WOOD QUALITY OF NORWAY SPRUCE GROWN IN PLANTATIONS IN QUEBEC

Donald Blouin

Research Assistant

Jean Beaulieu

Forestry Officer

Gaetan Daoust

Forestry Officer

Natural Resources Canada
Canadian Forest Service—Quebec Region
1055 du P.E.P.S.
P.O. Box 3800
Sainte-Foy, Quebec G1V 4C7

and

Jean Poliquin

Professor
Wood Science Department
Université Laval
Sainte-Foy, Quebec G1K 7P4

(Received September 1993)

ABSTRACT

This study was conducted as part of the genetic research program on Norway spruce [*Picea abies* (L.) Karst.] grown in Quebec. The objective of the study was to acquire more information on the wood density of Norway spruce grown in plantations and to determine whether the wood density could be used as a selection criterion for species improvement. To this end, 70-year-old commercial plantation-grown trees were first sampled in order to establish the wood density radial variation pattern and determine the existing relationships between the properties of juvenile wood and the average values of mature trees. Subsequently, the study of 22 provenances from central Europe introduced in Quebec was designed to verify the intra- and inter-provenance variation in wood density, determine the correlation between wood density and radial growth rates and origin, and estimate the impact of a selection of superior phenotypes on wood density. The study on 70-year-old trees showed that wood density declines from pith toward bark up to the eighth annual ring, stabilizes until the fourteenth annual ring, and increases thereafter. The simple regression equations calculated between the density of the juvenile wood and the mean density of the trees were significant with R^2 varying from 0.53 to 0.64. The study of the wood density of the trees in the provenance trial, 19 growing seasons after planting, showed the presence of a moderate negative correlation between radial growth rate and wood density. No significant difference was found among provenances with regard to the average density values of the juvenile wood. For the radial variation pattern of wood density and annual growth ring width, comparisons made it possible to identify significant differences between southwestern and northeastern European provenances. There is still, however, strong individual variability in these traits, with 65 to 85% of total variation being due to differences between trees from the same plot. A three-stage selection procedure would make it possible to maintain wood density, to reduce by half the deviation between the internal and external juvenile wood density, and to double the volume output, depending on the selection strategy chosen. These results confirm the potential for rapid growth

Wood and Fiber Science, 26(3), 1994, pp. 342–353

and the excellent wood quality of Norway spruce provenances that are well adapted to the soil and climate conditions in Quebec.

Keywords: Norway spruce, *Picea abies* (L.) Karst., wood quality, wood density, growth rates, intra- and inter-provenance variation, phenotypic selection.

INTRODUCTION

Norway spruce [*Picea abies* (L.) Karst.] is one of the main European forest species. It is a valuable resource for the veneer and lumber industries (Sell and Kropf 1990). It is also the most commonly planted exotic species in eastern North America. In Canada, this species can be found in the Maritimes, Ontario, and Quebec. In a study of the Norway spruce plantations dating from the early years of this century, MacArthur (1964) observed that, on appropriate sites, adapted provenances produced yields superior to indigenous spruce species. In light of these encouraging results, major reforestation efforts were undertaken with this species in Quebec. Over 163 million trees were planted between 1972 and 1990 (Paradis 1991).

In the Great Lakes and St. Lawrence forest region, Norway spruce shows maximum productivity on soils of fine to moderate texture, fresh loam, and loamy sand with moderate drainage (Camirand et al. 1983). On the basis of a test performed on 44 provenances and with full stocking of 2,500 saplings per hectare, Corriveau et al. (1988) estimated a mean annual growth of 4.7 m^3/ha/yr, 16 growing seasons after planting. The best adapted provenances achieved a mean annual growth of 6.4 m^3/ha/yr. On the other hand, Norway spruce is very susceptible to attacks from white pine weevil [*Pissodes strobi* (Peck)], an insect that can reduce the expected yield.

From the late 1960s to the early 1980s, approximately 150 provenances were established and tested in various experimental sites in Quebec. According to the results, several well-adapted, fast-growing provenances were recommended for the reforestation of the Great Lakes and St. Lawrence forest region (CAGAFQ 1983). In 1984, a Norway spruce genetic improvement program was initiated to develop high potential multiclonal varieties suited to the soil and climate conditions of southern Quebec (Daoust et al. 1987). Hardiness, volume yield, stem and crown quality, as well as resistance to insects and diseases, were the characteristics initially selected to reach the goals of the genetic improvement program. So far, very little interest has been shown in the wood quality of Norway spruce produced in Quebec. However, it has been recognized that an increase in volume should not be achieved at the expense of the quality of the inherent characteristics of the wood produced (Corriveau et al. 1990).

This study was conducted as part of the genetic research program on Norway spruce grown in Quebec. The objective of the study was to acquire more information on the density of Norway spruce grown in plantations and to determine whether the density could be used as a selection criterion for species improvement. To this end, 70-year-old trees were first sampled in order to establish the wood density radial variation pattern, and to determine the existing relationships between the properties of juvenile wood and the average values of mature trees. Subsequently, the study of 22 provenances introduced in Quebec was designed to verify the intra- and inter-provenance variation in wood density, determine the correlation between wood density and their radial growth rates and origin, and estimate the impact of a selection of superior phenotypes on wood density.

