ticular one, we need only complete the 9th row of *Table 2* and we can see immediately parent H has a general combining ability of 134/9 = 14.89. If the problem were solved by the least square method and by hand calculation, it would be much more laborious.

Another advantage of using this method is the ease of comparison. Just by observing the 9th row of *Table* 2, one can see immediately that male parent H is inferior only to male parent I but is superior to all others. By conventional procedure, comparison cannot be made until all parent effects are calculated.

This procedure gives an approximate solution for irregular mating schemes. The better the regularity, the better is the approximation. If the procedure is applied to balanced data, results from this procedure are identical to the least square estimates. Usually the discrepancies are too small to be significant.

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Pinus patula Schiede and Deppe progeny tests in Rhodesia Genetic control of nursery traits[1]

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Summary

A number of characteristics were assessed during the twelve-month nursery period of *Pinus patula* SCHIEDE and DEPPE seedlings raised for factorial (NCM II, 5 X 9) and reciprocal (diallel without selfs, 7 X 7) progeny tests. Both cotyledon number and length were under some general combining ability control with family heritabilities of 0.64 and 0.25 respectively and there was a high negative genetic correlation (—0.91) between them. Numbers of whorls and branches had family heritabilities of 0.55 and 0.45. Dominance effects were predominant in the genetic control of seedling height in the first six months of nursery life but general combining ability effects rose steadily and by 12 months dominance had disappeared and heritabilities were between 0.63 and 0.78; in addition, there was no correlation between seedling height at one and twelve months; thic suggests that different genes control height at the beginning and end of the nursery phase. The seed weight-seedling height relationship was strongest at three months but had almost disappeared by twelve months. There is sufficient variation and genetic control of these nursery traits to indicate that investigation of correlations with mature field characteristics could prove useful.

Key words: Pinus patula SCHIEDE and DEPPE, progeny tests, diailel, factoriai mating design, general combining ability, specific combining ability, maternal effects, reciprocal effects.

Zusammenfassung

In einer Baumschule in Rhodesien wurden bei einjährigen Sämlingen von *Pinus patula* SCHIEDE et DEPPE aus einem Kreuzungsdiallel (ohne Selbstungen) die Anzahl und Länge der Kotyledonen, die Anzahl der Quirle und Äste sowie die Höhe ermittelt. Sowohl die Anzahl als auch die Länge der Kotyledonen zeigten eine gute allgemeine Kombinationseignung mit Heritabilitäten (Familie) von 0,64 bzw. 0,25 und eine hohe negative Korrelation von — 0,91 zwischen beiden. Die Anzahl der Quirle und Äste wies Heritabilitäten von 0,55 bzw. 0,45 auf. In den ersten 6 Monaten herrschten bei der Höhe Dominanzeffekte vor, während sich danach die allgemeine Kombinationseignung bis zu Heritabilitäten zwischen 0,63 und 0,78 durchsetzte. Eine Korrelation zwischen der Sämlingshöhe im 1. und 12. Monat konnte nicht festgestellt werden. Daraus wird geschlossen, daß das Sämlingswachstum im ersten Jahr von verschiedenen Genen gesteuert wird. Die Korrelation Samengewicht — Sämlingshöhe war im 3. Monat am meisten ausgeprägt.

Introduction

A breeding programme for the genetic improvement of *Pinus patula* SCHIEDE and DEPPE in Rhodesia was started in 1958. Initially it was proposed that a polycross progeny test design would be used but in 1964 the plan was reviewed because it was felt that, particularly in the early stages of this programme, the progeny testing method used should not only identify the best general combiners, but should also yield information on population genetics. A revised plan was drawn up in which the polycross test was supplemented with factorial (NCM II) and reciprocal (diallel without selfs) mating designs. The review of progeny test methods, together with the adopted plan and the bases for analyses of variance, have been described by BURLEY, BURROWS, ARMITAGE and BARNES (1966). The controlled crosses for this test plan were completed in 1967 and the results of the nursery experiments are described here.

Materials

Nursery experiments were confined to the factorial and the reciprocal tests. In November 1967 seed was sown for the first part of the factorial test which consisted of 45 full-sib families with five tester clones used as pollen, on nine other clones as seed parents (see *Figure* 1). Seeds were soaked in water for 24 hours and those from the sinking fraction were sown singly in 8 cm (diameter) by 15.2 cm (depth) black polythene tubes which were filled with a uniform nursery soil mix. The experiment was laid out in a randomized complete block design with six replications of 30-seedling plots (10 X 3 tubes); the middle row of eight seedlings was the measured plot. Ungerminated or killed seedlings in the measured plot were replaced from the

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

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Pollen parent code No.

