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Effect of Seed Transfer on Selected Wood Quality Attributes of Jack Pine (*Pinus banksiana* Lamb.) †

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Abstract: So far, few studies have considered the impacts of seed sources transfer on jack pine (*Pinus banksiana Lamb.*) wood quality, although wood quality attributes (WQA) in general and the differences between juvenile and mature wood in particular will determine suitability of the produced wood for end-uses. The main objective of this study was to examine the possibility of selecting superior jack pine provenances based on selected WQA. Twenty-two provenances of jack pine were planted in 1964 in Petawawa Research Forest, ON, Canada, as part of a provenance test. The plantation location offers conditions close to optimum for jack pine growth. Transition ages at breast height, determined with tracheids length, were computed with a piecewise model. Measurements at age 42 from seed were subjected to analyses of variance. Radial variations from pith to bark, as well as trends with seed sources origin of the selected WQA were also considered. A ranking was made based on a selection index built with four WQA. The provenances matured between 8 and 14 years, corresponding to 17%–48% of juvenile wood proportion. Significant differences among provenances were observed for ring width, ring density, tracheid length, and diameter at breast height but not for tracheid diameter, tree height, transition age, and juvenile wood proportion. None of the provenances ranked the best with all the selected WQA, but it was possible to find provenances exhibiting both high growth rate and good wood quality. A surprising result of this study was that tracheid diameter initially enlarged for 8 years, before declining toward the bark. It is possible to select provenances for a higher growth rate and for good physical (i.e., related to wood density) and anatomical (i.e., related to tracheid dimensions) wood quality attributes.

Keywords: seed sources; provenance; ranking; transition age; wood quality attributes; physical properties; anatomical properties; growth rate; latitude

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1. Introduction

Jack pine (*Pinus banksiana* Lamb.) is an economically important tree species for Canada and the USA [1]. It is one of the most important species for the wood industries in Quebec [2] and offers an opportunity for wood quality management through provenance control [3–5]. However, effects of seed sources on jack pine wood quality have received little interest [6]. Ring width (RW) is commonly used to assess the impact of climate variations on tree growth. It has been found that jack pine seed sources acclimate positively to warmer and drier climate by increasing ring width [7]. Anything that affects tree growth also impacts its wood properties [4]. Therefore, one may expect wood quality attributes (WQA) in general and transition age (TA) in particular, to vary with seed sources.

A provenance test, i.e., plantings of seed sources originating from throughout the species range in the same environmental conditions, is a good silvicultural tool for selecting best performing seed sources for a given environment [3,5]. However, many extraneous factors (e.g., silvicultural management, tree-level genetic, edaphic conditions, herbivory and disease impacts, extreme climatic phenomena, and extreme natural disturbance) could alter the complex temperature–growth relationship induced by planting of seed sources in a given test location [4,5].

Together with ring density (RD), tracheid length (TL) is among the most important WQA in pulp [8] and solid wood [9] applications. TL allows a clear distinction between juvenile wood (JW) and mature wood (MW) through TA determination [10,11]. JW is found near the pith and shifts to MW toward the bark of older trees. JW is generally undesirable for solid wood products but can be managed in pulp industries [9]. This is due to shorter tracheid, thinner cell wall, lower latewood proportion, lower cellulose and higher lignin content, lower tangential and higher longitudinal shrinkage, and larger fibril angle of JW compared to MW [12]. The huge differences between the xylem of JW and that of MW is mainly due to the distance of the tracheid to the active living crown [13,14] and the age of cambial initial during xylogenesis [12]. Indeed, JW is formed under the strong regulatory influence of the growth hormones, especially indole-3-acetic acid (IAA, auxin) synthesized in the active living crown [15]. This explains why trees with deep crowns and the top of all trees are generally assumed to be entirely made of JW [14,16].

Transition age was found to occur at 14 years [10] in jack pine using TL. Loblolly pine (*Pinus taeda* L.) and slash pine (*Pinus elliottii*) trees grown on a same environment shared similar wood density TA, but TA was significantly different when these trees were grown in different geographical areas [17,18]. TA estimated from wood density was reported not to be influenced by seed sources in loblolly pine [19], but we are not aware of a previous study examining tracheid length TA in a provenance test. Since TA was found to be heritable [20], mapping lower TA seed sources can represent a first step in selecting early maturing trees [19] and, therefore, reduce juvenile wood proportion (JWP) in the harvest.

The main objective of this study was to examine the possibility of selecting superior jack pine provenances for an earlier TA from juvenile to mature wood, using TL. A second goal was to rank the provenances based on selected WQA (ring width, wood density, tracheid length, tracheid diameter, tree height, diameter at breast height, transition age, and juvenile wood proportion). Describing radial patterns of variation of the selected WQA was another goal of this study.

2. Materials and Methods

2.1. Sample Collection

The material came from a common garden plantation of jack pine in the Petawawa Research Forest, Ontario, Canada (lat. 45.58° N, long. 77.25° W, elev. 168 m). Seedlot provenances are mapped in Figure 1 and their origin, location, and climatic attributes are presented in Table 1. This plantation is part of a range-wide study initiated in 1966. Seed sources from 99 geographic origins were collected from native stands throughout the whole range of the species and planted at several locations in the USA and Canada [21]. The common garden plantation location in Petawawa offers conditions close to optimum for jack pine growth [3,22]. The experimental design was a triple square lattice design made of 10 blocks and one demonstration block near the edge of the plantation. Each seedlot or provenance was initially represented by a 10-tree-row plot planted at a spacing of 1.8 × 1.8 m. All seeds were sown in the Petawawa National Forest Institute (PNFI) nursery in 1964 and planted on the Petawawa Experiment Station in 1966, now known as Petawawa Research Forest. The provenance trial was thinned in the fall of 1987 to prevent growth stagnation. Regardless of mortality in adjacent trees, every third tree of the 10-tree-row plots was removed. Therefore, at least one side of every remaining tree was exposed to thinning [23].
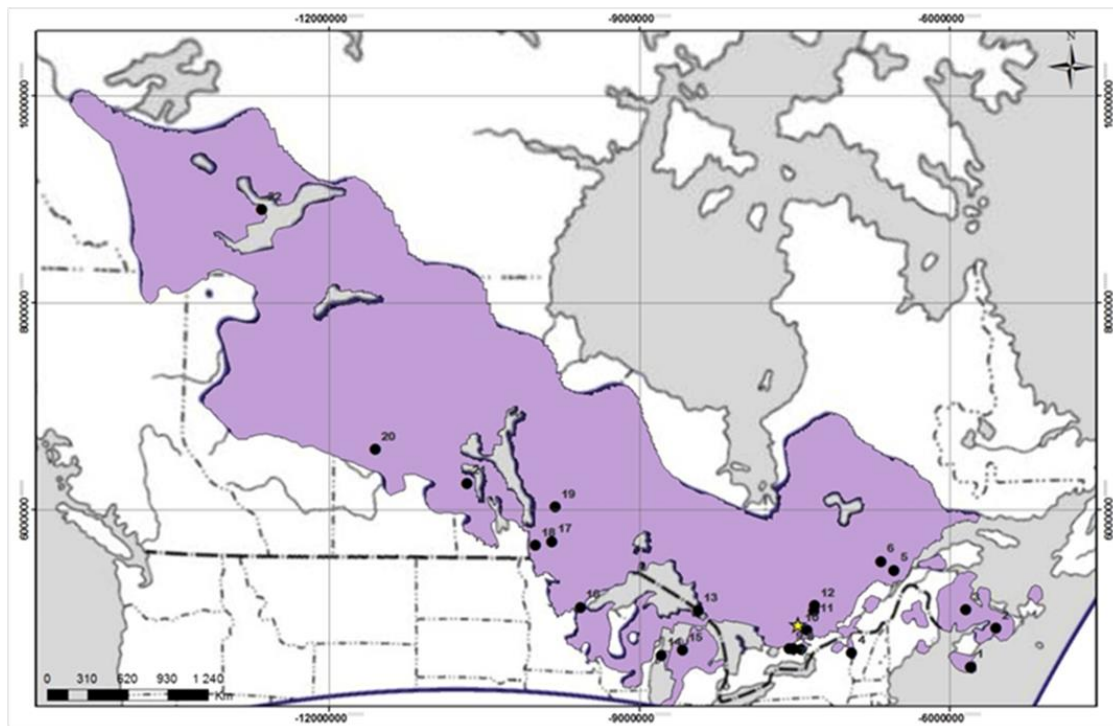
Figure 1. Map of the geographical locations of the provenances and the plantation site. The star indicates the provenance trial location.

