WOOD DENSITY IN RADIATA PINE CLONES ON FOUR DIFFERENT SITES

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ABSTRACT

Wood density was studied in 18 clones of radiata pine (**Pinus radiata** D. Don) replicated within and between four contrasting sites.

Clonal repeatabilities were high, generally 0.75 or greater, and it appears that the standard deviation of genotypic values is about 6-10% of the population mean. Notwithstanding appreciable clonal differences in the density gradient, clonal correlations were high between density in the first and second five rings from the pith.

Site effects were large, but not altogether consistent among different parts of the tree. Expression of site and genotypic differences was generally greater at breast height than higher up.

Clone-site interactions, although statistically significant, were minor, the most important involving a phosphate-deficient site and elsewhere. The clones which were severely distressed on this site showed a slightly greater density increase, in relation to another site, than the remainder.

Within sites density was very little affected by non-genetic differences in ring width, which accounted for less than 5% of the phenotypic variance at standard sampling positions.

Evidence for clonal relationships between density and growth rate in general is inconclusive. However, it appears that outside the first five rings there is a positive effect of height coupled with a negative relationship with diameter. This accords with mechanical considerations.

INTRODUCTION

Genetic experiments with forest trees have usually shown populations to contain much heritable variation in wood properties. Thus there is the prospect of improving the value of the wood by selective breeding provided that optimal wood properties can be defined by wood processors.

Heritability studies of wood characters have already been reviewed (Goggans, 1961; Hattemer, 1963; Zobel, 1964; Harris, 1965b). Density or specific gravity (oven-dry) was for various reasons the most widely studied character, and it has often shown a narrow-sense heritability of 0.5 or higher, despite its obvious complexity as a character.

Direct studies of the genetic variation in wood density in radiata pine (*Pinus radiata* D. Don) have hitherto been limited. Fielding and Brown (1960) and Dadswell *et al.* (1961) have estimated broad-sense heritability to be high, in the region of 0.7, which

accords with results for other pines. In all, four experiments were involved, containing a total of 50 clones at the most. However, these results, even if pooled, would still give imprecise estimates of the variance components. Hence, any prediction of gains in wood density that could be obtained through clonal selection would also be imprecise.

Furthermore, the success of selecting for wood density over a broad geographical region will depend not only on heritability at any one site, but also on the magnitude of genotype-site interactions. Previous clonal trials, with the exception of a very small experiment involving two microsites within a single locality (Pawsey and Brown, 1970), have been confined to single sites and therefore provided no estimates of interactions. Notwithstanding the strong genotypic effects within sites, wood density in radiata pine appears to show great environmental plasticity. Harris (1963, 1965a) found the mean density of outerwood (> 15 rings from pith) to range, within New Zealand, roughly from 0.5 to 0.4 g/cm^3 with a decrease of about 4°C in mean annual temperatures ($R^2 = 0.8$, $P < 0.001$). In addition, it appeared to be increased by phosphate deficiency. Near the pith, density also differed between sites although it was less closely related to temperature ($R^2 \cong 0.3$). It was of interest, therefore, to find out whether individual genotypes behave similarly in these respects.

The relationships between wood density and growth rate, particularly at the level of genotypes and in response to the stocking of stems within a stand, have remained obscure. Harris (1965a) observed on the average a weak but very highly significant negative association of phenotypic individual tree values between ring width and wood density, but this relationship differed among sites; Fielding and Brown (1960), in a similar but less extensive study with rather younger stands in Australia, observed a tendency towards a positive association. However, in ordinary plantations such as were involved in these studies, the genotypic and environmental correlations were fully confounded.

For the study reported in this paper wood samples were available from radiata pine clones replicated within and between contrasting sites. Not only could this trial provide further estimates of clonal and thence by inference genotypic variance in wood density, but also, despite imperfections, it gave an opportunity to study genotype-site interactions and to disentangle some genotypic and environmental interrelationships between density and growth rate.

MATERIAL AND METHODS

The Experiment

The experiment is described fully elsewhere (Burdon, 1971) and only briefly here. Eighteen clones were replicated as cuttings within and between four sites, at Glenbervie, Whakarewarewa (Whaka), Gwavas and Berwick State Forests. Not all clones were represented on all four sites, and the number of surviving cuttings (ramets) within clone-site subclasses ranged from one to six. The imbalance of the classification is illustrated by Table 1, which lists the numbers of trees from which at least one acceptable wood sample was obtained. The trial was assessed and wood samples taken 12 years after planting.

Of the sites, Glenbervie has the highest mean annual temperature and a highly infertile soil. Berwick has the lowest mean annual temperature, being at a higher latitude

TABLE 1—Numbers of ramets of each clone available for study of wood density, by sites

Clone No.	Site			
	Glenbervie	Whaka	Gwavas	Berwick
57	2	—	2	2
53	2	—	2	—
59	3	—	4	2
60	2	—	1	2
61	2	—	3	2
62	1	—	5	5
63	2	—	2	2
64	2	2	2	—
65	1	3	2	—
66	—	4	2	3
67	2	6	5	5
68	—	1	2	2
69	3	4	2	4
70	2	1	1	3
71	4	4	3	3
72	3	5	4	4
73	4	6	5	5
74	1	2	2	—
Totals	36	38	49	44

than the others, although the altitude is low. It also has a lower rainfall than the other sites.

