# WOOD STIFFNESS AND BENDING STRENGTH IN RELATION TO DENSITY IN FOUR NATIVE PROVENANCES OF PINUS RADIATA

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#### ABSTRACT

Static bending tests were conducted on small clear timber specimens from 20 trees of each of four native provenances of *Pinus radiata* D. Don: Año Nuevo, Monterey, and Cambria from mainland California, and Guadalupe Island. The specimens came from ≥5 m up the tree, with c. 24 rings from the pith. Individual specimens were cut from five equidistant positions from pith to bark, giving 400 specimens in all. Density (unextracted), modulus of elasticity (MoE), and modulus of rupture (MoR) were recorded for each specimen.

Density had the lowest coefficients of variation and MoE the highest. Provenances differed appreciably in density but not quite consistently across positions; while Guadalupe ranked top throughout, Cambria ranked lowest near the pith and Año Nuevo lowest towards the bark. MoE and MoR showed the same sort of pattern, albeit less pronounced in MoE. MoE was strongly correlated with density near the bark, but towards the pith the correlations were weaker and regressions on density less steep. MoR was even more strongly correlated with density, and with little pith-to-bark trend in regression slopes. Pith-to-bark increases were strong in all variables, and were evident in MoE and MoR even when adjusted for covariance on density. MoE in particular showed some negative skewness about its regression on density, especially near the pith, and this was believed to reflect compression wood. After adjusting for covariance on density, provenance differences in MoE and MoR were negligible, but significant differences remained among individual trees across positions.

**Keywords**: wood properties; stiffness; modulus of elasticity; bending strength; modulus of rupture; density; provenance; variation; *Pinus radiata*.

#### INTRODUCTION

Although the wood of *Pinus radiata* is a highly versatile material, its low bending stiffness (Walford 1991) tends to be a troublesome limitation, especially when the species is grown on the short rotations that are favoured by fertile sites and the silvicultural regimes that are designed for rapid attainment of piece-size specifications. Stiffness and bending strength are governed largely by basic density (i.e., specific gravity) (Harris *et al.* 1976; Bamber & Burley 1983), but stiffness can also be influenced strongly by microfibril angle (MFA) (Cave & Walker 1994; Addis Tsehaye *et al.* 1995; Walker & Butterfield 1996). The importance of

MFA relative to density as a determinant of stiffness will depend very much on the specific situation; if mean MFA (as a departure from the direction of the tracheid axis) varies widely in a range above about 10° it can become a major determinant (Walker & Butterfield 1996). Since MFA tends to decline sharply with ring number from the pith towards the bark, a corresponding gradient is to be expected in its importance as a determinant of stiffness, which will create a strong adverse effect of low tree age on mean stiffness. Empirically, Cown *et al.* (1999) found that, while MFA accounted for very little of the tree-to-tree variation in wood stiffness within the outerwood ("mature wood") zone (>10 rings from the pith), it was fully as important as wood density in accounting for the large majority of the tree-to-tree variation in wood stiffness in the corewood ("juvenile wood") zone (≤10 rings from the pith). Moreover, there is reason to believe the adverse effect of short rotations on stiffness, reflecting small numbers of rings from the pith, will be reinforced by a superimposed effect of height up the bole (Donaldson 1992; Megraw *et al.* 1999).

While MFA can be a major determinant of stiffness, it is typically far too expensive to measure to serve as a routine diagnostic tool for evaluating candidates for breeding or for segregating logs for processing. Determination of stiffness as such has the advantage of encapsulating the joint effects of density and MFA, plus those of specific defects. Measurement of stiffness has traditionally been done through static bending tests, which are slow and expensive. Recently, acoustic instruments have been developed for rapid indirect determination of stiffness (Booker & Sorensson 2000; Harris & Andrews 2000; cf. Ross & Pellerin 1991; Han 1996). However, this approach is still under development, with cross-calibration needing to be completed between acoustic methods and bending, while bending tests can be used to determine bending strength as well as stiffness.

Tree-to-tree variation in most wood properties is not only significant but is typically strongly heritable (e.g., Burdon 1992; Shelbourne 1997), which makes it easy to improve specific properties by selective breeding. However, significant provenance differences in wood properties are superimposed upon the tree-to-tree variation (Burdon & Low 1992; Burdon 1992), such that use of the Guadalupe provenance would allow much more rapid attainment of high target values for corewood density (Burdon 1992, Table 5). Also, anecdotal evidence (C.B.Low pers. comm.) has suggested some special wood-stiffness advantage in the Guadalupe provenance. While the Guadalupe provenance is of special interest for its high wood density (and any associated attributes) along with its good stem straightness (Low & Smith 1997), the other provenances were for various reasons also of interest.

This paper reports an empirical study of stiffness (modulus of elasticity — MoE) and, incidentally, of bending strength (modulus of rupture — MoR) in wood from four native provenances of *P. radiata*. For comparing the provenances these properties were studied in their own right and in relation to both radial position in the stem and density.

