AN EARLY PROGENY TRIAL IN PINUS RADIATA
4. WOOD DENSITY

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ABSTRACT

Variation in the density of the wood of **Pinus radiata** D. Don was studied in a progeny trial comprising 26 open-pollinated families arranged in nine randomised blocks. Samples of wood taken from different radii at breast height on 692 trees were divided into inner, middle, and outer segments, each containing five annual rings. The density of each segment and a mean for all 15 rings were determined for each tree.

Analyses of variance showed highly significant differences between families and between blocks. Point estimates for heritability ranged from 0.51 to 0.72.

On the basis of common knowledge, it may be assumed that on average each radial sample within a stem showed a consistent trend of density increasing with age, as xylem was deposited further and further from the pith. If, then, the variance of density is regarded as that of a point anywhere within the breast-height cross-sections of some 600 trees, a large part of the statistical effect of this trend may be extracted from the data as a linear regression component. With that concept, the linear regression component in this experiment accounted for 65% of the total variance in wood density. The mean density/age gradient was 7.87 $kg/m^3/yr$, with a standard deviation of 3.51 $kg/m^3/yr$. There were highly significant differences between the families in the gradient: its heritability was estimated as 0.27.

Density showed the usual weak, negative phenotypic correlation with radial growth-rate. A multiple regression analysis, relating density to the radius and height of the stem jointly, accounted for 2.2% of the total variation ($p < 0.001$), the partial regression coefficients being negative for radius and positive for height. In a similar analysis of the pooled within-families variance the regression coefficients were again negative for radius and positive for height, and the joint regression accounted for 16% of the total variation ($p < 0.001$).

Genetic, environmental, and phenotypic correlation coefficients were estimated for 10 characters. There appeared to be little or no association between density and external characters affecting log quality, but the different determinations of density showed consistently strong positive genetic correlation amongst themselves. This suggests that in each tree the same genes were acting on wood density, and acting in the same way, at all stages during the 15-year period.

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Both density and the density/age gradient were sensitive to differences in the environment, substantial contrasts occurring even between adjacent blocks of 0.27 ha.

It is concluded that wood density in **P. radiata** as represented by this trial should respond well to artificial selection. For this, the density of the first five annual rings, determined from 5-mm increment cores, provides a good index to genotypic value, at least up to the fifteenth annual ring.

INTRODUCTION

It is widely recognised that wood density (basic specific gravity) is an excellent index to the properties of wood as a raw material. This is true, whether one is comparing different species, genetically different populations within a species, genetically identical material grown on different sites, individual trees grown on the same site, or samples of wood taken from different positions within a single tree. Density varies in ways that are of practical importance to man, and that is the main reason why a great deal of research has been directed towards describing that variation and elucidating its causes.

As a species of great commercial importance, *Pinus radiata* has attracted a large part of this research effort in the Southern Hemisphere – e.g., in South Africa (Turnbull & du Plessis 1946; Turnbull 1947), in Australia (Fielding & Brown 1960; Dadswell *et al.* 1961; Nicholls *et al.* 1964; Nicholls 1967; Pawsey & Brown 1970), in New Zealand (Harris 1965; Burdon & Harris 1973; Cown 1974, 1980), and in Chile (Paz & Melo 1965; Ortiz 1965; Alfaro & Moreno 1974).

The literature provides a fairly good idea of how density varies from one site to another, of how it varies from tree to tree within sites, and of how it varies within individual trees. It is also clear, from studies of clones, that much of the tree-to-tree variation is genotypic; but as yet little has been published on the inheritance of wood density in *P. radiata* through sexual reproduction. This paper is based on an intensive study of 26 open-pollinated progenies; it presents fresh evidence of an additive-genetic variance component in wood density, and considers the implications of that component in the context of related studies.

METHODS

Wood samples were extracted with 5-mm increment borers from 692 trees in the progeny trial situated in Pigeon Valley near Wakefield, Nelson (described in detail in the first paper of this series, Bannister 1969). In choosing the trees for sampling, badly suppressed and possibly unhealthy trees were avoided, and every endeavour was made to minimise statistical imbalance. For this, a suitable sample of about the same number of trees would have been:

(26 families × nine blocks × three trees per plot).

As several plots were missing, however, it was thought best to try to compensate for the deficiencies in such a way that each family was represented by the same number of sample trees. In the event, this was almost achieved; 21 families were each represented by 27 sample trees, three families by 26 each, one by 24, and one by 23.

From each tree two 5-mm increment cores were taken close to breast height, and from directions approximately at right angles to one another. Their orientation

(Fig. 1) was determined by noting the direction in which the tree was leaning (in general this was north-east), by taking up a position on the opposite side of the tree, and then boring from bearings about 45° to the right (usually south) and 45° to the left (usually west). This was done to reduce, as much as practicable, the likelihood of compression wood being included in the samples.

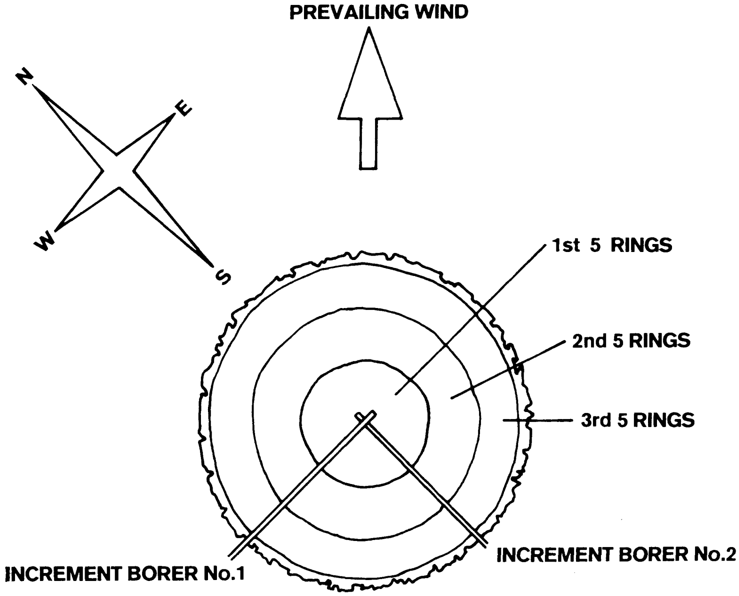

FIG. 1—Usual method of sampling within the tree.

The trees were 18 years old at the time of sampling. In the laboratory each sample (with a few exceptions) was cut into three pieces representing the first, second, and third segments of five rings each, in chronological order from the pith. The exceptions included cores in which the outermost rings were so compressed that they were indistinguishable. Such samples were cut into two, representing (for example) an inner five-ring segment and an outer nine- or ten-ring segment. For all the separate segments, numbering more than 4000 in total, density was measured by a standard procedure that requires the length of the sample (mm), its oven-dry weight (mg), and a constant representing the internal cross-sectional area of the particular increment borer.