Growth was fastest at Whaka, although two clones showed signs of an unidentified nutrient deficiency. There were no indications of appreciable nutrient deficiencies at either Gwavas or Berwick, although growth was much slower at the latter site. At Glenbervie the trees showed symptoms that are normally associated with acute phosphate deficiency. Foliar analyses (Burdon, MS, a) have revealed phosphorus levels which are typical of this condition. A notable feature at this site was the extreme difference in vigour between clones, some growing as rapidly as at Gwavas, and some failing almost completely.

Incomplete planting of surround rows, particularly at Whaka and Gwavas, made for large tree-to-tree differences in diameter growth.

Sampling Procedure

Discs, *ca.* 4 cm thick, were cut from each surviving tree at the following positions:

1. Breast height, i.e., 1.37 m above ground level.
2. Five complete annual growth stages down from the top of the tree, hereafter denoted t_5.

The t_5 discs, by definition, contained five complete annual growth rings. The breast height samples, with very few exceptions, all contained 10 growth rings.

All discs were taken clear of nodal swellings, visible compression wood associated with branch clusters, and any marked stem deformation or leader dieback at or near the specified sampling point. The discs from occasional suppressed trees were rejected.

From each disc a 0.3 cm slice was cut transversely in order to study the occurrence of compression wood (Burdon, in MS, b). From the remaining disc two sectors of 30-40° arc were cut. Wherever possible these sectors were diametrically opposed, subject to avoiding

obvious compression wood. The sectors from breast height were each cut into two specimens, one comprising the five outermost growth rings, and the other being the balance, which generally contained five rings. The sectors from each t_5 disc were not subdivided.

For purposes of later analysis the corresponding specimens from opposing sectors were treated as bulked samples (Table 2), because the locations of the two sectors from a disc were interdependent.

TABLE 2—Particulars of wood samples

Sample no.	Height	Specimen nos.	Growth rings
1	Breast height (1.37 m)	1 and 2	Outer 5, generally 6-10 from pith
2	Breast height (1.37 m)	3 and 4	Balance from above, generally 1-5 from pith
3	t_5 (generally 7-11 m)	5 and 6	1-5 from pith

Measurements

For each sample the following were obtained:

Density

The volume of each specimen was measured by water displacement while the wood was still green. After oven-drying at 103°C the specimens were each weighed, to the nearest 0.1 g. For each sample the weights and volumes of the two specimens were summed and their ratio calculated to give a single value for density, hereafter denoted S1, S2 or S3, according to position.

After the calculation of densities seven anomalous values (typically 0.05 g/cm^3 below normal) were discarded as outliers. All could be related to severe dieback or top breakage.

Ring Width

The radial thickness of each specimen was measured at the median point to the nearest 0.1 in. (2.5 mm), and the mean value for the sample calculated. This was then divided by the number of rings, and the quotient (mean ring width) is hereafter denoted R1, R2 or R3 according to position.

Analysis

Because of difficulties created by the highly unbalanced classification, clonal differences were analysed for one site at a time. For each site clonal repeatabilities were calculated from analysis of variance (Burdon, 1971) as $V_C/(V_C + V_E)$, where V_C is the between-clones component of variance, and V_E is the ramets-within-clones or error component. It is assumed, for wood density as studied here, that clonal differences are purely genetic in origin. If the clones are to be regarded as a random sample of the base population the repeatabilities may be accepted as estimates of "broad-sense heritability". However, the estimates obtained at the various sites are not independent of each other because of the number of clones in common among the sites.

Clonal, environmental and phenotypic coefficients of variation were calculated as

$$\sqrt{V_C} \div S \qquad \sqrt{V_E} \div S \qquad \sqrt{V_C + V_E} \div S$$

respectively, where S is the overall mean for the site in question.

Site means were calculated as the averages of clonal means, adjusted at those sites where clones were missing (Burdon and Low, 1973). The tests of significance of site differences (Burdon and Low, *ibid.)* are only approximate, so $P < 0.01$ is the preferred criterion of significance.

Tests for the general presence of clone-site interactions were made by the method of fitting constants (cf. Snedecor, 1956, 12.17), within the framework of unbalanced two-way analysis of variance. The allocation of degrees of freedom within the clasification was as shown in Table 3.

TABLE 3—Allocation of degrees of freedom

Source	Degrees of freedom
Total	(No. of ramets) — 1
Clones	17
Sites	3
Clone/site interactions	(No. of subclasses represented) — (17 + 3)
Error	(No. of ramets) — (No. of subclasses)

If, with the unbalanced classification, interactions are appreciable, the overall analysis of variance cannot be pursued further. This is because the mean squares for clones over all sites and for sites would be biased.

The interaction component of variance V_I, can be calculated from the expectation of mean squares. The expected interaction mean square is $(V_E + n_o V_I)$, where V_E is the error mean square and n_o is the appropriate mean of all clone-site subclasses that are represented (Snedecor, 1956, 10.16).