Table 1. Geographic and climatic description of the provenances (ranked in descending order of mean annual temperature) and the plantation site (*, Petawawa Research Forest).

ID	Origin, Province, or State	Seedlot	Lat.	Long.	Temp.	Prec.
14	Freesoil, Michigan	3271	44.1	86.1	8.3	747
1	Birchtown Brook, Nova Scotia	3202	43.5	65.2	6.7	1463
15	Fite Lake, Michigan	3272	44.3	85.2	6.7	795
8	Clare River, Ontario	3240	44.4	77	6.1	877
4	Upper Jay, New York	3223	44.2	73.5	5.6	984
7	Twin Lakes, Ontario	3239	44.4	77.5	5.6	721
2	Thomson Station, Nova Scotia	3206	45.4	63.5	5	1075
9	Kaladar, Ontario	3241	44.4	77.1	5	721
10	Douglas, Ontario	3242	45.3	76.6	5	755
3	Cains River, New Brunswick	3211	46.3	65.5	4.4	1180
11	Horry Lake, Québec	3247	46.2	76.1	4.4	768
*	Petawawa Research Forest	–	45.6	77.3	4.3	853
16	Cloquet, Minnesota	3279	46.4	92.3	3.9	758
12	Baskatong Lake, Québec	3248	46.5	76.1	3.3	865
13	Dunbar Forest, Michigan	3259	46.3	84.2	3.3	760
5	Port Alfred, Québec	3230	48.2	70.5	2.2	984
17	Kenora, Ontario	3282	49.5	94.3	2.2	655
18	Hadashville, Manitoba	3283	49.3	95.5	1.7	548
6	Alex River, Québec	3232	48.6	71.5	1.1	809
19	Red Lake, Ontario	3286	51	94.1	0.6	518
20	Big River, Saskatchewan	3288	53.5	107	0.6	410
21	Cowan, Manitoba	3290	52	100	0	455
22	Yellowknife, Northwest Territories	3297	62.3	114	−5.6	215

Lat.: latitude (north), Long.: longitude (west), Temp.: mean annual temperature (°C), Prec.: precipitation (mm).

In the fall of 2006, three trees were harvested in 17 provenances and two trees in five additional provenances for a total number of 22 provenances and 61 trees for the whole experiment. No blocking

structure was traceable with the harvested material. Furthermore, no local provenance was available in this study. Nevertheless, the collected material is highly valuable for the investigation of wood quality variation with seed sources. Indeed, jack pine offers an opportunity for wood quality management through provenance control [3,5–7], but mature stands made up of different sources of this species are very uncommon [5]. Morphological properties (tree height (TH) and diameter at breast height (DBH)) were recorded on the ground, and discs at breast height (1.3 m) were collected for all harvested trees. Mean annual temperature and mean annual precipitation at the seed origin are those measured during the establishment of the provenance test [21]. Mean annual temperature and mean annual precipitation at the test location was taken from Savva et al. [7].

2.2. Sample Preparation and Wood Quality Attribute Measurements

Two wedges centered on the pith were sawn bark to bark, in the north-south direction of the discs. One bark-to-bark wedge was extracted in a 2:1 solution of cyclohexane and ethanol for 24 h and in distilled water for another 24 h. Thereafter, the samples were rinsed with distilled water and air-dried under constraint to prevent any deformation. These extractives-free wedges were used for ring width and ring density measurements with an X-ray densitometer (Quintek Measurements Systems QMS model QTRS-01X, Knoxville, TN, USA). We used a 25 μm linear resolution step size. The mean value of the north and south radius (measured for every single ring) was computed for both ring width and ring density, to yield a unique pith-to-bark database for each tree. The boundary between earlywood and latewood was delineated using the maximum derivative method [24]. The other wedge was used for TL and tracheid diameter (TD) measurements. Wood sticks were taken from pith to bark at systematic rings (3, 6, 9, 12, 15, 20, 25, and 30) in a single pith-to-bark section. No particular direction was chosen in advance for anatomical (TL and TD) property measurements. The only rule observed was to avoid compression wood and knots that were visually detected. These sticks were macerated using a Franklin [25] solution of (1:1 *v/v*) hydrogen peroxide diluted to 30% and concentrated glacial acetic acid. Each stick was placed in a test tube, immersed in the Franklin's solution, and kept in hot distilled water (85–90 °C) until the stick turned white in appearance. A tracheid suspension was obtained by gently shaking the delignified wood stick with a laboratory blender. Anatomical features were measured in the suspension with a Fiber Quality Analyzer, LDA02 FQA (Op Test Equipment Inc. Hawkesbury, Ontario, Canada). A total of 4000 tracheids were measured in every sample. TL was measured as weight-weighted length (LLW) (Equation (1)), giving results reasonably comparable with true TL measurements and controlling for the bias caused by the large number of fines generated during the preparation process [26].

$$\text{LLW} = \frac{\Sigma_{ni} L_i^3}{\Sigma_{ni} L_i^2} \tag{1}$$

where LLW = weight-weighted length, *i* = 1, 2, 3 … N categories, *n* = fiber count in the (*i*[th]) category, *L* = contour length.

2.3. Statistical Analyses

2.3.1. Transition Age and Juvenile Wood Proportion

In a previous study, we found that a polynomial model that accounts for the autocorrelation among successive growth rings is a better choice than the piecewise model in determining TA based on TL [11]. However, the age span of the material used in this study did not allow using the polynomial model with TL. Therefore, we estimated TA with a piecewise model using the NLIN procedure of SAS® [27,28]. Equation (2) for JW and Equation (3) for MW were used to find the TA from Equation (4). The reliability of TA estimates was examined by graphical visual checking [29]. JWP at breast height (in tree basal area) was estimated following the procedure described by Alteyrac et al. [30]. Equation (5) described the juvenile wood radius (JWR), i.e., the cumulative ring width from pith to the year of

transition. Equation (6) made it possible to estimate the juvenile wood area (JWA), i.e., the basal area of JW in the tree. Equation (7) represented the tree radius (TR), i.e., the cumulative ring width from pith to the last calendar year of full ring (2006), and Equation (8) was the tree area (TAR), i.e., the whole basal area of the tree. JWP was computed with Equation (9) from results of Equations (6) and (8).

$$TL_{jw} = a_{jw} + b_{jw}(\text{CA}) \tag{2}$$

$$TL_{mw} = a_{mw} + b_{mw}(\text{CA}) \tag{3}$$

$$\text{TL} = a_{jw} + \text{TA}\left(b_{jw} - b_{mw}\right) + b_{mw}(\text{CA}) \tag{4}$$

$$\text{JWR} = \sum_{rfp=pith}^{rfp=TA} (\text{RW}) \tag{5}$$

$$\text{JWA} = \pi \times (\text{JWR})^2 \tag{6}$$

$$\text{TR} = \sum_{rfp=pith}^{rfp=2006} (\text{RW}) \tag{7}$$

$$\text{TAR} = \pi \times (\text{TR})^2 \tag{8}$$

$$\text{JWP} = 100 \times \left(\frac{\text{JWR}}{\text{TR}}\right)^2 \tag{9}$$

where TL = tracheid length, JW = juvenile wood, MW = mature wood, CA = cambial age, TA = transition age, JWR = juvenile wood radius, RW = ring width, JWA = juvenile wood area, TR = whole tree radius in 2006, TAR = whole tree basal area, JWP = juvenile wood proportion, and a and b are coefficients.

