

RELATIONSHIPS BETWEEN WOOD DENSITY AND ANNUAL GROWTH RATE COMPONENTS IN BALSAM FIR (*ABIES BALSAMEA*)

*Shinya Koga*¹

Visiting Scientist

and

S. Y. Zhang†

Research Scientist and Group Leader
Resource Assessment and Utilization Group
Forintek Canada Corp.
319 rue Franguet
Sainte-Foy, Quebec
Canada G1P 4R4

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ABSTRACT

This study examined relationships of wood density components with annual growth rate components (or annual ring width components) in juvenile wood and mature wood of balsam fir [*Abies balsamea* (L.) Mill.]. The relationships were studied at two different levels: 1) inter-tree level (between trees), and 2) intra-tree level (within a tree). In addition, juvenile-mature wood correlations for these characteristics were investigated. Wood density and annual ring width components of individual growth rings were measured by X-ray densitometry. Based on tree averages (at the inter-tree level), wood density is significantly correlated with its components (earlywood density, latewood density) and latewood percentage in both juvenile wood and mature wood; and earlywood density and latewood percentage are the two most important parameters in determining the overall wood density of the tree. Wood density, however, is not significantly correlated with annual growth rate (ring width) in either juvenile wood or mature wood, although a weakly negative correlation tends to strengthen in mature wood. This suggests that the relationship between wood density and annual growth rate in this species may vary with cambial age. Intra-ring wood density variation (IDV) shows a positive correlation with wood density traits, latewood width, and latewood percentage in both juvenile wood and mature wood, whereas a weakly negative correlation of IDV with ring width and earlywood width exists in balsam fir. Latewood traits are the most important parameters in determining the intra-ring wood density uniformity. At the intra-tree level (based on ring averages within a tree), relationships between wood density components and ring width components are similar to those found between the trees, although some relationships, to some extent, vary with tree. For each wood density trait, the juvenile-mature wood correlation is significant but moderate. For this species, earlywood density in juvenile wood seems to be the best parameter for predicting mature wood density.

Keywords: Balsam fir, wood density, ring width, earlywood, latewood, juvenile wood, mature wood, variation, correlation.

INTRODUCTION

Balsam fir [*Abies balsamea* (L.) Mill.] is one of the most important commercial species in eastern Canada and northeastern United

States. The wood of this species is used mainly for lumber production. Balsam fir lumber in Northern America is marketed with spruces and pines as Spruce-Pine-Fir lumber (Mullins and McKnight 1981). Among the S-P-F group, balsam fir has the lowest wood density and strength properties. Wood density in balsam fir is 17.5% and 21.4% lower than in black spruce and jack pine, respectively; and mod-

¹ Present Address: Department of Forest and Forest Products Sciences, Graduate School of Agriculture, Kyushu University, Tsubakuro 394, Sasaguri, Kasuya, Fukuoka, JAPAN 811-2415.

† Member of SWST.

ulus of rupture (MOR) in this species is 25.5% and 15.8% lower than in black spruce and jack pine, respectively (Jessome 2000).

As the forest industry in eastern Canada moves toward intensive silviculture, balsam fir has become a preferred species for precommercial thinning. Over the past decade, hectares of balsam fir stands thinned precommercially have increased dramatically in eastern Canada. This silvicultural treatment applied to young and dense balsam fir stands is intended primarily to accelerate the diameter growth of individual trees and shorten rotation age (Zarnovican and Laberge 1996). With large spacing and accelerated growth rate, wood quality of thinned balsam fir stands has become a concern in recent years. Since balsam fir wood is remarkably weaker than other species in the S-P-F group, any significant decrease in wood quality in this species may make this species too different from the others in the group. In 1995, a multidisciplinary project was initiated by Forintek to examine the impact of precommercial thinning on tree and wood characteristics, product quality, and value recovery in balsam fir (Zhang et al. 1998).

