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Genetic control of 1,5-year-old traits in Pinus patula Schiede et Deppe and a comparison of progeny test methods[1])

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Summary

The *Pinus patula* Schiede et Deppe breeding population in Zimbabwe Rhodesia is based on plus trees selected in stands which may be up to fourth generation since the species' first introduction as an exotic. Polycross, factorial and diallel mating plans have been used in progeny tests designed to elucidate the genetic structure of the population, to investigate genotype-environment interaction,to identify the best general combiners and to provide information on the efficiency of mating and environmental designs. At 1.5 years from planting, a large number of morphological characteristics were assessed. Statistical analysis showed a portion of the considerable variability expressed in all these traits to be under additive genetic control. Individual tree heritabilities were as high as 0.60 for branch traits. Specific combining ability was of little practical significance, nor were maternal or reciprocal effects important. Genetic correlations were generally favourable both in sign and magnitude. Genotype-environment interaction did not seriously affect ranking of parents but variation between sites in the scale of family differences contributed to large discrepancies in heritability estimates, for example 0.12—0.55 for height. There was evidence that the polycross test is reliable and the assumption of half-sib relationship within families is valid. The precision of component estimation was satisfactory ($CV < 50\%$) where individual tree heritability was over 0.10 and family heritability over 0.50; at the same time, an increase in the number of parents under test would lead to a proportionately greater improvement in precision where heritabilities are low. Although the triple lattice structure provided blocking efficiencies of up to 201 per cent, the design had only a small effect on parent ranking and therefore was of little practical use to the breeder. There were indications that within- and between-plot variances stabilized at three to five trees per plot; greater precision of ranking might have been accomplished had plots of this size and more replications been used.

Key words: Pinus patula Schiede et Deppe, progeny tests, diallel, NCM II, polycross, general combining ability, specific combining ability, maternd effects, reciprocal effects, heritability, genotype-environment interaction, genetic correlations, triple lattice design.

Zusammenfassung

Die Züchtungspopulation von *Pinus patula* Schiede et Deppe in Zimbabwe Rhodesien basiert auf in Beständen selektierten Plus-Bäumen, die z. T. bereits die vierte Generation seit Einführung dieser Exotenbaumart erreicht haben. Kontrollierte Mehrfachbestäubungen, sowie faktorielle und diallele Kreuzungspläne kamen bei der Nachkommenschaftsprüfung zur Anwendung, um die genetische Struktur der Population zu klären, das Bestehen von Interaktionen zwischen Genotyp und Umwelt zu untersuchen, die Bäume mit der besten allgemeinen Kombinationseignung auszulesen und Informationen über die Effizienz verschiedener experimenteller Ansätze bei der Prüfung von Kreuzungs- und Umwelteffekten zu erhalten.

Aus den 1.5 Jahre nach der Pflanzung gewonnenen Daten geht hervor, daß ein Großteil der Variation in vielen morphologischen Eigenschaften von allgemeiner Kombinationseignung gesteuert wird, wobei die Heritabilität in manchen Fällen 0.60 erreicht. Weder spezifische Kombinationseignung noch reziproke oder mütterliche Effekte erwiesen sich als signifikant. Die Genotyp/Umwelt-Interaktion war nur in Bezug auf ihre Wirkung auf die Heritabilitätsschätzung von Bedeutung.

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[1] The paper is adapted from part of the senior author's Ph. D. thesis (1973).

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Die Annahme, daß Nachkommen kontrollierter Mehrfachbestäubungen Halbgeschwister darstellen, bewahrheitete sich. Die Genauigkeit der Varianzkomponentenschätzung eines 9 × 5 faktoriellen Tests war im großen und ganzen zufriedenstellend. (Variationskoeffizient < 50%) Durch die Unterteilung von Blocks in einen Ansatz mit Dreisatzgitter konnte die Effizienz biz zu 100% gesteigert werden, doch war dies praktisch nur von geringer Bedeutung. Aus den Resultaten geht hervor, daß für eine Auswertung in diesem Alter Parzellen mit 3—5 Bäumen am günstigsten sein dürften.

Introduction

The genetic improvement programme for *Pinus patula* Schiede et Deppe in Rhodesia included the use of polycross, factorial and reciprocal mating designs for progeny testing the first population of plus trees selected in local stands. The aim was to identify clones with high general combining ability and to yield information on population genetics (Burley, Burrows, Armitage and Barnes, 1966). Controlled crosses for this part of the plan were completed in 1967 and the progeny tests were planted between 1967 and 1972 (Barnes, 1973). Barnes and Schweppenhauser (1978) have reported on the genetic control of nursery traits. In this paper we deal with the analysis and interpretation of data collected 1.5 years after planting the factorial and reciprocal tests. The assessments covered a large number of external morphological characteristics to provide an opportunity for later detailed investigation of juvenile-mature correlations. Measurements of height were made in adjacent polycross tests so that progeny test methods could be compared.

Materials

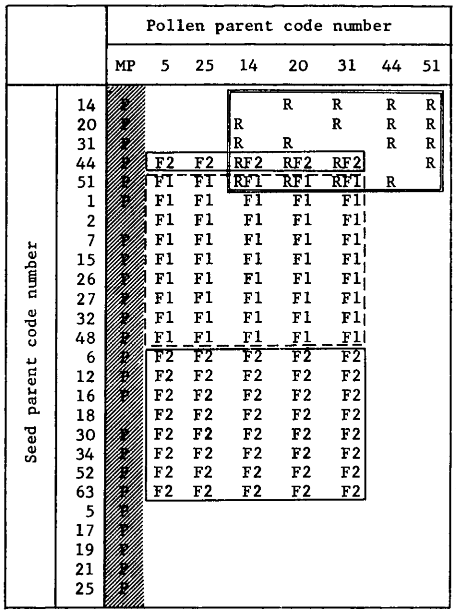
The plus tree population

The material for these tests came from a breeding population of plus tree clones, the ortets of which were selected in *P. patula* plantations in the Stapleford area of the Eastern Districts of Rhodesia. Individuals in the base population may be up to the fourth generation since introduction to southern Africa from Mexico (Barnes, 1973).

Mating plan

Mating plans for the polycross, factorial (design II of Comstock and Robinson, 1952) and reciprocal (diallel without selfs) are shown in *Figure 1.*

In the polycross, 24 plus tree clones were tested as female parents by crossing with a mixture of pollen from 20 parents which were from the same plus tree population. The controlled pollinations were made over a period of three years and the pollen mix had the same constituents every year. Pollen from each parent contributed by volume to the mix in inverse proportion to its viability which was tested by germination in a ten per cent sucrose solution (Dillon and Zobel, 1957). For the factorial test, a complete set of crosses was available between five of the tester clones used as pollen parents and 18 different clones used as seed parents. A complete diallel, without selfs, between five of the tester clones was used for the reciprocal test.



Seed parent code number	Pollen parent code number: MP	5	25	14	20	31	44	51
14	P				R	R	R	R
20	P			R		R	R	R
31	P			R	R		R	R
44	P	F2	F2	RF2	RF2	RF2		R
51	P	F1	F1	RF1	RF1	RF1	R	
1	P	F1	F1	F1	F1	F1		
2		F1	F1	F1	F1	F1		
7	P	F1	F1	F1	F1	F1		
15	P	F1	F1	F1	F1	F1		
26	P	F1	F1	F1	F1	F1		
27	P	F1	F1	F1	F1	F1		
32	P	F1	F1	F1	F1	F1		
48	P	F1	F1	F1	F1	F1		
6	P	F2	F2	F2	F2	F2		
12	P	F2	F2	F2	F2	F2		
16	P	F2	F2	F2	F2	F2		
18		F2	F2	F2	F2	F2		
30	P	F2	F2	F2	F2	F2		
34	P	F2	F2	F2	F2	F2		
52	P	F2	F2	F2	F2	F2		
63	P	F2	F2	F2	F2	F2		
5	P							
17	P							
19	P							
21	P							
25	P							

P - polycross test planted 1967/68 & 1968/69
F1 - factorial test planted 1968/69
F2 - factorial test planted 1969/70
R - reciprocal test planted 1968/69 & 1969/70

Figure 1. — Mating designs for *Pinus patula* progeny tests

Progeny test localities

Four test localities were selected in the Eastern Districts of Rhodesia. The first was at Stapleford which provided the type of environment where *P. patula* reaches its optimum development. The second was at Martin which is lower and hotter than Stapleford and where the species has a better early growth performance but tends to become less thrifty and subject to damage by various physical and biotic agencies in the second half of the 30-year rotation (Barnes and Mullin. 1976). The third and fourth sites were both at higher altitudes at Bende and Nyangui; *P. patula* is physiologically well adapted to these conditions but growth tends to be slower, particularly in the first ten years. Site data for the four localities are given in *Table 1.*

Environmental design

All tests consisted basically of three replications of ten-tree row plots established at a 2.44 m square spacing with a five-row external surround. Triple lattice designs were imposed on the main tests to contend with variation which was expected to stem from the large number of families and the heterogeneity of experimental sites.