### MATERIAL AND METHODS Sampling

The trees chosen were a subset of the sample described by Burdon *et al.* (1999). They comprised 20 unrelated individuals from each of four provenances—Año Nuevo, Monterey, and Cambria (all from mainland California), and Guadalupe Island — grown in a common-

garden experiment. The fifth native provenance, Cedros Island, was not included because its slower growth had led to almost complete suppression. In choosing trees for this study a wide spread of wood density within each provenance was ensured using preliminary determinations made on whole discs taken from the same zone up the bole (M.F.Lausberg unpubl. data).

The growing site was Cpt 918, Kaingaroa Forest, at 525 m altitude on the Kaingaroa Plateau (Burdon, Bannister, Madgwick & Low 1992). The layout was, for purposes of this study, fully random. The trees were 31-32 years old from planting. Those chosen were unrelated to each other, were of at least subdominant crown status (generally dominant or codominant), and were free from malformation, marked lean, and any obvious crookedness in the sampling zone. From each tree an 80- to 100-cm clear bolt was cut at  $\geq 5$  m from stump level, so that it contained about 24 annual growth rings. From each bolt a bark-pith-bark slab was cut from the centre. (Throughout the sampling procedure, efforts were made to keep the incidence of compression wood in specimens to a reasonable minimum.) From one side of the slab, representing a single radius of the log, five individual specimens were obtained at equidistant positions on the radius. These positions were numbered 1–5 from the pith. Final preparation entailed air drying, machining the specimens to  $300 \times 20 \times 20$ -mm dimensions, and then conditioning to equilibrium moisture content under  $20^{\circ}$ C and 65% relative humidity (moisture content c. 14%).

The classification was thus 4 provenances × 20 trees × 5 radial positions. Mechanical testing of specimens, under conditions of static bending, was as prescribed by Mack (1979), using an Instron universal testing machine. Variables recorded included:

- MoE (MPa), i.e., stiffness
- MoR (MPa), i.e., strength
- ring width (mm) where practicable (not generally reported here)
- type of failure, according to the scale:
  - 0 =compression failure on the compression face
  - 1 = shear along the neutral axis (induced by bending shear)
  - 2 = brash fracture (indicating short tracheids)
  - 3 = simple tension failure (suggesting short tracheids)
  - 4 = splintering failure (indicating long tracheids)
  - 5 = sloping grain failure.

Also recorded, but reported on only incidentally, were work values, i.e., energy expended in bending to proportional limit, maximum stress, and failure.

Of the 400 specimens, 21 were noted to be markedly resinous (10, 7, 2, and 2 in positions 1, 2, 3, and 4 respectively).

After mechanical testing the specimens were oven-dried in order to determine nominal density  $(D_n)$   $(kg/m^3)$ , as (oven-dry weight)  $\div$  (volume at test).

### **Data Analysis**

Initial study of the incidence of sloping grain failure among different positions, and comparisons of mean MoE and MoR including and excluding specimens with sloping grain failure, indicated that such a failure had little if any effect on the validity of measurements. Accordingly, no data were discarded because of this type of failure.

Preliminary plottings of MoE and MoR vs  $D_n$  (not shown) revealed some obvious outlier values. Density records were subsequently discarded for the 21 obviously resinous specimens, and for two specimens with highly anomalous values for both density (high) and MoE (low) in relation to the normal increases from pith to bark. In all, 29 of the 400 specimens had missing or discarded data for one or more of these three variables.

Univariate analyses of variance (ANOVAs) were then performed for  $D_n$ , MoE, and MoR, using SAS® PROC GLM to test for differences and obtain least-squares means. Effects in the model were provenance, position, tree within provenance, and provenance  $\times$  position. Tree within provenance was the only random effect, and so provenance was tested (with minor adjustments for the slight imbalance in the classification) against trees within provenances, all other tests being effectively against the residual. In addition to analyses for the whole classification, separate, one-way analyses were performed for each provenance and each position.

For each of the three variables overall correlations were calculated, using SAS® PROC CORR, between values at the different positions and means across positions. Corresponding pooled within-provenance correlations were also calculated using SAS® PROC GLM (MANOVA statement).

Bivariate analyses were also carried out, in order to study the degree to which effects of provenance, position, and provenance  $\times$  position interaction in MoE and MoR could be interpreted as being incidental to variation in  $D_n$ . This entailed treating MoE and MoR as dependent variables and  $D_n$  as the independent variable. Regressions were studied using SAS® PROC REG. In addition, analyses of covariance (ANCOVAs) were carried out using SAS® PROC GLM, to test for differences and obtain least-squares means upon adjusting for  $D_n$  and position (the latter could actually be treated as either a class or a metric variable), after preliminary tests for heterogeneity of regressions among classes or subclasses. In addition to analyses for the whole classification, separate, one-way ANCOVAs were performed for each provenance and each position. In general, curvilinearity of relationships was negligible.

In addition to testing for statistical significance of effects, and estimating means with and without covariance adjustments, variance components were estimated, in order to (1) illustrate the comparative contributions of the various effects to variation and (2) indicate the potential for genetic gain from selection of individual tress within populations. For (1), SAS PROC VARCOMP Method=Type 1 was used for single variables on the entire classification, using the artificial assumption of a fully random model. For (2), tree(provenance) was treated as the only random effect.