Effect of faster growth on wood quality has been a subject of great interest, and numerous studies have investigated the relationship between growth rate and wood density in many commercial species. However, very limited studies have investigated the effect of faster growth rate on wood quality in balsam fir. Zobel and van Buijtenen (1989) concluded that a negative relationship between growth rate and wood density was common for some genera including *Abies*, although this generalization has many exceptions. Kennedy (1995) noted that there seemed to be a negative relationship for *Abies* species in the Pacific Northwest. Zhang (1995) reported a negative correlation of growth rate with wood density and selected mechanical properties in two *Abies* species. Although previous studies suggest that there may exist a negative correlation between ring width and wood density in balsam fir, the intrinsic relationship between annual growth rate and wood quality is not well un-

derstood in this important commercial species. It is well known that the relationship between growth rate and wood quality within a species may vary with provenance (Dorn 1969), family (Abdel-Gadir et al. 1993; Zhang et al. 1996; Zhang 1998), cultivars (Koga et al. 1997), cambial age (Keith 1961; Zobel and van Buijtenen 1989; Zhang 1998; Koubaa et al. 2000), location (Hall 1984; Zhang 1998; Abdel-Gadir et al. 1993), silvicultural manipulations (Zobel and van Buijtenen 1989; Koga et al. 1996), and wood quality attributes (Zobel and van Buijtenen 1989; Zhang 1995).

As part of that multidisciplinary project, this study was intended to better understand the relationship between annual growth rate and wood density, one of the most important wood quality attributes in this species. To this end, this research thoroughly studied the intrinsic relationships of wood density components with annual ring width components (annual growth rate components). The relationships were examined at two different levels: 1) inter-tree level (between trees), and 2) intra-tree level (within a tree). In this study, juvenile wood and mature wood were investigated separately to see whether there is any difference in the relationships between juvenile wood and mature wood. In addition, juvenile-mature wood correlations were analyzed for each characteristic to evaluate the possibility for early selection. In another paper (Koga et al. 2001), effects of precommercial thinning on both annual growth and wood density in balsam fir were investigated.

MATERIALS AND METHODS

Materials used for this study came from a precommercial thinning trial located in the Bas Saint-Laurent Region of Québec. The trial was naturally regenerated from a clearcutting in 1955. At the end of the growing season in 1969, plots of heavy thinning, moderate thinning, and control were established. In the heavy thinning plots, all trees within a distance of 7 feet around each residual tree were removed; in the moderate thinning plots, all

trees within a distance of 5 feet around each residual tree were removed. The control plots had a stand density of approximately 20,000 trees/ha in 1969. At the beginning of the growing season in 1993, 18 sample trees (6 trees/plot) were collected from each thinning intensity as well as the control plots. In total, 54 sample trees ranging from 10 to 18 cm at the diameter of breast height were collected for this study. From each sample tree, a 4-cm-thick disk was collected at breast height for X-ray densitometry study. For further information on the trial and sample trees collected, refer to Schneider (2001).

A radial segment from pith to bark (1 cm longitudinally \times 1 cm tangentially \times radius) was removed from each disk at the north direction. The segments were trimmed to about 1.57-mm-thick (longitudinal) strips with a specially designed pneumatic-carriage twin-bladed saw. The sawn strips were extracted with cyclohexane/ethanol (2:1) solution for 24 h and then with hot water for another 24 h to remove extraneous compounds. After the extraction, the strips were air-dried under restraint to prevent warping. Using a direct reading X-ray densitometer, the air-dried strips were scanned to determine the basic wood density (oven-dry weight/green volume) for each ring from the pith to bark. The first few rings near the pith were excluded because they were so narrow that densitometry analysis could not be performed for these rings. Based on the densitometric profiles, earlywood and latewood boundary in each ring was defined by a predetermined fixed basic wood density (540 kg/m^3) as explained by Jozsa et al. (1987). Various ring width parameters (ring width, earlywood width, latewood width, latewood percentage) and ring density parameters (e.g., earlywood density, latewood density, and average wood density of individual growth rings) were obtained for each ring scanned.