Table 1. — Site data for the four *Pinus patula* progeny test localities.

	Locality			
	Martin	Stapleford	Bende	Nyangui
Latitude (°S)	19° 45'	18° 40'	18° 00'	18° 00'
Altitude (m)	1265	1770	1880	2120
Mean annual rainfall (mm)	1082	1750	1573	1550
Mean monthly max. temp. (°C)	22.9	19.2	17.7	14.7
Mean monthly temp. (°C)	17.7	15.1	13.0	11.5
Mean monthly min. temp. (°C)	12.6	11.1	8.3	7.3
Soil (parent material)	dolerite	granite	dolerite	shale
Previous land use	first rotation pine crop	first rotation pine crop	shifting cultivation	grassland

Table 2. — Descriptions of measured and derived 1.5-year traits

CODE	DESCRIPTION		UNIT
HT1	Height to leader bud minus post-planting	+	m
CAQ	Circular area of stem at a quarter of total height	+	cm^2
VFF	Volume form factor - $\left[\frac{1}{2}\ (CAQ + CAH)/CAQ\right] \times 10$	+	ratio
VOL	Total stem volume - (Total height x CAQ x VFF)	+	dm^3
STR	Stem straightness rating - (category 1 = best to 7 = worst; subtracted from 8 so that the straighter the stem the higher the numerical value: (Barrett and Mullin, 1968)	+	rating
SIN	Stem sinuosity index - (assessed on that part of the stem between the leader tip and the third whorl of branches from the tip) - (category 1 = slight deviation to 3 = severe deviation, multiplied by the frequency of deviations in the category, summed for the tree and subtracted from 30 so that the less the sinuosity of the stem the higher the numerical value)	+	index
BD1	Total branch x-sectional area } - in that whorl contributing most to the crown	-	cm^2
BL1	Total branch length } - in that whorl contributing most to the crown	-	m
BA1	Average branch angle (90^o = 10.0) } - in that whorl contributing most to the crown	+	9^o
AIL	Average internode length - (excludes that section between the ground and the first whorl)	-	cm
UIL	Uniformity index of internode length - (index constructed so that it is 10 when the longest internode = the average internode, and moves towards 0 as the difference increases) $\frac{n\bar{X} - Xmax}{(n-1)\bar{X}}$ where n = number of internodes, $\bar{X}$ = mean internode length, Xmax = length of longest internode	+	index
ABW	Average number of branches per whorl - (based on total number of branches on the tree)	-	number
UBW	Uniformity index of branches per whorl - (index constructed so that it is 10 when all whorls have the same number of branches and moves towards 0 as the difference increases) - see UIL above for formula	+	index
B/H	Number of branches per metre of height - (total number of branches/total height)	+	number
ARW	Average of 4 crown radii as a percentage of HT1 - (four radii measured at right angles and each at a point of maximum width)	-	ratio
ACH	Average of 4 crown heights as a percentage of HT1 - (four crown heights measured as the height of the point of maximum width on the 4 radii used for ARW above)	-	ratio
CGD	Displacement of the centre of gravity of the crown - (distance of "centre of gravity" from the stem $(\frac{RN - RS}{2})^2 + (\frac{RE - RW}{2})^2$ where RN, RS, RE and RW = crown radius to North, South, East and West respectively, expressed as a percentage of the average of the 4 crown radii)	-	index
BAQ	Branch/stem basal area index - (BD1 as a percentage of CAQ)	-	index
BEI	Branch efficiency index - (BD1 x BL1 as a percentage of VOL)	-	index

\+ = high value desirable
\- = low value desirable

Table 3. — Generalized form of the analysis of variance of the polycross test and the method of estimating heritability on individual tree and family mean bases.

SOURCE OF VARIATION	DEGREES OF FREEDOM	EXPECTATION OF MEAN SQUARE
Females (F)	(f-1)	$\sigma_T^2 + t.\sigma_\pi^2 + tr.\sigma_{FL}^2 + trl.\sigma_{FCY}^2 + trlc.\sigma_{FY}^2 + trly.\sigma_{FC}^2 + trlcy.\sigma_F^2$
Localities (C)	(c-1)	$\sigma_T^2 + t.\sigma_\pi^2 + tf.\sigma_R^2 + tr.\sigma_{FL}^2 + trl.\sigma_{FCY}^2 + trly.\sigma_{FC}^2 + tfrl.\sigma_{CY}^2 + tfr.\sigma_L^2 + tfrly.\sigma_C^2$
Years (Y)	(y-1)	$\sigma_T^2 + t.\sigma_\pi^2 + tf.\sigma_R^2 + tr.\sigma_{FL}^2 + trl.\sigma_{FCY}^2 + trlc.\sigma_{FY}^2 + tfrl.\sigma_{CY}^2 + tfr.\sigma_L^2 + tfrlc.\sigma_Y^2$
Lattices (L) in C in Y	cy(l-1)	$\sigma_T^2 + t.\sigma_\pi^2 + tf.\sigma_R^2 + tr.\sigma_{FL}^2 + tfr.\sigma_L^2$
C x Y	(c-1)(y-1)	$\sigma_T^2 + t.\sigma_\pi^2 + tf.\sigma_R^2 + tr.\sigma_{FL}^2 + trl.\sigma_{FCY}^2 + tfrl.\sigma_{CY}^2$
F x C	(f-1)(c-1)	$\sigma_T^2 + t.\sigma_\pi^2 + tr.\sigma_{FL}^2 + trl.\sigma_{FCY}^2 + trly.\sigma_{FC}^2$
F x Y	(f-1)(y-1)	$\sigma_T^2 + t.\sigma_\pi^2 + tr.\sigma_{FL}^2 + trl.\sigma_{FCY}^2 + trlc.\sigma_{FY}^2$
F x C x Y	(f-1)(c-1)(y-1)	$\sigma_T^2 + t.\sigma_\pi^2 + tr.\sigma_{FL}^2 + trl.\sigma_{FCY}^2$
F x L in C in Y	cy(f-1)(l-1)	$\sigma_T^2 + t.\sigma_\pi^2 + tr.\sigma_{FL}^2$
Replications (R) in L in C in Y	lcy(r-1)	$\sigma_T^2 + t.\sigma_\pi^2 + tf.\sigma_R^2$
Residual (π)	lcy(f-1)(r-1)	$\sigma_T^2 + t.\sigma_\pi^2$
Trees (T) in plots	frlcy(t-1)	σ_T^2
TOTAL	(tfrlcy-1)	

$$h_T^2 = \frac{4s_F^2}{s_T^2 + s_\pi^2 + s_{FL}^2 + s_{FCY}^2 + s_{FY}^2 + s_{FC}^2 + s_F^2}$$

$$h_F^2 = \frac{s_F^2}{\frac{s_T^2 + ts_\pi^2}{trlcy} + \frac{s_{FL}^2}{lcy} + \frac{s_{FCY}^2}{cy} + \frac{s_{FY}^2}{y} + \frac{s_{FC}^2}{c} + s_F^2}$$

Table 4. — Generalized form of the analysis of variance of the factorial test and the method of estimating heritability on individual tree and family mean bases.