Some alternative options for specifying models in SAS® PROC GLM were explored, without substantially altering the results.

#### **RESULTS**

Incidence of types of failure according to position is summarised in Table 1, categories 2–4 representing a scale of increasing desirability. No failures of types 0 and 1 were recorded. The two strongest trends were a decrease in proportion of brash fractures and an increase in splintering fractures with increasing position number from the pith. Incidence of both sloping grain failure and simple tension failure initially increased with position number, but then fell as splintering failure became more prevalent.

Type of failure	Position (from pith to bark along radius)					
	1	2	3	4	5	
2 – Brash fracture	62	37	25	12	4	
3 – Tension failure	8	. 19	26	33	20	
4 – Splintering failure	0	0	1	8	37	
5 – Sloping grain	10	24	27	25	18	
Total satisfactorily tested	70	80	79	79	79	

TABLE 1-Modes of failure, showing frequencies by position along stem radius.

Coefficients of variation, overall and within the main classes, were by far the lowest among the three variables for  $D_n$  (despite ensuring a good spread of density among trees within provenances) and highest for MoE (Table 2). They were considerably lower within positions than within provenances, but not substantially lower within provenance/position subclasses than within positions (details not shown), pointing to the predominant role of position among the sources of variation. Among provenances Cambria showed the highest values.

TABLE 2-Overall mean	s, and coefficients of variation	(CV), for $D_n$	, MoE, and MoR.
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Statistic	Class			
		$D_n$	MoE	MoR
Means	Overall	400.7 kg/m <sup>3</sup>	7851 MPa	68.2 MPa
CV (%)	Overall	13.8	35.9	27.3
C 7 (70)	Position: 1	9.61	22.8	19.4
	2	9.02	23.7	17.4
	$\frac{\overline{}}{3}$	9.57	20.5	14.7
	4	8.04	19.0	15.0
	5	9.91	19.0	16.0
	Provenance: Año Nuevo	13.1	33.1	26.0
	Monterey	12.9	36.6	26.5
	Cambria	16.0	40.1	32.1
	Guadalupe	11.7	34.3	24.0

Single-variable comparisons ("unadjusted" values for MoE and MoR) are summarised for positions, provenances, and provenance/position subclasses in Tables 3 and 4 respectively. All three variables differed strongly among positions  $(p \to 0)$ , and increased quite steadily with position number from the pith (Table 3). Overall provenance means differed significantly for  $D_n$  (p=0.0015) and unadjusted MoR (p=0.001), but not quite for MoE (p=0.07), with Guadalupe showing markedly higher values than the three other provenances (Table 3).

Provenance  $\times$  position interaction was extremely significant (p < 0.0001) for all three single variables (Table 4). This reflected some changes in relative values for the different provenances as position from the pith increased. In Position 1 Guadalupe showed clearly the highest values, with Cambria lower than Monterey and Año Nuevo. Proceeding outwards, the superiority of Guadalupe eventually became far less pronounced, while Año Nuevo became the lowest for all three variables. This had the effect of provenance differences being significant in Positions 1, 2, and 5, but not in Positions 3 and 4. When MoE was adjusted for

Category	$D_n$	MoE	(MPa)	MoR	(MPa)
	$(kg/m^3)$	Unadjusted	Adjusted	Unadjusted	Adjusted
Position					
1	341	4 813	6725	48.0	62.1
2 3	376	6 262	7034	58.7	64.3
3	392	7 287	7560	64.7	66.7
4	419	8 986	8391	74.6	70.0
5	465	11 426	9359	91.8	76.5
Differences					
F <sub>4.~275 d.f</sub> .†	289	310	20.0	324	16.9
p	$\rightarrow 0$				
Provenance					
Año Nuevo	385 b	7 352	7854	64.0 b	67.5
Monterey	399 b	7 784	7834	68.0 b	68.2
Cambria	391 b	7 494	7875	64.2 b	66.8
Guadalupe	419 a	8 286	7731	73.4 a	69.2
Differences					
F <sub>3,76 d.f.</sub> †	5.66	2.42	0.09	5.90	0.69
р	0.0015	0.07	0.97	0.001	0.56

TABLE 3-Least-squares position and provenance means overall, for density (D<sub>n</sub>), and for MoE and MoR both unadjusted and adjusted for covariance on density.

covariance on  $D_n$  some residual interaction was evident (p = 0.02), but the adjustment effectively eliminated such interaction in MoR (Table 4).

It was possible, by treating position as a metric rather than a categoric variable, to partition the combined sums of squares for position and provenance  $\times$  position interaction into three effects: (1) the overall linear effect of position, (2) heterogeneity among provenances of linear regressions on position, and (3) lack of fit. For all three variables in question ( $D_n$ , MoE. and MoR) the overall linear effect was very predominant, but the other two effects were still at least highly significant (p = 0.001 and 0.002 for heterogeneity of regressions on position for MoE and MoR respectively, otherwise p < 0.0001). Major contributions to this heterogeneity of regressions clearly came from the steep pith-to-bark increases for all three variables in the Cambria sample.