The interrelationships between characters were studied first at the level of ramets within clone-site subclasses. At each site, for a pair of characters, a test was made for heterogeneity of within-clone regressions. Then the significance of the pooled or average within-clone regression was tested and the coefficient of determination (R^2) and the slope (b) were calculated. After pooling within sites the regressions were tested for heterogeneity prior to pooling over all sites. Following the second pooling R^2 and b were similarly calculated.

The between-clone relationships, within sites, among pairs of characters were studied in two ways: (1) on the basis of clonal means, (2) using clonal components of variance and covariance. Clonal (genotypic) correlations were calculated from components as

$$W_{C_{(xy)}} \Big/ \sqrt{V_{C_{(x)}} \cdot V_{C_{(y)}}}$$

where $W_{C_{(xy)}}$ is the between-clones covariance component between the two characters, x and y, and $V_{C_{(x)}}$ is the between-clones variance component for x. The covariance components are calculated from the mean cross-products and the variance components are calculated from mean squares. However, correlations between clonal means are

almost identical to clonal correlations if repeatabilities are very high and if there is no within-clone association between characters. The significance of clonal correlations could often be inferred indirectly; for example, a significant negative relationship between clonal means in conjunction with a significant positive within-clone relationship would mean a significant negative clonal correlation. Also, it was possible to compare between-clone and within-clone regression slopes (t test).

More complex interrelationships among characters were pursued by multiple regressions of density on ring width and height for clonal means at each site. The values and standard errors of the partial regression coefficients were calculated, as well as the multiple R^2 values. Multiple regressions at the level of ramets within clone-site subclasses were not pursued because of the small numbers within subclasses.

Sites were too few to give firm evidence of interrelationships between density and growth rate at this level. Nevertheless, site means for density were graphed against those for ring width.

RESULTS

Table 4 lists clonal repeatabilities for density at each sampling position, by sites.

TABLE 4—Clonal repeatabilities for density, by sites (numbers of clones are listed in brackets)

Character	Site			
	Glenbervie (16)	Whaka (11)	Gwavas (18)	Berwick (14)
S1	0.90	0.57	0.87	0.88
S2	0.77	0.90	0.74	0.77
S3	0.74	0.77	0.74	0.85

Table 5 lists the clonal, environmental, and phenotypic coefficients of variation (%).

TABLE 5—Coefficients of variation (%) in density, by sites

Source	Character	Site			
		Glenbervie	Whaka	Gwavas	Berwick
Clonal (genotypic)	S1	10.7	6.9	7.8	8.4
	S2	7.9	9.6	6.6	8.1
	S3	6.5	7.9	6.0	5.7
Environmental	S1	3.6	5.9	2.9	3.0
(ramets within clones)	S2	4.4	3.2	4.0	4.5
	S3	3.8	4.2	3.4	2.4
Phenotypic	S1	11.2	9.3	8.3	8.7
	S2	9.0	10.0	7.7	9.3
	S3	7.6	9.0	7.0	6.4

All repeatabilities are very highly significant ($P < 0.001$), and with one exception, 0.74 or higher. The clonal coefficients tend to be lower for S3, indicating less expression of genotypic variation up the stem than at breast height.

Differences between sites in clonal coefficients of variation are harder to evaluate. They could either reflect differences in expression of genotypic variation or differences in the samples of clones represented. Comparing Glenbervie with Gwavas, with 16 out of 18 clones in common, it is evident that genotypic differences were expressed more at Glenbervie. At Whaka and Berwick more clones were missing, so the other comparisons cannot be interpreted satisfactorily.

The difference in density between sampling points within the the tree (S1 minus S2), showed moderate and statistically significant ($P < 0.05$) clonal repeatabilities at all sites, the value being 0.42, 0.42, 0.48 and 0.31 at Glenbervie, Whaka, Gwavas and Berwick respectively. This shows appreciable genotypic variation in the pith-to-bark density gradient. The clonal coefficients of variation, expressed as percentages of the mean differences at each site, were quite large (about 40%). For (S2 minus S3) there were no significant clonal repeatabilities, so there is no evidence of genotypic differences in any density gradient up the stem within the first five rings from the pith.

When the repeatabilities were calculated for ratios between the densities instead of differences the values were very similar, showing that the clonal differences were not essentially scalar in origin.

Table 6 shows correlations of clonal means for wood density between different positions within the stem. These correlations are generally very high and very highly significant† Surprisingly, there was no within-clone association between S1 and S2 at any site. With this and the high repeatabilities the tabulated correlations approximate to clonal correlations. These high correlations, despite clonal differences in density gradients, reflect the magnitude of clonal differences overall.

TABLE 6—Correlations between clonal means for wood density at different sampling positions by sites

Wood characters	Site			
	Glenbervie	Whaka	Gwavas	Berwick
S1/S2	0.87 ***	0.54 N.S.	0.78 ***	0.84 ***
S1/S3	0.84 ***	0.73 *	0.84 ***	0.91 ***
S2/S3	0.87 ***	0.83 ***	0.83 ***	0.78 ***

Site Differences

Table 7 shows the site means for each sampling position. In each case there were clearly significant differences between sites, although the pattern of differences varied

† N.S. denotes not significant $P > 0.05$
* denotes significant $P < 0.05$
** denotes highly significant $P < 0.01$
*** denotes very highly significant $P < 0.001$

according to position. For S1, Glenbervie showed the highest density and Gwavas the lowest, with Whaka and Berwick intermediate. For S2 Whaka, Gwavas and Berwick were all very similar, but substantially lower than Glenbervie ($P < 0.001$). For S3 Berwick was comparable with Glenbervie, both being higher than Whaka and Gwavas. At this latter position along the stem site differences, like clonal differences, were less pronounced.