Several of the initial results seemed to be anomalous. Of these, a few were replaced by acceptable values when the measurements were repeated; others seemed to be curiosities to be regarded with some suspicion, but were included in the analyses; and a few were so aberrant that they were rejected without compunction. Altogether, missing values upset the balance of the data for variation within trees for about 3% of the trees sampled. In some of the statistical analyses this was critical and resulted in one or more trees being excluded. In others, in which the behaviour of the whole tree was the prime consideration, it was considered better to retain a tree with, say, four values present and two missing than to discard it. For such analyses, therefore, estimated values were supplied wherever feasible.

ANALYSIS OF VARIANCE IN WOOD DENSITY

The mean was calculated for each pair of density measurements within the first, second, and third five-ring segments of each tree. From these were calculated (a) the arithmetic mean and (b) a weighted mean, for each tree. To obtain (b) each of the three means, determined within a single tree, was weighted by the cross-sectional area of the appropriate five annual rings.

The variance was then analysed, as described earlier (Bannister 1969), for each 5-year period separately, for the arithmetic-mean density, and for the weighted-mean density of each tree. The results (Table 1) showed that families contributed a highly significant component to the total variance, as did blocks; families × blocks may have contributed also.

TABLE 1—Results of variance-ratio tests, from analyses of variance in wood density

Source of variate	Variance component tested		
	Families (25 d.f.)	Blocks (8 d.f.)	Families × blocks (176 d.f.)
First 5 rings	***	***	n.s.
Second 5 rings	***	***	*
Third 5 rings	***	**	*
First 15 rings:			
arithmetic mean	***	***	*
weighted mean	***	***	*

***	significant at 0.1% level
**	significant at 1% level
*	significant at 5% level
n.s.	not significant
d.f.	degrees of freedom

Four variance components were estimated from each of the five analyses discussed above. In addition, it can be seen that an error (or trees-within-plots) component derived in this way must be compound, containing both a true trees-within-plots term and an exclusive error, which represents samples-within-trees. Partitioning of the variance was therefore carried a step further by going back to the original data and calculating the variance of samples within trees for each 5-year period separately.

Estimates of the various components are shown in Fig. 2; heritability estimates based on these, with their approximate 0.90 confidence limits shown in parentheses, are:

First five rings	0.60 (0.36–1.18)
Second five rings	0.68 (0.41–1.31)
Third five rings	0.51 (0.30–1.06)
First 15 rings:	
(a) arithmetic mean	0.72 (0.44–1.41)
(b) weighted mean	0.66 (0.40–1.28)

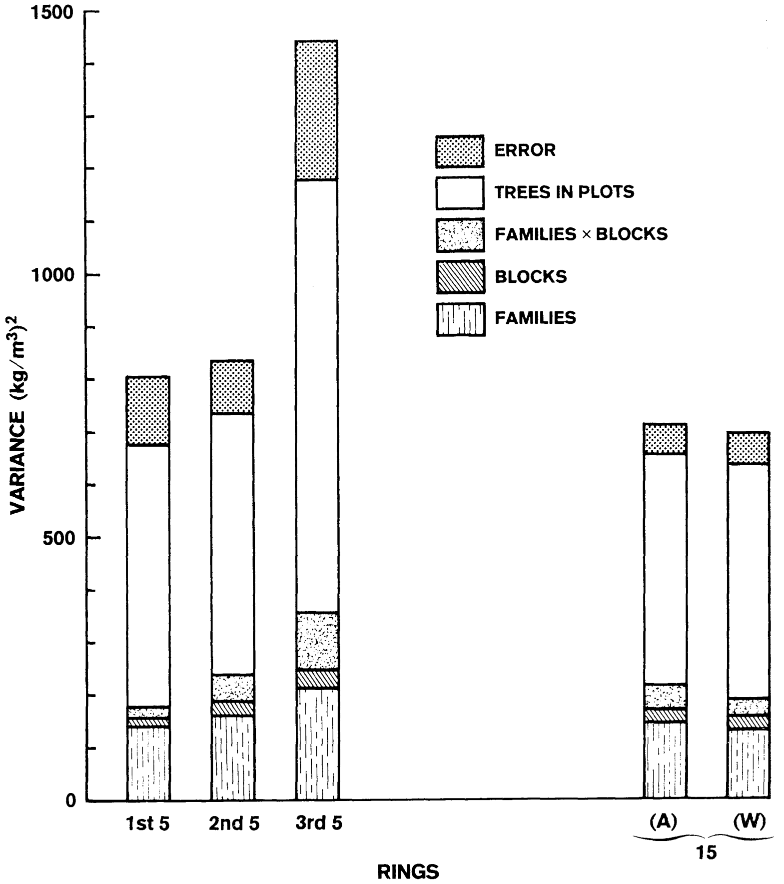

FIG. 2—Partitioning of the phenotypic variance in wood density into five components. For the three five-ring segments represented on the left, the error shown represents half of the sampling variance within trees. For the 15-ring analyses on the right, (A) represents the arithmetic mean, (W) the weighted mean, and the error represents one-sixth of the sampling variance.

GRADIENT OF WOOD DENSITY ON AGE

For the first, second, and third five-ring segments the over-all mean wood densities were 377.3, 406.5, and 453.9 kg/m^3 respectively. Since resin was not extracted from our samples, the first of these values may have been elevated a little by the presence of small but significant quantities of resinous heartwood; but whether or not one makes allowance for this, our results are well within the range reported by other workers, especially Harris (1965, 1969) and Cown (1980, also unpubl. data), who have repeatedly demonstrated a pattern of development in which density increases with age. Similar density/age gradients are found in most conifers (Spurr & Hsuing 1954), and in studies of wood quality they are sometimes expressed by the linear regression coefficient – a statistic that is commonly associated with a major part of the variation within the stem, and one that is regarded in practice as "a fair measure of the rate of transition from corewood to outerwood" (J. M. Harris, pers. comm.).

On this basis, comparable data from 31 sites sampled in a regional survey of Nelson and Westland (Cown, unpubl. data) show a mean gradient of 7.6 kg/m^3/yr; our results, using the over-all means of 692 trees on a single site, gave a mean of 7.66 kg/m^3/yr. Pursuing the idea that linear regression could account for much of the variation in our data, we fitted a straight line to each tree for which three pairs of co-ordinates were available, these being determined by three fixed points for age (at 2.5, 7.5, and 12.5 years) on the abscissa and by the appropriate densities on the ordinate. The regression coefficients estimated in this way showed a distribution, for trees-within-plots, that seemed on inspection to be approximately normal (Fig. 3).

