effects, the data provide lower estimates of numbers of recessive lethals than heretofore obtained, but the reduction is slight, typically less than one lethal per tree.

The model and the estimates obtained indicate greater variability in proportions of unsound seed than would be expected from sampling error alone. Our results suggest first, that maternal effects may differ markedly from ramet to ramet of the same tree and second, that numbers of lethals that are carried differ from one forest location to another. In turn, these observations have implications for sampling methodology.

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Short Note: Use of Kung's Method for Estimating Parental Effects in an Irregular Mating Design

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Abstract

Wood density parameters were determined by x-ray densitometry for a second generation progeny trial of *Pinus caribaea* var. *hondurensis* Barr. et Golf.. The mating design from which the trial originates is very irregular and represents only 29% of all possible crosses between the parents involved. An enhanced version of the program developed by Kung (1978) was used to calculate combining abilities.

Key words: *Pinus caribaea* var. *hondurensis*, combining abilities, wood density, incomplete partial diallel.

Zusammenfassung

Für eine Nachkommenschaftsprüfung mit *Pinus caribaea* var. *hondurensis* Barr. et Golf. in zweiter Generation wurden Holzdichte-Parameter durch Röntgenstrahlen-Dichtmessung bestimmt. Der Kreuzungsplan aus dem der Versuch hervorging, ist sehr unregelmäßig und umfaßt nur 29% aller möglichen Kreuzungen zwischen den beteiligten Eltern. Eine vergrößerte Version des von Kung (1978) entwickelten Programmes wurde zur Errechnung der Kombinationseignung benutzt.

Introduction

Pinus caribaea var. *hondurensis* Barr. et Golf. was introduced to Queensland plantations in the 1950's and has been the subject of intensive breeding since that time (see Nikles, 1973). One of the series of second generation progeny trials was intended to be an incomplete partial diallel among 19 parents. Biological and operational constraints reduced representation to 53 full sib families, the product of matings between 13 female and 14 male parents. The irregular and incomplete mating design of this trial, in which only 29% of all possible crosses are represented, lends itself to use of the method developed by Kung (1978). This approach is valuable because it circumvents problems associated with the calculation of heritabilities for such data (Simmonds, 1979).

Experimental materials and assessment procedures

Experiment 507/2A Genetics was planted in March 1973 near Cardwell, Australia (18°11'S, 146°00'E). It was duplicated on well and poorly drained sites. On each site, eight blocks were established. Each block comprised six plots, each of which contained one representative of each family. Four fertilizer treatments were applied at each site. In July, 1983, 8 mm increment cores were collected, bark to bark, at breast height from two randomly selected representatives of each family in the two most complete fertilizer treatments common to both sites. Thus, a total of eight cores were sampled for each family.

At the Oxford Forestry Institute, cores were prepared for and assessed by the x-ray densitometry techniques described by Hughes and Sardinha (1975). For each radius, mean weighted radius density, $\bar{p}$, was determined as (i)

$\bar{p} = \Sigma a_i p_i / \Sigma a_i$ and within radius variability, $\bar{v}$, as (ii)

$\bar{v} = \sqrt{(\Sigma a_i (p_i - \bar{p})^2 /) \Sigma a_i - 1))}$,

where p_i = density at the ith densitometer step;

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Table 1. — Analyses of variance results.

Source of variation	Degrees of freedom (missing values)	Parameter: Mean radius density — % Sum of squares	Significance	Within radius variability — % Sum of squares	Significance
Site	1	10.7	***	1.5	***
Fertilizer	1	3.0	**	0.0	ns
Residual (1)	5	1.8		3.8	
Family	42	40.4	***	34.4	***
Family*Fertilizer	42	4.6	ns	4.5	ns
Residual (2)	251(1)	34.1		42.7	
Radius	343(1)	5.9		13.7	
Total	685	100.5		100.6	
Total sum of squares		3.522		0.5915	

(*** = $p < 0.001$, ** = $p < 0.01$, * = $p < 0.05$, ns = not significant at $p < 0.05$)

Table 2. — Errors in the program listed as an Appendix by Kung (1978).

Program module	Location	Correction
Main program	prior to second call of subroutines	substitute for "IROW = ICOL" : "ITEMP = IROW IROW = ICOL ICOL = ITEMP
Subroutine ROWDIF	DO loop labelled 120	substitute "IROW" for "ICOL"
Subroutine ROWSUM	DO loop labelled 310	" " " "
Subroutine SIMEQU	DO loop labelled 410	" " " "
Subroutine SEPRAT	DO loop labelled 610	" " " "

a_i = area of ith densitometer step, assuming circular rings;

n = number of densitometer steps.

Statistical analyses

The results of analysis of variance of each parameter are summarized in *Table 1*. Rankings of families on each site and under each fertilizer level were similar (Spearman's rank correlation coefficient approximately 0.8 in all cases), so subsequent analyses considered only overall mean values.