TABLE 7—Site means for wood density in different sampling positions

Site	Character S1	S2	S3
Glenbervie	0.439 a	0.393 a **a**	0.368 a **a**
Whaka	0.405 b **bc**	0.342 b **b**	0.353 b **ac**
Gwavas	0.386 c **c**	0.346 b **b**	0.350 b **c**
Berwick	0.406 b **ab**	0.348 b **b**	0.365 a **ab**

Within columns, ordinary type letters in common indicate $P > 0.05$ for differences
Within columns, bold type letters in common indicate $P > 0.01$ for differences

Table 8 shows for each site the mean differences between sampling locations within trees and their significance (paired *t* tests based on clonal means for each location). At all sites there was a strong pith-to-bark density gradient as reflected by (S1 minus S2) ($P < 0.001$), which appears to be more marked at Whaka and Berwick than at Glenbervie and Gwavas. Within the first five rings from the pith (S2 and S3) there were highly significant differences ($P > 0.01$) along the stem at Glenbervie and Berwick but not at the other sites. Density was greater at breast height than further up the stem at Glenbervie, but the opposite at Berwick.

TABLE 8—Gradients in wood density, by sites

Gradient	Site Glenbervie	Whaka	Gwavas	Berwick
S1 minus S2	0.046 ***	0.063 ***	0.040 ***	0.058 ***
S2 minus S3	0.025 ***	— 0.011 N.S.	— 0.004 N.S.	— 0.017 **

Fig. 1 shows mean density for each sampling location plotted against mean annual temperature (Harris, 1965a) at the sites. The regression obtained by Harris for density of outerwood (> 15 rings from pith) on mean annual temperature is drawn in. In view of the closeness of our samples to the pith, densities would be expected to fall to well below the regression line. However, among these sites there are big departures from the regression slope, Berwick being the exception, particularly with S1 and S3.

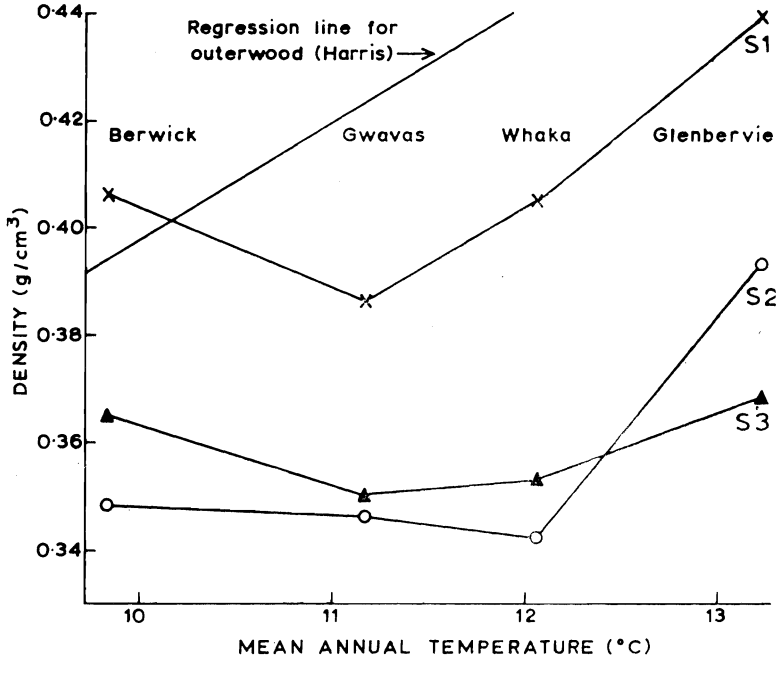

FIG. 1—Graph showing density vs mean annual temperature for each of the three sampling positions.

Clone-site

Table 9 shows calculated clone-site interaction components of variance for three sampling positions, both including and excluding Glenbervie. For S1 the estimate will be subject to some bias owing to heterogeneity of V_E between sites (Bartlett Test, $\chi^2_3 = 17.8$, $P < 0.001$). Interactions are present in each case, being strongest for S1 and weakest for S3. With Glenbervie omitted the interaction components are all reduced, but to a value that is non-significant only for S3.

TABLE 9—Variance components for clone-site interactions
$((g/cc)^2 \times 10^6)$

Character	Sites	
	All Sites	Omitting Glenbervie
S1	282 ***	176 ***
S2	151 ***	114 ***
S3	47 **	19 N.S.

Fig. 2 shows, by means of histograms, the relative magnitudes of different variance components. Interaction components, although significant, are small compared with clonal variances.