The boundaries of juvenile wood (until the 15th ring from the pith) and mature wood (from the 21st ring to the outermost ring) in this species were determined, based on the ra-

dial pattern of variation in wood density. Based on ring width and wood density data on individual growth rings from the pith to bark in each tree, weighted averages of wood density, earlywood density, and latewood density were computed for juvenile wood, mature wood, and whole tree as described by Barbour et al. (1992). Latewood percentage for each strip (tree) was calculated based on the total latewood width of the growth rings divided by the total width of the rings. In addition, intraring wood density variation was estimated using the equation given by Vargas-Hernandez and Adams (1991).

In total, eight characteristics were measured: ring width (RW) and its components including earlywood width (EW) and latewood width (LW), latewood percentage (LWP), wood density (WD) and its components including earlywood density (ED) and latewood density (LD), and the intra-ring wood density variation (IDV). For correlations between each pair of these characteristics at the inter-tree level (between trees), analyses were based on the tree average data for these characteristics in the 54 sample trees. Ring average data for these characteristics within a tree were used to calculate correlations at the intra-tree level (within a tree). All statistical analyses were performed using the Statistical Analysis System procedures (SAS Institute 1988).

RESULTS AND DISCUSSION

Variations between trees

Table 1 shows means and variations of eight characteristics for juvenile wood, mature wood, and whole tree in the 54 balsam fir trees. The mean basic wood density for the whole tree (351 kg/m^3) is slightly higher than that (335 kg/m^3) reported previously for this species (Jessome 2000). Ring width and earlywood width in juvenile wood are significantly larger than those in mature wood, but latewood percentage in juvenile wood is significantly lower than that in mature wood, although there are no differences in latewood

TABLE 1. Mean, standard deviation, and coefficient of variation of the eight characteristics in the 54 balsam fir sample trees.

Characteristic ¹	Juvenile wood			Mature wood			Whole tree		
	Mean	SD ²	CV ³	Mean	SD	CV	Mean	SD	CV
RW (mm)	2.58	0.54	20.7	1.47	0.40	26.9	2.06	0.36	17.5
EW (mm)	2.34	0.52	22.4	1.22	0.35	28.6	1.82	0.34	18.5
LW (mm)	0.24	0.07	27.3	0.24	0.07	29.1	0.24	0.06	24.1
LWP (%)	9.5	2.7	28.9	16.8	3.8	22.4	11.8	2.5	21.4
WD (kg/m ³)	335	23	6.8	359	38	10.5	351	21	5.9
ED (kg/m ³)	316	17	5.3	318	17	5.2	317	14	4.5
LD (kg/m ³)	552	23	4.2	574	26	4.5	564	22	3.9
IDV (kg/m ³)	70	11	16.1	99	12	12.6	79	10	12.4

¹ RW: ring width; EW: earlywood width; LW: latewood width; LWP: latewood percentage; WD: wood density; ED: earlywood density; LD: latewood density; IDV: intraring wood density variation.

² SD: standard deviation.

³ CV: coefficient of variation (%).

width between juvenile and mature wood. On the other hand, earlywood densities in juvenile wood and mature wood are quite comparable, although latewood density and wood density in mature wood are slightly higher than those in juvenile wood. This agrees with reports by Zobel and van Buijtenen (1989) and Kennedy (1995) that genus *Abies* generally has a radial pattern of very limited change in wood density from the pith to bark. Intra-ring wood density variation in the whole tree (79 kg/m³) is a little bit higher in balsam fir than in black spruce (58 kg/m³) (Zhang 1998), but considerably lower than in Douglas-fir (198 kg/m³) (Vargas-Hernandez and Adams 1991). This means that balsam fir shows a slightly larger variation in wood density within a growth ring than black spruce, but a smaller variation than Douglas-fir. As a result of a higher latewood density in mature wood, the intra-ring wood density variation in mature wood is significantly larger than that in juvenile wood (Table 1).

Variations in wood density and its components (ED, LD) among the 54 trees are quite comparable between juvenile and mature wood (Table 1). The coefficient of variation for wood density of the whole tree is almost equal to that reported by Jessome (2000). Compared to ring width and its components (EW, LW), wood density traits show a considerably smaller variation; the coefficients of variation for wood density traits are less than 11%, whereas the coefficients for ring width

and its component range from 21 to 29%. The same case was reported for other species (Jourdain and Olson 1984; Magnussen and Keith 1990; Park et al. 1989; Zhang et al. 1996; Zhang and Jiang 1998). Of the eight characteristics studied, latewood percentage and intra-ring wood density variation show an intermediate variation.

