PERFORMANCE OF SLASH x LOBLOLLY PINE INBRED AND OUTCROSSED F2 HYBRIDS IN QUEENSLAND, AUSTRALIA

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Abstract: -- The fitness and performance of inbred and outcrossed, full-sib F2 hybrids of *Pinus elliottii* x *P. taeda* were compared to that of *P. elliottii* controls and some putative F_1 hybrids in a replicated trial on a single site in south east Queensland, Australia. Data reported include cone and seed yields, seed viability, seedling cull percentages, abnormalities assessed at nine years and growth at ages from eight to 34 years. In terms of fitness, the outcrossed F2 hybrids had relatively high seed viabilities, low cull percentages and a low proportion of abnormal trees at age nine years compared to inbred Fes which also showed inbreeding depression in growth. The F2 hybrids did not exhibit hybrid vigour for growth on the trial site, whereas the putative F_1 hybrids appeared to do so in diameter and mean height at 34 years. However, the F_1 samples were very small, without plot structure and probably benefitted more than slash pine by loss of malformed trees via thinning. Both F2 hybrid populations appeared to show more phenotypic variation for eight-year diameter and height than the slash pine, with indications of transgressive segregants then and at 34 years.

Possible implications for hybrid breeding of these findings and other relevant information are outlined.

Keywords: *Pinus elliottii, P. taeda, P. elliottii* x *P. taeda* hybrids, inbred F2 hybrids, outcrossed F2 hybrids, hybrid breeding

INTRODUCTION

Pinus elliottii var. *elliottii* (slash) and *P. taeda* (loblolly) pines were introduced to Queensland for testing in the 1920s from the SE Georgia-NE Florida region, and were being planted operationally by the 1930s using seed collected locally. Soon afterwards, tree improvement was initiated via mass selection, followed by recurrent selection with progeny testing. In the case of slash pine, a series of clonal seed orchards was established, the first in 1953. In the 1950s, exploration of inter-specific hybridisation began following reports of such research in the USA, and the recognition of a few natural vigorous slash x loblolly (or reciprocal) pine hybrids in local plantations, and the possibility of capturing hybrid vigour.

Limited information is available on the relative performance of F_1 and outcrossed or inbred F2 hybrid populations of forest trees. Powell and Nikles (1996) reported on the six-year performance of populations of large numbers of F_1 and outcrossed F2 hybrid families of slash x *P. caribaea* var. *hondurensis* (PCH) and parental and backcross families from phenotypically-superior parents tested across 4 locations in south east and central Queensland. Averaged across the four sites, both F_1 and F2 hybrids were significantly superior to the high parent (PCH) but not from each other for under bark volume. At some locations the F2 was superior to the F_1 in under bark diameter and volume.

Slash x PCH F2 hybrid seedlings, derived from open-pollinated seed produced in a clonal orchard of select, mostly-unrelated F_1 clones (Nikles and Robinson 1989) have been planted operationally in south east Queensland since the mid 1980s with good results. Significant numbers of superior F2 phenotypes have been noted in these populations, as well as in other populations of outcrossed, polycross or full-sib F2 families planted between 1984 and 1987. Westvaco, a company planting *P. rigida* x *P. taeda* F2 hybrids operationally in north east USA, uses F2 seed from an orchard of select F_1 clones grafted in

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1987. Controlled-cross test results indicate that the eight-year growth of some F_2 families equals or surpasses the checks, which comprise some of the best F_1 families (pers. comm., Davis Gerwig, 1999). Thus outcrossed F_2 hybrids can be of value in commercial plantation programs and potentially provide superior families and clones for deployment or further breeding.

In South Africa, inbred backcross hybrids (F_1 trees crossed to a recurrent parent) of slash x PCH and slash x *P. cubensis* showed depression in growth (van der Sijde and Roelofsen 1986). Barnes and Mullin (1978) reported on three-year height performance of slash x loblolly and reciprocal F_1 hybrids grown on three sites in Rhodesia (Zimbabwe). They stated: "Over all [hybrid] families [20], heterosis was negative at the locality where environmental conditions were most favourable for growth and positive where conditions were marginal for the two species." However this hybrid is not used in Zimbabwe as there is no niche in which it can demonstrate sufficient hybrid vigour (Bridgewater et al. 1997).

