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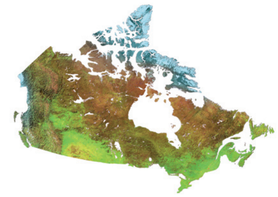

Wood density development in young open-pollinated eastern white pine (*Pinus strobus* L.) families

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Information Report LAU-X-131

2007

Natural Resources Canada, Canadian Forest Service

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Wood density development in young open-pollinated eastern white pine (*Pinus strobus* L.) families [electronic resource] / G.R. Larocque … [et al.].

(Information report, 0835-1570; LAU-X-131)
Electronic monograph in PDF format.
Mode of access: World Wide Web.
Issued also in French under title: Développement de la densité du bois chez des familles de jeunes pins blancs (*Pinus strobus* L.) en pollinisation libre.
Includes bibliographical references.
ISBN 978-0-662-47317-6
Cat. no.: Fo113-3/131E-PDF

1. White pine—Growth.
2. White pine—Quality.
3. White pine—Genetics.
I. LaRocque, G. (Guy), 1955-
II. Laurentian Forestry Centre
III. Series: Information report (Laurentian Forestry Centre: Online); LAU-X-131.

SD387.P65W6613 2007 634.9'75128 C2007-980250-8

Catalog Number Fo113-3/131E-PDF
ISBN 978-0-662-47317-6
ISSN 0835-1570

This publication is available in PDF at no charge from the Canadian Forest Service Bookstore at:
http://bookstore.cfs.nrcan.gc.ca

TTY: (613) 996-4397 (teletype for the hearing impaired)

Cette publication est également offerte en français sous le titre « Développement de la densité du bois chez des familles de jeunes pins blancs (*Pinus strobus* L.) en pollinisation libre » (numéro de catalogue Fo113-3/131F-PDF).

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ABSTRACT

The wood density development of open-pollinated families of juvenile eastern white pine (*Pinus strobus* L.) trees growing in mixed stands with grey alder (*Alnus incana*) was studied to determine the extent to which the variation in wood density was important among the families. The variation in the relationships between wood density and growth rate (ring width) and branch traits was also examined. White pine trees originated from 25 families located in southern Quebec, Canada, and Vermont, USA. The variation in relative wood density among families was very small. In fact, the statistical tests indicated that the family effect was significant only through its interaction with the block (effect). This suggested that the small variation in wood density among the families occurred only because of synergistic effects with growing site conditions. Despite the fact that some effects were statistically significant, the variation observed did not indicate that genetic selection for wood density could result in significant gains in wood quality of white pine. The relationship between wood density and average branch growth was more significant than the relationship between wood density and growth rate (ring width). These results highlighted the role of crown development in wood density development and supported the suggestion that wood density and growth rate (ring width) are not strongly genetically correlated.

RÉSUMÉ

Le développement de la densité du bois de familles de jeunes pins blancs (*Pinus strobus* L.) en pollinisation libre croissant en mélange avec l'aulne rugueux (*Alnus incana*) a été étudié afin de déterminer l'étendue de la variation inter-familiale de la densité du bois. La variation dans les relations entre la densité du bois et le taux de croissance (largeur des cernes) et les caractéristiques des branches a également été examinée. Les pins blancs provenaient de 25 familles croissant dans le sud du Québec (Canada) et au Vermont (É.-U.). La variation inter-familiale de la densité relative du bois était très faible. En fait, les résultats des tests statistiques ont indiqué que l'effet de la famille n'était significatif que lorsqu'il était en interaction avec celui du bloc (effet famille x bloc). Cela suggère que la faible variation inter-familiale de la densité du bois proviendrait uniquement des effets de synergie avec les conditions de croissance du site. Même si certains effets étaient statistiquement significatifs, la variation observée n'a pas indiqué que l'amélioration de la densité du bois par sélection génétique puisse déboucher sur des gains importants pour la qualité du bois de pin blanc. La relation entre la densité du bois et l'accroissement moyen des branches a été plus significative que la relation entre la densité du bois et le taux de croissance (largeur des cernes). Ces résultats ont mis en évidence le rôle du développement de la cime dans le développement de la densité du bois et supportent l'hypothèse voulant que la corrélation génétique entre la densité du bois et le taux de croissance (largeur des cernes) ne soit pas forte.