MATERIALS AND METHODS

Thirty-five trees in a Norway spruce plantation in Grand-Mère (Proulx plantation, Quebec, lat. 46°40′N, long. 72°40′W, alt. 130 m) dating from 1920 were systematically sampled. The average annual precipitation in Grand-Mère is 1,025 mm. The average annual temperature is 4.5 C; the average temperature

TABLE 1. *Geographic origin and averages by provenance of annual ring width and wood density of 22 provenances of Norway spruce established in Valcartier, Quebec.*

Provenance		Co-ordinates of origin[1]										
Number	Name	Lat. north	Long. east	Alt. (m)	IJW (mm)	OJW (mm)	JUVW (mm)	WIDD (mm)	IJD (kg/m³)	OJD (kg/m³)	JUVD (kg/m³)	DEND (kg/m³)
5390	Forest district of Marginea, Romania	47°45′	25°45′	670	3.7	3.5	3.6	0.2	353	329	344	24
5391	Forest district of Dorna Cindreni, Romania	47°21′	25°22′	975	3.4	2.8	3.2	0.6	357	345	352	12
5392	Forest district of Bicaz, Romania	46°50′	25°55′	1,150	3.8	3.5	3.7	0.3	354	336	348	18
5393	Forest district of Comanesti, Romania	46°17′	26°37′	780	3.7	3.7	3.7	0.0	369	348	361	21
5394	Forest district of Turda, Romania	46°35′	23°47′	1,110	3.4	3.0	3.3	0.4	358	336	351	22
5395	Forest district of Cimpeni, Romania	46°20′	23°00′	1,260	3.8	2.9	3.5	0.9	363	343	357	20
5397	Auce, Latvia	56°25′	22°50′	150	3.8	3.0	3.5	0.8	352	341	348	11
5398	Daugavpils, Latvia	55°50′	26°30′	250	3.6	2.8	3.3	0.8	367	349	360	18
5399	Jelgava, Latvia	56°40′	23°40′	100	3.7	2.9	3.4	0.8	361	341	354	20
5400	Skede, Latvia	57°00′	27°00′	180	3.4	3.4	3.4	0.0	352	337	345	15
5401	Tukums, Latvia	57°00′	23°05′	70	3.6	2.9	3.3	0.7	359	341	353	18
5403	Wilno, Lithuania	54°35′	24°15′	300	3.7	2.4	3.3	1.3	362	360	361	2
5404	Gorodokskii Leshos, Belorussia	55°30′	30°00′	200	3.6	2.8	3.3	1.2	360	353	358	7
5405	Glubokskii Leshos, Belorussia	55°15′	30°10′	200	3.6	2.9	3.3	0.7	354	349	352	5
5406	Minskii Leshos, Belorussia	53°50′	27°35′	660	3.7	3.0	3.4	0.7	356	340	350	16
5407	Forest district of Carlsfeld, Germany	50°25′	12°35′	920	3.3	3.4	3.3	−0.1	370	328	354	42
5408	Forest district of Rothenkirchen, Germany	50°20′	11°20′	555	3.6	3.4	3.5	0.2	371	328	356	43
3153	Forstamt Tannesberg, Germany	50°00′	12°30′	700	3.4	3.0	3.2	0.4	371	333	358	38
3154	Oberforsterei Rycerka, Poland	49°32′	19°00′	700	3.4	3.1	3.3	0.3	378	339	365	39
4027	Proulx plantation, Quebec, Canada	46°40′	72°40′[2]	130	3.4	3.2	3.4	0.2	367	336	357	31
4028	Proulx plantation, Quebec, Canada	46°40′	72°40′[2]	130	3.5	2.9	3.3	0.6	377	359	371	18
4076	Proulx plantation, Quebec, Canada	46°40′	72°40′[2]	130	3.8	3.0	3.6	0.8	369	354	357	35
Average					3.6	3.1	3.4	0.5	363	341	355	22
Standard deviation[3]					0.6	0.8	0.5	0.9	26	28	24	26

[1] Lat., latitude; Long., longitude; Alt., altitude.
[2] West longitude.
[3] Standard deviation of individual values.
IJW: growth ring width of inner juvenile wood, average for rings 1 to 9 from the pith; OJW: growth ring width of outer juvenile wood, average for rings 10 to 15 from the pith; JUVW: growth ring width of juvenile wood, average for rings 1 to 15 from the pith; WIDD: deviation between ring width of inner and outer juvenile wood; IJD: inner juvenile wood density; OJD: outer juvenile wood density; JUVD: juvenile wood density; DEND: deviation between inner juvenile wood density and outer juvenile wood density.

in July is 19.7 C and the coldest temperature recorded was −38.9 C. The length of the growing season varies from 140 to 160 days. The soil is deep alluvial sand. Increment cores 12 mm in diameter taken at breast height were cut into sections at every three annual growth rings from the pith to the eighteenth ring, and at every five or six rings from there to the bark, for a total of 14 core sections per tree. To estimate wood density, the samples were first immersed in water for a 24-h vacuum/pressure cycle to ensure that they had a moisture content higher than the fiber saturation point. The samples were weighed in air and then in water to determine the volume when saturated, according to Archimedes' principle. They were subsequently dried in an oven at 103 C, ±2 C, for 24 h. Oven-dry mass was measured after the samples had been placed in desiccation chambers containing phosphorous pentoxide (P_2O_5) and had reached ambient temperature. Weighing bottles were used to prevent any loss or absorption of moisture when the weighing was done with a Mettler PE160 digital precision scale (±0.0005 g). The weighing was done to calculate the wood density of the samples using the ratio of their oven-dry weight to their volume when saturated.

A test of 22 provenances of Norway spruce from central Europe (see Table 1) was established in 1969 at the Valcartier Forest Experiment Station (lat. 46°50′N, long. 71°30′W, alt. 150 m), located 40 km north of Quebec City. Three of these provenances were from the Proulx plantation at Grand-Mère, and the seed sources were unknown. They were withdrawn for the estimation of the relationships between provenance averages for each variable and their origin. The seedlings, four years old at the time of planting, were produced by and obtained from the Petawawa National Forestry Institute (lat. 46°80′N, long. 77°30′W, alt. 170 m). The average annual precipitation in Valcartier is 1,170 mm. The average annual temperature is 4 C; the average temperature in July is 15.4 C and the coldest temperature recorded was −41.7 C. The length of the growing season varies from 120 to 140 days. The soil is alluvial sand.

