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## Effects of thinning in progeny tests on estimates of genetic parameters in *Pinus radiata*

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### Summary

Data from two progeny tests of *Pinus radiata* were used to examine the effect of thinning on estimates of genetic variances and heritabilities. Each unthinned data set was modified by omitting trees which were subsequently thinned. Heritability estimates for unthinned data were much smaller than for the thinned data. Computer simulated row thinning and selective thinning regimes were also imposed on the otherwise unthinned data sets. Row thinning had no effect but selective thinning produced much higher heritabilities than the unthinned data. The implications of these results and their effects on the way progeny tests are measured are discussed.

*Key words:* *Pinus radiata*, progeny tests, thinning regimes, heritability estimates.

### Zusammenfassung

Daten von zwei Nachkommenschaftsprüfungen wurden dazu benutzt, die Auswirkung der Durchforstung zu Schätzungen der genetischen Varianzen und Heritabilitäten zu untersuchen. Die Daten jedes nicht durchforsteten Bestandes wurden durch das Weglassen der Bäume, die später geschlagen werden sollten, modifiziert. Heritabilitätsschätzungen für die Daten von nicht durchforsteten Beständen waren bedeutend niedriger als für durchforstete.

Eine vom Computer simulierte Reihendurchforstung, sowie selektive Durchforstungsverfahren wurden ebenso an Daten von sonst nicht durchforsteten Beständen vorgenommen. Die Reihendurchforstung zeigte keinen Effekt; die selektive Durchforstung erzeugte dagegen eine weitaus höhere Heritabilität als die Daten der nicht durchforsteten Bestände. Die Folgerung aus diesen Ergebnissen und deren Auswirkungen auf die Art und Weise, wie Nachkommenschaftsprüfungen gemessen werden sollten, stehen noch zur Diskussion.

### Introduction

Within a tree breeding program, population genetic parameters such as genetic and environmental variances and covariances are frequently estimated from data collected in progeny tests. Such estimates can be used to calculate the heritability which, in the narrow sense, is the ratio of the additive genetic variance to the total phenotypic variance (FALCONER 1981). This estimates the relative importance of the portion of the genetic variance which is available to recurrent selection programs to predict genetic change following selection. It is widely known that genetic variability is a property which is different for different

characteristics in different populations and at different times (FRANKLIN 1979).

The term "progeny testing" strictly applies to the case where the characteristics of progeny are used to assess the breeding value of their parents rather than to make inferences about the progeny themselves (TURNER and YOUNG 1969). Genetic parameters estimated from progeny tests thus apply to the parental population rather than the progeny population. Progeny tests can supply information about the breeding value rankings of parents as individuals as well as about genetic parameters of the parental population.

In forestry, progeny tests usually form a part of some larger forest and are usually thinned at some stage to maintain productivity and/or quality. What effect does this have on the genetic parameters to be estimated? It could be argued that the within-family variance would be reduced by the selective removal of smaller trees and that this would lead to the inflation of heritability estimates where this component of variance forms a large part of the denominator of the heritability ratio (see above). Plots in many progeny tests are small and there may be no justification in using selection theory based on the assumption of a normal distribution. If family differences are based on different distributions of tree size, then selective removal of smaller trees would remove family differences, and the heritability estimate would be reduced. There is also the problem of sampling trees to be measured within a plot. Sometimes the trees are so tall that to measure all trees in a plot would be prohibitively expensive. On what basis should the trees in a plot be selected for measurement in such cases?

Considering that these questions of the effects of thinning and of sampling within families are unresolved and that they affect the very basis of genetic parameter estimation, we were surprised to be unable to find any reference to them in forest genetics literature except for a few papers such as WILUSZ and GIERTYCH (1974) and JAMES (1979) who did not address the problem directly but were concerned with the effects of thinning on the genetic quality of seed collected subsequently. MAUGE *et al.* (1974) stated that total height was "still but slightly heritable" following thinning in a seedling seed orchard implying that the heritability should have been higher. It is not clear whether this implication refers to the thinning or to the time in-

terval between measurements. LEE (1974) studied the effects of partial measurement in a nursery trial of *P. ponderosa* LAWS and concluded that estimates for genetic gains were considerably in error when only a few seedlings were measured per plot. He also found that these estimates were improved if the tallest seedlings were measured rather than a random sample. KUNG (1977) considered the question of selecting one individual to measure in a multiple tree plot and suggested an adjustment could be made to the heritability estimates. He proposed that a synthetic within-plot variance could be obtained by adjusting the variance of the tallest tree per plot. The weakness of this approach is that plots are questionably assumed to be normally and identically distributed, and that he assumes it is always possible to select the tallest tree in a plot without measuring it.

