four-our five-year-old loblolly pine genetic test with five-tree plots. Within-plot variances for noncontiguous plots may have been slightly larger than those for row plots though it was no possible to statistically confirm this conclusion.

The significant advantages that the commonly used row plot may have over the noncontiguous arrangement are ease of layout and tracking in the field, and simplicity in silvicultural thinning by family. The efficiency advantage of noncontiguous plots, i.e., fewer trees needed to realize the same precision in a genetic test, seems to outweigh the advantages of row plots.

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Methods of estimating the average performance of families across incomplete open-pollinated progeny tests

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Summary

Six mathematical procedures are outlined and compared for relative accuracy in estimating the average performance of families from open-pollinated progeny data which are incomplete in the sense that families are represented in some but rarely all progeny tests. In this instance the data were records of stem volume and stem straightness (five-point visual score) from five open-pollinated progeny tests of *Pinus radiata* in South Australia. The methods were rank-score (RS), site-adjustment (SA) or standard site-adjustment (SSA) procedures compared with least-squares (LS), weighted least-squares (WLS) or shrunken least-squares (SLS) procedures. Logarithmic transformation was used to stabilise the variance of volume across sites.

The LS, WLS and SLS methods agreed very closely in their evaluation of families for all traits studied. The RS and SSA evaluations of families for volume agreed reasonably closely with least-squares evaluations, while the SA evaluations for volume were less accurate. All methods provided essentially the same evaluation of families for straightness.

Key words: progeny testing, non-orthogonality, genetic value, log transformation, least-squares.

Zusammenfassung

Es werden sechs mathematische Berechnungsarten beschrieben und bezüglich der relativen Genauigkeitsaussage des durchschnittlichen Wachstums von Kiefern, von denen ein Elternteil bekannt ist, miteinander verglichen. Die Daten sind jedoch keineswegs vollständig, da zwar einige Kiefernfamilien aufgeführt werden, aber nicht immer alle entsprechenden Nachkommenschaftsprüfungen durchgeführt wurden. Hierzu dienten als Ausgangspunkt die aufgezeichneten Daten über das Stammvolumen als auch diejenigen der Geradschäftigkeit (eine sogenannte „Fünf-Punkte-Beurteilung"), die okular in fünf verschiedenen Nachkommenschaftsversuchen mit der Kiefernart *Pinus radiata* in Südaustralien vorgenommen wurde. Die Methoden waren: Rang/Punktzahlen RS, Standortanpassung SA, Standard-Standortanpassung SSA, verglichen mit den kleinsten Quadraten LS, den gewichteten kleinsten Quadraten WLS und den geschrumpften kleinsten Quadraten SLS. Zur Stabilisierung der Volumen-Standort Varianz wurde die logarithmische Umwandlung angewandt.

Dabei wurde festgestellt, daß die LS-, WLS- und SLS-Verfahren sehr weit bezüglich der Wesensmerkmale aller untersuchten Familien übereinstimmten. Die RS- und SSA-Berechnungen für die Stammvolumen der jeweiligen Familien stimmten hinreichend mit der Auswertung der kleinsten Quadrate überein, während die SA-Ermittlungen der Volumen weniger genau waren. Dagegen ergaben sämtliche Berechnungsarten im wesentlichen dieselben Ergebnisse für die Ermittlung der Stammgeradheit der Familien.

Introduction

Most tree breeding programs rely on progeny testing in each generation to determine the genetic merit of new selections. These tests are usually established over a number of sites, and the analysis of data is primarily directed towards estimating the average relative performance of families across the range of conditions.

When the family × progeny test array of available data is complete (all families represented at all sites) the analysis is straightforward in that family performance can be obtained by simply averaging across sites. More often, the family × progeny test table is incomplete with a proportion of families represented at only a few sites, and in this case the non-orthogonality of the data can complicate

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the estimation of average family performance. If the non-orthogonality is slight, the problem may be avoided by discarding data to give orthogonality (Nikles *et al.* 1977). When the incompleteness is more substantial, average family performance is sometimes expressed relative to other 'control' families which happen to occur at all sites, but the success of this method depends directly on the stability of the controls (Silvey 1978). The most common approach is to use some type of mathematical procedure which adjusts for differences between the group of sites at which a family is represented and those where it is not.

