

controlling "thick root" productivity could be found in the 2 tested materials.

The need for further research on the subject and the limitations of the present test material was stressed. Still the investigation confirmed the hypotheses, that traditional breeding selections for above ground production will cause reductions in the ratios between root- and stem-biomass. By selections in young material only the "thin root" productivity is reduced, by selection in old stands mainly "thick root" productivity should be diminished. By selections in young material at present, it is suggested also to investigate the root biomass and select for total biomass production. On longer term, early test methods for the 2 physiologic different behaving "root/stem-ratios" should be developed.

7. Literature

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Genetic Control of Eighth Year Traits in *Pinus patula* Schiede and Deppe

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(Received 12th September 1991)

Summary

Polycross, factorial and diallel mating designs were used in the genetic improvement programme for *Pinus patula* SCHIEDE and DEPPE in Zimbabwe. Their function was to

elucidate genetic structure and control in economically important traits, to investigate genotype-environment interaction, to identify the best general combiners and to provide information on the efficiency of mating and experimental designs. Productivity, stem form and wood density traits were measured in the eighth year from planting in the field. Analysis of the data indicated that all traits were principally under multigenic control with dominance, maternal and reciprocal effects of no practical significance. Heritabilities were highest for wood density (up to 0.82

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on a family basis) but also high for stem volume (up to 0.63) and stem straightness (up to 0.69). Genotype-locality interaction was of practical significance for stem volume but was absent for wood density; it was intermediate for stem straightness. There was no genotype-year interaction for any trait. Selective thinning did not bias the estimates of genetic parameters when compared with systematic thinnings for any trait. Sub-blocking made little difference to the ranking of families but for some traits in some localities experiments could have been reduced in size by over 30% and achieved the same precision of ranking. The assumptions of half-sib relationship in polycross families was shown to be valid in that it ranked parents in almost the same order as the factorial test. There were no adverse genetic correlations of any consequence. Wood density appeared to vary independently of stem volume. Strong and usable juvenile-mature correlations were apparent even between nursery and eighth-year traits. Large seedlings with few long cotyledons in the nursery grew into large trees with high wood density and families with few branches and superior height in the second year developed into trees with high wood density and large volume by the eighth year.

Key words: Progeny tests, diallel, factorial mating design, polycross test, genetic correlations, juvenile-mature correlations, triple lattice design, genotype-environment interaction, general combining ability, specific combining ability.

Introduction

The genetic improvement programme for *Pinus patula* SCHIEDE and DEPPE in Zimbabwe (then Rhodesia) started in 1958. It included the use of polycross, factorial and reciprocal mating designs for progeny testing and estimating genetic parameters in the first generation of plus trees selected from unimproved plantations. The aim was to identify parents with high general combining ability (*gca*) and to provide genetic information on the local population (BURLEY *et al.*, 1966). Controlled crosses for this plan were completed in 1967 and progeny tests were planted between 1967 and 1972 (BARNES, 1973). Nursery assessments were made and the data analysed and published (BARNES and SCHWEPENHAUSER, 1978) as were the data from extensive assessments made at 1.5 years (BARNES and SCHWEPENHAUSER, 1979) and 4.5 years (BARNES *et al.*, in press) after planting in the field. In this paper we report on results of analyses of productivity, stem form and wood density traits measured at 7.5 years including estimates of juvenile-mature correlations and the comparative effects of systematic and selective thinning on the estimation of genetic parameters.

Materials and Methods

The plus tree population, mating design, progeny test localities and environmental design of the experiments have been fully described previously (see BURLEY *et al.*, 1966; BARNES, 1973; and BARNES and SCHWEPENHAUSER, 1979). For easy reference the mating design is repeated here in figure 1. Basic environmental design was randomized complete block with superimposed lattice at the principal localities with three replications of 10-tree line plots at 2.44 m square spacing. The polycross (controlled crosses between the seed parent and a 20-pollen mix) was repeated over two years at two localities and in each case was a double triple lattice. The factorial (controlled crosses between nine seed parents and five pollen testers) was planted at the same two localities in one year as single triple lattices. The diallel (controlled crosses among five

| | | Pollen parent code number | | | | | | | | |
|-------------------------|----|---------------------------|---|----|----|----|----|----|----|---|
| | | MP | 5 | 25 | 14 | 20 | 31 | 44 | 51 | |
| Seed parent code number | 14 | P | | | | | R | R | R | R |
| | 20 | P | | | | | R | | R | R |
| | 31 | P | | | | | R | R | | R |
| | 44 | P | | | | | R | R | R | |
| | 51 | P | F | F | | | RF | RF | RF | R |
| | 1 | P | F | F | F | F | F | | | |
| | 2 | P | F | F | F | F | F | | | |
| | 7 | P | F | F | F | F | F | | | |
| | 15 | P | F | F | F | F | F | | | |
| | 26 | P | F | F | F | F | F | | | |
| | 27 | P | F | F | F | F | F | | | |
| | 32 | P | F | F | F | F | F | | | |
| | 48 | P | F | F | F | F | F | | | |
| | 6 | P | | | | | | | | |
| | 12 | P | | | | | | | | |
| | 16 | P | | | | | | | | |
| | 30 | P | | | | | | | | |
| | 34 | P | | | | | | | | |
| | 52 | P | | | | | | | | |
| | 63 | P | | | | | | | | |
| | 5 | P | | | | | | | | |
| | 17 | P | | | | | | | | |
| | 19 | P | | | | | | | | |
| | 21 | P | | | | | | | | |
| | 25 | P | | | | | | | | |

P — polycross test planted 1967/1968 and 1968/1969
 F — factorial test planted 1968/1969
 R — reciprocal test planted 1968/1969

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

parents with reciprocals but without selfs) was planted as an integral part of the factorial experiment at the two main sites and extended to two additional localities on its own.