2.3.2. Variation and Ranking among Provenances

The eight WQA investigated in this study were: tree height, diameter at breast height, transition age, juvenile wood proportion, ring density, ring width, tracheid length, and tracheid diameter. The MEANS procedure of SAS$^{\circledR}$ was used to calculate means (from pith to 30th CA) on a tree basis of RD, RW, TL, and TD. One-way analysis of variance (Equation (10)) was used on the overall dataset to estimate the variance attributable to provenance [31]. The models were fitted using the MIXED procedure of SAS$^{\circledR}$ (α = 0.05 probability level).

$$Y_{ij} = u + P_i + \varepsilon_{ij} \tag{10}$$

where Y_{ij} = measured value of the *WQA*, μ = overall mean of the provenance, P_i = random effect of provenance i, and ε_{ij} = random error term associated with the jth tree of the ith provenance, $\varepsilon_{ij} \sim N (0, \sigma^2_{\text{residuals}})$.

Intraclass correlation coefficients (ICC) were calculated from variance parameter estimates computed with the MIXED model using Equation (11). The intraclass correlation coefficient informs us about the proportion of the total variance explained by provenances [31,32].

$$ICC = \frac{\sigma^2_P}{\sigma^2_P + \sigma^2_e} \tag{11}$$

where ICC = intraclass correlation coefficients, σ^2_P is the variance associated to provenances and σ^2_e the residual variance.

In order to rank the selection in terms of their ability to grow fast while keeping good wood quality, we created a selection index (SI) that encompasses WQA relevant to tree growth and wood

quality. This SI was built primarily on the WQA that significantly varied with provenance. However, tree height, a morphological property which is generally the most important growth trait considered by tree breeders (e.g., [5,8,33–36]) because it is more heritable than DBH or RW, was also included in the index, although it did not vary significantly with provenances. In a first step, average values of the selected WQA were computed on a provenance basis, and provenances were ordered in descending order. In a second step, the ordered provenances were ranked in descending order (from 22 to 1) with the provenance with the highest value of the selected WQA ranking 22nd and the provenance with the lowest value of the selected WQA ranking first. As it is customary in ranking procedures, equally ranked provenances were assigned a rank that corresponded to the average of their cumulative ranks. This ranking procedure allowed avoiding the issues related with the different measurement units (kg/m^3, mm, m), and the different orders of magnitude (see Table 2) of the selected WQA. In a third step, ranked values were weighted to have the final value of the selection index (Equation (12)). Given the relevance of volume production [8,34] and wood density [14] in most of the traditional wood industries, we gave a comparable weight to RW and RD (i.e., 0.333). Because it is less relevant that both RW and RD in wood industries, TL weighted only half the value of the formers (i.e., 0.167). Tree height also weighted only half the value of RW and RD (i.e., 0.167), because it did not vary significantly with provenances, and it is not a common variable in traditional wood industries. By doing so, growth-related WQA (RW and TH) weighted 0.5 of the final selection index, and physical (RD) and anatomical (TL) WQA weighted 0.5 of the final WQA for a total weight of 1. At the end of this process, selection indexes were ordered in descending order to identify the seven (one-third) best provenances.

$$\text{SI} = 0.333 \times rank_{RD} + 0.333 \times rank_{RW} + 0.167 \times rank_{TL} + 0.167 \times rank_{TH} \tag{12}$$

where SI = computed selection index, $rank_{RD}$ = rank for wood density, $rank_{RW}$ = rank for ring width, $rank_{TL}$ = rank for tracheid length, and $rank_{TH}$ = rank for tree height.

Table 2. Summary of average values of selected wood quality attributes.

ID	Origin, Province or State	Seedlot	RW	RD	TL	TD	TH	DBH	TA	JWP
1	Birchtown Brook, Nova Scotia	3202	2.03	454	2.7	37.2	15.4	14.8	10	43
2	Thomson Station, Nova Scotia	3206	2.63	475	2.5	33.7	16.5	20.0	14	42
3	Cains River, New Brunswick	3211	2.71	461	1.9	31.4	18.0	20.4	12	36
4	Upper Jay, New York	3223	3.56	456	2.5	37.3	17.5	27.7	13	28
5	Port Alfred, Quebec	3230	2.36	458	2.5	35.0	18.9	17.8	12	30
6	Alex River, Quebec	3232	2.66	469	2.7	36.3	18.0	21.7	11	28
7	Twin Lakes, Ontario	3239	2.81	485	2.5	37.2	17.3	21.4	13	37
8	Clare River, Ontario	3240	2.45	457	2.6	35.0	18.4	19.4	8	20
9	Kaladar, Ontario	3241	2.77	448	2.7	37.7	17.9	20.6	11	29
10	Douglas, Ontario	3242	3.18	468	2.5	37.8	18.1	25.0	8	17
11	Horry Lake, Quebec	3247	2.51	457	2.5	35.4	19.2	18.9	11	33
12	Baskatong Lake, Quebec	3248	2.79	458	2.7	37.2	18.1	21.7	9	22
13	Dunbar Forest, Michigan	3259	2.66	469	2.5	33.6	18.2	21.1	10	22
14	Freesoil, Michigan	3271	3.11	466	2.7	37.4	19.7	25.2	13	29
15	Fite Lake, Michigan	3272	2.96	466	2.9	30.0	19.3	22.6	11	27
16	Cloquet, Minnesota	3279	2.60	465	2.6	36.5	18.8	20.8	11	22
17	Kenora, Ontario	3282	2.68	450	2.7	36.6	19.1	21.9	11	23
18	Hadashville, Manitoba	3283	2.63	435	2.4	36.0	18.3	19.4	13	48
19	Red Lake, Ontario	3286	2.19	473	2.5	35.8	16.6	18.2	8	24
20	Big River, Saskatchewan	3288	2.45	456	2.6	35.3	18.2	18.4	10	28
21	Cowan, Manitoba	3290	2.17	458	2.4	36.1	15.9	16.1	8	17
22	Yellowknife, Northwest Territories	3297	2.95	457	2.6	34.9	17.4	22.6	11	28

RW: ring width (mm), RD: ring density (kg/m^3), TL: tracheid length (mm), TD: tracheid diameter (μm), TH: tree height (m), DBH: diameter at breast height (cm), TA: transition age (years), JWP: juvenile wood proportion in tree basal area (%).