In the 1960s, outcrossed and inbred full-sib F_2 hybrid families of slash and loblolly pines were produced in Queensland and planted in a replicated trial at a single location in 1965. This report outlines 34-year and earlier growth and fitness of these hybrids, a single control-crossed family of slash pine and a slash pine bulk from a young clonal seed orchard. Some putative slash x loblolly F_1 hybrids were found within the slash pine seed orchard bulk and were also measured and compared for performance. Possible implications for hybrid breeding of the study results and others are mentioned.

MATERIALS AND METHODS

Genetic Material

Pure species and hybrid populations were included in the experimental trial (slash pine and slash x loblolly outcrossed and inbred F_2 hybrids). No pure loblolly pine controls were available.

Outcrossed and inbred F_2 progeny were produced by controlled crossing between eight, phenotypically superior, slash x loblolly or reciprocal F_1 hybrid trees. These trees were selected at five or six years of age from three, unrelated, full-sib, F_1 hybrid families. Although not showing overall hybrid vigour, these families exhibited great variability with proportions of both small, malformed trees and oustanding trees of superior diameter and height. Details of the mating design are given in Table 1. Progeny produced from crossing between unrelated F_1 families were called outcrossed F_2 ($F = 0$), and progeny from crossing between full sibs within the same family were called inbred F_2 ($F = 0.25$) hybrids.

Table 1. Mating design used for the production of the F_2 hybrid families.

Seed parents		Pollen parents					
Select tree		TE-6	TE-7	ET-9	ET-10	ET- 11	ET-12
	Pedigree	T-2xE-15	T-2xE-15	E-40xT-67	E-40xT-67	E-9xT-10	E-9xT-10
TE-5	T-2xE-15	+[1]		+[2]		+[2]	
TE-6	T-2xE-15				+[2]		
ET-8	E-40xT-67	+[2]			+[1]		+[2]

Note: E = *P. elliottii*, T = *P. taeda*, [1] = inbred F_2, [2] outcrossed F_2, + = cross attempted and achieved, = cross not attempted. Seed parent species are given first in the select tree names and pedigrees.

Seed and Plant Production

Standard procedures were followed during the crossing, cone collection, seed processing and plant raising phases. However, neither sub-sampling of seedlots (several hundred seeds were obtained per family or bulk), nor replication in the nursery were implemented. For the nursery phase seed of eight F_2 hybrid families, a slash pine open-pollinated bulk seedlot from a young, clonal seed orchard (CSO) and two full-sib slash pine families were available.

Stratified seeds were sown in the Beerwah nursery in August 1964. Total numbers of germinants per family or bulk were recorded. Seedlings were observed for abnormalities in the nursery at two and six months after sowing, and the numbers of cull plants, i.e. spindly and malformed plants not achieving the standard for plantable stock, were recorded at the time of lifting, just prior to planting.

Experimental Field Trial

The experimental field trial was planted in May 1965 at a single uniform site, in the Beerburrum State Forest on the coastal lowlands in south-east Queensland, at latitude 27°S. The site previously carried a mixed-eucalypt forest typical of the extensive, well-drained, mid-slope positions in the eastern portion of the State Forest. The gradational soil-profile type sampled is known locally as yellow earth '; it is acidic, has low fertility and, with the phosphate fertiliser applied, is considered closer to optimal for slash pine than for loblolly pine of the Queensland land races.

Field layout followed a 'replicates in groups' design ie. three hybrid seed parent groups were formed, regardless of crosstype; these hybrid families along with slash pine controls were replicated three times in each group. A slash pine family (E-15 × E-40) was replicated in each group and nine plots of it were planted. Family plots were 7 x 7 trees. Spacing was 10 feet x 10 feet (approx. 3 × 3m). The trial was thinned during November 1978. However, due to varying proportions of abnormal trees among families and cross types, stockings of measurable and residual trees varied before and after thinning (see below).

Putative F_1 hybrid

Many years after planting the field trial, it was noted that the slash orchard bulk included a small proportion of putative slash x loblolly F_1 hybrids, distinguished principally on bark morphology. These hybrids must have resulted from pollination by loblolly pollen that drifted across the wide, orchard isolation area into the 4-year-old orchard where relatively little slash pine pollen was being produced. Eleven individual hybrids were identified at age 34 in the slash pine orchard bulk plots measured and were used to compare the growth performance of F_1 and the other F_2 hybrid and slash populations.