The experimental layout consisted of four randomized complete blocks. Each square plot had 36 trees spaced 1.8 m × 1.8 m. The total area of the layout was 1.03 ha.

To assess wood density, a 12-mm increment core was taken at breast height on the south side from five trees per plot in the fall of 1988, i.e., 20 trees per provenance for a total of 440 trees in the provenance trial. The core samples were numbered, then placed in polyethylene bags and kept in a freezer (−20 C) until they were used in the laboratory. The purpose of the sampling was to estimate the wood density variation within and among provenances and the relationships between the radial growth rates and their origin and wood density. Of the 19 provenances whose origin was known, nine had been selected by the breeders on the basis of their height growth and volume yield. Within these nine superior provenances, a mass selection of 75 trees had been made on the basis of their volume yield, stem and crown quality, as well as resistance to insects and diseases. These 75 trees had also been sampled to determine the wood density for the purpose of assessing the impact of this type of selection on the average wood density of the trees.

To account for the radial variation pattern in wood density observed in the genus *Picea* (Olesen 1977; Corriveau et al. 1990), the samples were divided into two categories. Since the trees were 23 years old at the time the samples were taken and since there was an average of 15 annual rings at breast height, the first nine rings, representing the density decline phase, were considered to be inner juvenile wood (IJW), while the six following rings, located near the bark and representing the stable stage, were considered to be outer juvenile wood (OJW). A third variable corresponding to the deviation between the inner juvenile wood density and that of the outer juvenile wood (DEND) was created.

Because of the large number of samples to be measured, the maximum moisture content method described by Keylwerth (1954) and used by Smith (1954) was chosen to estimate the wood density of unextracted wood. Complete saturation was achieved by immersing the samples in water. The samples were put through 24-h vacuum/pressure cycles until constant weight was obtained; up to 12 days were necessary in the case of samples of inner juvenile wood. Excess surface water was wiped off the samples with a damp cotton cloth before measuring the saturated mass. Oven-dry mass was obtained using the same procedure as for the trees from the Proulx plantation. The length of the samples was measured with a micrometer caliper to determine the average annual growth rate.

Analysis of variance based on a randomized complete block design and according to a random model was used to partition phenotypic variation. After verifying the basic assumptions about data normality and variance homogeneity, GLM and VARCOMP procedures (SAS 1988a) were used. Correlation and regression analyses measured the strength of the links between the wood characteristics using CORR and REG procedures. The normality of the data had been checked using the Shaparo-Wilk test (SAS 1988b) before the regression was performed.

RESULTS AND DISCUSSION

Mature trees from the Proulx plantation

Descriptive characteristics of the thirty-five 70-year-old trees from the Proulx plantation are presented in Table 2. Weighted values for wood density, according to the surface or width of the growth rings, were calculated but were not retained because of their weak influence on the estimated average density of the trees.

The average wood density of the Proulx plantation (387 kg/m^3) is similar to that of red spruce [*Picea rubens* Sarg.] (380 kg/m^3) and slightly greater than that of white spruce [*Picea glauca* (Moench) Voss] (354 kg/m^3), as reported by Jessome (1977). Also, similarities have been observed for other wood characteristics between Norway spruce and red spruce (Anonymous 1992).

Wood density radial variation pattern

In the genus *Picea*, the wood density radial variation pattern is known to be of type II, as described by Panshin and DeZeeuw (1980), i.e., starting from the pith, a density decline phase is followed by an increase in density, which then stabilizes as it nears the bark. This kind of variation pattern has been confirmed for Norway spruce in Europe (Olesen 1977) and for white spruce in Quebec (Corriveau et al. 1990). The wood density radial variation pattern of Norway spruce grown in the Proulx plantation in Quebec is shown in Fig. 1. The results of the analyses indicate that the transitions between the phases of decline, stabilization, and rapid increase in the wood density of Norway spruce grown in plantations in Quebec occur around the eighth and fourteenth annual rings from the pith. The rapid-increase stage is followed by a slow-increase stage, and the transition occurs around the twenty-fifth annual ring. Polge (1964) has shown that the wood density of many conifers declines from the pith toward the bark, and then increases again from ages ranging from 5 to 25 years, depending on the species. Clark and Saucier (1991) have reported that differences in wood density radial variation patterns of several species of southern pine in the United States are due largely to differences in geographic location of the plantation and not to differences between species. Thus, under the same soil and climate conditions, different species would have the same variation pattern.

In the case at hand, as in the case of white spruce grown in plantations in Quebec, the first 15 annual rings from the pith consist solely of juvenile wood, corresponding to the density decline and stabilization phases. This kind of density radial variation pattern may be explained by the internal structure of the annual ring. As stated by Elliott (1970), for distinct latewood species, the density of earlywood declines progressively from the pith to the bark, chiefly because of an increase in tracheid diameter, while the value of the density of latewood increases in the same direction, mainly because of an increase in wall thickness, the two phenomena being active over a period corresponding to the formation of juvenile wood. Most of the variation in density of each of the annual rings during this period is due to the proportion of tissue of early- and latewood and their respective density values.