SOURCE OF VARIATION	DEGREES OF FREEDOM	EXPECTATION OF MEAN SQUARE
Locality (C)	(c-1)	$\sigma_T^2 + t.\sigma_\pi^2 + tr.\sigma_{MPC}^2 + tpr.\sigma_{MC}^2 + tmr.\sigma_{PC}^2 + tmp.\sigma_R^2 + tmpr.\sigma_C^2$
Replications (R) in C	c(r-1)	$\sigma_T^2 + t.\sigma_\pi^2 + tmp.\sigma_R^2$
Pollen (paternal) parents (P)	(p-1)	$\sigma_T^2 + t.\sigma_\pi^2 + tr.\sigma_{MPC}^2 + tmr.\sigma_{PC}^2 + trc.\sigma_{MP}^2 + tmrc.\sigma_P^2$
Seed (maternal) parents (M)	(m-1)	$\sigma_T^2 + t.\sigma_\pi^2 + tr.\sigma_{MPC}^2 + tpr.\sigma_{MC}^2 + trc.\sigma_{MP}^2 + tprc.\sigma_M^2$
M x P	(p-1)(m-1)	$\sigma_T^2 + t.\sigma_\pi^2 + tr.\sigma_{MPC}^2 + trc.\sigma_{MP}^2$
P x C	(p-1)(c-1)	$\sigma_T^2 + t.\sigma_\pi^2 + tr.\sigma_{MPC}^2 + tmr.\sigma_{PC}^2$
M x C	(m-1)(c-1)	$\sigma_T^2 + t.\sigma_\pi^2 + tr.\sigma_{MPC}^2 + tpr.\sigma_{MC}^2$
M x P x C	(p-1)(m-1)(c-1)	$\sigma_T^2 + t.\sigma_\pi^2 + tr.\sigma_{MPC}^2$
Residual (π)	c(r-1)(mp-1)	$\sigma_T^2 + t.\sigma_\pi^2$
Trees (T) in plots	mprc(t-1)	σ_T^2
TOTAL	mprct-1	
$h_T^2 = \dfrac{2(s_P^2 + s_M^2)}{s_T^2 + s_\pi^2 + s_{MPC}^2 + s_{MC}^2 + s_{PC}^2 + s_{MP}^2 + s_M^2 + s_P^2}$		$h_T^2 = \dfrac{s_P^2 + s_M^2}{\dfrac{s_T^2 + ts_\pi^2}{trc} + \dfrac{s_{MPC}^2}{c} + \dfrac{s_{MC}^2}{c} + \dfrac{s_{PC}^2}{c} + s_{MP}^2 + s_P^2 + s_M^2}$

Table 5. — Generalized form of the analysis of variance of the reciprocal test and the method of estimating heritability on individual tree and family bases

SOURCE OF VARIATION	DEGREES OF FREEDOM	EXPECTATION OF MEAN SQUARE
Environments (C)	(c-1)	$\sigma_T^2 + t.\sigma_\pi^2 + tr\{2.\sigma_{sC}^2 + 2(p-2).\sigma_{gC}^2\} + t(p^2-p).\sigma_R^2 + tr(p^2-p).\sigma_C^2$
Replications (R) in C	c(r-1)	$\sigma_T^2 + t.\sigma_\pi^2 + t(p\ -p).\sigma_R^2$
General (g)	(p-1)	$\sigma_T^2 + t.\sigma_\pi^2 + tr\{2.\sigma_{sC}^2 + 2(p-2).\sigma_{gC}^2\} + tcr\{2.\sigma_s^2 + 2(p-2).\sigma_g^2\}$
Specific (s)	p(p-3)/2	$\sigma_T^2 + t.\sigma_\pi^2 + tr(2.\sigma_{sC}^2) + tcr(2.\sigma_s^2)$
Maternal (m)	(p-1)	$\sigma_T^2 + t.\sigma_\pi^2 + tr(2.\sigma_{r'C}^2 + 2p.\sigma_{mC}^2) + tcr(2.\sigma_{r'}^2 + 2p.\sigma_m^2)$
Reciprocal (r')	(p-1)(p-2)/2	$\sigma_T^2 + t.\sigma_\pi^2 + tr(2.\sigma_{r'C}^2) + tcr(2.\sigma_{r'}^2)$
g x C	(p-1)(c-1)	$\sigma_T^2 + t.\sigma_\pi^2 + tr\{2.\sigma_{sC}^2 + 2(p-2).\sigma_{gC}^2\}$
s x C	{p(p-3)/2}(c-1)	$\sigma_T^2 + t.\sigma_\pi^2 + tr(2.\sigma_{sC}^2)$
m x C	(p-1)(c-1)	$\sigma_T^2 + t.\sigma_\pi^2 + tr(2.\sigma_{r'C}^2 + 2p.\sigma_{mC}^2)$
r x C	{(p-1)(p-2)/2}(c-1)	$\sigma_T^2 + t.\sigma_\pi^2 + tr(2.\sigma_{r'C}^2)$
Residual (π)	c(r-1)(p²-p-1)	$\sigma_T^2 + t.\sigma_\pi^2$
Trees (T) in plots	cr(p²-p)(t-1)	σ_T^2
TOTAL	crt(p²-p)-1	
$h_T^2 = \dfrac{4s_g^2}{s_T^2 + s_\pi^2 + s_{r'C}^2 + s_{mC}^2 + s_{sC}^2 + s_{gC}^2 + s_{r'}^2 + s_m^2 + s_s^2 + s_g^2}$		$h_F^2 = \dfrac{s_g^2}{\dfrac{s_T^2 + ts_\pi^2}{trc} + \dfrac{s_{r'C}^2}{c} + \dfrac{s_{mC}^2}{c} + \dfrac{s_{sC}}{c} + \dfrac{s_{gC}^2}{c} + s_r^2 + s_m^2 + s_s^2 + s_g^2}$

The polycross was planted at Stapleford and Melsetter in 1967/68 as a double (two sets of three replications) 6 × 6 triple lattice in each locality and the whole experiment was repeated in 1968/69. There were only 24 polycross families. An extra 10 two-parent genetic checks and two commercial controls were used to make up the 36 families required for the design; their performance has been discussed elsewhere (BARNES, 1977).

The main factorial and reciprocal tests were planted together since they had some common crosses (see *Figure 1*). The 18 seed parents in the factorial were tested as two separate lots of nine (45 families) in 1968/69 and 1969/70 at Stapleford and Martin. Together with the 20 families of the reciprocal (three common with the factorial each year) and two genetic checks, this allowed the use of an 8 × 8 single triple lattice design for each combined experiment. The crosses of the reciprocal test were extended to the Bende and Nyangui sites in 1968/69 so as to provide additional information on genotype-environment interaction.

Assessments

Considerable importance has been attached to the 1.5-year field measurements. This is the earliest stage at which juvenile relationships with mature morphological characteristics are likely to be significant and, at the spacing used, the last stage at which trait expression will be free from the effects of competition. The measured and derived variates are listed in *Table 2*. These variates were selected as those which have most direct economic significance both in plantation management and in utilization (BARNES, 1973). Detailed measurements were restricted to the 1968/69 factorial and reciprocal tests; only height was measured in the other tests.

Statistical Methods

The generalized forms of the analyses of variance (and covariance) used for the polycross, factorial and reciprocal (BURROWS, pers. comm.)[1]) tests are shown in *Table 3, 4* and 5.

As establishment was good, it was not necessary to resort to complex methods to estimate missing values. The effect of missing trees on the coefficient 't' was allowed for by recalculation as

$$\frac{1}{p'-1}\left[N-\frac{\sum'^{n}_{i=1} n^2_i}{N}\right]$$

where p' is the number of plots
N is the total number of trees
n_i is the number of trees in the ith of a total of n plots (GANGULI, 1941).

The analyses, adjustment of family means and calculation of blocking efficiency for the triple lattice design were handled by the method described by COCHRAN and COX (1957).

For certain effects in the analyses there was no single variance to use in the denominator of the F-test. In these cases a term was constructed by addition and subtraction of appropriate mean squares and the number of degrees of freedom for the denominator was calculated using SATTERTHWAITE's (1946) approximation for complex variances.

Evidence of genotype-environment interaction was provided by significance of the appropriate mean square but a more meaningful expression of repeatability of performance of genotype over environment (R_E) was calculated as

$$R_E = \frac{s^2_i}{s^2_i + s^2_{ic}}$$

the intra-class correlation, where s^2_i is the variance of the effect i and s^2_{ic} is the variance of the interaction of the effect i with environment c. Spearman's rank correlation coefficient (r_S) was used to compare ranks over environments.

An expression to indicate the stability of parental ranking over different mating designs was derived by taking the normal scores (FISHER and YATES, 1957) for the ranked (ordinal) parental means, subjecting them to an analysis of variance and using the variance components to calculate a repeatability estimate (R_D) (BURROWS, pers. comm.)[4]). The generalized form of the analysis of variance is: —

Source of variation	*DF*	*EMS*
Females (F)	(f − 1)	$\sigma^2_{FD} + d\sigma^2_F$
Females (F) × Design (D)	(d − 1) (f − 1)	σ^2_{FD}

and the repeatability was calculated as: —

$$R_D = \frac{s^2_F}{s^2_F + s^2_{FD}}$$

The design source of variation in this analysis is not shown as the scores must sum to zero.