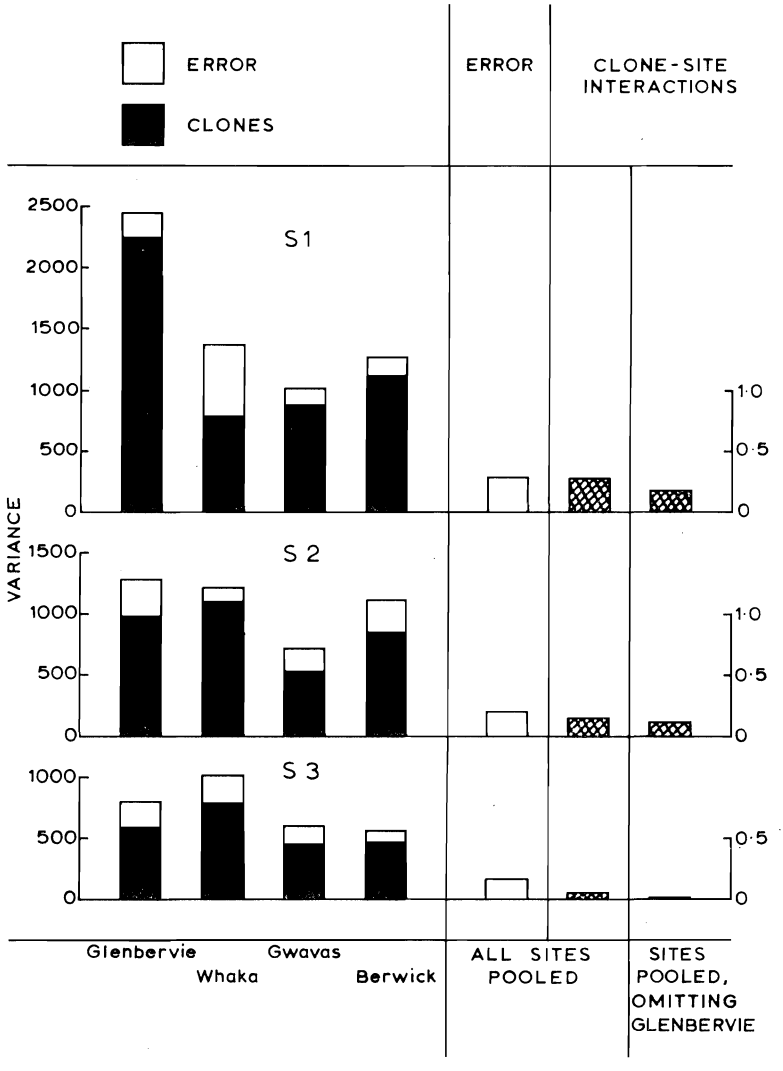

FIG. 2—Histogram representing variance components for wood density ((g/cc)^2 $\times$ 10^6), by sites and by sampling positions (i.e., S1, S2 and S3).

For each clone represented at Glenbervie the difference was calculated between the means there and at Gwavas. Among the clones with severely reduced vigour at Glenbervie, the increase in density compared with Gwavas was greater than in the remainder of the clones. This difference in increase (unpaired t tests) was marked for S1 (0.079 compared with 0.037, $P < 0.01$), but smaller and non-significant for S2 (0.061 compared with 0.038, $P < 0.1$) and S3 (0.023 compared with 0.014, $P > 0.2$).

Interrelationships Between Density and Growth Rate Parameters

Results of analysis of within-clone relationships between density and ring width are summarised in Table 10. Between sites there was no significant heterogeneity of regression slopes for any of the sampling positions. There was no significant heterogeneity of regression slopes among clones within sites, except for S1 at Whaka ($F_{9,15} = 2.58$, $P < 0.05$).

TABLE 10—Results of analysis of pooled within-clone regressions of density on ring width (cm)

Character	R^2	P	b
S1	0.099	**	— 0.0199
S2	0.118	**	+ 0.0196
S3	0.006	N.S.	+ 0.0046

In each case density was only weakly related to ring width, if at all. For S1 there was a weak although highly significant negative relationship, while for S2 there was a corresponding positive relationship. In S3 there appeared to be no relationship at all.

Because diameter is normally correlated with height, the within-clone relationships between S1 and R1, and S2 and R2 were then adjusted for variation in height. This was done, for each site, by treating the pooled within-clone relationships between the three characters as partial correlations (cf Snedecor, 1956, 14.6). Height was taken as at 1962 for considering S2 and R2. With S1 there were insufficient meaningful height measurements for this analysis at Glenbervie and Gwavas.

With the adjustment the positive within-clone associations between S2 and R2 were essentially unchanged. The same applied for the weak negative association between S1 and R1 at Berwick. For S1 at Whaka, however, the calculations indicated a strong negative within-clone correlation ($r_{S1\ R1.\ Height} = -0.7^{**}$) between S1 and R1 for constant height but a similar positive correlation between S1 and height for constant R1.

Table 11 presents the between-clone relationships between density and ring width.

