

GENETIC SURVEY OF *PINUS RADIATA*. 6: WOOD PROPERTIES: VARIATION, HERITABILITIES, AND INTERRELATIONSHIPS WITH OTHER TRAITS

R.D. BURDON and C.B. LOW

New Zealand Forest Research Institute,
Private Bag 3020, Rotorua, New Zealand

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ABSTRACT

Wood properties were studied in ≥ 4 trees \times 2 sites \times 50 wind-pollinated progenies \times 7 populations in a *Pinus radiata* D. Don provenance-progeny trial in Kaingaroa Forest in the central North Island of New Zealand. Specimens were taken at around 1.4 m height and contained rings 1–5 from the pith. Oven-dry wood density and ring width were determined throughout, and grain spirality in rings 2 and 5, compression wood, pith diameter, and tracheid lengths in subsamples. These data were analysed along with height and diameter data.

Wood density averaged about 10% higher in the slower-growing island populations (Guadalupe and Cedros) than in the Californian mainland ones. Compared with Monterey, Año Nuevo and Cambria averaged around 1.5% and 4% lower respectively, and the two New Zealand populations (Kaingaroa and Nelson) $\geq 1\%$ higher. Grain spirality was worst in Año Nuevo, but comparisons among other populations were complicated by site interaction (in contrast to other traits) and population differences in pith-to-bark spirality gradient. Compression wood was most prevalent in the island populations, and least in those from mainland California. Differences between local subdivisions of native populations were generally negligible.

Density showed within-population coefficients of variation (CV) of 6–7% but ring-5 spirality showed CVs of around 50% or more. Variances and narrow-sense heritabilities (h^2) appeared similar among populations. Ring-5 spirality gave \hat{h}^2 generally well over 0.5 within sites, but some unexplained family \times site interaction lowered across-sites \hat{h}^2 . Ring-2 spirality, which was studied within only one site, gave lower \hat{h}^2 and families varied appreciably in between-ring spirality differences. For density \hat{h}^2 was generally ≥ 0.65 , but with possibly less additive genetic variation in Año Nuevo than in Monterey and Cambria. Family \times site interactions appeared minimal. Estimates of \hat{h}^2 for density in the New Zealand populations, from sib-analysis and offspring-parent relationships respectively, agreed closely, suggesting essentially random mating.

Wood density showed a negative association (both genetic and within-family phenotypic correlations) with ring width, but a positive association with tree height, a situation that tends to be obscured by the strong association between height and diameter.

Keywords: variation; inheritance; provenance; heritability; correlation; genetic parameters; wood properties; wood density; spiral grain; *Pinus radiata*.

INTRODUCTION

Possible genetic improvement of wood properties in *Pinus radiata* is of considerable interest, for several reasons. The silvicultural attractiveness of the species has made it completely pre-eminent among commercial softwoods wherever it can be grown satisfactorily. That has led to it being used for a wide range of industrial processes and end purposes. While the wood is inherently versatile, and much can be achieved by segregation of log categories, there are still problems in producing raw material that is highly suitable for the various processes and end uses. More recently, improved seed orchard technology (Shelbourne *et al.* 1989) has made it feasible to produce different breeds or seedlots of *P. radiata* for specific situations.

Early studies on a number of conifers (*see* review by Zobel 1964; Zobel & Talbert 1984; Zobel & van Buijtenen 1989) pointed to considerable heritable genetic variation in certain wood properties, and preliminary studies on *P. radiata* (Dadswell *et al.* 1961; Nicholls 1965, 1967; Pederick 1971) indicated that this species was no exception.

Pinus radiata occurs naturally in five perfectly discrete populations, two being accepted as representing separate varieties (Axelrod 1980; Bannister & McDonald 1983), which makes the species more likely than most to show marked provenance differences in key wood properties.

The existence of intensive breeding programmes in *P. radiata* has potentially a three-fold significance in breeding for wood properties. Firstly, if any important wood properties are in adverse genetic correlation with the present main breeding goals, viz faster growth and/or improved tree form, undesirable side-effects on wood properties could be expected unless specific countermeasures are taken. Secondly, even without adverse genetic correlations, intensive selection of a small number of parents for producing commercial stock can lead to shifts in wood properties through genetic sampling effects. Thirdly, the existence of a pedigreed breeding programme provides an excellent context for undertaking genetic improvement of wood properties. Reinforcing these factors now is the ease of producing a range of specialised breeds within the species, through being able to mass-propagate material produced by controlled crossing (Shelbourne *et al.* 1989).

The relatively short rotations on which *P. radiata* can be grown to meet log size specifications, and the growing-cost advantages of shortening rotations, mean that corewood will tend to represent a high proportion of the log. At the same time, corewood properties in *P. radiata* tend to be limiting for a number of purposes. Prominent among the adverse properties of the corewood are low wood density (limiting for sawn timber, plywood, and some important pulp grades), spiral grain (affecting sawn timber and plywood), fibre length (believed to affect strength properties in timber and paper), and compression wood (affecting sawn timber, pulping, and paper properties). Thus, the pressure to shorten rotations creates a need for genetic improvement of wood properties, with a focus on the corewood properties.

An excellent opportunity to study the genetic control of wood properties in *P. radiata* was afforded by the availability of a large provenance-progeny trial (Burdon, Bannister, Low & Madgwick 1992), which sampled virtually the full natural range of the species. The experiment was designed as both a gene-resource collection (which could be subjected to preliminary evaluation of material) and the material for a comprehensive investigation of the quantitative genetic architecture of the species.

