

AN EARLY PROGENY TRIAL IN *PINUS RADIATA*

3. CHARACTERS AFFECTING LOG QUALITY

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Eleven characters of the stem and branches, studied in 26 open-pollinated families, showed highly significant additive-genetic variance ($P < 0.01$ or $P < 0.001$). Estimates of heritability ranged from 0.12 to 0.50.

For malformation, heritability was estimated as 0.17, but the assessment of this character was crude and, since the malformation may have had two or more independent origins, it may be best to regard this result merely as evidence that **some** genetic variation was involved.

Estimates of heritability for crookedness, butt sweep, number of branch clusters on the stem at age 7, and mean branch angle were from 0.4 to 0.5; those for the number, size, and distribution of the branches were from 0.1 to 0.2. These lower values reflect, in some degree, errors arising from the difficulties of sampling within the tree, but they also suggest that most of these characters were extremely sensitive to variations in the environment.

Genetic correlation coefficients were estimated for all possible pairs of characters. Although these correlations were not tested for significance, a comparison of 21 of them with their counterparts from an independent study by other New Zealand workers showed good agreement. Among the characters related to branching, several estimates of genetic correlation were close to +1 or -1. It is postulated that these represent associations resulting from pleiotropism rather than from linkage.

If these intimations of genetic correlation are at all accurate, they have important practical implications. Strong or even perfect genetic correlations, such as those indicated, could impose severe constraints on artificial selection, because one would expect directional selection applied to one character in a nexus of correlated characters to evoke correlated responses, some of which would be favourable and some detrimental to log quality.

INTRODUCTION

This paper reports some of the main results of a study begun in 1949. It is based on 26 open-pollinated progenies of *Pinus radiata*, planted in Pigeon Valley, in the Nelson district, to a randomised block design with 9 replications. Full details of the experiment may be found in preceding papers (Bannister 1969, 1979).

CHARACTERS, METHODS OF ASSESSMENT, AND ANALYSES

Malformation

In a first assessment, when the trees were 14 years old, only 2 categories were recognised: malformed and not malformed. For comparative purposes the families were ranked according to the percentage of trees free of malformation in each family total;

for tests of significance the number of trees free of malformation in each plot was expressed as a percentage of the total number in the plot, Bliss's angular transformation was applied, and the variance was analysed.

At 21 years of age the trees clearly varied widely in the severity of malformation, and they were scored numerically so that the data might be analysed as representing a variate with a continuous distribution. Three observers worked independently, using the scores 0.01, 1, 2, 3, and 4, according to the following criteria:

- 0.01 — a single stem with no fork and no evidence of serious disturbance to its growth. (The digit 0 would naturally have been chosen here, but the computer program used for the experiment interprets 0 as a missing tree; 0.01 was therefore chosen to indicate 0.)
- 1 — *either* a single fork below 1.4 m, with two stems free of malformation above; *or* a single fork above 16 m.
- 2 — a single fork between 1.4 m and 16 m, and at least one useful log developed above the fork.
- 3 — *either* a severe disturbance between 1.4 m and 16 m, resulting in the development of several competing leaders; *or* forked once between 1.4 m and 16 m, and a second fork above the first.
- 4 — *either* extremely severe malformation, leaving little or no merchantable bole; *or* clear evidence of forking having occurred at three or more different times during development.

To transform the original scores it was supposed that they themselves occupied an arbitrary scale, but represented some underlying biological variate with a continuous variation and a normal distribution. First, the overall frequency of each of the 5 original classes was expressed as a percentage of the total. The whole area under a normal distribution curve was then divided by ordinates, working from left to right, into 5 smaller areas proportional to the 5 frequencies. (Fig. 1; Pearson & Hartley 1958: 1-3). Finally the distance of the mean of each of these 5 areas from the origin of the curve was calculated, giving the 5 points of a new scale.

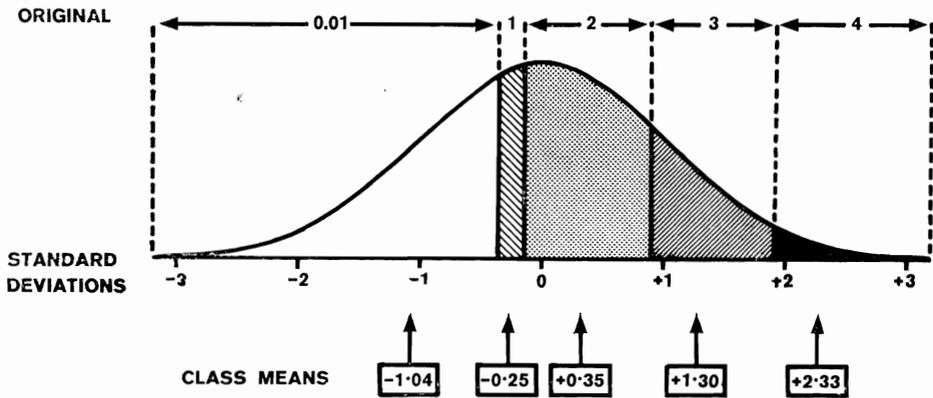


FIG. 1—Frequency distribution of the original malformation scores, and the derivation of a new scale.

