VARIATION IN THE RELATIONSHIP OF WOOD DENSITY WITH GROWTH IN 40 BLACK SPRUCE (*PICEA MARIANA*) FAMILIES GROWN IN NEW BRUNSWICK

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ABSTRACT

This study examined variation in the relationship of wood density with growth traits (DBH, tree height, and bole volume) in 15-year-old half-sib families of black spruce (*Picea mariana*) grown on two different sites located in northern New Brunswick. Effect of genotype and environment on wood density was also briefly discussed. Although a moderately negative relationship between wood density and growth generally exists, the relationship, to some extent, varies with genotype and environment. A nonsignificant or even a weak positive relationship between wood density and growth can be found in some families. Moreover, the negative relationship between wood density and growth appears to be weaker in families growing in a more favorable environment. This study indicates that it is possible to select some families that not only grow fast, but also maintain high wood density.

Keywords: Black spruce, wood density, growth traits, dry mass weight, variation, correlation, family, environment.

INTRODUCTION

With the steadily increasing proportion of improved and intensively managed plantations, and the move in forest management to shorter rotations, wood and fiber quality has become one of the major concerns in the forest products industry throughout the world (Bendtsen 1978; Kellogg 1989; Vargas-Hernandez and Adams 1991; Zhang 1994). Faced with this concern, tree breeders have realized that wood quantity and quality cannot be treated as independent factors, and therefore wood quality traits should be incorporated into any tree breeding programs where wood is to be the end product (Keith and Kellogg 1986; Magnussen and Keith 1990; Zobel and van

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Buijtenen 1989). Genetic improvement of some wood quality traits is particularly attractive since wood quality traits are generally strongly inherited (Weiner and Roth 1966; Zobel and van Buijtenen 1989).

Black spruce (*Picea mariana* (Mill.) B.S.P.) is one of the most important reforestation and commercial species from the Atlantic Coast to Manitoba (Canada Department of Forestry 1963; Rowe 1972). The wood of this species is highly valued both as lumber and as pulpwood in Canada and the United States (Mullins and McKnight 1981; Smyth and Brownright 1986). The oldest half-sib family tests for black spruce in New Brunswick were established in 1978 under the coordination of the New Brunswick Tree Improvement Council (NBTIC). Considering the importance of wood and fiber quality to the forest products industry, wood quality needs to be an integral part of this program and should be taken into consideration in overall planning and development (Morgenstern and Villeneuve 1986). To incorporate wood quality efficiently into the breeding program for optimal gains, however, it is necessary to study the genetic variation of wood quality and its relationship with growth traits (viz., DBH, tree height, and bole volume). A genetic study on key wood quality traits of black spruce was therefore initiated (cf. Zhang and Morgenstern 1996). The present paper and a previous one (Zhang and Morgenstern 1996) focused on wood density. This trait is widely regarded as one of the most important wood quality characteristics, having a major effect on both yield and quality of fibrous and solid wood products (Panshin and de Zeeuw 1980; Zobel and van Buijtenen 1989; Zhang and Zhong 1991; Zhang 1992, 1994; Zhang et al. 1992).

In a previous study by Zhang and Morgenstern (1996), heritability of wood density, relationship of wood density with growth, and the implications of these genetic parameters for wood quality improvement were discussed. The objective of the present study is to examine how and to what extent the relationship of wood density with growth traits in this species varies with genotype and environment. In addition, this study also examines how and to what extent genotype and environment influence wood density and other traits (e.g., earlywood density, latewood density, and latewood percent). The implications of these results for wood quality improvement were briefly discussed.

MATERIALS AND METHODS

Black spruce plus trees were selected by Fraser Inc. in northwestern New Brunswick in 1977. The materials used for this study came from a family test and the seed orchard that were located in different environments. The family test used was located at Larlee Brook, 50 km northeast of Edmundston (here called Location 1). The site for the family test was prepared by Marden Roller. The test consisted of 4-tree row plots with trees spaced at 2 × 2 m, replicated 10 times in a randomized block design. The seed orchard was located near the Fraser Inc. Nursery about 20 km northeast of Edmunston (called Location 2). This site was plowed and harrowed several times before the planting. For further information about the family test and the seed orchard, refer to the NBTIC report (Anon. 1978) and a paper by Zhang and Morgenstern (1995).