This paper addresses the population differences in several wood properties, variation and heritability of some of those properties within populations, and intercorrelations among wood properties and some growth and form traits. Comparisons among various estimates of heritability are used to help infer mating patterns in native populations (cf. Burdon, Bannister & Low 1992b, c; Burdon 1992; Moran *et al.*, 1988). Basic density was studied in most detail, since for various reasons it was regarded as the most crucial property (Harris *et al.* 1976). Grain spirality was also studied in some detail because it can be technically important and pilot results showed excellent prospects for its improvement. Limited attention was also given to compression wood incidence, pith diameter, and tracheid length.

Some of the results have been presented in brief preliminary reports (Burdon & Bannister 1973; Harris 1989; Burdon 1991). In addition, the experiment was used for a separate study of compression wood (Harris 1977).

MATERIALS AND METHODS

The Experiment

The experiment has been described in detail by Burdon, Bannister, Madgwick & Low (1992). Basically, it represented 50 wind-pollinated progenies (families) of each of the five natural populations (Año Nuevo, Monterey, and Cambria from the Californian mainland, and Guadalupe Island and Cedros Island) plus two New Zealand control populations (Kaingaroa and Nelson). The progenies of the Californian mainland populations were samples from five well-separated localities (subpopulations) within each of those populations (Forde 1964) and those from Cedros Island sampled the two disjunct subpopulations (Libby *et al.* 1968).

The experiment was replicated on two contrasting sites (A being warmer and of high site index, B being a cooler plateau site of lower site index) in Kaingaroa Forest, and over 3 planting years (stages) at each site. Subject to a minimal restriction imposed by the "interlocking block" layout, randomisation was complete within each site/stage block. For the first planting stage the Cedros Island population sample was not to hand, and so 50 supplementary Nelson progenies were used in its place.

Sampling and Determinations

Wood specimens were obtained, during or prior to the first thinning, in four blocks, Stage I and II on both sites (A and B), from the two superimposed "colour" replicates that were due to be thinned out. Trees that were suppressed, very butt-swept, badly leaning, or severely damaged were rejected for sampling. Out of the prescribed eight trees per progeny (plus four for each of the supplementary Nelson progenies) 91% were successfully sampled for the Californian mainland populations, 95% for the New Zealand ones, and 66% for Guadalupe; for Cedros 75% were successfully sampled out of the prescribed four trees per progeny.

Complete wood discs were obtained in the Stage I blocks 7 and 8 years from planting on Sites A and B respectively, at heights (near 1.4 m) that gave just five complete growth rings for each tree. The discs taken were 5 cm thick, and cut transversely into duplicate 2.5-cm discs. One of each pair of resulting discs was used for determining grain spirality, and the other for determining ring width and oven-dry wood density from two roughly opposing sectors.

In the Stage II blocks, bark-to-pith increment cores were taken. Unlike Stage I, where the sampling was destructive, it was possible to replace some trees missing from the prescribed genetic samples with ones that were to be left after thinning. Cores were taken from opposing radii across the axis of lean from each tree for determining ring width and oven-dry density. The cores were taken at breast height at ages 8 and 9 years from planting on Sites A and B respectively; almost all had five or more growth rings, rings in excess of the fifth being trimmed off. Borings were repeated as needed to obtain at least one core per tree without severe compression wood.

Oven-dry wood density was determined using the method of water displacement for the sectors (Stage I) and the method of maximum moisture content for the cores (Stage II). Values for duplicate samples were averaged for individual trees, except for occasional trees in which one sample was rejected because of severe compression wood (cf. Harris 1977).

Compression wood incidence was scored for each core (Stage II) on a 0–3 scale (0 = absent, 3 = severe), and the scores summed for the duplicate cores from each tree.

Grain spirality was determined at the outside of rings 2 and 5 in the Site-A specimens and for ring 5 only in the Site-B specimens. Measurements were made with a freely pivoted needle (slope of grain detector) at two opposing points of the circumference, which cancels the effects of errors in determining the orientation of the stem axis (Brazier 1965).

Ring width was expressed as an average for each tree for the five rings in duplicate sectors or cores. Pith diameter was measured directly on the Site A, Stage I discs.

Tracheid length was initially measured in 10 unrelated trees (i.e., one from each of 10 families) of each population from Site A, Stage I (thus omitting the Cedros population), choosing two trees from each extreme of density and six from the mid-range per population. Determinations were made on composite samples from the opposing disc sectors, on the second and fifth rings from the pith, each represented as both whole-ring and latewood-only samples, using the method of Harris (1966).

In the two New Zealand populations it was possible to sample the parental genotypes for wood density (for a description of the parental stands *see* Burdon, Bannister, Madgwick & Low 1992). For Nelson, both the parental ortets and ramets (grafts) were sampled. The ortets were sampled at 14 years from planting by taking single bark-to-pith 5-mm cores at breast height (1.37 m), and determinations were made by measuring core lengths and calibration of the borer for core diameters in order to measure core volumes. The ramets were grafts of which the scions had been taken from the ortets at the same age, and were planted at the Forest Research Institute, Rotorua. Duplicate bark-to-pith cores were taken which almost all contained 10 rings, and determinations were made by the method of maximum moisture content. Kaingaroa ortets were sampled at age 28 years from planting as single pith-to-bark cores that were subdivided into 5-ring segments for determining unextracted density by the method of maximum moisture content. Corewood segments that were resinous to the point of having higher unextracted density than outer segments were discarded for data analysis.

