

GENETIC VARIATION IN WOOD MECHANICAL PROPERTIES OF *CALYCOPHYLLUM SPRUCEANUM* AT AN EARLY AGE IN THE PERUVIAN AMAZON

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ABSTRACT

Calycophyllum spruceanum (Benth.) Hook. f. ex Shum. is an important timber species of the Peruvian Amazon Basin. Due to overexploitation in natural populations, users are turning to young trees of potentially lower quality. Therefore, variation in juvenile wood properties should be investigated to determine whether wood quality can be maintained or, if necessary, improved by breeding. A provenance/progeny test was established to evaluate genetic variation in growth and wood properties of young trees, the strength of their genetic control, as well as their interrelationships both at the genetic and phenotypic levels. This paper presents results obtained for ultimate crushing strength (σ_L), the static compliance coefficient (s_{11}) in longitudinal compression, the dynamic s_{11} in the longitudinal direction (determined by ultrasound), and air-dry density at 39 months. Results indicate that the mechanical properties of juvenile wood of this species are adequate for structural uses. There was significant variation in all wood properties due to families within provenances, and in all but dynamic s_{11} due to provenances. Families accounted for a larger percentage of the total phenotypic variance than provenances. Heritability estimates were higher for σ_L and static s_{11} than for dynamic s_{11} and density. Genetic correlations indicate that selecting trees with denser wood and/or faster growth would have a positive effect on some mechanical properties. A non-destructive ultrasonic method appeared suitable for estimating juvenile wood strength and stiffness of this species.

Keywords: Provenance, family, environment, heritability, phenotypic and genetic correlations, juvenile wood.

INTRODUCTION

Plantation forestry is an attractive management option in the tropics given the high growth rates normally observed. However, trees grown

under these conditions usually have a higher portion of juvenile wood compared with trees in natural stands, and this can affect wood properties (Zobel and Sprague 1998; Bowyer et al. 2003; Saranpää 2003). Understanding this variation and the factors involved is essential to main-

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tain or, if required, improve wood properties for specific uses (Tsoumis 1991). There has been relatively little research on genetic variation in wood properties of juvenile wood, their heritability, their correlation with tree growth, and their impact on end-use products (Zobel and Sprague 1998). This research is essential to design tree improvement programs that provide high-quality seed for plantation forestry in the tropics (Simons et al. 1994).

Strength and stiffness are important mechanical properties that determine the wood's suitability for structural uses (Jozsa and Middleton 1994). Wood density is usually a good predictor of strength and stiffness (Panshin and de Zeeuw 1980), but these properties can be influenced by other factors, including the variability among trees within species and environmental conditions that affect tree growth (Tsoumis 1991). Destructive methods are usually used to evaluate mechanical properties. However, a large number of living trees need to be evaluated using non-destructive methods in order to create breeding or production populations with trees possessing the best attributes. Non-destructive acoustical methods have been developed to evaluate wood properties (Herzig 1991; Bucur 2005), and several researchers have used these methods successfully (Kyokong and Bello 1977; Hernández et al. 1998; Oliveira et al. 2002; Ilic 2003).

Calycophyllum spruceanum (Bentham) Hooker f. ex Shumann (Rubiaceae family), known as capirona in Peru, is an important hardwood species for farming communities in the Peruvian Amazon (Sotelo Montes and Weber 1997). Its dense, diffuse-porous wood (Keenan and Tejada 1984) is mainly used for construction poles, charcoal, and firewood, but there is also demand in national and international markets for furniture, wall paneling, and parquet floors (Toledo and Rincón 1996). Capirona is a pioneer species that colonizes the floodplain and disturbed forests in the Amazon of Peru, Brazil, Ecuador, and Colombia (Linares et al. 1992). Trees can attain heights of 35 m and stem diameters of 1.8 m at breast height (Sears 2003). In Peru, farmers and industry have been harvesting the best canopy-level trees in accessible natural

populations, without considering management plans that would ensure that the genetic quality is maintained for subsequent generations. As a result, users are becoming dependent on young trees, which may have lower genetic quality for timber. In response to this problem, efforts have been made to set up seed orchards to produce high-quality seed for the establishment of small-scale forestry/agroforestry plantations in farming communities (Weber et al. 2001).

A provenance/progeny test of *C. spruceanum* was established in the Peruvian Amazon Basin, and results evaluated at 39 months indicated that there was significant variation in tree growth and wood density due to provenances and families within provenances. Wood density had a higher heritability than growth, and these variables were positively correlated at the genetic and phenotypic levels (Sotelo Montes et al. 2006). This paper presents additional results from the same provenance/progeny test. The main objectives were to (a) determine the relative magnitude of variation in juvenile wood mechanical properties (ultimate crushing strength, σ_L , and static and dynamic parallel compliance coefficients, s_{11}) due to provenances and families within provenances, (b) evaluate the heritability of the mechanical properties, (c) evaluate the phenotypic and genetic correlations among tree growth, wood density, and mechanical properties, and (d) evaluate the usefulness of non-destructive methods for predicting crushing strength and static stiffness. Results are compared with those of other species, and some practical implications are discussed.

MATERIALS AND METHODS

Sample region, study area, experimental design, and management of the provenance/progeny test

The sample region and provenance/progeny test are located in the Aguaytía watershed of the western Peruvian Amazon (Fig. 1). Open-pollinated seeds were collected on 200 selected mother trees of *Calycophyllum spruceanum* growing in natural stands located in seven geo-