This paper reports the results of an investigation into the effects of thinning in progeny tests on the estimation of genetic and phenotypic variances and their ratio - heritability.

### Materials and Methods

Data from two progeny tests of *Pinus radiata* D. DON planted near Canberra were used to examine the effect of thinning regime on genetic parameter estimation. The first data set was from a test of 15 open-pollinated families planted in three randomised blocks at Coree in the Australian Capital Territory in 1955. Blocks were not complete as a few families were not represented in all blocks. Each plot consisted of 25 trees planted in 5 rows of 5 trees. Diameters over bark, 1.3 m up the trunk were measured in 1975 and 1978. The trial was thinned in 1975 by removing one complete row of 5 trees per plot and selectively thinning the remainder of each plot to remove smaller and malformed trees. The objective of each thinning was to reduce the number of trees per plot by about one half.

The other data set was from a test of 100 open-pollinated families planted in an triple lattice at Kowen in the A.C.T. in 1954. Replications were not complete since a few families were unrepresented in some replications. Plots contained, as did the other test, 25 trees planted in 5 rows of 5 trees each. Diameter over bark was measured at 1.3 m up the trunk in 1973 and 1978. The trial was thinned in 1973 by removing one complete row in every second plot and selectively removing smaller and malformed trees from every plot. Kowen in particular is a very poor site and there were very few malformed trees, so the criterion for thinning was mainly size alone.

The following statistical model was fitted to the data from both tests to allow the estimation of genetic parameters.

$$Y_{ijk} = u + B_i + F_j + BF_{ij} + e_{ijk}$$

where  $Y_{ijk}$  = diameter at 1.3 m of the  $ijk$  th tree

$u$  = overall mean

$B_i$  = effect of the  $i$  th block

$F_j$  = effect of the  $j$  th family

$BF_{ij}$  = interaction between the  $i$  th block and the  $j$  th family

$e_{ijk}$  = within plot error

The genetic and phenotypic variances for diameter at 1.3 m over bark were estimated by equating the observed to the expected mean squares in the analysis of variance. Individual heritabilities were calculated, assuming families were half-sibs, as follows (FALCONER 1981):

$$h^2 = 4V_f / (V_f + V_{bf} + V_e)$$

where  $V_f$  = family variance component

$V_{bf}$  = family  $\times$  block interaction variance component

$V_e$  = residual mean square

To allow examination of the effect of thinning regime on the genetic parameters, three additional analyses were carried out. For each data set, the 1978 measurements were used to determine which trees remained after thinning had been carried out. The previous set of measurements (i.e. those from the year in which the thinning was actually carried out) was re-analysed using data only from those trees present after thinning. In other words, the 1975 data for the Coree trial and the 1973 data for the Kowen trial were analysed including only those trees present in 1978.

Computer simulation was used to impose two alternative thinning regimes on the measurements for the year of actual thinning for each data set. The first simulated thinning was a systematic thinning, i.e. the first and fourth row in each plot were removed. This is essentially random with respect to diameter. The second simulated thinning was selective, i.e. all trees in each plot were ranked and the required number of trees per plot to be retained were selected from the largest available.

The computer simulated thinnings reduced the number of trees remaining in each plot to approximately the same number left after the actual thinnings. The above model was fitted to each reduced data set for analysis.

Analysis of covariance between all data before thinning and data 3 or 5 years after thinning were carried out. From these analyses, the family covariance components were estimated. The genetic correlation between the data before and 3 to 5 years after thinning was then calculated as:

$$r_g = \frac{V_{ij}}{\sqrt{V_{ii} \cdot V_{jj}}}$$

(FALCONER 1981, TURNER and YOUNG 1969 — corrected) where  $V_{ij}$  is the family covariance component for characters  $i$  and  $j$ ,  $V_{ii}$  and  $V_{jj}$  are the family variance components for characters  $i$  and  $j$  respectively.

### Results

Table 1 presents the heritabilities, genetic and phenotypic variances for the test at Coree. Results for the Kowen test are presented in Table 2.