The tests received their first thinning at this assessment and therefore the opportunity was taken to take measurements for a more detailed stem analysis and wood samples for density determination from the thinned trees as well as assessing the usual characteristics of height, diameter and stem straightness. The measured and derived traits are described in table 1.

The generalized form of the fully random models of the analyses of variance and covariance, the statistical procedures and the genetic interpretation of the results have also been given previously (BARNES, 1973; BARNES and SCHWEPENHAUSER, 1978 and 1979). The genetic correlations were estimated from the maternal parents component in the analysis of covariance.

All traits were assessed on every tree in each plot except for volume (OBV8), form factors (FFO8 and FFU8) and wood density (BDB8) which were assessed only on the five trees per plot that were felled in a thinning immediately after the general assessment. Thinning was on a systematic basis in that every other tree in the plot was re-

Table 1. — Descriptions of measured and derived traits.

| TRAIT | DESCRIPTION | UNIT |
|----------------------------|---|-------------------|
| Nursery traits | | |
| CON | Number of cotyledons at 6 weeks | count |
| COL | Average length of cotyledons at 3 months | mm |
| NH12 | Total seedling height at 12 months | cm |
| 1.5-year-old-traits | | |
| HT12 | Height to leader bud minus post-planting | m |
| CAQ2 | Circular area of stem at a quarter of total height | cm ² |
| VOL2 | Total stem volume - (total height x CAQ x VFF) | dm ³ |
| SIN2 | 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 20 so that the less the sinuosity of the stem the higher the numerical value) | index |
| BD12 | Total branch x-sectional area in that whorl contributing most to crown | cm ² |
| BL12 | Total branch length in that whorl contributing most to crown | m |
| BA12 | Average branch angle (90° = 10.0) in that whorl contributing most to crown | 9° |
| AIL2 | Average internode length - (excludes that section between the ground and the first whorl) | cm |
| ABW2 | Average number of branches per whorl - (based on total number of branches on the tree) | number |
| B/H2 | Number of branches per metre of height - (total number of branches/total height) | number |
| 4.5-year-old traits | | |
| HGT5 | Total height | m |
| CAQ5 | Circular area of stem at breast height (1.3 m) | cm ² |
| VOL5 | Total stem volume over bark - (total height x CAQ x 0.45) | dm ³ |
| STR5 | 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 |
| BBA5 | Total branch basal area of 2 whorls nearest breast height | cm ² |
| AIL5 | Average internode length (for lower 10 whorls) | m |
| B/H5 | Branches per metre run of stem (for lower 10 whorls) | number |
| ABW5 | Average number of branches per whorl (for lower 10 whorls) | number |
| 7.5-year-old traits | | |
| HGT8 | Total height | m |
| CAQ8 | Circular area of stem at breast height (1.3 m) | cm ² |
| STR8 | Stem straightness rating - (category 1 = best to 7 = worst; subtracted from 8 so that the straighter the stem the higher the numerical value) (Barrett & Mullin, 1968) | rating |
| OBV8 | Total over bark volume (based on HGT8 and CAQ8 at 10,30,50,70 and 90% of HGT8) | dm ³ |
| BRK8 | Bark percent (based on total volume) | percent |
| FF08 | Over bark form factor based on over bark diameter at breast height | ratio |
| FFU8 | Under bark form factor based on under bark diameter at breast height | ratio |
| BDB8 | Basic density - determined from full 10 cm-thick disc taken at breast height | g/cm ³ |

moved except that if a second generation selection occurred in a thinned tree position, it was left and the adjacent tree was taken so as to reduce all plots to five trees. Selective thinnings however were carried out in the second triple lattice of the polycross in each locality and each year. Selection was based on the usual silvicultural practice of removing small and malformed trees with

some attention being paid to the spacing of the remaining crop. The aim was to compare the effects of the two types of thinning on the genetic structure of the experiments at this and subsequent assessments through estimation of the genetic variances from measurements on the remaining trees in directly comparable experiments.

Table 2. — Analyses of variance of eighth-year traits in the *Pinus patula* polycross tests at Stapleford and Martin planted in 1967 and 1968.