3. Results

3.1. Radial Pattern of Wood Quality Attributes

RD initially steadily decreased for approximately 6 years, followed by a sharp increase up to 17 years before lowering again (Figure 2a). Standard error of the mean (SE) for RD was relatively large and constant from pith to the 30th ring from pith (RFP). TL was longer in MW compared to JW, and followed Sanio's law [37], as shown by its rise from pith to bark (Figure 2b). SE for TL was small throughout the 30 rings. There was an initial expansion of RW for 4 years, followed by a consistent contraction until 15 years, before continuing to decrease at a lower rate (Figure 2c). RW did not vary a lot for a given cambial age among the sampled trees, as shown by the small SE. TD initially enlarged for 8 years, before declining toward the bark (Figure 2d). As for TD, its SE was small throughout the 30 rings.
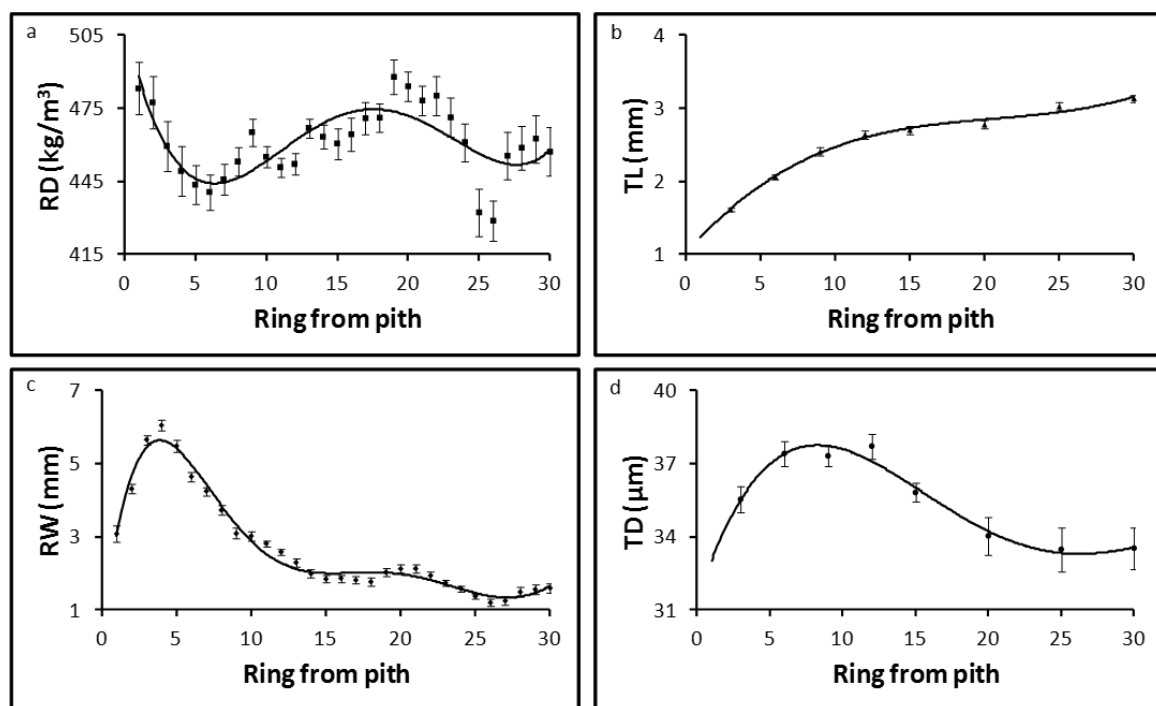

Figure 2. Radial variation pattern of selected wood quality attributes with standard errors (SE) bars: (**a**) radial variation of ring density (RD), (**b**) radial variation of tracheid length (TL), (**c**) radial variation of ring width (RW), (**d**) radial variation of tracheid diameter (TD).

3.2. Overall Wood Quality of the Provenances

Descriptive statistics on average WQA are presented in Table 2. TL was longer and RW thinner in MW compared to JW, regardless of the provenance. Overall, TD was narrower and RD higher in MW compared to JW.

TA ranged from 8 to 14 years depending on the provenance, with an average TA of 11 years (Table 2). JWP ranged from 17% to 48% of the tree basal area at breast height, depending on the provenance, with an average JWP of 29% (Table 2). TA and JWP ranges were wider, 6–22 years and 9–63%, respectively, when single trees were considered (results not shown).

3.3. Variation among Provenances

When taking the overall mean at breast height, TL, RW, and RD, were significantly different among provenances, while TD did not vary significantly among provenances (Table 3). The overall mean of DBH was significantly different among provenances, while that of TH, TA, and JWP did not

vary significantly among provenances (Table 3). In all cases, there was a highly significant variation among trees within provenances, as shown by the residuals (Table 3). ICC indicated that a good proportion of the total variance was explained by the provenance for RW, RD, and DBH. In contrast, the proportion of total variance represented by the provenance for the remaining WQA, including TL and TH, was limited (Table 3).

Table 3. Analysis of variance of selected wood quality attributes (WQA) for juvenile wood, mature wood and whole pith-to-bark section.

WQA	Sources of Variation						ICC
	Random Effects						
	Provenances			Residuals (Trees)			
	Estimate	Z Value	Pr > Z	Estimate	Z Value	Pr > Z	
Juvenile Wood							
RW	0.09	1.54	0.0619	0.25	4.47	<0.0001	0.26
RD	768.9	2.76	0.0029	356.5	4.42	<0.0001	0.68
TL	0.01	1.27	0.1020	0.04	4.41	<0.0001	0.21
TD	0.30	0.27	0.3939	7.98	4.50	<0.0001	0.04
Mature Wood							
RW	0.07	1.85	0.0319	0.13	4.47	<0.0001	0.34
RD	559.6	2.17	0.0151	724.1	4.44	<0.0001	0.44
TL	0.02	1.65	0.0498	0.06	4.47	<0.0001	0.30
TD	1.54	0.64	0.2602	15.0	4.47	<0.0001	0.09
Whole Pith-to-Bark Section							
DBH	5.82	2.08	0.0187	8.4	4.44	<0.0001	0.41
RW	0.08	2.01	0.0224	0.13	4.46	<0.0001	0.38
RD	63.2	1.73	0.0420	142.9	4.46	<0.0001	0.31
TL	0.02	1.95	0.0253	0.04	4.48	<0.0001	0.08
TD	1.08	0.48	0.3158	15.3	4.51	<0.0001	0.07
TH	0.37	0.89	0.1871	2.4	4.49	<0.0001	0.13
TA	0.08	0.06	0.4745	9.3	4.26	<0.0001	0.01
JWP	16.6	0.64	0.2621	155.9	4.20	<0.0001	0.10

DBH: diameter at breast height (cm), RW: ring width (mm), RD: ring density (kg/m^3), TL: tracheid length (mm), TD: tracheid diameter (μm), TH: tree height (m), TA: transition age (years), and JWP: juvenile wood proportion in tree basal area (%), ICC: intraclass correlation coefficient.

When the whole pith-to-bark section was segregated between JW and MW, there was a significant variation of RW and RD (though only marginal in the JW for RW) among provenances (Table 3). Both RW and RD significantly vary in the mature wood, and a marginal significant variation was also found for TL in this wood zone (Table 3). TD did not vary among provenances, independently of the wood zone. There was more variation among trees within provenances than among the provenances (Table 3) in both JW and MW. The ICC indicated that a high proportion of the total variance was explained by the provenance for RD, particularly in the JW (Table 3). The variance induced by the provenance also represented a good proportion of the total variance, for mature RW (Table 3).