INTRODUCTION

Several breeding programs for eastern white pine (*Pinus strobus* L.) have been established throughout northeastern North America in the last few decades. As part of these programs, studies were conducted to examine the genetic variability in different attributes, such as genetic traits related to productivity (e.g., Abubaker and Zsuffa 1991; Beaulieu et al. 1996; Li et al. 1997; Joyce et al. 2002) or physiological characteristics (e.g., Abubaker and Zsuffa 1991). Much less attention, however, has been given to genetic variation in wood quality, particularly in wood density, which is known to be under strong genetic control in many tree species (Megraw 1985; Zobel and Talbert 1991). Some studies (e.g., Olson et al. 1981; Struve et al. 1984; Brisbin and Rast 1988) examined wood quality characteristics of eastern white pine trees originating from natural stands or plantations. However, very few studies quantified the extent of genetic variation in wood density among different provenances of eastern white pine, such as those by Lee (1974) and Gilmore and Jokela (1978), in comparison with other species. Moreover, as far as the literature is concerned, the extent of genetic control on this trait remains to be determined, as there is still a lack of information on the extent of genetic variation in wood density among the numerous provenances in northeastern North America. In addition, as suggested by St. Clair (1994a), the simultaneous examination of different traits, including those based on productivity, morphology and physiology, may contribute to superior genetic gains as opposed to the sole examination of stem volume traits. Therefore, it is important to examine if wood density is genetically related to other traits. For instance, is there a relationship between wood density and crown development attributes, and how is wood density related to tree growth rate?

In particular, the last question remains controversial (e.g., Jozsa and Brix 1989; Sheriff and Rook 1990; Zhang and Zhong 1991; Barbour et al. 1992; Johansson 1993; DeBell et al. 1994; Zhang 1995). Several studies indicated that growth rate and wood density were negatively correlated in different species (e.g., Corriveau et al. 1987, 1990; Petty et al. 1990; Johansson 1993; DeBell et al. 1994; Zhang 1995). However, the relationship has not been clearly demonstrated for all species (Rozenberg et al. 2001). Low correlations were often obtained or were limited to some species only (e.g., Senft et al. 1985; Barrett and Kellogg 1986; Haygreen and Bowyer 1989; Larocque and Marshall 1995; Zhang 1995). Growth rate and wood density are both heritable traits, but are not necessarily strongly genetically correlated, particularly in some pine species (Zobel 1971; Zobel and Talbert 1991). Moreover, the strength of the relationship may vary among families for the same species (e.g., Zhang et al. 1996). In addition, there is no causal relationship between growth rate and wood density (Larson 1962, 1967; Megraw 1985). In fact, any long-term or short-term factor that affects wood density originates from effects on crown development (Larson 1962, 1964a, 1969).

Studies conducted for other species have concluded that crown development in terms of shoot elongation or changes in crown dimensions may indicate the extent to which different populations adapt to different abiotic and biotic growth conditions (e.g., Williams 1987; Bridgwater 1990; Kaya and Isik 1997; Larocque 2000; Day et al. 2002; Isik et al. 2002). As far as wood density is concerned, its relationship with crown development has long been recognized, and significant correlations or relationships were derived for different species (e.g., St. Clair 1994a, 1994b; Larocque and Marshall 1995; Amarasekara and Denne 2002). However, for different species, the same type of relationship still remains to be compared among families or provenances, including eastern white pine.