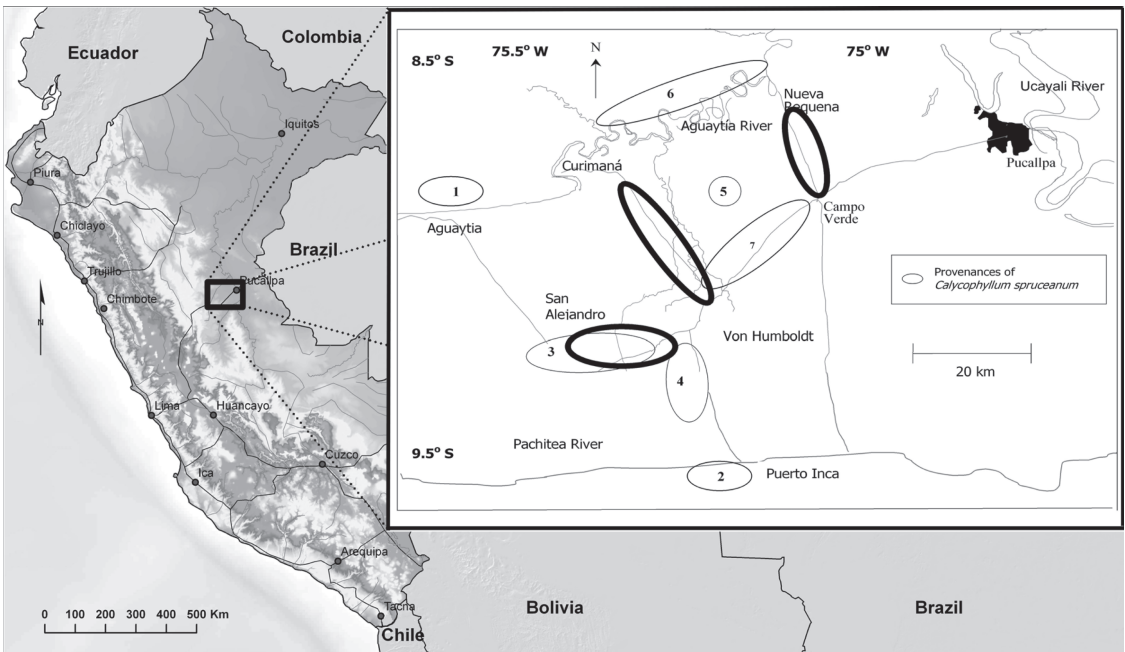


Fig. 1. Geographic location of the sample region and study area in the Aguaytía watershed of the Peruvian Amazon. Inset shows the location of the seven provenances of *Calycophyllum spruceanum* and the three planting zones (bold ellipses).

graphic locations (provenances) distributed in the lower, middle, and upper parts of the watershed. Seeds collected from the same mother tree are referred to as a family because they share the same maternal parent. The test was established on sites with upland, non-alluvial soils. In general, soil fertility and mean annual rainfall increase from the lower to the upper parts of the watershed. Details about the distribution of *C. spruceanum* in the sample region, sampling procedures, tree selection criteria, and the climate and soils in the sample region and study area are given elsewhere (Sotelo Montes et al. 2006).

The experimental design was a randomized complete block with 15 replications: five replications were established on different farms in each of the lower, middle, and upper parts of the watershed (hereafter called planting zones). In each replication, each of the 200 families was randomly assigned to one of 200 experimental plots, with two trees per plot. Spacing was 2.5 by 2.5 m within and between rows. Two rows of border trees surrounded the experimental design

on each site. Dead trees were replaced during the first dry season, but data collected on replants were not included in the analyses. Although each replication was established on a relatively homogenous site, the size of the replication with border rows was relatively large (~0.3 ha), and this could have resulted in fairly large microenvironmental differences within replications. Management practices included a cover crop, fertilizer application, branch pruning, and manual weeding (Sotelo Montes et al. 2006). One tree in each experimental plot was selectively thinned 39 months after planting, based on tree form (primarily stem bifurcations in the canopy) and growth.

Traits measured in the provenance/progeny test

Measurements of mechanical properties were made on the thinned trees of only six of the fifteen replications: three each in the middle and upper zones of the watershed. The other nine

replications (two each in the middle and upper zones, and the five in the lower zone) were excluded because mean diameter of the trees was too small to provide enough samples of sufficient size for mechanical tests. Prior to thinning, tree height was measured to the nearest cm using a meter stick or a telescopic measuring pole. After thinning, stem diameter at breast height (dbh, 1.3 m above ground level, outside the bark) was measured to the nearest 0.1 cm using calipers for small trees and diameter tape for larger trees.

Although the thinned trees were not randomly selected from the two trees in each experimental plot, it is unlikely that this would affect the results about the relative magnitude of variation in wood properties due to provenances and families within provenances, as well as the correlations between tree growth and wood properties. The following reasons can be advanced to support this assumption: (1) Wood properties were not used as selection criteria in the thinning. (2) Mean height of the thinned trees was essentially the same as the mean height of all trees in the six replications (8.6 m and 8.4 m, respectively). Dbh was only measured on the thinned trees, but as it was highly correlated with height (Sotelo Montes et al. 2006), we expect the same results. (3) Wood samples were obtained from the lower stem, well below the stem bifurcations in the canopy. This sampling procedure was used for all plots so it should not have any significant bias on mean height, dbh, or wood properties of any particular family.

Air-dry density, ultimate crushing strength in the longitudinal direction (σ_L), and static and dynamic parallel compliance coefficients (static and dynamic s_{11} , respectively) were determined from one wood sample per tree. The static and dynamic s_{11} are the reciprocals of the static (E_s) and dynamic (E_d) modulus of elasticity, respectively.

Sampling of wood specimens for determination of air-dry density, σ_L and static s_{11} involved two steps. In the first step, a 45-cm-long stick was prepared: this was located close to the bark, in the south-facing quadrant of the stem, between 75 and 120 cm above ground level. Cross-

sections of the sticks were 2.5×2.5 cm for larger trees (group A, dbh greater than approximately 7.0 cm), and 2.0×2.0 cm for smaller trees (group B, dbh less than approximately 7.0 cm). Sticks were stored under controlled conditions (60% relative humidity – RH, 20°C) for approximately 6 months to attain equilibrium moisture content (EMC mean = 12.2%) before processing. In the second step, one defect-free sample without the pith was prepared from each stick. Two sizes were used for measurements: $8 \times 2 \times 2$ cm for the larger trees, and $6 \times 1.5 \times 1.5$ cm for the smaller trees. This was done in order to sample the maximum number of trees in each planting zone, and to have the last two growing seasons represented in the samples. As a result, data would have to be adjusted to eliminate any difference in air-dry density and mechanical properties due to sample dimension.