| SOURCE OF VARIATION | DF ¹ | TRAIT CODE | | | | | | | | | | |
|--|-----------------|--------------------|-------|-------|-------------------------------|-------|-------------------|--------|------------------------------|-------|-------------------|-------|
| | | BASED ON ALL TREES | | | BASED ON SYSTEMATIC THINNINGS | | | | BASED ON SELECTIVE THINNINGS | | | |
| | | HGT8 | CAQ8 | STR8 | OBV8 | BRK8 | FFO8 | BDB8 | OBV8 | BRK8 | FFO8 | BDB8 |
| Families (F) | 23 | 2** | 5*** | 2*** | 4*** | 1** | 0 | 5*** | 2 | 2** | 0 | 9*** |
| Localities (C) | 1 | 34 | 1 | 0 | 15 | 65** | 57 | 20*** | 5 | 56* | 44 | 17*** |
| Years (Y) | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 13*** | 0 | 2 | 0 | 21*** |
| Lattices (L)/C/Y | 4 | 0 | 0 | 0 | - | - | - | - | - | - | - | - |
| Replications (R)/L/C/Y | 16 | 2 | 1*** | 1*** | 1 | 7*** | 0 | 4*** | 1* | 2 | 1 | 0 |
| C x Y | 1 | 7*** | 2*** | 3** | 6*** | 0 | 1*** | 0 | 8*** | 1 | 0 | 0 |
| F x C | 23 | 2*** | 1* | 0 | 2 | 0 | 1 | 1 | 5** | 1 | 2 | 0 |
| F x Y | 23 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| F x C x Y | 23 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 2 |
| F x L in C in Y | 92 | 0 | 0 | 0 | - | - | - | - | - | - | - | - |
| Residual (π) | 436 | 2 | 1 | 2 | 2 | 5 | 2 | 3 | 2 | 5 | 2 | 5 |
| Trees in plots (T) | 5017 | 50 | 88 | 89 | 71 | 22 | 39 | 53 | 77 | 30 | 51 | 45 |
| TOTAL VARIANCE | | 3.600 | 0.445 | 1.234 | 2647 | 5.045 | 2.89 ² | 0.1083 | 2321 | 5.266 | 2.97 ² | 0.120 |
| SIGNIFICANCE OF F TEST FOR FAMILIES AT SEPARATE LOCALITIES COMBINED OVER YEARS | | | | | | | | | | | | |
| Martin | | *** | *** | * | *** | NS | NS | ** | *** | NS | ** | *** |
| Stapleford | | *** | *** | ** | *** | ** | NS | ** | *** | *** | * | *** |
| MEANS, RANGES, STANDARD ERRORS, COEFFICIENTS OF VARIATION AND REPEATABILITY OVER LOCALITIES AND YEARS | | | | | | | | | | | | |
| Overall - mean | | 13.5 | 1.9 | 4.8 | 117 | 7.7 | 0.46 | 3.5 | 102 | 7.9 | 0.46 | 3.5 |
| - range - from | | 12.5 | 1.6 | 4.4 | 98 | 7.3 | 0.45 | 3.3 | 81 | 7.1 | 0.44 | 3.4 |
| - range - to | | 14.1 | 2.3 | 5.1 | 137 | 8.4 | 0.47 | 3.6 | 123 | 8.9 | 0.47 | 3.8 |
| - s.e. | | 0.10 | 0.04 | 2.08 | 6.1 | 0.20 | 0.0049 | 0.04 | 6.0 | 0.22 | 0.0055 | 0.04 |
| Martin - mean | | 14.3 | 2.0 | 4.8 | 132 | 6.4 | 0.49 | 3.4 | 112 | 6.7 | 0.48 | 3.4 |
| - s.e. | | 0.14 | 0.06 | 0.10 | 10.1 | 0.25 | 0.0079 | 0.05 | 9.5 | 0.31 | 0.0089 | 0.95 |
| - CV(%) indiv. tree | | 10.9 | 35.3 | 25.1 | 41.8 | 17.1 | 8.0 | 8.7 | 45.8 | 18.6 | 9.0 | 9.1 |
| Stapleford - mean | | 12.7 | 1.8 | 4.7 | 101 | 9.0 | 0.44 | 3.6 | 91 | 9.2 | 0.43 | 3.6 |
| - s.e. | | 0.15 | 0.06 | 0.12 | 7.0 | 0.29 | 0.0057 | 0.05 | 6.7 | 0.31 | 0.0065 | 0.06 |
| - CV(%) indiv. tree | | 11.1 | 33.0 | 20.51 | 37.3 | 14.3 | 7.0 | 7.7 | 43.1 | 18.1 | 8.0 | 8.7 |
| Repeatability of θ parents - Re | | 0.40 | 0.80 | 0.98 | 0.91 | 1.00 | 0.98 | 0.82 | 0.83 | 0.97 | 0.96 | 0.98 |
| over localities - rs | | 0.42 | 0.59 | 0.44 | 0.63 | -0.08 | 0.19 | 0.72 | 0.25 | -0.03 | -0.03 | 0.81 |
| over years - Ry | | 0.91 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 0.97 | 1.00 | 0.98 | 0.99 | 1.00 |
| - rs | | 0.79 | 0.84 | 0.71 | 0.78 | 0.40 | 0.01 | 0.74 | 0.63 | 0.42 | 0.23 | 0.81 |
| HERITABILITIES | | | | | | | | | | | | |
| Localities combined - family | | 0.50 | 0.81 | 0.69 | 0.63 | 0.53 | 0.00 | 0.73 | 0.36 | 0.54 | 0.02 | 0.82 |
| - tree | | 0.12 | 0.21 | 0.08 | 0.19 | 0.15 | 0.00 | 0.33 | 0.10 | 0.21 | 0.00 | 0.57 |
| Martin - family | | 0.85 | 0.86 | 0.50 | 0.59 | 0.00 | 0.18 | 0.66 | 0.70 | 0.16 | 0.47 | 0.71 |
| - tree | | 0.32 | 0.25 | 0.05 | 0.21 | 0.00 | 0.04 | 0.33 | 0.24 | 0.06 | 0.14 | 0.43 |
| Stapleford - family | | 0.85 | 0.87 | 0.65 | 0.73 | 0.66 | 0.33 | 0.69 | 0.65 | 0.53 | 0.43 | 0.74 |
| - tree | | 0.26 | 0.27 | 0.11 | 0.38 | 0.47 | 0.07 | 0.47 | 0.27 | 0.23 | 0.12 | 0.72 |
| EFFICIENCY OF TRIPLE LATTICE DESIGN | | | | | | | | | | | | |
| Mean blocking efficiency (%) | | | | | | | | | | | | |
| Martin | | 105 | 104 | 104 | 105 | 118 | 103 | 106 | 107 | 115 | 103 | 125 |
| Stapleford | | 160 | 117 | 105 | 116 | 127 | 103 | 110 | 109 | 114 | 105 | 113 |
| rs of adjusted & unadj. family means over environment and yrs | | 0.98 | 0.98 | 0.99 | 0.99 | 0.96 | 0.97 | 0.99 | 0.97 | 0.98 | 0.99 | 0.99 |

¹) Degrees of freedom for OBV8, BRK8, FFO8 and BDB8 are 8, 276 and 1093 and 8, 280 and 1087 for R, π and T in the systematic and selectively thinned sections respectively.