A detailed study that examined the branch and wood density development of juvenile eastern white pine was conducted to better understand the extent of genetic variation among different families and to determine if there were significant relationships between wood density and growth rate or crown development attributes. Specific objectives of this study were: (1) to compare the radial development in wood density of juvenile white pine trees of different families and (2) to examine the variation in the relationships between branch development traits and wood density among different families.

MATERIALS AND METHODS

This study was based on two experimental sites consisting of mixed plantations of eastern white pine and grey alder (*Alnus incana*) located in different climatic conditions. The first site was established in Valcartier (46° 56' N, 71° 30' W), north of Quebec City, and the second one was established in St-Joseph-de-Lévis (46° 40' N, 71° 10' W), east of Quebec City and about 25 km from the Valcartier site. The Valcartier site, on abandoned farmland measuring about 0.86 ha in area, was originally colonized by several species such as balsam fir (*Abies balsamea* (L.) Mill.), black spruce (*Picea mariana* (Mill.) B.S.P.) and trembling aspen (*Populus tremuloides* Michx.), before clearcutting in the spring of 1988. The soil texture consisted of sandy loam (15 cm) sitting over loamy sand, which provides good drainage conditions. Different treatments were performed before planting. After the residual stumps were removed in the spring of 1989, the site was ploughed and disc harrowed and chips from non-commercial timber were spread. Fertilizers (850kg ha^{-1} of 12-8-14+3.5 Mg) and lime (600 kg ha^{-1}) were then applied to prevent nutrient deficiency and improve soil pH.

The Lévis site, 2.2 ha of farmland, was located on a hill sitting on gravelly loam. As the drainage conditions varied greatly from the top of the hill to the bottom, three blocks were delimited to ensure homogeneous drainage conditions within each block. The first block was located at the top of the hill on well-drained soil, the second block on the middle of the hill on poorly to very poorly drained soil and the third block at the bottom of the hill on very poorly drained soil. Different treatments were conducted before planting. In the spring of 1989 ploughing and discing were performed following glyphosate (5 L ha^{-1}) application. Seedlings were planted in June 1989, when Simazine 80W was applied (6 kg ha^{-1}).

White pine seedlings were planted alternatively with grey alder on both experimental sites. For the present study, grey alder was used as a companion species to provide shade to juvenile eastern white pine. This plantation system was used to prevent white pine weevil attacks (Stiell and Berry 1985). White pine seedlings originated from 25 families within 5 geographical provenances (Table 1). Spacing was 1.5 m between the white pine and grey alder seedlings in the rows. The rows were separated by a distance of 2 m. The rows were laid out within each block so that each white pine seedling was surrounded by four grey alders. Four blocks, one at Valcartier and three at Lévis, were established. Linear plots of 4 white pines for each family were randomly located within each block. The seedlings were surveyed in July 1990 to record problems (mortality, damage, etc.) and brushing and weeding were performed in 1990 and 1991 on both sites.

Table 1. List of white pine families planted in three blocks at the Lévis site and one block at the Valcartier site

Geographical origin	Family numbers	Latitude N (°')	Longitude W (°')	Elevation (m)
Lac Emery, QC, Can.	183, 184, 185, 186, 187	46 53	73 14	274
Little River, VT, U.S.A.	422, 425, 426, 427, 428	44 29	73 06	110
Rivière-de-l'Aigle, QC, Can.	630, 633, 635, 638, 639	46 21	76 10	213
Lac Kipawa, QC, Can.	661, 662, 664, 743, 745	47 03	78 57	335
Lac Balsam, QC, Can.	731, 733, 736, 737, 739	46 15	76 54	244

Branch trait measurements were conducted in 1995 for the first five whorls from the top (1991-1995). Three types of branches from each whorl were targeted for measurements. First, the longest and shortest branches were identified and one additional branch was selected randomly. Then, the diameter at the branch base and the annual branch increment (whorl length) were measured for all the selected branches. Thus, the number of branch length measurements varied from one for the whorl at the top of the trees to five on the fifth whorl at the base of the crown.