TABLE 2. *Descriptive statistics of the characteristics of the 35 Norway spruce trees from the Proulx plantation at Grand-Mère, established in 1920.*

Characteristics	Unity	Average	Standard deviation	Interval
IJW	mm	5.1	0.9	3.7–6.8
OJW	mm	3.3	0.7	2.4–6.3
JUVW	mm	4.4	0.7	3.4–6.4
MW	mm	2.4	0.4	1.9–3.5
IJD	kg/m^3	356	26	318–414
OJD	kg/m^3	344	26	291–405
JUVD	kg/m^3	351	24	307–412
MD	kg/m^3	387	23	344–437

IJW: growth ring width of inner juvenile wood, average for rings 1 to 9 from the pith; OJW: growth ring width of outer juvenile wood, average for rings 10 to 15 from the pith; JUVW: growth ring width of juvenile wood, average for rings 1 to 15 from the pith; MW: whole tree growth ring width; IJD: inner juvenile wood density, average for rings 1 to 9 from the pith; OJD: outer juvenile wood density, average for rings 10 to 15 from the pith; JUVD: juvenile wood density, average for rings 1 to 15 from the pith; MD: whole tree density.

Relationships between the juvenile wood density and that of mature wood

The purpose of genetic improvement is to select superior individuals, develop offsprings that combine desired characteristics and mass produce improved individuals. Making a selection at a young age accelerates the improvement process. The length of the experiment is often considered to be a limiting factor, mainly in temperate regions. Corriveau et al. (1987) have found a moderate positive correlation in white spruce between juvenile wood density and mature wood density, at both the individ-

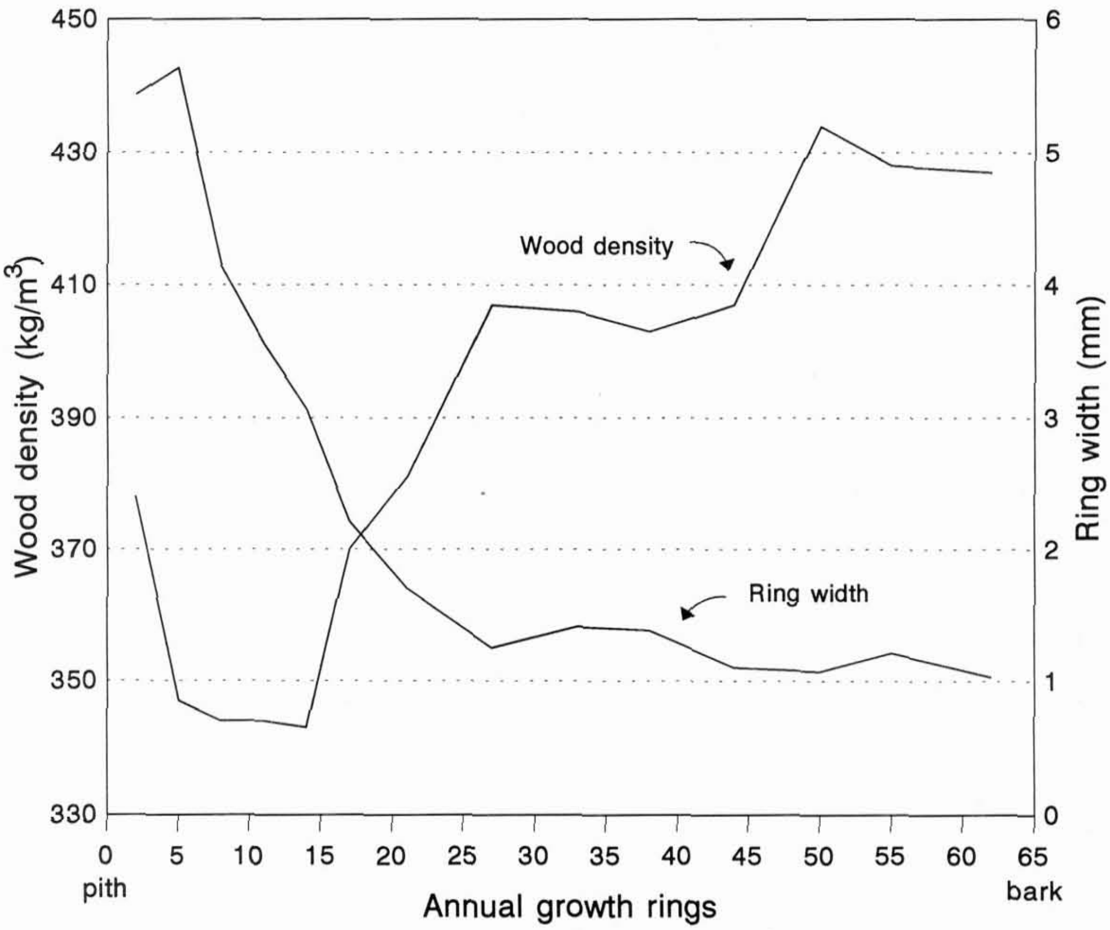

FIG. 1. Radial variation of wood density and annual growth ring width for 35 Norway spruce trees from the Proulx plantation at Grand-Mère, Quebec.

ual and population levels. This means that a mass selection can be made at a young age for the purpose of genetic improvement of wood density or wood mass production in the species. Nepveu and Birot (1979) have also obtained high simple and canonical correlations between juvenile wood and mature wood for Norway spruce growing in France.

To determine whether the juvenile wood data are representative of those for mature wood for Norway spruce grown in plantations in Quebec, simple regression equations were calculated between the juvenile wood density and the whole tree density as well as between the juvenile wood density and that of mature wood. The results, presented in Table 3, show the annual ring sections and the grouped values for rings 1 to 9, 10 to 15, and 1 to 15, representing, respectively, the inner juvenile wood density, the outer juvenile wood density, and the average juvenile wood density.