Genetic Interpretation

The components of variance and covariance which are derived from these analyses can be interpreted genetically provided that a basic set of assumptions concerning the parent population and the progenies can be met. These assumptions are well known (see, *e.g.* COCKERHAM, 1963) and appear to be valid for this material (BARNES, 1973) provided that inferences are drawn about the potential population of plus trees only and not about the local *P. patula* population as a whole.

The construction of heritability estimates, on both individual tree (h^2_T) and family mean (h^2_F) bases, for the three test designs are shown in *Tables 3, 4* and 5. Standard errors of heritability estimates were calculated as

$$\sqrt{[P^2V_G + G^3V_P - 2PG\mathrm{cov}(P,G)]\ /P^4}$$

where P is the phenotypic variance,
G is the genotypic variance,
V_P is the variance of P
V_G is the variance of G (GORDON *et al., 1972)*

Phenotypic, genotypic and genetic (additive) correlations were estimated from the analyses of covariance and standard errors were calculated as

$$\sqrt{\frac{m^2_{12}}{m_{11}\,m_{22}}\left[\frac{\mathrm{var}\,(m_{12})}{m^2_{12}} + \frac{\mathrm{var}\,(m_{11})}{4m^2_{11}} + \frac{\mathrm{var}\,(m_{22})}{4m^2_{22}} - \frac{\mathrm{cov}\,(m_{12}, m_{11})}{m_{12}\,m_{11}} - \frac{\mathrm{cov}\,(m_{12}, m_{22})}{m_{12}\,m_{22}} + \frac{\mathrm{cov}\,(m_{11}, m_{22})}{2m_{11}\,m_{22}}\right]}$$

where m_{12} is the covariance of two traits, say x and y
m_{11} is the variance of x
m_{22} is the variance of y (MODE and ROBINSON, 1959)

Results

Analyses of selected traits in the factorial, reciprocal and polycross tests are given in *Tables 6, 7* and *8*. Figures for the percentage contribution of variance components have been used; with the total variance and expectations of mean squares in *Tables 3, 4* and 5, they provide a concise and, at the same time complete, record. Negative estimates of components have been entered as zero. Heritabilities for height in individual tests are given in *Table 9* and genetic, genotypic and phenotypic correlations in *Table 10*.

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Table 6. — Analysis of variance of 1.5-year traits in the *Pinus patula* factorial progeny tests at Stapleford and Martin.

Source of variation	Degrees of freedom	Trait code/1																		
		Stem						Branch								Crown			Branch efficiency	
		HT1	CAQ	VFF	VOL	STR	SIN	BD1	BL1	BA1	AIL	UIL	ABW	UBW	B/H	ARW	ACH	CGD	BAQ	BEI
Percentage contributions to the total variance/2 and significance of the F tests on the mean squares for combined environments																				
Environments (C)	1	1	0	4 *	0	0	0	3	1	1	7 *	2 *	5 **	6 **	0	9 *	0	0	8	5
Paternal parents (P)	4	1	1	1	2	1	0	8 ***	15 ***	0	13 **	2 *	17 ***	0	20 **	1 *	1	1	22 ***	33 ***
Maternal parents (M)	8	4 *	3	1 *	4	0	1	5 **	2 *	3	4 **	3 **	4 **	0	7 **	1	2 *	0	20 ***	16 **
M x P	32	1	0	1	0	0	1	2	3 *	0	1 **	0	0	0	0	1	3 **	0	8	9 *
P x C	4	3 **	1	1 *	1	0	3 **	0	0	1	2	0	0	1 *	1	0	2 **	0	0	0
M x C	8	0	1	0	2	2	5 ***	0	0	1	0	1	1	1	0	0	0	1 *	2	0
M x P x C	32	1	1	0	1	1	0	0	0	1	0	0	0	1	1	0	0	0	3	5
Residual (π)	252	11	9	1	11	19	10	7	5	8	4	0	1	0	2	3	9	4	37	31
Trees in plots (T)	2419	78	84	91	79	77	80	75	74	85	69	92	72	91	69	85	83	94	-	-
TOTAL VARIANCE		0.1267	6.817	0.2791	26.15	0.4934	2.718	8.991	1.913	0.9179	20.11	0.2038	0.3860	0.1126	12.72	48.26	126.5	58.38	581.4	97.09
:Significance of F tests for separate environments																				
Martin Paternal parents (P)		***	***	***	***		***	***	***	**	***	**	***	**	***	*	***		***	***
Martin Maternal parents (M)		***	***	*	***	*	***	**	**	***	***	***	***	*	***	***	***		***	**
Martin M x P								*	**										***	***
Stapleford Paternal parents (P)		*	**		**	*		***	***		***	**	***	*	***	**	**		***	***
Stapleford Maternal parents (M)			***	*	***	*		***	**		**	**	***		***			*	***	***
Stapleford M x P		**								*	*				*					
Means, ranges, standard errors, CVs and repeatability over environments																				
Overall mean		1.9	7.1	7.3	11.2	4.5	27.8	5.4	4.0	7.1	21.1	9.0	4.2	9.4	16.6	32.0	48.1	12.5	76.9	20.7
Range of 5 pollen parent means - from		1.8	6.6	7.2	10.2	4.4	27.5	4.4	3.4	7.0	19.2	8.9	3.9	9.4	14.4	31.3	45.9	11.8	62.1	13.8
- to		2.0	7.6	7.4	12.7	4.6	28.1	6.4	4.9	7.2	22.9	9.0	4.5	9.5	18.4	32.8	50.1	13.4	91.5	29.3
Standard error		0.02	0.15	0.02	0.30	0.05	0.10	0.16	0.07	0.05	0.20	0.02	0.02	0.01	0.15	0.32	0.06	0.38	2.00	0.75
Range of 9 seed parent means - from		1.8	6.3	7.2	9.5	4.3	27.3	4.5	3.7	6.9	19.0	8.9	4.0	9.4	15.1	30.9	44.5	11.6	64.1	15.6
- to		2.0	7.7	7.4	12.7	4.8	28.4	6.4	4.4	7.5	22.4	9.1	4.4	9.4	18.1	33.1	50.3	13.5	96.2	27.9
Standard error		0.03	0.20	0.03	0.41	0.07	0.13	0.21	0.09	0.07	0.26	0.02	0.03	0.02	0.20	0.43	0.80	0.51	2.69	1.00
CV(%) individual tree - Martin		19.8	35.8	6.7	45.7	13.2	6.6	55.5	33.5	13.0	18.9	4.5	13.1	2.9	20.7	20.3	23.9	59.1	-	-
- Stapleford		17.7	37.1	7.5	44.7	16.1	5.1	51.1	32.7	14.1	20.6	5.4	15.2	4.0	21.8	21.1	26.6	63.1	-	-
Repeatability of ♀ parents over environments $-R_E$		0.91	0.47	1.00	0.65	0.39	0.20	0.95	0.96	0.69	0.90	0.88	0.87	0.35	1.00	0.85	0.94	-	0.94	0.98
$-r_S$		0.82	0.40	0.75	0.45	0.00	0.35	0.82	0.82	0.53	0.90	0.80	0.68	-0.05	0.90	0.65	0.73	-0.35	0.88	0.90
Heritabilities																				
Heritability localities combined - family		0.44	0.45	0.38	0.53	0.19	0.13	0.74	0.78	0.37	0.83	0.68	0.90	0.12	0.91	0.35	0.30	0.15	0.72	0.74
- tree		0.10	0.07	0.04	0.12	0.03	0.02	0.26	0.34	0.05	0.37	0.10	0.44	0.01	0.54	0.04	0.06	0.01	-	-
Martin - family		0.59	0.44	0.51	0.57	0.21	0.70	0.57	0.68	0.55	0.77	0.70	0.88	0.42	0.87	0.30	0.51	0.18	0.60	0.61
Stapleford - family		0.34	0.52	0.29	0.51	0.24	0.02	0.76	0.78	0.18	0.82	0.47	0.85	0.22	0.87	0.18	0.34	0.23	0.71	0.74
Efficiency of triple lattice design																				
Blocking efficiency (%) - Martin		150	124	101	129	115	107	126	125	112	156	102	109	103	105	163	201	110	111	110
- Stapleford		113	120	101	121	103	115	110	102	93	118	107	99	103	101	111	102	97	109	103
r_S of adjusted and unadj. ♀ means		1.0	0.88	0.98	0.95	0.83	1.00	0.99	0.99	0.99	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.95	0.99	1.00

/1 See Table 2 for trait descriptions
/2 Negative components entered as zero

The analyses, means, heritabilities and correlations are based on unadjusted data. Means adjusted through the triple lattice analyses have been used in practice but here, where theory rather than practical precision is of interest, it is more informative to indicate the value of the triple lattice design through the estimates of blocking efficiency and rank correlations of adjusted and unadjusted family means (*Table 6*). The differences in significance of F ratios in analyses of adjusted and unadjusted means were small for all traits and the effects of lattice adjustment on the variance and covariance components and their standard errors were generally so small that there were negligible changes in heritabilities and correlations. In the occasional instance where there was a larger change in the component estimate, the significance of the difference was difficult to judge because of the impracticability of analysing the adjusted data in such a way as to allow the estimate of genetic components of variance unconfounded with the environmental components of the lattice design (BARNES, 1973). Overall means and ranges of the different traits are shown

Table 7. — Analysis of variance of 1.5-year traits in the *Pinus patula* reciprocal progeny tests at Stapleford and Martin.