Statistical Analysis

Analyses of variance were used to test for statistical significance and to estimate variance components, basically as described by Burdon, Bannister, Madgwick & Low (1992). Among the effects, subpopulations (if significant) were nested within populations, and families were

nested within populations (or subpopulations), populations being a fixed effect, subpopulations arguably a random effect, and families a random effect. Two classes of block effect, sites and stages, were in cross-classification with the genotypic effects. For some variables, e.g., wood density, stages was definitely a fixed effect, the different weightings between stages of various rings between sectors and cores creating systematic differences between the samples of Stage I and Stage II. Sites were in theory a fixed effect, but unless they or stages differed significantly the site/stage blocks could be treated collectively as a single random effect, generating random interactions with genotypic effects.

Among the traits, compression wood scores, and to a lesser extent spirality, showed positive skewness but, because normalising transformations had minimal effect on the results, all results presented are for untransformed variables. Analyses of variance were repeated in selected cases as analyses of covariance, adjusting sums of squares for within-class covariance, ring width being a commonly used covariate.

Heritabilities were estimated using the sib-analysis method as set out by Burdon, Bannister & Low (1992b) using the provisional assumption of random mating—in other words, that the progenies were half-sib families. Estimates made under this assumption can be designated apparent heritabilities. Where appropriate, standard errors for estimates were calculated (Falconer 1981, Ch. 10). For wood density in the two New Zealand populations, where parental information was available from both ortets and ramets, offspring-parent regression analysis could be used (Becker 1984). The correlation method of Franklin (1974) was used as a cross-check on the regression method, having a special advantage where there was appreciable heterogeneity of variances between parental and offspring material. Comparisons among the different types of heritability estimate could be used to help infer the more exact mating patterns that had generated the wind-pollinated progenies.

Such information could, in turn, be used to revise the assumed coefficients of genotypic relationship in the families, and hence to propose adjustments to the “apparent” heritabilities (Burdon, Bannister & Low 1992b). Inbreeding can be expected to cause greater upward bias, when random mating is assumed, in estimates of additive genetic variance and heritability from sib-analysis than in those from offspring-parent regressions or correlations.

The other relevant items of information to be considered in inferring mating patterns and the coefficients of relationship have been addressed by Burdon, Bannister & Low (1992b, Table 3).

Genetic correlations between traits were likewise estimated mainly by sib-analysis, as set out by Burdon, Bannister and Low (1992d), for those involving wood density in the New Zealand populations; however, supplementary estimates were made using offspring-parent relationships (Becker 1984).

RESULTS

Subpopulation Differences

Differences between local subdivisions of the Californian mainland populations and Cedros were clearly very minor. Half the tests for statistical significance give $F < 1$, and the occasional significant tests ($\alpha = 0.05$) were so few as to suggest Type I errors, which would reflect chance effects of sampling rather than true biological differences. Indeed, the estimated overall variance for wood density among subpopulations, for what it was worth,

was below 5 (kg/m³)². Thus, while such differences were presumably not zero they were too small to be of consequence or to be estimated satisfactorily with the samples involved. Accordingly, the results are not presented in detail and the subpopulation classification is henceforth disregarded.

Population Differences

Wood density differed markedly between populations (Table 1), the island populations showing roughly 10% higher density than the Californian mainland populations, at least in the first five rings from the pith. Among the latter Monterey had the highest density and Cambria the lowest, while the New Zealand populations were marginally higher than any mainland one. These differences were expressed very consistently over blocks, although the Stage I samples (sectors) averaged about 14 kg/m³ higher than the Stage II samples (cores) and the warmer Site A averaged about 9 kg/m³ higher than Site B.

TABLE 1—Population averages for wood density (kg/m³), compression wood scores (sums of 0–3 scores for duplicate cores), and pith diameter (mm).

Population	Basic density (all 4 blocks)	Compression wood		Pith diameter (Site A, Stage I)
		Site A	Site B	
Año Nuevo	321 bc	1.04 ab	1.42 a	3.7 a
Monterey	326 b	1.00 ab	1.51 ab	4.0 a
Cambria	313 c	0.96 a	1.65 abc	4.1 ab
Kaingaroo	328 b	1.24 ab	1.76 abc	4.2 ab
Nelson	329 b	1.48 bc	1.87 c	4.4 b
Guadalupe	358 a	2.36 c	2.30 d	3.5 a
Cedros*	360 a	2.68 c	1.88 bc	–

Values within a column that are suffixed by a letter in common do not differ significantly ($\alpha=0.05$ comparisonwise, protected t-tests), “a” denoting the most desirable value(s) for the trait.

* Samples available from only the two Stage II blocks.

Compression wood scores (Table 1) showed a greater overall expression of population differences at Site A than at Site B. At both sites the mainland populations averaged the lowest (i.e., most desirable) scores, with Kaingaroo being marginally higher and Nelson slightly higher still. Of the island populations Cedros showed the highest scores at Site A, with Guadalupe slightly lower there, but at Site B Guadalupe averaged highest with Cedros essentially the same as Nelson.

Ring widths varied according to stem diameter differences which have already been reported by Burdon, Bannister & Low (1992a), so are not reported in detail here. Briefly, the New Zealand population showed the highest values, ahead of the mainland populations which differed little, with Guadalupe appreciably lower and Cedros considerably lower again.

Population differences in pith diameters (Table 1) were marginally significant statistically ($p \leq 0.05$), the New Zealand populations having the highest values and Guadalupe the lowest. Given a within-population correlation with ring width of 0.4, and the population differences in ring width or diameter growth, the population differences in pith diameter could confidently be regarded as essentially incidental to growth-rate differences.