The results obtained show significant relationships between the juvenile wood density and the average whole tree density. The coefficients of determination (R^2) range from 0.29 to 0.58 for individual rings. For grouped rings, the coefficients of determination range from 0.53 to 0.64. Since the regression equations are significant, the wood density radial variation pattern is expected to be sufficiently constant from one tree to the next to allow the average value of a mature tree to be predicted

TABLE 3. *Regression analysis of the whole tree density according to the juvenile wood density of the 35 Norway spruce trees from the Proulx plantation at Grand-Mère.*

Regression equation[1]	Coefficient of determination R^2	Standard error of estimate	Value of F	$P > F$
TRED = 244 + 0.379•D^{13}	0.29	20	13.51	0.0008
TRED = 214 + 0.499•D^{46}	0.34	19	17.17	0.0002
TRED = 194 + 0.560•D^{79}	0.58	15	45.82	0.0001
TRED = 212 + 0.508•D^{1012}	0.38	18	20.32	0.0001
TRED = 220 + 0.488•D^{1315}	0.48	17	30.45	0.0001
TRED = 160 + 0.637•IJD	0.53	16	36.98	0.0001
TRED = 156 + 0.671•OJD	0.58	15	45.98	0.0001
TRED = 119 + 0.762•JUVD	0.64	14	59.73	0.0001
OJD = 97.1 + 0.692•IJD	0.48	19	30.72	0.0001
DMAT = 185.4 + 0.630•JUVD	0.34	22	16.87	0.0002

[1] All wood density variables are in kg/m^3.

TRED: whole tree density; D^{13}: wood density for rings 1 to 3; D^{46}: wood density for rings 4 to 6; D^{79}: wood density for rings 7 to 9; D^{1012}: wood density for rings 10 to 12; D^{1315}: wood density for rings 13 to 15; IJD: inner juvenile wood density, rings 1 to 9; OJD: outer juvenile wood density, rings 10 to 15; JUVD: juvenile wood density, rings 1 to 15; DMAT: mature wood density, rings 16 and over.

on the basis of the average density of the 9 or 15 annual rings near the pith. Significant relationships also exist between the inner juvenile wood density and that of the outer juvenile wood and between the juvenile wood density and that of the mature wood.

These results are very interesting because they suggest that a very effective selection could be made at a young age. Since wood density has been recognized as a strongly inherited characteristic (Zobel 1961; Kennedy 1966; Corriveau et al. 1991), there is every reason to use this criterion in the selection and improvement of Norway spruce in Quebec.

Test of 22 provenances of Norway spruce in Valcartier

The average annual ring width and wood density values per provenance, together with the average values for all the trees in the experimental site at the Valcartier Forest Station, are presented in Table 1.

The juvenile wood density (first 15 annual rings) of the Valcartier trees is similar to that of the juvenile wood of the Proulx plantation trees, with an overall average of 355 kg/m^3. In addition, the analysis of the average data for the inner and outer juvenile wood densities of the trees sampled suggests similarities in radial variation pattern, i.e., the same age for the transition from the inner juvenile period to the outer juvenile period. Using the regression equations developed from the Proulx plantation data, it can be predicted that, at the age of 70, the average wood density of the trees from the provenance trial should be around 386 kg/m^3, i.e., a value comparable to that obtained for the Proulx plantation (387 kg/m^3).

The deviation between the inner juvenile wood density and that of the outer juvenile wood (DEND) is an indication of the density radial variation pattern, with a slight deviation representing a more homogeneous, better quality wood. Per provenance, the deviation between the inner juvenile wood density and that of the outer juvenile wood ranges from 2 to 43 kg/m^3, thus reflecting a great disparity between provenances with respect to this characteristic.

Correlations between growth and wood characters

Individual level.—As far as the correlations at the individual tree level are concerned, the inner juvenile wood density ($r = -0.43$; $P < 0.001$) and that of the outer juvenile wood ($r = -0.48$; $P < 0.001$) are negatively related to the widths of respective annual rings. This confirms the tendency of a decline in wood density to be associated with an increase in annual ring width as observed in Norway spruce (Olesen

TABLE 4. *Pearson correlation coefficients for 19 provenances of Norway spruce of known origin established in Valcartier, Quebec.*

	IJW	OJW	JUVD	WIDD	IJD	OJD	JUVD
DEND	−0.50	0.51	0.02	−0.67*	0.71**	−0.78**	0.22
JUVD	−0.06	−0.30	−0.26	0.25	0.84**	0.44	
OJD	0.39	−0.66*	−0.19	0.74**	−0.11		
IJD	−0.35	0.08	−0.20	−0.22			

IJW: growth ring width of inner juvenile wood; OJW: growth ring width of outer juvenile wood; JUVW: growth ring width of juvenile wood; WIDD: deviation between ring width of inner and outer juvenile wood; IJD: inner juvenile wood density; OJD: outer juvenile wood density; JUVD: juvenile wood density; DEND: deviation between inner juvenile wood density and outer juvenile wood density.

* Significant at $P < 0.05$ after Bonferroni correction.

** Significant at $P < 0.01$ after Bonferroni correction.

df = 19.

1976, 1977) and in white spruce (Keith 1961; Chang and Kennedy 1967; Beaulieu and Corriveau 1985; Wang et al. 1985; Corriveau et al. 1990, 1991). Despite this tendency, Corriveau et al. (1987) have noted that it is possible to maintain a gain in volume yield by selecting populations or trees having both greater-than-average wood density and ring width. In the case at hand, the fact that this link is only moderate suggests that it is possible to identify individuals that deviate from this general tendency.