In this study we have used stem volume and straightness data from five open-pollinated progeny tests of *Pinus radiata* D. Don in South Australia to compare six methods of analysing incomplete progeny data. These methods are identified as rank-score (RS), site-adjustment (SA), standard site-adjustment (SSA), least-squares (LS), and weighted (WLS) and shrunken (SLS) least-squares. No allowance was made for family × progeny test interactions. RS, SA and SSA are simple procedures which require no elaborate computations and have been used in practical tree breeding in Australia, but to our knowledge their accuracy has not been previously tested. Least-squares are more reliable methods which make simultaneous adjustment for incompleteness of data in estimating both family and site effects, but for large data sets they require substantial computing facilities. LS has been used to analyse incomplete progeny data in plant breeding (Patterson 1978, Silvey 1978, Patterson and Silvey 1980), and WLS and SLS have been used for the same purposes in animal breeding (Cunningham 1965, Harvey 1968, Miller *et al.* 1968), although in animal breeding the methods are used under different names (discussed later). No use of the methods of WLS or SLS has apparently been made in forestry.

The aim of this study was to determine the accuracy of the simpler procedures by comparing them with least-squares. The advantage of using a logarithmic transformation in analysing growth data is also demonstrated.

Progeny Data

The open-pollinated progeny tests are identified as *tests* 5031, 5042, 5408, 5410 and 5411 (Australian Progeny Trial numbers) and were established between 1969 and 1971 across five sites in the south-east of South Australia (as detailed by Cotterill and Zed 1980). *Appendix 1* shows the highly incomplete family × progeny test table. There are 65 families represented in one or more of the five progeny tests but only one family (10954) occurs in all tests. The sites can be regarded as representative of the environmental conditions in the breeding region.

Each test has a randomised complete blocks design with single-row plots (Cotterill and Zed 1980). The number of block replications in each test is given in *Table 1*. The height and diameter (at 1.3 m) of all trees in *test* 5031 were measured at 10$^1/_2$ years after planting and at 7$^1/_2$ years for the other tests. Stem volume was estimated from height and diameter by a simple conical function. Stem straightness was assessed as a five-point visual score (1 = worst, 5 = best stem straightness).

Mathematical Procedures

The data were reduced to class means before analysis. This does not waste information since records on individual trees are not considered when calculating any standard errors of the effects of different families. Within a test the families were randomly assigned to plots in experimental blocks, so the relevant error for comparing families is the family × block interaction. Calculation of this experimental error involves only plot means. When the effects of families are being estimated across sites the family × site interaction is the appropriate error for estimating the standard errors of the relative performances of the families.

Log Transformation

Differences in the age at assessment and environmental conditions were reflected in large differences between-sites for stem volume and the standard deviations of the volume data varied almost proportionally to the means *(Table 1)*. This causes problems in assessing progeny test data where the objective is to analyse the effects of families across sites. A correlation between the site means and family effects would tend to make the family, site (and block) effects multiplicative rather than additive. Under these circumstances a log transformation is effective in both stabilising the variance and achieving additivity. In this instance we used base 10 logarithms but any base would have been satisfactory. The effect of this transformation on the variances of the different sites is shown in *Table 1*.

The means for straightness were relatively uniform across sites *(Table 1)* and preliminary analyses showed that log transformation was not required. Analysis of only raw straightness data is reported here.

Rank-score

This is a non-parametric method derived from the quartile ranking used by Eldridge (1974). Families at a particular site are grouped into quartiles, and those in the upper quartile are given a score +1, those in the middle half are scored zero, and those in the lower quartile −1. The mean score for each family is then found by averaging these scores across sites. In this study, families at each site (or test) were ranked in reverse order of merit and these ranks were converted to scores by dividing by the number of families at the site. The rank-scores for each family were then averaged across all sites.

Site-adjustment

In this method an attempt to remove the effects of sites was made by expressing the plot mean data as deviations from the site means. The deviations for each family were first averaged within-sites and then across-sites. The method is equivalent to the herdmate-comparison used in animal breeding (Miller *et al.* 1968).

Standard Site-adjustment

The problem of unequal variances across sites can be reduced by dividing the previously mentioned deviations from the site means by the site standard deviations (means and standard deviations given in *Table 1)*, thereby converting the data to standard normal deviates. The standard normal deviates for each family were averaged within-sites and then across-sites.