Immediately adjacent to the experimental field trial was a block of 'slash' progeny from the clonal seed orchard (same seedlot as in the trial), planted at the same time and spacing, and also thinned. To further examine the relative diameters of the slash and putative F_1 hybrids, this block was sampled in 1999 in the following manner: all putative hybrids in the block (23) were identified visually and then measured for diameter breast height (DBH); to remove any possible bias, the corresponding nearest three slash pine trees to each hybrid were also measured (n = 69) for comparative purposes.

Measurements and Assessments

Various measurements and assessments were undertaken regularly after planting. Those reported here are outlined in Table 2.

Abnormalities, not strongly evident in the nursery (except for a very low proportion of albinism in some families), were first noted in the field at four years of age. These were assessed at nine years following a 4-point scale: normal (4), slight to moderately affected (3), moderate to severely affected (2) and severely affected (1). Normal plants had no visual signs of abnormalities. Slightly affected plants had shortened needles and a combination of dead branch tips, drooping branches and corky bark that was deeply fissured in small squares. The third class included the latter traits, plus with the main leader collapsed beyond recovery. The fourth class included all symptoms described above and plants only 30cm high or dead. The pure slash pine family was not assessed, although the orchard bulk was.

Table 2. Summary of measurements and assessments undertaken in the field trial.

Time of measure or assessment	Age (years)	Parameter, measure or assessment unit, plot sample (rows x trees)
September 1973	8.33	Total height, m, 7 x 7; DBH, cm, 7 x 7
January 1974	8.67	Abnormalities, classes 1-4, 7 x 7
June 1978	13.08	Predominant height, m, 5 x 5; DBH, cm, 5 x 5
March 1999	33.83	Predominant height, m, 5 x 5; DBH, m, 5 x 5

Volumes per hectare were calculated using equations for slash pine, and were adjusted for the number of stems enabling a better comparison between different pure and hybrid populations, particularly after thinning. These volumes are reported as mean annual increments (MAI).

Data Analysis

Cone, seed and plant yields and abnormalities

Cone yields (percent), numbers of seeds per cone and per gram, seed viability and percentages of culled plants calculated from count or weight data for families were averaged by cross type. Standard errors were not calculated, as subsample data were unavailable. The percentage of plants in each abnormality class was calculated from plot data, and family and cross-type averages determined.

Slash pine versus putative F_1 hybrid

The heights and diameters of the putative hybrids identified in the three slash pine CSO plots in the field trial (n= 11) in 1999 were analysed separately from the pure slash pine of the same plots for each of the three measures. Comparisons between the two crosses were undertaken for unbalanced data in PROC GLM, in SAS (SAS 1994), with cross as a random effect in the model. For comparison of slash pine (n = 69) with the putative hybrids (n = 23) in the block adjacent to the experimental trial, the average diameter of the three slash pines corresponding to each hybrid was used and differences were tested by a similar procedure to that described above.

Slash pine versus F2 hybrids

Differences between slash pine from the seed orchard, slash pine of the full-sib family, and the F2 inbred and outcrossed hybrid populations were tested via PROC GLM in SAS (SAS 1994), using plot means and cross as a random effect in the model. The identities of all putative hybrids in the slash pine, CSO stock were not known at the 1973, 1974 and 1978 measures or assessments (all prior to the late 1978 thinning), so these slash CSO means would be biased. However, those putative hybrids identified in 1999 were excluded from the CSO bulk plots in prior years.

RESULTS AND DISCUSSION

Cone and Seed Yields and Some Seedling Characteristics

Although statistical testing was not possible, there appeared to be no substantial differences between the inbred and outcrossed F_2 and slash pine families in cone yields and seeds per cone, nor between inbred and outcrossed F_2 hybrids in numbers of seeds per gram (Table 3). Slash pine had fewer seeds per gram as expected since it is known to have larger seeds than loblolly pine. However, germination percentages of two of the three inbred F_2 families appeared substantially lower than those of the outcrossed F_2s and the slash pine families (Table 3). The relatively low percentage for the slash pine CSO seed may reflect probable inclusion of unidentified F_1 hybrids, as indicated by the presence of putative hybrids in the trial plots and adjacent block, and/or the seed from the young orchard included some selfs.