3.4. Ranking of Provenances

When focusing on the overall mean at breast height, only TL, RW, and RD were significantly different among provenances. DBH also showed a significant difference among provenances. However, both DBH and RW represent radial growth. Therefore, only RW was used in ranking, together with RD and TL. RW is a valuable WQA that describes radial growth, a feature that is often considered in breeding programs [8,34]. RD is the most studied WQA, used in both solid wood and pulp industries [4]. TL is one of the most important WQA for paper products because it has a significant impact on the

quality of pulp and paper and fiber-based products such as wood-plastic composites and fiberboards. Despite not varying significantly with provenances, TH was used in the final ranking because it is the trait that tree breeders usually use to select superior trees or sources (e.g., [5,8,33–35]). The best and the second-best provenances (Fite Lake, MI, and Freesoil, MI, respectively) were the only ones that ranked among the seven best provenances with all the four WQA considered (Table 4). Except for the seventh-best provenance (Dunbar Forest, MI) which was among the seven best provenances for only one WQA, all other best provenances (Douglas, ON; Twin Lakes, ON; Alex River, QC; and Baskatong Lake, QC) ranked among the seven best provenances for two WQA (Table 4). Very interestingly, the four best provenances shared a similar latitude (44.1–45.3 N, Table 4) and were located at the south-eastern edge of jack pine distribution. These provenances ranked among the first five highest mean annual temperature (Table 1), had higher mean annual temperature and lower latitude (except Douglas, ON, which was comparable for latitude) than the common plantation (Table 4). The fifth-, sixth- and seventh-best provenances shared a lower mean annual temperature and higher latitude than the common plantation (Table 4). Their temperatures were in the lower range of all available provenances (Table 1).

Table 4. Top seven provenances when ranked in order of selected wood quality attributes and as cumulative selection index among these selected wood quality attributes.

ID	Origin, Province or State	RW Rank	RD Rank	TL Rank	TH Rank	SI	Final Rank	Temp.	Lat.
15	Fite Lake, Michigan	19	15.5	22	21	18.7	1	6.7	44.3
14	Freesoil, Michigan	20	15.5	18.5	22	18.6	2	8.3	44.1
10	Douglas, Ontario	21	17	7.5	11.5	15.8	3	5	45.3
7	Twin Lakes, Ontario	17	22	7.5	5	15.1	4	5.6	44.4
6	Alex River, Quebec	11.5	18.5	18.5	9.5	14.7	5	1.1	48.6
12	Baskatong Lake, Quebec	16	11	18.5	11.5	14.0	6	3.3	46.5
13	Dunbar Forest, Michigan	11.5	18.5	7.5	13.5	13.5	7	3.3	46.3
*	Petawawa Research Forest	–	–	–	–	–	–	4.3	45.6

RW: ring width, RD: ring density, TL: tracheid length, TH: tree height, SI: selection index, Temp.: mean annual temperature (°C) of the provenance, Lat.: latitude (Nord) of the provenance.

4. Discussion

4.1. Radial Patterns and Mean Values of the Selected Wood Quality Attributes

Radial variation of TD has been reported for several conifer tree species but not yet for jack pine. These species include radiata pine (*Pinus radiata* D. Don) [38], Norway spruce (*Picea abies* L. Karst.) [39,40], and eastern white cedar (*Thuja occidentalis* L.) [41]. In all these studies, TD and TL have been found to share a similar increasing pattern from pith to bark. In our study on jack pine, TL followed such an increasing pattern, in agreement with a previous report on five Canadian conifers, including jack pine [10], but TD showed a different radial trend by initially enlarging for 8 years, before declining toward the bark, as seen in Figure 2d. Since this radial pattern of TD was unexpected, we estimated a Pearson correlation coefficient between TD and TL. The purpose of this estimation was to see if jack pine TD and TL were highly correlated, despite their different radial patterns. This correlation was very low and non-significant ($r = 0.012$, $p = 0.80$), contrary to what is expected in other conifers [42,43]. It would be very interesting to study the longitudinal variation of jack pine TD in a functional viewpoint, to see if it concurs with the predictions of the hydraulic optimality models, as has been found for many coniferous species [44,45]. This radial pattern of TD specific to jack pine should also be confirmed using different datasets. The radial patterns of jack pine RD and RW followed trends previously described [46]. A variation as large as that of RD found for jack pine during the first 30 RFP has also been reported for eastern white cedar [41].

4.2. Overall Wood Quality of the Provenances

All seed sources presented larger average RW than the 1.8 mm [47] and the 2.2 mm [46] reported for jack pine, apart from the Birchtown Brook, NS provenance for the second (2.2 mm) case. This may be due to the optimum growth at the test location [3,22], and the thinning treatment of 1987 [23].

Since competition was controlled in the plantation, one will expect improved growth, compared to natural stands [48,49]. Furthermore, only the first 30 RFP, with a large proportion of wide juvenile rings were analyzed in this study, due to the age of the plantation. Zhang and Koubaa [46] sampled trees that were older than 25 RFP and were considered to be mature trees. The data published by Jessome [47] came from trees sampled during more than 60 years, and one can hypothesize that these trees were mature. Similarly to RW, all seed sources presented higher RD than the 430 kg/m^3 [50], 444 kg/m^3 [47], and 447 kg/m^3 [46], excluding the Hadashvile, MB provenance in the later (444 kg/m^3 and 447 kg/m^3) cases. Once again, the lower age of trees may explain the greater RD found in this study. Indeed, the radial pattern of jack pine RD (Figure 2a) belongs to the type II as described by Panshin and de Zeuuw [51], in which the closer to the pith, the higher the RD. Furthermore, the method used to measure RD may influence the results; we measured RD on extracted clear samples with X-ray densitometry, the same method used by Zhang and Koubaa [46], while Jessome [47] and Isenberg, Harder, and Louden [50] measured air-dry specific gravity. As for anatomical properties, although all seed sources were in the range (1.6–5.7 mm) for TL, none of them reached the mean value (3.5 mm) reported by Isenberg, Harder, and Louden [50]. Large RW, as found in this study are known to favor the development of shorter tracheids, as a result of a higher frequency of anticlinal division of cambial initials, to keep pace with the higher circumferential and radial growth rate [52]. All seed source values for TD were in the reported range (28–40 μm) of the species [50]. All provenances of this 42-year-old plantation from seed grew comparably or taller than the 18 m reported for a 60-year-old jack pine stand [50]. They also grew taller than the 14.7–17.1 m reported by Magnussen, Smith, and Yeatman [36] in a 34-year-old provenance test established in the Petawawa Research Forest that had only provenances from Ontario. The warm-origin seed sources (e.g., Freesoil and Fite Lake) grew taller, in agreement with their expected high growth potential [5]. All provenances in this study had larger DBH than reported (12–14.7 cm) in the Magnussen, Smith, and Yeatman [36] study, but they generally grew less than the 22 cm reported for diameter at breast height at 60 years [50], omitting eight provenances (Upper Jay, NY; Alex River, QC; Douglas, ON; Baskatong Lake, QC; Freesoil, MI; Fite Lake, MI; Kenora, ON; and Yellowknife, NT). These differences are understandable, considering the older and younger age (42 years) of the plantation compared to the Magnussen, Smith, and Yeatman [36] study (34 years) and the Isenberg, Harder, and Louden [50] study (60 years), respectively. Average TA of all harvested trees was comparable to a previous determination of TA in jack pine using TL and a piecewise model [10].