Source of variation	Degrees of freedom	Trait code/1												
		Stem					Branch						Crown	
		HT1	CAQ	VOL	STR	SIN	BD1	BL1	BA1	AIL	ABW	B/H	ARW	ACH
Environments (C)	1	10.0	0.0	3.6	2.6	0.0	5.3*	5.7*	4.5	7.1*	2.6	0.0	9.0	0.0
Replications in C	4	0.5	0.0	0.0	3.4**	9.1***	0.3	0.2	2.0**	0.3	0.0	2.9***	0.5	19.5***
General (g)	4	1.6	5.4*	5.0	2.0	3.4	6.3*	8.4	0.0	11.1*	3.0	7.4*	3.8	1.0
Specific (s)	5	0.4	0.9	1.4	0.9	0.9	0.9	0.0	2.4	0.0	0.0	1.6	0.0	0.3
Maternal (m)	4	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.4	0.1	0.7	0.1
Reciprocal (r)	6	1.2	3.9*	2.8*	0.0	0.6	0.6	0.3	0.0	0.8	0.5*	0.0	0.0	0.0
g x C	4	3.3*	0.4	1.7	0.0	2.7*	0.1	0.0	1.8	1.7	0.0	0.7	0.0	0.8
s x C	5	0.0	0.0	0.0	0.2	0.0	0.0	2.0	0.0	0.0	2.9*	0.0	2.6	0.0
m x C	4	1.3*	0.8	1.6*	0.0	0.0	0.0	0.0	0.0	0.2	0.2*	0.0	0.0	0.6
r x C	6	0.0	0.0	0.0	0.9	0.0	0.0	0.0	2.5*	0.0	0.0	0.4	3.7	0.0
Residual in C	76	12.1	7.4	10.0	7.9	5.9	4.4	2.8	4.0	5.4	0.2	3.0	28.2	14.4
Trees in plots	1072	69.6	81.2	73.9	81.8	77.4	82.1	80.6	82.8	73.4	90.2	83.9	51.5	63.3
TOTAL VARIANCE		0.1380	6.2334	26.1884	0.4591	2.3087	12.3241	1.6888	1.0543	17.1727	0.2955	10.7414	67.0089	145.5054
Heritability - family		0.18	0.40	0.36	0.31	0.40	0.68	0.73	0.00	0.74	0.43	0.64	0.29	0.18
- individual tree		0.07	0.21	0.21	0.09	0.15	0.27	0.36	0.00	0.48	0.12	0.30	0.17	0.05

/1 See Table 2 for trait descriptions.

Table 8. — Analysis of variance of 1.5-year height (HT1) in the *Pinus patula* polycross progeny tests at Stapleford and Martin.

Source of variation	DF	VC(%)
Families (F)	23	1.1
Localities (C)	1	0
Years (Y)	1	0
Lattices (L) in C in Y	4	2.9*
Replications (R) in L in C in Y	1	2.0***
C x Y	1	8.3***
F x C	23	0.8
F x Y	23	0
F x C x Y	23	2.0*
F x L in C in Y	92	0.1
Residual (π)	436	8.5***
Trees in plots (T)	5114	74.3
Total variance		1.2884
Overall mean		1.46
Range of 24 family means - from		1.35
- to		1.57
Standard error		0.03
Heritability - family		0.42
- individual tree		0.05

Table 9. — Heritability estimates and coefficients of variation for 1.5-year height (HT1) in individual *Pinus patula* polycross, factorial and reciprocal tests.

Test type	Locality	Planting year	Family composition	Heritability		CV (%)
				Family $\hat{h}^2_F$	Tree $\hat{h}^2_T$	
Polycross	Stapleford	1968/69	24 common half-sib families	0.82	0.34	20.8
	Stapleford	1969/70		0.71	0.21	19.8
	Martin	1968/69		0.51	0.15	23.3
	Martin	1969/70		0.16	0.03	27.3
Factorial	Stapleford	1969/70	5♂ x 9♀ common tester series	0.34	0.08	17.7
	Martin	1969/70		0.59	0.24	19.8
Factorial	Stapleford	1970/71	5♂ x 9♀ common tester series	0.37	0.09	26.7
	Martin	1970/71		0.23	0.05	18.9
Reciprocal	Stapleford	1969/70	5 x 5 common diallel without selfs	0.66	0.37	17.0
	Stapleford	1970/71		0.55	0.37	22.5
	Martin	1969/70		0.23	0.12	17.5
	Martin	1970/71		0.42	0.26	18.4
	Bende	1969/70		0.30	0.14	29.0
	Nyangui	1969/70		0.73	0.55	19.1

in *Table 6;* individual family values are not given but their rankings have been used in the repeatability estimates discussed below.

Only the combined analyses (over environments and years) are shown here. Significance of F ratios for most traits in the various parental groups was higher for individual environments; this is indicated in these Tables by the higher heritabilities for individual environments.

Discussion

Genetic control of the traits

In the individual (within environment) factorial tests, significant differences ($p = < .05$) were found between parents within both the maternal and paternal groups for every measured or derived trait (Barnes, 1973). Over the two localities, Stapleford and Martin, heritabilities were highest for the branch size, number and distribution characteristics *(Table 6)* with maximum values of $\hat{h}^2_T = 0.54$ and $\hat{h}^2_F = 0.91$ for number of branches (B/H). Stem volume (VOL) was also under strong genetic control and consequently the branch efficiency indices (BAQ and BEI), for the construction of which both stem size and branch measurements were used, were equally heritable. The crown characteristics for symmetry (CGD), shape (ACH) and width (ARW) had the lowest heritabilities.

Specific combining ability effects were not important in either the factorial *(Tables 6)* or the reciprocal *(Table 7)* tests, neither was there an indication of maternal or reciprocal effects of any practical significance in the latter. The mean square for these three sources of variation was occasionally statistically significant but at no more than the predicted frequency when taken over all traits.

Even at this early stage, variability was high for most of the stem and branch characteristics *(Table 6)*. The sizes of the coefficients of variation for some of the derived traits are not good indications of the practical importance of the amount of variation. For example, for sinuosity (SIN) the index was rarely higher than about 4.0 but it is subtracted from 30 to make higher values desirable; the CV is therefore low because the mean is artificially high although the amount of variation is important.

It is encouraging that some degree of additive genetic control has been found in so many 1.5-year traits. Even where heritability and variation are low it may still prove to be useful in early selection if juvenile-mature correlations are found to exist.

Genetic, genotypic and phenotypic correlations

Before an interpretation can be made of the practical significance of the genetic correlations between traits, it is necessary to decide whether a high or low value in each

Table 10. — Genetic, genotypic and phenotypic correlations between selected 1.5-year traits /1 in the factorial test at Martin.

