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# Effects of radial growth, tree age, climate, and seed origin on wood density of diverse jack pine populations

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**Abstract** Several models of the effects of silviculture, radial growth, and tree age on wood density have been developed, but they have rarely considered the roles of diverse seed origins and climate. We developed a model to test the effects of radial growth, tree age, climate, and seed-source origins on wood density in 21 diverse populations of jack pine in a common garden in Petawawa, Ontario, Canada over the last 24 years using a linear mixed-effects model. Although we found significant differences in wood density among diverse seed origins, there were no differences between seed origins having the same ring age and ring width, indicating an indirect effect on wood density of seed-source origin via radial growth. High variation in wood density among trees within the same population and between populations indicated high genetic control of wood density. The climate effect was significant on wood density in all populations, but smaller when radial growth was controlled. Climate effect did not differ significantly among populations. Precipitation in July negatively affected latewood density, whereas precipitation in May in the current year and September of the previous year negatively affected earlywood density. We concluded that a single model of jack pine wood density and radial growth could be used, either controlling for climate effects or not, as the relationship between wood density and radial growth is preserved among the diverse populations, and the climate effect controlling for radial growth in the model was only slight.

**Keywords** *Pinus banksiana* · Tree ring · Wood density · Radial growth · Dendroclimatology · Provenance

## Introduction

Jack pine (*Pinus banksiana* Lamb.) is an economically important tree species for Canada and the USA. It is widely used for pulp and wood production and contributes to the carbon balance and mitigation of climate change. Jack pine grows in the cold-temperate and boreal forests of North America. It is a shade-intolerant species and usually grows on dry, sandy, gravelly or thin soil sites (Rudolph and Laidly 1990). This serotinous species usually regenerates after periodic stand-replacing wild fires.

Wood density is an important wood quality attribute. It is a measure of the total amount of solid-wood substance in a piece of wood. Therefore, it can be used to predict end-use characteristics of wood, such as strength, stiffness, hardness, pulp yield, and paper-making quality (Zobel and van Buijtenen 1989). Density variation is also important for end use. For instance, high uniformity is positive for veneer peeling and slicing. Wood density within tree rings varies greatly from earlywood to latewood. Within-ring density

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distribution is more homogeneous in juvenile wood, mainly due to lower latewood density and lower latewood percentage by width.

Wood density is controlled genetically and environmentally. Whereas the radial growth of forest species is significantly influenced by environmental factors (Becker et al. 1994; Savva et al. 2008), reports on the effects of environmental factors on wood density are inconsistent (Guilley et al. 2004). For example, some studies of broad-leaved species showed a direct control of wood density by environmental factors (Berges et al. 2008), while others assumed that the effects of ecological factors on wood density are included in the effects on tree rings (Zhang et al. 1993). The problem often lies in high inter-tree variability in the relationship between wood density and radial growth, which is not considered in studies of plot averages, potentially masking the true relationship (Zobel et al. 1960; Berges et al. 2008).

The correlation patterns between wood density and radial growth are also complicated. For example, in radiata pine, the genetic correlation between ring density and radial growth was positive for cambial ages 3–9 and negative thereafter, whereas the phenotypic correlation between radial growth and wood density was positive from rings 5–9 and negative thereafter (Zamudio et al. 2002). A study of black spruce demonstrated that average ring density and earlywood density were negatively correlated with ring width, especially in juvenile wood (Koubaa et al. 2000). This correlation tends to weaken as the tree ages. It is therefore important to account for between-tree and within-tree variations that might partially explain the relationship between wood density and tree growth to obtain the least biased estimate of this relationship.

Several studies of coniferous species have examined the effects of silvicultural practices on wood density. For Canadian eastern softwoods, practices that improve radial growth generally have a negative impact on wood density (Zhang and Koubaa 2008). It was shown that thinning treatments negatively affected wood density and positively affected earlywood growth in jack pine (Barbour et al. 1994). However, most studies have focused on the effects of initial spacing, thinning, and fertilization (e.g., Barbour et al. 1994; Tasissa and Burkhart 1998; Kang et al. 2004; Jaakkola et al. 2005), and studies on the effects of diverse seed-source origins on wood density are lacking. A provenance plantation, i.e., plantings of seeds originating from throughout the species range in the same environmental conditions, is a good silvicultural tool for selecting best-performing seed-source origins for a given environment (Matyas 1999). A recent study of height, diameter, and survival data in jack pine populations in Canada concluded that northern seed sources were currently growing at below-optimum temperatures and would benefit from transfer to warmer environments (Parker et al. 2006). Another study in southern Ontario, Canada found that the radial growth of southern seed sources of jack pine would benefit from a slight northward transfer (Savva et al. 2007). Studies on the effects of seed-source origins on wood density would also be useful for breeding purposes. For example, tree families and/or provenances could be selected for better wood quality traits, thereby facilitating prediction of product qualities, such as pulp yield and mechanical properties of lumber.

We studied jack pine from 21 provenance locations throughout the species range and planted in Petawawa, Ontario, Canada. We tested a number of hypotheses by developing models of wood density characteristics as a function of radial growth, accounting for between- and within-tree variability.

The objectives of this study were to:

1. Develop models of the relationships between wood density characteristics and radial growth in diverse jack pine populations in a common garden in Petawawa, Ontario, Canada, controlling for within- and between-tree variability.
2. Test the effects of seed-source origins and climate on wood density characteristics, controlling for radial growth.
3. Determine the main climatic factors affecting earlywood density, latewood density, and average ring density.

We hypothesized that seed-source origin would affect wood density characteristics indirectly via ring width, as previously observed for other silvicultural treatments (Pape 1999; Guilley et al. 2004). We predicted that wood density characteristics of jack pine populations would be controlled more by precipitation than by temperature. It was earlier observed that radial growth in same populations is significantly influenced by precipitation, because jack pine grows in dry sandy soils with low water-storage capacity (Savva et al. 2008). In addition, we predicted that monthly precipitation/growth relationship patterns would differ between radial growth and wood density characteristics.