4.3. Variation among Provenances

The lack of difference observed for TA determined with TL in this provenance test concurs with results obtained with ring density TA of loblolly pine [19]. The fact that all the trees of this experiment shared similar in-situ environmental conditions may explain this lack of TA variation among provenances, as reported elsewhere [17,18]. Since JWP is directly related to TA, we expected variation of both to behave similarly, as observed for TA-JWP variations on white spruce [11]. When looking at anatomical properties, TL significantly varied with provenance, while TD did not. The lack of TD across-provenance variation may be explained by the functional role of tracheid diameter in tree growth. Indeed, the primary role of cell expansion is to ensure an efficient transport of water along the stem, by overcoming hydraulic resistance (friction) that increases with tree height [53–55]. Thus, tracheid widening essentially varies with the distance from the apex [44,56]. Since water requirements and distance from the apex can reasonably be assumed to be similar at breast height in this even-aged plantation, one can expect TD to be comparable, regardless of seed origin. Furthermore, tracheid dimensions are known to vary with RW [14,52,57], but the variations of TL are more pronounced compared to those of TD [42]. Variations of RW among provenances were small (Figure 2c), although significant. This may also explain the lack of significant variation of TD with provenances. The significant variation of TL with provenances observed in the present study concurs with a previous one on jack pine [58]. We found a significant effect of provenance on RD. The total variance explained

by provenance for RD was also high, especially in the JW. However, when comparing provenances, only the Hadashville provenance, which had the lowest density, was significantly different from the Twin Lakes, Thomson station, and Red Lake provenances, which presented the higher densities (Table 2). Thus, excluding the Hadashville provenance invalided the significant variation at the tree level, but not at the juvenile and mature wood levels. Savva, Koubaa, Tremblay, and Bergeron [6] also documented a significant variation of RD with seed origin in jack pine planted in the Petawawa Research Forest, but the differences vanished when adjusted for RW and cambial age differences. We cannot ascribe the significant RD variation to solely RW differences in this study. Indeed, average RW of the Hadashville and Thomson Station seeds were similar, while the Twin Lakes and the Red Lake seeds presented larger and smaller average RWs than the Hadashville seeds, respectively. Since tree height is known to vary with provenances [5,8,33–36], the lack of variation observed in this study was unexpected. This absence of significant difference might be due to the number of sampled trees per provenance (2–3) and to the thinning treatment of 1987 [23], which may have levelled tree heights among provenances. Indeed, one chooses to remove (and to keep) trees arbitrarily (although following established rules) in a thinning experiment. Therefore, trees remained after the thinning may not reflect the dominance naturally established before the thinning event. Although our provenances cover a wide range of jack pine seed sources, we only had access to 2–3 trees per provenance in a single plantation. Therefore, although some differences among provenances are significant, care must be taken when generalizing the results to jack pine provenance tests across its whole range. Also, given the material tested and the analyses performed, one cannot assure if the statistically significant differences observed in this study will necessarily translate into practically meaningful differences if a selection/breeding program were implemented.

4.4. Ranking of Provenances

As wood quality can be defined only in light of the final product desired [59], we had to make arbitrary (although justified) choices in this ranking procedure. The main objective was to have a selection index that gives higher weight to the most relevant wood property in many wood industries (i.e., wood density) and to the more commonly measured growth parameter (radial growth represented here by ring width). However, we also had to consider less common, although highly relevant properties for both wood industries (i.e., tracheid length) and volume estimation (i.e., tree height). Ranking of the provenances requires that one choose which is the most important character to consider in determining which seed sources should be retained for reforestation. Our research found that TL, RW, RD, and DBH were influenced by provenance, whereas TD, TH, TA, and JWP were not. Therefore, if one is more interested in growth rate, one would primarily look at RW and DBH. Those who are looking for better physical properties would choose provenances based on RD, while TL should be used to select provenances with better anatomical properties. As trees' radial growth (DBH and RW) differed more between seed sources compared to TL or RD, one could consider a two-step selection or tandem selection, first for volume production and successively for RD and TL [8,34]. However, if one is interested in choosing provenances that present an overall higher wood quality, one must first determine the respective relevance of each WQA for the end use. We did this by constructing an index that gives equal weight to radial growth (RW) and physical wood properties (RD), while anatomical wood properties (TL) and tree height (TH) weighted only half as much as the former ones. By doing so, Fite Lake, MI; Freesoil, MI; and Douglas, ON ranked first-, second-, and third-best provenance, respectively. In order, Twin Lakes, ON; Alex River, QC; Baskatong Lake, QC; and Dunbar Forest, MI were the fourth-, fifth-, sixth-, and seventh-best provenances. Our finding that warm-origin jack pine populations (Fite Lake, Freesoil, Douglas, and Twin Lakes) tended to grow best (both radially and longitudinally) at the common plantation (which lies in a cooler environment than southern provenances) and that cool-origin populations (Alex River, Baskatong Lake, and Dunbar Forest) tended to grow best (both radially and longitudinally) at the common plantation (which lies in a warmer environment than northern provenances) concurs with results on five northern conifers, including jack

pine [5]. Since TL is known to increase with TH [44,52,60], we expected provenances that ranked best for TH to have a comparable ranking for TL, as seen for Fite Lake and Freesoil. All best-performing provenances presented a mix of high radial growth and high physical properties, high radial growth and long tracheid, or high physical properties and long tracheid. Based on the known correlations among RW, RD, and TL (see Mvolo et al. [43]), one would have expected that RW and RD do not go in the same direction. However, the positive response of tree species to climate change seems to operate at the whole-tree level. Indeed, in a recent study, Reich et al. [33], found that both photosynthetic and growth response to warming followed the same trend, suggesting that the physiological carbon gain response to warming plays an important role in longer-term integrated growth responses. It may therefore be that the four best-performing provenances in this study are growing under warmer than optimal conditions [5], while the fifth-, sixth-, and seventh-best performing provenance are growing under cooler than optimal conditions [5]. Moving these provenances to the common plantation may have triggered a whole-plant better performance [33].

Although increasing yield and quality is essential in forestry nowadays, use of transferred material must be done cautiously. Indeed, the advantages and concerns about seed sources movement and climate change (e.g., maladaptation of species or genotype, hybridization, gene pool dilution, species loss via interspecific competition, introduction of pests and diseases, loss of resilience, and creation of artificial systems depending on human intervention) [61] and the implementation tools of seed sources movement [5,62] have to be considered uppermost [4] in this exercise. Since some of the provenances in this study presented a combination of wider ring and higher RD (e.g., Freesoil, MI) or wider ring and longer TL (e.g., Fite Lake, MI) in the juvenile wood, one could also improve the quality of wood through an early selection of the best provenances for RD and TL, without neglecting the primarily objective of increasing yield (RW). Furthermore, the high variance in the residuals (trees) showed that there was a great heterogeneity between trees of the same provenance. This suggested that an intraprovenance selection could be worthwhile [8,34], in agreement with other jack pine provenance tests in the Petawawa Research Forest [6,36]. However, only two to three trees were sampled per provenance in this study. Furthermore, we only had access to one common location. Since variation among provenances is only one part of the genetic control, one would need to have access to replicated progeny tests to estimate the heritability of these traits and the genetic correlations among the traits to estimate the genetic gains that one could expect from genetic improvement. Moreover, one must be aware about the fact that environment, and not origin, is generally the main variable explaining WQA [4,23]. Zobel and Van Buijtenen [4] summarized this concept saying that "one cannot accurately predict the influence of the source of seed upon wood until the trees are grown in the particular environment of interest".