Forty half-sib black spruce families were sampled from Location 1, and 16 of these families were sampled from Location 2. At the end of the 1992 growing season, 8–12 (depending on the availability) 15-year-old trees per family were sampled from different blocks at the two locations. In total, 343 trees were sampled from Location 1, and 190 trees from Location 2. For each of the trees sampled, diameter at breast height (DBH) and tree height (TH) were measured, and bole volume (BV) was calculated based on DBH and TH (Honer et al. 1983).

Wood density was measured using X-ray densitometric technique. A radial segment from the pith to the bark was taken from each tree. The radial segment was extracted in the laboratory and then sawn into a 2-mm-thick (longitudinal) × 10-mm-wide (tangential) strip for the X-ray densitometric analysis. Each strip was scanned from the pith to the bark at air-dry condition. The first few growth rings near the pith were excluded because they were usually too narrow and the growth ring boundary was so ambiguous that densitometric analysis could not be performed. Based on the microdensitometric profiles, various ring density parameters (e.g., earlywood density, latewood density, and average wood density of individual rings) and ring width parameters (earlywood width, latewood width, and ring width) were obtained. Based on the intra-ring wood variables, intra-ring density variation (IDV) was estimated using the equation given by Vargas-Hernandez and Adams (1991).

After wood density data on individual growth rings were obtained, weighted averages were computed for overall wood density (WD), earlywood density (EW), and latewood density (LD). In addition, latewood percent (LP) for each strip was calculated based on the total latewood width of the growth rings divided by the total width of the rings across the radial strip. Based on bole volume (BV) and overall wood density (WD), dry mass weight (DMW = BV × WD) was computed for each tree as an index of gross fiber yield.

In order to evaluate genetic and environmental effects on wood density and other traits, the GLM procedure of the SAS packages was used to carry out analysis of variance of the unbalanced data. Various variance components and covariances were estimated from the appropriate mean square and mean cross-products also using SAS procedures (cf. Zhang and Morgenstern 1996). Relationships between wood density and growth traits were examined using phenotypic correlations since a previous study by Zhang and Morgenstern (1996) indicated that phenotypic correlations were generally comparable with genetic ones in this species. Variance components and covariances obtained were used to compute phenotypic correlations as follows (Falconer 1981):

$$r_p(xy) = \frac{COV_{pf}(xy)}{[\sigma^2_{pf}(x)\sigma^2_{pf}(y)]^{1/2}}$$

where $r_p(xy)$ is the phenotypic correlation (based on family means); $COV_{pf}(xy)$ is the phenotypic covariance (based on family means) between traits x and y; $\sigma^2_{pf}(x)$, $\sigma^2_{pf}(y)$ are the phenotypic variances for traits x and y, respectively (based on family means).

RESULTS AND DISCUSSION

Genetic and environmental effects on wood density and growth traits

As shown in Table 1, overall wood density (361 kg/m^3) for families grown in the seed orchard (Location 2) is lower than that (399 kg/m^3) for families from Location 1 (the family test). This results largely from the difference in growth rate between the two locations. As indicated by either ring width or DBH (Table 1), families from Location 2 grew faster than those from Location 1 because of the more favorable environment. As shown in Fig. 1, with increasing ring width, latewood width in this species remains more or less constant or even tends to decrease slightly, while earlywood width increases proportionally. As a result, latewood percent decreases significantly with increasing ring width (growth rate) (see Table 1). This means that higher growth rate will result in lower latewood percent, thus lower wood density. In other words, wood density is negatively related to growth rate, as reported previously by Zhang and Morgenstern (1996).

Similarly, earlywood density at Location 2 (343 kg/m^3) is also appreciably lower than at Location 1 (376 kg/m^3). This is associated with its larger earlywood width because earlywood density in this species decreases gradually with increasing width (see Fig. 2). This case, however, does not hold true in latewood. Although latewood width at Location 2 is much smaller than at Location 1, latewood densities at both locations are quite comparable (569 kg/m^3 and 567 kg/m^3). This suggests that latewood density is significantly less related to its width as compared with earlywood density. As shown

TABLE 1. *Variation of wood density and other traits among the families from two locations.*