Table 3. Average cone and seed yields and seed germination and seedling cull rates for the outcrossed F_2 and inbred F_2 hybrids, full-sib slash pine family and the slash pine from the clonal seed orchard.

Cross type	Family	No. of flowers/cones		Ave. no. seeds		Bed germination	Culls
		Pollinated	Collected	Per cone	Per gram		
Outcrossed F_2 hybrid	TE-5xET-9	9	7	104	32	80.5	8.8
	TE-5 xET-11	7	6	99	30	75.1	NA
	TE-6xET-10	7	6	111	37	80.7	8.7
	ET-8 xTE-6	5	4	130	37	85.0	15.7
	ET-8xET-12	6	6	120	36	87.2	11.0
	Overall		85%	113	34	81.7	11.1
Inbred F_2 hybrid	TE-5xTE-6	7	7	87	35	61.5	5.6
	TE-6xTE-7	7	5	107	41	71.9	18.5
	ET-8xET-10	8	6	143	41	57.2	22.0
	Overall		82%	116	39	63.5	15.4
Slash pine families	E-15xE-9	9	9	109	27	86.4	4.4
	E-15xE-40	9	6	129	28	82.0	0.4
	Overall		83%	119	27.5	84.2	2.4
Slash pine seed orchard	bulk	bulk	NA	NA	22	74.0	0.50

The slash pine samples had much lower cull percentages than the F_2 hybrids, for which the outcrossed hybrids tended to have lower values (Table 3). Thus it is possible that the first strong sign of inbreeding depression in the life cycle of inbred (F = 0.25) F_2 s occurs at the seed germination stage, whereas for outcrossed (F=0) F_2 hybrids, hybrid breakdown may be delayed until late in the nursery phase.

Abnormalities in the F_2 Hybrids Versus Slash Pine

Although differences could not be tested, the slash pine CSO bulk exhibited a low incidence of abnormal trees, while the inbred F_2 families had the highest and the outcrossed F_2 families showed intermediate values (Table 4). However, abnormalities may vary considerably among families (Table 4). These observations, together with results shown in Table 3, indicate inbreeding generally gave detrimental effects in the inbred F_2 population. Abnormalities in the CSO slash pine may have been largely among the putative F_1 hybrids included since QFRI records show the three F_1 hybrid families which gave the parents of the F_2s in this study all showed abnormal trees (varying proportions) in the field.

Table 4. Percentage abnormal types in each of four abnormality classes: Normal, slight, moderate and severe, assessed during January 1974 in populations of three cross types.

Cross type	Family	Normal	Slight abnormality %	Moderate abnormality %	Severe abnormality %
Outcrossed F2 hybrid	TE-5 xET-9	75	8	7	10
	TE-5xET-11	81	13	4	1
	TE-6xET-10	77	12	6	5
	ET-8xTE-6	89	7	1	3
	ET-8xET-12	95	0	4	1
	Mean	83.4	8.0	4.4	4.0
Inbred F2 hybrid	TE-5 x TE-6	58	13	11	18
	TE-6xTE-7	67	16	6	10
	ET-8xET-10	49	20	15	16
	Mean	58.0	16.3	10.6	14.7
Slash orchard	bulk	94	2	1	3

Numbers of Measurable Trees per Plot by Cross Type

The average numbers of measurable trees per plot varied among cross types (Table 5), reflecting the variation in occurrence of abnormal trees which could not be measured, and the thinning at 13.5 years of age. These differences would be expected to influence mean diameters and volumes per hectare.

Table 5. Average numbers of trees measured for diameter per plot by cross type and year.

Cross type	Average number of trees measured per plot by age at measure (49-tree plot at 8yr, 25-tree plot thereafter, except slash orchard at 34 yr)		
	8 yr	13 yr	34 yr
Outcrossed F2 hybrid	44.2	22.7	16.9
Inbred F2 hybrid	39.0	19.4	15.3
Slash orchard	39.3	17.3	24.3'
Slash family	46.9	21 7	1 6.7

' For the slash orchard stock only, whole plots (7 rows x7 trees) were measured in 1999 to maximise the number of putative F_1 hybrids available to study. However, on a net, 25-tree-plot basis, which would have been comparable to the other cross types, the average number of measured trees was 12.4 approx. Note that all populations were thinned at 13.5 years of age.