TABLE 11—Clonal relationships between wood density and ring width

Site	No. of Clones	Wood Character	Density on Ring Width (cm) (weighted clonal means) b	r	P	Total Genotypic Correlation (R_G)	
Glenbervie	16	S1	— 0.087	— 0.46	< 0.2	— 0.6	N.S.
		S2	— 0.039	— 0.21	N.S.	— 0.8	N.S.
		S3	— 0.008	— 0.08	N.S.	— 0.2	N.S.
Whaka	11	S1	— 0.014	— 0.04	N.S.	0.2	N.S.
		S2	0.047	0.48	< 0.2	0.2	N.S.
		S3	0.039	0.48	< 0.2	0.6	N.S.
Gwavas	18	S1	— 0.017	— 0.09	N.S.	—	
		S2	— 0.006	— 0.04	N.S.	— 0.3	N.S.
		S3	— 0.063	— 0.36	< 0.2	—	
Berwick	14	S1	— 0.126	— 0.35	N.S.	— 0.5	N.S.
		S2	— 0.079	— 0.37	N.S.	— 0.7	N.S.
		S3	— 0.102	— 0.53	*	— 0.9	*

Except at Whaka, where the number of clones was small and where some had become partially suppressed, the relationships were all negative, but they were significant only for S3 at Berwick. No genotypic correlations could be obtained for S1 and S3 at Gwavas because the estimates of V_G for ring width were zero or negative. The genotypic correlations tended to be higher than the correlations of clonal means, but the errors of estimation are very large. Moreover, the various estimates are not independent and therefore cannot be regarded as cumulative evidence. The regressions for clonal means are generally steeper than the within-clone regressions, but significantly so only for S3 at Berwick.

Results of the analysis of multiple regressions of S1 and (S1 minus S2) on R1 and height are summarised in Tables 12 and 13. At Glenbervie and Whaka the simple regressions of S1 on both height and R1 were weak, but there were quite strong multiple regressions, with negative partial regressions on diameter and positive partial regressions on height. However, the addition of height to ring width gave very little improvement of fit at Gwavas and Berwick. When (S1 minus S2) was considered instead of S1 the

TABLE 12—Coefficients of determination (R^2) for regressions of density parameters on growth rate parameters, using unweighted clonal means

Dependent Variable	Independent Variable(s)	Site							
		Glenbervie		Whaka		Gwavas		Berwick	
S1	Height	0.04	N.S	0.11	N.S.	0.007	N.S.	0.05	N.S.
	R1	0.12	N.S.	0.29	N.S.	0.07	N.S.	0.20	N.S.
	Height and R1	0.46	*	0.66	*	0.08	N.S.	0.21	N.S.
S1 minus S2	Height	0.007	N.S.	0.03	N.S.	0.000	N.S.	0.001	N.S.
	R1	0.21	N.S.	0.58	*	0.17	N.S.	0.19	N.S.
	Height and R1	0.49	*	0.76	**	0.18	N.S.	0.33	N.S.

TABLE 13—Partial regression coefficients in multiple regressions of density parameters on growth rate parameters

Dependent Variable	Site	Independent Variable	
		R1 (cm) ± S.E.	Height (m) ± S.E.
S1	Glenbervie	— 0.146 ± 0.045	0.0134 ± 0.0046
	Whaka	— 0.100 ± 0.028	0.0089 ± 0.0031
	Gwavas	— 0.051 ± 0.046	— 0.0022 ± 0.0049
	Berwick	— 0.189 ± 0.126	0.0034 ± 0.0112
S1 minus S2	Glenbervie	— 0.081 ± 0.023	0.0062 ± 0.0024
	Whaka	— 0.104 ± 0.021	0.0055 ± 0.0023
	Gwavas	— 0.051 ± 0.029	— 0.0005 ± 0.0031
	Berwick	— 0.150 ± 0.064	0.0027 ± 0.0017

relationships were, if anything, stronger. The smaller variability among clones at Gwavas and Berwick for height and diameter growth (Burdon, 1971) would have made for weaker relationships. The lack of any positive effect of height at Gwavas is probably related to disturbances in height growth among trees growing on a very exposed stand margin.

A similar multivariate analysis of the interrelationships between S2, R2 and 1962 heights (t_5) showed practically no significant regressions at all. This is consistent with (S1 minus S2) showing appreciable regressions.

Fig. 3 shows the mean density plotted against mean ring width for each sampling location at each site. The method of calculating means was immaterial. The indications are of a negative relationship, albeit incomplete. To consider the first five rings from