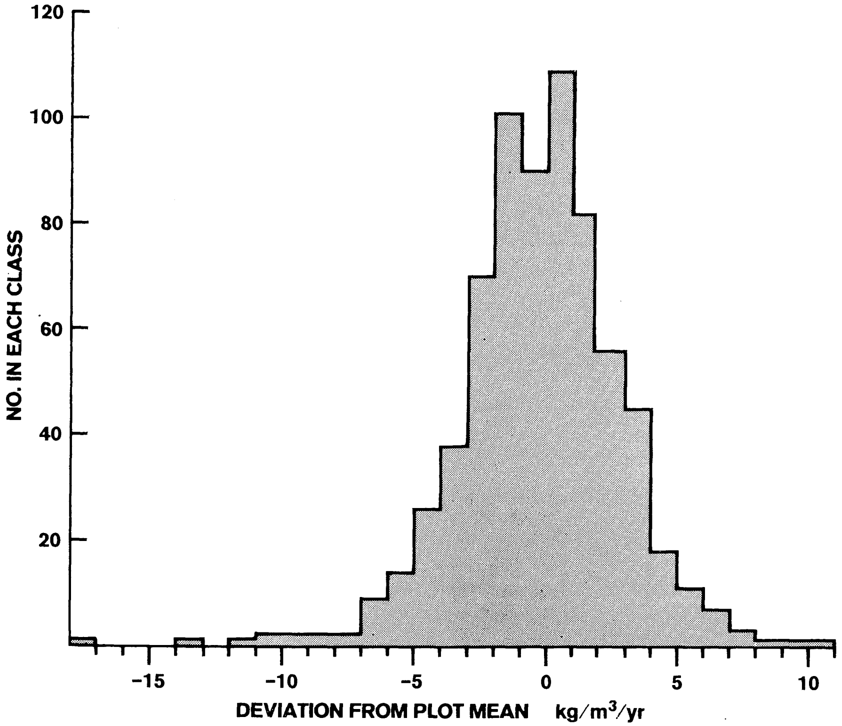

FIG. 3—Distribution of the trees-within-plot (i.e., error) component of variation in the gradient of density on age. The mean over all was 7.87 kg/m^3/yr; the plot means varied from 2.63 to 15.79; and this histogram represents 83% of the phenotypic variance.

Analysis of their variance showed the following:

Families	. . . significant at 0.1% level;
Blocks	. . . significant at 1% level;
Families × blocks	. . . significant at 5% level.

Estimates from this analysis included the following:

Mean gradient	. . .	7.87 kg/m^3/yr
Phenotypic variance	. . .	12.34 (kg/m^3/yr)^2
Standard deviation	. . .	3.51 kg/m^3/yr
Heritability	. . .	0.27 (0.90 confidence limits about 0.15 and 0.69)

It is reasonable to postulate, therefore, that there is an important additive-genetic component in the tree-to-tree variation of the density gradient. Its effect can perhaps be best appreciated by referring to Fig. 4.

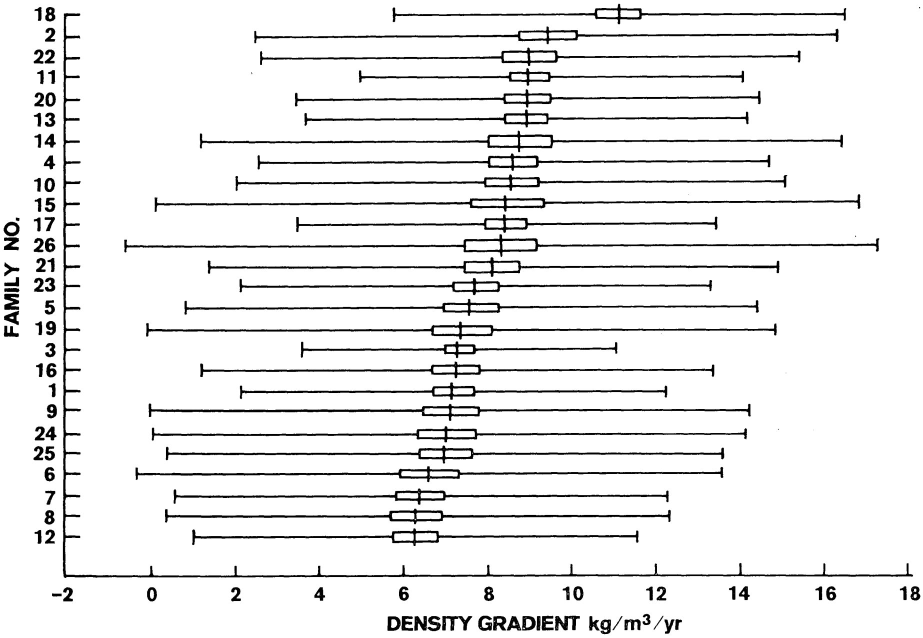

FIG. 4—Variation of 26 families, ranked according to mean gradient of wood density on age. For each family the vertical shows the mean, the hollow box shows one standard error above and below the mean, and the single horizontal lines show two standard deviations above and two below the mean.

ANALYSIS OF AGE AND FAMILY EFFECTS

The analyses described so far involved a piecemeal approach to a complex subject. Useful though they were, we also wanted a comprehensive analysis – one that would give a sense of the true proportions of the components as interrelated parts of the whole. In particular, we wanted a synthetic assessment of within-tree and between-tree variation at breast height, in the light of family and age effects. In choosing a model, we discarded the data from 94 trees so that the data from the remaining 598 trees would be balanced with respect to families and trees-in-families, ignoring block effects, with simplifying assumptions as follows:

(a) Although the error variances calculated separately from the first, second, and third five-ring segments were not homogenous, their heterogeneity would not be enough to vitiate the analysis;

(b) Blocks, family × block subclasses, and several other possible interactions could reasonably be regarded as absorbed into a single variance component – i.e., "trees-in-families";

(c) The fact that all three age-classes were based on the same sample of 598 trees, instead of each being based on a separate independent sample of 598 trees, could be ignored in view of the large number of trees in comparison with the number of observations within each tree; even with perfect within-tree correlation ($\rho = 1$), the bias would be tolerable;

(d) Most of the covariance of density and age could be expressed as one or more linear regression components of the variance of density, dependent on age;

(e) The residual variances about the linear regression lines undoubtedly included random effects, and probably curvilinear effects also; but, since discrimination of these was precluded by the lack of degrees of freedom, the actual residuals were best treated as random components;

(f) The rate of increase in basal area was constant.

The technique used was to subtract 7.5 from each of the values for age so that this, a fixed and independent effect, assumed the values –5, 0, and 5, with a mean of 0; and then to partition the sums of squares for density by the analysis of variance and covariance, facilitated by fitting an orthogonal polynomial (Fisher & Yates 1957). Table 2 gives the design for the analysis, Tables 3 and 4 the numerical results, and the broad interpretation of these is shown in Fig. 5.