Increment cores were taken at stump height in the summer of 2001 on both sites. Average height and dbh of the white pines in all the families were 2.5 m and 22.6 mm, respectively. All the trees that were alive in 2001 in each plot were sampled. Thus, a total of 292 cores were collected for ring density measurement. The cores were then sawn to a thickness of 1.57 mm. Following extraction in an alcohol-benzene solution, relative density was measured using a direct reading X-ray densitometer by Forintek Canada Corp. in Quebec City. Ring width, ring density and minimum and maximum ring densities were computed from the 100 readings performed for each ring. Additional information about the direct reading X-ray densitometer can be found in Jozsa and Myronuk (1986).

The three blocks within the experimental set-up at the Lévis site and the experimental set-up at the Valcartier site were merged to form a randomized four complete block design. This decision was supported by the examination of the plots of each variable against the overall family means, which indicated that no bias was introduced into the block x family interaction.

For each ring, the corresponding average branch increment rate for all the branches measured for each whorl was matched with ring width, ring density and minimum and maximum ring densities to examine the degree to which the effect of branch increment rate on wood formation differed among the families. The following mixed model of analysis of covariance was performed with the SAS GLM procedure (SAS Institute Inc. 2001):

$$Y_{ijk} = \mu + ß_i + f_j + W_{ij} + (a_j - \alpha)\tau_{ijk} + \gamma_{ijk} + e_{ijk} \quad (1)$$

where Y_{ijk} is the dependent variable for the k^{th} tree (k=1,…,4) from the j^{th} family (j=1,…,25) in the i^{th} block (i=1,…,4);
μ the overall mean effect;
$ß_i$ the fixed effect of block i;
f_j the random effect of the j^{th} family; it is assumed that f_j is ~ $N(0,\sigma^2{}_f)$;
W_{ij} the random effect due to the interaction between the i^{th} block and the j^{th} family; it is assumed that ω_{ij} is ~ $N(0, \sigma^2{}_{ij})$;
τ_{ijk} the average branch increment rate associated with the k^{th} tree from the j^{th} family in the i^{th} block;
a_j the slope of the j^{th} family in the relationship between ring density and ring width;
α the common slope for all the families in the relationship between ring density and ring width;
γ_{ijk} the cambial age associated with the k^{th} tree (k=1,…,4) from the j^{th} family (j=1,…,25) in the i^{th} block (i=1,…,4);
e_{ijk} the random error term associated with the k^{th} tree in the j^{th} family in the i^{th} block; it is assumed that e_{ij} is ~ $N(0, \sigma^2{}_e)$.

The comparison of ring density among families was also conducted by using the GLM procedure in SAS (SAS Institute Inc. 2001) to fit the following mixed ANCOVA model with ring width as a covariate:

$$Y_{ijk} = \mu + ß_i + f_j + r_{ij} + (a_j - \alpha)W_{ijk} + \gamma_{ijk} + e_{ijk} \quad (2)$$

where y_{ijk} is the dependent variable for the k^{th} tree (k=1,…,4) from the j^{th} family (j=1,…,25) in the i^{th} block (i=1,…,4);
μ the overall mean effect;
$ß_i$ the effect of block i;
f_j the random effect of the j^{th} family; it is assumed that f_j is ~ $N(0,\sigma^2_f)$;
r_{ij} the random effect due to the interaction between the i^{th} block and the j^{th} family; it is assumed that r_{ij} is ~ $N(0, \sigma^2_{ij})$;
W_{ijk} the ring width associated with the k^{th} tree from the j^{th} family in the i^{th} block;
a_j the slope of the j^{th} family in the relationship between ring density and ring width;
α the common slope for all the families in the relationship between ring density and ring width;
γ_{ijk} the cambial age associated with the k^{th} tree (k=1,…,4) from the j^{th} family (j=1,…,25) in the i^{th} block (i=1,…,4);
e_{ijk} the random error term associated with the k^{th} tree in the j^{th} family in the i^{th} block; it is assumed that e_{ij} is ~ $N(0, \sigma^2_e)$.