Growth up to Rotation Age

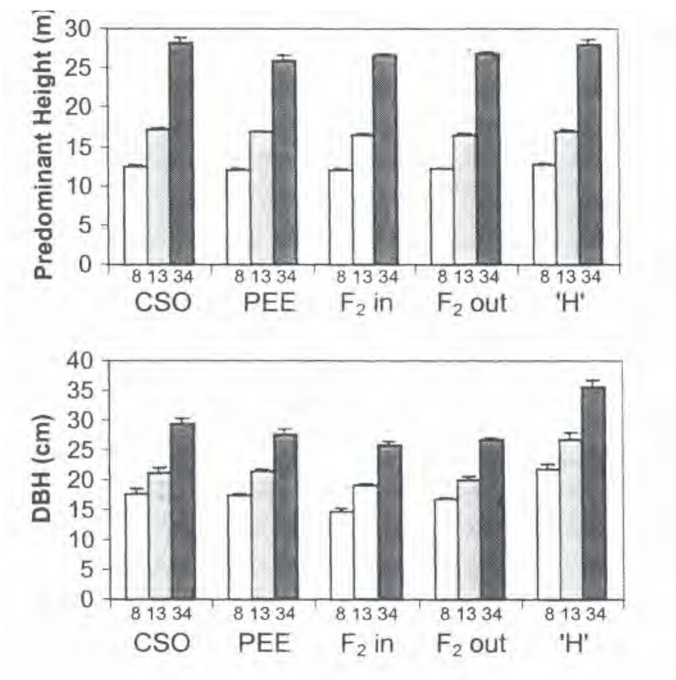
Slash versus putative F_1 hybrids

The putative F_1 hybrids measured in the block of orchard stock adjacent to the experimental trial (n=23) exceeded the pure slash pine there in DBH (P = 0.004), the only parameter measured in this material. Likewise, in the experimental field trial, the putative F_1 (n=11) had greater mean DBH than the pure slash pine progeny from the CSO (P=0.009) at 34 years of age. However, predominant height did not differ significantly between the two cross types (Figure 1), while mean height at 34 years did (Figure 2).

Thus, although the sample sizes were small, the putative F_1 hybrids appeared to exhibit hybrid vigour for DBH relative to slash pine at 34 years on this site. (If loblolly pine had been present, it may have been surpassed also because the site is considered more suited to slash than to loblolly pine). However this result probably reflects exclusion of malformed hybrids removed by thinning, as the putative F_1s did not show hybrid vigour at ages 8 and 13 years (before thinning) (Figure 1).

Slash, F_1 and F2 populations compared

Results of the comparisons of slash pine, F2 and putative F_1 hybrids for growth at 8, 13 and 34 years are summarised in Figure 1, and for 34-year mean height in Figure 2.



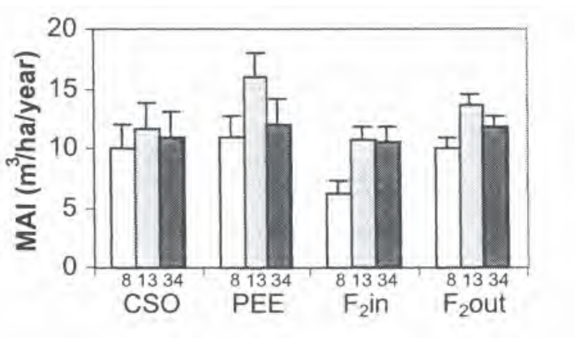


Figure 1. Least squares means estimates of predominant height, DBH and MAI (volume) per hectare, for slash pine from a clonal seed orchard (CSO), a single slash pine control-cross family (PEE), inbred F2 (F2 in), outcross F2 (F2 out), and putative F_1 slash x loblolly hybrids ('H') at 8, 13 and 34 years. (n=11 for 'H', but larger for the other populations).

Linear contrasts not shown indicated that growth differences in DBH or predominant height were confined to several cases of DBH variation only with only one exception (CSO slash pine vs outcrossed F2 for predominant height at 13 years). This suggests there were sufficient numbers of tall trees in all groups such that predominant heights usually did not differ between them. The generally superior DBH of the slash pine CSO sample (Figure 1) was probably due to the inclusion of unidentified putative F1 hybrids, as mentioned above. The inbred F2 group was significantly lower in DBH than one or both slash pine samples at all three ages, whereas the outcrossed F2 group of five families was surpassed in DBH by the CSO slash pine only, and only at 34 years of age. The outcrossed F2 population was not significantly different in DBH (nor height) from the slash family at any of the three ages.