Correlations between trees

The present study examined only phenotypic correlations because the trial where the sample trees were collected has no genetic structure. Table 2 shows the correlation coefficients between all pairs of the eight characteristics in juvenile wood (upper triangle) and mature wood (lower triangle). In juvenile wood, ring width is positively correlated with both earlywood width and latewood width. But, its correlation with earlywood width ($r = 0.99$) is much stronger than with latewood width ($r = 0.29$). This suggests that in the juvenile wood of balsam fir, earlywood width is critically important in determining the ring width. In fact, earlywood width alone explains 98% (r^2) of the variation in ring width. Table 2 also shows that in juvenile wood, earlywood width is not significantly correlated with latewood width. As a result, a significantly negative correlation between ring width and latewood percentage ($r = -0.49$) was found. The above correlations between ring width and its components

TABLE 2. Coefficients of correlation (p-value given in parentheses) between all pairs of the eight characteristics measured in juvenile wood (upper triangle) and mature wood (lower triangle).

Characteristic ¹	RW	EW	LW	LWP	WD	ED	LD	IDV
RW		0.99 (0.0001)	0.29 (0.0317)	-0.49 (0.0002)	-0.10 (0.4943)	-0.15 (0.268)	0.01 (0.9367)	-0.32 (0.0191)
EW	0.98 (0.0001)		0.18 (0.1954)	-0.58 (0.0001)	-0.18 (0.1967)	-0.25 (0.0737)	-0.05 (0.7384)	-0.39 (0.0038)
LW	0.66 (0.0001)	0.55 (0.0001)		0.66 (0.0001)	0.67 (0.0001)	0.70 (0.0001)	0.49 (0.0002)	0.54 (0.0001)
LWP	-0.46 (0.0004)	-0.57 (0.0001)	0.33 (0.0159)		0.67 (0.0001)	0.76 (0.0001)	0.46 (0.0005)	0.75 (0.0001)
WD	-0.21 (0.1246)	-0.32 (0.0198)	0.29 (0.0345)	0.58 (0.0001)		0.83 (0.0001)	0.40 (0.003)	0.39 (0.0033)
ED	-0.32 (0.0177)	-0.42 (0.0016)	0.30 (0.0302)	0.80 (0.0001)	0.58 (0.0001)		0.35 (0.0093)	0.36 (0.0073)
LD	0.51 (0.0001)	0.42 (0.0015)	0.73 (0.0001)	0.21 (0.134)	0.31 (0.0239)	0.19 (0.1794)		0.83 (0.0001)
IDV	0.17 (0.2258)	0.05 (0.69555)	0.62 (0.0001)	0.46 (0.0005)	0.43 (0.0011)	0.21 (0.1309)	0.79 (0.0001)	

¹ RW: ring width; EW: earlywood width; LW: latewood width; LWP: latewood percentages; WD: wood density; ED: earlywood density; LD: latewood density; IDV: intra-ring wood density variation.

in juvenile wood hold true in mature wood except for a significantly positive relationship between earlywood width and latewood width in mature wood (Table 2).

Wood density is positively correlated with earlywood density, latewood density, and latewood percentage in juvenile wood (Table 2). Wood density in juvenile wood (or juvenile wood density) shows the strongest correlation with earlywood density ($r = 0.83$), followed by latewood percentage ($r = 0.40$) and latewood density ($r = 0.39$). Earlywood density alone explains 69% (r^2) of the variation in juvenile wood density. These relationships hold true in mature wood as well. In mature wood, however, the correlation of wood density with latewood percentage ($r = 0.58$) is comparable to that of wood density with earlywood density. These results indicate that in this species, a positive correlation of wood density with its components (ED, LD) and latewood percentage exists in both juvenile wood and mature wood; but the magnitude of the correlation may differ between juvenile wood and mature wood. A similar case was found in black spruce (Zhang 1998; Koubba et al. 2000). Overall, this study indicates that for balsam fir, earlywood density and latewood percentage are the most important parameters in determining the overall wood density of the tree.

