Inheritance of Wood Specific Gravity in an Unimproved Loblolly Pine Population: 20 Years of Results

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Abstract

In a 20-year-old loblolly pine (*Pinus taeda* L.) genetic test population, unextracted juvenile wood, unextracted mature wood, and unextracted weighted specific gravity were all found to be under substantial genetic control ($h^2 = 0.44$ for juvenile wood specific gravity and $h^2 = 0.45$ for mature wood and weighted specific gravity). All three characteristics were highly genetically correlated ($r_G \geqq 0.88$), indicating that selection for one of these traits will result in a substantial correlated response in the other two traits. The heritability of juvenile wood specific gravity observed in 20-year-old trees was similar to that found at age 7 in the same population. However, both estimates were lower than the heritability of juvenile wood specific gravity calculated at age 10. Coefficients of genetic prediction relating parental mature wood specific gravity and specific gravities of their progeny were in line with heritability values calculated for the age 7 and age 20 measurements. The observed heritabilities and variances indicate that substantial genetic gain can be made by selection for wood specific gravity in loblolly pine.

Key words: Pinus taeda L., Wood specific gravity, juvenile-mature correlations, heritability.

Zusammenfassung

In einer zwanzig Jahre alten *Pinus taeda* L. Nachkommenschaft aus einem genetischen Test wurde gefunden, daß das unextrahierte juvenile Holz sowie das unextrahierte spätere Holz und das gewichtete spezifische Gewicht unter starker genetischer Kontrolle waren. ($h^2 = 0.44$ für das spezifische Gewicht juvenilen Holzes und $h^2 = 0.45$ für das spätere Holz und für das gewichtete spezifische Gewicht des Holzes). Alle 3 Merkmale waren genetisch eng korreliert ($r_G \geqq 0.88$), was bedeutet, daß sich eine Selektion auf eines dieser Merkmale gleichzeitig auf die anderen zwei eng korrelierten Merkmale auswirkt. Die Heritabilität des spezifischen juvenilen Holzgewichtes, welches bei den 20jährigen Bäumen beobachtet wurde, war derjenigen, die im Alter von 7 Jahren in der gleichen Population gefunden wurde, ähnlich. Jedenfalls waren beide Schätzwerte niedriger, als die Heritabilität der spezifischen juvenilen Holzdichte, die im Alter von 10 Jahren errechnet wurde. Die Koeffizienten der genetischen Vorhersage, daß das spezifische Gewicht des späteren Holzes der Eltern mit dem spezifischen Gewicht der Nachkommen in Zusammenhang zu bringen ist, stimmen mit den Heritabilitäten im Alter 7 bzw. 20 überein. Die beobachteten Heritabilitäten und ihre Veränderungen zeigen, daß beim spezifischen Gewicht von *Pinus taeda* wesentliche genetische Gewinne möglich sind.

Introduction

Wood specific gravity has been shown to be a highly heritable characteristic in many species of forest trees. Heritability estimates for juvenile wood specific gravity of loblolly pine (*Pinus taeda* L.) are generally on the order of $h^2 = 0.4$ to 0.7 (GOGGANS, 1961; STONECYPHER *et al.*, 1973, CHUNTANAPARB, 1973). Specific gravity is a complex trait influenced by length and diameter of cells, cell wall thickness, relative proportions of springwood and summerwood, cellulose and lignin content, and extractives content (KOCH, 1972). It is highly correlated with the major strength properties of sawn timber (PEARSON and GILMORE, 1980) and pulp and paper properties (BAREFOOT *et al.*, 1964; KIRK *et al.*, 1973; BLAIR *et al.*, 1976). Collectively, these considerations make wood specific gravity a desirable trait to include in many selection and breeding programs. However, the desirability of including wood specific gravity in a selection and breeding program is not without debate. Countering arguments include the high cost of measuring specific gravity and the occasional reports of negative genetic correlations between specific gravity and growth traits (NAMKOONG *et al.*, 1969). Wood specific gravity is used as a selection criterion in the establishment of some loblolly pine seed orchards in the N. C. State-Industry Pine Tree Improvement Program (JETT and TALBERT, 1982).