Surprisingly, the inbred F2 group was significantly inferior to the outcrossed F2 hybrids only in DBH at eight years of age, and there was essentially no difference between the outcrossed and inbred F2 populations after this. However, this is likely to be due to the fact that there were more severely-abnormal plants present in the inbred F2 that were not measured (Tables 4 and 5). This probably resulted in inflation of the height and diameter means for the inbred population. Also the thinning of late 1978 may have benefitted the inbred Fes more than the outcrossed F2 hybrids with respect to 34 year growth parameters. These factors would tend to reduce apparent differences between outcrossed and inbred F2 hybrids, and between these hybrids and slash pine. Thus it is considered that the full, negative impact of inbreeding in the inbred F2 hybrids has been underestimated in this study as a result of the exclusion of very inferior trees from measurement.

Volume per hectare, integrating DBH and height growth with stocking of measured trees expressed as MAIs, showed few significant differences via linear contrasts illustrated in Figure 1. At 8 years, the inbred F2 was significantly inferior in MAI to all the other populations (though only marginally to the slash CSO: $P = 0.127$). There were no other differences. However, with age the inbred F2 differences declined: at 13 yr, it was inferior to the PEE and outcrossed F2 only, at low levels of significance (P =

0.064 and P = 0.093 respectively), while at 34 yr there were no signficant differences between populations. Perhaps the lower stockings of measured, viable trees in the slash CSO and inbred F2 populations enabled stand growth to be less inhibited by competition among trees. On this site, considered more suited to slash than loblolly pine, there was no F2 hybrid vigour for volume.

At 34 years the putative F_1 hybrids (n=11) had significantly greater mean height than all but the CSO slash (P = 0.078 for the latter comparison); there were no other significant differences but a tendency for the F2 hybrids to be poorer (Figure 2). The similar mean heights of all but the putative F_1 hybrids may have been due to the loss of many highly inferior trees in the hybrids via the thinning at 13.5yr.

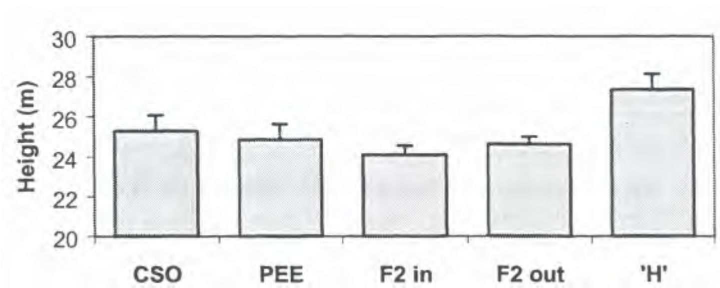


Figure 2. Least squares means estimates of height at rotation age (34 years) ± standard errors for slash pine clonal seed orchard bulk (CSO), slash pine control-cross (PEE), inbred F2 (F2 in), outcrossed F2 (F2 out), and putative slash x loblolly F_1 hybrids (`H'). (n = 7 for 'H' but larger for the other populations).