## Materials and methods

### Study material

We studied a common-garden plantation of jack pine in the Petawawa Research Forest, Ontario (45.58°N, 77.25°W). This plantation is part of a range-wide provenance experiment initiated in 1966. Seed sources from 99 geographic origins were collected from native stands throughout the geographic range of the species and planted at several locations in the USA and Canada (Holst 1967). For this test, all seeds were sown in nurseries in Petawawa in 1964 and transferred to the planting sites in 1966. The experimental plantation was laid out in a triple square lattice design comprising 10 blocks (replications) and one demonstration block near the edge of the plantation. Each block contained one plot per provenance, randomly assigned within the block. Each plot initially contained 10 trees of the same provenance in a single row planted at a spacing of 1.8 m × 1.8 m. The mineral soil of the plantation site is an acidic, light-textured sandy loam overlying granite sand and stony till sediments (Wilde 1946; Hills and Pierpoint 1960). The trial plantation 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.

### Ring-width and wood density characteristics measurements

Cores of tree rings from 21 *Pinus banksiana* provenances were collected from the Petawawa common-garden plantation in 2006 (Table 1; Fig. 1). About 14–20 trees were sampled for each provenance and only 5 trees each for two of the northernmost provenances with low survivorship. For many trees, two-radius cores were collected. A total of 410 cores were taken from 285 trees at approximately 50 cm above ground. This height above base represented a loss of about 3–5 years' growth in relation to total tree age. The provenances were sampled from six blocks on average, depending on survivorship, while the northernmost provenances with lower survivorship were sampled from only an average of three blocks.

Each increment core was wrapped in a plastic bag and kept frozen until preparation. After air drying, cores were sawn to 1.57 mm in thickness and extracted with a cyclohexane-ethanol solution 2:1 (v/v) for 24 h, then extracted in distilled water for another 24 h to remove resinous substances and water-soluble carbohydrates (Grabner et al. 2005). Extractives can account for anywhere from 1 to 20% of the oven-dry weight of wood (as cited in Singleton et al. 2003), and they are unevenly distributed from pith to bark (Zobel and van Buijtenen 1989). Considering that factors such as tree age, growth rate, genetics, and site conditions could also influence their presence (Singleton et al. 2003), we controlled for extractives and water content by removing them prior to analysis. This would also allow more accurate comparisons of change in wood density with age.

Annual ring width, ring density, and earlywood and latewood density were measured with a QTRS-01X Tree-Ring Scanner (QMC, Knoxville, Tennessee), which uses X-ray technology to determine annual density profiles. During scanning, precautions were taken to eliminate incomplete or false rings and rings with compression wood or branch tracers. We used a linear resolution step size of 0.04 mm for measurements. Transition between earlywood and latewood was determined according to the inflexion point method (Koubaa et al. 2002), as follows. Matlab software was used to model intra-ring wood density profiles using 6th order polynomials. Earlywood–latewood transition was defined as an inflexion point, obtained by equalling the second derivative of the polynomial function to zero. For each 6th order polynomial function, the second derivative gave 4 solutions, only one of which was of interest. Few restrictions were specified in the Matlab program to obtain this unique solution: the solution should be included in a positive slope and in the range of 40–90% of ring-width proportion. The measured tree-ring series were cross-dated and quality-checked for each tree using COFECHA software (Holmes 1983). Correlation analysis and COFECHA output showed that the tree-ring series were correctly cross-dated. About 5% of the poor-quality cores (e.g., fragmented, not cross-datable, rotten) were not retained for further analysis. A total of 7,124 tree rings were studied.

### Climate data

Climate data near seed-source origins for the Canadian seed sources were downloaded from Environment Canada's website (http://www.ec.gc.ca/) and from the National Climate Data Center (http://www.ncdc.noaa.gov/oa/ncdc.html) for the American seed sources and were used as climate normals for the sites nearest the seed origins and the plantation site in Petawawa, Ontario, Canada for 1971–2000. Mean annual monthly temperature and precipitation data for 1975–1999 for the Petawawa study site, according to the weather station nearest the plantation site, were downloaded from Environment Canada's website (http://www.ec.gc.ca/).

### Developing ring-width and wood density characteristics chronologies

Ring-width and wood density characteristics chronologies were developed with ARSTAN software (Cook 1985) for each provenance using individual tree-ring series of the provenances. In this analysis, cores from the same tree were treated separately to maximize climatic signal, because averaging tree core values might decrease the signal-to-noise ratio. To minimize the post-thinning effect

**Table 1** Description of seed-source origins and annual tree-ring characteristics of the 21 jack pine provenances planted in Petawawa, Ontario, Canada over the period from 1975 to 1999