TABLE 2 - Design for the analysis of variance in wood density, incorporating effects of regression on age

Source of variation	Symbol for mean square[1]	Degrees of freedom[2]	Expectations of mean squares[1,3,4]
Families	F	f-1	$\sigma^2_w + wa\sigma^2_{t:f} + wat\sigma^2_f$
Age: linear	AL	1	$\sigma^2_w + w\sigma^2_{art:f} + w(a-1)L^2_{alt:f} + wt\sigma^2_{arf} + wt(a-1)L^2_{alf} + wft\sigma^2_{ar} + wft(a-1)L^2_{al}$
Age: residual	AR	a-2	$\sigma^2_w + w\sigma^2_{art:f} + wt\sigma^2_{arf} + wft\sigma^2_{ar}$
Age: linear x families	ALF	f-1	$\sigma^2_w + w\sigma^2_{art:f} + w(a-1)L^2_{alt:f} + wt\sigma^2_{arf} + wt(a-1)L^2_{alf}$
Age: residual x families	ARF	(a-2)(f-1)	$\sigma^2_w + w\sigma^2_{art:f} + wt\sigma^2_{arf}$
Trees in families	T:F	f(t-1)	$\sigma^2_w + wa\sigma^2_{t:f}$
Age: linear x trees in families	ALT:F	f(t-1)	$\sigma^2_w + w\sigma^2_{art:f} + w(a-1)L^2_{alt:f}$
Age: residual x trees in families	ART:F	(a-2)f(t-1)	$\sigma^2_w + w\sigma^2_{art:f}$
Error	W	aft(w-1)	σ^2_w
Total		waft-1	

[1] Age: linear is regarded as a fixed effect; all other components are random

[2] f = No. of families = 26; a = No. of fixed points for age = 3; t = No. of trees per family = 23; w = No. of observations in smallest subclass = 2

[3] For further details of components see Table 4

[4] For derivation of coefficients of L^2 (regression) terms <u>see</u> Appendix 1

TABLE 3—Analysis of variance in wood density

Source of variation	Symbol for mean square	Degrees of freedom	Mean square	F ratio
Families	F	25	22 563.00	6.8***
Age: linear	AL	1	3 625 404.20	55.2†
Age: residual	AR	1	65 727.04	85.5***
Age: linear × families	ALF	25	4 354.98	2.6***‡
Age: residual × families	ARF	25	768.39	1.9**
Trees in families	T : F	572	3 307.73	9.9***
Age: linear × trees in fams.	ALT : F	572	1 334.88	3.4***
Age: residual × trees in fams.	ART : F	572	399.05	1.2**
Error	W	179§	333.10	
Total		3587		

*** significant at 0.1% level
** significant at 1% level
† F = AL/(AR + ALF − ARF); approximate degrees of freedom 1, 1.14; P = 0.07
‡ F = ALF/(ARF + ALT : F − ART : F); approximate degrees of freedom 30, 166
§ This would be the correct number for the balanced classification as shown; the actual mean square of 333.1 is a pooled estimate from separate analyses, with 2054 degrees of freedom.

TABLE 4 - Estimates of components of variance in wood density

Symbol for component	Estimate		Nature of variance component
	Initial	Final[1]	
σ^2_f	139.53	139.53	variance of family means for mean density
L^2_{al}	1486.66	1672.49	variance within trees attributable to mean linear regression for 598 trees (a fixed effect)
σ^2_{ar}	54.31	54.31	residual variance about the over-all mean regression line
L^2_{alf}	28.81	32.41	variance within trees, attributable to differences between families in the density/age gradient
σ^2_{arf}	8.03	8.03	pooled residual variance about the 26 mean-of-family regression lines
$\sigma^2_{t:f}$	495.77	495.77	pooled variance of trees within families, for mean density
$L^2_{alt:f}$	233.96	263.21	pooled within-trees variance, attributable to differences between trees within families in the density/age gradient
$\sigma^2_{art:f}$	32.97	32.97	pooled residual variance about the individual-tree regression lines
σ^2_w	333.10	333.10	pooled variance of samples within tree x age subclasses
Total variance	2813.14	3031.82	

[1] Initial estimates for the L^2 terms were increased by 1/8: *see* Appendix 2

Although the validity of our model may be challenged on theoretical grounds, we believe that this analysis demonstrates to some extent the complexity of the influences that contribute to variation in wood density, and we emphasise one salient feature of it in particular: if the variance of wood density is regarded as that of infinitesimal samples (or points, in the geometrical sense) distributed throughout the breast-height cross-sections of the 598 trees, the fitting of a straight regression line to the data for each tree accounts for 65% of the total variance. From a statistical point of view the method appears to invoke one or two unfamiliar ideas, which have already generated doubt and controversy. Further comment may be found in the Discussion and Appendixes 1 and 2.

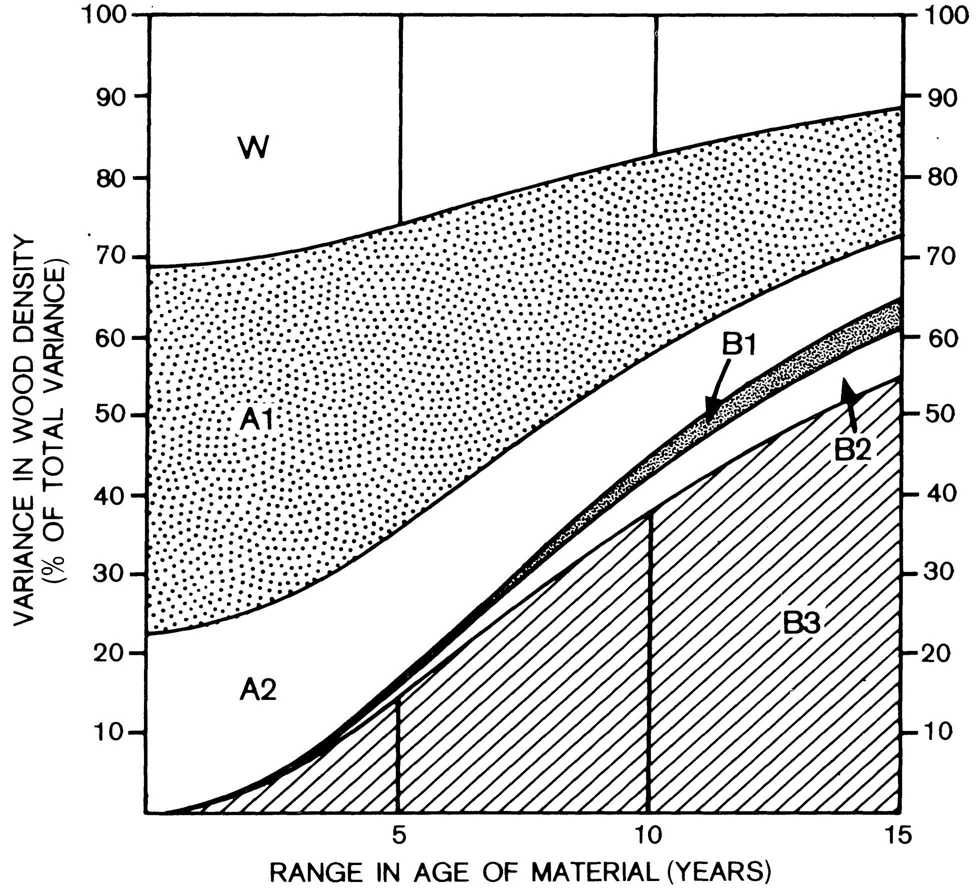

FIG. 5—Proportions of the total variance in wood density attributable to different sources:

Between-trees components

A1: additive-genetic variance of mean density;

A2: non-additive-genetic and environmental variance of mean density;

Within-trees components

B1: additive-genetic variance of the density/age gradient;

B2: non-additive-genetic and environmental variance of the density/age gradient;

B3: variance arising from the mean density/age gradient, over all;

W: mean variance of samples of the same age, within trees.