5. Conclusions

This study is one of the few studies considering the effects of seed provenance on wood quality in a common garden for jack pine. Generally, there is more focus on growth than on the impacts of seed transfer in wood quality. Yet, wood quality attributes in general and the differences between juvenile and mature wood, in particular, will determine the suitability for end-use products. We considered geographical variation of jack pine wood quality, including transition age and juvenile wood proportion. The geographical effect was also investigated for growth through ring width, diameter at breast height, and tree height. Anatomical wood properties, i.e., tracheid length and diameter, and a physical wood property, i.e., ring density, were also used to determine the effect of geographical variation on wood quality. Only ring width, ring density, tracheid length, and diameter at breast height were significantly influenced by the geographical origin of the trees, while tracheid diameter, tree height, transition age, and juvenile wood proportion were not. This suggests that trees could be selected both for radial growth superiority and wood quality. The selection must focus on attributes with relevant importance for the end-use products of interest. However, despite opportunities related to the selection of best-performing seed sources, concerns about the response to climate change have to be considered.

References

1. Rudolph, T.D.; Laidly, P.R. Jack pine. In *Sylvics—Volume 1: Conifers*; Burns, R.M., Honkala, B.H., Eds.; Agriculture Handbook; USDA, Forest Service: Washington, DC, USA, 1990; p. 654.

2. MRNF. *Ressources et Industries Forestières: Portrait Statistique 2017*; Ministère des Forêts, de la Faune et des Parcs. Direction du Développement de L'industrie des Produits du Bois: Québec, QC, Canada, 2017; p. 133.

3. Matyas, C. Modeling climate change effects with provenance test data. *Tree Physiol.* **1994**, *14*, 797–804. [CrossRef] [PubMed]

4. Zobel, B.J.; Van Buijtenen, J.P. (Eds.) *Wood Variation: Its Causes and Control*; Springer Series in Wood Science; Springer: Berlin, Germany, 1989; p. 363.

5. Pedlar, J.H.; McKenney, D.W. Assessing the anticipated growth response of northern conifer populations to a warming climate. *Sci. Rep.* **2017**, *7*. [CrossRef] [PubMed]

6. Savva, Y.; Koubaa, A.; Tremblay, F.; Bergeron, Y. Effects of radial growth, tree age, climate, and seed origin on wood density of diverse jack pine populations. *Trees Struct. Funct.* **2010**, *24*, 53–65. [CrossRef]

7. Savva, Y.; Denneler, B.; Koubaa, A.; Tremblay, F.; Bergeron, Y.; Tjoelker, M.G. Seed transfer and climate change effects on radial growth of jack pine populations in a common garden in Petawawa, Ontario, Canada. *For. Ecol. Manag.* **2007**, *242*, 636–647. [CrossRef]

8. Beaulieu, J. Genetic variation in tracheid length and relationships with growth and wood traits in eastern white spruce (*Picea glauca*). *Wood Fiber Sci.* **2003**, *35*, 609–616.

9. Bendtsen, B.A.; Senft, J. Mechanical and anatomical properties in individual growth rings of plantation-grown eastern cottonwood and loblolly pine. *Wood Fiber Sci.* **1986**, *18*, 23–38.

10. Fujiwara, S.; Yang, K.C. The relationship between cell length and ring width and circumferential growth rate in five canadian species. *IAWA J.* **2000**, *21*, 335–345. [CrossRef]

11. Mvolo, C.S.; Koubaa, A.; Beaulieu, J.; Cloutier, A.; Mazerolle, M.J. Variation in Wood Quality in White Spruce (*Picea Glauca* (Moench) Voss). Part I. Defining the juvenile–mature wood transition based on tracheid length. *Forests* **2015**, *6*, 183–202. [CrossRef]

12. Zobel, B.J.; Sprague, J.R. (Eds.) *Juvenile Wood in Forest Trees*; Springer: Berlin, Germany, 1998; p. 300.

13. Anfodillo, T.; Deslauriers, A.; Menardi, R.; Tedoldi, L.; Petit, G.; Rossi, S. Widening of xylem conduits in a conifer tree depends on the longer time of cell expansion downwards along the stem. *J. Exp. Bot.* **2012**, *63*, 837–845. [CrossRef]

14. Larson, P.R.; Kretschmann, D.E.; Clark, A., III; Isebrands, J.G. *Formation and Properties of Juvenile Wood in Southern Pines: A Synopsis*; General Technical Report, FPL-GTR-129; United States Department of Agriculture, Forest Service, Forest Products Laboratory: Madison, WI, USA, 2001; p. 42.

15. Savidge, R. Intrinsic regulation of cambial growth. *J. Plant Growth Regul.* **2001**, *20*, 52–77. [CrossRef]

16. Larson, P.R. A biological approach to wood quality. *Tappi* **1962**, *45*, 443–448.

17. Clark, A., III; Saucier, J.R. Influence of initial planting density, geographic location, and species on juvenile wood formation in southern pine. *For. Prod. J.* **1989**, *39*, 42–48.

18. Saucier, J.R. Forest Management and wood quality. In Proceedings of the Southern Plantation Wood Quality Workshop, Athens, Greece, 6–7 June 1989; p. 104.

19. Szymanski, M.B.; Tauer, C.G. Loblolly pine provenance variation in age of transition from juvenile to mature wood specific gravity. *For. Sci.* **1991**, *37*, 160–174.

20. Loo, J.A.; Tauer, C.G.; McNew, R.W. Genetic variation in the time of transition from juvenile to mature wood in loblolly pine (*Pinus taeda* L.). *Silvae Genet.* **1985**, *34*, 14–19.

21. Holst, M.J. *All-Range Jack Pine Provenance Experiment*; Internal Report Pet-ps-6; Petawawa Forest Experiment Station: Chalk River, ON, Canada, 1967.

22. Parker, W.H.; Thomson, A.M.; Lesser, M.R. *Identification of Jack Pine Seed Sources to Compensate for Loss of Growth Resulting from Climate Change: Part 2*; Living Legacy Research Program-Lakehead University: Lakehead, ON, Canada, 2006; p. 169.

23. Savva, Y.; Bergeron, Y.; Denneler, B.; Koubaa, A.; Tremblay, F. Effect of interannual climate variations on radial growth of jack pine provenances in Petawawa, Ontario. *Can. J. For. Res.* **2008**, *38*, 619–630. [CrossRef]

24. Koubaa, A.; Zhang, S.Y.; Makni, S. Defining the transition from earlywood to latewood in black spruce based on intra-ring wood density profiles from X-ray densitometry. *Ann. For. Sci.* **2002**, *59*, 511–518. [CrossRef]

25. Franklin, G.L. Preparation of thin sections of synthetic resins and wood-resin composites, and a new macerating method for wood. *Nature* **1945**, *155*, 51. [CrossRef]

26. Fries, A.; Ericsson, T.; Morling, T. Measuring relative fibre length in Scots pine by non-destructive wood sampling. *Holzforschung* **2003**, *57*, 400–406. [CrossRef]

27. SAS Institute Inc. *SAS® 9.4 Statements*; SAS Institute Inc.: Cary, NC, USA, 2013.

28. Yang, K.C. Impact of spacing on width and basal area of juvenile and mature wood in *Picea mariana* and *Picea glauca*. *Wood Fiber Sci.* **1994**, *26*, 479–488.