A moderate positive correlation ($r = 0.55$; $P < 0.001$) exists between the inner juvenile wood density and that of the outer juvenile wood. The weak relationship ($r = 0.21$; $P < 0.001$) between inner juvenile ring width and outer juvenile ring width suggests that this last parameter is not strongly genetically controlled and that the result is rather the response of the trees to the environmental conditions existing at different growing periods (Larson 1969).

Provenance level.—The Pearson correlation coefficients for the provenance averages are presented in Table 4. A Bonferroni (Wright 1992) correction was made to the probability level to allow for the fact that 22 tests were conducted simultaneously. The provenances from the Proulx plantation whose exact origins are unknown were eliminated for these calculations. There is, therefore, a significant negative relationship between ring width and outer juvenile wood density, whereas no relationship exists for the inner juvenile wood. It seems that the negative relationship between ring width and wood density becomes clearer once the trees have reached a certain age. According to Olesen (1977), the influence of ring width on wood density increases with the distance from the pith, making it the main factor influencing wood density in mature wood. Thus, the parameters affecting the inner juvenile wood density appear to be controlled more by physiological factors because of the proximity of the crown and its hormonal control (Larson 1969).

It is also worth noticing that there is no significant relationship between the average densities of the inner and outer juvenile wood of the provenances. This is contrary to the results reported by Corriveau et al. (1987) for white spruce in Quebec. In the case at hand, the absence of relationships at the provenance level suggests that not all the provenances have the same radial variation pattern. The deviation between the value of the inner juvenile wood density and that of the outer juvenile wood density (DEND) is strongly negatively related to the outer juvenile wood density, whereas it is positively related to the inner juvenile wood density. Thus, provenances with homogeneous wood (low deviations) tend to have high outer juvenile wood density, while provenances with more heterogeneous wood (high deviations) tend to have the lowest outer juvenile wood densities. If the positive relationships that exist between the density of the annual ring sections and the average value of the trees in the Proulx plantation are corroborated in the provenance trial, it can be expected that, in the long term, the provenances with more homogeneous wood, and thus the highest outer juvenile wood densities, will have a higher average tree density.

Partition of intra- and inter-provenance variation

The presence of a significant provenance-block interaction is an indication of the influence of the microsite conditions on the provenance yield. This significant interaction makes it impossible to draw conclusions about the effect of individual factors on the characteristics as a whole. It is possible, however, to identify some provenances belonging to the superior group in all the blocks, despite their change in rank.

In addition, for these characteristics, most of the variation occurs among the trees of a single plot. Indeed, its variance component accounts for 65 to 85% of the total variation. The strong individual variations suggest that mass selection should be used to improve the wood density of Norway spruce. This type of variation is well-known in conifers. Hence, Zobel et al. (1972), in a study on the density of the wood of southern pines, have noted that the most significant changes in wood density are achieved through selection of superior individuals rather than through selection of provenances. The results of Corriveau et al. (1990) have also confirmed the relevance of individual selection based on wood density in fast-growing populations for the production of genetically improved wood.

The morphological and allozymic studies conducted by Lagercrantz and Ryman (1990) have identified three possible refuges for Norway spruce ranging from southwestern to northeastern Europe during the last ice age some 10,000 years ago. On the basis of these results, we did an a priori comparison to determine whether the provenances from southwestern Europe (Germany, Poland, Romania) differed from those from northeastern Europe (Latvia, Lithuania, Belorussia). The results of the contrasts showed that the deviation between the inner juvenile wood density and that of the outer juvenile wood differed significantly between the southwestern European provenances and the northeastern provenances. The western provenances (Germany, Poland, Romania) have high density deviations, whereas the eastern provenances (Latvia, Lithuania, Belorussia) show low density deviations. Similarly, the deviation between the width of the inner juvenile rings and that of the outer juvenile rings differs significantly between the two groups of provenances, with density deviation and ring width deviation increasing inversely while still being linked to growth conditions. Significant differences are also found in the outer juvenile wood density, with the provenances from the Baltic region having the highest outer juvenile wood densities. The provenances from Latvia, Lithuania and Belorussia come from regions with climate conditions similar to those of Quebec. They are therefore well adapted to the climate conditions of the experimental site, and this can be seen from a lower variation in juvenile wood density and a higher outer juvenile wood density.

The high proportion of juvenile wood in plantation-grown trees is known to cause problems for the veneer and lumber industries (Bendtsen 1978; Senft et al. 1985). Any means of reducing the proportion or improving the characteristics of juvenile wood, such as reducing the variation in wood density or decreasing the average value of wood density, represents an opportunity for improving the quality of plantation-grown wood.

Impact of selection for vigor on wood density

Selections based solely on vigor criteria were made in the past for the local improvement program in the provenance trial under study.

An examination of the results of a three-stage selection (see Table 5) shows the resulting gains in wood density, diameter, height growth, and volume yield of the trees.

In the first selection stage, 9 of the 19 provenances of known origin were chosen for height growth and volume yield. This type of selection offers hope of an increase in height growth and volume yield of the order of 10 and 14%,

TABLE 5. *Comparative results of a three-stage selection and deviations between the overall average and the average of the provenances and trees selected for the various characteristics of the Norway spruce provenances established in Valcartier, Quebec.*

	DIA (cm)	IJD (kg/m³)	OJD (kg/m³)	JUVD (kg/m³)	DEND (kg/m³)	HEIGHT (m)	VOL (dm³)
Overall average	8.5	363	341	355	22	6.7	23.0
Stage 1 of selection[1]	9.0	357	343	352	13	7.4	26.3
Deviation[2]	+6%	−2%	+1%	−1%	−41%	+10%	+14%
Stage 2 of selection[3]	12.0	348	331	342	18	9.3	53.8
Deviation[4]	+33%	−3%	−3%	−3%	+38%	+26%	+104%
Stage 3 of selection[5]	11.6	358	345	353	13	9.1	49.1
Deviation[6]	+29%	0%	+1%	0%	0%	+23%	+87%

DIA: diameter at breast height; IJD: inner juvenile wood density; OJD: outer juvenile wood density; JUVD: juvenile wood density; DEND: deviation between inner juvenile wood density and outer juvenile wood density; HEIGHT: total height; VOL: volume per tree.