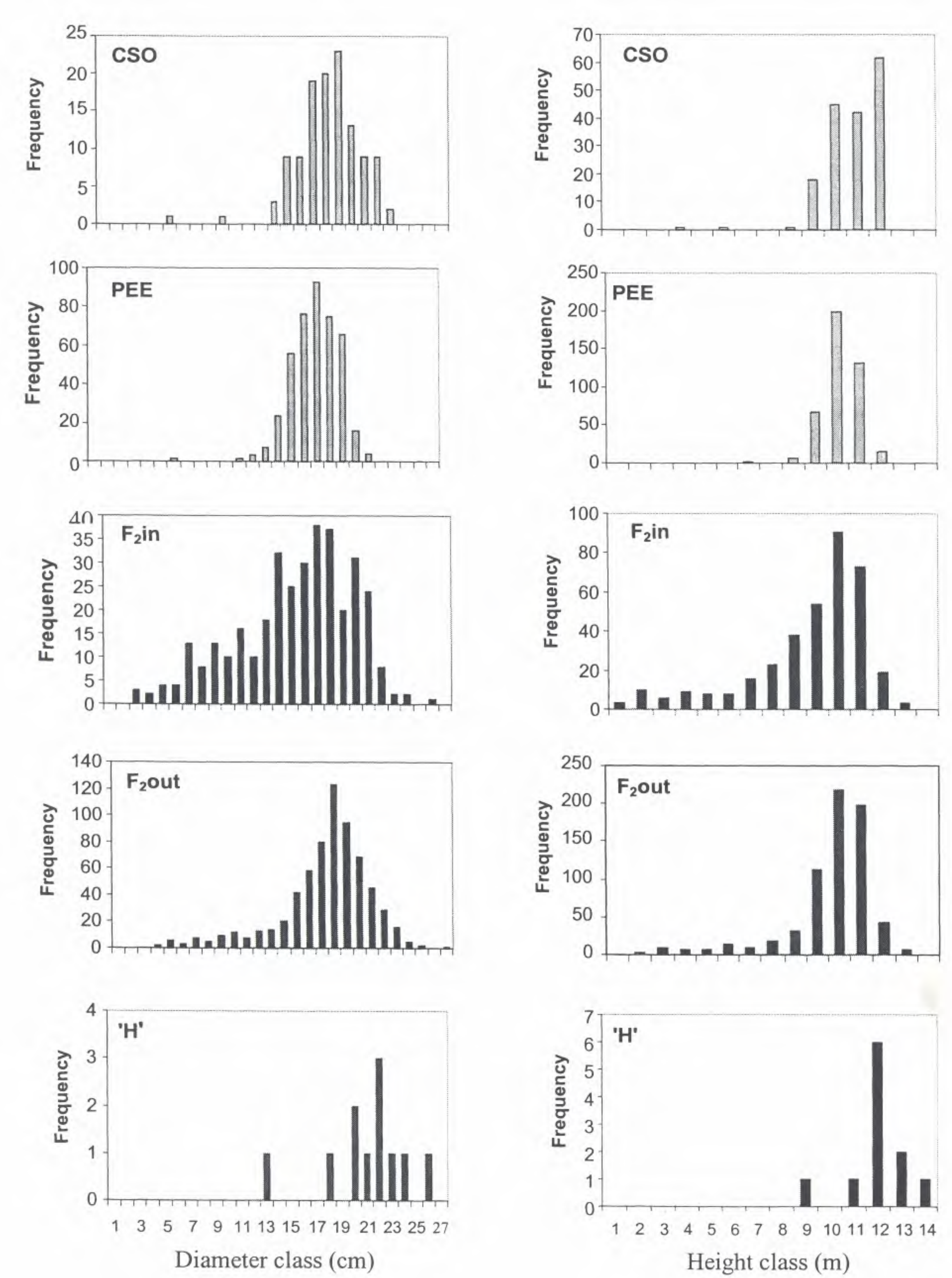
Figure 3 presents the frequency distributions of DBH and height for the different populations at eight years of age, the latest time when whole plots were measured (Table 2). Clearly, the outcrossed (especially) and inbred F2 populations appear to have had wider ranges of tree sizes than the comparable, slash pine CSO stock in both DBH and height. (The single, full-sib family of pure slash pine had relatively narrow ranges, as expected). The high frequencies of small trees in the inbred (especially) and outcrossed F2 hybrid populations reflect their percentages of abnormals (Table 4). Of interest is the fact that the putative F_1 and both types of F2 hybrids included a few - several trees phenotypically beyond the upper range of the CSO slash pine in diameter and height. In fact, the most outstanding tree found in the trial at rotation age (in a combination of DBH, height and stem quality) was an outcrossed F2 tree (in family TE-5 x ET-11) with a DBH of 48.9cm at age 34 years, whereas the most vigorous slash pine nearby was only 39.9cm in DBH.

CONCLUSIONS

It would be unwise to draw strong, broad inferences from the results of this study because of the limited numbers of families, the single test site and the confounding effects of varying numbers of abnormal trees among cross types and of thinning on estimates of growth. However, there are indications that the inbred F2 hybrid of slash x loblolly pine exhibited inferior fitness i.e. lower seed viability, higher plant cull rates, and higher proportions of abnormal trees than the outcrossed F2. It is considered the inbreds performed more poorly than is indicated by the growth data presented because of lower numbers of measurable trees per plot than in the outcrossed F2 and slash family.

