silvae Genet.* **29**, 5–6.

Macdonald, E. and Hubert, J. 2002 A review of the effects of silviculture on timber quality of Sitka spruce. *Forestry* **75**, 107–138.

Mattsson, S. 2002 Effects of site preparation on stem growth and clear wood properties in boreal Pinus sylvestris and Pinus contorta. *Acta Universitatis Agriculturae Sueciae, Silvestria*, **240**, 1–37.

Megraw, R.A., Bremer, D., Leaf, G. and Roers, J. 1999 Stiffness in loblolly pine as a function of ring position and height, and its relationship to microfibril angle and specific gravity. *Connection between silviculture and wood quality trough modelling approaches and simulation software, Proceedings of IUFRO WP S*, **5**, 01–04.

Mullin, T.J., Andersson, B., Bastien, J.-C., Beaulieu, J., Burdon, R., Dvorak, W. *et al.* 2011 Economic importance, breeding objectives and achievements. In *Genetics, Genomics and Breeding of Conifers*, CRC Press, New York, pp. 40–127.

Mvolo, C.S., Koubaa, A., Beaulieu, J., Cloutier, A., Defo, M. and Yemele, M.-C. 2019 Phenotypic correlations among growth and selected wood properties in white spruce (*Picea glauca* (Moench) Voss). *Forests* **10**, 589.

Paradis, N., Auty, D., Carter, P. and Achim, A. 2013 Using a standing-tree acoustic tool to identify forest stands for the production of mechanically-graded lumber. *Sensors* **13**, 3394–3408.

Pretzsch, H. 2020 Density and growth of forest stands revisited. Effect of the temporal scale of observation, site quality, and thinning. *For. Ecol. Manag.* **460**, 117879.

Sattler, D.F., Comeau, P.G. and Achim, A. 2014 Within-tree patterns of wood stiffness for white spruce (*Picea glauca*) and trembling aspen (*Populus tremuloides*). *Can. J. For. Res.* **44**, 162–171.

Sattler, D.F. and Stewart, J.D. 2016 Climate, location, and growth relationships with wood stiffness at the site, tree, and ring levels in white spruce (*Picea glauca*) in the Boreal Plains ecozone. *Can. J. For. Res.* **46**, 1235–1245.

Schimleck, L., Mora, C. and Daniels, R. 2003 Estimation of the physical wood properties of green *Pinus taeda* radial samples by near infrared spectroscopy. *Can. J. For. Res.* **33**, 2297–2305.

Telewski, F. 1989 Structure and function of flexure wood in *Abies fraseri*. *Tree Physiol.* **5**, 113–121.

Ukrainetz, N.K., Ritland, K. and Mansfield, S.D. 2008 Identification of quantitative trait loci for wood quality and growth across eight full-sib coastal Douglas-fir families. *Tree Genet. Genomes* **4**, 159–170.

Watt, M.S., Zoric, B., Kimberley, M.O. and Harrington, J. 2011 Influence of stocking on radial and longitudinal variation in modulus of elasticity, microfibril angle, and density in a 24-year-old *Pinus radiata* thinning trial. *Can. J. For. Res.* **41**, 1422–1431.

Wessels, C., Malan, F. and Rypstra, T. 2011 A review of measurement methods used on standing trees for the prediction of some mechanical properties of timber. *Eur. J. For. Res.* **130**, 881–893.

Wheeler, N.C., Steiner, K.C., Schlarbaum, S.E. and Neale, D.B. 2015 The evolution of forest genetics and tree improvement research in the United States. *J. For.* **113**, 500–510.

White, T.L., Adams, W.T. and Neale, D.B. 2007 *Forest Genetics*. Cabi.

Wielinga, B., Raymond, C.A., James, R. and Matheson, A.C. 2009 Effect of green density values on Pinus radiata stiffness estimation using a stress-wave technique. *N. Z. J. For. Sci.* **39**, 71–79.

Wolak, M.E. 2019 Nadiv: an R package to create relatedness matrices for estimating non-additive genetic variances in animal models. *Methods Ecol. Evol.* **3**:792–796.

Wu, H.X., Eldridge, K.G., Matheson, A.C., Powell, M.B., McRae, T.A., Butcher, T.B. *et al.* 2007a Achievements in forest tree improvement in Australia and New Zealand 8. Successful introduction and breeding of radiata pine in Australia. *Aust. For.* **70**, 215–225.

Wu, H.X., Powell, M.B., Yang, J.L., Ivković, M. and McRae, T.A. 2007b Efficiency of early selection for rotation-aged wood quality traits in radiata pine. *Ann. For. Sci.* **64**, 1–9.

Xiang, W., Leitch, M., Auty, D., Duchateau, E. and Achim, A. 2014 Radial trends in black spruce wood density can show an age-and growth-related decline. *Ann. For. Sci.* **71**, 603–615.

Zhou, H. and Smith, I. 1991 Factors influencing bending properties of white spruce lumber. *Wood Fiber Sci.* **23**, 483–500.

Zobel, B.J. and Jett, J.B. 2012 *Genetics of Wood Production*. Springer Science & Business Media.

Zobel, B.J. and Van Buijtenen, J.P. 2012 *Wood Variation: Its Causes and Control*. Springer Science & Business Media.