This diagram was derived from the analysis shown in Tables 2, 3, and 4. A1 and B1 were based on 3.5 σ^2_f and 3.5 L^2_{alf} respectively (Table 4). The choice of 3.5 instead of the usual 4 for half-sib models is explained elsewhere (Bannister 1969).

EFFECT OF GROWTH RATE

The relationship between density and radial growth-rate has been examined in many studies. For *P. radiata* it is well established that, as a general rule, these characteristics are negatively correlated – i.e., trees that are increasing in radius more rapidly than the average tend to produce at the same time wood of lower-than-average density;

but for trees on the same site the correlation is usually very weak, seldom accounting for more than 5% of the variation in density (Harris 1965).

This relationship was examined in the samples described here. The results, listed in Table 5, show a close similarity to Harris's (1965) data from the same district – especially so when it is understood that the Pigeon Valley samples came mostly from the corewood of young trees of widely varying crown class, whereas Harris's came from the mature outerwood of selected dominants more than 30 years of age. The data from recent surveys of the Nelson region by D. J. Cown (unpubl. data), and much more closely comparable with our own, lead to exactly the same conclusion.

TABLE 5—Relationship between wood density and radial growth rate in the Nelson district: results from Pigeon Valley are original, others from Harris (1965)

Origin of sample	No. of trees	Mean radial increment (cm)	Mean density (kg/m^3)	Regression: y =	Test of regression
Rabbit Island	50	6.78	449	$490 - 6.06x_1$	*
Tasman	50	5.08	480	$524 - 8.69x_1$	*
Golden Downs:					
275 m	50	5.68	414	$464 - 8.74x_1$	***
640 m	50	4.87	429	$467 - 7.84x_1$	n.s.
Pigeon Valley:					
First 5 rings	691	8.73	378	$402 - 2.76x_1$	**
Second 5 rings	692	3.54	407	$429 - 5.93x_1$	**
Third 5 rings	671	2.00	455	$479 - 11.55x_1$	**
Weighted mean of first 15 rings	692	14.23	407	$419 - 0.86x_1$	*

y = density (kg/m^3)
x_1 = radial increment (cm)
n.s. = not significant
*** = significant at 0.1% level
** = significant at 1% level
* = significant at 5% level

In contrast with the covariance of density and **radial** growth-rate, the covariance of density and **height** growth-rate has received little attention. Moreover, since there is commonly a positive association between radial growth and height growth, a multiple regression model incorporating growth in both dimensions is potentially more informative than simple regression models. Unfortunately, our data are not entirely suitable because the imbalance in the sub-classes would render a two-factor, trivariate analysis intractable; moreover, our data for diameter seem to suffer from a partial confounding of genetic and environmental effects. We can therefore present only a tentative interpretation of the correlation patterns, based on the model

$$y = a + b_1x_1 + b_2x_2$$

in which y = weighted mean density of first 15 rings at breast height (kg/m^3)
a = a constant (the intercept at $x_1 = 0$, $x_2 = 0$; kg/m^3)
x_1 = radius of first 15 rings at breast height (cm)
x_2 = height at 17 years of age (m)
and b_1 and b_2 are the partial regression coefficients for radius and height respectively.

We examined the data from 691 trees (reduced from the original total because of a missing datum) in three ways:

(a) By supposing that they represented the phenotypic variation of a random sample from a single population – i.e., ignoring their experimental classification (Table 6);

(b) By analysing the joint regression within each family separately and pooling the within-family sums of squares and degrees of freedom (Table 7);

(c) By analysing the joint regression of the family means (Table 8).

TABLE 6—Over-all analysis of variance in wood density with regression on radius and height of stem

Source of variation	Degrees of freedom	Sum of squares	Mean square	Snedecor's F
Regression on radius alone	1	293 779	293 779	4.43*
Extension to include height in joint regression	1	749 456	749 456	11.29***
Total from joint regression	2	1 043 235	521 618	7.86***
Residual	688	45 651 885	66 354	
Total	690	46 695 120		

*** significant at 0.1% level

* significant at 5% level

TABLE 7—Analysis of pooled within-family variance in wood density, with regression on radius and height of stem

Source of variation	Degrees of freedom	Sum of squares	Mean square	Snedecor's F
Regression on radius alone	26	1 495 084	57 503	1.04
Residual from above	639	35 198 690	55 084	
Extension to include height in joint regression	26	4 231 685	162 757	3.22***
Total joint regression	52	5 726 769	110 130	2.36***
Mean joint regression	2	1 462 430	731 215	8.57***
Heterogeneity of family regressions	50	4 264 339	85 287	1.69**
Residual from joint regressions	613	30 967 005	50 517	
Total	665	36 693 774		

*** significant at 0.1% level

** significant at 1% level

TABLE 8—Analysis of family-means variance in wood density, with regression on radius and height of stem

Source of variation	Degrees of freedom	Sum of squares	Mean square	Snedecor's F
Regression on radius alone	1	49 258	49 258	4.45*
Extension to include height in joint regression	1	11 743	11 743	0.86
Total joint regression	2	61 006	30 503	2.23
Residual	23	314 781	13 686	
Total	25	375 787		

* significant at 5% level

To summarise, we draw attention to two main features of these results:

(1) In all three analyses the coefficient of determination – i.e., the proportion of the total sum of squares that is attributable to a regression – is higher for the joint regression effect than for the simple regression on radius alone (Table 9);

(2) The partial regression coefficients for radius (height constant) are all negative, whereas those for height (radius constant) are positive for the first two analyses (Tables 6, 7) and negative, although not significantly so, for the family-means analysis (Table 8).

Apart from these results, we know of only two published studies, one on slash pine (Squillace *et al.* 1962) and one on *P. radiata* (Burdon & Harris 1973), that have examined density in a similar multiple regression relationship. Although different in detail, all three reports are consistent in suggesting that, on a single site –

(a) For trees of the same height, density and diameter are negatively correlated;

(b) For trees of the same diameter, density and height are positively correlated.