Measurements of σ_L , static s_{11} and air-dry density were based on procedures in ASTM 1994, except for the sample dimensions. Air-dry volume of each sample was calculated from its length and cross-sectional area, and air-dry weight was measured to the nearest 0.001 g. The ratio of air-dry weight to volume was used to estimate air-dry density (kg/m^3). Parallel-to-grain compression tests were then carried out on a MTS ALLIANCE RT/50 machine. Strain in the longitudinal direction was measured over a span of 50 mm (group A) or 40 mm (group B) in the central part of the sample, using a two-side clip gauge provided with a Sangamo DG1.0 linear displacement sensor. Cross-head speed was set to 0.67 mm/min for group A and 0.50 mm/min for group B in order to obtain a similar elastic strain rate of approximately 0.3%. The σ_L was obtained from the maximum load at failure and cross-sectional area of the sample. Test results were also used to calculate the compliance coefficients in the longitudinal direction (static s_{11}). Finally, the samples were oven-dried at 103°C for 48 h and then cooled to room temperature over phosphorous pentoxide. Oven-dry weight was then measured to the nearest 0.001 g and EMC was calculated.

The dynamic s_{11} was determined for trees from 101 families. Families were selected for the

dynamic s_{11} measurements using a stratified random sampling procedure. The number of families per stratum (provenance) was proportional to the total number of families in the stratum. The dynamic s_{11} was determined for 441 trees, of which 323 were also used for the determination of σ_L , static s_{11} and air-dry density of the specimen. A 10-mm increment core was extracted at breast height from each tree after thinning. The core extended from bark to bark through the pith following the north-south orientation. The longitudinal direction of each core was marked immediately after extraction. Subsequently, the cores were conditioned at 20°C and 60% RH for about 6 months to attain an EMC of 11.7%. A 20-mm-long segment of the core from the south side of the tree, close to the bark, was then prepared for the test.

The dynamic s_{11} was measured using an ultrasonic method described in detail by Herzig (1991) and Yang and Fortin (2001). Each segment was placed between two ultrasonic transducers (transmitter and receiver), and a 1 MHz frequency wave was propagated in the longitudinal direction through the segment. The time taken by the wave to pass through the segment was read to the nearest 10^{-6} of second. Three replicated measurements were made on each segment, and time readings were only accepted when a maximum amplitude and well-defined transmitted wave onset could be seen on the oscilloscope display. The distance of wave propagation was equal to the diameter of the segment: this was measured to the nearest 0.001 mm. A correction factor was applied to the calculation of wave velocity through the core in order to compensate for the error caused by the presence of the coupling medium (neoprene membrane) and the transport of electric waves within the measuring circuit (Herzig 1991; Yang and Fortin 2001). A plexiglas core, with the same dimension as the wood core, was used as a reference to determine the correction factor. The dynamic s_{11} was calculated using the following equation: $s_{11} = (\rho v^2)^{-1} (\text{MPa})^{-1}$, where ρ = air-dry density (kg/m^3) at time of testing, and v = velocity (m/s) of wave propagation. The air-dry density used in this formula was determined using X-ray

densitometry for a 20-mm-long section of wood sampled at breast height and carefully matched to the 20-mm-long segment (hereafter called either density of the slice or ρ_{20}). It should be noted that the values were not corrected to take into account the effect of Poisson's ratio on the wood segments, so they are approximate values for dynamic s_{11} (Bucur 1981). Finally, the EMC of the segments was determined after the test following the procedure previously described.

Statistical analyses

The SAS® statistical package, version 9.1 (SAS Institute Inc. 2002–2003), was used for all statistical analyses. Data transformations were not required to satisfy the assumptions of analysis of variance and other analyses. Analyses of tree height and stem diameter are reported elsewhere (Sotelo Montes et al. 2006).

Analyses of variance of dynamic s_{11} and covariance of the other wood properties were carried out across and by planting zones (GLM procedure, partial sums of squares estimation method). Variance of dynamic s_{11} was analyzed according to a mixed linear model with the following sources of variation: zone, replication within zone [Rep(Zone)], provenance (Prov), family within provenance [Fam(Prov)], and the interactions [Prov*Zone, Prov*Rep(Zone), Fam(Prov)*Zone]. For density, σ_L and static s_{11} , the model also included dimension (Dim) and equilibrium moisture content (EMC) of the wood sample as covariates because σ_L and static s_{11} were significantly affected by EMC in the middle zone of the watershed ($P = 0.012$ and 0.026 with 283 and 393 trees, respectively). Zone was treated as a fixed factor and the others as random factors. Some F-ratios involved more than one mean square in the denominator ("quasi" F-ratios), and were tested with approximate degrees of freedom. Analyses were also carried out within each zone if there was a significant difference in the wood property due to zones and/or a significant interaction between zones and provenances/families.

Data for density of the compression specimen, σ_L and static s_{11} were adjusted across zones for Dim and EMC (based on covariate relationships) but not for dynamic s_{11} and density of the slice (ρ_{20}). Variance components were estimated using the VARCOMP procedure with the restricted maximum likelihood method. Phenotypic correlations (Pearson r) were calculated at the tree level (CORR procedure). Simple and multiple linear regressions (REG procedure) using the same sample size (323 trees) were used to develop models for predicting σ_L and static s_{11} from the independent variables ρ_{20} and dynamic s_{11} . For the multiple linear regression models, the stepwise method was used and they were compared using Akaike's information criterion (AIC), the model with the lowest value for AIC being the best model. Narrow sense heritability (h_i^2) based on individual trees, genetic correlations, and their standard errors were estimated using formulas described elsewhere (Becker 1984; Falconer and Mackay 1996). Phenotypic correlations include both genetic and environmental effects, whereas genetic correlations reflect only genetic effects (Falconer and Mackay 1996). Trait values were standardized (Steel et al. 1997) for calculation of genetic correlations. Heritability (h_i^2) was estimated assuming partial inbreeding (Sotelo Montes et al. 2006); in this case, additive genetic variance was estimated as $3\sigma_f^2$. These assumption and estimation methods have been used for some other tropical hardwood species (Hodge et al. 2002; Hodge and Dvorak 2004) in order to provide a conservative estimate of h_i^2 .