For each dependent variable, the best linear unbiased prediction (BLUP) approach was used to estimate the mean for each family.

RESULTS

Ring relative density for all families decreased with increasing cambial age. On average, it decreased from 0.31 to 0.27 when cambial ages increased from 4 to 13 (Figure 1a). However, the decrease from cambial ages 4 to 7 was more pronounced than the decrease observed for the other ages. For each cambial age, the variation among families remained very small, as indicated by the standard deviation. This is supported by the results of the ANCOVA based on the relationship of ring relative density with average branch increment, which indicated that the variance component of the family effect was not statistically significant (Table 2). The cambial age effect, average branch increment covariate and variance component of the block*family effect were statistically significant. Similar results were obtained for the ANCOVA with ring width as covariate (Table 3). However, the covariate ring width was not significant and the proportion of the variability explained by the model was lower (R^2=0.32 vs 0.43).

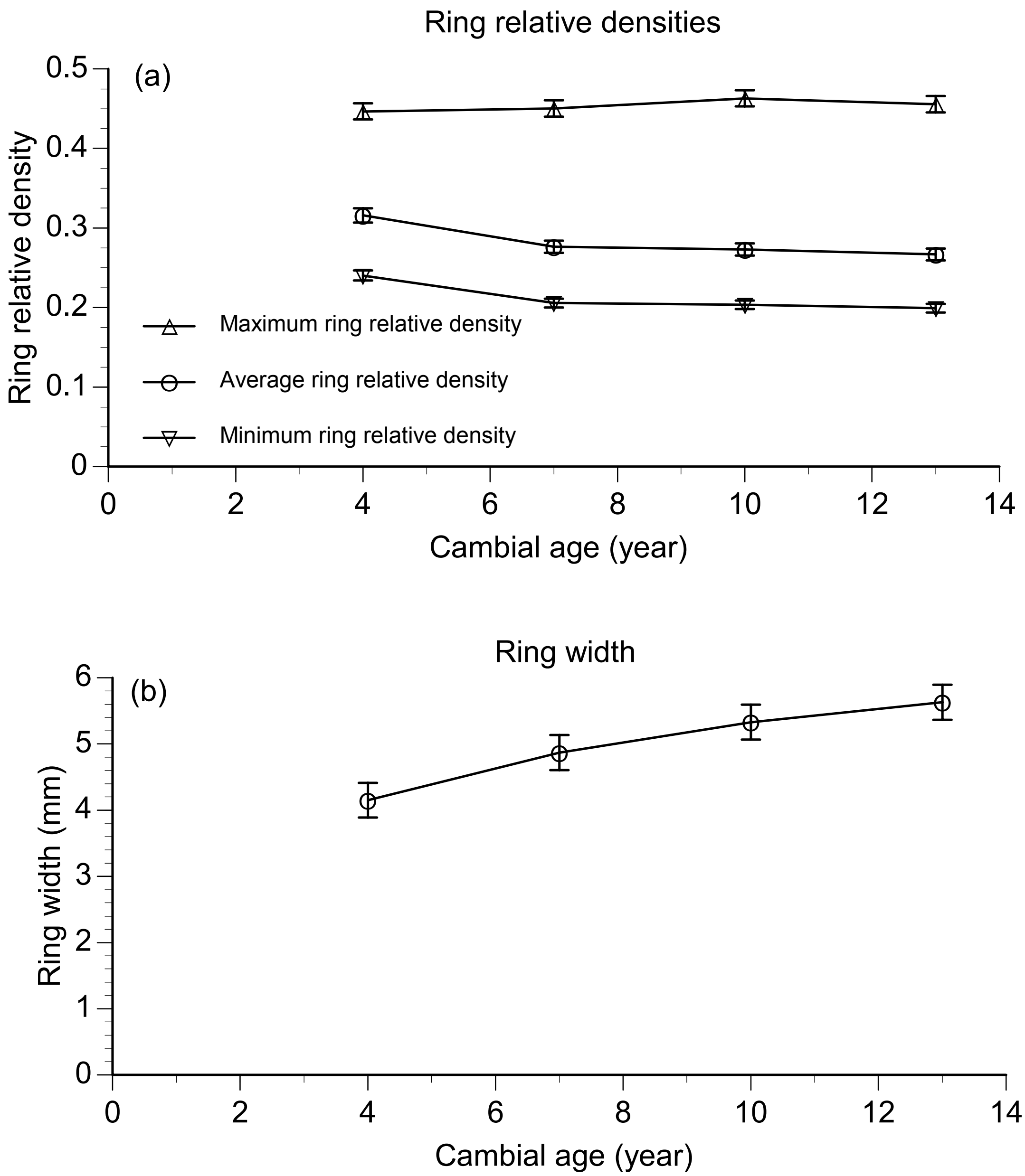

Figure 1. Average ring density, minimum and maximum ring densities (a) and ring width (b) for 25 white pine families at four cambial ages. Error bars represent standard deviation.

Table 2. Observed significance associated with the analysis of covariance for ring width, average ring relative density, minimum ring density and maximum ring density as a function of average branch whorl increment for different cambial ages in 25 eastern white pine families

	P<F			
	Average ring relative density	**Minimum ring density**	**Maximum ring density**	**Ring width**
Fixed effects				
Block	0.10	0.09	<0.01	<0.01
Meanvertincr*	<0.01	<0.01	<0.01	<0.01