This led to the following transformation:

Transformed score	Original score
0.01	0.01
0.950	1
1.657	2
2.786	3
4	4

For each tree the sum of the transformed scores of the 3 observers was used as a variate representing the degree of malformation, and the variance was analysed. For graphical illustration the families were ranked from the lowest to the highest incidence of malformation, using percentages from the 1963 assessment and mean scores from the 1970 assessment. Strong contrasts between families were evident (Fig. 2).

Crookedness

When the trees were 14 years old, 5 independent observers, working independently, assessed the whole of the visible part of the stem except for 2 m at the base. Scores, ranging from 0 for "straight" to 9 for "extremely crooked", were assigned to trees subjectively. Full details of this work have been published separately (Bannister 1979).

Butt sweep or lean

When the trees were 18 years old, 4 observers assessed this character, working independently and using a subjective scoring system like the one used for crookedness. The purpose was to represent the extent to which each stem deviated from a vertical posture, between ground level and a point 2 m above ground level. A few trees were strongly curved in the first 2 m of the stem, but most showed little curvature; on the other hand, practically all of them leaned visibly towards the north-east. Direct measurements were made on 120 trees using a plumb-bob; deviations from the vertical ranged from 0° to 20°. The subjective scores and their approximate equivalents in degrees were:

Subjective score	Lean as measured (degrees)
0	0.0
1	0.5
2	4.5
3	7.5
4	10.2
5	12.6
6	14.8
7	17.0
8	18.9
9	20.7

The frequency distribution of the original scores showed a strong positive skewness; the square-root transformation was applied and the sum of the transformed scores of the 4 observers was the variate used for statistical analysis.

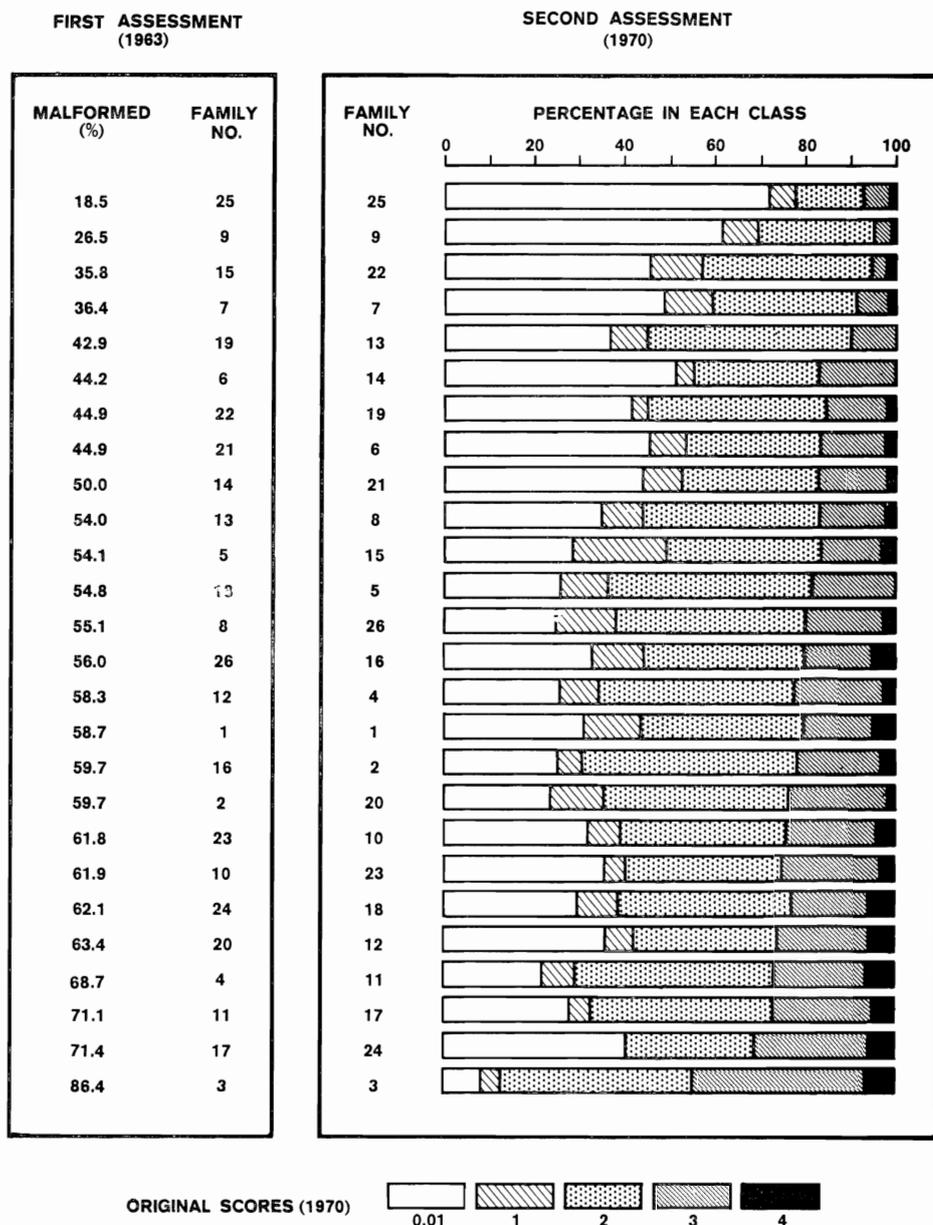


FIG. 2—Comparison of families for incidence and severity of malformation at 21 years of age. The results for malformation at 14 years of age are also shown.