Tree-within-provenance differences across positions were extremely significant (p < 0.0001) for all three unadjusted variables. Repeatability of least-squares tree means—which could be calculated as (F-1)/F (Baker 1986, p. 36), F being the variance ratio in testing for tree-within-provenance effects — was 0.85, 0.77, and 0.79 for  $D_n$ , MoE, and MoR respectively. Average repeatability of such tree-to-tree differences, from any one position to another, could be calculated as  $\sigma_t^2/(\sigma_t^2 + \sigma_e^2)$ , where  $\sigma_t^2$  and  $\sigma_t^2$  are the tree-within-provenance and residual variances respectively, the values being 0.54, 0.46, and 0.43 for  $D_n$ , MoE, and MoR respectively.

Tree-to-tree differences were also reflected in between-position correlations (Table 5). Most of these correlations were strong and positive, but were weaker with increasing

<sup>†</sup> Model without covariance adjustment: provenance, tree(provenance), position, provenance  $\times$  position. Figures for provenances in a column that are suffixed with a letter in common do not differ significantly ( $\alpha = 0.05$  comparisonwise). Suffix letters omitted in absence of significant differences within column.

TABLE 4—Least-squares provenance means, position by position, for density  $(D_n)$ , and for MoE and MoR both unadjusted and adjusted for covariance on density.

Position	Provenance	$D_n$	MoE (	(Mpa)	MoR	(Mpa)
		$(kg/m^3)$	Unadjusted	Adjusted	Unadjusted	Adjusted
1	Año Nuevo	330 b	. 4710b	4 871	46.3 bc	48.3
	Monterey	345 b	4 780 b	4 728	48.4 b	47.7
	Cambria	326 b	4 142 b	4 360	41.9 c	44.8
	Guadalupe	366 a	5 691 a	5 331	56.1 a	51.1
	Differences - p	0.001	0.006	0.05	0.0001	0.05
2	Año Nuevo	372 b	6 514 a	6 640	58.2 b	59.0
	Monterey	373 b	6 143 ab	6 249	58.3 b	59.2
	Cambria	358 b	5 573 b	6 046	51.6 c	55.6
	Guadalupe	404 a	6 791 a	6 082	65.8 a	59.6
	Differences - p	0.0002	0.08	0.46	0.0002	0.24
3	Año Nuevo	382	6 782	7 036	61.4	63.3
	Monterey	393	7 483	7 476	66.0	65.9
	Cambria	386	7 547	7 696	63.1	64.2
	Guadalupe	407	7 347	6 977	68.1	65.3
	Differences - p	0.10	0.38	0.25	0.12	0.68
4	Año Nuevo	410	8 506	8 854	71.8	73.1
	Monterey	423	9 295	9 179	76.4	75.7
	Cambria	415	8 828	8 976	72.6	73.6
	Guadalupe	431	9 3 1 8	8 931	77.8	75.5
	Differences - p	0.24	0.40	0.88	0.28	0.71
5	Año Nuevo	436 b	10 221	11 369	83.2 b	90.9
	Monterey	464 a	11 518	11 539	91.9 a	92.1
	Cambria	477 a	11 590	11 080	92.7 a	89.3
	Guadalupe	482 a	12 354	11 660	99.2 a	94.7
	Differences - p	0.006	0.02	0.46	0.006	0.15
Provenai	$nce \times position - p$	< 0.0001	< 0.0001	0.02	< 0.0001	0.50

Figures for provenances within a column that are suffixed with a letter in common do not differ significantly ( $\alpha = 0.05$  comparisonwise). Suffix letters omitted in absence of significant differences within column.

difference in position. Among correlations between individual positions the highest values tended to involve the intermediate positions; this evidently reflected the time-series nature of the correlations and some inherent "noisiness" of the Position 1 data. Correlations between means and individual positions tended to be higher than those between individual positions, which would be expected from the fact that each individual position contributed to a mean. Interestingly, the correlations involving means tended to be higher than even the correlations between neighbouring positions, suggesting that components of purely random "noise" variation were indeed contributing strongly to imperfect correlations between positions. Among the variables the correlations tended to be highest for D<sub>n</sub> and lowest for MoE. Pooled within-provenance correlations were not greatly different and so are not shown.

Regressions of MoE on  $D_n$  were strongly heterogeneous among positions (Table 6), becoming much steeper as position out from the pith increased but with some corresponding decrease, to large negative values, in intercepts. While the fitted regressions never quite

TABLE 5—Between-position	n correlations	(overall) f	or each	variable.
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Pos	ition			Position		
		1	2	3	4	5
Density						
2	2	0.74				
3	3	0.50	0.63	_		
4	1	0.42	0.64	0.72	auth	
	5	0.41	0.42	0.56	0.64	_
	Mean	0.79	0.84	0.81	0.83	0.76
MoE						
2	2	0.53				
<u> </u>	3	0.31	0.53			
	4	0.19	0.43	0.63	_	
4	5	0.23	0.27	0.54	0.50	
I	Mean	0.54	0.73	0.82	0.78	0.78
MoR						
2	2	0.72				
2	3	0.46	0.59			
4	4	0.24	0.44	0.73		
4	5	0.37	0.33	0.56	0.57	Manage
ľ	Mean	0.68	0.76	0.85	0.78	0.79

p = 0.05,  $r \approx 0.22$ ; p = 0.01,  $r \approx 0.28$ ; p = 0.001,  $r \approx 0.36$ 

Mean denotes average over all positions for the tree, including the position involved in the correlation.