Trait[1]	Location 1			Location 2		
	Mean	Family range	CV (%)[2]	Mean	Family range	CV (%)
WD (kg/m^3)	399	366–450	8.1	361	347–392	6.8
ED (kg/m^3)	376	352–429	6.3	343	332–358	5.6
LD (kg/m^3)	569	412–598	8.0	567	551–589	3.4
RW (m, ×0.001)	4.05	3.20–4.89	19.6	4.62	4.17–5.02	16.4
EW (m, ×0.001)	3.54	2.84–4.49	24.0	4.26	3.91–4.74	18.5
LW (m, ×0.001)	0.51	0.36–0.75	52.8	0.36	0.21–0.64	47.6
LP (%)	13.3	8.8–19.0	55.0	7.94	4.77–14.17	50.4
IDV (kg/m^3)	65.8	50.1–87.4	40.0	59.0	45.1–77.7	24.5
DMW (kg)	2.858	1.645–5.559	44.8	5.210	4.127–6.677	39.8
TH (m)	4.33	3.65–5.23	13.6	5.48	5.18–5.98	12.8
DBH (m, ×0.01)	6.33	5.11–9.44	17.6	8.06	7.43–8.96	16.1
BV (m^3, ×0.001)	7.269	4.099–14.974	48.3	14.569	11.499–19.081	41.9

[1] WD: average wood density; ED: earlywood density; LD: latewood density; RW: ring width; EW: earlywood width; LW: latewood width; LP: latewood percent; IDV: intra-ring density variation; DMW: dry mass weight; TH: tree height; DBH: diameter at breast height; BV: bole volume (same in Tables 2, 3 & 4).
[2] CV: coefficient of variation.

in Fig. 3, latewood density, unlike earlywood density, does not decrease with increasing width. Compared with Location 2, a comparable latewood density, but a remarkably higher earlywood density at Location 1, means a larger intra-ring density variation (see Table 1). Although overall wood density at Location 1 is remarkably higher than at Location 2, dry mass weight per tree at Location 2 is still much higher because of its faster growth in both diameter and height and thus much higher volume.

Among various traits listed in Table 1, density traits (WD, ED, and LD) show remarkably smaller phenotypic variation (CV < 10%) than growth traits (TH and DBH, CV ranging from 10% to 20%). The same result was reported in other species (Jourdain and Olson 1984; Magnussen and Keith 1990; Park et al. 1989). Dry mass weight in black spruce shows much larger variation (CV about 50%) than DBH and tree height, and its variation is almost comparable with that in bole volume. Furthermore, latewood width and thus latewood percent show much higher variation (CV over 50%) than either earlywood width or ring width. A sim-

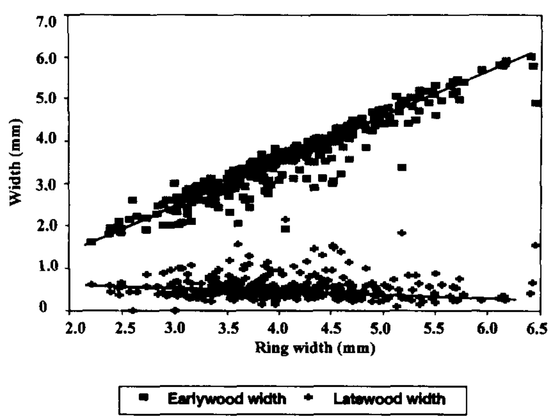

FIG. 1. Variation of earlywood width and latewood width with ring width.

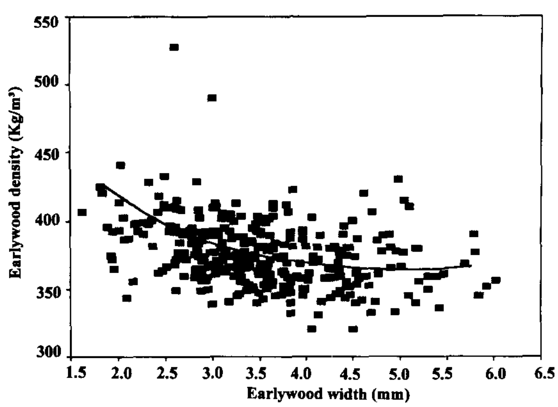

FIG. 2. Variation of earlywood density with earlywood width.