29. Wang, M.; Stewart, J.D. Determining the transition from juvenile to mature wood microfibril angle in lodgepole pine: A comparison of six different two-segment models. *Ann. For. Sci.* **2012**, *69*, 927–937. [CrossRef]

30. Alteyrac, J.; Cloutier, A.; Zhang, S.Y. Characterization of juvenile wood to mature wood transition age in black spruce (*Picea mariana* (Mill.) B.S.P.) at different stand densities and sampling heights. *Wood Sci. Technol.* **2006**, *40*, 124–138. [CrossRef]

31. Singer, J.D. Using SAS PROC MIXED to fit multilevel models, hierarchical models, and individual growth models. *J. Educ. Behav. Stat.* **1998**, *24*, 323–355. [CrossRef]

32. Falconer, D.S.; Mackay, T.F.C. (Eds.) *Introduction to Quantitative Genetics*, 4th ed.; Pearson Education Limited: Harlow, UK, 1996; p. 464.

33. Reich, P.B.; Sendall, K.M.; Rice, K.; Rich, R.L.; Stefanski, A. Geographic range predicts photosynthetic and growth response to warming in co-occurring tree species. *Nat. Clim. Chang.* **2015**, *5*. [CrossRef]

34. Beaulieu, J.; Corriveau, A. Variabilité de la densité du bois et de la production des provenances d'épinette blanche, 20 ans après plantation. *Can. J. For. Res.* **1985**, *15*, 833–838. [CrossRef]

35. Magnussen, S.; Yeatman, C.W. Height growth components in inter- and intra-provenance jack pine families. *Can. J. For. Res.* **1989**, *19*, 962–972. [CrossRef]

36. Magnussen, S.; Smith, V.G.; Yeatman, C.W. Tree size, biomass, and volume growth of twelve 34-year-old Ontario jack pine provenances. *Can. J. For. Res.* **1985**, *15*, 1129–1136. [CrossRef]

37. Sanio, K. Über die Grösse der Holzzellen bei der gemeinen Kiefer (*Pinus sylvestris*). *Jahrb. Wiss. Bot.* **1872**, *8*, 401–420.

38. Cown, D.J. Variation in tracheid dimensions in the stem of a 26-year-old radiata pine tree. *Appita* **1975**, *28*, 237–245.

39. Brändström, J. Micro and ultrastructural aspects of Norway spruce tracheids: A review. *IAWA J.* **2001**, *22*, 333–353. [CrossRef]

40. Kučera, B. A hypothesis relating current annual height increment to juvenile wood formation in Norway spruce. *Wood Fiber Sci.* **1994**, *26*, 152–167.

41. Bouslimi, B.; Koubaa, A.; Bergeron, P.Y. Anatomical properties in *Thuja occidentalis*: Variation and relationship to biological processes. *IAWA J.* **2014**, *35*, 363–384. [CrossRef]

42. Bannan, M.W. The length, tangential diameter, and length/width ratio of conifer tracheids. *Can. J. Bot.* **1965**, *43*, 967–984. [CrossRef]

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

44. Mvolo, C.S.; Koubaa, A.; Defo, M.; Beaulieu, J.; Yemele, M.-C.; Cloutier, A. Prediction of tracheid length and diameter in white spruce (*Picea glauca* (Moench) Voss). *IAWA J.* **2015**, *36*, 186–207. [CrossRef]

45. Olson, M.E. Xylem hydraulic evolution, I.W. Bailey, and Nardini & Jansen (2013): Pattern and process. *New Phytol.* **2014**, *203*, 7–11. [PubMed]

46. Zhang, S.Y.; Koubaa, A. *Les Résineux de L'est du Canada: Écologie Forestière, Caractéristiques, Transformation et Usages*; Publication Spéciale SP-526F; FPInnovations: Québec, QC, Canada, 2009; p. 400.

47. Jessome, A.P. *Résistance et Propriétés Connexes des Bois Indigènes*; Forintek Canada Corp: Sainte-Foy, QC, Canada, 2000; p. 37.

48. Goudiaby, V.; Brais, S.; Grenier, Y.; Berninger, F. Thinning effects on jack pine and black spruce photosynthesis in eastern boreal forests of Canada. *Silva Fenn.* **2011**, *45*, 595–609. [CrossRef]

49. Morris, D.M.; Bowling, C.; Hills, S.C. Growth and form responses to pre-commercial thinning regimes in aerially seeded jack pine stands: 5th year results. *For. Chron.* **1994**, *70*, 780–787. [CrossRef]

50. Isenberg, I.H.; Harder, M.L.; Louden, L. *Pulpwoods of the United States and Canada, Volume I: Conifers*; Institute of Paper Chemistry: Appleton, WI, USA, 1980; p. 219.

51. Panshin, A.J.; de Zeuuw, C. *Textbook of Wood Technology: Structure, Identification, Properties, and Uses of the Commercial Woods of the United States and Canada*, 4th ed.; McGraw-Hill Book Co.: New York, NY, USA, 1980; p. 722.

52. Larson, P.R. (Ed.) *The Vascular Cambium: Development and Structure*; Springer: Berlin, Germany, 1994; p. 725.

53. Anfodillo, T.; Petit, G.; Crivellaro, A. Axial conduit widening in woody species: A still neglected anatomical pattern. *IAWA J.* **2013**, *34*, 352–364. [CrossRef]

54. Rosner, S. Hydraulic and biomechanical optimization in Norway spruce trunkwood—A review. *IAWA J.* **2013**, *34*, 365–390. [CrossRef]

55. West, G.B.; Brown, J.H.; Enquist, B.J. A general model for the structure and allometry of plant vascular systems. *Nature* **1999**, *400*, 664–667. [CrossRef]

56. Olson, M.E.; Anfodillo, T.; Rosell, J.A.; Petit, G.; Crivellaro, A.; Isnard, S.; León-Gómez, C.; Alvarado-Cárdenas, L.O.; Castorena, M. Universal hydraulics of the flowering plants: Vessel diameter scales with stem length across angiosperm lineages, habits and climates. *Ecol. Lett.* **2014**, *17*, 988–997. [CrossRef] [PubMed]

57. Bannan, M.W. Anticlinal divisions and cell length in conifer cambium. *For. Prod. J.* **1967**, *17*, 63–69.

58. King, J.P. Seed Source Variation in Tracheid Length and Specific Gravity of Five-Year-Old Jack Pine Seedlings. In Proceedings of the Eighth Lake States Forest Tree Improvement Conference, Madison, WI, USA, 12–13 September 1967; pp. 5–9.

59. Savidge, R.A. Tree growth and wood quality. In *Wood Quality and Its Biological Basis*; Barnett, J.R.J., Ed.; Blackwell: Boca Raton, FL, USA, 2003; pp. 1–29.

60. Carlquist, S. (Ed.) *Ecological Strategies of Xylem Evolution*; University of California Press: Berkeley, CA, USA, 1975; p. 259.

61. Aubin, I.; Garbe, C.M.; Colombo, S.; Drever, C.R.; McKenney, D.W.; Messier, C.; Pedlar, J.; Saner, M.A.; Venier, L.; Wellstead, A.M.; et al. Why we disagree about assisted migration: Ethical implications of a key debate regarding the future of Canada's forests. *For. Chron.* **2011**, *87*, 755–765. [CrossRef]

62. Pedlar, J.H.; McKenney, D.W.; Beaulieu, J.; Colombo, S.J.; McLachlan, J.S.; O'Neill, G.A. The implementation of assisted migration in Canadian forests. *For. Chron.* **2011**, *87*, 766–770. [CrossRef]