All grain spirality variables (Table 2) showed very highly significant ($p < 0.001$) differences between populations within sites, and the within-ring values were still very highly significant, although generally slightly less pronounced, after adjusting for positive individual covariance on ring width. The pattern of differences, however, was rather complex. There were marked population differences in differential spirality between rings 2 and 5, and in ring 5 there were some obvious population \times site interactions which were associated with greater spirality overall at Site B. Among the populations, Año Nuevo stood out as having consistently the greatest spirality, and the New Zealand populations appeared to have relatively high spirality in ring 5, but otherwise there was no consistent pattern of differences among the populations. Given the apparently large interactions between just the two sites, no attempt was made to infer the statistical significances of population differences across sites.

TABLE 2—Population averages for grain spirality variables ($^{\circ}$)

Population	Both sites Ring 5	Site B Ring 5	Site A			
			Ring 5	Ring 2	Average	Difference
Unadjusted values						
Año Nuevo	4.76	4.95 b	4.56 d	7.35 c	5.95 c	2.79 ab
Monterey	2.86	3.70 a	2.03 ab	5.24 ab	3.63 ab	3.21 ab
Cambria	3.22	3.90 a	2.55 bc	4.72 a	3.63 ab	2.17 bc
Kaingaroa	4.10	4.97 b	3.22 c	4.65 a	3.94 ab	1.43 c
Nelson	3.78	4.90 b	2.66 bc	5.39 b	4.02 ab	2.73 ab
Guadalupe	2.54	3.62 a	1.47 a	5.20 ab	3.32 a	3.73 a
Adjusted for within-family covariance on ring width						
Año Nuevo	4.81	5.04 b	4.58 d	7.36 c		
Monterey	2.90	3.75 a	2.04 ab	5.24 ab		
Cambria	3.28	3.97 a	2.58 bc	4.74 a		
Kaingaroa	3.84	4.56 b	3.12 c	4.57 a		
Nelson	3.60	4.61 b	2.58 b	5.32 ab		
Guadalupe	3.20	4.61 b	1.78 a	5.45 b		

Values within a column that are suffixed by a letter in common do not differ significantly ($\alpha = 0.05$ comparisonwise, protected *t*-tests), "a" denoting the most desirable value(s) for the variable.

Tracheid length differences (Table 3) were marginally significant ($p < 0.05$) overall in ring 2, but not after adjusting for individual covariance on ring width. In ring 5, however, they were very highly significant ($p < 0.001$) and were essentially unaffected by covariance adjustments. Despite sharper resolution of population differences in ring 5, the pattern of population differences was similar to that for ring 2. The population samples fell into two groups—Nelson and Guadalupe which had markedly shorter tracheids, and the rest. An independent follow-up sample of 10 trees from each of the Nelson and Guadalupe populations was studied (Table 3). For ring 2 these latter values were consistent with those observed for the remaining populations, but for ring 5 they were clearly inconsistent with the observed mean for the Cambria sample.

Variations and Heritabilities within Populations

Wood density

Estimated narrow-sense heritabilities (h^2) for wood density from sib-analysis (Table 4) were all very highly significant ($p < 0.001$), and were consistently high (all >0.5) and

TABLE 3—Means (mm) of population samples for tracheid-length variables. Figures in parentheses are values adjusted for within-population covariance on ring width; figures in square brackets apply to follow-up sample studied in the light of anomalous results.

Population	Whole ring		Latewood only		
	Ring 2	Ring 5	Ring 2	Ring 5	
Año Nuevo	1.68 (1.67)	2.44	1.80 (1.79)	2.58	
Monterey	1.73 (1.72)	2.44	1.80 (1.78)	2.66	
Cambria	1.71 (1.71)	2.65	1.88 (1.88)	2.84	
Kaingaroo	1.74 (1.71)	2.54	1.84 (1.80)	2.87	
Nelson	1.53 (1.53)	2.16	1.68 (1.68)	2.46	
	[1.72]	[2.48]			
Guadalupe	1.57 (1.62)	2.09	1.66 (1.73)	2.38	
	[1.64]	[2.35]			
LSD	0.149	—	0.146	—	0.221
p population diffs	<0.05	>0.05	<0.05	>0.05	<0.001

TABLE 4—Estimates of genetic parameters for wood density from sib-analysis by populations, assuming half-sib families.

Population(s)	Between-families variance ($\hat{\sigma}_f^2$)	Within-families variance ($\hat{\sigma}_w^2$)	Narrow-sense heritability ($\hat{h}^2 \pm$ s.e.)	Phenotypic variance ($\hat{\sigma}_p^2$)	$\hat{CV}_p\%$
Año Nuevo	60	266	0.74 \pm 0.21	326	5.6
Monterey	128	405	0.96 \pm 0.26	533	7.1
Cambria	115	364	0.96 \pm 0.26	479	7.0
Pooled within mainland*	101	345	0.89	446	6.6
Kaingaroo	55	360	0.53 \pm 0.19	415	6.2
Nelson	98	318	0.94 \pm 0.22	416	6.2
Pooled within New Zealand	76	339	0.73	416	6.2
Guadalupe†	148	641	0.75 [\pm 0.25]	791	7.9
Cedros	156	361	1.21 \pm 0.37	517	6.3

* Arithmetic averages of statistics for component populations.

† Arithmetic averages of within-block statistics, which will be marginal over-estimates.