RESULTS AND DISCUSSION

Means and coefficients of variation of wood mechanical properties and density

Mean air-dry density of *Calycophyllum spruceanum* wood was significantly greater ($P < 0.001$, 323 trees, paired t-test) for the slice ($\rho_{20} = 761 \text{ kg/m}^3$) than for the compression specimen (717 kg/m^3). It is likely that the mean density of ρ_{20} was greater because (a) density increases from the pith to the bark (Sotelo Montes et al. unpublished data), (b) the 20-mm slices and the compression specimens were obtained close to the bark, but the compression specimens varied more in the radial position given the machining requirements (orientation of samples, jointing, and planing), (c) the slices were obtained at 1.3 m above ground whereas the compression specimens were obtained between 0.75 and 1.2 m above ground, and (d) density was estimated by two different procedures and with a different number of trees and families.

Mean values for σ_L and density of juvenile wood in the present study (Table 1) were lower than those reported by Keenan and Tejada (1984) for mature wood of *C. spruceanum*. This was expected based on differences in density and other properties between juvenile and mature wood (Tsoumis 1991). However, the specific strength (ratio of σ_L to density of the compression specimen) of *C. spruceanum* juvenile wood (70) was similar to that of mature wood (72, Keenan and Tejada 1984). This means that when adjusted for differences in density, both juvenile and mature woods of *C. spruceanum* have a similar strength in parallel compression, even though they might differ in several charac-

TABLE 1. Descriptive statistics of density, ultimate crushing strength (σ_L), static and dynamic parallel compliance coefficients (s_{11}) for *Calycophyllum spruceanum* wood at 39 months.^a

Trait	Mean	CV ^b	Range	N ^c
Air-dry density (kg/m^3)	718	5.9	250.0	676
Ultimate crushing strength, σ_L (MPa)	50.1	10.1	28.2	676
Static s_{11} (TPa^{-1})	75.3	18.2	77.2	676
Dynamic s_{11} (TPa^{-1})	77.3	15.7	72.2	441

^a Data for density, σ_L and static s_{11} are adjusted for dimension and equilibrium moisture content of the wood sample (as covariates).

^b Coefficient of variation.

^c Number of trees.

teristics, including microfibril angles, proportion of rays, fiber length, cell-wall thickness, as well as the content of lignin, extractives, and other chemical constituents (Skaar 1988; Tsoumis 1991; Lei et al. 1997; Zobel and Sprague 1998; Evans et al. 2000; Bowyer et al. 2003). The specific strength of wood varies among species. For example, compared with other tropical hardwoods, the specific strength in parallel compression of juvenile wood of *C. spruceanum* was lower than that of *Tectona grandis* wood evaluated at 8 years in plantation (78, air-dry density = 580 kg/m³; Rivero 2004), and similar to mature wood of *Cariniana domestica*, *Copaifera officinalis*, and *Terminalia guianensis* grown in natural stands (71, 70, and 72, respectively, with air-dry density = 720, 730, and 740 kg/m³, respectively; Keenan and Tejada 1984).

Juvenile wood of *C. spruceanum* is relatively stiff, which is also important for structural uses. Its specific stiffness in parallel compression (ratio of static modulus of elasticity [E_s] to density of the compression sample = 18494) was higher than the specific stiffness in static bending of juvenile wood of *T. grandis* (17812; Rivero 2004). It was also higher than the specific stiffness in static bending of *C. officinalis* mature wood, but lower than that of *C. domestica* and *T. guianensis* mature wood (16529, 22345, and 18957, respectively; Keenan and Tejada 1984).

The dynamic s_{11} is usually lower than the static s_{11} , as observed in mature wood of conifers (Bodig and Jayne 1982) and hardwoods (Bucur 1983; Oliveira et al. 2002). The difference between the dynamic and static s_{11} tends to be smaller in parallel compression tests than in bending tests (Herzig 1991). This is because the ultrasonic method, which is used to determine the dynamic s_{11} , deals mostly with elastic effects (Bucur 1983), whereas the static bending test deals with shear effects (Ilic 2001). Moreover, the difference between the dynamic and static s_{11} in static bending tests is smaller for increment cores than for standard specimens (Bucur 1983).

The mean values for the dynamic and static s_{11} (75.3 and 75.4 TPa⁻¹, respectively; data not tabled) were not significantly different (paired

t-test, $P = 0.80$) when compared using the same sample size (323 trees). However, when the mean dynamic and static s_{11} were expressed as specific values (i.e., divided by their density) and compared for the same number of trees, the specific dynamic s_{11} was about 6% lower than the specific static s_{11} , and this difference was statistically significant (paired t-test, $P < 0.001$). This result is consistent with previous values reported for other hardwood species (Bodig and Jayne 1982; Bucur 1983; Hernández and Restrepo 1995; Hernández et al. 1998; Oliveira et al. 2002; Bucur 2006).

The CVs for the static and dynamic s_{11} of *C. spruceanum* wood (Table 1) were similar to those reported for other species (Hernández and Restrepo 1995; Bucur 2005). Judging from the CVs, there was relatively more variation in the static and dynamic s_{11} than in σ_L .

Variation in wood mechanical properties and density

Environmental conditions affect tree growth and can indirectly produce variation in mechanical properties (Tsoumis 1991). For example, significant differences between sites were observed in dbh and E_d of juvenile wood of selected clones of *Cryptomeria japonica* (Nakada et al. 2003). However, in the present study, there were no significant differences in density and mechanical properties between the two planting zones (Table 2). Similar results were observed for basic density of cross-sectional disks (Sotelo Montes et al. 2006) and density of wood slices (Sotelo Montes et al. unpublished data) sampled at breast height in trees from the same two zones. The environmental difference between the two planting zones was probably not large enough to produce significant differences in these wood properties, even though there were significant differences in tree growth between zones (Sotelo Montes et al. 2006).