Although the F2 hybrids did not exhibit hybrid superiority for growth on the trial site, the normal trees of the outcrossed F2 hybrid population, especially, grew well and included several trees with heights and diameters beyond the range of the largest slash pine trees i.e. putative transgressive segregants, which could be useful in breeding and propagation populations of a tree improvement program. This provides support for the suggestion of Barnes and Mullin (1978) based on their study of 3-year height of 20 F1

Figure 3. Frequency distributions for diameter (LHS) and height (RHS) at age 8.
Note: CSO = slash pine orchard bulk; PEE = slash pine full-sib family E-15xE-40; F2 in & F2 out = 3 and 5 inbred (F = 0.25) and outcrossed (F = 0), full-sib slashxloblolly hybrid families respectively; 'H' = putative F_1 hybrid (n = 11 for 'H' but larger for other populations).



hybrid families that "prospects seem to be good for using the hybrid to assemble diverse populations, to maintain vigour and to provide opportunities for selection in breeding programmes."

The results of Powell and Nikles (1996) and of Westvaco (pers. comm. Davis Gerwig, 1999) with other pines suggest that the loss of hybrid vigour between F_1 and F_2 generations, where the latter are produced by random mating in an F_1 family (Falconer and Mackay,1996, p 257), can be largely avoided or minimised by using superior, preferably unrelated, F_1 parents to produce F_2 hybrids of some *Pinus* species. Results of the present, single-site study did not confirm this suggestion and could reflect inadequacies of the study, that the slash x loblolly hybrid is too wide a cross, or other factors.

The indications of this and the other studies should encourage the study of outcrossed F_2 hybrid populations from superior parents of more species within *Pinus,* and among species of a wide range of genera. If such studies confirm the present indications, then superior, outcrossed F_2 families of some interspecific hybrids could be of particular value in developing breeding and/or propagation populations in cases where F_1 hybrids have low viability and/or are very difficult to propagate vegetatively, but can be grafted or airlayered successfully for CSOs. Furthermore, advancing the F_2 hybrids via parental selection and avoidance of inbreeding for some further generations might yield high-performing, stabilised hybrids or composites retaining a high proportion of the maximum hybrid vigour. Thus the need to maintain separate parental populations for recurrent, F_1 hybrid production would be avoided.

ACKNOWLEDGEMENTS

The authors acknowledge the contributions made at various stages of this long term study by P.C. Bowyer, T.R. Chard (deceased) and M.U. Slee, and by S.L. Chamberlin in processing this document.

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hybrid families that "prospects seem to be good for using the hybrid to assemble diverse populations, to maintain vigour and to provide opportunities for selection in breeding programmes."

The results of Powell and Nikles (1996) and of Westvaco (pers. comm. Davis Gerwig, 1999) with other pines suggest that the loss of hybrid vigour between F_1 and F_2 generations, where the latter are produced by random mating in an F_1 family (Falconer and Mackay,1996, p 257), can be largely avoided or minimised by using superior, preferably unrelated, F_1 parents to produce F_2 hybrids of some *Pinus* species. Results of the present, single-site study did not confirm this suggestion and could reflect inadequacies of the study, that the slash x loblolly hybrid is too wide a cross, or other factors.

The indications of this and the other studies should encourage the study of outcrossed F_2 hybrid populations from superior parents of more species within *Pinus,* and among species of a wide range of genera. If such studies confirm the present indications, then superior, outcrossed F_2 families of some interspecific hybrids could be of particular value in developing breeding and/or propagation populations in cases where F_1 hybrids have low viability and/or are very difficult to propagate vegetatively, but can be grafted or airlayered successfully for CSOs. Furthermore, advancing the F_2 hybrids via parental selection and avoidance of inbreeding for some further generations might yield high-performing, stabilised hybrids or composites retaining a high proportion of the maximum hybrid vigour. Thus the need to maintain separate parental populations for recurrent, F_1 hybrid production would be avoided.

ACKNOWLEDGEMENTS

The authors acknowledge the contributions made at various stages of this long term study by P.C. Bowyer, T.R. Chard (deceased) and M.U. Slee, and by S.L. Chamberlin in processing this document.

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