The bulk of studies investigating inheritance of wood specific gravity have dealt primarily with measurements taken on wood from young trees. Therefore, samples consisted largely or entirely of juvenile wood. Numerous papers have been published on the characteristics of juvenile wood and differences between juvenile and mature wood (DADSWELL, 1957; PAUL, 1957; ZOBEL, 1976; ZOBEL *et al.*, 1978). Compared to mature wood, juvenile wood can be characterized as having lower specific gravity, shorter tracheids, thinner cell walls and a lower proportion of summerwood. The transition from juvenile to mature wood is a gradual process, but generally occurs in a zone from 7 to 11 rings from the pith in loblolly pine.

Because of dissimilarities in juvenile and mature wood specific gravities, inheritance patterns for the two traits might be expected to be somewhat different. During the summer of 1979, a study was initiated to investigate the inheritance of mature wood specific gravity in loblolly pine. The test population was the Loblolly Pine Heritability Study, established jointly in 1960 by N. C. State University and International Paper Company on the company's Southlands Experiment Forest in Decator Country, Georgia. The study is designed to investigate inheritance patterns in a nonselected natural loblolly pine population. A summary of information from the Heritability Study through age 7 is given in STONECYPHER *et al.* (1973). This paper reports results of the mature wood specific gravity study and their relationship to results obtained in earlier studies of juvenile wood specific gravity involving the same test population.

Materials and Methods

Parent Trees

Parent trees for the Heritability Study were chosen from unthinned naturally regenerated stands of loblolly pine

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growing on the Southlands Experiment Forest. Trees were approximately 35 years of age at the time the study was initiated, and were selected essentially at random, with the exception that they had to be safe to climb and they had to be producing cones. At the time trees were chosen, 12 mm "bark to bark" increment cores were taken from each tree at breast height, and unextracted specific gravity was determined for the mature wood segments.

Genetic Test Design

During the winter of 1959—1960, an open-pollinated genetic test of 280 parent trees was established in a randomized complete block design at two locations on the Experimental Forest. Although the test sites are separated geographically by only a few miles, the plantings were established on two quite different soil types. Soils at the location 1 planting site are classified as Norfolk loamy sand and Lakeland sand. The area had been under cultivation for two years prior to test establishment; there was no site preparation prior to planting. Location 2 soils are predominately Orangeburg sandy loam, and supported a natural loblolly pine-shortleaf pine (*Pinus echinata* Mill) stand. Site preparation consisted of removal of the residual stand followed by burning.

To better partition of environmental variation in the study associated with large replication size, families were divided into 10 sets, each set containing 28 families. Families in each set were planted together in each replication. There are two replications per location. Families were planted in 25 tree-square plots.

Sampling Procedures

Wood samples have been taken from the open-pollinated study at three different times. Initial sampling was done after 7 growing seasons, when 8 mm "bark to bark" increment cores were taken at breast height (4.5 feet) from all families in each of 4 sets in all replications. Seven trees were sampled per family plot. Unextracted juvenile wood specific gravity was determined for each sample tree. Detailed analyses of these data may be found in Chuntanaparb (1973).

After 10 growing seasons in the field, thinning was prescribed for 5 of the 10 family sets in the study. Because of differences among replications in growth rate, only 1 replication at each location was thinned. Breast height wedges were taken from approximately 5 thinned trees in each family plot, and unextracted juvenile wood specific gravity was measured for each tree. Results of these assessments have been reported in detail by Barker (1973) and Chuntanaparb (1973).

During the 20th growing season, 12 mm bark to bark increment cores were obtained at breast height from 15 families in each of 3 sets in all 4 replications of the study. Sets and families sampled were chosen so that they were in common with both the age 7 and age 10 assessments. Because of sampling procedures and the thinning which was conducted at age 10, very few trees measured for specific gravity in the age 7 assessment were included in the age 20 assessment. Cores taken at age 20 were divided into juvenile and mature wood segments (using an arbitrary division at 10 rings from the pith) and specific gravity was determined for both juvenile and mature wood segments. A weighted breast height specific gravity was determined by averaging juvenile and mature wood values for each tree, weighted by the basal area represented by each segment.

Table 1. — Variance components and heritability estimates for age twenty assessment of juvenile wood, mature wood, and weighted breast height specific gravity.