For each progeny test, the heritability estimates for the data set following thinning are higher (1978 data for each test) than before thinning. In 1978, the heritabilities were 0.21 for Coree and 0.34 at Kowen, compared with 0.12 for Coree and 0.24 for Kowen before thinning in 1975 and 1973 respectively (see Tables 1 and 2 for standard errors). Is this due to the thinning or to a normal development of the genetic parameters with time (FRANKLIN 1979)? When the pre-thinning data were analysed using only the trees which were still alive in 1978, the heritabilities were 0.21 and 0.33 for Coree and Kowen respectively. These figures are extremely similar to the 1978 heritability estimates for the two trials, suggesting there has been essentially no change in heritability from the time of thinning until 1978 in either trial.

There is, however, a considerable difference in heritability estimates at the time of thinning depending on whether the thinned trees are included in the data set or not. At Coree the heritability estimate was 0.12 if thinned trees were included and 0.21 if they were not. At Kowen estimates for corresponding data were 0.24 and 0.33. Since the actual thinning carried out was a combination of row and selective thinning, the next question was whether the change in the estimates was due to the random part of the thinning or to the selective part.

In each case the elimination of rows in the pre-thinning data by computer (random with respect to diameter) pro-

Table 1. — Estimates of genetic parameters for diameter measured in centimetres in progeny test number 15 planted at Coree, A.C.T. in 1956. The progeny test was measured in 1975 before being thinned later in the same season. Data "after actual thinning" were obtained by removing from the 1975 unthinned data set trees which were absent in data collected in 1978, three years after thinning had been carried out in the field.

	Number of trees*	$h^2$	SE	Additive Genetic Variance	Phenotypic variance
1975 data					
Before thinning	23.4	0.12	0.065	1.11	35.8
After actual thinning	14.8	0.21	0.105	1.68	32.0
After simulated row thinning	13.9	0.15	0.089	1.28	33.3
After simulated selective thinning	15.0	0.31	0.135	1.42	18.3
1978 data					
After actual thinning	14.8	0.21	0.106	2.18	41.2

\* Harmonic mean of number of trees per plot

Table 2. — Estimates of genetic parameters for diameter measured in centimetres in progeny test number 8 planted at Kowen, A.C.T. in 1954. The test was measured in 1973 before it was thinned later in the same season. Data "after actual thinning" were obtained by removing from the 1973 unthinned data set trees absent in the 1978 data set, five years after the test was thinned in the field.

	Number of trees*	$h^2$	SE	Additive Genetic Variance	Phenotypic variance
1973 data					
Before thinning	14.3	0.24	0.059	1.87	31.2
After actual thinning	8.3	0.33	0.080	2.57	30.8
After simulated row thinning	8.4	0.22	0.068	1.69	31.0
After simulated selective thinning	7.6	0.56	0.132	2.38	16.9
1978 data					
After actual thinning	8.3	0.34	0.079	4.01	47.7

\* Harmonic mean of trees per plot

duced very little change in the heritability estimates: from 0.12 to 0.15 at Coree, and 0.24 to 0.22 at Kowen. But the selective elimination of the smallest trees by computer (i.e. selective thinning) produced a very large change: from 0.12 to 0.31 at Coree, and from 0.24 to 0.56 at Kowen. This difference between selective and random thinning contrasts with LEE's (1974) results where he concluded the reverse. However, LEE used plot means as the basis for his analysis rather than individual seedlings. This means that the phenotypic variance is underestimated by an amount which varies according to the way in which the selection is carried out.

The actual thinnings carried out in 1975 at Coree and in 1973 at Kowen were combinations of random and selective thinnings. It is interesting therefore to see that the heritability estimates obtained from data omitting the thinned trees at the time of thinning were between the random and selective computer simulated thinnings: 0.21 for Coree and 0.33 for Kowen.

The genetic and phenotypic variances were not materially affected by the simulated random row thinning in either data set. But the genetic variances were increased and phenotypic variances decreased by the simulated selective thinning. Actual thinning increased the genetic variance, but left the phenotypic variance unchanged.

The genetic correlations between diameter immediately before thinning and 5 and 3 years after thinning were 0.9915 for Kowen and 0.8070 for at Coree. This implies, not unreasonably, that virtually the same genes are controlling diameter 3 or 5 years after thinning as were controlling it before thinning.