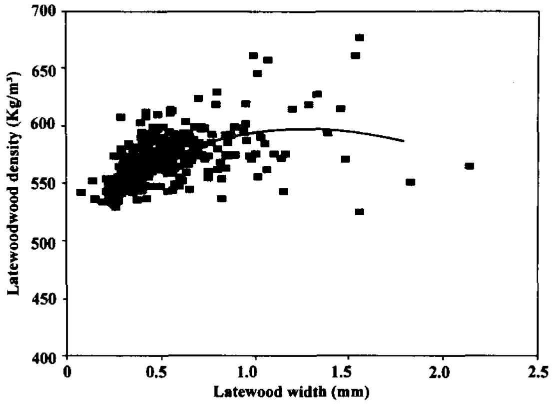

FIG. 3. Variation of latewood density with latewood width.

ilar case was found in European oak (Zhang et al. 1994). The high variability in latewood width and latewood percent implies that these traits are under poor genetic control in black spruce (Zhang 1995b). As a result, selection for increasing latewood percent cannot improve overall wood density remarkably, as reported by Zhang and Morgenstern (1996).

Large differences in overall wood density and other traits among the families are clearly shown in Table 1 as well. For instance, overall wood density among the 40 families from Location 1 ranges from 366 kg/m³ to 450 kg/m³, and dry mass weight from 1.645 kg to 5.559 kg. A similar case holds true at Location 2. A significant effect on wood density, earlywood density, and latewood density by genotype and environment has been reported in many species (McKimmy 1966; McKimmy and Nicholas 1971; Jourdain and Olson 1984; Yanchuk et al. 1984; Zobel et al. 1960; Zobel and van Buijtenen 1989; Abdel-Gadir et al. 1993).

The objective of tree breeding programs is to increase bole volume through genetic selection for height and diameter growth (Zobel and van Buijtenen 1989; Yanchuk and Kiss 1993). However, dry mass weight as an index of gross fiber yield appears to be of importance to the pulp and paper industry. As shown above, significant differences in overall wood density exist among the families studied. This suggests that there is potential for additional gain in gross fiber yield if wood density is incorporated into the breeding program. A previous study by Zhang and Morgenstern (1996) indicates that it is feasible and economically justifiable to incorporate wood density into breeding programs. Selection for dry mass weight instead of bole volume would increase genetic gain in gross fiber yield substantially. If selection is

TABLE 2. *The differences in wood density, bole volume, and dry mass weight among 40 families (Location 1).*

Family	WD (kg/m³)	BV (m³, ×0.001)	R[1]	R[2]	DMW (kg)
42	374	14.974	1	1	5.559
61	366	9.532	2	4	3.508
80	388	9.324	3	3	3.570
34	395	9.323	4	2	3.657
41	396	8.915	5	6	3.530
65	407	8.887	6	5	3.539
32	404	8.500	7	7	3.364
19	376	8.497	8	8	3.160
38	359	8.297	9	13	3.022
48	384	8.066	10	11	3.057
85	402	7.878	11	9	3.124
79	386	7.824	12	17	3.003
62	393	7.796	13	10	3.060
47	409	7.759	14	15	3.013
33	398	7.708	15	14	3.016
7	400	7.539	16	12	3.031
60	410	7.521	17	18	2.990
25	399	7.494	18	19	2.953
31	397	7.473	19	20	2.911
58	413	7.358	20	16	3.012
43	375	7.355	21	23	2.723
12	377	6.871	22	28	2.554
52	419	6.836	23	22	2.848
49	408	6.699	24	24	2.722
53	450	6.606	25	21	2.900
77	397	6.448	26	27	2.567
40	405	6.445	27	25	2.586
37	409	6.376	28	29	2.548
72	404	6.284	29	30	2.531
68	387	6.228	30	33	2.381
23	421	6.142	31	26	2.574
73	421	5.979	32	31	2.477
51	381	5.897	33	34	2.264
70	391	5.643	34	36	2.223
64	422	5.705	35	32	2.397
39	421	5.390	36	35	2.244
26	409	5.310	37	37	2.153
24	402	5.165	38	38	2.063
84	401	4.747	39	39	1.904
10	412	4.099	40	40	1.645

[1] Ranking according to bole volume.
[2] Ranking according to dry mass weight.