| No. | Provenance origin[a] | Latitude, N/Longitude, W | Elevation, m a.s.l. | Mean annual temp (°C) | Mean max. daily temp (°C) | Total annual precipitation (mm) | Mean tree-ring width ± SD, mm | Average density ± SD ($kg\ m^{-3}$) | Earlywood density ± SD ($kg\ m^{-3}$) | Latewood density ± SD ($kg\ m^{-3}$) |
|---|---|---|---|---|---|---|---|---|---|---|
| 57 | Miller Lake, ON | 45.1/81.5 | 198 | 6.6 | 10.8 | 830 | 2.48 ± 1.45 | 522 ± 68 | 408 ± 45 | 784 ± 95 |
| 75 | Gladstone, MI | 46.0/86.5 | 198 | 5.6 | 10.4 | 725 | 2.60 ± 1.27 | 504 ± 62 | 391 ± 37 | 785 ± 103 |
| 62 | Cowganda Lake, ON | 47.7/80.7 | 335 | 2.2 | 8.2 | 785 | 2.42 ± 1.13 | 512 ± 66 | 389 ± 40 | 789 ± 108 |
| 70 | Nokomis, WI | 45.6/89.8 | 472 | 6.4 | 12.0 | 847 | 2.42 ± 1.04 | 515 ± 62 | 401 ± 40 | 777 ± 102 |
| 61 | Benny, ON | 46.8/81.6 | 396 | 3.7 | 8.8 | 899 | 2.41 ± 1.05 | 500 ± 56 | 386 ± 38 | 780 ± 84 |
| 47 | Harry Lake, QC | 46.4/76.2 | 183 | 3.7 | 9.9 | 909 | 2.48 ± 1.35 | 523 ± 84 | 389 ± 55 | 806 ± 115 |
| 48 | Baskatong Lake, QC | 46.8/76.1 | 244 | 3.3 | 9.2 | 1,015 | 2.49 ± 0.97 | 500 ± 60 | 378 ± 40 | 786 ± 87 |
| 79 | Cloquet, MN | 46.7/92.6 | 390 | 4.6 | 11.2 | 807 | 2.36 ± 0.99 | 517 ± 67 | 402 ± 42 | 781 ± 101 |
| 45 | York River, ON | 45.2/77.7 | 320 | 4.0 | 10.5 | 843 | 2.29 ± 1.00 | 537 ± 82 | 403 ± 56 | 787 ± 88 |
| 55 | Clark Point, ON | 44.1/81.8 | 180 | 6.7 | 11.8 | 1,121 | 2.31 ± 1.08 | 517 ± 68 | 400 ± 47 | 774 ± 102 |
| 63 | Nellie Lake, ON | 48.8/80.8 | 305 | 0.9 | 7.4 | 776 | 2.30 ± 1.07 | 514 ± 70 | 386 ± 46 | 806 ± 96 |
| 81 | Fort Frances, ON | 48.8/93.5 | 338 | 2.9 | 8.8 | 721 | 2.29 ± 1.04 | 535 ± 75 | 405 ± 53 | 804 ± 112 |
| 86 | Red Lake, ON | 51.0/94.1 | 354 | 0.9 | 6.4 | 640 | 2.20 ± 1.05 | 526 ± 70 | 404 ± 46 | 804 ± 94 |
| 68 | Waupaca, WI | 44.3/89.0 | 290 | 6.8 | 12.7 | 782 | 2.18 ± 1.04 | 517 ± 79 | 398 ± 49 | 751 ± 113 |
| 18 | St. Alexandre, QC | 47.7/69.7 | 91 | 3.5 | 8.7 | 983 | 2.33 ± 1.12 | 512 ± 85 | 398 ± 62 | 787 ± 78 |
| 49 | Capitachouare River, QC | 47.8/76.7 | 457 | 2.8 | 7.9 | 950 | 2.01 ± 1.14 | 518 ± 70 | 391 ± 45 | 780 ± 115 |
| 30 | Port Alfred, QC | 48.3/70.9 | 251 | 2.3 | 7.9 | 951 | 2.05 ± 1.06 | 504 ± 72 | 386 ± 52 | 751 ± 114 |
| 20 | Toulnoustook River, QC | 49.7/68.4 | 76 | 1.5 | 6.3 | 1,014 | 1.91 ± 1.03 | 535 ± 82 | 405 ± 60 | 772 ± 96 |
| 15 | Patapedia Depot, QC | 48.1/67.5 | 366 | 2.3 | 8.0 | 1,027 | 1.57 ± 0.96 | 518 ± 82 | 389 ± 53 | 755 ± 116 |
| 37 | Lac Des Loutres, QC | 49.6/72.2 | 229 | −0.9 | 4.5 | 954 | 2.28 ± 1.24 | 533 ± 77 | 404 ± 51 | 805 ± 94 |
| 36 | Ducharme River, QC | 49.4/74.0 | 381 | 0.0 | 5.2 | 961 | 1.68 ± 0.97 | 534 ± 84 | 399 ± 65 | 790 ± 109 |

# indicates the number of provenance

[a] Michigan (MI), Minnesota (MN), Ontario (ON), Quebec (QC), Wisconsin (WI)

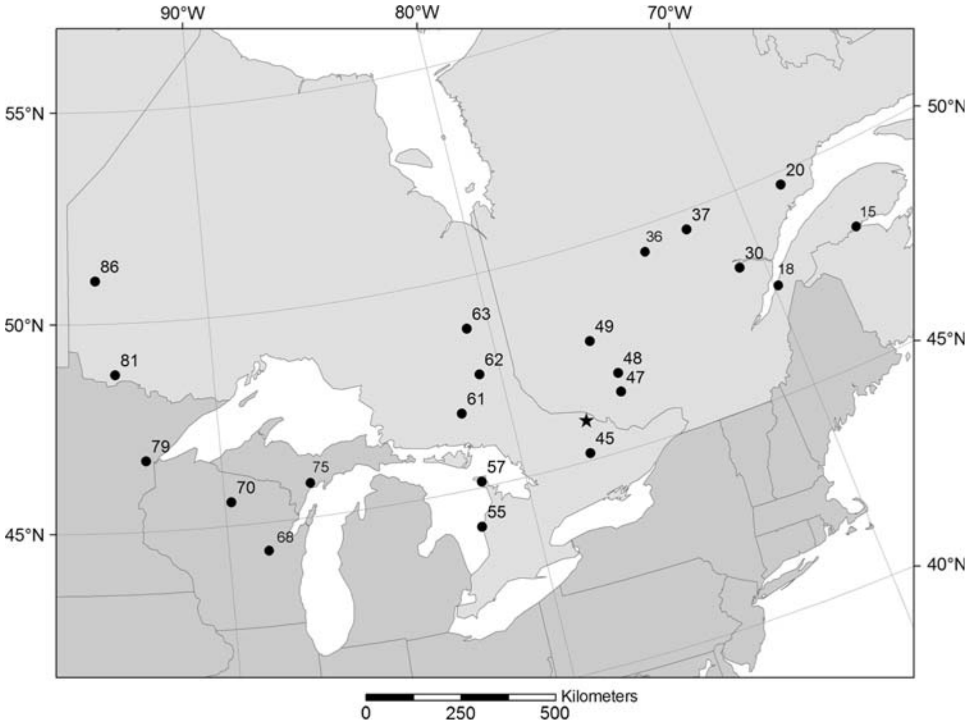

**Fig. 1** Map of the geographic locations of the jack pine populations studied in a common garden in Petawawa, Ontario, Canada. The study site is indicated by a *star* and the studied provenances (21) are indicated by *circles*

and highlight inter-annual high-frequency variations, a spline function with a 50% frequency response of 30 years was fitted to the individual tree-ring series and indices were calculated as the differences between observed and expected values for each provenance. Flexible cubic spline curves effectively remove the long-term trend and the effect of local disturbance events (Cook et al. 1990), such as the long-term after-thinning effect, but at the risk of removing possible low-frequency climatic information. Considering that the tree-ring chronologies of jack pine populations were insufficiently long to analyze low-frequency variations or stand thinning history, we used spline curves for detrending to reduce the long-term effect of thinning. We referred to the obtained tree-ring chronologies as individual standard chronologies. Tree-ring chronologies usually contain autocorrelation, i.e., current year growth dependent on previous year growth. Tree-ring data autocorrelations were removed using an autocorrelation model. The obtained tree-ring chronologies were referred to as residual chronologies. Average residual wood density characteristics chronologies were then calculated for the diverse seed origins.