TABLE 9—Summary of regression analyses showing coefficients of determination and signs of regression coefficients

	Table 6 (over-all)	Table 7 (within-families)	Table 8 (family-means)
Source of sum of squares			
Regression on radius alone	0.006	0.041	0.131
Effect of including height	0.016	0.115	0.031
Joint regression on radius and height	0.022	0.156	0.162
Signs of partial regression coefficients			
b_1 = Radius (height constant)	—	—	—
b_2 = Height (radius constant)	+	+	—

To what extent this pattern of phenotypic correlation is determined by genetic correlation, and to what extent the environment mediates to reinforce or oppose genetic correlation, we cannot say; the data and our analyses are inconclusive. More recent work (C. J. A. Shelbourne, pers. comm.; M. D. Wilcox, pers. comm.) suggests that in *P. radiata* there is generally a negative genetic correlation between density and diameter; R. D. Burdon and others (unpubl. data), also working with *P. radiata,* found evidence that when genetic covariances between density, diameter, and height are considered jointly there is a **negative** genetic correlation between density and diameter, associated with a **positive** genetic correlation between density and height.

The picture is certainly complex, but it appears to be quite compatible with the mechanical requirements of the tree trunk (Schniewind 1962; Burdon & Harris 1973) and with the behaviour of the cambium in a physiological context (Larson 1963).

CORRELATIONS

Estimates of covariance components for wood density, the density gradient, and other characters were obtained by a process analogous to that used for estimating variance components (Bannister 1969). Correlation coefficients were then estimated for 30 pairs of characters, representing wood density and log quality (Table 10; *see also* Bannister 1980).

Study of this table suggests that the five wood-density characters form a coherent group. Amongst themselves, the wood-density measurements show a moderate to strong phenotypic correlation and a consistently high genetic correlation, suggesting that the density of the wood undergoing deposition was under the influence of essentially the same genes at all times during the 15-year period.

The correlations between density and the density/age gradient are not so easily interpreted. Those involving the first and third five-ring segments are probably not to be trusted, because a regression coefficient b, based on only three density values a_1, a_2, and a_3 at positions 2.5, 7.5, and 12.5 on the abscissa, is

$$(a_3 - a_1)/10$$

and therefore any biological correlation between b and a_1 or b and a_3 is confounded with an automatic mathematical correlation. The coefficients involving the second segment and the mean of all three segments, however, are free from such confounding and may be looked at with more confidence. They suggest that, in our samples, the genotypic and environmental variances acted in concert to promote a positive phenotypic correlation between the mean density and the mean gradient of the first 15 rings.

If there were any genuine correlations between wood density and log-quality characters in this study they were conspicuously weak. Estimates by C. J. A. Shelbourne (pers. comm.) and by M. D. Wilcox (pers. comm.) for comparable pairs of characters also clustered close to zero. Cumulatively, therefore, the evidence suggests that the variation of wood density is independent of variation in the external characters (malformation, crookedness, etc.) listed in Table 10.

TABLE 10—Estimates of genetic, environmental, and phenotypic correlation coefficients

Characters combined in pairs		r_A	r_E	r_P
Density first 5 rings	: Density second 5 rings	0.81	0.18	0.58
	: Density third 5 rings	0.69	-0.03	0.37
	: Density first 15 rings	0.92	0.58	0.79
	: Density gradient	-0.10	-0.48	-0.30
	: Malformation	-0.18	0.04	-0.03
	: Crookedness	-0.15	-0.02	-0.09
	: Butt sweep	-0.33	0.30	-0.05
	: No. branch clusters	0.25	-0.11	0.08
	: Height first stem cone	-0.18	0.05	-0.04
Density second 5 rings	: Density third 5 rings	0.93	0.46	0.73
	: Density first 15 rings	0.95	0.73	0.88
	: Density gradient	0.38	0.27	0.30
	: Malformation	-0.02	-0.20	-0.11
	: Crookedness	-0.02	-0.24	-0.11
	: Butt sweep	-0.24	0.10	-0.10
	: No. branch clusters	0.01	-0.02	0.00
	: Height first stem cone	-0.20	0.11	-0.03
Density third 5 rings	: Density first 15 rings	0.91	0.48	0.72
	: Density gradient	0.16	0.79	0.70
	: Malformation	-0.03	-0.02	-0.02
	: Crookedness	0.10	-0.01	0.04
	: Butt sweep	-0.17	0.04	-0.06
	: No. branch clusters	-0.16	-0.09	-0.12
	: Height first stem cone	-0.19	0.13	0.02
Density first 15 rings (weighted mean)	: Density gradient	0.25	0.08	0.15
	: Malformation	-0.10	-0.15	-0.11
	: Crookedness	-0.07	-0.18	-0.12
	: Butt sweep	-0.32	0.20	-0.10
	: No. branch clusters	0.11	-0.15	0.00
	: Height first stem cone	-0.14	0.10	-0.01

r_A additive-genetic correlation coefficient
r_E environmental correlation coefficient
r_P phenotypic correlation coefficient

DISCUSSION

Sampling Variance at Breast Height (within-trees)

Several workers have examined the variation of samples of the same age structure, representing different parts of each cross-section at a standardised height in the stem. Some of the within-tree variances abstracted from their measurements have represented circumferential variation of density within a single annual ring, but more often they have been based on two or more increment cores taken from different radii within each cross-section, or on different sectors cut from a complete cross-sectional disc. Some of these results (expressed as $(\text{kg/m}^3)^2$) are: 66 (Fielding & Brown 1960); 50 R. D. Burdon, pers. comm.); 127 (M. D. Wilcox, pers. comm.); and a series, from five trees only, ranging from 29 to 272 (D. J. Cown, unpubl. data). It has been disturbing, therefore, to find substantially higher values in our own data: for the three successive five-ring segments these were 280, 258, and 512, with an over-all mean of 333. On the face of it, our error variances appear excessively large, and we have sought an explanation for this discrepancy.

During the laboratory work, several checks were made on the repeatability of the density determinations. These included finding the density for a sample of 60 cores, with a mean length of 33 mm, by two methods – the one already described and the maximum-moisture technique (Smith 1954). The variance of the resulting data was separated into a between-cores component, V_C, and a within-cores component, V_W, which gave an estimate of r, the repeatability:

$$r = \frac{V_C}{V_C + V_W} = 0.955,$$

and this was reassurance that the errors of measurement were within tolerable limits. The actual estimate of V_W, representing the measurement-error variance, was 62 $(\mathrm{kg/m^3})^2$. The measurement technique therefore contributed probably less than one-quarter of the within-tree variance for samples of the same age.