TABLE 6–Statistics for regressions of MoE (MPa) and MoR (MPa) on density (D<sub>n</sub>) (kg/m<sup>3</sup>), by positions.

Position	No. of specimens	R	$\mathbb{R}^2$	Slope	Intercept (Mpa)	CV <sub>e</sub> (%)
MoE						
1	68	0.55	0.30	18.3	-1428	19.2
2	73	0.57	0.32	24.9	-3118	19.6
3	76	0.54	0.29	23.8	-2041	17.4
4	75	0.69	0.48	35.0	5718	13.8
5	79	0.84	0.71	40.5	-7396	13.8
Heterogeneity o	f regressions: F	3,270 d.f.* 7.28				
	p	< 0.00	01			
MoR						
1	69	0.78	0.51	0.221	-27.7	12.3
2	74	0.80	0.63	0.238	-31.1	10.6
3	75	0.68	0.46	0.192	-10.5	10.8
4	76	0.68	0.47	0.226	-20 5	11.0
5	79	0.86	0.75	0.275	-35.9	8.1
Heterogeneity o	of regressions: F	0.00				

<sup>\*</sup> Model: Provenance, tree(provenance), position, provenance×position, D<sub>n</sub>, D<sub>n</sub>×position.

intersected within their own data ranges, they did so within the total range of  $D_n$ , those for Positions 4 and 5 intersecting with the remainder (Fig. 1). Coefficients of determination ( $R^2$ ) increased markedly towards the bark (Positions 4 and 5), with decreases in the total and error

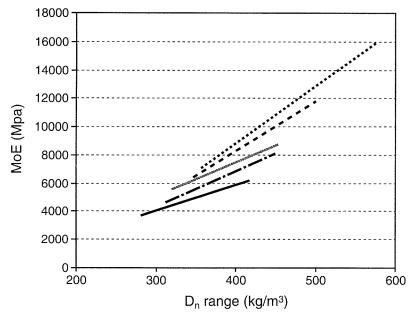


FIG. 1—Regressions of MoE (MPa) on D<sub>n</sub> (kg/m³), for each of the five positions from near the pith towards the bark. Regressions are drawn for the ranges of D<sub>n</sub> represented in the data. Position 1——; Position 2———; Position 3——; Position 4———; Position 5 ……

coefficients of variation. Regressions of MoR on  $D_n$  were mildly heterogeneous among positions, but without showing any clear trend (Table 6). Values of  $R^2$  tended to be higher and coefficients of variation lower than those involving MoE, without such marked trends with position.

Among provenances there was no statistically significant heterogeneity of regressions of either MoE or MoR on  $D_n$  (Table 7). Likewise, there was no heterogeneity among provenances for individual positions (p ranging from 0.1 to 0.9) despite the apparently wide variation in slopes and  $R^2$  values in the latter (details not shown). For individual provenances, across positions, the coefficients of determination and regression slopes on  $D_n$  (Table 7) were higher than those for individuals across provenances within positions (Table 6), largely reflecting the substantially higher total coefficients of variation resulting from bulking data from all five positions.

Differences among positions, while much reduced by the covariance adjustment (Table 3), remained extremely significant (p < 0.0001), although reservations must attach to such comparisons in view of the heterogeneity of regression slopes among positions.

After adjusting for covariance on  $D_n$ , provenance differences in both MoE and MoR were essentially obliterated (Tables 3 and 4), except perhaps in Position 1. Across-positions differences among trees within provenances, however, were still extremely significant (p < 0.0001) after the adjustment; repeatabilities of adjusted means were 0.70 and 0.71 for MoE and MoR respectively, and average repeatabilities of tree differences from any one position to another were 0.33 and 0.35 for MoE and MoR respectively.

TABLE 7–Statistics for regressions of MoE (MPa) and MoR (MPa) on density (D<sub>n</sub>) (kg/m<sup>3</sup>), by provenances.

Provenance	No. of specimens	R	R <sup>2</sup>	Slope	Intercept	$CV_e$
MoE						
Año Nuevo	94	0.84	0.70	40.0	-8 071	18.1
Monterey	95	0.86	0.74	47.7	-11 216	18.5
Cambria	91	0.90	0.82	43.7	-9 588	17.2
Guadalupe	91	0.89	0.77	59.2	-12720	17.2
Heterogeneity of re	gressions: F <sub>3</sub>	3,271 d.f. *0.37 0.77				
MoR						
Año Nuevo	97	0.87	0.76	0.282	-45.0	12.7
Monterey	95	0.93	0.86	0.327	-62.2	9.8
Cambria	91	0.92	0.85	0.301	53.5	12.3
Guadalupe	91	0.89	0.79	0.317	-59.2	10.9
Heterogeneity of re	gressions: F	3.274 d.f.*0.10 0.95				

<sup>\*</sup>Model: provenance, tree(provenance), position, provenance×position, density, provenance×density.