$\hat{h}^2 = 4 \hat{\sigma}_f^2 / (\hat{\sigma}_f^2 + \hat{\sigma}_w^2)$, assuming σ_A^2 (additive genetic variance) = $4\sigma_f^2$

$CV_p =$ Phenotypic coefficient of variation = $\sigma_p / (\text{population mean})$

$\sigma_p^2 = \sigma_f^2 + \sigma_w^2$

generally very high (>0.7). Estimates tended to be higher for native populations than for the New Zealand ones, but confidence limits of estimates for individual populations were clearly quite wide. Variances and the phenotypic coefficient of variation were highest in the Guadalupe population, and they tended to be comparatively low in the New Zealand populations. Among the mainland populations the estimated variance components differed appreciably ($p < 0.05$, Bartlett test, for within-families variances), both components being markedly lower in Año Nuevo. Results for Cedros, which gave an out-of-bounds value for \hat{h}^2 , were clearly less precise on account of a smaller sample. Site interaction was clearly

minimal (F ratios clustering around 1) within populations, estimates of variances and heritabilities being virtually unaffected by alternative procedures for pooling estimates across blocks.

The values for trees contained sampling errors, which could be estimated assuming random variation between duplicate cores/sectors, albeit with a likely upward bias through the opposing positions of the duplicates. Accepting a sampling error variance of 30 at the designated sampling position on the tree (40 in Guadalupe and 35 in Cedros), the estimates of the biological phenotypic variance would be reduced and those of "biological" \hat{h}^2 raised by nearly 0.1.

Comparing heritability estimates for wood density in the New Zealand populations, from sib-analysis and offspring-parent relationship respectively (Table 5), the overall agreement was very close. While sib-analysis gave a lower \hat{h}^2 in Kaingaroa but a higher \hat{h}^2 in Nelson, the average for the two populations (weighted according to numbers of families involved) was very close to 0.75 whatever the method or sample of material. In any case the discrepancies for individual populations were well within likely estimation error, the sib-analysis estimates having larger standard errors than those listed for the estimates from offspring-parent regression.

Offspring-parent heritability estimates for the Kaingaroa population, involving different core segments from the ortets, are shown in Table 6. Those obtained by the regression method tended to decline outwards from the pith, unlike those from the correlation method,

TABLE 5—Estimates of narrow-sense heritability (h^2) for wood density in New Zealand populations using alternative methods of estimation (assuming half-sib families).

Sample	Method	Kaingaroa			Nelson		
		Progenies	\hat{h}^2	s.e.	Progenies	\hat{h}^2	s.e.
Stage I	Sib-analysis	50	0.63	0.29	100	0.81	0.21
	O/P regression*	35	0.89	0.18	49	0.61	0.08
	O/P correlation	35	0.86	•	49	0.70	•
Stages I and II	Sib-analysis	50	0.53	0.19	50	0.94	0.22
	O/P regression	34	0.80	0.13	49	0.68	0.12
	O/P correlation	34	0.85	•	49	0.68	•

* O/P denotes offspring-parent.

TABLE 6—Estimates of narrow-sense heritability (h^2) for wood density in the Kaingaroa population from relationships between offspring values in rings 1–5 from pith and parental (ortet) values in successive core segments. Values in parentheses are standard errors.

Ortet segment (rings from pith)	Stage I only			Stages I and II		
	No. of progenies	Method		No. of progenies	Method	
		Regression	Correlation		Regression	Correlation
1–5	35	0.89 (0.18)	~0.86	34	0.80 (0.13)	~0.85
6–10	38	0.65 (0.17)	~0.7	36	0.44 (0.13)	~0.49
11–15	24	0.76 (0.14)	~1.0	22	0.72 (0.13)	~0.88
16–20	18	0.43 (0.10)	~0.9	18	0.44 (0.11)	~0.78

which presumably reflects the tendency for variances to increase outwards from the pith (cf. Bannister & Vine 1981)—such variances were parental in nature and contributing to denominators of the heritability estimates.

Other traits

Heritability estimates for pith diameter were very imprecise with the small sample involved, particularly for individual populations. Overall, the indications were that $h^2 \approx 0.35$.

Estimates of heritability for the grain spirality variables were almost all very high within sites (Table 7), and coefficients of variation tended to be extremely high, particularly at Site A for ring-5 spirality and the spirality differential between rings 2 and 5. The within-site heritability estimates for individual populations (not shown in detail) were very imprecise because of the very small family samples, and so no satisfactory comparisons of the estimates could be made between populations. Estimates were actually slightly higher for the New Zealand material than for the Californian mainland samples (Tables 7 and 8), but this comparison carries little statistical weight. Among populations the phenotypic coefficients of variation for spirality (not shown in detail) varied little, those for ring 5 at Site B all falling between 40% and 46% except for a value of 54% for Guadalupe.

TABLE 7—Pooled estimates of within-site variances and narrow-sense heritability (assuming half-sib families) for spirality variables.

		Variance		Heritability		$\hat{CV}_p \dagger$
		$\hat{\sigma}_f^2$	$\hat{\sigma}_p^{2*}$	\hat{h}^2	(p)	
Californian mainland populations only						
Site A,	Ring 2	0.24	3.54	0.34	(>0.05)	33
	Ring 5	1.59	5.12	1.24	(<0.001)	74
	Average	0.71	3.04	0.94	(<0.01)	40
	Difference	0.94	5.27	0.71	(<0.05)	84
Site B,	Ring 5	0.56	3.65	0.62	(<0.05)	46
All populations except Cedros						
Site A,	Ring 2	0.63	3.73	0.67	(<0.05)	36
	Ring 5	1.55	5.36	1.16	(<0.001)	83
	Average	0.82	3.12	1.05	(<0.001)	48
	Difference	1.06	5.29	0.81	(<0.01)	87
Site B,	Ring 5	0.95	3.98	0.96	(<0.001)	46

* Pooled within-population values

† $CV_p = \text{phenotypic coefficient of variation} = \sigma_p / (\text{overall mean})$

Other statistics as designated for Table 4.