Cambial age	<0.01	<0.01	0.74	<0.01
Random effect				
Family	0.93	0.88	0.64	0.09
Family x block	<0.01	<0.01	<0.01	<0.01
R^2	0.43	0.41	0.36	0.39

* Average branch whorl increment

Table 3. Observed significance associated with the analysis of covariance for ring density as a function of ring width for different cambial ages in 25 eastern white pine families

Fixed effects	P<F
Block	0.07
Ring width	0.15
Cambial age	<0.01
Random effect	
Family	0.54
Block x family	<0.01
R^2	0.32

Average minimum ring relative density decreased with cambial age for all families. On average, it decreased from 0.24 to 0.19 for cambial ages 4 to 14 (Figure 1a). The pattern of variation in minimum ring density with cambial age is similar to that of variation in ring density (and the variation for each cambial age was very small). Only the cambial age effect and variance component of the family*block effect were statistically significant (Table 2). The covariate average branch whorl increment was statistically significant and 41% of the variability in minimum ring density was explained by the model. Average maximum ring relative density remained fairly constant with cambial age, varying between 0.44 and 0.46 (Figure 1a). This pattern explains why the cambial age effect was not statistically significant (Table 2). The block effect and variance component of the family*block effect and the covariate average branch increment rate were significant. Average ring width for all families increased with cambial age, increasing on average from 4.1 to 5.6 mm for cambial ages 4 to 13 (Figure 1b). Except for the family, all the fixed effects and the variance components of the family x block effect were statistically significant (Table 2). The covariate average branch increment rate was also significant and 39% of the variability in ring width was explained by the model.