In the juvenile wood of balsam fir, earlywood density has a significantly positive correlation with latewood density ($r = 0.35$, $p = 0.0093$), but no significant correlation between earlywood density and latewood density ($r = 0.19$, $p = 0.18$) exists in mature wood (Table 2). The same result was found in black spruce (Koubba et al. 2000). However, a negative relationship between earlywood density and latewood density was reported in the juvenile wood of black spruce (Zhang and Morgenstern 1995) and in both juvenile wood and mature wood of Douglas-fir (Abdel-Gadir et al. 1993).

Wood density in balsam fir is not significantly correlated with ring width in either juvenile wood ($r = -0.1$) or mature wood ($r = -0.21$), although a weakly negative correlation tends to strengthen in mature wood (Table

2). Earlywood density is negatively correlated with earlywood width and ring width in both juvenile wood and mature wood, but only in mature wood the correlations ($r = -0.42$ and -0.32 , respectively) are statistically significant. Furthermore, latewood density shows no correlation with ring width in juvenile wood ($r = 0.01$), but a significantly positive correlation in mature wood ($r = 0.50$). Latewood density and latewood width show a strongly positive correlation in both juvenile wood ($r = 0.49$) and mature wood ($r = 0.73$). Based on these results, the insignificant correlation between wood density and ring width in juvenile wood could be explained; earlywood density, which is the most important parameter in determining wood density in juvenile wood, is not significantly correlated with ring width despite a negative correlation between latewood percentage and ring width. The tendency to a weakly negative relationship in mature wood could also be explained, because latewood percentage and earlywood density, which are the two most important parameters in determining mature wood density, are strongly and negatively correlated with ring width; but latewood density shows a significantly positive correlation with ring width. As mentioned before, Zobel and van Buijtenen (1989) and Kennedy (1995) concluded that for the genus *Abies* wood density generally tended to decrease with increasing ring width. Zhang (1995) found that two *Abies* species tended to have a negative correlation between ring width and wood density. In the present study, only the results for mature wood agree with those reports. Keith (1961), Zhang (1998), and Koubba et al. (2000) reported that the correlation between wood density and growth rate in black spruce tended to weaken with cambial age. Although our result is in contrast with these reports, the relationship between wood density and growth rate in balsam fir also seems to vary with cambial age. In other words, the negative correlation tends to increase with cambial age from juvenile wood to mature wood. In spite of the tendency to a weakly negative relationship in mature wood,

TABLE 3. Percentages of the trees which have a significantly (S), non-significantly (NS) positive or negative correlation between each pair of the characteristics in juvenile wood and mature wood.

	Juvenile wood				Mature wood			
	Negative		Positive		Negative		Positive	
	S (%)	NS (%)	NS (%)	S (%)	S (%)	NS (%)	NS (%)	S (%)
RW × EW	0	0	0	100	0	0	0	100
RW × LW	6	28	51	15	0	11	46	43
RW × LWP	63	28	9	0	89	9	2	0
EW × LW	6	39	46	9	0	26	59	15
RD × ED	0	0	0	100	0	0	2	98
RD × LD	6	22	50	22	0	0	37	63
RD × LWP	0	4	41	55	0	0	0	100
ED × LD	7	46	41	6	2	24	55	19
RW × RD	15	33	48	4	54	46	0	0
RW × ED	7	20	54	19	31	46	23	0
EW × ED	9	26	48	17	41	46	13	0
RW × LD	24	50	24	2	0	28	61	11
LW × LD	0	19	46	35	0	0	6	94
IDV × RW	46	48	6	0	28	56	9	7
IDV × EW	70	22	8	0	48	39	11	2
IDV × LW	0	24	37	39	0	0	7	93
IDV × LWP	0	4	16	80	0	2	11	87
IDV × RD	11	26	48	15	0	0	17	83
IDV × ED	24	52	17	7	2	28	55	15
IDV × LD	0	0	13	87	0	0	0	100

it appears to be of no practical importance because the correlation coefficient ($r = -0.21$) is quite low (Table 2). Overall, this study suggests that faster growth rate would not reduce wood density significantly in this species.