Development of Kung's method

The program by Kung (1978) contains a number of errors: corrections are detailed in *Table 2*. The program solves simultaneous equations by Gaussian elimination, a method which returns only approximate solutions. Consequently, general combining abilities (GCA's) thus derived do not sum to zero as they should. An enhanced program, developed from Kung's original, uses Crout's factorization method to return accurate solutions to the equations.

The revised program, which is available from the author on request, also lists expected cross performances and calculates the parameters and correlation coefficient of the linear regression of observed on expected performances. Simmonds (1979, p. 111) demonstrated their use in estimating the relative importance of specific combining ability (SCA). Ratios of SCA and GCA are also listed. Gordon (1980) suggested that, for any trait under consideration, these should generally be less than one for useful inferences to be drawn from an incomplete partial diallel.

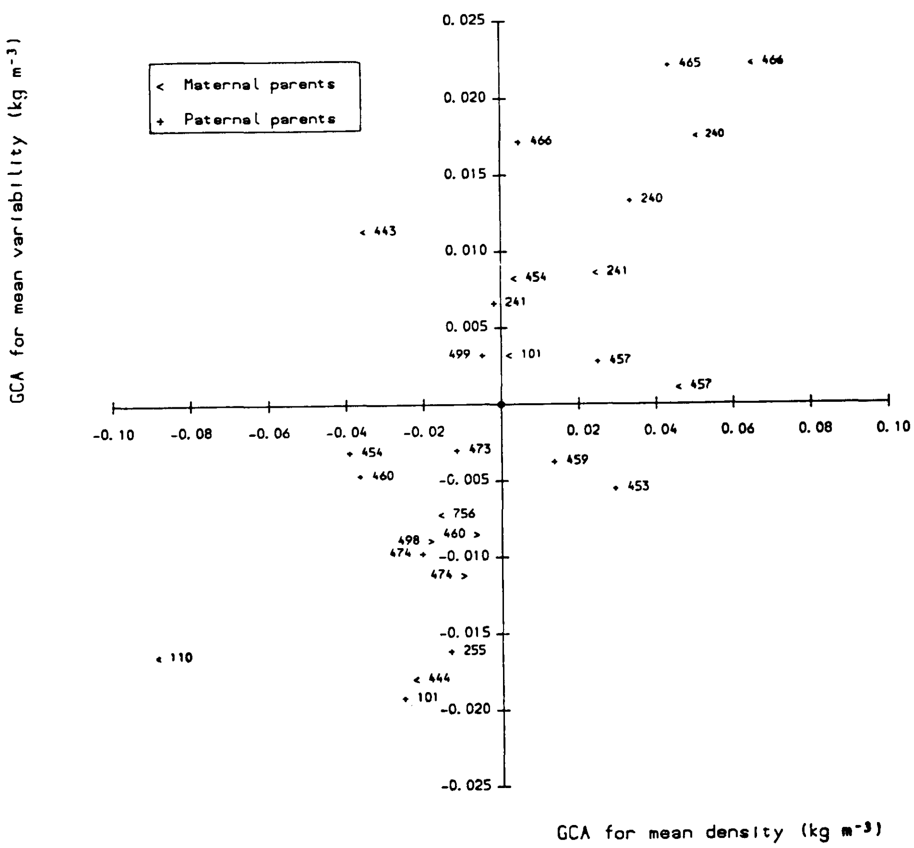

Figure 1. — Parental GCAs: density vs. variability.

A limitation of the method is that it does not allow estimation of the precision of the parameters. The jacknifing techniques described by MILLER (1964) may be useful for this purpose but were not attempted here. The application of least-squares analysis does provide an estimate of the error associated with these parameters. This analysis was performed with mean density data through the regression directives of the GENSTAT statistical package. The standard errors of the estimates thus derived were about 7% of the overall mean.

Application of the method

GCA values were calculated for family mean density and variability. In both cases, correlations between expected and observed values are high (0.90 and 0.87 respectively), suggesting that SCA effects are generally unimportant. The same conclusion is suggested by the SCA/GCA ratios, which are generally less than one.

Within tree uniformity of density is desirable for most end uses (e.g. OLSON and ARGANBRIGHT, 1977), and, within the range of density present, increased mean density is also desirable. A simple mean of unweighted joint selection for both parameters is to plot GCA values for each as in *Figure 1*. In this case, desirable parents are those combining above average GCA for density with less than average GCA for variability, that is, those falling in the lower right quadrant.

In this trial only the paternal parents 453 and 459 satisfy these criteria, but 457, as both mother and father, is only slightly above average in variability. These results suggest that, in the absence of more complete information, KUNG's method offers a soundly based approach to interpreting data from incomplete mating designs.

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