Component	Trait: Juvenile Wood Specific Gravity	Mature Wood Specific Gravity	Weighted Specific Gravity
σ^2_L	.029027 1/	.088625	.027652
$\sigma^2_{R(L)}$	.001214	.002140	.017685
σ^2_S	.003971	.003813	.007942
σ^2_{LxS}	.000930	.007268	.003379
$\sigma^2_{R(L)xS}$	.001491	.007296	.001912
$\sigma^2_{F(S)}$	.008997	.014290	.010072
$\sigma^2_{F(S)xL}$	.004099	.000712	−.001821
$\sigma^2_{F(S)xR(L)}$	.011039	.008500	.009614
σ^2_E	.057142	.104509	.07099
σ^2_P	.081277	.128011	.088855
h^2	.44	.45	.45
S.E.(h^2)	.157	.148	.171
$\bar{X}$ =	.402	.549	.473

σ^2_L = Variance due to differences between locations

$\sigma^2_{R(L)}$ = Variance due to differences between replications in locations

σ^2_S = Variance due to differences among sets

σ^2_{SxL} = Variance due to sets by location interaction

$\sigma^2_{R(L)xS}$ = Variance due to sets by replication in location interaction

$\sigma^2_{F(S)}$ = Variance due to families in sets

$\sigma^2_{F(S)xL}$ = Variance due to families in sets by locations interaction

$\sigma^2_{F(S)xR(L)}$ = Varance due to families in sets by replications in location interaction

σ^2_E = Variance among trees within plots

σ^2_P = Phenotypic variance = $\sigma^2_{F(S)} + \sigma^2_{F(S)xL} + \sigma^2_{F(S)xR(L)} + \sigma^2_E$

h^2 = heritability = $\frac{4\sigma^2_{F(S)}}{\sigma^2_P}$

S.E(h^2) = Standard error of the heritability

1/ Actual variance component values are multiplied by 100.

Statistical Analysis

Analyses of variance were performed on an individual tree basis. The general form of the analysis for the study data collected at age 7 and age 20 may be found in Stonecypher *et al.* (1973). Data collected at age 10 involved only 1 replication per location; thus genetic and genotype × replications in location effects are confounded. The appropriate analysis may be found in Chuntanaparb (1973). In order to evaluate any changes in variance component estimates and heritabilities with time, data collected in the age 7 and age 10 assessments were reanalyzed, including only those sets and families that were sampled at all three ages. This also permitted genetic correlations between specific gravity measured at younger ages and at age 20. Therefore, estimates and heritabilities presented here differ slightly from those reported by Chuntanaparb (1973) for the age 7 measurements and Barker (1973) and Chuntanaparb (1973) for the age 10 asessment. Standard errors of heritability estimates for the age 20 data were calculated using formulae given by Becker (1975).

Parental mature wood specific gravity values and the values of their open-pollinated progeny were related using Baradat's (1976) "coefficient of genetic prediction" (CGP). Parent-offspring regressions are often used to calculate heritability values, but because mature wood speci-

Table 2. — Heritability estimates for age 20 assessment of unextracted juvenile wood, mature wood, and weighted specific gravity by and across test locations.*

	Heritability Location 1	Location 2	Combined
Juvenile Wood Specific Gravity	.25 (.299)	.54 (.346)	.44 (.157)
Mature Wood Specific Gravity	.59 (.225)	.36 (.206)	.45 (.148)
Weighted Specific Gravity	.54 (.240)	.30 (.225)	.45 (.171)

*Standard errors of heritability estimates are in parentheses (   ).

fic gravities of 35 year-old trees and mature and juvenile wood specific gravities of younger trees are somewhat dissimilar traits, the CGP is a more appropriate statistic here. In this procedure, the genetic value of a trait (progeny specific gravity values) are related to the phenotypic value of another trait (parental mature wood specific gravity) in the following way:

$$CGP = \frac{Cov(A_1A_2)}{\sigma P_1 \cdot \sigma P_2}, \quad \text{where}$$

CGP = coefficient of genetic prediction

$Cov(A_1,A_2)$ = covariance of traits A_1 and A_2

$\sigma P_1, \sigma P_2$ = square root of phenotypic variances of traits A_1 and A_2, respectively

Results and Discussion

Means, variance components, and heritability estimates for unextracted juvenile and mature wood specific gravity, and weighted unextracted specific gravity are shown in *Table 1*. Heritabilities for all three traits are essentially the same, with $h^2 = 0.44$ for juvenile wood specific gravity and $h^2 = 0.45$ for mature wood and weighted specific gravity. These results indicate that selection at age 20 for any of the three characteristics assessed would result in genetic gain in this test population. For a given selection intensity, selection for mature wood specific gravity would be expected to give greater genetic gain than selection for juvenile wood specific gravity because of the greater phenotypic variation (σ^2_P) for the mature wood characteristic *(Table 1)*.