		HT1	CAQ	VOL	SIN	BD1	BL1	BA1	AIL	ABW	B/H	BAQ
		Genetic correlation (standard error)										
HT1	Genotypic/phenotypic correlation		■ 0.96 (0.06)	■ 0.96 (0.04)	■ -0.67 (0.24)	-0.18 (0.42)	0.35 (0.41)	0.48 (0.32)	0.51 (0.28)	-0.33 0.36	■ -0.60 (0.25)	-0.22 (0.42)
CAQ		0.87 0.87		■ 1.01 (0.02)	■ -0.63 (0.32)	-0.50 (0.44)	-0.11 (0.54)	■ 0.76 (0.29)	0.16 (0.42)	-0.60 (0.37)	-0.40 (0.36)	-0.42 (0.43)
VOL		0.92 0.93	0.98 0.97		■ -0.71 (0.23)	-0.29 (0.42)	0.09 (0.47)	0.57 (0.30)	0.36 (0.34)	-0.58 (0.31)	-0.55 (0.27)	-0.32 (0.40)
SIN		-0.48 -0.39	-0.61 -0.38	-0.63 -0.47		■ -0.55 (0.31)	■ -0.73 (0.30)	0.10 (0.36)	■ -0.89 (0.14)	0.06 (0.43)	■ 0.83 (0.14)	-0.17 (0.40)
BD1		-0.04 0.03	0.19 0.17	0.16 0.15	-0.61 -0.42		■ 0.61 (0.28)	■ -0.98 (0.10)	■ 0.62 (0.27)	-0.05 (0.40)	■ -0.54 (0.29)	■ 1.09 (0.08)
BL1		-0.01 0.12	0.06 0.16	0.06 0.15	-0.41 -0.31	0.75 0.78		-0.42 (0.38)	■ 0.87 (0.19)	0.39 (0.39)	■ -0.56 (0.33)	■ 0.84 (0.22)
BA1		0.55 0.36	0.39 0.24	0.43 0.26	0.04 0.03	-0.54 -0.55	-0.15 -0.21		-0.35 (0.34)	0.10 (0.37)	0.41 (0.31)	■ -1.07 (0.12)
AIL		0.37 0.45	0.58 0.50	-0.13 -0.13	-0.78 -0.60	0.73 0.60	0.42 0.46	-0.19 -0.14		-0.22 (0.36)	■ -0.93 (0.07)	0.44 (0.36)
ABW		-0.31 -0.17	-0.33 -0.16	-0.36 -0.21	-0.31 -0.07	0.34 0.27	0.78 0.65	-0.09 -0.07	-0.11 -0.05		0.56 (0.26)	0.29 (0.29)
B/H		-0.43 -0.44	-0.64 -0.50	-0.64 -0.55	-0.70 -0.61	-0.51 -0.45	-0.04 -0.13	0.16 0.15	-0.90 -0.85	0.51 0.48		-0.30 (0.38)
BAQ		-0.36 -0.23	-0.21 -0.20	-0.22 -0.19	-0.25 -0.23	0.77 0.71	0.50 0.49	-0.74 -0.57	0.40 0.29	0.25 0.16	-0.26 -0.22	

/1 See Table 2 for trait descriptions

■ - genetic correlations of interest due to their size or relative statistical significance

trait is desirable. This is obvious for all traits except those describing branch distribution where few branches in closely spaced whorls have been considered to be desirable, *i.e.* internode length (AIL) and branches per whorl (ABW) should be low and number of branches (B/H) high.

The genetic and genotypic correlations are similar in sign and size as would be expected given the high levels of general combining ability *(Table 10)*. It is the genetic correlations which are of greatest interest to the breeder. Taken with the desirability sign *(Table 2)*, nearly all the correlations of interest (judged by size and/or relative statistical significance) among these juvenile traits were either neutral or favourable to the breeder. The only exceptions were where height (HT1), basal area (CAQ), and therefore volume (VOL), were associated with an increase in leader sinuosity (SIN) and where height was negatively correlated with the number of branches per metre of stem (B/H). Otherwise, efficient trees tended to be those with narrow crowns which consisted of many, evenly distributed, wide-angled, small diametered, short branches. A large branch basal area tended to be negatively correlated with volume and therefore it should be possible to breed for large efficient trees.

In view of these correlations, there will probably be considerable scope for rapid improvement through multiple trait selection although it will be necessary to break the few negative value relationships.

Genotype-environment interaction

The level of genotype-environment interaction can be gauged from the significance of the F ratio of the interaction terms, from the size of the intra-class correlation (repeatability) and from the parent rank correlations between environments *(Tables 6* and *7)*. Interaction can be important both when it is caused by a change in the ranking of families and when it is due to a change in the scale of differences in separate environments. At the same time, F ratios can be statistically significant but of little practical value if the general combining ability at all environments is low.

The overall indication from the analyses is that, insofar as parental ranking is concerned, genotype-environment interactions are unimportant in most of the juvenile traits which were measured except for stem cross-sectional area (CAQ) and consequently volume (VOL) which was derived from CAQ itself, height (HT1) and form factor (VFF). However, the rank correlation over sites for height (HT1) was high (0.82) compared with CAQ (0.40) and it remains to be seen which will be the better predictor of eventual productivity; if it is height then the high interaction of CAQ will be unimportant. The only other instance where there was a statistically significant and substantial interaction was for sinuosity (SIN) in the factorial test *(Table 6)* but this was not a genuine interaction; flocks of perching birds did extensive damage to branches and leading shoots in the Stapleford test which completely confounded the assessment for sinuosity; this was indicated also by the family heritability of 0.02 compared with 0.70 for the same test at Martin.

Changes in the scale of differences between families within environments have contributed to considerable variation in size of the heritability estimates for the same trait in different tests. This expression of genotype-environment interaction is illustrated by the comparison of heritabilities and the associated coefficients of variability for height (HT1) in indivdual tests *(Table 9)*. If the assumption is made that general combining ability control remains constant over environments, the expectation would be for heritability to decrease with greater heterogeneity of the within-test environment, *i.e.* as the genetic components are less and less precisely estimated. In the factorial and reciprocal tests, higher CVs were, in several instances, associated with higher heritabilities which indicates a difference in genetic response between environments. This has implications in the siting of progeny tests to obtain the most precise assessments of genetic worth and for estimating and securing genetic gain. The aim should be to identify critical environments but, at the same time to watch for reversals in ranking; if these occur, it may be necessary to test over a number of critical environments to gain the information required.

The only estimate of genotype-year interaction is in the analysis of height (HT1) in the polycross test over years and environments (*Table 8)*; the interaction variance was zero which was not unexpected given that planting took place in only two years. The high year-environment interaction in this analysis was due entirely to differences in nursery and field cultural practices between years and environments.

Mating design

The groups of parents under test as females in the factorial and polycross tests were drawn from the same population of plus trees. Therefore, although the parental groups in each test were not identical in composition, they were random samples from the same population and, as such, could provide estimates of the same population parameters. A similar argument can be applied to the parents used as males (testers) in both tests. The comparisons are best made with components estimated from the combined analysis of each test over sites because of the large differences in within-test site homogeneity. Heritability estimates provide an overall comparison but it is also necessary to check on the relative contributions of the family and tree (within plot) sources since they contain the genetic contributions. Coefficients of variation were used for the latter so that both these comparisons were free from the effects of scale. The relevant terms, taken or calculated from the height (HT1) data in *Tables 6* and *8*, are:

	Heritability		Coefficient of variation (%)	
	Family	Tree	Family	Tree
Factorial	0.44	0.10	5.04	16.57
Polycross	0.42	0.05	2.60	21.19

The heritability estimates from the two different tests are very similar; the family coefficient of variation in the polycross is almost exactly half that in the factorial which is as expected because it estimates a quarter of the additive variance compared with a half in the factorial; and the tree coefficient of variation is larger in the polycross by an amount which is only slightly more than would be expected to account for the additional quarter of the additive variance.

The conclusion from these comparisons is that the males in the pollen mix used for the polycross acted in a random manner and that the assumption of a half-sib relationship within polycross families is valid for *P. patula*.

The main practical requirement of a mating design is for it to provide an accurate ranking of the progeny tested parents for general combining ability. It was possible to compare the ranking for height (HT1) of the 16 parents which were common to the factorial and the polycross tests (*Figure 1*). In the factorial, eight of the parents were planted in the 1968/69 and eight in the 1969/70 test. As there was no indication of strong genotype-year interaction, the parents were ranked in one continuous series after correcting their means by use of genetic checks in the form of the 17 common additional families of the reciprocal test. The comparison was made through the repeatability (R_D) of the ranking by the relevant factorial tests (three replications of five full-sib families per parent over two sites) by three (in lattices in sites in years), six (over lattices in sites in years), twelve (over lattices over years in sites) and 24 (over lattices, sites and years) replicates of the polycross.

When only three replications of the polycross were used, although average repeatability, of ranking was 0.48, the six individual comparisons varied from zero to 0.71 (*Figure 2*). With increasing replication, the polycross, improved in its ability to repeat the ranking until at 24, the average repeatability was 0.76 with a narrowed range of individual comparisons of 0.71 to 0.80. If the line in *Figure 2* is extrapolated, the repeatability, when there is an equivalent number of 30 replications in the polycross, is 0.86 which suggests that more plots per tested parent are required in the polycross than in the factorial to give an equivalent accuracy in ranking. This would be expected because the higher proportion of genetic variance in the within plot source contributes to the standard error of the difference between parental means.