[1] Average values of 9 selected provenances.

[2] Deviation of average between stage 1 of selection and overall average of trees in provenance trial.

[3] Average values of 75 individuals selected according to height.

[4] Deviation of average between stage 2 and stage 1 of selection.

[5] Average values of 43 individuals selected according to wood density.

[6] Deviation of average between stage 3 and stage 1 of selection.

respectively. It also reduces the deviation between the inner juvenile wood density and the outer juvenile wood density by 41%, as provenances with strong height growth produce wood with more homogeneous density. It also helps to maintain a juvenile wood density equal to the average, indicating an absence of link between height growth of the provenances and average juvenile wood density.

In the second selection stage, 75 trees from the 9 provenances chosen in the first stage were selected on the basis of height growth, diameter, stem and crown quality, and insect and disease-resistance criteria. This selection resulted in a twofold increase in volume yield but reduced wood density by some 3% and increased the density deviation by 38% compared with the average of the selected provenances. This type of selection reduces the quality of the wood, mainly the homogeneity of the juvenile wood density, which is not desirable.

In the third and last stage, we selected 43 trees from the 75 already selected, choosing only those having a juvenile wood density greater than a standard deviation below the overall average and a wood density deviation less than a standard deviation above the overall average. This group of 43 trees, with an average juvenile wood density and an average deviation between inner juvenile wood density and outer juvenile wood density equal to the average of the nine provenances selected in the first stage, shows an improvement in the order of 23% for height growth and 87% for volume yield. Thus, these results show that if wood quality characteristics are taken into account, it should be possible to maintain appreciable gains in height growth and volume yield without sacrificing wood quality characteristics. In doing so, we reduce the genetic basis of the breeding population as compared with that developed in the second stage of sampling. More selection work should be done to restore the size of the breeding population and more emphasis should be put on maintaining the level of expected gains.

CONCLUSIONS

The wood density radial variation pattern for Norway spruce is similar to that observed for white spruce grown in plantations (Corriveau et al. 1990). This radial variation pattern between trees is sufficiently constant to make relatively accurate predictions ($R^2 = 0.64$) about the average wood density of a 70-year-old tree on the basis of the juvenile wood density of the first 15 annual rings near the pith. A mass selection of young Norway spruce grown in plantations in Quebec can thus be made with sufficient confidence. It is recommended, however, that this selection be made among provenances with high volume yield.

The results also show that annual ring width is negatively linked to wood density at the individual as well as at the provenance level. But since this relationship is moderate, individuals deviating from this general tendency and having a high radial growth rate and high wood density can be identified.

On the basis of these results, a three-stage selection strategy applied to the material under study produced the following gains: the selection of the nine provenances with strong height growth (first stage) makes it possible to maintain the juvenile wood density, reduce by 41% the deviation between the inner juvenile wood density and the outer juvenile wood density, and increase height growth by 10% and volume output by 14%. A mass selection based on height growth (second stage) and wood density (third stage) within the selected provenances produced a group of individuals having a juvenile wood density and a deviation between the inner juvenile wood density and the outer juvenile wood density equal to the average of the selected provenances. It also produced height growth and volume output of 23% and 87% greater than the average of the selected provenances. These results are an indication of the productivity and wood quality potential of the Norway spruce grown in plantations in Quebec.

This kind of improvement program would make it possible to maintain the superior wood quality of Norway spruce while increasing its volume yield in order to maximize returns from reforestation programs.

ACKNOWLEDGMENTS

We wish to acknowledge the assistance of the following organizations and persons: the Natural Sciences and Engineering Research Council of Canada (NSERC) for the graduate studies grant awarded to Donald Blouin, under which a part of this work was carried out; the Wood Science Department of Université Laval for the technical support received for laboratory work; the Canadian Forest Service–Quebec Region for having made available the material from the Valcartier provenance trial facility and for their technical help; the Stone Consol company for having made available the mature tree material from the Proulx plantation at Grand-Mère; Ariane Plourde, project leader at the Canadian Forest Service–Quebec Region, and Michel Beaudoin, professor in the Wood Science Department of Université Laval, for their recommendations on the first draft of the manuscript; and Professor Robert Krahmer and an anonymous reviewer for their valuable comments.

REFERENCES

ANONYMOUS. 1992. Mise à l'essai des classes de bois de l'épinette de Norvège. For. Tech., Forestry Canada—Maritimes Region. 2(3):1 and 8.

BEAULIEU, J., AND A. CORRIVEAU. 1985. Variabilité de la densité du bois et de la production des provenances d'épinette blanche, 20 ans après plantation. Canadian J. Forest Res. 15:833–838.

BENDTSEN, B. A. 1978. Properties of wood from improved and intensively managed trees. Forest Prod. J. 28(10):61–72.

CAMIRAND, R., C. CAMIRÉ, AND B. BERNIER. 1983. Performance of *Picea abies* (L.) Karst. in plantation in Quebec, Canada: II. Nutrition–growth relationships. Plant Soil 73:17–26.

CHANG, C. I., AND R. W. KENNEDY. 1967. Influence of specific gravity and growth rate on dry wood production in plantation-grown white spruce. Forest. Chron. 43(1): 165–173.