Seed parent code No.	5	14	20	25	31	44	51
5		X	X	X	X	X	X
14	X		X	X	X	X	X
20	X	X		X	X	X	X
25	X	X	X		X	X	X
31	X		X	X		X	X
44	X	X	X	X	X		X
51	XO	XO	XO	XO	XO	X	
1	O	O	O	O	O		
2	O	O	O	O	O		
7	O	O	O	O	O		
15	O	O	O	O	O		
26	O	O	O	O	O		
27	O	O	O	O	O		
32	O	O	O	O	O		
48	O	O	O	O	O		

Figure 1. — Mating designs for two *Pinus patula* progeny tests.
O — Factorial (NCM II, 5 ♂ testers × 9 ♀) sown 1967.
X — Reciprocal (diallel without selfs, 7 × 7) sown 1969.

surround rows or, where this was not posible, with a seedling raised from excess seed sown in nursery beds.

In October 1969 it was possible to sow a complete reciprocal test (a diallel with reciprocals but without selfs), except for one of the 42 crosses, between seven tester clones (see *Figure 1*). Experimental procedure was exactly as that described for the factorial above but the layout in the nursery was a randomized complete block design with three replications of 60-tree plots (10 × 6 tubes) which gave a 32-tree (8 × 4 tube) inner measured plot.

Seedling survival and growth in the 1967 factorial test was uneven due to damping-off problems in the early stages and analysis was ultimately confined to five trees per plot, which were selected by accepting the first five original seedlings in the line as representing the plot.

Stock for both progeny tests was raised in Rupere nursery on the John Meikle Forest Research Station, latitude 18° 14' and altitude 1.000 m above sea level.

Assessments

Cotyledon number and length, seedling height at various stages, and branch and whorl number were the characteristics measured. The trait codes and descriptions are given in *Table 1*.

Average full and empty seed weights were known for each parent and the difference between these was taken as the gametophyte tissue plus embryo weight, *i.e.* seed weight excluding the coat.

Statistical method and results

The generalized forms of the analyses of variance used for the factorial and reciprocal mating and environmental designs are shown in *Tables 2* and *3*. In the factorial test, s^2_P and s^2_M each estimate a quarter of the additive, and s^2_{MP} a quarter of the dominance, variance. Heritability on an individual tree basis was estimated as: —

$$\hat{h}^2_T = \frac{2(s^2_P + s^2_M)}{s^2_T + s^2_\pi + s^2_{MP} + s^2_M + s^2_P}$$

and family heritability as: —

$$\hat{h}^2_F = \frac{s^2_P + s^2_M}{\dfrac{s^2_T + ts^2_\pi + s^2_{MP} + s^2_P + s^2_M}{tr}}$$

where the notation is as defined in *Table 2*.

In the reciprocal test, s^2_g and s^2_s estimate a quarter of the additive and dominance variance respectively. Family heritability was estimated as: —

$$\hat{h}^2_F = \frac{s^2_g}{\dfrac{s^2_\pi}{r} + s^2_{r'} + s^2_m + s^2_s + s^2_g}$$

where the notation is as defined in *Table 3*.

The proportional contribution of variance components, significance of F ratios, overall means and ranges, standard errors and heritabilities for all traits are given in *Tables 4* and *5*.

The best estimates of genetic correlations (Falconer, 1960) in this material are obtainable from the seed parent

Table 1. — Descriptions and codes for nursery traits assessed in *Pinus patula* progeny tests

Trait code	Description	Age at assessment (months)	Unit of assessment
CON	number of cotyledons	1½	Count
COL	average length of cotyledons	3	mm
NWH	number of whorls of branches	12	Count
NBR	total number of branches	12	Count
NH1 to NH12	total seedling height total seedling height	1 to 12	cm cm