Re — intra-class correlation

rs — Spearman's rank correlation coefficient

Results and Discussion

Analyses of variance for selected 7.5-year-old traits in the polycross, factorial and diallel tests combined over localities are given in tables 2, 3 and 4 respectively. The data indicate the percentage contribution of each source to total variation and the total variance itself; this, with the degrees of freedom, makes it possible to construct an approximation to the complete analysis of variance table. Negative estimates have been entered as zero. Significance for the F-test for families in the analysis of variance for individual localities has also been shown for the polycross and factorial tests. Other statistics given for these two tests are family means, ranges, standard errors, coefficients of variation, repeatability over localities and years, heritabilities, blocking efficiencies and Spearman's

rank correlation coefficients for adjusted and unadjusted means. Genetic, genotypic and phenotypic correlations between eighth-year traits are given in table 5 and those between nursery and eighth, second and eighth and fifth and eighth year traits in tables 6, 7 and 8 respectively. In each of these tables, those genetic correlations where the standard errors are approximately a third or less of the correlation coefficient itself, and therefore likely to be of practical significance, are highlighted.

The analyses, means heritabilities and correlations are based on unadjusted data. Means adjusted by using the triple lattice design have been used to rank families and parents for second generation selections but here, where general principles are under discussion, it is more informative to indicate the value of the triple lattice design

Table 3. — Analysis of variance of eight-year traits in the *Pinus patula* factorial progeny tests at Stapleford and Martin.

| SOURCE OF VARIATION | DEGREES OF FREEDOM | TRAIT CODE | | | | | | |
|--|--------------------|------------|------|------|-------|------|--------|------|
| | | HGT8 | CAQ8 | OBV8 | BRK8 | STR8 | FFO8 | BDB8 |
| PERCENTAGE CONTRIBUTION TO TOTAL VARIANCE AND SIGNIFICANCE OF THE F TESTS ON THE MEAN SQUARES FOR COMBINED LOCALITIES | | | | | | | | |
| Locality (c) | 1 | 59*** | 8* | 32** | 90** | 1 | 50*** | 28** |
| Paternal parents (p) | 4 | 0 | 8** | 5* | 0 | 2 | 0 | 6** |
| Maternal parents (m) | 8 | 0 | 2 | 1 | 0 | 4 | <1* | 7*** |
| m x p | 32 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| p x c | 4 | 0 | 1 | 1 | 0 | 2** | <1** | 0 |
| m x c | 8 | 1 | 1 | 1 | <1** | 0 | 0 | 0 |
| m x p x c | 32 | 1* | 1 | 1 | 0 | 0 | 0 | 1 |
| Residual (π) | 252 | 5 | 5 | 9 | 3 | 7 | 4 | 7 |
| Trees in plots | 1041 ¹ | 33 | 72 | 49 | 6 | 83 | 46 | 52 |
| TOTAL VARIANCE | | 4.98 | 0.47 | 3239 | 18.33 | 1.58 | 0.0028 | 1493 |
| SIGNIFICANCE OF F TESTS FOR SEPARATE LOCALITIES | | | | | | | | |
| Martin - paternal parents (p) | | ** | *** | *** | | *** | ** | *** |
| - maternal parents (m) | | *** | *** | ** | *** | *** | * | *** |
| m x p | | | * | | | | | |
| Stapleford - paternal parents (p) | | | *** | *** | | *** | ** | *** |
| - maternal parents (m) | | | | | * | *** | | *** |
| m x p | | ** | ** | ** | | | | |
| MEANS, RANGES, STANDARD ERRORS, COEFFICIENTS OF VARIATION AND REPEATABILITY OVER LOCALITIES | | | | | | | | |
| Overall - mean | | 13.6 | 2.0 | 122 | 9.1 | 4.7 | 0.47 | 320 |
| - range 5 ♀ parents - from | | 13.4 | 1.7 | 102 | 8.9 | 4.4 | 0.46 | 305 |
| - to | | 13.8 | 2.2 | 136 | 9.3 | 4.9 | 0.47 | 330 |
| - s.e. | | 0.08 | 0.03 | 3.1 | 0.12 | 0.06 | 0.0021 | 2.0 |
| - range 9 ♀ parent - from | | 13.2 | 1.8 | 111 | 8.5 | 4.4 | 0.45 | 302 |
| - to | | 14.0 | 2.1 | 133 | 9.5 | 5.3 | 0.47 | 336 |
| - s.e. | | 0.11 | 0.04 | 4.1 | 0.16 | 0.08 | 0.0028 | 2.7 |
| Martin - mean | | 4.8 | 2.1 | 145 | 6.2 | 4.6 | 0.49 | 306 |
| - s.e. | | 0.13 | 0.06 | 6.8 | 0.14 | 0.10 | 0.0044 | 8.5 |
| - CV(%) indiv. tree | | 9.8 | 33.7 | 37.8 | 16.6 | 25.1 | 8.4 | 12.3 |
| Stapleford - mean | | 12.4 | 1.8 | 99 | 12.0 | 4.9 | 0.44 | 335 |
| - s.e. | | 0.17 | 0.06 | 4.6 | 0.28 | 0.13 | 0.0036 | 8.3 |
| - CV(%) indiv. tree | | 11.5 | 33.2 | 37.7 | 13.2 | 27.6 | 7.6 | 8.4 |
| Repeatability of ♀ parents - Re | | 0.75 | 0.66 | 0.53 | 0.36 | 1.00 | 0 | 0.95 |
| over locality - rs | | 0.35 | 0.58 | 0.47 | -0.02 | 0.70 | 0.35 | 0.85 |
| HERITABILITIES | | | | | | | | |
| Localities combined - family | | 0.23 | 0.69 | 0.54 | 0.07 | 0.68 | 0 | 0.81 |
| - tree | | 0.04 | 0.22 | 0.18 | 0.02 | 0.14 | 0 | 0.36 |
| Martin - family | | 0.60 | 0.75 | 0.57 | 0.39 | 0.63 | 0.50 | 0.59 |
| Stapleford - family | | 0.06 | 0.52 | 0.39 | 0.29 | 0.68 | 0 | 0.74 |
| EFFICIENCY OF TRIPLE LATTICE DESIGN | | | | | | | | |
| Blocking efficiency (%) - Martin | | 113 | 108 | 104 | 117 | 112 | 102 | 102 |
| - Stapleford | | 147 | 119 | 117 | 235 | 109 | 102 | 149 |
| rs of adjusted and unadj. + means | | 0.98 | 0.98 | 0.98 | 0.95 | 1.0 | 0.98 | 1.00 |

¹⁾ 2342 degrees of freedom for HGT8 and CAQ8
 Re — intra-class correlation coefficient
 rs — Spearman's rank correlation coefficient

through the blocking efficiency term and to use variance components for construction of genetic parameters unconfounded with the environmental correlations of the lattice design (BARNES, 1973).