Least-squares

If the effect of the ith family is represented by a_i and the jth block by b_j, then within a site the model

$$Y_{ij} = \mu + a_i + b_j + \varepsilon_{ij} \qquad (1)$$

is fitted to the plot means (Y_{ij}) for each trait, choosing the a_i and b_j constants to minimise the sum of squares of the ε_{ij}'s. This is straightforward as the families and blocks are orthogonal within a site. To enable results to be generalised over a breeding region it is necessary to estimate family performance across a range of sites. If the effect of the k^th^ site is designated t_k, then across-sites the model

$$Y_{ik} = \mu + a_i + t_k + e_{ik} \qquad (2)$$

is fitted to the family means (Y_{ik}) for each trait. Usually the families and the sites will not be orthogonal necessitating some least-squares fitting of constants. The technique of fitting constants for non-orthogonal data was first considered by YATES (1933) and more recently by PATTERSON (1978). The a_i constants fitted for family effects in model (2) are unbiased, and if the progeny tests have equal precision, they will be minimum variance estimators with variance equal to the residual mean square divided by the number of sites across which a family occurs. For open-pollinated progeny tests the a_i constants for each family can be considered as least-squares estimates of general combining ability and $2a_i$ as least-squares estimates of breeding value.

There are many algorithms available for fitting least-squares constants. In this study it was simplest to remove the site effects with covariates and then proceed with a one-way analysis classified by families. Only a 4 × 4 matrix is then inverted.

Weighted Least-squares

One assumption made in the previous method of least-squares is that each progeny test has the same precision. This is not correct for the present data as the number of block replications varied from test to test (*Table 1*). If there are large differences in precision, more notice should be taken of the more precise tests. We have done this by weighting the data inversely proportional to the residual mean square for the site, which leads to a weighted least-squares analysis. Again it is only necessary to invert a 4 × 4 matrix if a covariate analysis is used. The precision of each progeny test is obtained from a two-way analysis using model (1).

Shrunken Least-squares

In this method families are considered to be distributed about some overall mean with variance σ^2_a. This information is then combined with the experimental data to give estimates of family effects which are 'shrunk' towards the overall mean by an amount which depends on the effective replication of each family and σ^2_a. We used the equation:

$$a^*_i = [\sigma^2_a/(\sigma^2_a + \sigma^2_i)]\ a_i \qquad (3)$$

where a^*_i is the shrunken least-squares estimate of the effect of the i^th^ family, a_i is the unweighted least-squares estimate obtained using model (2), and σ^2_i is the effective variance of the a_i. Both σ^2_a and σ^2_i were obtained from the unweighted least-squares analysis using the method given by HUITSON (1966). In the case of equation (3) the a^*_i are shrunk towards zero which is the overall mean of the a_i. The a^*_i estimates are more conservative for the purpose of family recommendations in the sense that poorly replicated families (with a larger σ^2_i) are shrunken more towards zero than those which are better replicated.

Table 1. — **Number of block replications in the randomised blocks designs of each progeny test, and the means and standard deviations (s.d.) for stem volume, stem volume after transformation of data using base 10 logarithms, and stem straightness.**

	Progeny test				
	5031	5042	5408	5410	5411
Replications	12	6	14	10	10
Volume (dm³)					
Mean	165	98	76	89	45
s.d.	34.2	18.0	13.2	13.8	12.3
Volume after transformation ($\log_{10}$ dm³)					
Mean	2.21	1.99	1.88	1.95	1.64
s.d.	0.093	0.084	0.078	0.069	0.098
Straightness (1 to 5-point visual score)					
Mean	3.04	2.79	2.90	2.55	2.48
s.d.	0.508	0.365	0.326	0.316	0.361

Table 2. — **Mean-squares and, in brackets, F-ratios from unweighted least-squares analysis of progeny data using model (2). Volume is after transformation of data using base 10 logarithms.**

Source of variation	d.f	Mean squares	
		Volume	Stem straightness
Family	64	0.0032 (2.1)	0.0767 (4.4)
Site	4	0.7227 (481.8)	0.9869 (57.1)
Residual	145	0.0015	0.0173

The method of shrunken least-squares has been outlined by LINDLEY and SMITH (1972) and is similar to the methods of regressed least-squares used by HARVEY (1968), and weighted least-squares used by CUNNINGHAM (1965) and MILLER *et al.* (1968). We refer to the methods as shrunken least-squares to avoid the ambiguity of the word 'regressed' and confusion with the method of weighted least-squares used in this study.