Table 2. — Generalized form of the analysis of variance of the factorial test

Source of variation	Degrees of freedom	Expectation of mean square
Pollen (paternal) parents (P)	(p-1)	$\sigma^2_T + t.\sigma^2_\pi + tr.\sigma^2_{MP} + tmr.\sigma^2_P$
Seed (maternal) parents (M)	(m-1)	$\sigma^2_T + t.\sigma^2_\pi + tr.\sigma^2_{MP} + tpr.\sigma^2_M$
M X P	(p-1)(m-1)	$\sigma^2_T + t.\sigma^2_\pi + tr.\sigma^2_{MP}$
Replications (R)	(r-1)	$\sigma^2_T + t.\sigma^2_\pi + tmp.\sigma^2_R$
Residual (π)	(r-1)(mp-1)	$\sigma^2_T + t.\sigma^2_\pi$
Trees in plots (T)	mpr(t-1)	σ^2_T
TOTAL	mprt-1	

Table 3. — Generalized form of the analysis of variance of the reciprocal (diallel without selfs) test[1]

Source of variation	Degrees of freedom	Expectation of mean square
General (g)	(p-1)	$\sigma^2_\pi + 2r.\sigma^2_s + 2r(p-2).\sigma^2_g$
Specific (s)	p(p-3)/2	$\sigma^2_\pi + 2r.\sigma^2_s$
Maternal (m)	(p-1)	$\sigma^2_\pi + 2r.\sigma^2_{r'} + 2pr.\sigma^2_m$
Reciprocal (r')	(p-1)(p-2)/2	$\sigma^2_\pi + 2r.\sigma^2_{r'}$
Replications (R)	(r-1)	$\sigma^2_\pi + (p^2-p).\sigma^2_R$
Residual (π)	$(r-1)(p^2-p-1)$	σ^2_π
TOTAL	$r(p^2-p)-1$	

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[1]) Model suggested by Dr. P. M. Burrows, University of South Carolina, Clemson, S.C., U.S.A.

Table 4. — Analysis of variance of three nursery traits in the *Pinus patula* factorial progeny test

Source of variation		Degrees of freedom	Trait code/1 CON	COL	NH12
Percentage contribution of variance component/2 and significance of F ratio/3					
Pollen parents		4	1	0	16 ***
Seed parents		8	11 ***	5 *	12 ***
Interaction		32	4 ***	9 **	4 **
Residual		220	0	6	13
Trees in plots		1080	84	80	55
Total variance			0.4924	11.1501	26.5757
Means, ranges, standard errors and heritabilities					
General mean			5.14	22.19	15.74
Range of five pollen parent means	- highest		5.23	22.40	18.28
	- lowest		5.00	21.81	13.72
	- s.e.		0.0386	0.2144	0.3419
Range of nine seed parent means	- highest		5.66	23.48	19.38
	- lowest		4.87	22.78	13.28
	- s.e.		0.0518	0.2877	0.4587
Heritability	- family		0.64	0.25	0.78
	- tree		0.24	0.09	0.56

1) See Table 1 for code description.
2) Negative components entered as zero.
3) * — p <0.05, ** — p <0.01, *** — p <0.001.

component in the factorial test. The standard error of the genetic correlation coefficient was calculated using the expression given by MODE and ROBINSON 1959. The phenotypic correlation was based on the 45 family means. Genetic and phenotypic correlations were estimated for all combinations of the three traits measured, cotyledon number, cotyledon length and height at 12 months and they are given in *Table 6*.

Discussion and conclusions

Cotyledon number is the earliest expressed and most easily measured nursery trait. It has been found to be under genetic control in some conifers and used for verification of hybrids (*e.g.* SILEN *et al.*, 1965; SORENSEN, 1966) and identification of seed source (*e.g.* FRANKLIN and GREATHOUSE, 1968). Both the factorial and reciprocal tests show cotyledon number to have been under some general combining ability (*gca*) control in *P. patula* ($\hat{h}^2_T = 0.24$ and $\hat{h}^2_F = 0.64$). This was highest for the seed parents in the factorial where the variance was so much greater than that for the pollen parents that some maternal influence was suspected. However, the maternal effect was not significant in the reciprocal test and the greater variation was therefore probably due to unequal sampling of the population under test. Specific combining ability (*sca*) was also significant and, in both tests, contributed about two thirds as much as the additive effects. Over 50 per cent of the variation in cotyledon number remained unaccounted for by genetic effects and was probably attributable to the intra-ovular environment at the time of development of the embryo.