Height to first cone on stem

This character was measured with a Blume-Leiss hypsometer, when the trees were 21 years old. It is an index to the detrimental effect of "cone holes" on timber quality (see Fielding 1945; Bannister 1959: 73-5, 1962: 360-3).

Branching frequency

Complete counts of the number of branch clusters on each stem were made when the trees were 5 and 7 years old. Some results have already been presented (Bannister 1969); the importance of branching frequency, as dealt with in this paper, lies in its interrelationships with other characters that influence log quality.

Other branch characters

Since it was far from clear what counts or measurements would best characterise the variation, the trees were sampled at 20 years of age for a series of branch measurements. Sampling within the tree was restricted for two reasons: (a) the physical difficulty of climbing and working more than a few metres from the ground; (b) many of the branches below the 2-m level had been removed in pruning. The method adopted was to take the first 2 intact, consecutive branch clusters above 2 m. In these clusters, the diameter of every branch more than 3 mm thick was measured with calipers as close to the trunk as practicable. Generally the cross-section of a branch is practically circular, but close to the trunk, and especially for the larger branches, it tends to be elliptical, with the longer axis in the vertical plane. The horizontal dimension was the one used throughout this work. "Branch angle" was measured with a celluloid protractor and represents the angle enclosed between a branch and the distal part of the stem. Other records included the height above ground level of each of the 2 branch clusters.

Sampling within families was arranged to give as nearly as possible a total of 27 trees per family. With that requirement predominant, sampling within plots was restricted whenever possible to 3 trees per plot, in all 652 trees were sampled.

The characters derived from these measurements may be described as follows:

- (a) Number of branches in two consecutive clusters: this was simply a direct count, which is the equivalent of $2 \times$ (mean no. of branches per cluster).
- (b) Sum of all branch diameters in two consecutive clusters: this is one way (crude but possibly useful) of expressing "knottiness" around the circumference of the stem.
- (c) Mean diameter of branches: for this, three statistics were derived from the measurements of each tree.

These were:

- (i) the arithmetic mean of all the diameters measured;
- (ii) the arithmetic mean of the square roots of the diameters;
- (iii) the arithmetic mean of the natural logarithms of the diameters of 4 branches, comprising the 2 biggest branches in the upper cluster, and the 2 biggest in the lower cluster.

Preliminary analyses using these three alternatives showed them to be virtually equivalent for characterising mean branch diameter. Therefore in all the analyses reported here this character is represented by the arithmetic mean of all the diameters without transformation.

- (d) Mean branch angle: the statistic used was the arithmetic mean of all the branch angles recorded within each tree.

Analyses

The analysis of variance and the estimation of variance components were carried out using two different models. The first was a 2-way classification with Trees nested

in the Family-Block sub-classes; the method for analysing this has been described in the preceding papers of this series (Bannister 1969, 1979). The second model was a 1-way classification with Trees nested in Plots and Plots nested in Families.

According to the model chosen, the Phenotypic variance, σ^2_P , was estimated as:

either $\sigma^2_P = \sigma^2_f + \sigma^2_b + \sigma^2_{fb} + \sigma^2_w$

or $\sigma^2_P = \sigma^2_f + \sigma^2_{p:f} + \sigma^2_w'$

where σ^2_f = Families component of variance

σ^2_b = Blocks component of variance*

σ^2_{fb} = Families \times Blocks component of variance

σ^2_w = Error component of variance

$\sigma^2_{p:f}$ = Plots-in-Families component of variance

Heritability (h^2) was estimated as $h^2 = (3.5 \sigma^2_f) / \sigma^2_P$; the choice of 3.5 as the coefficient has been explained previously (Bannister 1969).

Repeatability of the family means (r_f) was calculated as:

$$r_f = (n\sigma^2_f) / (\text{Mean square for Families})$$

where σ^2_f = Families component of variance

and n = Number of trees per family. The denominator was extracted from the 2-way analysis of variance.

The Blocks component was usually very small and the fully nested analysis gave estimates for the Plots-within-Families component that were very similar to those for the Family \times Block interaction component in the 2-way analyses. So, considering each character in turn: if the F-ratio for Blocks showed P substantially greater than 0.05, the components estimated from the simpler, nested model were used; but if it showed P close to, or less than, 0.05 those from the 2-way model were preferred. In fact, wherever the 1-way model was chosen, the important results — namely the estimates of Families variance and Phenotypic variance — were practically the same by both methods.

Analyses of covariance, leading to the calculation of genetic, environmental, and phenotypic correlation coefficients, were made using a method analogous in every respect to that used for the 2-way analysis of variance in this experiment (Bannister 1969).