Genetic control of traits

All 3 tests, the polycross, the factorial and the diallel,

showed very large environmental followed by significant *gca* variation for productivity, stem straightness and basic density traits. The diallel showed that maternal and reciprocal effects were unimportant and both the diallel and the factorial tests that specific combining ability (*sca*) was not of practical significance. Heritabilities were highest for basic density followed generally by volume

Table 4. — Analyses of variance of eight-year traits in the *Pinus patula* diallel progeny tests at Stapleford, Martin, Bende and Nyangul.

| SOURCE OF VARIATION | DEGREES OF FREEDOM | TRAIT CODE | | | | | | |
|-----------------------|--------------------|------------|--------|---------|-------|---------|---------|--------|
| | | HGT8 | CAQ8 | OBV8 | STR8 | BRK8 | FFO8 | BDB8 |
| Localities (c) | 3 | 64.5*** | 8.2*** | 32.6*** | 3.8** | 74.6*** | 87.7*** | 6.0** |
| Replications in c | 8 | 1.4** | 0.8 | 1.1 | 0.5 | 6.8*** | 0.4* | 0.5 |
| General (g) | 4 | 1.2* | 8.7*** | 8.7 | 1.0 | 0.4 | 0.2 | 4.6*** |
| Specific (s) | 5 | 0.4* | 1.1** | 1.9* | 0.1 | 0 | 0 | 0 |
| Maternal (m) | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Reciprocal (r) | 6 | 0.3 | 0.5** | 0.6 | 0.6* | 0 | 0 | 0 |
| g x c | 12 | 0.7* | 0.8* | 1.4 | 0.1 | 0 | 0.7 | 0.5 |
| s x c | 15 | 0 | 0 | 0 | 0 | 0.4 | 0 | 0 |
| m x c | 12 | 0.3* | 0.4* | 0.6 | 0.6** | 0.3 | 0 | 0.3 |
| r x c | 18 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Residual in c | 152 | 3.8 | 3.4 | 18.5*** | 5.8 | 7.9*** | 0.7 | 0 |
| Trees in plots | 2150 | 27.6 | 76.3 | 34.6 | 87.4 | 9.6 | 60.1 | 88.11 |
| TOTAL VARIANCE | | 4.14 | 0.4616 | 2137 | 1.178 | 37.72 | 26.16 | 2054 |
| Heritability - family | | 0.45 | 0.76 | 0.64 | 0.33 | 0.32 | 0.23 | 0.83 |
| - individual tree | | 0.14 | 0.38 | 0.52 | 0.04 | 0.09 | 0.02 | 0.20 |

Table 5. — Genetic, genotypic and phenotypic correlations between selected eighth-year traits in the factorial test at Martin.

| | | HGT8 | STR8 | CAQ8 | OBV8 | BRK8 | BDB8 | FFU8 |
|------|----------------------------------|--|----------------|----------------|----------------|-----------------|-----------------|-----------------|
| | | GENETIC CORRELATION (and STANDARD ERROR) | | | | | | |
| HGT8 | GENOTYPIC/PHENOTYPIC CORRELATION | | 0.05 (0.38) | 0.46 (0.29) | 0.94 (0.11) | -0.45 (0.32) | -0.38 (0.34) | 0.83 (0.22) |
| STR8 | | 0.37 0.19 | | 0.17 (0.37) | 0.39 (0.39) | -0.12 (0.38) | 0.19 (0.38) | -0.56 (0.31) |
| CAQ8 | | 0.42 0.49 | 0.00 0.03 | | 0.81 (0.15) | 0.59 (0.27) | 0.11 (0.38) | 0.00 (0.40) |
| OBV8 | | 0.60 0.60 | 0.12 0.05 | 0.91 0.86 | | -0.04 (0.42) | 0.00 (0.42) | -0.32 (0.42) |
| BRK8 | | -0.28 -0.22 | -0.20 -0.25 | 0.28 0.23 | -0.01 -0.05 | | 0.28 (0.37) | -0.56 (0.28) |
| BDB8 | | -0.05 -0.07 | 0.31 0.14 | 0.17 0.13 | 0.22 0.13 | 0.22 0.13 | | -0.82 (0.22) |
| FFU8 | | 0.45 -0.28 | 0.08 -0.02 | -0.21 -0.14 | -0.01 0.00 | 0.00 0.02 | -0.33 -0.28 | |

Table 6. — Genetic, genotypic and phenotypic correlations between nursery and eighth-year traits at Martin.