There was statistically significant variation in all wood properties due to families within provenances, although variation in air-dry density of the compression specimen was barely significant (Table 2). In addition, variation due to prov-

TABLE 2. Analysis of covariance of air-dry density, ultimate crushing strength (σ_L) and the static parallel compliance coefficient (static s_{11}), and analysis of variance of the dynamic parallel compliance coefficient (dynamic s_{11}) for *Calycophyllum spruceanum* wood at 39 months.^{a,b}

Source of variation	DF	Density		σ_L		Static s_{11}		DF	Dynamic s_{11}	
		P > F	VAR	P > F	VAR	P > F	VAR		P > F	VAR
Zone	1	0.065	—	0.140	—	0.143	—	1	0.237	—
Rep(Zone)	4	0.368	—	0.110	—	0.461	—	4	0.293	—
Prov	6	<0.001	3.8	0.001	4.6	0.005	2.6	6	0.098	4.7
Fam(Prov)	189	0.054	7.7	<0.001	18.2	<0.001	15.2	94	0.014	6.9
Prov*Zone	6	0.999	0.0	0.909	0.1	0.995	0.0	6	0.339	0.0
Prov*Rep(Zone)	23	0.161	0.0	0.126	0.0	0.230	0.0	24	0.170	1.3
Fam(Prov)*Zone	154	0.088	8.2	0.154	1.9	0.713	0.0	89	0.726	0.0
Dim	1	0.198	—	0.599	—	0.922	—	—	—	—
EMC	1	0.916	—	0.339	—	0.307	—	—	—	—
Residual	289	—	80.3	—	75.2	—	82.2	216	—	87.1
Total	674	—	100.0	—	100.0	—	100.0	440	—	100.0

^a Dimension (Dim) and equilibrium moisture content (EMC) of the wood sample are covariates for density, σ_L and static s_{11} .

^b DF = degrees of freedom; P > F = significance of F ratio; VAR = percentage of the total phenotype variance explained by the variance component.

ences was significant for all properties except dynamic s_{11} . Families within provenances accounted for a larger percentage of the total phenotypic variance (VAR) than provenances, especially for σ_L and static s_{11} . In addition, the percentage of variance explained by families within provenances was larger for static than for dynamic s_{11} . Moreover, provenance and family rankings in mechanical properties and density were relatively stable across zones, judging by the fact that variation due to the interactions (provenance by zone, family within provenance by zone) was not statistically significant. These results suggest that greater gains in wood mechanical properties could be achieved by selecting the best families within provenances after having selected the best provenances. However, the most appropriate strategy depends on several factors, including the amount of phenotypic variance in the trait, its heritability, and its genetic correlations with other traits (discussed below), as well as economic considerations (Namkoong et al. 1988).

Genetic variation in mechanical properties has also been observed in other hardwood species. For example, significant variation has been reported for juvenile wood of hybrid poplar clones (Hernández et al. 1998) and families of *Eucalyptus grandis* (Santos et al. 2003), and for mature wood of clones of *C. japonica* (Fujisawa et

al. 1994) and provenances of *T. grandis* (Bhat and Priya 2004).

The dimension of specimens (covariate Dim in Table 2) did not have a significant effect on density, σ_L or static s_{11} in the analysis of covariance across zones. This is consistent with previous research investigating the effect of sample dimension on wood properties (Hernández 1993; Ilic 2003), and is likely related to the fact that the samples had the same length:width ratio (4:1).

Heritability of juvenile wood mechanical properties and density

Estimates of narrow-sense heritabilities (h_i^2) were moderately high for σ_L (0.51) and static s_{11} (0.47), and relatively low for air-dry density of the compression specimen (0.24) and dynamic s_{11} (0.22) (Table 3). Therefore, considering only h_i^2 , selection would be most effective if based on σ_L , slightly less effective if based on static s_{11} , and least effective if based on air-dry density and dynamic s_{11} .

Other researchers have also reported moderate to high h_i^2 values for strength and stiffness in parallel to the grain compression of juvenile wood. For example, h_i^2 was 0.57 for σ_L of *Eucalyptus grandis* (Santos et al. 2003). Broad-sense heritability of a trait is generally higher

TABLE 3. Heritability of density, ultimate crushing strength (σ_L), static and dynamic parallel compliance coefficients (s_{11}) for *Calycophyllum spruceanum* wood at 39 months.^a

Trait	Heritability	Standard error	Number of trees
Density (kg/m ³)	0.24	0.17	676
σ_L (MPa)	0.51	0.18	676
Static s_{11} (TPa ⁻¹)	0.47	0.18	676
Dynamic s_{11} (TPa ⁻¹)	0.22	0.19	441

^a Data for density, σ_L and static s_{11} are adjusted for dimension and equilibrium moisture content of the wood sample (as covariates).

than its narrow-sense heritability because its numerator includes both additive and non-additive genetic variances (Falconer and Mackay 1996). Broad-sense heritability was 0.47 for σ_L , 0.34 for static s_{11} (both determined using small, clear standard samples) and 0.66 for dynamic s_{11} (determined using increment cores) of juvenile wood from hybrid poplar clones (Hernández et al. 1998), and ranged from 0.60 to 0.86 for E_d (determined by a non-destructive method) of mature wood from *C. japonica* clones (Fujisawa et al. 1992).