Intra-ring wood density variation (IDV) is moderately and positively correlated with wood density in both juvenile wood ($r = 0.39$) and mature wood ($r = 0.43$), as shown in Table 2. This means that trees with a higher wood density have a larger intra-ring wood density variation. IDV is also positively correlated with wood density components (ED, LD) in both juvenile and mature wood, and its correlation with latewood density is remarkably strong in both juvenile wood ($r = 0.83$) and mature wood ($r = 0.79$). This suggests that IDV, to a large extent, depends on the latewood density. The correlations of IDV with latewood width and latewood percentage are strongly positive in both juvenile and mature wood, while its correlation with ring width and earlywood width is weakly negative

in juvenile wood or insignificant in mature wood.

Correlations within a tree

Table 3 lists percentages of the trees that have a significantly or non-significantly positive or negative correlation between each pair of the eight characteristics studied. Relationships of ring width with its components and latewood percentage within a tree seem to follow the same tendency as those found between the trees (Table 2). As shown in Table 3, a significantly positive correlation between ring width and earlywood width was found in all the 54 trees studied (100%). This applies to both juvenile wood and mature wood (on average, $r = 0.99, 0.99$, respectively). Most trees also show a positive correlation between ring width and latewood width in both juvenile wood and mature wood (on average, $r = 0.16, 0.32$, respectively). A moderately negative correlation between ring width and latewood

percentage was observed in both juvenile and mature wood of over 90% of the trees studied (on average, $r = -0.57, -0.63$, respectively). There is an insignificant correlation between earlywood width and latewood width in both juvenile wood and mature wood of most trees. An insignificant correlation in mature wood within a tree is different from that found between the trees (Table 2).

As shown in Table 3, almost all trees have a strongly positive correlation between ring density and earlywood density in both juvenile and mature wood (on average, $r = 0.90, 0.79$, respectively), whereas between ring density and latewood density, most trees show a positive correlation in juvenile wood and mature wood (on average, $r = 0.23, 0.51$, respectively), although a negative correlation was found in the juvenile wood of a small percent of the trees studied. Furthermore, almost all trees show a positive correlation between ring density and latewood percentage in both juvenile wood and mature wood (on average, $r = 0.55, 0.85$, respectively) although the correlation is insignificant in the juvenile wood of some trees. Overall, the relationships between ring density, and its components and latewood percentage within a tree seem to be in line with those at the inter-tree level (Table 2). Most trees show no correlation between earlywood density and latewood density in both juvenile wood and mature wood (Table 3). The result for juvenile wood is different from that found at the inter-tree level.

The relationships between wood density and ring width also vary with tree as well as cambial age. In mature wood, for example, 54% of the trees studied have a significantly negative correlation between ring width and wood density, whereas the remaining trees have a negative but insignificant correlation (on average, $r = -0.47$). In juvenile wood, an insignificant correlation was observed in most trees (on average, $r = 0.07$). In some trees, however, even a weakly positive correlation exists. The same case was found in black spruce (Zhang et al. 1996). As a whole, the correlation between ring width and wood den-

sity within a tree seems to be similar to that found between the trees, but the negative correlation in mature wood within a tree is stronger than that between the trees. The correlations of earlywood density with ring width and earlywood width in both juvenile and mature wood are similar to those of ring density with ring width (Table 3). On the other hand, a significant correlation between latewood density and ring width was not observed in either juvenile wood or mature wood of most trees; but between latewood density and latewood width, a significantly positive correlation or a tendency to a positive correlation was observed in both juvenile and mature wood of most trees (on average, $r = 0.33, 0.67$, respectively). Overall, the results indicate that wood density in juvenile wood is not affected significantly by growth rate within individual trees, but wood density in mature wood would be more affected by growth rate. Zhang et al. (1996) reported that the relationship between wood density and growth rate varied with family (genotype) and location. Since trees studied were obtained from one location only, further studies may be needed to verify these relationships in juvenile wood and mature wood.