Results and Discussion

Ordinary analysis of variance of data using model (2) revealed that both families and sites had a significant effect on all traits studied, but that sites had an overwhelming effect on volume (*Table 2*). The magnitude of the effects of sites on volume and the corresponding reduced relative contribution of families to the overall sums of squares makes this growth trait a stringent evaluation of the efficiency and reliability of the various methods in removing the variation due to sites and extracting information on families from the incomplete data. To take the opposite extreme, when there are only small site effects the relative performance of families could be reliably deduced by simply averaging the incomplete data across sites. In the case of straightness, site effects made a much smaller contribution to the overall sums of squares and this trait therefore provides a less stringent evaluation of the various methods. This is evident from subsequent results.

Assumptions made by the various methods of analysing incomplete data are summarised in *Table 3*. RS assumes

Table 3. — Assumptions made by the methods of rank-score (RS), site-adjustment (SA), standard site-adjustment (SSA), least-squares (LS), shrunken (SLS) and weighted (WLS) least-squares.

Assumption	RS	SA	SSA	LS	SLS	WLS
1. Additivity of family and site effects	No	Yes	Yes	Yes	Yes	Yes
2. Uniform variance across sites	No	Yes	No	Yes	Yes	No
3. Random distribution of families across sites	Yes	Yes	Yes	No	No	No
4. Random family effects	No	No	No	No	Yes	No

only that there is a random distribution of families across sites (or expressed another way, that the 'quality' of the families at each site in compatible) and is therefore quite a robust procedure. WLS is also robust assuming only additivity of family and site effects, as implicit in model (2). Even when non-additivity is present in the data, least-squares analysis of cell means (or in this case family means) using model (2) should still provide reliable comparisons between treatments (Urquhart and Weeks 1978). SA can be considered an approximation to the fitting of constants by LS but requires the assumption of random distribution of families across sites.

Of the six methods we prefer WLS due to its providing minimum variance unbiased estimates of the effects of families under the additive model, and we have used WLS to evaluate the relative accuracy of the other methods. Since the purpose of progeny testing is to rank families in order of merit, the association between the ranking according to WLS versus ranking according to the other methods has been used to judge 'relative accuracy'.

Despite theoretical differences in complexity the six methods were found to rank families in about the same order for volume and almost exactly the same order for straightness. The actual relationships between rankings according to the method of WLS and rankings according to each of the other methods are quantified in *Table 4* by Spearman's rank correlations. A rank correlation of 1.0 indicates complete agreement in the order of the ranks while zero indicates complete disagreement. *Table 4* also gives, for each trait, the number of the top 10 families as selected by WLS which would have been selected by each of the other methods. The top 10 families are used here because that happens to be the number of families actually retained from these combined progeny tests in breeding *P. radiata* in South Australia.

Table 4. — Spearman's rank correlations between weighted least-squares and other methods of estimating family performance from non-orthogonal data; and the number of families correctly allocated into the top 10 positions by various methods, accepting the method of weighted least-squares as optimal. Volume data were transformed logarithmically before analysis.

Method	Rank correlations		No. families correctly allocated into top 10	
	Volume	Straightness	Volume	Straightness
Rank-score	0.89	0.99	6	9
Site-adjustement	0.82	0.99	8	9
Standard site-adjustment	0.91	0.99	8	9
Least-squares	0.97	0.99	9	9
Shrunken least-squares	0.97	0.99	10	9

Each of the least-squares procedures gave essentially the same rankings of families (rank correlations between WLS and LS or SLS were 0.97 for volume and 0.99 for straightness; *Table 4)* and little real advantage seems to have been achieved by using the slightly more complicated SLS or WLS procedures compared to unweighted LS. This finding agrees with that of Miller *et al.* (1968) who reported rank correlations of 0.99 between LS and SLS rankings of dairy sires determined from incomplete progeny data. For both volume and straightness LS and SLS selected either nine or all of the 10 families chosen by WLS *(Table 4)*. It was noticeable that SLS is more conservative in recommending families which are not well replicated. For instance, WLS ranked *families* 80055, 50078 and 50047 first, second and third respectively, for volume, but because 800055 was represented at only two sites *(Appendix 1)* SLS reduced it to rank third behind 50078 and 50047 which were both represented at three sites.