The most plausible suggestion may be that the samples were inordinately affected by compression wood. While reasonable vigilance was maintained in the laboratory, and any badly affected samples were rejected, there remains the speculation that more compression wood than usual came to be included in the samples that were accepted. If that is true, it has certain implications that should be considered. On the one hand, it might be contended that the inclusion of compression wood in studies of wood density – on a random-sampling basis, say – might not be a bad thing. After all, compression wood and "normal" wood are both natural; they occur intermingled in the tree, in the log, in the veneer, in the scantling, and in the digester; and hardly anyone separates them except the scientist who objects to his "normal" wood being "contaminated". From one point of view, therefore, studies based on allegedly normal wood (i.e., rigorously excluding compression wood) could be accused of bias; whereas the one reported here – if indeed it did deal with a greater admixture of compression wood than usual – could be regarded as somewhat more realistic than is usual in studies of this kind.

On the other hand, there is the possibility that the incidence and severity of compression wood are under some sort of variable genetic control (Shelbourne *et al.* 1969; Burdon 1975). If this is correct, it would be quite proper in studying the genetics of wood properties to discriminate carefully between different categories of wood within the tree: a sampling procedure that failed to do so might lead to very obscure or even misleading results. But as far as the present study is concerned, if compression wood contributed anything more than usual to the variation it looks as though it did so only at the level of samples within the smallest subclasses, and that the analysis of variance relegated it tidily to the error term. Wherever it was possible to compare estimates of variance components, other than that for error, with those of other workers there was no suggestion of discordance.

Effect of the Environment

The sensitivity of wood density to differences in the environment, on an extensive scale, has been well demonstrated by Harris (1965). The study reported here was relatively intensive, encompassing a mere 2.4 ha on a single site, and in it the highly significant differences between the nine blocks are noteworthy. Values for the blocks with the highest and lowest means, and for the over-all mean, were:

Block means	*First 5 rings*	*Second 5 rings*	*Third 5 rings*
Highest	387.9	415.3	464.3
Mean	377.3	406.5	453.9
Lowest	367.2	394.2	439.2

Even more remarkable were the differences in the mean density gradient from block to block. The highest was that of Block IV at 9.5 kg/m^3/yr; the lowest was that of the adjacent Block V at 7.5 kg/m^3/yr. The average distance between the trees represented by these two mean gradients was only 50 m, so it may be postulated that seemingly small fluctuations in the environment can have profound effects on the density/age relationship. This is best illustrated by Block IV. For the first five rings its mean density was the lowest but one; for the second five rings it was slightly above the over-all mean; and for the third five rings its density was easily the highest of all nine blocks.

Environmental effects of this order lead one to wonder what caused them. The only suggestion that can be offered at present, from long familiarity with the terrain, is that the block-to-block variation of the density gradient may have been related to soil moisture, the moister patches of ground being associated on average with the gentler density gradients and the drier patches with the steeper density gradients.

The analyses of variance depicted in Fig. 2 showed a component that would be formally described as "genotype × environment interaction", which was generally significant at the 5% level. In this and comparable randomised-block experiments, however, each block inevitably covers quite a large area of ground, and within our blocks the environment showed appreciable heterogeneity. We therefore regard the "family × block" term as being essentially an additive component of the external environmental variance, rather than a genuine interaction. Its rapid increase with age, especially from the second to the third five-ring segment, was probably engendered largely by increasingly severe competition within the stand.

Sources of Variation in Density for Different Kinds of Sample

Special attention should be drawn to certain features of the analysis shown in Tables 2–4 and Fig. 5. Consider the wood in a sample of, say, 1000 fifteen-year-old logs, and suppose that their density varies in the same way as that of the trees described in this paper. One use for all this raw material might be to convert it into a pile of chips at a pulp mill, and in this condition more than half of the chip-to-chip variation in density would have originated within the tree, and especially in the density/age relationship (see B1, B2, B3 near the right-hand side of Fig. 5); most of this may be recognised as the mean linear regression within trees – an **unvarying** characteristic of the sample – whereas the between-trees sources of variation, both genetic and environmental, would tend to be less important. Another use might be to convert the logs into sawn timber, in which event the range in the mean age of the wood in each piece would probably be about 5 to 10 years; the components of the piece-to-piece variation in the density of the timber would then be more or less in the proportions shown in the central part of Fig. 5. Yet another use might be as round or half-round posts; then the components of the post-to-post variation in density would be in the proportions shown in the extreme left of Fig. 5.

Complex as all this may seem, it still does not show the full picture. One complication, not included in the analysis, is that the cross-sectional area and the volume of the wood deposited in the different years of the range are not constant (our simplified model assumed that they were); and if fluctuations in annual increment were taken into account the partitioning of the variance would be rather different.

Another complication arose because our samples yielded only three points for the examination of the density/age relationship within each tree. One degree of freedom was used to estimate each mean, and one to estimate each linear regression, leaving only one for the "residual variance". As explained earlier, this residual was regarded as a random component (Table 2); but it is abundantly clear from other results, notably those of Harris (1965, 1969) and D. J. Cown (unpubl. data), that the typical mean regression for a more-or-less random sample of trees from a single site takes a graphical form that is not a straight line but a curve. One such curve, derived from Harris (1969, Fig. 3), was analysed by the method of orthogonal polynomials (Fisher & Yates 1957). This partitioned the variance in mean density at breast height, over the range 0–17 years, into three highly significant components ($p < 0.001$) and a remainder, with coefficients of determination as follows:

Linear	0.63
Quadratic	0.08
Cubic	0.24
Residual	0.05

This conforms with the common assertion (e.g., Harris *et al.* 1976) that the relationship is "essentially linear", but it also suggests that there is at least one important curvilinear component in the regression, and that in our data the paucity of observations for each regression line resulted in substantial under-estimation of the total regression effect. With ideal data, one might be able to fit an accurate curve for each tree in a random sample; but the radial pattern within the individual tree appears to vary widely, and the mathematical form of the curve may differ radically from tree to tree. If that is so, it might preclude the application of the "family of curves" concept of Day (1966) or the "longitudinal-growth model" of Graybill (1976).

Finally, it should be emphasised that our data and Fig. 5 represent a range of only 0–15 years, whereas in practice large volumes of wood are supplied as logs with a range of 0–30 years and more. Our results should therefore be considered as representative only of thinnings, top logs, or short-rotation pulpwood; but in the context of general knowledge about the density/age gradient beyond the age of 15 we suggest that extrapolation from our data would probably lead to a fairly accurate conception of how density varies in material grown on a 25-year rotation.

Artificial Selection for Wood Density

The importance of wood density as a character with potential for artificial selection in *P. radiata* has often been raised in the literature. In a recent statement Harris *et al.* (1976) concluded that it would be quite appropriate to use the mean density of the first five annual rings as a criterion. The results presented here support their view, and indeed they go somewhat further. Although they show samples from the first five rings to be rather poor for predicting the later performance of the **phenotype** – confirming the results of Harris (1965) and D. J. Cown (unpubl. data) – they seem to be much more dependable as indexes to the **genotypic value** of a group or of an individual (Table 10).