TABLE 3. *Phenotypic correlations between wood density and other traits at Location 1 (lower triangle) and Location 2 (higher triangle).*

	WD	ED	LD	RW	EW	LW	LP	IDV	DMW	DBH	TH	BV
WD		0.93	0.50	−0.28	−0.44	0.79	0.82	0.53	−0.17	−0.33	−0.21	−0.32
ED	0.83		0.28	−0.17	−0.28	0.57	0.58	0.21	−0.14	−0.28	−0.20	−0.12
LD	−0.09	−0.27		−0.30	−0.39	0.51	0.58	0.82	−0.15	−0.22	−0.15	−0.08
RW	−0.31	−0.26	−0.05		0.98	−0.08	−0.37	−0.44	0.55	0.65	0.25	0.58
EW	−0.43	−0.33	−0.17	0.95		−0.29	−0.56	−0.57	0.53	0.65	0.26	0.06
LW	0.43	0.26	0.38	−0.03	−0.35		0.94	0.72	−0.01	−0.13	−0.10	−0.13
LP	0.49	0.34	0.43	−0.36	−0.64	0.92		0.81	−0.17	−0.31	−0.16	−0.28
IDV	−0.01	−0.04	0.54	−0.27	−0.48	0.69	0.76		−0.16	−0.27	−0.10	−0.24
DMW	−0.24	−0.26	−0.08	0.53	0.57	−0.24	−0.38	−0.27		0.95	0.79	0.99
DBH	−0.39	−0.39	−0.08	0.60	0.66	−0.30	−0.47	−0.29	0.95		0.63	0.96
TH	−0.26	−0.28	−0.06	0.35	0.41	−0.24	−0.34	−0.21	0.85	0.74		0.78
BV	−0.37	−0.37	−0.08	0.55	0.61	−0.29	−0.44	−0.27	0.99	0.96	0.84	

made for dry mass weight, the ranking of most families (32 of 40 families) will be different from that based on bole volume (Table 2). Based on dry mass weight, for instance, family No. 53 will jump to the 21st position among the 40 families from the 25th position (based on bole volume) because this family has the highest wood density. On the contrary, family No. 38 will drop to the 13th position from the 9th position (based on bole volume) because of its lowest wood density. Furthermore, Table 2 also clearly shows that among the 40 families studied, it is still possible to select families that have both high bole volume and high wood density (e.g., families No. 65, 32, 85, and 47).

Variation of the relationship between wood density and growth among the families from the two locations

As shown in Table 3, wood density at both locations shows a negative (phenotypic) correlation with growth traits (ranging from −0.17 to −0.39), which is quite comparable with the genetic one reported previously by Zhang and Morgenstern (1996). Wood density at both locations is also negatively related to dry mass weight (−0.17 and −0.24). This negative relationship is reasonable if a very strong positive correlation between bole volume and dry mass weight and a moderately negative correlation between bole volume and wood density are taken into consideration. Moreover, earlywood density at two locations is negatively related to earlywood width (−0.28 and −0.33), but latewood density is positively related to latewood width (0.51 and 0.38), as shown in Figs. 2 and 3. Both earlywood density and latewood density, as shown in Table 3, are strongly and positively correlated with average wood density at Location 2. Although most correlation coefficients at the two locations are relatively comparable, the relationships of wood density with latewood density and intra-ring density variation are remarkably different at two locations. The correlations of wood density with latewood density and intra-ring density variation are negative and very weak at Location 1, while the correlations between them at Location 2 are positive and relatively strong.

Although a moderately negative correlation between wood density and growth generally exists (Table 3), it does not mean that this negative correlation exists in every family. As shown in Table 4, the relationship of wood density with DBH varies significantly with both family and location. For instance, a significantly negative relationship between wood density and DBH exists in family No. 47; but the relationship is not significant or even positive in families No. 10, 43, 61, and 65. A similar case applies to the relationships of wood density with tree height, bole volume, and dry mass weight (Table 4). This clearly shows that

TABLE 4. *Phenotypic correlations of wood density with growth traits in different families (No) from Location 1 (first row) and Location 2 (second row).*