Thus, if the 4 components of covariance for 2 characters x and y were as follows:

cov_f = covariance of family means

cov_b = covariance of block means

cov_{fb} = residual covariance of plot means

cov_w = covariance of trees within plots,

then cov_P = phenotypic covariance

$$= \text{cov}_f + \text{cov}_b + \text{cov}_{fb} + \text{cov}_w;$$

cov_A = additive-genetic covariance

$$= 3.5 \text{cov}_f \text{ (using the same coefficient as in estimating heritability — see Bannister 1969);}$$

and cov_E = environmental covariance

$$= \text{cov}_P - \text{cov}_A.$$

* Normally, in a tree breeding context, excluded from σ^2_P

From the last 3 covariance estimates and the 6 analogous variance estimates the 3 correlation coefficients were derived as:

$$r_P = \frac{\text{COV}_P}{\sqrt{\sigma_{P(x)}^2 \cdot \sigma_{P(y)}^2}} = \text{phenotypic correlation coefficient,}$$

$$r_A = \frac{\text{COV}_A}{\sqrt{\sigma_{A(x)}^2 \cdot \sigma_{A(y)}^2}} = \text{genetic correlation coefficient,}$$

and $r_E = \frac{\text{COV}_E}{\sqrt{\sigma_{E(x)}^2 \cdot \sigma_{E(y)}^2}} = \text{environmental correlation coefficient,}$

where $\sigma_P^2 =$ phenotypic variances of x and y respectively,
 $\sigma_A^2 =$ additive-genetic variances of x and y respectively,
 and $\sigma_E^2 =$ environmental variances of x and y respectively
 $= (\sigma_P^2 - \sigma_A^2).$

RESULTS

For the first assessment of malformation the analysis of variance showed no differences between the blocks, but very highly significant differences between the families ($P < 0.001$). For the experiment as a whole the number of stems free of malformation comprised 44.9% of the total; taking the families separately, the percentages ranged from 13.6 to 81.5.

The second assessment of malformation generally confirmed the results of the first, and allowed a more detailed comparison of the families (Fig. 2).

The 2-way analyses of variance showed the following:

1. The Families component was in every case highly significant ($P < 0.001$ or $P < 0.01$);
2. The Blocks component was small or non-existent;
3. The Family \times Block component was highly significant ($P < 0.01$) for 7 of the 11 characters examined, but it was invariably small, ranging from 2.3 to 6.5% of the phenotypic variance.

At the same time the 1-way analyses showed:

1. The Families component in each case was significant, as in the 2-way analyses;
2. The Plots-in-Families component was generally comparable in size and significance with that of Families \times Blocks in the 2-way analyses;
3. The Phenotypic variance was very similar to that estimated by the 2-way analyses.

As one might have expected from these results, the two methods of analysis gave almost identical estimates of heritability for each character. Table 1 shows heritability estimates together with estimates of some associated parameters. Estimates of correlation coefficients are shown in Tables 2, 3, and 4.

TABLE 1—Mean, standard deviation, and heritability estimates for stem and branch characters

Character	Mean	σ_A^\dagger	σ_E^\dagger	σ_P^\dagger	h^2^\ddagger		90% confidence limits for h^2	
Malformation‡	2.65	1.27	2.77	3.04	0.17		0.09	0.43
Crookedness‡	17.48	2.84	3.11	4.21	0.44	(0.23)*	0.28	0.87
Butt Sweep‡	6.04	0.98	0.97	1.38	0.50	(0.24)	0.31	0.95
Number of Branch Clusters, age 5 years	8.08	1.12	1.42	1.81	0.38		0.23	0.75
Number of Branch Clusters, age 7 years	12.27	2.03	2.07	2.90	0.49	(0.86)	0.31	0.93
Height to First Cone on Stem (m)	11.12	2.31	4.29	4.88	0.23	(0.41)	0.13	0.51
Total Number of Branches in Two Clusters	13.60	1.11	3.06	3.25	0.12	(0.26)	0.05	0.68
Mean Branch Diameter (mm)	27.76	2.61	6.47	6.98	0.15	(0.21)	0.07	0.66
Sum of all Branch Diameters in Two Clusters (mm)	375.09	42.42	113.90	121.54	0.12		0.06	0.48
Mean Branch Angle‡	61.04	4.61	5.30	7.02	0.43	(0.08)	0.25	0.95
Distance between Two Consecutive Branch Clusters (m)	0.77	0.18	0.40	0.44	0.17		0.08	0.63

* Values in parentheses from Shelbourne *et al.* (unpubl.).

† σ_A = additive-genetic standard deviation

σ_E = environmental standard deviation
(for derivation see "Analyses")

σ_P = phenotypic standard deviation

h^2 = heritability

‡ For units see the section following the Introduction

TABLE 2—Estimates of phenotypic correlation coefficients for stem and branch characters