Only one disadvantage, it seems, is likely to detract from selecting for higher wood density: a negative **genetic** correlation between that and volumetric growth rate. Evidence so far is neither plentiful nor unequivocal (C. J. A. Shelbourne, pers. comm.; M. D. Wilcox, unpubl. data) but most of the results, including the preliminary analyses of our own data, point to the correlation being real. If there is such a correlation, it will have an important bearing on the strategy of selection: for a specified amount of improvement in wood density it will be necessary to weigh not only the technical and economic advantages of that improvement itself, but also the economic disadvantage of it as an impediment to the improvement of volumetric growth rate. In this connection it should be understood that, if growth rate is measured as tonnes of cellulose per hectare per year, an increase in density could be accompanied by an actual loss in volumetric production without any loss of productivity; but the point is that selection should be considered, not just for its likely effects on density and volume separately, but in terms of what it may do to the quality and yield of the crop as a whole. We agree completely with Harris *et al.* (1976) that there is a need for more careful thought and research into the interrelated elements of *P. radiata* culture – silvicultural methods, rotation, volume, wood density, yield, quality, and economics.

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APPENDIX 1

COEFFICIENTS OF REGRESSION COMPONENTS IN EXPECTATIONS OF MEAN SQUARES

Suppose we have n observations on a normally distributed variate y, each paired with an associated observation on a normally distributed covariate x. If the covariance with x is ignored, the sum of the squared deviations of y from its mean, $\bar{y}$, is simply $\Sigma(y-\bar{y})^2$, and the variance, $\sigma^2{}_y$, is given by

$$\sigma^2{}_y = \Sigma(y-\bar{y})^2/(n-1) \quad \text{..........} \quad (1)$$

If we now consider the deviations $(y-\bar{y})$ as attributable partly to the influence of the covariate x and partly to a random variation independent of x, we may suppose that

$$\sigma^2{}_y = \sigma^2{}_w + L^2 \quad \text{..........} \quad (2)$$

where L^2 is the linear-regression component of variance of y and $\sigma^2{}_w$ is the residual variance about the y/x regression line.

Moreover, by an analysis of variance of the form shown in Table A it should be possible to estimate the two terms on the right-hand side of Equation (2).

Determination of the coefficient k in Table A proved a stumbling block, but by an empirical approach we find that Equation (2) is satisfied as follows:

(a) In the simplest, i.e., bivariate normal, case (Table A),

$$k = n-1;$$

and hence k may be interpreted as

"one less than the number of pairs of observations".

(b) In the more complex situation considered in this paper, y is a random variate, x is a fixed effect with $a = 3$ levels, and

$$\begin{aligned} n &= w \times a \times f \times t \\ &= 2 \times 3 \times 26 \times 23 \\ &= 3588. \end{aligned}$$

Here k is the product of two factors. One of these is $(a - 1)$, i.e.,

"one less than the number of levels of the independent variate".

The other factor is analogous to the coefficient of a variance component that is completely independent of x. For example, if our expectations of mean squares included a variance component $\sigma^2{}_{at:f}$, the coefficient for that would be

$$n/(a \times t \times f) = w = 2.$$

At the corresponding level in the analysis the linear-regression component $L^2{}_{alt:f}$ has the coefficient

$$\left[n/(a \times t \times f)\right] (a-1) = w(a-1) = 4.$$

We have looked unsuccessfully for theoretical proof of this finding, but its application – at least to the analysis shown here – seems valid.

APPENDIX 2

EFFECT OF GROUPING DATA INTO THREE AGE CLASSES

The regression model used in our nine-component analysis is that of a random variate y with a regressor x at three fixed levels. Expressing these levels with the year as the unit of time, the range of x is 10 years. It may need explaining, however, that these three levels are in a sense quite artificial. A more elaborate study of the same raw material might have been made by dividing each of the original increment cores into five segments of three annual rings each. In such an event, the mid-point of each segment on the scale of x would have led to x having five fixed levels and a range of $(13\frac{1}{2} - 1\frac{1}{2})$, i.e., 12 years. Similarly, in principle (although not in practice) each increment core could have been divided into 15 segments of one annual ring each. Then x would have had 15 fixed levels and a range of $(14\frac{1}{2} - \frac{1}{2})$, i.e., 14 years.

But time is really a continuum. One can envisage a process of dividing it into progressively smaller and smaller classes: years could be divided into months, so that x would have 180 fixed levels and a range of $14\,{}^{11}/_{12}$ years, and so on. Ultimately the class interval would be infinitesimal, and x would have an infinitely large number of fixed levels and a range of 15 years.

In our judgment, the most realistic statistical concept for the linear regression of density on age, within this 15-year period, is one in which the observations for y are normally distributed about the regression lines, while x has an infinitesimal class interval and the same number of observations in each class (i.e., its frequency distribution can be portrayed by a rectangle). Two questions arise:

(1) Does our crude statistical reduction of the 15-year continuum to three fixed points introduce any inaccuracy into the estimates?

(2) If so, can we counteract or eliminate it?

The answers, we conclude, are:

(1) Estimation of the regression coefficients is not affected; but the analysis of variance, on its own, leads to under-estimation of the regression-component (L^2) terms. That part of the deviation of y attributable to the influence of x may be represented as $b(x - \bar{x})$, where b is the regression coefficient and $(x - \bar{x})$ is the deviation of x from its mean. It follows that the mean square of the deviations attributable to the regression may be represented as $\Sigma(b(x - \bar{x}))^2/n$, where n is the number of pairs of y and x, and this can be re-written as

$$b^2\ \Sigma(x - \bar{x})^2/n.$$

In other words, our estimates of the L^2 terms represent b^2 multiplied by the variance of the fixed effect, x.

Now a variate with a rectangular distribution and a range of 1 has the variance 1/12. Our material, with an equally uniform distribution, an infinitesimal class interval, and a range of 15, has the variance $(1/12 \times 15^2)$, i.e., $18\frac{3}{4}$. Grouping all our observations on x into three classes and using the mid-points of those classes as the only values for x in the calculations leads, in effect, to the following:

$$\begin{aligned}\Sigma(x-\bar{x})^2/3 &= \left[(2\tfrac{1}{2}-7\tfrac{1}{2})^2 + (12\tfrac{1}{2}-7\tfrac{1}{2})^2\right]/3 \\ &= 16\,{}^2/_3.\end{aligned}$$

Thus the regression components taken directly from the analysis of variance are based partly on an erroneous value for the variance of x.

(2) The effect of the initial error can be eliminated simply by multiplying each regression-component estimate by $(18\tfrac{1}{2})/(16\,{}^2/_3)$, i.e., 1.125.

TABLE A—Analysis of variance incorporating a regression component

Source of variation	Degrees of freedom	Expectations of mean squares
Regression	1	$\sigma^2_w + kL^2$
Residual	n - 2	σ^2_w
Total variance	n - 1	$\sigma^2_y = \sigma^2_w + L^2$