Table 6. — Genetic and phenotypic correlations between three traits in the factorial test

TRAIT		CON	COL	NH12
		Genetic correlation (and s.e.)		
CON	Phenotypic correlation		-0.91 (0.23)	-0.39 (0.24)
COL		-0.10		-0.87 (0.16)
NH12		0.00	0.35*	

* Significant at the 5% level.

Cotyledon length, with family and individual tree heritabilities of 0.25 and 0.09 respectively, was under less genetic control than cotyledon number although both additive (seed parent) and dominance effects were significant. The high negative genetic correlation (—0.91) suggests that fewer cotyledons were compensated for by greater length. The relatively large and precisely estimated genetic correlation (0.87) between cotyledon length and seedling height at 12 months was surprising, especially considering the relatively low heritability of cotyledon length. This suggests that even traits under relatively low *gca* control could be useful in establishing juvenile-mature correlations.

Both branch traits, number of whorls and total number of branches, were under appreciable general combining ability control with family heritabilities of 0.55 and 0.45 respectively.

Table 5. — Analysis of variance of 12 nursery traits in the *Pinus patula* reciprocal progeny test

Source of variation		Degrees of freedom	Trait code/1 CON	NWH	NBR	NH1	NH2	NH3	NH4	NH5	NH6	NH7	NH10	NH12
Percentage contribution of variance component/2 and significance of F ratio/3														
General (g)		6	17 **	37 ***	26 ***	1	0	0	0	0	5	19 **	42 ***	41 ***
Specific (s)		14	12 *	12 **	10 *	18 **	21 **	13 *	14 *	18 **	17 **	8 *	0	1
Maternal (m)		6	2	0	0	4	2	0	2	4	4	3	3 *	2
Reciprocal (r)		14	9 *	1	2	10 *	10 *	8	11 *	14 *	17 **	14 **	1	3
Residual (π)		80	60	50	62	67	67	79	73	64	57	56	54	53
Total variance			0.0796	0.0566	0.4778	0.0491	0.1435	0.3820	0.3453	0.4256	0.4349	0.3927	7.9215	11.7938
Means, ranges, standard errors and heritability														
Overall mean			5.08	0.49	1.46	2.60	3.94	6.16	7.73	8.93	9.61	9.85	15.70	19.43
Range of seven parent means	highest		5.37	0.66	1.82	2.69	4.13	6.49	8.04	9.30	10.05	10.30	17.75	21.75
	lowest		4.87	0.29	0.77	2.51	3.81	5.97	7.52	8.67	9.32	9.34	13.71	17.27
Standard error			0.0517	0.0398	0.1277	0.0429	0.0730	0.1296	0.1188	0.1227	0.1171	0.1099	0.4872	0.5896
Range of 41 family means	highest		5.73	0.97	2.65	3.03	4.43	6.95	8.82	10.44	11.21	11.06	21.55	26.20
	lowest		4.70	0.00	0.00	2.23	3.40	5.46	7.00	8.15	8.75	8.67/4	10.53	12.73
Standard error			0.1268	0.0975	0.3129	0.1052	0.1788	0.3173	0.2910	0.3007	0.2869	0.2693	1.1933	1.4442
Heritability			0.29	0.55	0.45	0.03	0.00	0.00	0.00	0.01	0.09	0.30	0.66	0.63

1) See Table 1 for code description.
2) Negative components entered as zero.
3) * — p <0.05, ** — p <0.01, *** — p <0.001.
4) Reason for decrease in range limits not known but may be change in soil level in tube.

By 12 months seedling height showed considerable variation, highly significant parental differences and large family (0.78) and individual tree (0.56) heritabilities. Specific, maternal and reciprocal effects were not significant in the reciprocal test at this stage but the significant interaction effect in the factorial indicated the presence of dominance.

The whole series of height measurements (NH1 to NH12) in the reciprocal test indicated a progressive change in the form of genetic control. *Figure 2* shows that *sca* effects accounted for most of the total genetic variance in the early stage of nursery height growth but they steadily declined in importance until, at 12 months old, they were minimal. The *gca* curve was the complete reverse, *i.e.* additive effects were almost non-existent in the early stages but accounted for nearly all the genetic variance after ten months. The F ratio for maternal effects did not reach significance at any stage except at seven months when it was significant at the five per cent level; the effects due to this source were constant, but very small, throughout the nursery period. Reciprocal effects, on the other hand, were significant at all but one measurement up to seven months after which they dropped to near zero.