	Crookedness	Butt Sweep	No. of Branch Clusters, age 5 years	No. of Branch Clusters, age 7 years	Height to First Cone on Stem	Total No. of Branches in Two Clusters	Mean Branch Diameter	Sum of all Branch Diameters in Two Clusters	Mean Branch Angle	Distance between Two Consecutive Branch Clusters
Malformation	0.48	0.08	-0.20	-0.29	0.03	-0.05	0.03	-0.01	0.02	-0.01
Crookedness		0.42 (0.30)*	-0.28	-0.35 (-0.10)	0.06 (0.10)	-0.01 (-0.02)	0.08 (0.18)	0.06	0.09 (0.09)	0.11
Butt Sweep			-0.12	-0.10 (-0.08)	-0.05 (0.04)	-0.03 (-0.00)	0.09 (0.11)	0.06	0.10 (-0.04)	-0.02
Number of Branch Clusters, age 5 years				0.76	-0.11	-0.03	-0.25	-0.22	0.17	-0.42
Number of Branch Clusters, age 7 years					-0.23 (-0.30)	-0.07 (-0.11)	-0.26 (-0.11)	-0.24	0.16 (0.12)	-0.34
Height to First Cone on Stem						0.01 (0.03)	0.18 (0.13)	0.13	-0.15 (0.04)	0.15
Total No. of Branches in Two Clusters							-0.10 (-0.05)	0.64	0.23 (-0.09)	0.14
Mean Branch Diameter								0.67	-0.58 (-0.28)	0.38
Sum of all Branch Diameters in Two Clusters									-0.27	0.38
Mean Branch Angle										-0.23

* Values in parentheses are from Shelbourne et al. (unpubl.).

TABLE 3—Estimates of genetic correlation coefficients for stem and branch characters

	r_f^\dagger	Crookedness	Butt Sweep	No. of Branch Clusters, age 5 years	No. of Branch Clusters, age 7 years	Height to First Cone on Stem	Total No. of Branches in Two Clusters	Mean Branch Diameter	Sum of all Branch Diam. in Two Clusters	Mean Branch Angle	Dist. between Two Consec. Branch Clusters
Malformation	0.67	0.36	0.08	-0.47	-0.51	0.51	-0.05	0.26	0.16	0.02	0.41
Crookedness	0.84		0.84 (0.87)*	-0.55	-0.48 (-0.17)	-0.19 (-0.10)	0.41 (0.26)	0.11 (0.55)	0.36	0.47 (0.09)	0.38
Butt Sweep	0.86			-0.18	-0.08 (-0.33)	-0.49 (0.51)	0.38 (0.31)	-0.29 (0.22)	0.06	0.74 (0.37)	-0.36
Number of Branch Clusters, age 5 years	0.73				0.95	-0.01	-0.60	-0.76	-0.96	0.12	-0.93
Number of Branch Clusters, age 7 years	0.80					-0.19 (-0.34)	-0.60 (-0.15)	-0.75 (-0.80)	-0.95	0.16 (0.77)	-0.92
Height to First Cone	0.70						0.17 (0.51)	0.94 (0.83)	0.95	-0.56 (-0.48)	0.78
Total No. of Branches in Two Clusters	0.47							-0.07 (-0.71)	0.58	0.50 (0.35)	0.46
Mean Branch Diameter	0.50								0.86	-0.51 (-0.77)	1.11
Sum of All Branch Diameters in Two Clusters	0.44									-0.09	1.23
Mean Branch Angle	0.80										-0.26

* Values in parentheses are from Shelbourne *et al.* (unpubl.)† r_f = repeatability of the family means

TABLE 4—Estimates of environmental correlation coefficients for stem and branch characters

	Crookedness	Butt Sweep	No. of Branch Clusters, age 5 years	No. of Branch Clusters, age 7 years	Height to First Cone on Stem	Total No. of Branches in Two Clusters.	Mean Branch Diameter	Branch Diam. in Two Clusters, Sum of all	Mean Branch Angle	Dist. between Two Consec. Branch Clusters.
Malformation	0.56	0.09	-0.11	-0.22	-0.08	-0.05	-0.01	-0.04	0.02	-0.10
Crookedness		0.02 (0.13)*	-0.09	-0.24 (0.02)	0.18 (0.06)	-0.15 (0.06)	0.08 (0.15)	-0.04	-0.21 (-0.15)	0.00
Butt Sweep			-0.08	-0.12 (0.65)	0.19 (-0.14)	-0.18 (0.11)	0.26 (0.05)	0.06	-0.46 (0.08)	-0.04
No. of Branch Clusters, age 5 years				0.63	-0.16	0.13	-0.11	-0.02	0.20	-0.26
No. of Branch Clusters, age 7 years					-0.27 (-0.53)	0.11 (-0.03)	-0.10 (0.82)	-0.02	0.16 (-0.34)	-0.12
Height to First Cone on Stem						-0.03 (-0.21)	0.01 (-0.06)	-0.03	0.04 (0.04)	0.00
Total No. of Branches in Two Clusters							-0.10 (0.20)	0.65	0.17 (0.06)	0.09
Mean Branch Diameter								0.64	-0.64 (-0.22)	0.22
Sum of All Branch Diameters in Two Clusters									-0.35	0.20
Mean Branch Angle										-0.23

* Values in parentheses are from Shelbourne *et al.* (unpubl.)