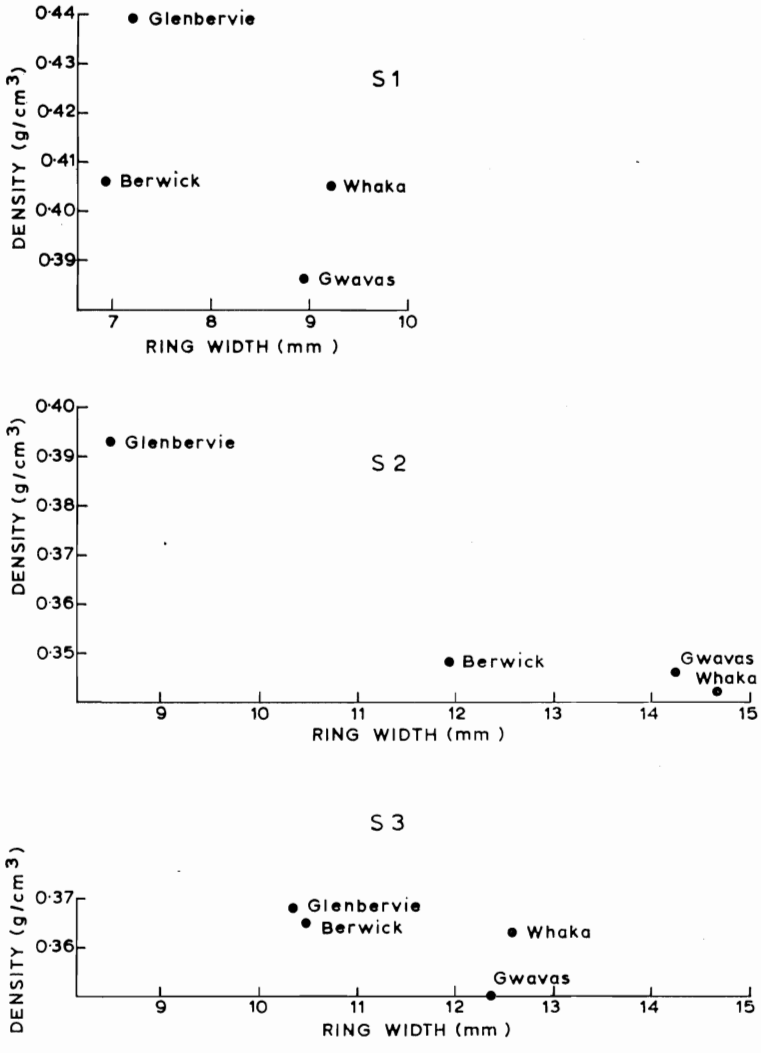

FIG. 3—Graphs showing mean density vs mean ring width, by sites.

the pith, however, it is noteworthy that at Berwick the lower density at breast height than at t_5 is associated with wider rings, while at Glenbervie the higher density at breast height is associated with narrower rings.

DISCUSSION

We must stress that this study was concerned solely with "normal wood" (reaction wood being excluded as far as possible) at specified locations within stems. Although limited by the age of the trees to the first 10 rings from the pith, the investigation involved the zone of wood that creates many of the worst problems of utilisation and in which improvement would be most welcome.

No attempt was made to estimate within-tree sampling error because the pairs of opposing sectors were treated as single composite samples. Compared with the sampling errors involved in other studies, those here would tend to be reduced by taking entire sectors instead of increment cores. Against this, however, the residual variance was probably inflated by having to accept all trees unless they were suppressed or had serious stem deformation at the sampling points. It has been common practice to minimise the possible influence of reaction wood by avoiding trees either with stem defects or growing at stand margins.

To consider the appropriate weighting for individual growth rings, a sector weights each ring roughly according to its cross sectional area. This weighting, however, is not constant in that the widths of outer rings relative to the inner rings vary between trees. Competition between trees normally reduces most the widths of the outer rings, which are of the highest density. Hence if competition does increase density within individual rings, this effect will tend to be masked in the mean density of a sector. Similarly, a broken top will reduce growth and thence decrease the contribution of the outer rings to the properties of the sector.

Genotypic Differences

The high clonal repeatabilities accord with earlier work, and further demonstrate the strong genotypic variation in wood density. Insofar as the clones might approximate to a random population sample with respect to density, the repeatabilities may be accepted as estimates of broad-sense heritability. Differences in error variance, the possible causes for which have been discussed, would contribute to the variations in repeatabilities. However, when broad-sense heritability is almost complete, the real interest will centre on the genotypic component of variance. This parameter is subject to large errors of estimation, and our repeatabilities do not represent independent estimates because they all relate to a single group, in whole or in part, of 18 clones. Hence, rather than calculate confidence limits for the estimates from this experiment we will consider the results as part of the cumulative evidence.

Table 14 lists various point estimates of genetic parameters in different experiments, together with some corresponding coefficients of variation. Generally, the phenotypic and clonal coefficients were higher in this experiment than in others, so the clones under study may have been a sample of more than average variability.

This study was concerned with total genotypic variance which governs the expected response to selection of clones for vegetative propagation. Such a response should be considerable. However, the response to selection under orthodox seed propagation depends on the purely additive genetic variance, for which this trial provided no estimates.

TABLE 14—Estimates by various workers of clonal variances ((g/cc)^2 × 10^6) and coefficients of variation for wood density in radiata pine

Authors	No. of Clones	Rings from Pith	V_C	CV_C%	Type of Samples	Remarks
Fielding and Brown	9	9-17 (approx)	*ca.* 550	*ca.* 6	Cores	Parameters are rough estimates from presented data
	9	8-17 (approx)	*ca.* 350	*ca.* 5	Cores	
	10	1-11 (approx)	430	5.2	Cores	
Pawsey and Brown	6	1-13 (approx)	200	3.7	Cores	
Nicholls and Brown	20	2-8	407	—	Cores	Variance is mean of separate estimates for individual rings
Burdon and Harris	11-18	1-5	530-1110	6.9-10.7	Sectors	Separate estimates for each of four sites
(Current study)	11-18	6-10	790-2250	6.6-9.6	Sectors	
	11-18	1-5 (up stem)	440-780	6.0-7.9	Sectors	

The appreciable repeatabilities for (S1 minus S2) indicate that the objectionable pith-to-bark density gradient could be reduced by clonal selection. Nevertheless, selection for higher density within the first five rings from the pith should still be effective for the next five.