### Relationship between climate and wood density characteristics

The relationships between climate and wood density characteristics for the provenances were determined by calculating the correlation coefficients between the average residual chronologies of wood density characteristics and the mean monthly temperature and precipitation data for Petawawa for 1975–1999. We chose to calculate correlation coefficients instead of response functions because we were interested in the magnitude and direction of the relationships rather than a simulation of the relationships for the experimental site. Mean monthly temperature and precipitation data over a 16-month period from June of the previous year to September of the current year were chosen as predictor variables for current-year wood density characteristics indices.

### Provenance effect on annual wood density characteristics

Mixed linear models were used to test for significant differences in wood density characteristics among provenances. Each wood density characteristic for each year was tested separately. The provenance effect was used as a fixed effect in the models, and trees nested within a block were treated as a random effect. Data for two cores from the same tree were averaged and treated as one sample in the analysis. A first-order autocorrelation model was used to account for temporal variations in model residuals. The model expresses the current observation $e_{yklm}$ in year $y$ for tree $k$ in provenance $l$ in block $m$ as a linear function of the independent and identically distributed noise term $a_{yklm}$:

$$\begin{aligned} e_{yklm} &= \rho e_{(y-1)klm} + a_{yklm}, \\ a_{yklm} &\sim N\left(0, \sigma_a^2 I\right) \end{aligned} \quad (1)$$

where $\rho$ is a single correlation parameter representing the lag-1 correlation and takes values from $-1$ to 1.

### Wood density characteristics models

Relationships between wood density characteristics, radial growth, tree age, seed origin, and climate were modeled for the last 24 years (1975–1999). The first 9 years of growth (1966–1974) were not included in the model because the changes in ring width with age were described as a hump of the Hugershoff function that had a nonlinear effect on wood density characteristics in this juvenile period. In addition, the high variation in wood density characteristics in the juvenile period is generally due to compression wood (Barbour et al. 1994). Including this juvenile period in the model would require a more complicated nonlinear function and might increase unexplained variations in the model.

Wood density characteristics models can be used to predict wood density characteristics for a given ring width, tree age, seed-source origin (Model 1), and climate (Model 2). The two models were developed separately to estimate the variation explained by adding climate variables to wood density Model 1. Results for the provenance effect on wood density characteristics, described in the previous section, could differ from the results of models of the provenance effect on the relationships between wood density characteristics, tree growth and tree age, as described below. This is because Model 1 describes the provenance effect on ring density at similar ring age and ring width. Therefore, it determines how the wood density characteristics of trees having the same ring width and age would differ by provenance, while the analysis described in the previous section determines statistical differences in wood densities by provenance.

### Effects of seed-source origin, ring width, and tree age on wood density characteristics (Model 1)

The linear mixed model of a density characteristic ($X_{yklm}$) (g/cm$^3$) in year $y$ for tree $k$ in provenance $l$ in block $m$ with ring width $z_{1yklm}$ (mm), (centered) tree age $z_{2yklm}$ (years), and their interaction $(z_1z_2)_{yklm}$ is

$$\begin{aligned} X_{yklm} &= (A_0 + a_{0k}) + (A_1 + a_{1k})z_{1yklm} + (A_2 + a_{2k})z_{2yklm} \\ &\quad + (A_3 + a_{3k})(z_1z_2)_{yklm} + e_{yklm} \\ a_k &= \{a_{0k}, a_{1k}, a_{2k}, a_{3k}\} \sim N(0, (\sigma_0^2, \\ &\quad \sigma_1^2, \sigma_2^2, \sigma_3^2)),\ e_{yklm} \sim N(o, \sigma^2) \end{aligned} \tag{2}$$

where $A_0$, $A_1$, $A_2$, and $A_3$ are the respective fixed effects for the intercept and slopes, a$_k$ is the random-effects vector (assumed independent for different trees), and $e_{yklm}$ is the within-group error (assumed independent for different $y$, $k$, $l$, and $m$ values and independent of random effects). Random effects and error are assumed as normally distributed with means of zero and variances of $\sigma_0^2, \sigma_1^2, \sigma_2^2, \sigma_3^2$, and $\sigma^2$, respectively. The block effect was not included in these models because the variation explained by the block effect was close to zero. Additionally, the likelihood ratio test showed insignificant differences between the two models with trees as a random effect and with trees nested in block as a random effect. Including the block effect would result in loss of degrees of freedom in our models, but would not decrease mean square residual. Therefore, the final model did not include the block effect.

Because wood formation in a given year depends on the previous year's wood formation, we used an autoregressive model of order 1 AR(1) to account for residual autocorrelations (Box et al. 1994, Koubaa et al. 2005), as described above (see Eq. 1).

Model residuals for average ring density were characterized by high heteroscedasticity. Therefore, the variance function was used to model within-group heteroscedasticity of average wood density. The variance function is

$$g(z_{1yklm}, \delta) = z_{1yklm}^{\delta}, \tag{3}$$

where $\delta$ is a power of the absolute value of the variance covariate ring width $z_{1yklm}$. This variance function allows giving higher weight to lower ring widths.

The provenance effect ($p_{yklm}$) was tested in the model as an additive effect, as follows:

$$X_{yklm} = \text{Eq.}1 + A_4 p_{yklm} \tag{4}$$

where, $A_4$ is the fixed effect for seed-source origins. However, because the effect of seed-source origins was not significant in the models of wood density characteristics, it was not included in the final models, described by Eq. 2.

Several models were tested for each wood density characteristic by excluding random terms or fixed effects, and the best model was chosen based on the Akaike information criterion (AIC) (Sakamoto et al. 1986), the Bayesian information criterion (BIC) (Schwarz 1978), and the log likelihood (Searle et al. 1992).