DISCUSSION

Malformation

The morphology of malformation can be reduced — albeit laboriously — to quantitative terms, but the contribution of genetic variation is extremely difficult to assess. The main trouble is that one seldom knows how the malformation originated. Thus two malformed trees, with features that superficially appear to be identical, may have become malformed independently and for quite different reasons. Among possible causes one might list storm damage, fungous diseases, drought, frost, hail, nutritional disorders, and even a genetic predisposition in some trees to fork despite being in perfect health. A further complication is that genotypes may well vary widely in their ability to replace a damaged apical shoot with a single dominant leader, so that what may cause an irreversible change in the growth habit of one tree may result in nothing more than a temporary aberration in that of another.

With such obscurity surrounding its genesis and development, it may well be unrealistic, more often than not, to treat malformation as a single character. Even so it may *sometimes* happen that most of the malformation in a particular stand originates from a single cause. In such an event, phenotypic variation of the kind described here could be the outward expression of a cryptic genetic variation, characterised by an effectively continuous and normal distribution of genotypic classes and a varying threshold for some essential ingredient or end-product of metabolism.

In this study the results were statistically not entirely satisfactory because the variate showed some evidence of positive skewness and discontinuities in the frequency distribution, but the striking differences between families, coupled with the results from the analysis of variance, leave little room for doubting the existence of an underlying genetic variation. The cause or causes of the malformation are not known, but it should be noted that from about the eighth to the tenth year the stand seemed to be assailed each summer by die-back of the leaders; that the affected leaders resembled those described by Stone & Will (1965) as suffering from boron deficiency; and that the experiment was sited on the Moutere Gravels, a soil formation that has provided many examples of boron deficiency in crops such as apples, hops, and raspberries (Atkinson 1936; Askew & Monk 1953), as well as in *Pinus radiata* (Appleton & Slow 1966).

It is suggested, therefore, that some of the malformation seen in this experiment may have been caused by a chronic, sub-acute, short-term deficiency in the supply of boron to the leading shoots, at a stage when relative growth rates were at their greatest. Now if this had been in fact the only cause of the malformation, a straightforward genetic interpretation would be as follows: the individual genotypes varied either in their boron requirements or in their ability to translocate boron to the leading shoot, so that in times of shortage the more demanding or less efficient trees would have been prone to die-back, whereas the more frugal would have survived unscathed.

In reality, however, such an explanation would almost certainly be too facile. The fungus *Diplodia pinea* is almost ubiquitous in New Zealand plantations, and several workers have reported that it is intimately associated with shoot die-back (e.g., Marks & Minko 1969; Wright & Marks 1970; Chou 1976a, b). Opinions may differ on whether this fungus is a primary pathogen or a wound parasite, or whether it is part of a complex

disease syndrome, but it must certainly be considered as an alternative and possibly major factor in the development of malformation in this experiment. In view of this and other possibilities, it seems likely that the method of assessment resulted in two or more quite different patterns of genetic variation being treated as one. It was therefore rather surprising that the analysis pointed so clearly to the existence of genetic variation; but this, it is suggested, may have been a variation with respect to one particular cause of malformation — one that was quantitatively more important than any other in the history of the stand.

Heritabilities

As shown in Table 1, the estimates of heritability for Crookedness, Butt Sweep, Number of Branch Clusters, and Mean Branch Angle, are all between 0.43 and 0.50; those for the remaining branch characters lie between 0.12 and 0.17, and the heritability for Height to First Cone is 0.23. It is not at all clear how this grouping should be interpreted. It may have been caused partly by chance and partly by the problems of sampling branch clusters and individual branches within the tree. For example, Distance between Clusters (or Clearwood Length) had an estimated heritability of 0.17, but this was based on only one measurement per tree; the phenotypic variance therefore included all the within-tree variance (or "special environmental variance" of Falconer 1960: 143-9). Had it been possible to express this character in another way, such as (Height of Stem)/(Number of Branch Clusters at age 7 years), the estimate of heritability would have been much higher than 0.17. On the other hand, it seems probable that some branch characters (Mean Diameter, for example) are particularly sensitive to variations in the environment, and might therefore be expected to show relatively low heritability.

Various heritability estimates have been made by other workers, but they were based on families that represented different kinds of genetic sample; the trials were assessed at different ages; and different methods of assessment were used for several characters. Nevertheless, it may be instructive to compare some of the estimates in this study with the corresponding estimates of Shelbourne *et al.* (unpubl.), which are included in Table 1. These workers found relatively low heritabilities for Crookedness and Butt Sweep. As they observed, their sample of female parents had been the result of stringent selection to minimise the expression of both these characters, and it seems quite possible that the variance of their family means was much lower than that of ordinary populations. At the same time, the phenotypic variance of their material would have been determined in part by the male parents, which one may suppose to have been approximately random samples of ordinary populations. Thus their heritability ratios for these characters may represent abnormally low values in the numerator and only slightly lower-than-normal values in the denominator.

For Number of Branch Clusters there appears to be a consistent trend of heritability increasing as age increases. In the Pigeon Valley trial the estimate rose from 0.38 at 5 years to 0.49 at 7 years, and in the trees studied by Shelbourne *et al.* (unpubl.) reached 0.86 at 12 years. Although the first two values may be a little lower, and the last a little higher, than the heritabilities of most ordinary populations, one would expect them to show this sort of trend for two reasons. First, the total number of branch clusters on the stem is the cumulative expression of an annual rhythm (Bannister 1962), and this is subject to a good deal of special environmental variance. Consequently, the greater

the number of annual cycles included in the count of branch clusters, the higher are the repeatability and the heritability (Falconer 1960: 140-9). Secondly, the special environmental variance appears to be largely the reflection of instability in the patterns of growth shown by individual trees during the juvenile phase, contrasted with relatively stable patterns in the adult phase (Bannister 1962). As a result, the phenotypic variance of young trees is largely environmental in origin, and heritability is low, whereas in adult trees, especially if the juvenile height increments are excluded, heritability is high.