Phenotypic and genetic correlations between the tree's growth and wood mechanical properties and density

Phenotypic correlations (Pearson r, Table 4) indicated that denser wood tended to have

greater strength and stiffness (i.e., lower value of static and dynamic s_{11}), as reported for mature wood in a number of other hardwood species (Bodig and Jayne 1982; Tsoumis 1991; Hernández et al. 1998; Bowyer et al. 2003; Hernández 2007). In diffuse-porous hardwoods, generally there is little or no relationship between tree growth and the wood's density or mechanical properties (Saranpää 2003). For example, no significant correlation was observed between tree growth and (a) the mechanical properties of several diffuse porous hardwoods (Zhang 1995), (b) density and dynamic s_{11} for mature wood of *Alnus acuminata* H.B.K. (Hernández and Restrepo 1995), and (c) bending properties, E_s and σ_L for juvenile wood of *Alnus rubra* Bong (Lei et al. 1997). Hernández et al. (1998) noted a weak negative correlation between growth rate and juvenile wood density of hybrid poplar clones, with a correlation between growth rate and mechanical properties that was either weak and negative or not significant. However, due to the positive correlation between growth and density in *C. spruceanum* (Weber and Sotelo Montes 2005; Sotelo Montes et al. 2006), larger trees also tended to have wood with greater strength and stiffness.

Genetic correlations indicated the same general relationships as those shown by the phenotypic correlations (Table 4). However, with the

TABLE 4. Pearson and genetic correlations between ultimate crushing strength (σ_L), static and dynamic parallel compliance coefficients (s_{11}), and the tree's height, stem diameter at breast height (dbh) and density for *Calycophyllum spruceanum* wood at 39 months. The significance (for Pearson r) or standard error (for genetic correlations) is given in parentheses, followed by the number of trees involved in the calculation.^a

Trait	Pearson correlations			Genetic correlations ^b		
	Height	Dbh	Density	Height	Dbh	Density
σ_L	0.210	0.094	0.697	0.085	0.143	<u>0.749</u>
	(0.009)	(0.014)	(<0.001)	(0.338)	(0.255)	(0.146)
Static s_{11}	674	676	676	674	674	674
	-0.156	-0.067	-0.443	-0.238	-0.204	<u>-0.360</u>
Dynamic s_{11}	(<0.001)	(0.080)	(<0.001)	(0.358)	(0.278)	(0.322)
	674	676	676	674	674	674
	-0.282	-0.266	-0.445	<u>-0.507</u>	<u>-0.753</u>	UND ^c
	(<0.001)	(<0.001)	(<0.001)	(0.247)	(0.162)	
	438	441	323	438	438	

^a Data for density, σ_L and static s_{11} are adjusted for dimension and equilibrium moisture content of the wood sample.

^b Genetic correlations that are larger than their standard error are underlined.

^c UND = undefined: Estimate of variance component for dynamic s_{11} was zero (using 323 trees), so correlation is undefined and standard error cannot be calculated.

exception of the dynamic s_{11} , all genetic correlations with tree height and dbh had large standard errors and cannot be considered statistically significant. These results suggest that any gain in growth following selection and breeding could also bring about some gain, albeit small, in wood stiffness.

Predictive ability of non-destructive methods

The phenotypic correlations between wood strength and stiffness were strong, and in agreement with the results of previous studies (Bodig and Jayne 1982; Tsoumis 1991; Bowyer et al. 2003). As expected, the correlation between σ_L and static s_{11} ($r = -0.812$, $n = 676$, $P < 0.001$) was stronger than that between σ_L and dynamic s_{11} ($r = -0.567$, $n = 323$, $P < 0.001$). This is because σ_L and static s_{11} were measured from the same specimen, whereas dynamic s_{11} was measured from an increment core (even though it was extracted close to the static specimen).

The non-destructive ultrasonic method appears to be useful for estimating the static strength and stiffness of juvenile wood of *C. spruceanum* (Table 5). Dynamic s_{11} explained approximately 30% of the variation in σ_L and static s_{11} ($R^2 = 0.322$ and 0.303 , respectively, $P < 0.001$). Stronger relationships in these properties were, however, reported for other hardwood species at older ages (Bucur 1983; Hernández et al. 1998; Oliveira et al. 2002).

Wood density might also be a useful criterion for the indirect selection of *C. spruceanum* trees

with desirable wood mechanical properties (Table 5). Indeed, density (ρ_{20}) of the wood slice was more effective for predicting σ_L than static s_{11} ($R^2 = 0.304$ and 0.124 , respectively, $P < 0.001$).

The inclusion of both ρ_{20} and dynamic s_{11} as independent variables in a multiple regression model did improve the ability of these non-destructive methods to predict σ_L , based on Akaike's information criterion (Table 5). Indeed, the multiple linear regression model had the lowest value for Akaike's information criterion, indicating that it was better than the simple linear regression models (AIC = 869 for the multiple regression model using dynamic s_{11} and ρ_{20} , 916 for the simple regression model using dynamic s_{11} , and 923 for the simple regression model using ρ_{20}). Although both independent variables were statistically significant ($P < 0.001$) and together explained approximately 42% of the variation in σ_L , most of this variation was explained by dynamic s_{11} (32%). For predicting static s_{11} when dynamic s_{11} was in the equation, the additional variation explained by ρ_{20} was not significant ($P = 0.07$, multiple regression not shown in Table 5). Therefore, dynamic s_{11} was better than ρ_{20} for predicting both σ_L and static s_{11} .

In conclusion, dynamic s_{11} was the best predictor of static s_{11} , and σ_L was better predicted when considering both dynamic s_{11} and ρ_{20} as independent variables. However, these results are based on juvenile wood and cannot be extrapolated to mature wood.

TABLE 5. Simple and multiple linear regressions for predicting ultimate crushing strength (σ_L) and static parallel compliance coefficient (static s_{11}) of *Calycophyllum spruceanum* wood at 39 months. Independent variables include air-dry density of the slice (ρ_{20}) and dynamic s_{11} , which were measured using non-destructive methods.

Dependent variable	Regression equation ^a	R ^{2b}	CV ^c
σ_L	$4.2 + 0.060 (\rho_{20})$	0.304	8.3
σ_L	$69.8 - 0.26 (\text{dynamic } s_{11})$	0.322	8.2
σ_L	$33.9 + 0.039 (\rho_{20}) - 0.18 (\text{dynamic } s_{11})$	0.417	7.7
Static s_{11}	$153.8 - 0.103 (\rho_{20})$	0.124	16.7
Static s_{11}	$23.4 + 0.69 (\text{dynamic } s_{11})$	0.303	14.9

^a Pr >|t| < 0.001 for regression coefficients in all models with 323 trees. Means for dependent and independent variables: $\sigma_L = 49.9$ MPa, static $s_{11} = 75.4$ TPa⁻¹, dynamic $s_{11} = 75.3$ TPa⁻¹, $\rho_{20} = 761$ kg/m³.