Variance components for families in sets by location interaction ($\sigma^2_{F(S)xL}$) are small or slightly negative for all three characteristics *(Table 1)*. As a result, heritability figures for the combined location analysis are intermediate to those obtained for individual location analysis *(Table 2)*. Locations reversed themselves in the strength of inheritance of juvenile and mature wood specific gravity. The inheritance of weighted specific gravity closely paralleled that of mature wood gravity at both locations. This was to be expected because of the relatively large basal area represented by the mature wood segment as compared to the juvenile wood segment.

Table 3. — Genetic correlation (r_G) between juvenile wood, mature wood, and weighted specific gravity for the age 20 assessment (combined locations).[1]

	Juvenile	Mature	Weighted
Juvenile		.88	.97
Mature			.99

1/Genetic correlations were calculated as

$$r_G = \frac{\sigma_{f_{xy}}}{\sigma_{f_x} \cdot \sigma_{f_y}},$$

where r_G = genetic correlation

$\sigma_{f_{xy}}$ = family component of covariance for traits X and Y

σ_{f_x} = square root of family component of variance for trait X

σ_{f_y} = square root of family component of variance for trait Y

Table 4. — Means, variance components, and heritability estimates for juvenile wood specific gravity sampled at age 7, 10, and 20 in the same test population.

Component 1/	Age 7	10 3/	20
σ^2_L	.001092 2/	.037457	.029027
$\sigma^2_{R(L)}$	-.001770	--	.001214
σ^2_S	-.000960	-.002239	.003971
σ^2_{SxL}	-.002033	.007061	.000930
$\sigma^2_{R(L)xS}$	.007302	--	.001491
$\sigma^2_{F(S)}$	.006152	.012817	.008997
$\sigma^2_{F(S)xL}$	.000457	.000636	.004099
$\sigma^2_{F(S)xR(L)}$	.006382	--	.011039
σ^2_E	.049234	.053325	.057142
σ^2_P	.062225	.066775	.081277
h^2	0.40	0.76	0.44
$\bar{\bar{X}}$ =	.353	.364	.402

1) Variance components are as defined in *Table 1*.

2) Actual variance component values are multiplied by 100.

3) Estimates of several variance components can not be determined because only one replication was sampled per location at age 10.

Genetic correlations among the three characteristics assessed at age 20 are shown in *Table 3*. All genetic correlations are high; those for juvenile or mature wood specific gravity and weighted specific gravity approach unity. This is not unusual in light of the autocorrelations involved, as the juvenile and mature wood segments are a component of the weighted specific gravity figures. However, the high genetic correlation between juvenile and mature wood specific gravity ($r_G = 0.88$) is encouraging to those involved in breeding programs to improve specific gravity traits. The high genetic correlation, combined with comparable heritability estimates for the two characteristics, indicate that selection for either juvenile or mature wood specific gravity would result in substantial correlated response in the other trait.

Results of the age 20 assessment of juvenile wood specific gravity compare favorably with those of the age 7 measurements *(Table 4)*. Family variance and phenotypic variance increased from age 7 to age 20 but effects on heritability were small ($h^2 = 0.40$ at age 7 vs. $h^2 = 0.44$ at age 20). These results were not unexpected because wood produced at essentially the same period in the stand's life was being sampled at both ages. Increases in variance were likely to be at least partially due to deposition of extractives in the juvenile wood segment; this was also reflected in the increase in mean juvenile wood specific gravity from .353 to .402 during the 13 year period. Increases in unextracted juvenile wood specific gravity with age of sample have been reported previously for loblolly pine (ZOBEL *et al.*, 1972).