### Effects of climate, ring width, and tree age on wood density characteristics (Model 2)

The climate variables that best correlated with wood density characteristics (see the section on "Relationship between climate and wood density characteristics") were used to test the effect of climate on wood density characteristics while controlling for radial growth. The linear mixed model of the density characteristic ($X_{yklm}$) (g/cm$^3$) in year $y$ for tree $k$ in provenance $l$ in block $m$ with ring width

$z_{1yklm}$ (mm), (centered) tree age $z_{2yklm}$ (years), their interaction$(z_1z_2)_{yklm}$, and climate variables $v_{1y}$ and $v_{2y}$ is

$$\begin{aligned} X_{yklm} &= (A_0 + a_{0k}) + (A_1 + a_{1k})z_{1yklm} + (A_2 + a_{2k})z_{2yklm} \\ &\quad + (A_3 + a_{3k})(z_1z_2)_{yklm} \\ &\quad + (A_4 + a_{4k})v_{1y} + (A_5 + a_{5k})v_{2y} + e_{yklm} \\ a_k &= \{a_{0k}, a_{1k}, a_{2k}, a_{3k}, a_{4k}, a_{5k}\} \\ &\sim N(0, (\sigma_0^2, \sigma_1^2, \sigma_2^2, \sigma_3^2, \sigma_4^2, \sigma_5^2)),\ e_{yklm} \sim N(o, \sigma^2) \end{aligned} \tag{5}$$

where $A_0$, $A_1$, $A_2$, $A_3$, $A_4$ and $A_5$ are the respective fixed effects for the intercept and slopes, $a_k$ is the random-effects vector, assumed independent for different trees, and $e_{yklm}$ is the within-group error, assumed independent for different *y*, *k*, *l*, and *m* values and independent of random effects. Random effects and error are assumed to be normally distributed, with means of zero and variances of $\sigma_0^2, \sigma_1^2, \sigma_2^2, \sigma_3^2, \sigma_4^2, \sigma_5^2$, and $\sigma^2$, respectively.

The autoregressive moving average model AR(1) was the same as in Eq. 1 and the variance function was the same as in Eq. 3. All random effects were tested for exclusion using AIC, BIC and a likelihood ratio test. Thus, both models accounted for between-tree and within-tree variability. Assumptions of normality and homogeneity of residuals were met for both models. The analyses were carried out using the NLME package in R software (Pinheiro and Bates 2000).

## Results

### Provenance effect on wood density characteristics

A significant effect of seed-source origins was found on absolute annual wood density characteristics ($p < 0.0001$), average ring density, earlywood density, and latewood density. Highest average ring density (537 kg m$^{-3}$) with intermediate ring width (2.29 mm) was found for the provenance located at York River, Ontario, slightly south of the plantation site (Table 1). Lowest ring density (500 kg m$^{-3}$) with earlywood density (378 kg m$^{-3}$) and relatively high ring width (2.49 mm) was found for the provenance located slightly north of the plantation site at Baskatong Lake, Quebec. Highest earlywood density (408 kg m$^{-3}$) with relatively high ring width (2.48 mm) was found for the southern provenance of Miller Lake, Ontario. Highest latewood density (806 kg m$^{-3}$) with relatively high ring width (2.48 mm) was found for the provenance of Harry Lake, Quebec, located near the provenance plantation. Lowest latewood density (751 kg m$^{-3}$) with relatively low ring width (2.05 mm) was found for the provenance of Port Alfred, Quebec.

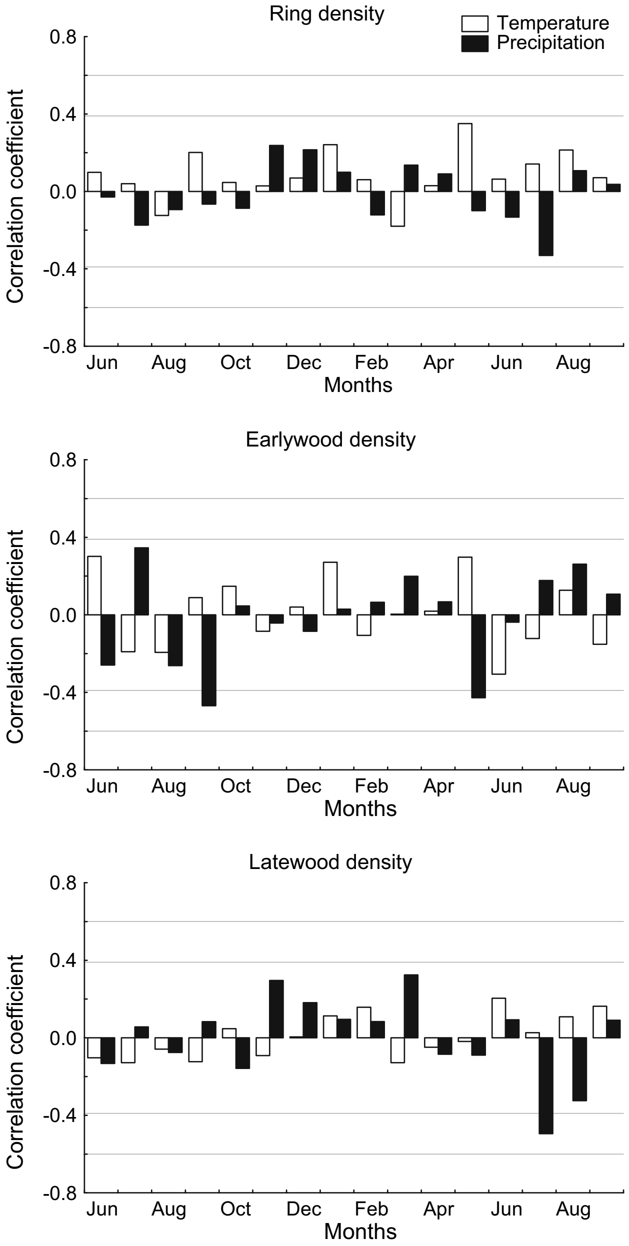

**Fig. 2** Correlation coefficients relating mean monthly temperature and precipitation to average ring density and earlywood and latewood chronologies of jack pine populations for 1975–1999. Horizontal lines indicate significance levels ($p < 0.05$ and $p < 0.001$). Correlation coefficients were calculated for 16 months from June of the previous growth year to September of the current growth year

### Relationship between wood density characteristics and climate

Individual chronologies of ring density and earlywood and latewood density were highly correlated among the diverse seed-source origins, indicating that similar climatic factors affected high-frequency variations in each wood density characteristic. Correlation coefficients of individual residual chronologies and average-provenance residual chronologies varied from 0.85 to 0.95 for average ring density, from 0.66 to 0.92 for earlywood density, and from 0.54 to 0.96 for latewood density ($p < 0.05$), reflecting a common climate signal in the density chronologies for the diverse populations.

Wood density characteristics of the different populations responded differently to climate factors (Fig. 2). Latewood and earlywood density were highly sensitive to climate variations. Latewood density was negatively correlated with precipitation in July of the current growth year, whereas earlywood density was negatively correlated with precipitation in September of the previous growth year and precipitation in May of the current growth year. Average ring density was not significantly correlated with climate variables for the Petawawa area.