Relationships between IDV and other traits within a tree are similar to those found between the trees. As shown in Table 3, most trees studied show a positive correlation between IDV and latewood traits (LW, LWP, and LD) in juvenile wood, and a positive correlation occurs in the mature wood of almost all trees. Most trees studied show a negative correlation of IDV with ring width and earlywood width in both juvenile and mature wood (Table 3). However, the relationships of IDV with ring density and earlywood density within individual trees are different from those found between the trees. In juvenile wood, most trees have an insignificant correlation between IDV and ring density. In mature wood, however, a significantly positive correlation or a tendency to a positive correlation was observed in all the trees studied (on average, $r = 0.63$). This suggests that increased ring density in juvenile wood may not affect the intra-ring uniformity.

In mature wood, however, increased ring density would increase the intra-ring wood density variation. Most trees studied show no relationship between IDV and earlywood density. Overall, this study indicates that in balsam fir, latewood traits (LW, LD, and LWP) are the most important parameters in determining the intra-ring variation, especially in mature wood.

Correlations between juvenile wood and mature wood

Breeding programs usually take many years to complete a cycle. Therefore, selections at an early age will reduce the length of breeding cycle and thus lead to being cost-effective. To pursue selections at an early age, it is important to understand the relationships between juvenile wood and mature wood. This study examined only phenotypic correlations between juvenile and mature wood in balsam fir. However, earlier studies (Corriveau et al. 1987; Zhang and Morgenstern 1995) found that the phenotypic correlations were similar to the genetic ones. Table 4 shows the phenotypic correlations for all pairs of the eight characteristics studied between juvenile and mature wood in balsam fir.

Correlations between juvenile and mature wood for each of the eight traits are all positive and statistically significant ($p < 0.01$). Among them, the juvenile-mature wood correlation for latewood width is the highest ($r = 0.71$); latewood width in juvenile wood explains 51% of the variation in latewood width in mature wood. The juvenile-mature wood correlation for either ring width or earlywood width is weak ($r = 0.38, 0.37$, respectively). The correlations for wood density traits (WD, ED, LD) and latewood percentage are moderate ($r = 0.41, 0.51, 0.57, 0.51$, respectively). The juvenile-mature wood correlation for wood density is appreciably weaker than those reported for other species including white spruce (Corriveau et al. 1987), black spruce (Koubaa et al. 2000), Norway spruce (Nepveu and Biron 1979; Blouin et al. 1994), and

Douglas-fir (Abdel-Gadir et al. 1993; Keller and Thoby 1977). Wood density in juvenile wood explains only 16% of the variation in mature wood density. This means that in balsam fir mature wood density cannot be predicted reliably from juvenile wood density.

In fact, either earlywood density or latewood percentage in juvenile wood is more closely correlated with mature wood density ($r = 0.54, 0.50$, respectively) than juvenile wood density. This indicates that in this species, earlywood density or latewood percentage in juvenile wood may serve as a better parameter than juvenile wood density to predict mature wood density, although the correlations are still moderate. It is particularly true for latewood percentage because that can be measured easily. On the other hand, mature wood density is weakly and negatively correlated with ring width in juvenile wood ($r = -0.30$). This suggests that selection for an increased growth rate in juvenile wood may result in a decrease in mature wood density.

As shown in Table 4, the juvenile-mature wood correlation for IDV is moderate ($r = 0.52$) and comparable to that for wood density traits (WD, ED, LD). IDV in mature wood is also moderately correlated with wood density traits (WD, ED, LD), latewood width, and latewood percentage in juvenile wood ($r =$ from 0.40 to 0.55). For IDV in mature wood, latewood density in juvenile wood serves as the best predictor, explaining 31% of the variation. On the other hand, IDV in mature wood tends to have a weakly negative correlation with ring width and earlywood width ($r = -0.20, -0.26$, respectively). It should be noted that selection for an increased growth rate in juvenile wood would result in a slight increase in the intra-ring uniformity in mature wood.