| | | NURSERY TRAITS | | | | | |
|--------------------|------|---|-----------------|----------------|----------------|----------------|-----------------|
| | | CON | | COL | | NH12 | |
| | | GENETIC CORRELATION (AND STANDARD ERROR) GENOTYPIC AND PHENOTYPIC CORRELATIONS | | | | | |
| EIGHTH YEAR TRAITS | HGT8 | -0.45 -0.46 | (0.32) -0.28 | -0.41 -0.05 | (0.41) 0.03 | -0.31 -0.34 | (0.34) -0.25 |
| | CAQ8 | -0.69 -0.43 | (0.23) -0.37 | 0.42 0.23 | 0.39 0.19 | 0.51 0.26 | (0.32) 0.13 |
| | OBV8 | -0.53 -0.43 | (0.32) -0.42 | 0.26 0.11 | (0.48) 0.03 | 0.29 0.06 | (0.41) -0.06 |
| | STR8 | -0.20 -0.31 | (0.38) -0.19 | 0.06 -0.01 | (0.45) 0.03 | 0.49 -0.36 | (0.31) -0.11 |
| | BRK8 | -0.45 -0.20 | (0.34) -0.04 | 0.74 0.53 | (0.26) 0.46 | 0.56 0.38 | (0.27) 0.36 |
| | BDB8 | -0.18 -0.12 | (0.39) -0.01 | 0.93 0.23 | (0.23) 0.25 | 0.74 -0.15 | (0.21) 0.10 |

Table 7. — Genetic, genotypic and phenotypic correlations between second-year and eight-year traits at Martin.

| | | SECOND YEAR TRAITS | | | | | | | | | |
|--------------------|------|---|----------------------------------|----------------------------------|-----------------------------------|-----------------------------------|-----------------------------------|-----------------------------------|----------------------------------|-----------------------------------|-----------------------------------|
| | | HTI2 | CAQ2 | VOL2 | SIN2 | BDI2 | BLI2 | BAI2 | AIL2 | ABW2 | B/H2 |
| | | GENETIC CORRELATION (AND STANDARD ERROR) GENOTYPIC AND PHENOTYPIC CORRELATIONS | | | | | | | | | |
| EIGHTH YEAR TRAITS | HGT8 | 0.77 (0.16) 0.30 0.51 | 0.77 (0.21) 0.25 0.43 | 0.67 (0.22) 0.21 0.43 | 0.04 (0.37) 0.14 0.05 | -0.57 (0.30) -0.41 -0.32 | -0.03 (0.45) -0.40 -0.23 | 0.64 (0.23) 0.20 0.35 | 0.12 (0.37) -0.11 0.05 | 0.13 (0.36) -0.18 -0.03 | -0.08 (0.36) 0.00 -0.07 |
| | CAQ8 | 0.61 (0.25) 0.65 0.62 | 0.84 (0.19) 0.72 0.61 | 0.73 (0.20) 0.71 0.65 | -0.46 (0.30) -0.41 -0.35 | 0.09 (0.41) -0.05 -0.09 | -0.09 (0.45) -0.46 -0.37 | 0.20 (0.36) 0.20 0.21 | 0.11 (0.37) 0.34 0.28 | -0.42 (0.32) -0.68 -0.53 | -0.26 (0.34) -0.60 -0.50 |
| | OBV8 | 0.99 (0.12) 0.60 0.58 | 1.25 (0.21) 0.65 0.52 | 1.05 (0.11) 0.64 0.58 | -0.35 (0.37) -0.77 -0.23 | -0.46 (0.38) -0.24 -0.24 | -0.18 (0.49) -0.58 -0.41 | 0.72 (0.24) 0.29 0.34 | 0.18 (0.40) 0.27 0.23 | -0.42 (0.36) -0.75 -0.54 | -0.29 (0.37) -0.56 -0.46 |
| | STR8 | 0.35 (0.36) -0.12 -0.02 | 0.47 (0.37) -0.23 -0.03 | 0.36 (0.36) -0.25 -0.06 | -0.26 (0.35) 0.29 0.05 | 0.13 (0.41) -0.45 -0.26 | 0.52 (0.39) -0.40 -0.23 | 0.45 (0.37) -0.08 -0.18 | 0.04 (0.38) -0.53 -0.36 | 0.05 (0.37) -0.14 -0.07 | 0.15 (0.36) 0.43 0.30 |
| | BRK8 | -0.13 (0.39) 0.10 0.07 | 0.06 (0.44) 0.13 0.07 | 0.10 (0.39) 0.16 0.10 | -0.52 (0.29) -0.36 -0.28 | 0.67 (0.26) 0.32 0.32 | 0.00 (0.46) 0.09 0.10 | -0.57 (0.27) -0.30 -0.36 | 0.19 (0.37) 0.11 0.12 | -0.50 (0.30) -0.09 -0.13 | -0.34 (0.33) -0.14 -0.17 |
| | BDB8 | 0.28 (0.38) 0.29 0.19 | 0.32 (0.42) 0.02 0.03 | 0.40 (0.36) 0.14 0.12 | -0.70 (0.24) 0.07 -0.05 | 0.28 (0.40) -0.48 -0.25 | 0.00 (0.46) -0.48 -0.30 | -0.24 (0.37) 0.24 0.15 | 0.37 (0.34) -0.28 -0.06 | -1.01 (0.08) -0.56 -0.51 | -0.70 (0.21) 0.05 -0.32 |

Table 8. — Genetic, genotypic and phenotypic correlations between fifth- and eighth-year traits at Martin.