The change in relative contributions of *gca* and *sca* variance during the course of nursery growth was not unexpected. In the early stages, when a seedling's performance is dependent upon a few primary biochemical, physiological and morphological properties, a small number of genes controls height growth and, if present, a dominance effect at a single locus could be clearly expressed. The reversal in importance of *gca* and *sca* effects occurred immediately after the first dormant period *(Figure 3)* six or seven months from sowing. From this point on, a seedling's performance becomes dependent upon an increasing number of attributes, for example, secondary needle size and number, branching characteristics, root system development and efficiency of mycorrhizal association (Marx and Bryan, 1971); very many more genes become indirectly involved in height growth and even if dominance is present at some

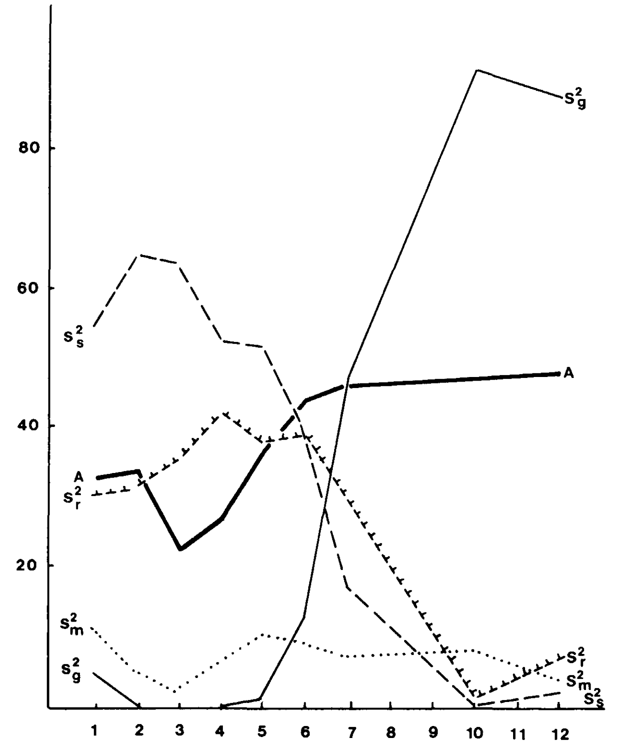

Figure 2. — Relative contributions of genetic components to total family variance for nursery height from one to twelve months in the reciprocal test.

S^2_g — General combining ability.

S^2_s — Specific combining ability.

S^2_m — Maternal effects.

S^2_r — Reciprocal effects.

A — Contribution of total family genetic variance. ($S^2_g + S^2_s + S^2_m + S^2_r$) to total plot variance.

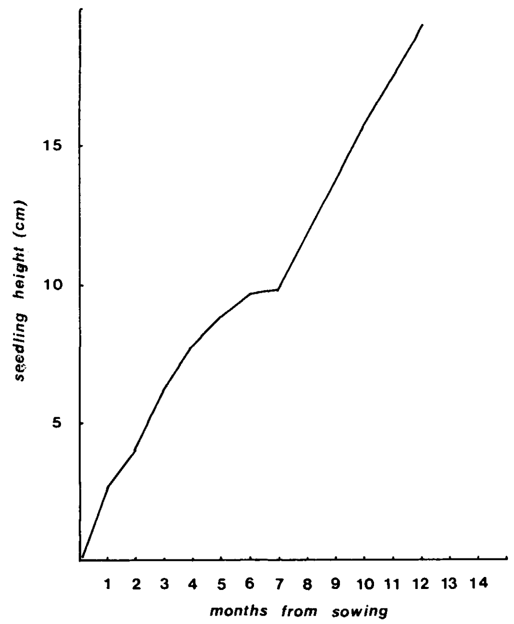

Figure 3. — Nursery height/age relationship in the reciprocal test.