CONCLUSIONS

Based on the present study on balsam fir, the following conclusions can be drawn:

1. There are significant differences in means of ring width, earlywood width, latewood

TABLE 4. Juvenile-mature wood correlations for all pairs of the eight characteristics in balsam fir.*

	Juvenile wood				Mature wood			
	RW	EW	LW	LWP	WD	ED	LD	IDV
Ring width (RW)	0.38 (0.0048)	0.39 (0.0031)	0.19 (0.1785)	-0.26 (0.0565)	-0.30 (0.029)	-0.05 (0.7045)	0.05 (0.7353)	-0.20 (0.15)
Earlywood width (EW)	0.33 (0.0139)	0.37 (0.0061)	0.10 (0.4684)	-0.30 (0.025)	-0.36 (0.0083)	-0.09 (0.5045)	-0.01 (0.9251)	-0.26 (0.0569)
Latewood width(LW)	0.37 (0.0054)	0.29 (0.035)	0.71 (0.0001)	0.37 (0.0061)	0.30 (0.0259)	0.31 (0.0212)	0.45 (0.0007)	0.41 (0.0023)
Latewood percentage (LWP)	0.06 (0.666)	-0.02 (0.8598)	0.49 (0.0002)	0.51 (0.0001)	0.50 (0.0001)	0.29 (0.0333)	0.37 (0.0065)	0.52 (0.0001)
Wood density (WD)	0.13 (0.3393)	0.06 (0.6915)	0.50 (0.0001)	0.41 (0.0023)	0.40 (0.0024)	0.33 (0.0156)	0.40 (0.0025)	0.40 (0.0028)
Earlywood density (ED)	0.17 (0.2268)	0.07 (0.6087)	0.59 (0.0001)	0.51 (0.0001)	0.54 (0.0001)	0.51 (0.0001)	0.46 (0.0005)	0.44 (0.0008)
Latewood density (LD)	0.20 (0.1385)	0.15 (0.2703)	0.43 (0.0014)	0.23 (0.0941)	0.18 (0.1913)	0.11 (0.422)	0.57 (0.0001)	0.55 (0.0001)
Intra-ring wood density variation (IDV)	0.06 (0.6788)	0.00 (0.983)	0.35 (0.0087)	0.34 (0.012)	0.26 (0.055)	0.10 (0.4584)	0.42 (0.0018)	0.52 (0.0001)

* *p* value is given in parentheses.

- percentage, and IDV between juvenile wood and mature wood, whereas juvenile wood and mature wood are very comparable in means of latewood width and earlywood density.
2. Wood density and its components show a much smaller inter-tree variation than ring width and its components. Latewood percentage and IDV have an intermediate variation among the trees.
 3. For each wood density trait, the juvenile-mature wood correlation is significant but moderate. For this species, earlywood density in juvenile wood seems to be the best parameter for predicting mature wood density.
 4. Based on tree averages (at the inter-tree level), a significant correlation between ring width and its components exists in both juvenile and mature wood. Earlywood width is by far the most important parameter in determining ring width in balsam fir. In addition, a moderately negative correlation between ring width and latewood percentage exists in both juvenile and mature wood. Wood density, like ring width, is significantly correlated with its components and latewood percentage in both juvenile and mature wood. Earlywood density and latewood percentage are the two most important parameters in determining the overall wood density of the tree. Wood density, however, is not significantly correlated with annual growth rate (ring width) in both juvenile and mature wood, although a weakly negative correlation tends to strengthen in mature wood. IDV shows a positive correlation with wood density traits, latewood width, and latewood percentage, but a weakly negative correlation with ring width and earlywood width. Latewood traits (LW, LD, LWP) are the most important parameters in determining the intra-ring uniformity.
 5. Although most relationships between wood density and ring width components at the inter-tree level are comparable between juvenile and mature wood, relationships between limited characteristics are appreciably different between juvenile and mature wood. This suggests that some relationships may vary with cambial age in this species.
 6. Most relationships between wood density and ring width components within a tree (at the intra-tree level) are similar to those at the inter-tree level, although a negative relationship between wood density and annual growth rate in the mature wood of the tree seems to be stronger than that between the trees. Relationships between some of the wood density and ring width components within a tree, to some extent, vary with tree.

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