| | | FIFTH YEAR TRAITS | | | | | | | |
|--------------------|------|---|----------------------------------|---------------------------------|-----------------------------------|-----------------------------------|-----------------------------------|-----------------------------------|-----------------------------------|
| | | HGT5 | CAQ5 | VOL5 | STR5 | BBA5 | AIL5 | B/H5 | ABW5 |
| | | GENETIC CORRELATION (AND STANDARD ERROR) GENOTYPIC AND PHENOTYPIC CORRELATIONS | | | | | | | |
| EIGHTH YEAR TRAITS | HGT8 | 0.93 (0.06) 0.79 0.83 | 0.61 (0.23) 0.13 0.47 | 0.74 (0.16) 0.46 0.59 | 0.20 (0.61) 0.51 0.38 | -0.49 (0.31) -0.32 -0.26 | 0.31 (0.32) 0.22 0.30 | -0.19 (0.34) -0.22 -0.23 | 0.16 (0.37) -0.11 0.02 |
| | CAQ8 | 0.57 (0.26) 0.71 0.62 | 0.89 (0.08) 0.93 0.90 | 0.85 (0.11) 0.93 0.89 | 0.25 (0.60) 0.28 0.28 | -0.14 (0.38) 0.24 0.14 | 0.21 (0.34) 0.61 0.49 | -0.34 (0.32) -0.74 -0.60 | -0.42 (0.33) -0.76 -0.53 |
| | OBV8 | 0.99 (0.11) 0.80 0.68 | 1.02 (0.07) 0.87 0.80 | 1.05 (0.06) 0.90 0.83 | 0.49 (0.61) 0.41 0.36 | -0.58 (0.33) 0.02 -0.08 | 0.39 (0.35) 0.64 0.50 | -0.51 (0.31) -0.77 -0.60 | -0.45 (0.37) -0.77 -0.50 |
| | STR8 | 0.05 (0.38) 0.15 0.10 | 0.38 (0.34) -0.11 -0.03 | 0.27 (0.35) -0.05 0.01 | 1.56 (0.83) 0.68 0.49 | -0.86 (0.17) -0.71 -0.52 | -0.47 (0.29) -0.38 -0.32 | 0.11 (0.36) 0.19 0.16 | -0.70 (0.25) -0.12 -0.13 |
| | BRK8 | -0.26 (0.36) -0.10 -0.09 | 0.31 (0.35) 0.21 0.17 | 0.17 (0.37) 0.16 0.12 | -0.47 (0.62) -0.21 -0.15 | 0.76 (0.21) 0.45 0.38 | -0.17 (0.35) 0.07 0.07 | -0.17 (0.35) -0.07 -0.09 | -0.08 (0.38) -0.06 -0.09 |
| | BDB8 | -0.05 (0.39) 0.21 0.13 | 0.34 (0.35) 0.20 0.17 | 0.23 (0.36) 0.23 0.18 | 0.67 (0.78) 0.03 -0.15 | -0.11 (0.39) -0.42 -0.29 | 0.44 (0.30) 0.01 0.11 | -0.77 (0.18) -0.18 -0.26 | -0.90 (0.15) -0.44 -0.40 |

and then by stem straightness. Heritability was higher for height than diameter.

Although the change in the sizes of the heritability estimates for height (HGT) and basal area (CAQ) has varied within trials with increasing age, if the estimates for combined trials are taken, there has been a trend for

| | Age (years) | | |
|-----|-------------|------|------|
| | 1.5 | 4.5 | 7.5 |
| HGT | 0.44 | 0.33 | 0.23 |
| CAQ | 0.45 | 0.62 | 0.69 |

family heritability for height to decrease and that for basal area to increase as shown below.

The increase for CAQ may have been due to inflation of the differences between families brought about by competition between the 10-tree line plots; once suppression of a slower growing family by a faster growing one starts, the difference is accelerated as competition becomes more severe. HGT is less affected by competition and therefore heritability would be unlikely to increase for the same reason. The tendency for its heritability to decrease with age has been found with other coniferous species (FRANKLIN, 1979) where the explanation given was that rapidly developing phenotypes were slowing down while less rapidly developing phenotypes were catching up.

Genotype-environment interaction

Taken over the 3 tests, genotype-locality interaction of most practical significance in the productivity traits was

evidenced by the often low repeatability for volume over localities in the polycross and factorial; it was least for basic density where repeatability was always very high, as has been found for other tropical pines (e.g. BARNES *et al.*, 1977, PLUMPTRE, 1984; ZOBEL and VAN BUIJTENEN, 1984); and it was intermediate for stem straightness. The polycross test showed that genotype-year interaction was unimportant.

Systematic versus selective thinning

It would be expected that smaller trees would be removed in a selective rather than in a systematic thinning and that if there were some *sca* effects in productivity traits or correlations between these and say basic density, then there would be significant differences in the genetic parameters estimated from trees removed or remaining in the two types of thinnings. Neither *sca* effects nor such correlations were indicated from these experiments and the differences in heritability estimates from the two types of thinning were, as then expected, minimal.

The triple lattice design

Use of triple lattice design had virtually no advantage over the straight randomized complete block in the precision of ranking families in the polycross and factorial tests as shown by the high repeatability of adjusted by unadjusted means. On the other hand, there were some substantial blocking efficiency effects, e. g. height at Stapleford in the polycross (160%) and basic density in the factorial at Stapleford (149%). This indicated that if the experiments had been about a third smaller in size, they would have achieved the same degree of precision as in this randomized complete block.

Mating design

The results here confirm the earlier findings (BARNES and SCHWEPPENHAUSER, 1979) that the assumption of half-sib relationships in the polycross families is valid and that the test is a reliable one for these traits in *P. patula*. Table 9 shows how the polycross and factorial ranked the female and male parents that were common to both tests for CAQ8. The rankings were precisely the same for the 5 male parents over both localities. The 8 female parents were tested against only 5 males and therefore the same degree of precision could not be expected; nevertheless, in the combined analysis, the highest- and lowest-ranked 4 parents were the same in both tests.

Genetic correlations

Among the eighth year traits (Table 5) only 3 correlations had small enough standard errors to be of significance. These were between height (HGT8) and basal area (CAQ8) and volume and under-bark form factor, both traits derived from the measured variates and therefore auto-correlated. Height was slightly better predictor of volume than basal area perhaps due to the lesser effect of competition on this trait. Of greater interest is the small size and statistical insignificance of correlation between any of the growth traits and basic density of the wood (BDB8) and the lack of a significant correlation between stem height and basal area.

The juvenile-mature correlations show some interesting relationships. Seedlings with fewer cotyledons (CON) tend to have larger stem basal area (CAQ) by the eighth year and seedlings with long cotyledons (COL) and greater height at 12 months in the nursery (NH12) develop into trees with higher wood density.