Ring-5 spirality was the only variable measured at both sites, and it showed appreciable family \times site interaction (Table 8). While the across-site heritability estimates were thus eroded compared with within-site estimates (Table 7) they were still high, averaging c. 0.65.

For all the tracheid length variables the observed between-tree coefficients of variation were around 9%.

TABLE 8—Estimates of genetic parameters, by populations, for grain spirality in ring 5 over both sites.

Population	Variance				Narrow-sense heritability*	
	$\hat{\sigma}_f^2$	$\hat{\sigma}_{fs}^2$	(p)	$\hat{\sigma}_{p\ddagger}^2$	$\hat{h}^2\ddagger$	(p)
Año Nuevo	0.81	0	(>0.5)	5.31	0.61	(<0.05)
Monterey	0.56	1.22	(0.009)	4.24	0.53	(<0.05)
Cambria	0.54	0.75	(0.06)	3.46	0.62	(<0.05)
Kaingaroa	1.19	1.60	(0.025)	6.42	0.74	(<0.01)
Nelson	0.94	0.60	(0.05)	4.55	0.82	(<0.001)

* Assuming half-sib families

† Estimated by pooling family-site interaction with error, which causes only minor bias (Burdon, Bannister & Low 1992b).

σ_{fs}^2 = family \times site interaction variance.

Other statistics as designated for Table 4.

Intercorrelations between Traits

Estimates of genetic correlations between wood density and growth-rate variables obtained by alternative methods are shown for individual populations in Table 9. The estimates based on growth data from the entire experiment were made using the method of Burdon (1977); applying this method to the augmented data sample for the less heritable traits assumed independence of within-family samples for wood density and the growth traits instead of being a small subsample (around eight out of almost 40), and so the resulting estimates are subject to bias (albeit of uncertain magnitude). The absolute magnitudes of the correlation estimates varied markedly according to both population and the method used, which clearly reflected wide (if mostly ill-defined) confidence limits for individual estimates, such that very few would be statistically significant in themselves. The Cambria population showed highly anomalous values, and the correlation statistics proved to be dominated by a single progeny of particularly low density and poor growth. Nevertheless there was an overall trend, particularly in the New Zealand populations, for density to show markedly more positive, or less negative, genetic correlations with height than with diameter/ring width. Assuming a genetic correlation over all populations between height and diameter/ring width of c. 0.7 (Burdon, Bannister & Low 1992d) this points to an average partial genetic correlation between density and ring width/diameter for constant height of around -0.4, and a corresponding correlation between density and height for constant ring width (or stem

TABLE 9—Alternative estimates of genetic correlations between wood density and growth variables.

Sample(s)	Method*	Other trait	Population				
			Año Nuevo	Monterey	Cambria	Kaingaroa	Nelson
Wood specimen trees only	1	Ring width	-0.02	0.13	0.71	-0.28	-0.38
		Height	0.42	-0.11	1.16	0.23	0.25
All trees for growth variables	2	Diameter	-0.11	-0.08	0.51	-0.29	-0.45
		Height	-0.01	0.25	0.57	-0.03	-0.02
Ortet cores/seedling sample trees	3	Ring width	-	-	-	-0.37	-0.35
		Height	-	-	-	0.22	0.17

*Methods: 1: conventional sib-analysis

2: method of Burdon (1977)

3: using offspring-parent covariances

diameter) of around 0.4; the values of such estimates vary slightly according to which of the various alternative figures are accepted for overall average genetic correlations of density with ring width and with height. Considering the New Zealand populations specifically and accepting a more conservative genetic correlation of around 0.5 between height and ring width, the corresponding partial correlations would appear to be around -0.5 and 0.5 respectively. For the native populations, which showed appreciable inbreeding (Burdon, Bannister & Low 1992a, b), the estimates of additive genetic correlations between wood density and growth-rate traits were presumably biased towards zero because, unlike wood density, growth rate shows inbreeding depression, and the depression varies according to family (Wilcox 1983).

The phenotypic within-family sample correlations involving ring width, on the one hand, and height and diameter, on the other, averaged over all populations around 0.1 and -0.1 respectively, although there were some marked and unexplained differences between experimental blocks. With an overall correlation between height and ring width of c. 0.6, this points to partial correlations of density with ring width for constant height of -0.2 and with height for constant ring width of 0.2.

Genetic correlations between density and two tree-form traits (straightness and branch habit quality) appeared to be close to zero. Density and spirality showed a very weak pooled within-population phenotypic correlation ($r = -0.05, p > 0.1$).

Within populations, spirality showed a weak positive phenotypic association with ring width at Site A, but a stronger association at Site B (Table 10). Spirality was moderately correlated between rings 2 and 5. Tracheid length showed a moderate-to-strong positive association with ring width in ring 2 but not in ring 5 (Table 11). Its association with density

TABLE 10—Pooled within-population phenotypic correlations among spirality and ring-width variables, Site A (254 d.f.)

		Spirality			
		Ring 2	Ring 5	Average	Difference
Ring width		0.08	0.18 **	0.16 (0.32 ***)	-0.11
Spirality	Ring 2		0.38 ***	0.80 ***	0.44 ***
	Ring 5			0.86 ***	-0.66 ***
	Average				-0.19 **

Value in parentheses relates to Site B

* $p < 0.05$

** $p < 0.01$

*** $p < 0.001$

TABLE 11—Average within-population phenotypic correlations (R) involving tracheid-length variables.