## Discussion and Conclusion

The results show conclusively that the method employed for thinning materially affects the estimate of heritability for tree size through its effects on the estimates of additive and phenotypic variances. Row thinning, or the random removal of trees from a plot did not seem to affect the estimates of the variances themselves but increased the standard errors of the heritability estimates because the estimates were based on a smaller number of trees. Selective thinning, on the other hand, increased the estimate of genetic variance and decreased the estimate of the phenotypic variance. The combination of row and selective thinning yielded estimates of heritability which fell between those obtained for random and selective thinning carried out separately by computer simulation. There was essentially no difference in heritability estimates made immediately after thinning and those made three and five years later. Although the additive and phenotypic variances increased over this period, they did so at the same rate. This is consistent with FRANKLIN'S (1979) proposal about changes in these variances during the later part of what he calls the "mature genotypic phase" of stand development. Without considering the fact that thinning had taken place, it might have been inferred that a great increase in genetic variability had taken place in both progeny tests between the time of thinning and 1978. In fact, there has been a discontinuity, caused by the thinning, in the development of the genetic variability. Although additive genetic variance continued to increase in the years after actual thinning, so did the phenotypic variance and thus the heritability remained the same. Because of the change in

stand structure caused by the actual thinning, we cannot be sure how the additive and phenotypic variances would have behaved if the actual thinning had not taken place. Genes which affect competitive ability would gradually become important as between-tree competition increased before thinning. Thinning presumably reduces the amount of between-tree competition for resources so the genes affecting competitive ability could then become relatively less important than before the thinning. The extremely high genetic correlations between data obtained before thinning and data obtained several years after thinning suggests that this change in relative importance of genes affecting competitive ability is not very great. But the effect of this change on genetic variances is unknown. The next question is; how do these results affect the inferences drawn from progeny tests?

Progeny tests usually supply information about the parents both as individuals and as a population. Neither form of thinning affects the relative rankings of the parents with respect to their breeding values. The information provided about the performance of the parents as individuals is largely unaffected by thinning operations. However, the estimates of parental population parameters are considerably affected by selective thinning, although they are not by random thinning. So some account must be taken of thinning procedures when making inferences about the parental population as a whole.

Heritability estimates taken from an unthinned progeny test should not be used to estimate genetic change if breeding is to be done with trees chosen in selectively thinned tests unless due allowance is made. Similarly, estimates from selectively thinned tests should be used only with allowance for thinning if unthinned or randomly thinned tests are the basis of the breeding program. Presumably, the level of selection at thinning will also have an effect on the heritability estimates. Consequently, selections should be made from trials which have faced exactly the same thinning treatment as those from which the heritability estimate was obtained. If this provides too stringent a condition on the application of the estimates, then it is probably better not to thin the progeny trials selectively at all.

The problem of selecting individuals within a plot for measuring expensive or difficult traits is similar to the problem of selective thinning. If the data are to be used only for rankings and not for parameter estimation then selection of trees for measurement should have little ef-

fect. This contention is supported by the extremely high genetic correlation between diameter before thinning and 3 or 5 years after thinning at both sites. It is also in agreement with LEE's (1974) results in a nursery trial of *P. ponderosa*, and with KUNG's (1977) more theoretical results. Selecting individuals to measure difficult traits has a similar effect on heritability estimates as selective thinning if the selection is based on some character which is genetically related to the difficult trait. If diameter is measured only in what appear to be the fattest trees, then the heritability estimate will be inflated. If height is measured only in the fattest trees, the heritability will be inflated by an amount proportional to the correlation between diameter and height. It follows that if trees must be selected for measurement, then some inflation of heritability estimates must be accepted, although rankings of families are unlikely to be affected. KUNG (1977) states that it is easier to choose the tallest tree in a plot than to choose randomly. If the trees are so tall that it is not possible to measure them all, then it is probably too difficult to be sure that the tallest one and not the second tallest one has been chosen. The effect of such mistakes on KUNG's results are unknown. For making estimates of genetic variances, measurements of less than a whole plot should be made at random, although for ranking families some systematic selection of trees within a plot for measurement is acceptable.

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## Identification of Hybridity of *Casuarinas* grown in Taiwan<sup>1)</sup>

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#### Abstract

Seven morphological traits, branchlet anatomic structure of *Casuarina glauca*, *C. equisetifolia* and their putative

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hybrids and growth characters of their seedlings were evaluated to compare the differences within and among the four taxa grown at Yun-lin County, Taiwan. Hybrid index scales based on morphological and growth traits were constructed for parent trees and open-pollinated progenies to illustrate the occurrence of introgressive hybridization during the several decades of composite planting. The evidence of introgression can be verified by the variability of number and shape of rib as well as the significant correlation among traits. The theoretical reasoning