These comparisons show that, although the polycross is a reliable test method for *P. patula*, there can be no saving in test size over the factorial if equal accuracy is required.

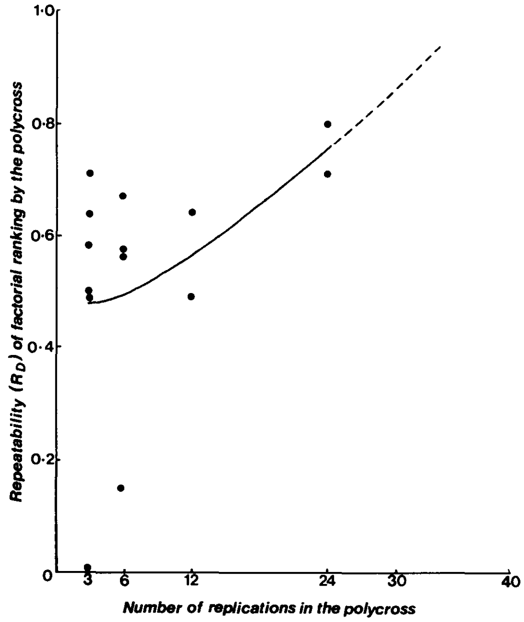

Figure 2. — Effect of replication number on the ability of the polycross test (one half-sib family per parent) to repeat the ranking of 16 parents by the factorial test (6 replications of 5 full-sib families per parent).

Accuracy of component estimation

Standard errors of variance components are usually large and therefore it was to be expected that the accuracy of additive variance, and heritability, estimation would be low. *Figure 3* shows, for the traits measured in the factorial, the relationship between the size of the family and tree heritabilities and their standard errors expressed as coefficients of variation (CV%). Estimates with CV's of less than 50% are considered to be good (NAMKOONG and ROBERDS, 1974). Where $\hat{h}^2_T$ was over 0.10 and $\hat{h}^2_F$ was over 0.40, the 5 ♂ × 9 ♀ factorial gave a satisfactory estimate, particularly for $\hat{h}^2_F$ when it was over 0.75.

The number of parents tested is the element in the factorial design which has greatest influence over the standard error of the heritability estimate. The effect of increasing

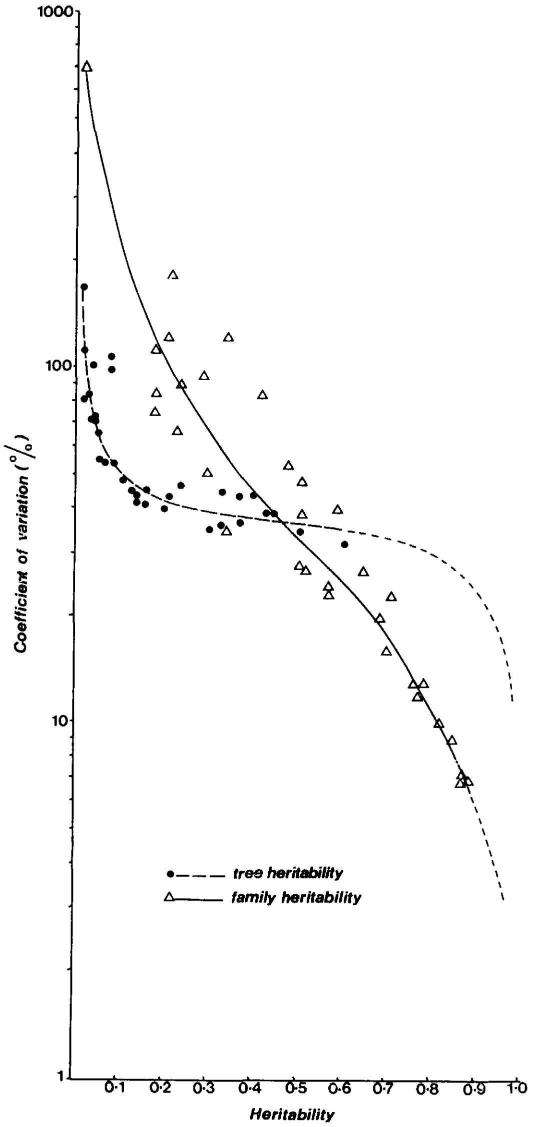

Figure 3. — Relationship of heritability and its coefficient of variation in the factorial test (5 ♂ × 9 ♀) for all traits at Stapleford and Martin.

the number of female parents on the CVs of $\hat{h}^2_T$ and $\hat{h}^2_F$ for two traits is shown in *Figure 4*. For B/H, where heritability was high, there would be little gained but for HT1, where heritability was lower, the CVs could be more than halved by increasing the maternal parents to 100.

These results suggest that, for the broad range of heritabilities in which the breeder is likely to be interested, even the relatively small 5 ♂ × 9♀ factorial provides component estimates with satisfactory accuracy. However, if a trait were associated with particularly high variability or economic value, smaller heritabilities may be of interest and then appreciably greater accuracy in their estimation could be obtained by increasing the number of parents tested. Large tests become difficult to handle but, as there appears to be no genotype-year interaction, tests in successive years could be combined in analyses for ranking and component estimation provided the same tester males and genetic checks were used.

Environmental design

Progeny tests with forest trees involve large numbers of families which must be grown at wide spacing for long periods often on heterogeneous sites. The triple lattice design was incorporated in these tests to increase environmental precision and reduce overall experiment size. The practical benefits of the design concern the precision with which parents are ranked for general or specific combining ability, the tests of significance of effects and the accuracy with which genetic and environmental components of variance and covariance are determined.

Blocking efficiency is a measure of the effectiveness of the lattice design in increasing precision; it indicates the precision of the latter in relation to the randomised complete block analysis. In the factorial, blocking efficiency varied from 93 to 201 per cent *(Table 6);* the latter figure indicates that the lattice design with three replications was equivalent in sensitivity to a randomized complete block with six replications. For the polycross test the range of blocking efficiencies over the eight individual lattices was from 103 to 135 per cent for height (HT1). The lattice structure was more efficient at Martin than at Stapleford and the highest blocking efficiencies were usually, but by no means invariably, associated with those traits under least genetic control.

The practical significance of a high blocking efficiency can best be judged by the effect on the parental ranking. In the factorial, the rank correlation of unadjusted and adjusted means varied with trait from 0.83 to 1.00. In the polycross, for height in individual tests the rank correlation had the same range. With such marginal changes in ranking, the lattice structure was not of much practical significance in increasing precision in either test. This was predictable in the factorial where each parent was represented by five full-sib families in each of three replications but was unexpected in the polycross where there was only one half-sib family per parent per replication.

The F ratios in the analysis of variance of adjusted means were also only marginally increased and the effects on the components of variance and covariance were small in most heritability estimates and genetic correlations and their standard errors (Barnes, 1973).

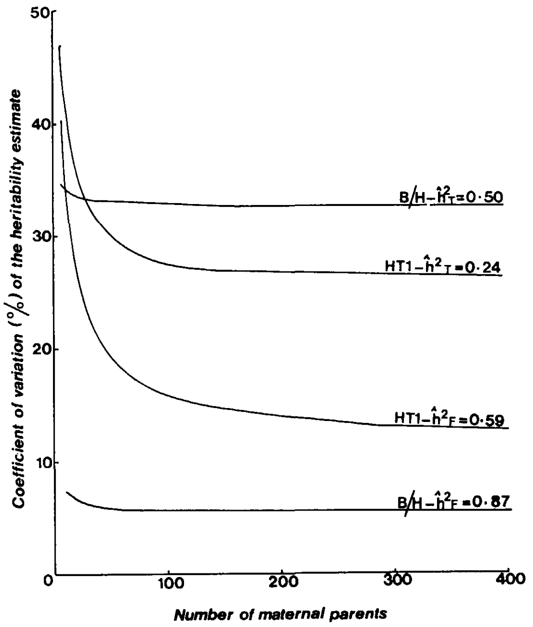

Figure 4. — Effect of increasing the number of maternal parents on the coefficients of variation of the heritability estimates for height (HT1) and number of branches (B/H) in the factorial test at Martin.

In general, the lattice structure failed to provide benefits in these tests and, given the relatively inflexible nature of the design in practice in the field, it has been of doubtful value.