CLARK, A., AND J. R. SAUCIER. 1991. Influence of planting density, intensive culture, geographic location, and species on juvenile wood formation in southern pine. Georgia Forest Research Paper, Athens, GA.

COMITÉ D'AMÉLIORATION GÉNÉTIQUE DES ARBRES FORESTIERS DU QUÉBEC (CAGAFQ). 1983. Amélioration génétique des essences résineuses au Québec: Recherche et développement. A. Corriveau et G. Vallée, eds. Service canadien des forêts et ministère de l'Énergie et des Ressources du Québec, Sainte-Foy, Québec, Canada.

CORRIVEAU, A., J. BEAULIEU, AND G. DAOUST. 1988. Phenotypic stability and productivity of Central European Norway Spruce provenances in Quebec, Canada. IUFRO working party S 2.02-11 meeting, Tjornarp, Sweden (unpublished).

———, ———, AND ———. 1991. Heritability and genetic correlations of wood characters of Upper Ottawa Valley white spruce populations grown in Quebec. Forest. Chron. 67(6):698–705.

———, ———, AND F. MOTHE. 1987. Wood density of natural white spruce populations in Quebec. Canadian J. Forest Res. 17:675–682.

———, ———, ———, J. POLIQUIN, AND J. DOUCET. 1990. Densité et largeur des cernes des populations d'épinettes blanches de la région forestière des Grands Lacs et du Saint-Laurent. Canadian J. Forest Res. 20: 121–129.

DAOUST, G., J. BEAULIEU, AND A. CORRIVEAU. 1987. Rooting ability of cuttings from sexually mature Norway spruce. Canadian Forestry Service, Laurentian Forestry Centre, Sainte-Foy, Québec, Canada. Information Report LAU-X-75.

ELLIOTT, G. K. 1970. Wood density in conifers. Commonwealth Agricultural Bureaux, Technical Communication No. 8, Oxford, England.

JESSOME, A. P. 1977. Résistance et propriétés connexes des bois indigènes au Canada. Laboratoire des produits forestiers de l'Est. Rapport technique de foresterie No. 21, Ottawa, Ontario, Canada.

KEITH, C. T. 1961. Characteristics of annual rings in relation to wood quality in white spruce. Forest Prod. J. 11(3):122–126.

KENNEDY, R. W. 1966. Intra-increment variation and heritability of specific gravity, parallel-to-grain tensile strength, stiffness, and tracheid length, in clonal Norway spruce. Tappi 49(7):292–300.

KEYLWERTH, R. 1954. A contribution to qualitative growth analysis. Holz Roh-Werkst. 12(3):77–83 (taken from Smith 1954).

LAGERCRANTZ, U., AND N. RYMAN. 1990. Genetic structure of Norway spruce (*Picea abies*): Concordance of morphological and allozymic variation. Evolution 44(1): 38–53.

LARSON, P. R. 1969. Wood formation and the concept of wood quality. Yale University School Forest Bulletin No. 74, New Haven, CT.

MACARTHUR, J. D. 1964. Norway spruce plantations in Québec. Canadian Department of Forestry. Forest Research Branch. Publication No. 1059, Ottawa, Ontario, Canada.

NEPVEU, P., AND Y. BIROT. 1979. Les corrélations phénotypiques juvénile-adulte pour la densité du bois et la vigueur chez l'épicéa. Annales des Sciences Forestières 36(2):125–149.

OLESEN, P. O. 1976. The interrelation between basic density and ring width of Norway spruce. Forstlige Forsogsvaesen i Danmark 34(4):339–359.

———. 1977. The variation of the basic density level and tracheid width within the juvenile and mature wood of Norway spruce. Forest tree improvement, Arboretet Horsholm, Denmark, No. 12.

PANSHIN, A. J., AND C. DEZEEUW. 1980. Textbook of wood technology, 4th ed. McGraw-Hill Book Co., New York, NY.

PARADIS, C. 1991. Programme de surveillance dans les plantations. Pages 14–17 *in* Insectes et maladies des arbres. Service de la protection contre les insectes et les maladies, ministère des Forêts, and Forestry Canada, Laurentian Forestry Centre, Sainte-Foy, Québec, Canada.

POLGE, H. 1964. Le bois juvénile des conifères. Revue Forestière Française 6:474–505.

SAS INSTITUTE INC. 1988a. SAS user's guide: Statistics, version 6.03 edition. SAS Institute Inc., Cary, NC.

———. 1988b. SAS user's guide: Basic, version 6.03 edition. SAS Institute Inc., Cary, NC.

SELL, J., AND F. KROPF. 1990. Propriétés et caractéristiques des essences de bois. Lignum, Union suisse en faveur du bois, Le Mont, Suisse.

SENFT, J. F., B. A. BENDTSEN, AND W. L. GALLIGAN. 1985. Weak wood, fast-grown trees make problem lumber. J. Forestry 83(8):477–484.

SMITH, D. M. 1954. Maximum moisture content method for determining specific gravity of small wood samples. USDA Forest Products Laboratory, Forest Science No. 2014.

WANG, E. I. C., T. MUELLER, AND M. M. MICKO. 1985. Drainage effect on growth and wood quality of some bog-grown trees in Alberta. Forest. Chron. 61(6):489–493.

WRIGHT, S. P. 1992. Adjusted *P*-values for simultaneous inference. Biometrics 48:1005–1013.

ZOBEL, B. J. 1961. Inheritance of wood properties in conifers. Silvae Genetica 10(3):65–70.

———, R. C. KELLISON, M. F. MATTHIAS, AND A. V. HATCHER. 1972. Wood density of the southern pines. Technical Bulletin No. 208. School of Forest Resources, North Carolina State University, Raleigh, NC.