The two estimates for Mean Branch Angle are 0.08 and 0.43. At first sight the difference between these may seem important, but it is probably more artificial than real. Shelbourne *et al.* (unpubl.) obtained their value of 0.08 by measuring on each tree the angle of the largest branch in each of the two clusters nearest to ($0.33 \times$ height of tree) above ground level. Thus their Mean Branch Angle represented the upper extremity of the branch-size distribution. In the present study the value of 0.43 was based on the mean of about 12, rather than 2, branches per tree. Moreover, the sampling of the population of branches within each tree was designed to represent that population as a whole, rather than a small atypical fraction of it. One has to conclude that the radical differences in methods frustrate any attempt to find statistical or biological significance in the contrast between these two estimates.

The foregoing are just a few samples of the problems that arise if one tries to compare results from different experiments. However, quite apart from these difficulties, the overriding consideration in comparing heritability estimates must be their intrinsic sampling errors. There is no ready means for judging the size of these errors in the estimates of Shelbourne *et al.* (unpubl.), but from the degrees of freedom and the general proportions of the variance components in their analyses it is reasonable to assume that they were of much the same order as those encountered in the present study. If one does make that assumption, and considers the confidence limits listed in Table 1, then for most of the 7 characters the 90% confidence interval from one experiment would overlap that from the other. Then, if one were to expand the intervals according to the more stringent criterion of 95% confidence, even the biggest of the apparent differences (that for Mean Branch Angle) would become statistically insignificant.

From what has just been said it should be clear that comparing heritability estimates from different experiments *in detail* can serve no real purpose unless they are based on exceptionally accurate statistics. Nonetheless, a *series* of independent estimates for any one character can give a useful indication of its heritability *in a general sense* (see, for example, Lerner 1958: 64, for several characters in poultry); and if the object of a selection programme is to improve two or more characters concurrently, one needs heritability estimates applicable to each stage of the work in order to achieve maximum efficiency (Falconer 1960: 324-7). The estimates presented in this paper should therefore be regarded as a modest but unique contribution to what is still a very imperfect knowledge of heritability in *P. radiata*.

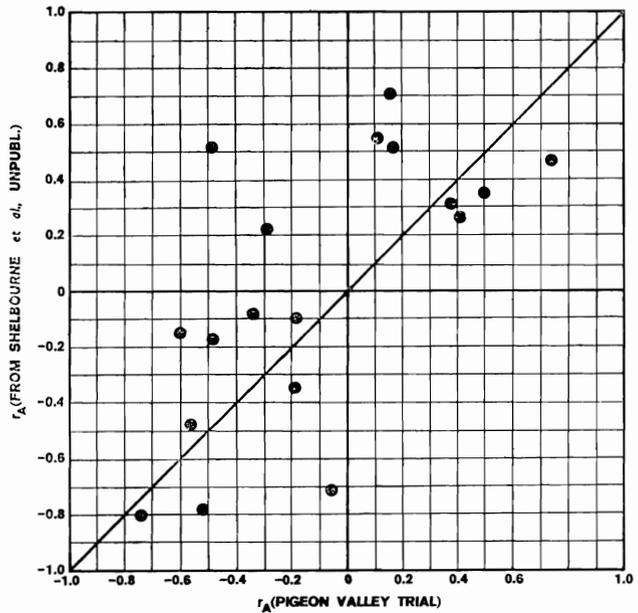
Correlation coefficients

As the confidence limits in Table 1 show, the heritabilities were very imprecisely estimated. Using the same data, the estimation of genetic correlation coefficients is bound to be even less satisfactory, so that intuitively one may doubt whether any of the

coefficients in Table 3 is significantly different from zero. Formal tests have not been attempted because the lack of orthogonality in the data makes the calculations formidable (Tallis 1959); but the results are presented because it may be worth while to compare them with those from other genetic analyses within the same species.

In particular, the phenotypic and genetic correlation coefficients for 21 character-pairs from Shelbourne *et al.* (unpubl.) are in remarkably good agreement with those reported here (Tables 2 and 3). The genetic correlation coefficients are of special interest; the strength of the association between the two independent sets of estimates, as given by the ordinary correlation coefficient r , is 0.70 (see also Fig. 3). The phenotypic correlation coefficients, as one might expect from their greatly superior degrees of freedom, are in even closer agreement, with $r = 0.87$. In the light of these comparisons it is considered that the patterns of morphological variation found in the two experiments were essentially the same, both at the genotypic level and at the phenotypic level, and that the correlation coefficients from the one lend credence to those from the other.