A heritability of $h^2 = 0.76$ for juvenile wood specific gravity measured at age 10 is much higher than values at either age 7 or age 20 *(Table 4)*. The higher heritability figure at age 10 appears to be due largely to an increase in the families in sets variance component ($\sigma^2_{F(S)}$). Only one replication was sampled per location at age 10, which resulted in a confounding of the families in sets × replications in location ($\sigma^2_{F(S)} \times R(L)$) and families in sets ($\sigma^2_{F(S)}$) components of variance. Therefore, the calculated heritability of juvenile wood specific gravity actually estimated the value[1])

$$h^2 = \frac{4(\sigma^2_{F(S)} + \sigma^2_{F(S)xR(L)})}{\sigma^2_{F(S)} + \sigma^2_{F(S)xL} + \sigma^2_{F(S)xR(L)} + \sigma^2_E}$$

rather than the appropriate formula

$$h^2 = \frac{4\sigma^2_{F(S)}}{\sigma^2_{F(S)} + \sigma^2_{F(S)xL} + \sigma^2_{F(S)xR(L)} + \sigma^2_E}$$

A reduction of the component $\sigma^2_{F(S)}$ by the amount of $\sigma^2_{F(S)xR(L)}$ estimated at age 7, the sampling age closest to age 10, would result in a heritability figure at age 10 of $h^2 = 0.39$, much in line with heritability for juvenile wood specific gravity obtained at age 7 and age 20. An analysis of the age 20 data using only those replications sampled at age 10 yielded estimates of $h^2 = .63$ and $\sigma^2_{F(S)} = .013037$, similar to values obtained for the age 10 analysis. The above emphasizes the problems associated with sampling only one replication per location when conducting genetic studies.

Genetic correlations between juvenile wood specific gravity at age 7 and age 20 were high *(Table 5)*. Correlations with age 20 traits for age 7 measurements are higher than for age 10 measurements. This could be the result of a smaller sample size at age 10, giving a less precise estimate of family performance and thereby reducing the correlation.

Coefficients of genetic prediction (CGP) for parental mature wood specific gravities and progeny specific gravities across locations at all three assessment ages are shown in *Table 6*. For the age 7 and age 20 measurements, CGP values compare favorably with heritability estimates based on sibling analyses *(Table 2 and 4)*. This is a result of the strong genetic correlation between the various wood specific gravities measured, and the substantial heritabilities observed for the same characteristics. These values are similar to those reported by JETT and TALBERT (1982) for selected loblolly pine parents and and their 8-year-old progenies in the N. C. State University-Industry Cooperative Tree Improvement Program. A CGP of 0.14 was obtained for the age 10 assessment of juvenile wood specific gravity, lower than calculated CGP's at other ages, and much lower than the heritability of $h^2 = 0.76$ calculated from the half-sib analysis at the same age. Reasons for the lower CGP at age 10 undoubtedly include the smaller sample size at that age (5 trees in each of 2 replications at age 10 vs. 7 trees in each of 4 replications at ages 7 and 20), and the inability to account for the families in sets by replications in locations interactions at age 10, which would bias estimates of family performance and lower the CGP.

Table 5. — Genetic correlations (r_G) between juvenile wood specific gravity measurements at age 7 and 10 and specific gravities at age 20.

	Juvenile Wood Specific Gravity	
Age 20 Trait	Age 7	Age 10
Juvenile Wood Specific Gravity	.94	.77
Mature Wood Specific Gravity	.82	.68
Weighted Specific Gravity	.99	.89

[1]) See *Table 1* for explanation of variance components.

Table 6. — Coefficients of genetic prediction (CGP) for unextracted parental mature wood specific gravity and unextracted progeny specific gravities at ages 7, 10, and 20.

	CGP		CGP
Age 7		Age 20	
Juvenile Wood Specific Gravity	0.37	Juvenile Wood Specific Gravity	0.36
Age 10		Mature Wood Specific Gravity	0.43
Juvenile Wood Specific Gravity	0.14		
		Weighted Specific Gravity	0.48