Table 9. — Ranking of the 8 common female and 5 common male parents for circular area at breast height (CAQ8) by the factorial (F) and polycross (P) tests at Stapleford (A) and Martin (B) separately and combined.

| Parent | Test | | | | | |
|-----------------------------|------|---|---|---|-------|---|
| | A | | B | | A + B | |
| | F | P | F | P | F | P |
| 8♀ tested against 5♂ | | | | | | |
| 1 | 1 | 5 | 3 | 4 | 3 | 4 |
| 7 | 6 | 4 | 8 | 6 | 7 | 6 |
| 15 | 3 | 2 | 2 | 5 | 2 | 2 |
| 26 | 8 | 8 | 6 | 8 | 8 | 8 |
| 27 | 2 | 7 | 1 | 1 | 1 | 3 |
| 32 | 4 | 3 | 7 | 7 | 5 | 7 |
| 48 | 7 | 6 | 4 | 3 | 6 | 5 |
| 51 | 5 | 1 | 5 | 2 | 4 | 1 |
| 5♂ tested against 9♀ | | | | | | |
| 5 | 1 | 1 | 1 | 1 | 1 | 1 |
| 14 | 2 | 3 | 2 | 2 | 2 | 2 |
| 20 | 3 | 2 | 3 | 4 | 3 | 3 |
| 25 | 4 | 4 | 4 | 3 | 4 | 4 |
| 31 | 5 | 5 | 5 | 5 | 5 | 5 |

Height and basal area in the second and eighth years were well-correlated in all combinations. Low numbers of branches in the second year (ABW2 and B/H2) were an excellent prediction of high wood density (BDB8) by the eighth year. This was surprising and could be a useful correlation, particularly given the tendency for branch number also to be negatively correlated with growth and high density with less stem sinuosity (SIN2). The only other large genetic correlation with a low standard error in this table was a positive and desirable one between branch angle (BA12) and stem volume (OBV8).

The genetic correlations between the fifth and eighth year traits (Table 8) are precisely similar to those between the second and eighth except that, in addition, straight trees with thin bark have smaller branches but are not necessarily smaller.

The consistent indication of a high negative correlation between branch number and wood density calls for an explanation. The production of low density juvenile wood continues throughout the tree's life in the proximity of the live crown (see ZOBEL and VAN BUIJTENEN, 1984). Few branches have been associated with longer branches in these tests in the second year (BARNES and SCHWEPPENHAUSER, 1979). Higher wood density may therefore be correlated with few branches because of the less dense and more distant crown at the point of stemwood production.

Conclusions

The conclusions drawn from this eighth year assessment should be read in conjunction with those derived from analysis of the nursery (BARNES and SCHWEPPENHAUSER, 1978) second year (BARNES and SCHWEPPENHAUSER, 1979) and fifth year (BARNES *et al.*, in press) assessments. The results

from these tests are being used to investigate some theoretical questions of mating and environmental design of progeny tests and of sampling the base population; these studies are in progress at the Oxford Forestry Institute and among other things, indicate that some caution is required in interpretation of the data when the population is represented by such small number of parents.

The practically significant conclusions from analyses of selected economically important traits in these *P. patula* tests in the eighth year are: —

1. Heritabilities are high for wood density, stem volume and stem straightness;
2. Specific combining ability, maternal and reciprocal effects are not of practical significance;
3. Genotype-locality interaction may be sufficiently pronounced in volume production traits to be used whereas it is absent in wood density;
4. Genotype-year interaction is not important;
5. Data from trees selectively rather than systematically thinned from progeny tests do not give significantly biased estimates of genetic parameters;
6. Sub-blocking with a lattice design does not give any useful improvement in ranking of families but appreciably smaller tests could be used to get the same precision in assessing some traits in some localities if the characteristics of the test site could be predicted;
7. The polycross mating design with half-sib families being produced by controlled pollination with a 20-pollen mix is an efficient method for determining *gca* and ranking families;
8. Both height and basal area are closely genetically correlated with stem volume within and between second, fifth and eighth years;
9. There is no genetic correlation of practical significance between wood density and stem volume;
10. In the nursery, seedlings with few long cotyledons and greater height develop into large trees with high density by the eighth year;
11. Trees with few branches and superior height in the second year develop into trees with high wood density and large volume by the eighth year;

It is emphasized that these interpretations of the data are only up to the eighth year. This is half a pulpwood and

one quarter of a sawlog rotation. FRANKLIN (1979) recognized 3 phases in stand development for four North American conifer species, juvenile-genotypic, mature-genotypic and co-dominance-suppression based on trends in additive genetic variance. He found that genetic correlations were high within and low between phases and he cautioned against juvenile selection in those populations. With the close spacing and rapid growth rate of *P. patula*, these tests in the eighth year can be said to be in the mature-genotypic phase. Genetic correlations between and within the first two phases are high and useable. It will be interesting to see whether they remain high for the fifteenth year traits which is the age at which the next assessment is scheduled.

Acknowledgement

The authors wish to thank the Zimbabwe Forestry Commission for permission to use this data and publish the results and Dr. JEFF BURLEY and JACQUELINE BIRKS for reviewing the manuscript.

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Influence of Selection for Volume Growth on the Genetic Variability of Southwestern Ponderosa Pine

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(Received 22nd November 1991)

Summary

Genetic variability between 18 select and 50 non-select neighbour trees in three ponderosa pine (*Pinus ponderosa*

DOUGL. ex LAWS. var. *scopulorum* ENGELM.) geographical sources in the Southwest was characterised by isozyme analysis using starch gel electrophoresis. Twenty six isozyme loci in 15 enzymes were assayed. Measures of genetic diversity showed that the select and neighbour trees did not differ in isozyme variability. Contingency chi-square analysis did not detect any differences in allozyme frequencies between the select and neighbouring

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