FIG. 3—Estimates of r_A (the additive-genetic correlation coefficient) made independently in two separate studies for 21 pairs of characters (see Table 3). If the results had been in perfect agreement the 21 points would all lie on the diagonal. In fact, quite a strong association is indicated ($r = 0.7$).



If the correlations shown in Table 3 are real, they hold important implications for artificial selection. For example, a programme aiming for straightness alone would, if successful in itself, be expected to produce several correlated responses:

- (1) reduced malformation,
- (2) reduced butt sweep,
- (3) greater branching frequency (number of clusters),
- (4) fewer branches per cluster,
- (5) steeper branching angle,
- (6) shorter distances between clusters.

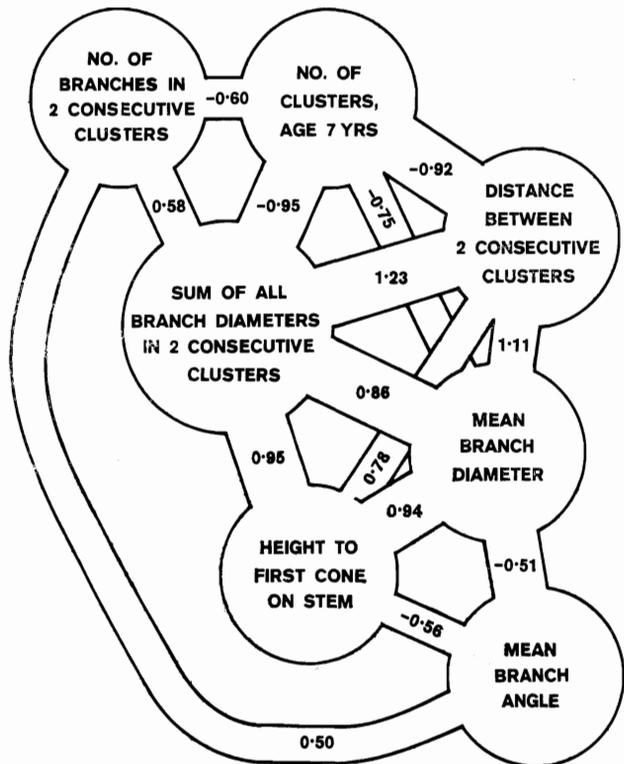
Another programme, concentrating on increasing the distance between clusters (clearwood length) would be expected to produce:

- (1) increased malformation,
- (2) increased crookedness, but less butt sweep,
- (3) lower branching frequency,
- (4) increased height to first stem cone,
- (5) more branches per cluster,
- (6) greater mean branch diameter,
- (7) steeper branching angle.

In either programme some of the correlated genetic responses would be desirable and some undesirable.

A salutary example of the uncertainties involved is provided by the genetic correlation coefficient for Mean Branch Angle and Crookedness, which in the present study is 0.47 (Table 3). If one plots the 26 pairs of family means on a graph, one gets a picture of 25 points constituting an amorphous group in the middle and one, all by itself, in the right upper corner. Evidently the "genetic covariance" implicit in the coefficient was generated almost entirely by one family. Therefore the primary problem with such a coefficient is whether the outlier should be included or excluded: the answer can have a profound effect on the estimate.

FIG. 4—Estimates of genetic correlation coefficients involving 7 characters related to branching. Parallel lines linking any 2 circles represent an apparent correlation and enclose the appropriate estimate. All estimates between -0.5 and $+0.5$ have been excluded.



Special attention should be drawn to several branch-related characters that seem to be inherited as a coherent group (Fig. 4). In this diagram it should be realised that some of the characters (*No. of branches in 2 consecutive clusters*, *Sum of all branch diameters . . .*, and *Mean diameter of branches*) are related to each other as a result of the initial arithmetic, quite apart from any genetic correlation; so, too, are *Number of clusters at 7 years* and *Mean distance between clusters*.

Arithmetical relationships, however, could hardly account for 6 or 7 of these estimates of genetic correlation being so close to unity, and it seems possible that many of these characters are the outcome of a process that is under unified genetic control. As Lerner (1958) noted: "It is very likely that many metric traits are conditioned in part by the same fundamental processes, either on the level of primary gene action or early in ontogeny. Correlation due to pleiotropy may occur when the phenotypic expressions of the correlated traits are dependent on alleles with general effects on metabolic efficiency, or on the same hormones."

Thus, the branching system seems to be governed by powerful biological constraints. Because of these, a tree breeder attempting to modify the branching would probably find himself in an inescapable dilemma: before implementing any selection policy he would need to consider the likely consequences for the phenotype, to weigh the expected improvement in some characters against the probable deterioration in others, and finally — if the indications were promising enough — to make the best compromise possible.

ACKNOWLEDGMENTS

I wish to thank R. Keizer, C. B. Low, I. Rennie, J. Riley, and M. H. Vine for technical assistance in the field; T. P. Whiston and C. R. van der Voort for help and instruction in the use of computers; Dr B. Weir for advice on genetic correlation; Mrs F. Robertson and her key-punch operators, who provided valiant service in managing the data; Dr C. J. A. Shelbourne for permission to use his unpublished data; Dr W. J. Libby for suggesting the method used to transform the malformation scores; and Dr R. D. Burdon for helpful criticism and discussion.

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