Site Effects

This experiment has firmly established the large influence of site on wood density, since it avoided the usual confounding of genotype and environment. The high-density at the warm, phosphate-deficient Glenbervie site accords with the results of Harris (1965a). Although Harris did not observe as close a relationship between density and mean annual temperature in corewood as in outerwood, the relatively high density at Berwick is still interesting. At this site both S1 and S3 were conspicuously high, and they reflect a 5-year period during which there were two quite severe droughts. This suggests that water stress may be conducive to increased density.

The amount of variation up the stem in the five rings from the pith was surprising, since it has been generally accepted that such variation is unimportant. It should be appreciated, though, that along the stem the corresponding rings from the pith are produced in different years and therefore under slightly different weather conditions. Moreover, the micro-environment can change during the life of a stand. Such environmental fluctuations might well cause changes in wood properties along the stem. An alternative interpretation, which would not preclude the one given above, is that site effects are expressed more strongly near the ground than higher up the stem.

Genotype-Site Interactions

Considering the large effects of both genotype and site the clone-site interactions were strikingly small, particularly as the sites included one (Glenbervie) which had generated gross interactions for vegetative vigour (Burdon, 1971). Predictably, Glenbervie appears to be the main (but not the sole) source of interactions for wood density. Also, the indications are that any effects of phosphate deficiency on density are largely indirect, the increased density being a consequence of the reduced vigour which itself resulted from the deficiency.

Interrelationships Between Density and Growth Rate Parameters

A notable finding is the very small influence of non-genetic variations in ring width on wood density. From the pooled regression calculated for S1 the mean expectation is that a difference in ring width of 1 cm would reduce density by 0.02, a difference that is small in relation to the usual pith-to-bark density gradient. Any bias in the sampling procedure would hardly influence the broad conclusions that are to be drawn. There was one indication that clones can differ in their density/ring width relationships, although little weight should be given to an isolated case of significance. Moreover, the prime interest is in the average behaviour of genotypes.

The weak but highly significant positive within-clone association between density and ring width in the first five rings at breast height merits comment. Even allowing for some minor artifact of the sampling procedure, the relationship appears to be very different from that in the next five rings. The essential difference may be that variations in the width of the second five rings would reflect competition far more than those in the first five. Competition, since it affects diameter far more than height, influences the shape of the stem. But it may also be noted that the first five rings would be produced

within the green crown, whereas subsequent rings would tend to be produced below this zone, by a distance that could be related to both height and diameter growth. It is still possible that beyond the tenth ring there may be a stronger relationship between density and ring width. However, at this position density would always be high enough to be acceptable.

Evidence concerning the genotypic interrelationships between density and growth rate parameters is very limited. However, the indications are that there is a general negative association between density and rate of growth, at least for a constant height of tree. The negative partial regressions of density on ring width coupled with the positive partial regression on height mean that clones with tall, thin boles had higher densities. This effect appeared to operate only after the first few years of growth. The fact that it was not marked at Berwick may reflect the earlier stage of development resulting from the slower growth rate.

There appears to be a within-clone effect of height on the density of the second five rings; although there is little statistical evidence there were the anomalously low densities in the trees severely affected by dieback or breakage. Further to this particular observation, however, it would be desirable to study wood density in topped stems. There is as yet no certainty whether the three-way interrelationship operates more strongly between clones than within clones. However, it is unlikely that any influence of within-clone variation in height would mask a large effect of ring width on density for constant height. This is partly because, barring breakage or severe dieback, the variation in height was predominantly clonal (Burdon, 1971).

Site-to-site relationships between density and ring width were not pursued because there were so few sites. In broad terms, however, the picture is consistent with the within-clone relationships.

The picture that appears to be emerging, at least outside the first five rings, is consistent with common sense mechanics. However, although we analysed density as the dependent variable, the causal relationships are uncertain. There are, perhaps, better grounds for regarding height as an independent variable than for so regarding diameter. With a genotype of inherently high density, for instance, we would expect diameters to be correspondingly small if photosynthetic capacity is fixed.

CONCLUSIONS

1. Tree-to-tree variation at given positions within the stem is predominantly genetic, as evidenced by high clonal repeatabilities within sites (generally > 0.75).
2. Indications are that the genotypic standard deviation for wood density is typically 6-10% of the population mean.
3. Appreciable genotypic differences in the pith-to-bark density gradient are indicated by moderate clonal repeatabilities (0.3 to 0.5); notwithstanding, there are still close genotypic correlations between density in the first and second five rings.
4. It is now established that site can strongly influence wood density, though not altogether consistently among different parts of the tree; this means that density can vary along the stem at a given position in relation to the pith.
5. Both site and genotype differences appear to be less marked up the stem than at breast height.
6. Clone-site interactions, although statistically significant, were only minor, so that

selection for density at any one site should be effective over a wide geographical range.

7. The most important but by no means all of the observed interactions arose with respect to a phosphate-deficient site and elsewhere.
8. It appears that with phosphate deficiency wood density increases partly in relation to the degree of distress in the individual genotype.
9. Within sites the net effects on wood density of non-genetic variation in ring width appear to be very minor, and not even consistent among different parts of the stem.
10. Between genotypes, at least, density appears to show a negative partial regression on ring width but a positive partial regression on tree height. Such a pattern is mechanically plausible, but it was evident only after the first five rings from the pith.

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