DISCUSSION

The decrease in ring relative density and minimum relative density with cambial age may appear unusual, as both wood density attributes normally increase with age. However, this pattern is in agreement with the description of Panshin and de Zeeuw (1980) for white pine. Few studies compared wood density development among different families or provenances of eastern white pine. Gilmore and Jokela (1978) observed significant differences among different provenances of eastern white pine originating from areas covering the natural range of eastern white pine. Lee (1974) observed significant differences in wood relative density among 15 provenances of eastern white pine that originated from the entire area of the natural distribution of white pine. Significant differences in wood relative density were also observed among 98 provenances of eastern white pine by Olson et al. (1981). The lack of significant family variation in the present study may appear unusual, as significant family variations were obtained for different pine species (Zobel and Jett 1995). The two reasons that may explain these results are the age of the trees and the relative geographical proximity of the families examined. When the wood density measurements were conducted, the white pines were still very young and growing under relatively homogeneous site conditions. It is possible that the changes in gene expressions related to phenotype effects were minimal at the juvenile stage of tree development. The genes involved in the development of meristems, which ultimately affect cell development, are known to change with age (Woo et al. 1994; Kaya and Isik 1997; Day et al. 2002). Regarding geographical proximity, the families examined in the present study originated from relatively close populations. Thus, it is possible that the variation in family differences that may exist in the natural range of distribution of white pine was not captured in the present study. The studies cited above included more provenances that originated from a wider range of geographical locations than the present study.

The analysis of covariance between ring density and ring width indicated a non-significant relationship between wood density and ring width (Table 3), which is in contrast with significant relationships obtained for other species (e.g., DeBell et al. 1994; Larocque and Marshall 1995; Zhang 1995; Zhang and Morgenstern 1995; Lindstrom 1996; Simpson and Denne 1997; Hannrup et al. 2000). However, the white pine sample trees studied were still very young. It is possible that the significance of the relationship between ring density and ring width may increase with age (e.g., Larocque and Marshall 1995; Simpson and Denne 1997). Nevertheless, the strength of the relationship between ring density and growth rate remains controversial in light of the existing literature (see Jozsa and Brix 1989; Zhang and Zhong 1991; Barbour et al. 1992; Johansson 1993; DeBell et al. 1994; Zhang 1995). In fact, some authors claim that there is no causal relationship between wood density and growth rate (e.g., Larson 1962, 1967; Megraw 1985). Short- and long-term factors that influence wood density development act through the intermediary of crowns (Larson 1962, 1964a, 1964b, 1969).

The absence of a significant relationship between ring density and ring width and the significant relationship between ring density and branch whorl increment rate support the hypothesis that there is a stronger causal relationship between wood density and crown development than that between ring density and growth rate. Several studies highlighted the influence of crown development on wood characteristics without necessarily obtaining highly significant relationships (e.g., Cameron and Watson 1999; Gartner et al. 2002). As suggested by Amarasekara and Denne (2002), several parameters influence wood density, which can be affected differently by physiological processes occurring within crowns. Thus, basic measures such as crown width or branch whorl growth rate do not reflect the complexity of the physiological factors, such as synthesis and translocation of auxins and photosynthates (see Larson 1962, 1964a, 1964b, 1967, 1969), involved in wood formation. Thus, future studies that aim at achieving a better understanding of the role of crowns in wood formation should integrate these physiological factors.

CONCLUSION

The extent of genetic variation in wood density among young open-pollinated white pine families was examined. Despite some statistically significant effects, the variation observed was not pronounced. The relatively close geographical origins of the families examined may explain the small variation obtained in wood relative density among the different families. However, it may be premature to conclude that wood density of young white pine is not characterized by high genetic variability compared with other variables such as growth rate. The trees examined were still very young, with a small proportion of mature wood. Thus, the re-examination of wood density when the trees are much older may highlight differences among families. Nevertheless, the results of the present study indicate that the examination of wood density in juvenile white pine cannot be used to select genetically superior families for wood quality improvement.

ACKNOWLEDGEMENTS

Sincere thanks are extended to the Canadian Forest Service and Forintek Canada Corp. for the support both organizations provided for the field work and ring density measurements. The contributions of Mr. René Pâquet, technician at the Laurentian Forestry Centre, for field measurements, Dr. Peng Li, formerly of the Canadian Forest Service, for planning the experimental designs in the field, Mr. Gilles Chauret, professional at Forintek Canada Corp, for ring density measurements, and Mr. Maxime Boucher, professional statistician, for his assistance with statistical analyses, were greatly appreciated.

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