^b R² = Coefficient of determination of model. All models are significant at P = 0.001.

^c CV = Coefficient of variation of model (%).

CONCLUSIONS

Results indicate that (a) juvenile wood of *C. spruceanum* is relatively strong and stiff, (b) there is genetic variation in juvenile wood mechanical properties, and (c) a greater proportion of this variation occurs among families within provenances rather than among provenances. Heritability estimates suggest that selection would be more effective for ultimate crushing strength and the static parallel compliance coefficient than for air-dry density of the specimen and the dynamic parallel compliance coefficient. Genetic correlations indicate that selecting trees with faster growth and denser wood will increase both strength and stiffness of the wood. These results, combined with results from another study of genetic variation in tree growth, suggest that there is potential to simultaneously improve tree growth, density, and some mechanical properties of juvenile wood of this species. In addition, the non-destructive ultrasonic method appears suitable for estimating mechanical properties of juvenile wood. Additional research is needed to evaluate (a) genetic correlations between mechanical properties of juvenile and mature wood; (b) heritability of mechanical properties of mature wood; (c) genetic correlations among tree growth, density and mechanical properties of mature wood; and (d) the ability of the non-destructive ultrasonic method to predict mechanical properties of mature wood of this species.

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REFERENCES

- AMERICAN SOCIETY FOR TESTING AND MATERIALS (ASTM). 1994. Standard methods of testing small clear specimens of timber. ASTM D143-94. Annual book of ASTM Standards 4.10. Philadelphia, PA. Pages 23-52.
- BECKER, W. A. 1984. Manual of quantitative genetics, 4th ed. Academic Enterprises, Pullman, WA. 191 pp.
- BHAT, K. M., AND P. B. PRIYA. 2004. Influence of provenance variation on wood properties of teak from the Western Ghat region in India. IAWA J. 25(3):273-282.
- BODIG, J., AND B. A. JAYNE. 1982. Mechanics of wood and wood composites. Van Nostrand Reinhold, New York, NY. 736 pp.
- BOWYER, J. L., R. SHMULSKY, AND J. G. HAYGREEN. 2003. Forest products and wood science: An introduction, 4th ed. Iowa State Press, Ames, IA. 564 pp.
- BUCUR, V. 1981. Détermination du module d'Young du bois par une méthode dynamique sur carottes de sondage. Ann. Sci. For. 38(2):283-298.
- . 1983. An ultrasonic method for measuring the elastic constants of wood increment cores bored from living trees. Ultrasonics 21(3):116-126.
- . 2005. Ultrasonic techniques for nondestructive testing of standing trees. Ultrasonics 43(4):237-239.
- . 2006. Acoustics of wood, 2nd ed. Springer-Verlag, Berlin, Germany. 400 pp.
- EVANS, J. W., J. F. SENFT, AND D. W. GREEN. 2000. Juvenile wood effect in red alder: Analysis of physical and mechanical data to delineate juvenile and mature wood zones. Forest Prod. J. 50(7-8):75-87.
- FALCONER, D. S., AND T. F. C. MACKAY. 1996. Introduction to quantitative genetics. Addison Wesley Longman Limited, Edinburgh, UK. 480 pp.
- FUJISAWA, Y., S. OHTA, K. NISHIMURA, AND M. TAJIMA. 1992. Wood characteristics and genetic variations in Sugi (*Cryptomeria japonica*). Clonal differences and correlations between locations of dynamic moduli of elasticity and diameter growths in plus-tree clones. Mokuzai Gakkaishi 38(7):638-644.
- , ———, ———, T. TODA, AND M. TAJIMA. 1994. Wood characteristics and genetic variations in Sugi