Estimated variance components, assuming a fully random model, illustrate the preeminence of position as a source of variation (Table 8). Tree-within-provenance variances were comparable in magnitude to residual variances, and provenance and position × provenance variances were the smallest. The rankings of the variables for coefficients of variation held for all effects.

TABLE 8-Estimates of variances and coefficients of variation (CV) for individual effects for each variable, assuming fully random model.

Effect	Variable				
	$D_n$	MoE	MoR		
Variance					
Position	2217	6 406 856	270.6		
Provenance	132	85 453	15.5		
Tree(provenance)	622	1 016 105	47.6		
Position × provenance	71	111 713	4.5		
Residual	560	1 604 735	63.4		
Percentage total variance					
Position	60.6	69.5	67.4		
Provenance	3.8	0.9	3.9		
Tree(provenance)	17.7	11.0	11.8		
Position × provenance	2.0	1.2	1.1		
Residual	15.9	17.4	15.8		
CV%					
Position	11.5	32.2	24.1		
Provenance	2.9	3.7	5.8		
Tree(provenance)	6.2	12.8	10.1		
Position × provenance	2.1	4.3	3.1		
Residual	5.9	16.1	11.7		

Estimated among-tree variances were markedly higher for individual positions than overall, with or without covariance adjustments for density (Table 9). However, this would reflect a combination of underlying effects including both true tree × position interaction and the "noise" variation for determinations on individual specimens.

TABLE 9-Estimates of among-tree variances and coefficients of variation (CV), by position, for the respective variables, with and without covariance adjustments for density in the cases of MoE and MoR.

Position	$D_n$ (kg/m <sup>3</sup> )	Unadj	usted	Adjusted	
	(kg/III*)	MoE (MPa)	MoR (MPa)	 МоЕ (MPa)	MoR (MPa)
Variances					
1	875	1 061 531	63.3	863 324	34.3
2	919	2 044 272	80.1	1 498 072	37.2
3	1079	2 289 583	91.7	1 588 425	50.2
4	1121	3 266 276	132.7	1 585 082	68.8
5	1869	4 448 470	188.8	1 423 525	53.2
Overall*	622	1 016 105	47.6	504 549	17.5
CV%					
1	8.7	21.4	16.6	19.2	12.2
2	8.0	22.9	15.3	19.7	10.5
3	8.4	20.8	14.8	17.3	11.0
4	8.0	20.1	15.4	14.0	11.1
5	9.3	18.5	15.0	10.5	8.0
Overall*	6.2	12.8	10.1	9.1	6.2

<sup>\*</sup> Adjusting for position as well as density.

Where MoE was anomalously low in relation to  $D_n$  there were often major anomalies in the work values to the various specified points (details not shown). Paradoxically, they were often much higher than for specimens with more typical MoE values. Some such specimens also had anomalously wide growth rings and high  $D_n$ , relative to other positions within the tree. Yet among the remaining specimens, without anomalous work values, there was overall an extremely significant (p < 0.0001) negative relationship (details not shown) between density and ring width after fitting effects of provenance, tree within provenance, and the individual-tree linear regressions of  $D_n$  on position number. This relationship, however, was evident only in the Año Nuevo and Monterey samples.

#### DISCUSSION

Important to the interpretation of results is an understanding of the nature and sources of "noise" variation. Because the specimens were unextracted, resin content would have been a source of upwards bias in density determinations, even though density figures for the obviously resinous specimens were discarded. This bias would have been greater in the inner positions, which would have included some heartwood. It would also have varied from tree to tree, especially in the zone where heartwood occurred (cf. Cown *et al.* 1992). There was likely to be some provenance variation in this respect; Burdon & Young (1991), studying 5-mm increment cores, found Guadalupe to have the highest resin content, and Año Nuevo

and Cambria the lowest, these differences being evident mainly towards the pith. The expected effects of high and variable resin content will be:

- distortion of provenance comparisons for density,
- reduction in apparent pith-to-bark (position) variation in density,
- · reduction of apparent MoE and MoR in relation to density,
- increased, and negatively skewed, variation about regressions of MoE and MoR on D<sub>n</sub>,
- some flattening of fitted regression slopes for MoE and MoR on density.

All except the first two of these effects can also arise, at least for MoE, through high and variable microfibril angles depressing stiffness in some of the specimens. Whether such an effect relates to the presence of mild compression wood is unconfirmed.

The indications are that resin content has not caused major bias in the provenance comparisons for density. The differences observed in Position 1 (Table 4) are similar to those observed in corewood specimens that had no heartwood (Burdon & Low 1992) or resinextracted specimens (Burdon & Young 1991), the main exception being that the Monterey mean was relatively high in this study, in accordance with the high resin contents observed in Monterey heartwood (Burdon & Young 1991). Also, the pattern of variation between consecutive positions (except possibly Positions 2 and 3 (Tables 3–5; Fig. 1)) suggests no serious bias from elevated resin contents near the pith. The method of taking and preparing specimens in this study would have facilitated avoiding unnecessarily resinous material.