Summary and Conclusions

These results indicate that breast height unextracted juvenile, unextracted mature, and unextracted weighted specific gravity are under substantial genetic control in a nonselected 20-year-old loblolly pine population. Calculated heritabilities were essentially the same for all three traits, with $h^2 = 0.44$ for juvenile wood specific gravity, and $h^2 = 0.45$ for mature wood and weighted tree specific gravities. Genotype by location interaction effects were small. Genetic correlations were high, with $r_G = 0.88$ between juvenile wood specific gravity and mature wood specific gravity. Equivalent heritabilities and the high genetic correlation indicate that substantial genetic gain can be made in mature wood specific gravity through selection for juvenile wood specific gravity. In advanced generation loblolly pine improvement programs, most selections are made at young ages (10-years-old or younger) before most trees begin to produce mature wood. Several workers have emphasized the need to select for increased juvenile wood specific gravity in pines, especially for trees harvested at young ages (PEARSON and GILMORE, 1980; BLAIR *et al.*, 1976; ZOBEL, 1976). However, mature wood will still comprise a substantial proportion of wood harvested on rotations of 20 years or more. Selection to increase specific gravity of the juvenile wood component in loblolly pine will give a correlated increase in the mature wood component.

Results of the age 20 specific gravity measurements compare quite favorably with measurements of juvenile wood specific gravity made at age 7 in the same genetic test. Heritabilities for juvenile wood specific gravity were similar at both assessments ($h^2 = 0.40$ at age 7 and $h^2 = 0.44$ at age 20), and genetic correlations between the age 7 measurement and the three specific gravity traits assessed at age 20 were high. A heritability estimate of $h^2 =$

0.76 for juvenile wood specific gravity based upon an age 10 sample in this population appears to be inflated because only one replication was sampled per test location, and therefore the estimate of the families component of variance ($\sigma^2_{F(S)}$) was confounded with the families by replication in locations component ($\sigma^2_{F(S)xR(L)}$).

Coefficients of genetic prediction (CGP) relating parental mature wood specific gravity and progeny specific gravities at ages 7 and 20 were high (CGP = 0.37 and 0.48 at ages 7 and 20, respectively) and were much in line with heritability estimates based upon sibling analyses. The CGP value for the age 10 sample of juvenile wood specific gravity (CGP = 0.14) was lower, probably as a result of inadequate sample size and the inability to account for families in sets by replication in locations interactions.

Wood specific gravity is one of the most heritable economically important characteristics in loblolly pine. Although it is more difficult to assess on large numbers of trees than other important traits such as height, stem straightness, or pest resistance, high heritabilities and considerable variation in wood specific gravity in loblolly pine indicate selection for the trait will result in substantial genetic gain.

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Variabilité génétique individuelle de la Qualité du Bois chez Betula pendula Roth

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Résumé

Nous avons étudié la variabilité et les corrélations intercaractères sur 46 familles de *Betula pendula* issues de croisements contrôlés. Le dispositif (6 blocs complets) est installé en Finlande du sud; les descendants étaient âgés de 12 ans après la graine.

Dans un premier temps, nous avons évalué la variabilité génétique par analyse de variance dans les descendants et par régression entre les parents moyens et les moyennes de descendances, ceci dans le but d'utiliser l'ensemble de l'information disponible. Ensuite, nous avons estimé les paramètres génétiques classiques à partir d'un plan factoriel complet de 4 mères et de 5 pères extraits de l'échantillon précédent.

Nous avons mesuré 564 descendants et 12 arbres-parents. Les mesures ont porté sur la croissance et la qualité du bois appréciée à partir de carottes de sondage (rétractibilités radiale, longitudinale, tangentielle et volumétrique; infradensité du bois; anisotropie de ces propriétés; rendement en fibres).

Sur le terrain, nous avons aussi étudié la possibilité d'estimer la qualité du bois à partir d'un pénétromètre (Pilodyn).

Les principaux résultats sont les suivants:

— la variabilité familiale est forte pour l'infradensité, la rétractibilité du bois; elle est moyenne pour la production en volume; elle n'est pas significative pour le rendement en fibres.

— la sélection en forêt pour l'infradensité du bois et surtout pour la rétractibilité volumétrique est possible.

— il y a un léger effet dépressif de l'autofécondation sur la production de matière sèche.

— il existe des effets maternels pour la croissance en hauteur.

— l'aptitude spécifique à la combinaison est assez faible.

— la liaison interfamille est favorable entre croissance et rétractibilité volumétrique; elle est nulle entre infradensité et croissance; cependant, elle est positive entre infradensité et rétractibilité.

— L'impact de l'âge sur les propriétés physiques du bois

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