In progeny testing there is always a limit on the number of trees which can be planted to represent each family. In these *P. patula* tests the limit was 30 per family per test and a distribution of 10-tree plots in three replications was selected; we considered smaller plots would be imprudent in the absence of knowledge of the relevant contribution of genetics and environment to the between-plot variance (Evans *et al.*, 1961; Shiue and Pauley, 1961). More recently, it has been suggested that, even with single-tree plots, the environmental component of error variation will rarely be so small in relation to the genetic component that a failure might result in the assumption of normality in the analysis of variance. In addition, genetic segregation in quantitative traits creates a continuous range of variation and, except at extreme allelic frequencies, genotype values will not deviate substantially from normality (Franklin, 1971). Therefore it appears that smaller plots could safely be considered.

In these tests, where the variance of a family mean is

$$\frac{s^2_{\pi}}{r} + \frac{s^2_T}{tr},$$

the within-plot, between-tree environmental contribution to s^2_T was generally large and contributed as much to the variance of a family mean as did s^2_{π}; but there is no prospect of reducing s^2_T while the total number of trees remains the same since its divisor in the variance estimate is the product of trees per plot and replications. However, s^2_{π} could be made smaller by reducing plot size and increasing the number of replications provided that the small number of trees per plot remains a good estimate of s^2_T and s^2_{π} does not start to get large because of a greater contribution from s^2_T. The data for height (HT1) at Martin, a trait with larger than average plot to plot variation, was used to illustrate the relationship of the between- and within-plot CVs with numbers of trees per plot (*Figure 5*). CVs of both sources of variation become relatively stable at three to five trees per plot and this suggests that a considerable improvement in precision could be obtained for the assessment of juvenile traits in *P. patula* by decreasing plot size to this order and making a corresponding increase in the number of replications. The practical implications of such a reduction have been discussed elsewhere (Barnes, 1973).

Conclusions

The conclusions drawn from these assessments must to some extent be provisional because the tests were only 1.5 years old. However, the importance of assessment at this age should not be underestimated; the trees are already nearly 2 m high and approaching the end of their competition-free growing period. Practically and theoretically this is the point at which it would be best to assess juvenile characteristics in *P. patula* if correlations with economically important traits in the mature tree are found to exist and are to be used. In addition, it is better to examine certain aspects of genetic and environmental design before competition sets in.

The most important general conclusions from the analysis are: —

1) Many economically important external morphological characteristics are under some degree of genetic control in the 1.5-year-old tree.

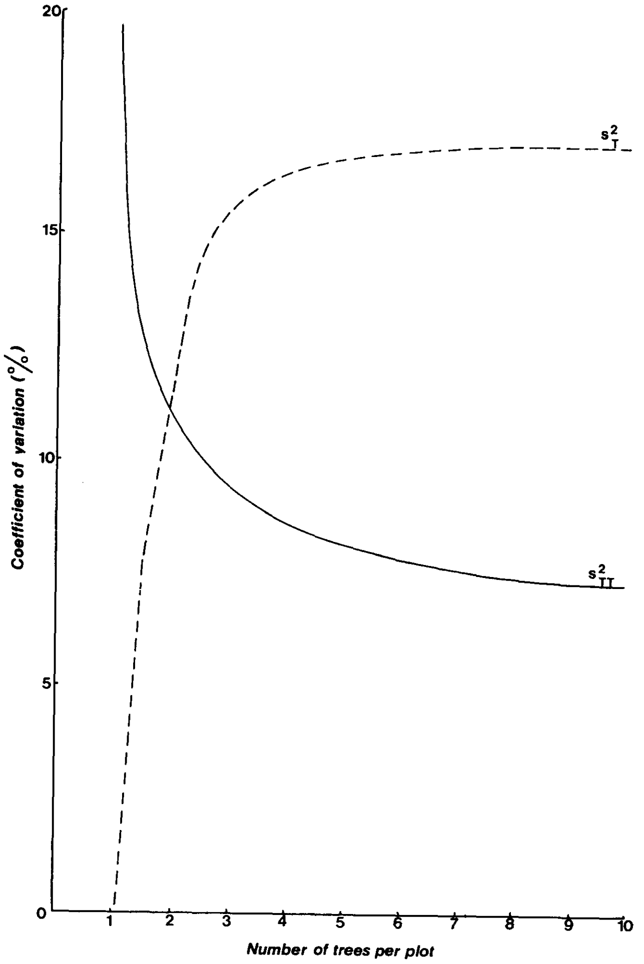

Figure 5. — Relationship of within-plot (s^2_T) and between-plot (s^2_{π}) coefficients of variation and plot size for height (HT1) in the factorial test at Martin.

2) There is little specific combining ability control or maternal or reciprocal effect on the traits of interest.
3) There is still a large amount of variability in the breeding population even in traits subjected to stringent selection in allocating plus tree status.
4) Given 1) and 3) above, the prospects are promising for gain in subsequent generations and for useful juvenile-mature correlations in at least some important traits.
5) Genetic correlations are largely favourable in sign and magnitude and this should make multiple trait selection effective.
6) Genotype-environment interactions are apparently not-important at this stage in their effect on the relative ranking of parents but their influence on heritability estimates and precision of parental ranking make site selection for progeny testing of critical importance.
7) The assumption of half-sib relationship in polycross families is valid and the polycross is a reliable test method for *P. patula*.
8) A 45-family factorial test allows acceptably accurate estimation of environmental and genetic components of variation when individual tree heritability is over 0.1; an increase to 100—200 families would improve precision for traits with heritabilities of less than 0.1.
9) The triple lattice design is not necessarily of practical benefit to the breeder even when blocking efficiency is as high as 200 per cent; however, given (10) below, with

smaller plots and the same number of replications, the triple lattice structure could permit smaller experiments with no loss of precision.

10) Optimum plot size for precision of ranking at 1.5 years is probably from three to five trees; these small plots allow more replication and greater precision.

Acknowledgements

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Short Note: Winter Injury in a Scotch Pine (Pinus sylvestris L.) Clonal Seed Orchard

By D. F. Van Haverbeke[1])

(Received May 1979)

Summary

Scotch pine clonal seed orchard trees, 3 to 6 years old, sustained varying amounts of crown damage following prolonged drought stress and severe winter conditions in eastern Nebraska, U.S.A. Damage was greatest in the northwestern portion of the orchard, direction of prevailing winter winds. Primary branch tips and secondary branchlets of trees were killed by desiccation in the north and northwest portions of the crowns. Significant differences in injury were detected among clones and provenances, with greater variation between provenances than among clones within provenances. Provenances from most northerly and southerly regions incurred most damage. Age of trees was not significant.

Key words: Seed orchard, winter injury, *Pinus sylvestris*

Zusammenfassung

Drei bis sechs Jahre alte *Pinus sylvestris* in einer Klon-Samenplantage im östlichen Teil Nebraskas, U.S.A. erlitten nach längerer Einwirkung von Trockenheit und strengen winterlichen Bedingungen Schädigungen im Kronenbereich. Am schlimmsten waren die Schäden im nordwestlichen Teil der Samenplantage in der vorherrschenden Richtung der Winterwinde. Durch Austrocknung waren die Spitzen von Haupt- und Nebenästen der Bäume abgestorben. Signifikante Unterschiede in den Schäden wurden zwischen Klonen und Herkünften entdeckt. Die Unterschiede zwischen den Herkünften waren größer, als die zwischen Klonen innerhalb der Herkünfte. Die Herkünfte der nördlichsten und südlichsten Regionen wiesen die meisten Schäden auf. Das Alter der Bäume war nicht entscheidend.

Introduction

Young Scotch pine (*Pinus sylvestris* L.) trees in an eastern Nebraska, U.S.A. clonal seed orchard were observed with varying amounts of crown damage in the early spring of 1977. Damage was confined to the north and northwest portions of the crowns and was restricted to the killing of primary branch tips and secondary branchlets. The grafted trees ranged in height from 1.2 to 3.0 m. Evaluations were made early spring 1977 to determine the cause of the damage, and whether or not it was related to location within the orchard, age, clone, or provenance.

Study Site and Methods

The orchard, located about 50 km northeast of Lincoln, Nebraska, was established during 1971—74 from trees selected within a range-wide Scotch pine provenance test planted in Nebraska in 1962 (Read 1971, Van Haverbeke 1974) (*Table 1*). The orchard is on a Sharpsburg silty clay loam with a zero to 2 percent slope to the southeast. It is ex-

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