The use of covariance adjustments of MoE and MoR for  $D_n$  was a means of exploring the degree to which different sources of variation in MoE and MoR could be interpreted as incidental to the effects of variation in density. Where effects of  $D_n$  could not fully account for variation in MoE and/or MoR, there was no direct evidence concerning other mechanisms, making surmise inevitable. That MoE was more variable than MoR in relation to  $D_n$  (Table 6) is consistent with an important role of MFA in determining stiffness, given that MoR as a variable that relates to the vagaries of specimen failure (including sloping grain failure) is inherently more subject to "noise" variation. The decline, from the pith towards the bark, in the error coefficient of variation ( $CV_e$ ) for the regression of MoE on  $D_n$  (Table 6) is also consistent with such an effect, given that MFA tends to exceed 10° (above which stiffness tends to decline markedly) much more frequently in corewood than in outerwood (Donaldson 1992; Walker & Butterfield 1996; Cown et al. 1999). This latter line of evidence, however, is tenuous, since a similar relative decline in  $CV_e$  is shown by MoR, and resin content could elevate  $CV_e$  for both MoE and MoR in the inner positions.

As an incidental point, the high work values in specimens of anomalously low MoE (sometimes associated with anomalously wide growth rings) suggest the presence of compression wood, and that this wood had a considerable capacity to stretch. The relationship, at the level of residual effects, between density and ring width is inherently ambiguous because the occurrence of compression wood will tend to make it positive whereas it is likely to be negative in the absence of compression wood. This ambiguity, together with the likelihood that some cases of compression wood were not recognised, could explain the inconsistent pattern among the provenance samples. The results also support the interpretation that brash fracture, which predominated in the core, was due primarily to shortness of the tracheids.

Position differences for the individual variables (Tables 3 and 4) conformed to the classical expectations of a pith-to-bark increase. However, the pre-eminently linear relationships of  $D_n$ , MoE, and MoR on position number was in some degree fortuitous; the effect of the curvilinear relationships of these variables to ring number from the pith was evidently offset by a countervailing effect of a curvilinear relationship between ring numbers and position number which would reflect the pith-to-bark decline in ring width. Comparisons among positions after adjusting for covariance on  $D_n$  are complicated by the heterogeneity of regression slopes, particularly for MoE (Table 6). However, given how the regressions radiate largely from beyond the lower range of  $D_n$  for MoE (Fig. 1), plus the fact that the incomplete overlap between positions in  $D_n$  reduces the power of tests for covariance-adjusted differences, it is concluded that there are genuine differences in MoE and MoR between positions in relation to  $D_n$ . Such differences would be expected on a priori grounds, given how MFA falls and tracheid length rises from the pith outwards (Walker & Butterfield 1996: Cown et al. 1999).

In similar vein, it is of note that when positions are bulked within provenances the fitted regressions of MoE and MoR on  $D_n$  are markedly steeper with higher coefficients of determination (Tables 6 and 7).

Differences among provenances for  $D_n$  (Tables 3 and 4) were in general agreement with previous results (Burdon & Low 1992), at least for the corewood. The increasing values, relative to the other provenances, shown by Cambria proceeding towards the bark are of interest. It is likely that they reflect at least in part the greater susceptibility of this provenance to needle cast (Burdon, Bannister & Low 1992), since experimental simulation of such defoliation has increased density and tracheid length while reducing diameter growth (Cown 1977), and average disc diameter was lower for the Cambria trees sampled for this study (Lausberg unpubl. data). In this connection, it may also be noted that among the provenances the overall least-squares mean ring width (after fitting effects of position, tree, and tree × position) was lowest in the Cambria specimens (9.2 mm, compared with 10.6 mm, 10.0 mm, and 9.5 mm in Año Nuevo, Monterey, and Guadalupe respectively — details not shown), which may also relate to the high coefficients of variation for the wood properties in Cambria (Table 1).

The relatively low outerwood density in Año Nuevo (Table 4) is noteworthy, and it may reflect environmental plasticity that is in some degree specific to this provenance. Given the environmental plasticity of branching pattern in this provenance (Burdon *et al.* 1997), it may be no coincidence that the growing site was relatively cool, and that New Zealand *P. radiata* (which has derived mainly from Año Nuevo) tends to have low outerwood density on cool sites (Cown *et al.* 1991). However, it may also reflect the highest overall least-squares mean ring width shown by the Año Nuevo sample.

That a spread of densities was ensured among trees within provenances would tend to reduce the statistical significance of provenance differences for the individual variables (it would also tend to inflate between-position correlations (Table 5)). However, it should not in principle affect the tests for differences in MoE and MoR after adjusting for covariance on D<sub>n</sub>, although imperfect determinations of density (largely through not having extracted resin) would cause some residual bias. Also, the notable lack of heterogeneity of regressions among provenances (Table 7) was reassuring. Overall, any provenance differences in MoE and MoR in relation to density are clearly very minor. While the covariance-adjusted means

for Position 1 were almost statistically significant, this was both an isolated case and involved the position where variable resin content (cf. Burdon & Young 1991) was most likely to have affected the efficiency of the covariance adjustment.