## Wood density models

### *Effects of seed-source origin, ring width, and tree age on wood density characteristics (Model 1)*

Although wood density characteristics differed significantly among the diverse provenances, provenance effects on the relationships between wood density characteristics, ring width, and tree age were not significant, indicating that ring density characteristics did not differ significantly among provenances with the same ring age and ring width. This suggests that the significant differences in wood density characteristics among the provenances were caused by the earlier observed differences in ring width among the provenances (Savva et al. 2007). The developed models showed significant effects of radial growth, age, and their interaction on wood density characteristics (Table 2). As expected, the effect of radial growth was negative on average ring density and earlywood density and positive on latewood density. The opposite relationships were found between wood density characteristics and tree age. The interaction term between radial growth and tree age was positive for average ring density and latewood density and negative for earlywood density. The random effects of the model accounting for between-tree variability explained a large part of the variation in density characteristics. The relative variability of random effects was calculated as the ratio of standard deviation of the random effect to the absolute value of the corresponding fixed effect. Random variation among trees to the intercept explained about 6.5, 6.2, and 7.7% of the variation relative to the fixed effect of the intercept for average ring density, earlywood density, and latewood density, respectively. Random among-trees variation was high for the estimates of ring-width effect, ranging from 32 to 49% for wood density characteristics, with age effect showing the highest values, at from 46 to 58%. Exclusion of these random effects from the model resulted in low $p$-values of the likelihood ratio tests and higher AIC and BIC values, indicating the need to retain them in the model. Intra-tree variation was highest for latewood density ($\rho = 0.43$) and lower for earlywood density ($\rho = 0.29$) and average ring density ($\rho = 0.28$).

We examined the relationships between observed and predicted values of wood density characteristics and found that, in general, the model accurately described wood density characteristics for the studied period (Figs. 3, 4; Table 2). However, the model of average ring density and earlywood density did not describe high densities very accurately, and the latewood density model did not describe low values very accurately, suggesting that other unaccounted for environmental and genetic factors might have affected these characteristics (Fig. 3).

### *Effects of climate, ring width, and tree age on wood density characteristics (Model 2)*

Although there were significant correlations between wood density characteristics by provenance and climate factors (Fig. 2), the inclusion of the climate variables in the model of wood density characteristics, ring age, and ring width improved the models only slightly, according to the fit statistics, and only slightly reduced the mean residuals, and therefore the unexplained variance (Table 2). These climate effects were significant in the models, suggesting that they directly affected wood density characteristics, although the effects were low when ring width was statistically controlled. This indicates that climate effects on wood density characteristics are partially accounted for by ring width in the model, since both ring width and wood density characteristics were found to be affected mainly by precipitation. Model residuals were reduced by 2.5% for mean ring density, by 2.8% for earlywood density, and by 0.7% for latewood density compared to the model without climate effects (Model 1). The directions of the relationships between wood density characteristics, tree ring, and tree age were the same as in Model 1 without climate effects. For wood density characteristics, random variation among trees to the intercept ranged from 6.5 to 7.6%, to ring width from 36 to 53%, and to tree age from 44 to 100%. Random variation to the interaction term was 18% for latewood density relative to the appropriate fixed terms. Random variation to climate variables was high only for latewood density (33%). Intra-tree variation was about the same as in Model 1 without climate effects.

A comparison between observed and predicted wood density characteristics demonstrated that Model 2 described wood density characteristics relatively accurately for

**Table 2** Coefficients and fit statistics of models of the average ring density, earlywood density and latewood density with ring width, and tree age (Model 1), and climate effects (Model 2) of jack pine populations in a common garden, Petawawa, Ontario, Canada[a]

| Coefficient | Average ring density (g $\text{cm}^{-3}$) | | Earlywood density (g $\text{cm}^{-3}$) | | Latewood density (g $\text{cm}^{-3}$) | |
|---|---|---|---|---|---|---|
| | Model 1 | Model 2 (with climate effects) | Model 1 | Model 2 (with climate effects) | Model 1 | Model 2 (with climate effects) |
| Estimates for fixed effects[b] | | | | | | |
| A0 | 0.5404 (0.0030) | 0.5467 (0.0029) | 0.4107 (0.0022) | 0.4146 (0.0022) | 0.7393 (0.0048) | 0.7438 (0.0048) |
| A1 | −0.0085 (0.0008) | −0.0118 (0.0009) | −0.0073 (0.0007) | −0.0085 (0.0007) | 0.0271 (0.0016) | 0.0248 (0.0016) |
| A2 | 0.0032 (0.0003) | 0.0036 (0.0003) | 0.0021 (0.0002) | 0.0013 (0.0001) | −0.0052 (0.0004) | −0.0044 (0.0004) |
| A3 | 0.0005 (0.0001) | 0.0003 (0.0001) | −0.0003 (0.0001) | Ins. | 0.0036 (0.0002) | 0.0033 (0.0002) |
| A4 | | 0.0040 (0.0004) | | −0.0048 (0.0004) | | −0.0073 (0.0008) |
| A5 | | −0.0066 (0.0005) | | −0.0051 (0.0005) | | |
| Estimates for modelling autocorrelation and heteroschedasticity[c] | | | | | | |
| $\rho$ | 0.28 | 0.28 | 0.29 | 0.26 | 0.43 | 0.43 |
| $\delta$ | −0.59 | −0.59 | | | | |
| Standard deviations for random effects[b] | | | | | | |
| a0 | 0.0352 | 0.0349 | 0.0255 | 0.0257 | 0.0566 | 0.0568 |
| a1 | 0.0031 | 0.0044 | 0.0023 | 0.0033 | 0.0132 | 0.0132 |
| a2 | 0.0014 | 0.0017 | 0.0012 | 0.0013 | 0.0024 | 0.0024 |
| a3 | 0.0003 | Ins. | Ins. | Ins. | 0.0006 | 0.0006 |
| a4 | | Ins. | | Ins. | | 0.0024 |
| a5 | | Ins. | | Ins. | | |
| Residual | 0.067 | 0.0653 | 0.0364 | 0.0354 | 0.0762 | 0.0757 |
| Fit statistics[d] | | | | | | |
| AIC | −23,544 | −23,807 | −26,732 | −26,924 | −16,888 | −16,950 |
| BIC | −23,468 | −23,718 | −26,664 | −26,842 | −16,819 | −16,867 |
| LogLik | 11,783 | 11,917 | 13,376 | 13,474 | 8,454 | 8,487 |