- (*Cryptomeria japonica*) III. Estimation of variance components of the variation in dynamic modulus of elasticity with plus-tree clones. *Mokuzai Gakkaishi* 40(5):457–464.
- HERNÁNDEZ, R. E. 1993. Influence of moisture sorption history on the swelling of sugar maple wood and some tropical hardwoods. *Wood Sci. Technol.* 27(5):337–345.
- . 2007. Influence of accessory compounds, wood density and interlocked grain on the compressive properties of hardwoods. *Wood Sci. Technol.* 41(3):249–265.
- , AND G. RESTREPO. 1995. Natural variation in wood properties of *Alnus acuminata* H.B.K. grown in Colombia. *Wood Fiber Sci.* 27(1):41–49.
- , A. KOUBAA, M. BEAUDOIN, AND Y. FORTIN. 1998. Selected mechanical properties of fast-growing poplar hybrid clones. *Wood Fiber Sci.* 30(2):138–147.
- HERZIG, L. 1991. Évaluation du module d'Young de bois d'épinette par méthode ultrasonore sur carottes de sondage. M.Sc. thesis, Département des sciences du bois, Université Laval, Québec, Canada.
- HODGE, G. R., AND W. S. DVORAK. 2004. The CAMCORE international provenance/progeny trials of *Gmelina arborea*: genetic parameters and potential gain. *New For.* 28(2-3):147–166.
- , ———, H. URUEÑA, AND L. ROSALES. 2002. Growth, provenance effects and genetic variation of *Bombacopsis quinata* in field tests in Venezuela and Colombia. *For. Ecol. Manage.* 158(1-3):273–289.
- ILIC, J. 2001. Relationship among the dynamic and static elastic properties of air-dry *Eucalyptus delegatensis* R. Baker. *Holz Roh-Werkst.* 59(3):169–175.
- . 2003. Dynamic MOE of 55 species using small wood beams. *Holz Roh-Werkst.* 61(3):167–172.
- JOZSA, L. A., AND G. R. MIDDLETON. 1994. A discussion of wood quality attributes and their practical implications. Special Publication No. SP-34. Forintek Canada Corporation. Western Laboratory, Vancouver, BC, Canada.
- KEENAN, F. J., AND M. TEJADA. 1984. Tropical timber for building materials in the Andean Group countries of South America. International Development Research Centre, Ottawa, Canada.
- KYOKONG, B., AND E. D. BELLO. 1977. Relationship of dynamic modulus of elasticity with static modulus of elasticity and modulus of rupture of *Dipterocarpus grandiflorus* and *Shorea polysperma*. *Pterocarpus* 3(1):43–54.
- LEI, H., B. L. GARTNER, AND M. R. MILOTA. 1997. Effect of growth rate on the anatomy, specific gravity, and bending properties of wood from 7-year-old red alder (*Alnus rubra*). *Can. J. For. Res.* 27(1):80–85.
- LINARES, C., E. MENESES, AND J. DIAZ. 1992. Monografía sobre capirona: *Calycophyllum spruceanum*. Proyecto Forestal ITTO PD 37/88: Utilización industrial de nuevas especies forestales en el Perú. Cámara Nacional Forestal, Dirección General de Forestal y Fauna, Lima, Peru.
- NAKADA, R., Y. FUJISAWA, AND Y. HIRAKAWA. 2003. Effects of clonal selection by microfibril angle on the genetic improvement of stiffness in *Cryptomeria japonica* D. Don. *Holzforchung* 57(5):553–560.
- NAMKOONG, G., H. C. KANG, AND J. S. BROUARD. 1988. Tree breeding: Principles and strategies. Monographs on Theoretical and Applied Genetics. Springer-Verlag, New York, NY. 180 pp.
- OLIVEIRA, F.G.R., J.A.O. CAMPOS, AND A. SALES. 2002. Ultrasonic measurements in Brazilian hardwood. *Materials Research* 5(1):51–55.
- PANSHIN, A. J., AND C. DE ZEEUW. 1980. Textbook of wood technology, 4th ed. McGraw-Hill, New York, NY. 736 pp.
- RIVERO, J. G. M. 2004. Propiedades físico-mecánicas de *Gmelina arborea* Roxb. y *Tectona grandis* Linn. F. proveniente de plantaciones experimentales del Valle del Sacta—Cochabamba, Bolivia. <http://www.monografias.com/trabajos16/gmelina-arborea/gmelina-arborea.shtml> [accessed 10 October 2005].
- SANTOS, P. E. T., I. O. GERALDI, AND J. N. GARCIA. 2003. Estimates of genetic parameters for physical and mechanical properties of wood in *Eucalyptus grandis*. *Scientia Forestalis* 63:54–64.
- SARANPÄÄ, P. 2003. Wood density and growth. Pages 87–117 in J. R. BARNETT and G. JERONIMIDIS, eds. Wood quality and its biological basis. Blackwell Publishing Ltd., Oxford, UK.
- SAS INSTITUTE INC. 2002-2003. SAS/STAT users' guide, version 9.1. SAS Institute Inc., Cary, NC.
- SEARS, R. R. 2003. New forestry on the floodplain: The ecology and management of *Calycophyllum spruceanum* (Rubiaceae) on the Amazon landscape. Ph.D. thesis, Graduate School of Arts and Sciences, Columbia University, Ithaca, NY. 246 pp.
- SIMONS, A. J., D. J. MACQUEEN, AND J. L. STEWART. 1994. Strategic concepts in the domestication of non-industrial trees. Pages 91-102 in R. B. LEAKEY and A. C. NEWTON, eds. Tropical trees: The potential for domestication and the rebuilding of forest resources. HMSO Books, London, UK.
- SKAAR, C. 1988. Wood-water relations. Springer-Verlag, New York, NY. 283 pp.
- SOTELO MONTES, C., AND J. C. WEBER. 1997. Priorización de especies arbóreas para sistemas agroforestales en la selva baja del Perú. *Agroforestería en las Américas* 4(14): 12–17.
- , R. E. HERNÁNDEZ, J. BEAULIEU, AND J. C. WEBER. 2006. Genetic variation and correlations between growth and wood density of *Calycophyllum spruceanum* at an early age in the Peruvian Amazon. *Silvae Genet.* 55(4-5):217–228.
- STEELE, R. G. D., J. H. TORRIE, AND D. A. DICKEY. 1997. Principles and procedures of statistics—A biometrical approach, 3rd ed. McGraw-Hill Series in Probability and Statistics. McGraw-Hill, Boston, MA. 672 pp.
- TOLEDO, E., AND C. RINCÓN. 1996. Utilización industrial de nuevas especies forestales en el Perú. Cámara Nacional Forestal, Instituto Nacional de Recursos Naturales, Orga-

- nización Internacional de las Maderas Tropicales, Lima, Peru.
- TSOUMIS, G.T. 1991. Science and technology of wood: structure, properties, utilization. Van Nostrand Reinhold, New York, NY. 400 pp.
- WEBER, J. C., AND C. SOTELO MONTES. 2005. Variation and correlations among stem growth and wood traits of *Calycophyllum spruceanum* Benth. from the Peruvian Amazon. *Silvae Genet.* 54(1):31–41.
- , ———, H. VIDAURRE, I. K. DAWSON, AND A. J. SIMONS. 2001. Participatory domestication of agroforestry trees: an example from the Peruvian Amazon. *Development in Practice* 11(4):425–433.
- YANG, J-L, AND Y. FORTIN. 2001. Evaluating strength properties of *Pinus radiata* from ultrasonic measurements on increment cores. *Holzforschung* 55(6):606–610.
- ZHANG, S. Y. 1995. Effect of growth rate on wood specific gravity and selected mechanical properties in individual species from distinct wood categories. *Wood Sci. Technol.* 29(6):451–465.
- ZOBEL, B. J., AND J. R. SPRAGUE. 1998. Juvenile wood in forest trees. Springer Series in Wood Science. Springer-Verlag, Berlin, Germany. 300 pp.