The tree-to-tree differences across positions in MoE and MoR (Tables 8 and 9), even after covariance adjustment, are noteworthy. They must be interpreted in the light of the provenance × position interaction being a fixed effect. While coefficients of variation for MoE and MoR suggest that corewood differences may have contributed strongly, the corewood differences are also likely to be of practical importance in their own right. In any event, the tree-to-tree differences in adjusted values suggest a real potential for genetic improvement by selection within populations.

Interpretation of the tree-to-tree variation in terms of the potential for genetic gain in MoE and MoR must be very tentative. Expected genetic gain is the product of: the selection intensity (in standard deviations), the operative heritability (h<sup>2</sup>), and the phenotypic standard deviation (or coefficient of variation (CV) if the expectation is to be expressed in percentage gain). While we obtained no heritability estimates in this study, the behaviour of the betweenposition correlations and other statistics for MoE and MoR relative to those for  $D_n$  suggests general agreement with the preliminary heritability estimates of Matheson et al. (1997) (for small clearwood specimens) and Jayawickrama (in prep.) (acoustic determinations on standing trees). Assuming on this basis  $h^2 = 0.4$  and CV = 20% for MoE, the expected genetic gain per unit standard deviation of phenotypic selection would be ≈8% — if MoE is considered across positions the heritability is likely to be higher but the CV lower ( $\approx 13\%$ ). For MoR, assuming  $h^2 = 0.6$ , CV = 16%, the corresponding expectation would be 9–10% (CV ≈ 10% across positions). An important limiting factor could be selection intensity achievable, because of determination costs and the need to select for other traits, but acoustic determination of MoE (Booker & Sorensson 2000; Harris & Andrews 2000; cf. Ross & Pellerin 1991; Han 1996) promises a major reduction in the costs and therefore an increase in possible selection intensity.

Selection for density, which is highly heritable (Burdon & Low 1992; Burdon 1992) is of course an option for indirect improvement of MoE and MoR. How effective it would be will depend on the strength of its genetic correlations with these variables. Our study gave no estimates of these correlations, but the indications are that they would be very imperfect in the corewood and especially for MoE, which would make indirect selection through density significantly inefficient. However, given the comparative coefficients of variation for the three wood properties, and provided there are close genetic correlations with density as is likely in the outerwood, a genetic gain in density should be accompanied by at least proportionate gains in MoE and MoR.

No direct comparisons were available with New Zealand land-race material which had been removed from the trial. However, it was possible to compare MoE and MoR along with density between this study and other sites in New Zealand (see Bier & Britton 1999). Our values of MoE relative to D<sub>n</sub> were, for each of our sampling positions, well above the country-wide regression on D<sub>n</sub> (details not shown). Two possible reasons for this discrepancy, which are not mutually exclusive, are (1) a lower incidence of compression wood in our material, and (2) that Bier's results were based on MoE/Dn relationships established from breast-height specimens rather than at 5.5 m. Our sampling protocols probably made it easier to avoid compression wood (cf. Walford 1985). But probably more important is that the

lower part of the butt log tends to both contain more compression wood (Burdon 1975) and have higher microfibril angle ring for ring from the pith (Donaldson 1992, Fig. 1) with consequently lower MoE. Anomalously low MoE in relation to ring from pith has been shown clearly for the lower butt log zone in *P. taeda* L. by Megraw *et al.* (1999) and appears to be not inconsistent with what would be expected from Donaldson's MFA data (1992) for *P. radiata*. Moreover, Donaldson (1996) found that in cuttings with some maturation ("physiological ageing"), in which the lower boles tend to show characteristics that are typical of higher up the bole in seedlings, breast-height MFA tended to be lower than in seedlings.

For MoR, however, our values ranged from being slightly above the country-wide regression for Position 5 to markedly below it for Position 1. It is likely that in studies reported by Bier & Britton (1999) outerwood received heavier weightings in deriving site means than in deriving overall means in this study, which might explain the apparent disparity between their MoR results and ours.

Thus there is no convincing evidence that, for MoE and MoR in relation to density, the native provenances differ materially from the New Zealand "land-race" stocks.

#### CONCLUSIONS

Stiffness and to a lesser extent strength show much higher coefficients of variation than density. Both stiffness and strength are strongly correlated with density, except that stiffness is very imperfectly so in the corewood zone. It appears that, because of the higher coefficients of variation in stiffness and strength, genetic gains from selection for density could be accompanied by at least proportionate gains in stiffness and strength, despite imperfect correlations with density.

Despite the strong overall correlations with density, stiffness and strength increased, even in relation to the increasing density, from the pith towards the bark. The pattern is consistent with microfibril angle and tracheid length being important additional determinants of stiffness and strength respectively, especially in corewood.

Provenance differences in stiffness and strength, while present, appear to have been essentially incidental to provenance differences in density. Tree-to-tree differences across positions in stiffness and strength are evident within provenances, even after adjusting for covariance on density. The nature of these differences further indicates that within-population selection may be used to give genetic gains beyond those accruing just from gains in density.

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