[a] Ins. indicates insignificant effects. Standard errors of the estimates are in parentheses

[b] See Eq. 2 for abbreviations of the Model 1 and Eq. 5 for abbreviations of the Model 2. For the average ring density, climate factors in Model 2 were the mean monthly temperature in May (with estimates A4 and a4) and precipitation in July (A5 and a5). For the earlywood density, climate factors in Model 2 were the mean monthly precipitation in May of the current year (A4 and a4) and the mean precipitation of September of the previous year (A5 and a5). For the latewood density, a climate factor of Model 2 was the mean monthly precipitation in July of the current year (A4 and a4)

[c] $\rho$ is an estimate of the autoregressive function of the first order (see Eq. 1). $\delta$ is an estimate of the power of the variance covariate, i.e. tree-ring width (see Eq. 3)

[d] AIC indicates the Akaike Information Criterion (AIC), BIC is the Bayesian Information Criterion and LogLik is the log likelihood

the studied period (Fig. 4), and did not substantially improve on Model 1, which did not consider climate effects. The RMS errors did not differ considerably between the two models, at 0.002, 0.001, and 0.005 g/$\text{cm}^3$ for ring density, earlywood density, and latewood density, respectively. The model was unable to accurately describe relationships at the tree level due to the high between-tree variability observed. In any case, relationships at the population level are actually more important for predicting end-use properties. The remaining high-frequency variation, which was not taken into account by either model, is probably related to other factors, such as microclimate, microtopography, genetics, and so forth.

## Discussion

### Effect of seed-source origin on wood density characteristics

This study developed models of wood density characteristics for diverse jack pine populations planted at Petawawa, Canada over the past 24 years. These models accounted for a relatively high variation in wood density characteristics. Although the estimates of wood density characteristics were slightly biased, the models reproduced wood density characteristics profiles for the studied years that were similar to observed wood density characteristics

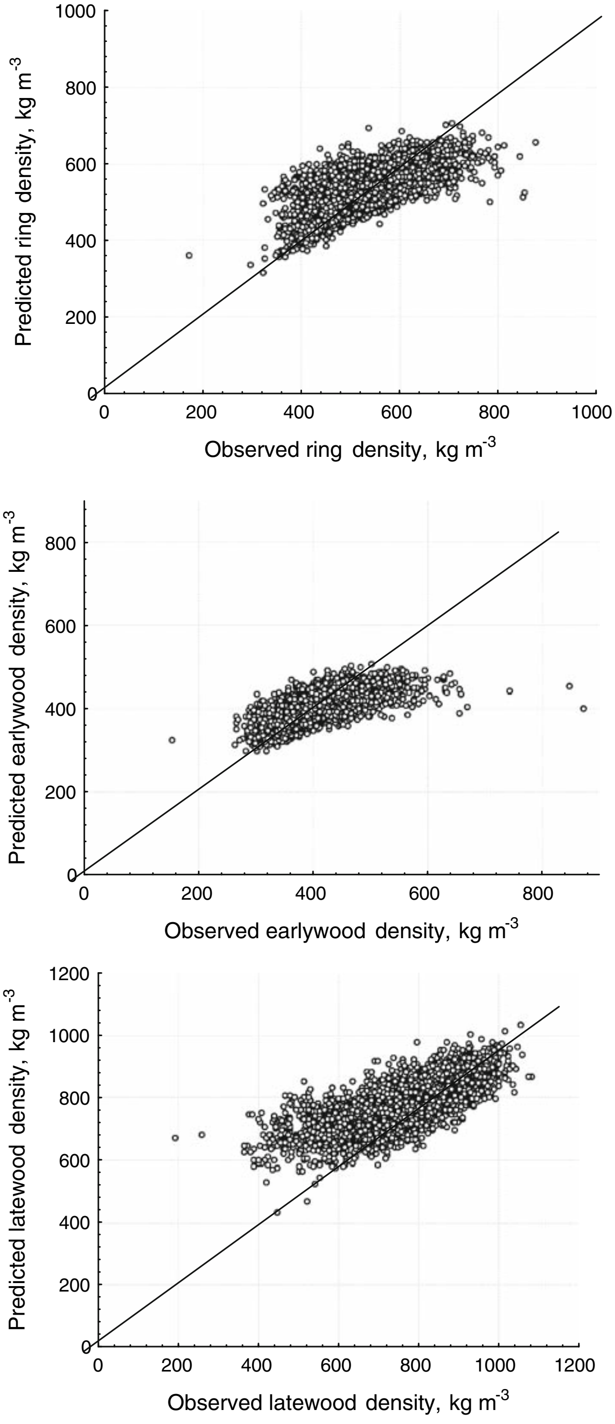

**Fig. 3** Predicted values of wood density characteristics plotted versus observed values of individual tree rings of jack pine populations from a common garden in Petawawa, ON using Model 1, which does not account for climate variations (see Eq. 2). The *solid line* indicates the 1:1 ratio