		Tracheid length			Density	Ring width
		Whole ring Ring 5	Latewood only			
			Ring 2	Ring 5		
Whole ring	Ring 2	0.46	0.70	•	0.07	0.40
	Ring 5	-	•	0.79	0.17	0.04
Latewood only	Ring 2		-	0.41	0.18	0.58
	Ring 5			-	0.35	0.10

r (or R) = 0.26, 0.34, and 0.43 for $p = 0.05, 0.01, \text{ and } 0.001$ respectively.

was weak except for latewood-only length in ring 5. Tracheid lengths in latewood were closely correlated with whole-ring values, but ring-2 lengths were only moderately correlated with ring-5 lengths.

DISCUSSION

Wood Density

The population differences reported by Burdon & Bannister (1973), Matziris (1979), and Nicholls & Eldridge (1980) were confirmed. The higher density in the island populations has an interesting parallel in *P. caribaea* Morelet var. *hondurensis* (Birks & Barnes 1990; Wright 1990) and in Guadalupe it persists from the core into the outerwood (Burdon & Young 1991b). The selective pressures that have operated in the New Zealand populations have, if anything, increased wood density.

The results indicated that the high heritability that has been reported for wood density in *P. radiata* (see Bannister & Vine 1981) holds for all populations. In accordance with the results of Burdon, Bannister & Low (1992b) the apparent heritabilities in native populations tended to be higher than in the New Zealand material; this suggests appreciable non-random mating in natural stands, particularly as one might expect the New Zealand populations to show if anything higher genetic variances and heritabilities because of their mixed Californian ancestry (cf. Libby 1992). Among the mainland populations there are strong indications of less genetic variation in Año Nuevo, since both $\hat{\sigma}_f^2$ and $\hat{\sigma}_w^2$ were lower and the latter, while being predominantly genetic, is based on many more degrees of freedom. The higher phenotypic variances in Monterey and Cambria populations than in the New Zealand material, even if genuine, are ambiguous since they could reflect either the effects of inbreeding (Burdon, Bannister & Low 1992c, d) or the high proportion of Año Nuevo ancestry in the New Zealand material (Burdon, Bannister & Low 1992a; Burdon 1992). It is difficult to make detailed interpretations of the results from the island populations, however, because the samples were much less complete.

The excellent agreement overall between \hat{h}^2 from sib-analysis and offspring-parent regressions respectively in the New Zealand populations provides no evidence of appreciable "full-sibbing" (i.e., small effective numbers of pollen parents per seed parent). Full sibbing will produce an upwards bias in \hat{h}^2 , since the additive genetic coefficient of relationship in full-sib families is $1/2$ compared with $1/4$ in half-sib families, yet the covariance of offspring on a single known parent is independent of the number of pollinators per parent. This use of comparisons of heritability estimates from sib-analysis with those from offspring-parent regressions depends on the assumption that the parents of study material were fully outbred which is supported by the results of Plessas & Strauss (1986) and Moran *et al.* (1988). Inbreeding, while it would tend to bias upwards the estimates (of both additive genetic variance and heritability) from both methods, would do so to a greater degree with sib-analysis; selfing at a rate z would be expected to inflate the apparent heritability by a factor of $(1 + z)$ or more in offspring-parent estimates and by around a factor of $(1 + z)^2$ or more in sib-analysis estimates (Burdon, Bannister & Low 1992b, c) unless both z and heritability are very high.

Of special interest are the genotypic relationships between density and growth rate variables. There appear to be some strong partial correlations such that high wood density

is associated, within populations, with a tall slender growth habit, and low density with a squat habit. This was particularly so in the New Zealand populations in which the differences in the growth rate variables were less likely to reflect maladaptation. While the evidence was not strong in itself it corroborates the results of Burdon & Harris (1973) and Bannister & Vine (1981), and what is implicit in results for many other conifers (e.g., Bridgwater *et al.* 1983; Vargas-Hernandez & Adams 1990; Corriveau *et al.* 1991).

The pattern of partial correlations would explain the apparent slight increase in density in the New Zealand populations which must have derived (Burdon, Bannister & Low 1992a; Burdon 1992) from Año Nuevo and, to a lesser extent, Monterey. The intense crown competition in plantations presumably favoured in the medium to long term the taller-growing genotypes that would tend to have higher density.

The relationship between density and stem diameter growth can presumably be modified by competitive influences, particularly as a closed stand gets older. The competitive advantage of tall-growing genotypes with high wood density is likely to be reflected in good long-term diameter growth despite an inherently slender growth habit. This will make it difficult to establish the true trade-off between wood density and per-hectare stem volume production (cf. King & Burdon 1991).

Compression Wood

The rejection and replacement of specimens containing severe compression wood undoubtedly created a downwards bias in the scores, but it should only have damped down the provenance differences. The higher scores for the Californian mainland and New Zealand populations at Site B than at Site A probably reflect the toppling that particularly affected these populations as a result of the “Wahine” storm in 1968, in contrast to Cedros (which was less vulnerable because the trees were shorter) and Guadalupe (Burdon, Bannister & Low 1992a).