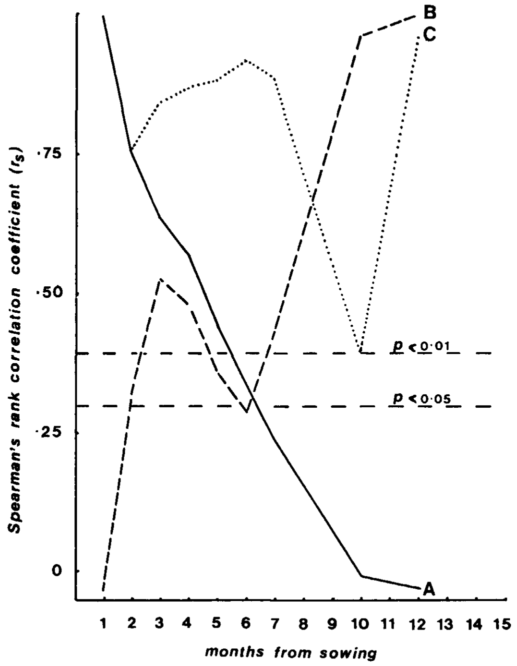

Figure 4. — Nursery height rank correlations for the 41 families in the reciprocal test.

A — Correlation of rank at one month with rank at each succeeding month.

B — Correlation of rank at 12 months with rank at each preceding month.

C — Correlation of rank at each month with rank at the preceding month.

of the loci concerned, its effect is likely to be obscured. It is interesting also that there was no correlation in the family ranking for nursery height at one and twelve months *(Figure 4)*. The major change in ranking occurred at the point where *sca* and *gca* effects changed over in relative importance and this suggests that different genes were taking over control.

The reasons for the relatively high contribution of reciprocal rather than maternal effects to the variation of height in the first six months of nursery growth are not clear. With other species in the genus, correlations have been found between seed weight and at least early nursery height performance (*e.g.* Snyder, 1969; Perry, 1976) and these may persist in some species for up to eight or ten years (Anon., 1974). Hundred-seed weight among the seven parents in this reciprocal test ranged from 0.893 to 1.510 g and it would have been expected that this amount of variation would have resulted in significant maternal effects. Instead, reciprocal effects were significant for most of the first six months of nursery height growth. This suggests an interaction of reciprocal effects, that is, neither maternal nor paternal cytoplasmic effects were acting in an additive manner. Recent electron microscope studies in the pines have shown that the embryonal cytoplasm is a "neocytoplasm" composed of contributions from the nucleoplasm of the female gamete, the perinuclear zone of the egg nucleus and part of the cytoplasm associated with the male gamete (Singh and Johri, 1972). The implications of this are that the reciprocal effect could have been due to male-female cytoplasmic interaction as well as to an interaction between the male genetic and the female cytoplasmic (embryonic or female gametophyte) contributions.

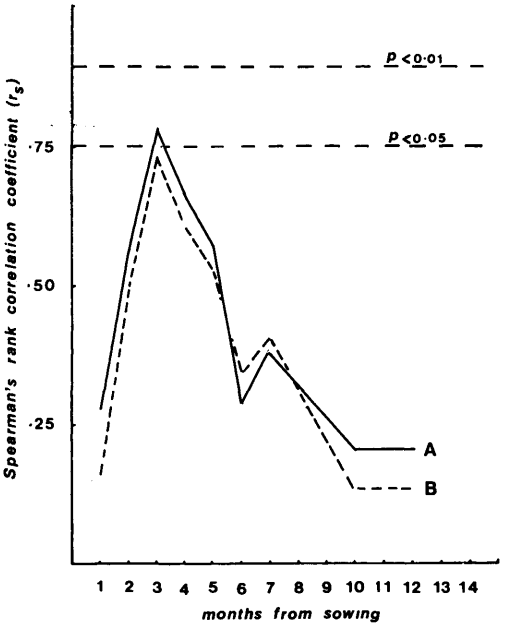

Figure 5. — Correlation of seed weight and seedling height in the reciprocal test based on average seed weight and mean height for each of the seven parents used as female.

A — Total seed weight.

B — Seed weight without seed coat.

The effect of seed weight was examined further by rank correlation with each height measurement during the nursery phase. Although the overall curve *(Figure 5)* indicated the expected type of relationship, the correlation coefficient barely attained significance at the five per cent level when it was at its highest. Female gametophyte (plus embryo) weight for one hundred seeds for the seven parents varied from 0.535 to 0.772 g, markedly less than the 0.893 to 1.510 g range for total seed weight, but its relationship with seedling height was almost exactly the same *(Figure 5)*.

There are few problems with the nursery performance of *P. patula* and none of the traits measured in these progeny tests has any presently known economic significance. Interest centres rather on their potential value in providing aids to early selection if correlations with economically important mature characteristics are found. There is more than sufficient genetic content in the control of all these nursery traits to indicate careful investigation of such relationships.

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