It may be unreasonable to discard a promising variety because little is known about it, as could occur with SLS. On the other hand Patterson and Silvey (1980) have argued that a family is more likely to be chosen by LS if its test means exceed its true mean. For the purpose of family recommendations and estimating responses from selection the more conservative SLS estimates may be preferred because they remove this potential bias of LS. The correction is however dependent on having good estimates of the various components σ^2_a and σ^2_i for use in equation (3).

The methods of RS and SSA showed comparable accuracy (rank correlations with WLS were 0.89 to 0.91 for volume and 0.99 for straightness; *Table 4)* while SA was marginally less reliable for volume (rank correlation with WLS equalled 0.82). In analyses not reported here we have found the accuracy of SA is further reduced when the method is used to analyse raw volume data not transformed logarithmically, because unlike RS and SSA, the method of SA requires the assumption of uniform variance across sites *(Table 3)*. Nevertheless, RS, SA and SSA all selected

Appendix 1. — Representation of families across progeny tests.

Family[A]	Progeny test					Family	Progeny test				
	5031	5042	5408	5410	5411		5031	5042	5408	5410	5411
30040	X	X				50267				X	X
50001				X	X	50268				X	
50006				X		50269				X	
50009				X	X	80055	X	X			
50010				X	X	10935	X	X			
50012				X	X	10948		X			
50013				X	X	10954	X	X	X	X	X
50015				X	X	10956	X	X		X	X
50016				X		10957	X	X			
50017					X	10994	X	X		X	X
50018				X	X	12001		X			
50022				X		12038		X			
50024				X		12040		X			
50028			X	X	X	12112	X	X			
50030			X	X		12130	X	X			
50031			X	X	X	12187	X	X			
50039	X		X	X	X	12197	X	X			
50042			X	X	X	12236	X	X			
50043	X		X	X	X	12247	X	X			
50044			X	X	X	12294	X	X			
50045			X	X	X	12315	X	X			
50047			X	X	X	12349	X	X			
50048			X	X	X	12351	X	X			
50077			X	X	X	12373	X	X			
50078			X	X	X	12374	X	X			
50079			X	X	X	12378	X	X			
50080			X	X		12403	X	X			
50082	X		X	X	X	12408	X	X	X		
50126				X		12412	X	X			
50127			X	X	X	12419	X	X		X	X
50176			X	X	X	12423		X			
50177			X	X	X	12447	X	X			
50178				X	X						

[A] Families identified by Australian Plus Tree Register numbers.

six to eight families correctly for volume (log transformed) and nine correctly for straightness (*Table 4*). We have calculated that these inaccuracies in the RS, SA or SSA rankings of families would reduce expected genetic gain from selecting the top 10 families (according to WLS rankings) by less than only 5% for volume and 1% for straightness. The calculations were made by simply averaging WLS breeding values of the 10 families chosen according to each method.

The choice between the simpler methods or least-squares is open to debate. In this study we have found that while the simpler methods are not exact, particularly for traits which show strong site effects, they probably rank families with sufficient accuracy for most practical breeding purposes. Of course the degree of incompleteness of the data will also affect the relative accuracy of alternative methods. Differences between the simpler methods and least-squares would be expected to be less when the family × progeny test Table is more complete.

We could argue that the amount of effort required in the field to establish and measure progeny tests is sufficient justification for carrying out the additional computations required by the least-squares procedures. This is in view of the fact that most breeders have access to suitable computing facilities to calculate the least-squares estimates.

The six methods can also be applied to control-pollinated progeny data, although the simpler methods would be unsatisfactory where there is incompleteness in both the crossing scheme and the representation of full-sib families across sites. If there were substantial incompleteness across both crossing scheme and sites then even the least-squares estimates would not be very reliable (URQUHART and WEEKS 1978). GILBERT (1967) described the application of an unweighted LS approach for analysing progeny data from incomplete crossing schemes, and HARVEY (1960 and 1968) outlined the application of LS and SLS procedures using the more complex models needed to analyse full-sib progeny data from a range of sites.

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