No	DBH	TH	BV	DMW
10	−0.54	−0.29	−0.47	−0.38
	+0.01	−0.51	−0.18	+0.07
12	−0.52	−0.20	−0.48	−0.31
	−0.79**	−0.64*	−0.83**	−0.79**
25	−0.57	−0.61	−0.66	−0.59
	−0.30	−0.71*	−0.43	−0.27
31	−0.52	−0.64	−0.61	−0.57
	−0.68*	−0.68*	−0.71*	−0.65*
34	−0.77*	−0.11	−0.61	−0.51
	−0.35	−0.45	−0.34	−0.21
37	−0.83*	−0.78	−0.78	−0.73
	−0.49	+0.51	−0.35	−0.17
43	−0.67	−0.51	−0.65	−0.57
	+0.13	+0.20	+0.21	+0.32
47	−0.81*	−0.80*	−0.73	−0.65
	−0.63*	−0.35	−0.56	−0.47
48	−0.56	−0.57	−0.54	−0.49
	−0.49	−0.15	−0.44	−0.21
61	+0.27	+0.35	+0.18	+0.35
	−0.58	−0.33	−0.57	−0.42
62	−0.32	+0.38	−0.23	+0.04
	−0.23	−0.22	−0.23	−0.11
64	−0.19	−0.06	−0.16	0.00
	−0.27	−0.40	−0.31	−0.22
65	−0.61	−0.72*	−0.57	−0.54
	+0.17	+0.25	+0.20	+0.31
72	−0.34	+0.18	−0.11	+0.14
	−0.46	−0.45	−0.47	−0.40
77	−0.03	+0.31	+0.16	+0.31
	−0.11	+0.29	+0.04	+0.21
79	−0.31	+0.02	−0.26	−0.15
	−0.82*	−0.18	−0.74	−0.71
Mean	−0.46	−0.25	−0.38	−0.29
	−0.37	−0.24	−0.36	−0.23

*–significant at the 0.05 level; **–significant at the 0.01 level.

even in a species where a negative correlation between wood density and growth exists, it is still possible to select some genotypes (families) where the negative relationship is not significant or negligible. By doing so, selection for bole volume would not result in significant reduction in wood density simultaneously. Dorn (1969) reported that the relationship of wood properties with growth in *Pinus sylvestris* varied appreciably with provenance. Growth rate in some provenances showed a larger effect on wood properties than in others. Furthermore, a negative correlation between wood density and tree height in this species is appreciably weaker (−0.25 and −0.24 for Locations 1 and 2, Table 4) than that between wood density and DBH (−0.46 and −0.37). This implies that selection for tree height in this species may have less negative impact on wood density compared to selection for DBH. Similar results were reported in other species (Allen 1977; Park et al. 1989; Vargas-Hernandez and Adams 1991). Some studies (Squillace et al. 1962; Shelbourne et al. 1972; Sohn and Goddard 1974) even reported a positive relationship between wood density and tree height in the species where a negative relationship exists between wood density and tree diameter.

The relationship between wood density and growth, to some extent, also varies with location (Table 4). Wood density, for instance, is negatively related to DBH in families No. 10, 43, and 65 from Location 1; but a positive relationship exists in these families from Location 2 (the seed orchard). A similar case was noticed in the relationships of wood density with tree height, bole volume, and dry mass weight. As a whole, a negative relationship between wood density and DBH in the families grown in the seed orchard is appreciably weaker (−0.37) than that for families grown in the family test site (−0.46); and this, to a lesser extent, applies to the relationships of wood density with tree height, bole volume, and dry mass weight (Table 4). It appears that in a species where a negative relationship between wood density and growth exists, the negative relationship tends to be weaker in the trees growing in a more favorable environment. In other words, growth rate of the trees growing in a favorable environment probably has less negative impact on wood density than that of the trees growing in a less favorable environment. This appears to be reasonable from the physiological point of view. This result means that the relationship between wood density and growth rate found at one location does not necessarily apply to others since environment, to some extent, can influence the relationship.

A study by Hall (1984) on 12 black spruce stands from different locations in Newfoundland indicated that the relationship of wood density with tree diameter varied remarkably with location; and the relationship could be significantly negative, nonsignificant or significantly positive, depending on the location.

The relationship of wood density with growth rate is not only of scientific interest, but of crucial importance to tree breeders and forest managers (Zobel and van Buijtenen 1989). This relationship directly influences genetic gains, economic return of a breeding program, and the quality of wood from intensively managed plantations. Although a tremendous amount of research has been undertaken on the relationship of wood density with growth rate over the decades, various controversial results have been reported (cf. Spurr and Hsuing 1954; Zobel and van Bujitenen 1989; Zhang and Zhong 1991; Zhang 1995a). Even in a single species, various contradictory reports on the relationship can be found, as documented by Zhang (1995a). The present study, as well as limited information available so far (cf. Zhang 1995a), suggest that the relationship of wood density with growth rate, to some extent, may vary with genotype and environment, and silvicultural manipulations may modify the relationship (Zobel and van Buijtenen 1989; Zhang 1995a). These may be part of the reasons why various controversial results have been obtained even in a single species.

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