The higher (i.e., more adverse) scores in New Zealand trees than in Californian mainland material may just reflect greater vigour (cf. Burdon & Harris 1973; Kininmonth & Whitehouse 1991). The higher scores in Guadalupe and Cedros, despite good stem straightness, are noteworthy. They may reflect a high propensity of these populations to actively straighten stems by forming compression wood (cf. Burdon 1975), or the effects of boron deficiency which could have been corrected before too many of the Cedros trees reached breast height at Site B (Burdon, Bannister & Low 1992a). It is also possible that compression wood, real or apparent, occurred after attack by the aphid *Pineus laevis* (Maskell) which affected some of the young Guadalupe trees (cf. van der Sijde *et al.* 1985); this accords with much older Guadalupe trees, which were survivors of considerable suppression, having relatively little compression wood in cores containing around 20 rings (Burdon & Young 1991b).

Separate studies (Burdon 1975; Burdon & Young 1991a) have indicated marked tree-to-tree genetic variation, and therefore heritability, for propensity to form compression wood.

Grain Spirality

Grain spirality variables showed a remarkable combination of very high within-site heritabilities (cf. Pederick 1971) and high coefficients of variation. Despite some appreciable

adverse phenotypic correlations with the low-heritability trait, ring width, this would suggest outstanding prospects for genetic improvement. There are several caveats, however.

The magnitude of genotype-site interaction, at the level of both provenances and individual families, is very puzzling. We know of no precedent in *P. radiata* for this amount of interaction to occur in a trait of very high within-site heritability. While the observed progeny \times site interaction would not unduly erode genetic gains, other sites may be involved in even greater interaction.

The determinations were made at single sampling points, but the genetic gains will depend on how representative the determined values are of the tree. Concerns were raised by strong provenance and progeny differences in differential spirality between rings 2 and 5, and have been reinforced by the wide tree-to-tree differences in the detailed pattern of within-tree variation (Cown *et al.* 1991).

A third caveat attaches to the fact that while a left-handed spiral is the norm it does not have a strict bound of zero, raising the possibility that intensive selection might even incur significant right-handed spirality.

Nevertheless, it seems unlikely that the effects of these three factors would be sufficient to vitiate genetic improvement of spirality.

Tracheid Length

The pattern of population differences is unclear, because the results of the follow-up determinations did not confirm the anomalously low values initially obtained for Nelson. A rare sampling event in the initial results is suspected. It is possible, though, that in the fifth ring Cambria has genuinely longer tracheids and Guadalupe genuinely shorter ones than the other populations.

The 9% within-population phenotypic coefficient of variation suggests, in the light of the estimated 7% additive genetic coefficient of variation (Burdon & Young 1991a), a narrow-sense heritability of ~ 0.6 for observed values. Outside ring 2 tracheid length appeared to vary essentially in its own right and not as a concomitant of ring width.

Adjustments to Heritability Estimates

The relevant statistics for adjusting estimates of additive genetic variance and heritability, in order to correct for non-random mating, are listed in Table 12, insofar as they are known or could be reasonably guessed. Applying these adjustment factors to \hat{h}^2 for density (Table 4) brought the sib-analysis estimates for New Zealand and native-population material closer into line, and down to around 0.65 to 0.7 overall. However, it brought the sib-analysis estimates slightly below those from offspring-parent regressions (Table 5). For grain spirality (Tables 7 and 8) such adjustments accentuated the higher \hat{h}^2 values in New Zealand material compared with Californian mainland samples, a feature that may reflect the generally greater spirality in the New Zealand material.

None of the adjustments, however, generated or eliminated clear discrepancies in \hat{h}^2 among population groups, given the confidence intervals of point estimates, or materially changed the picture concerning the very high heritability for these variables.

TABLE 12—Basis for proposed adjustment factors for genetic parameter estimates, relative to those obtained assuming random mating, for wood density and grain spirality.

Parameter (or estimate)	Population group			
	Mainland	New Zealand	Guadalupe	Cedros
Self-fertilisation equivalent (%)*	20	2	45	35
Field losses (%)†	3	2	15	35
Likely selective loss of inbreds (%) ‡	9	≥1	25	25
Residual “selfing” (%)	12	≤1	20	10
Full-sibbing (%)§ (a)	20	10	25	20
(b)	10	5	20	10
Coefficients of relationship among families				
(a)	0.36	0.28	0.41	0.35
(b)	0.34	0.27	0.40	0.32
Adjustment factors¶				
(a) $\hat{\sigma}^2_A$	0.70	0.90	0.61	0.72
\hat{h}^2	0.74	0.90	0.67	0.76
(b) $\hat{\sigma}^2_A$	0.74	0.94	0.62	0.77
\hat{h}^2	0.79	0.94	0.69	0.81

* General inbreeding, defined as 2F (see Moran *et al.* 1988; also Plessas & Strauss 1986) for native populations, New Zealand figure assumed (cf. Burdon & Bannister 1973)

† Among total trees planted

‡ Including, in addition to likely selective losses in field, elements in germination and up till planting out (the latter probably small)—subjective estimate

§ Assumed reciprocal of effective number of unrelated pollen parents.

(a) Assuming high values—value for New Zealand is a compromise between 20% indicated by $\hat{\sigma}^2_f / \hat{\sigma}^2_{c(f)}$ (Burdon, Bannister & Low 1992c) and almost zero indicated in this paper (Table 5) and Burdon, Gaskin, Zabkiewicz & Low (1992) by comparing \hat{h}^2 from different methods,

(b) assuming lower values

|| In relation to genetic parameters for non-inbred parents

¶ Assuming fully additive inheritance and using algorithms of Burdon, Bannister & Low (1992b, Eqn 1–3). Adjustment factor for apparent h^2 varies linearly, from that for σ^2_A as $h^2 \rightarrow 0$ to that shown for $h^2 = 1$, requiring iteration for exact solutions.

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