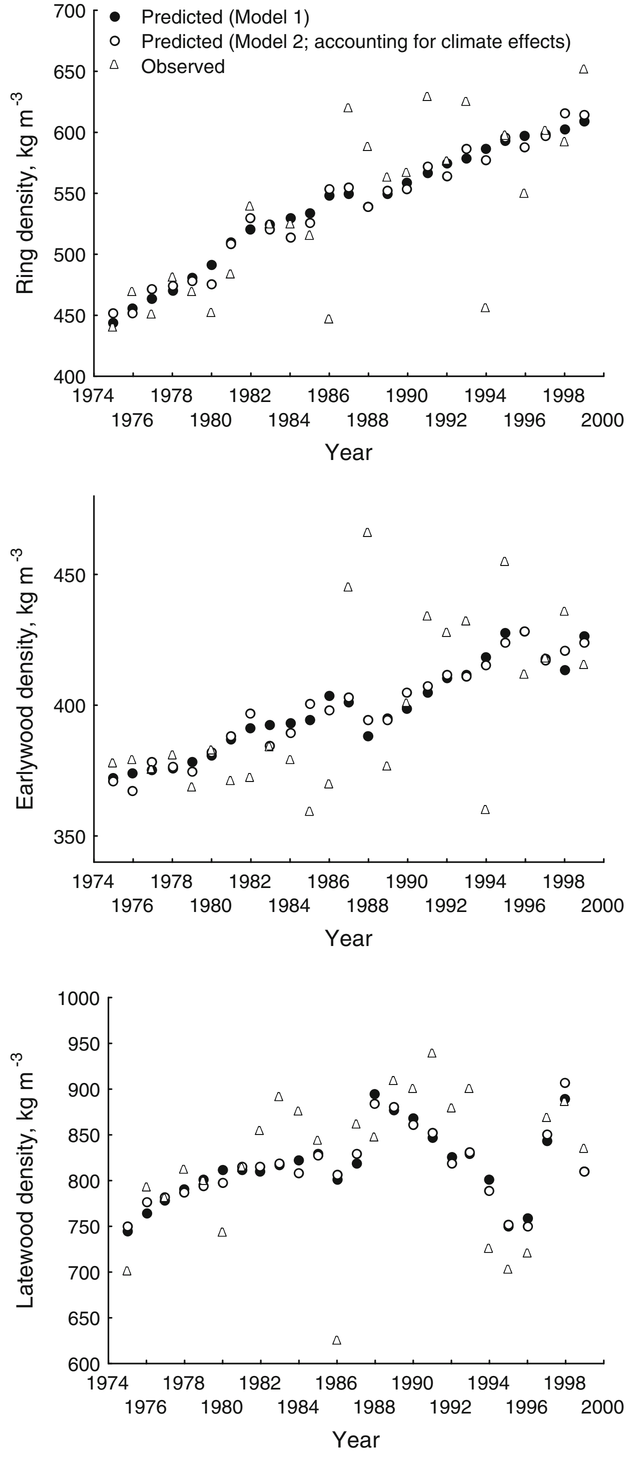

**Fig. 4** Measured and predicted values of wood density characteristics of jack pine populations from a common garden in Petawawa, ON using Model 1 and Model 2 (accounting for climate effects) and plotted against the year for a randomly selected tree. Data are plotted for the provenance Red Lake, ON tree #3 in block #6

profiles. Despite the significant differences in wood density characteristics by provenance, the seed origin effect on wood density characteristics was not significant when radial growth was statistically controlled. This indicates that seed-source origin affects wood density characteristics indirectly through radial growth, given that significant differences in radial growth by provenance were found previously (Savva et al. 2007). Thus, rings of provenances of the same age and width have the same wood density characteristics. Model 1 can be used to predict wood density characteristics of diverse jack pine populations when the radial growth parameters are known. These results are consistent with several studies on the effects of a variety of silvicultural treatments on wood density of coniferous and broad-leaved species. A study of Douglas fir found that 26% of variation in wood density was explained by radial growth and only 6% by provenance for a fixed ring width (Rozenberg et al. 1999). One study tested five thinning regimes on wood density of *Picea abies* and demonstrated no differences between treatments in wood density for a fixed ring width (Pape 1999). A recent study showed that thinning of jack pine in New Brunswick, Canada did not affect models relating wood density, radial growth, and tree age (Schneider et al. 2008).

### Effect of climate on wood density characteristics

We showed that climate factors significantly affected wood density components. This effect of climate factors was direct on wood density characteristics and indirect via ring width, because we found a slightly significant effect of climate factors on wood density characteristics at a fixed ring width. Including climate effects in the model reduced residuals by only 0.7–2.8%, depending on wood-density characteristics. These results indicate that some climate factors affecting wood density characteristics also affected ring width of the provenances. The model was improved slightly by including climate effects for latewood density compared to other wood density components.

High inter-correlation between indexed wood density chronologies (i.e., when tree age was removed) of the provenances indicated that the diverse populations responded similarly to climate variations, but that climate factors affecting wood density characteristics differed among the three wood density components. Wood density characteristics were affected more by precipitation than by temperature. It was earlier shown that the radial growth of jack pine provenances was also affected more by precipitation than by temperature (Savva et al. 2008). Jack pine typically grows in sandy soils, which are characterized by low water-storage capacity. High temperatures during the summer can considerably decrease soil moisture. Studies of pines growing in dry soils have shown a decrease in photosynthate production and carbohydrate storage due to an efficient and rapid stomatal control of transpiration water loss (e.g., Lebourgeois et al. 1998), most likely promoting hardening and thickening of cell walls in wood.

### Within-tree variability of wood density characteristics

Our study also showed high autocorrelation of wood density characteristics. Dependence of current year wood density characteristics on previous year wood density characteristics was high for average ring density and earlywood density and highest for latewood density. This means that if a given year's climate conditions favored cell wall thickening and latewood density formation, it is highly probable that latewood density would be high in the next growth year, most probably due to a high capacity to use accumulated photosynthates and stored carbohydrates in the next year.

### Effect of between-tree variability on wood density characteristics

This study also revealed a strong genetic control of wood density characteristics through the high variability among trees within and between provenances. This is because the environmental conditions were the same for the studied populations, and we controlled for ring width in the models, which might be affected by tree position in the stand. Therefore, we attributed the high random variation mainly to tree genetics. In the wood density characteristics models, random tree effects for the age variable were highly significant, explaining up to 58% of the variation in wood density characteristics relative to fixed effects. Random tree effects were also highly significant for the radial growth variable, explaining up to 100% of the variation in wood density characteristics relative to fixed effects. This finding is consistent with those of Mutz et al. (2004) and Guilley et al. (2004), who found a large variation in wood density due to tree effects. A study on Douglas fir by Rozenberg et al. (1999) compared the effects of fertility and cloning on wood density and found that differences in wood density among clones were much higher than differences between fertility treatments. Variation in wood density due to radial growth was 20%, while variation due to clone differences was 34%, indicating that wood density is under genetic control. A study of Scots pine provenances in Siberia also found high between-tree variability in ring width and wood density (Savva et al. 2002). Furthermore, a study of jack pine in New Brunswick, Canada found remarkably high heritability of wood density (Zhang and Chui 1996).

## Conclusions

This study demonstrated that the relationships between wood density characteristics and radial growth were preserved among diverse populations and that the climate effect on wood density characteristics was only slight when radial growth was statistically controlled in the model. This indicates that single models of wood density characteristics and radial growth of jack pine can be used whether or not climate effects are included. If climate warming were to result in decreased summer precipitation, it would negatively affect radial growth and positively affect the wood density characteristics of jack pine in southern Ontario, Canada.

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