Three-year height performance of Pinus elliottii Engelm. var. elliottii x P. taeda L. hybrid families on three sites in Rhodesia

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Summary

Pinus elliottii Engelm. var. elliottii and P. taeda L. are important exotics in Rhodesia and each has desirable attributes. Reciprocal hybrid crosses were planned between eight clones from the breeding populations of each species. The cross P. elliottii X P. taeda produced an average 25 viable seeds per cone whereas the reciprocal produced less than one. Progeny tests, each comprising 20 full-sib hybrid families between four P. elliottii female, and five P. taeda male parents, and nine open-pollinated half-sib non-hybrid families from the parents, were planted at three localities. An analysis of three-year height measurements showed that there was more within-family variation in the hybrid than there was in the non-hybrid families. General cambining ability variance remained high in the hybrids although there was a statistically significant amount of specific combining ability associated with certain clones. Over all families, heterosis was negative at the locality where environmental conditions were most favourable far growth and positive where conditions were marginal for the two species. The prospects for using hybrids between P. elliottii and P. taeda to assemble diverse populations for selection are good and may have special value where the species are grown as exotics when there may be increased chances of finding a "hybrid habitat".

Key *words:* Pinus elliottii Engelm., P. taeda L., hybrids, cross-ability, heterosis, hybrid habitat, general combining ability, specific combining ability.

Zusammenfassung

Pinus elliottii Engelm. var. elliottii und Pinus taeda L. sind wirtschaftlich wichtige Baumarten in Rhodesien. Nach Kreuzung von 8 P. elliottii-Klonen und 8 P. taeda-Klonen in sog. Samenplantagen konnten bei den P. elliottii X P. taeda-Kombinationen ungefähr 25 keimfähige Samen pro Zapfen erzielt werden, während in umgekehrter Richtung im Durchschnitt nur weniger als 1 Samen pro Zapfen zu erzielen war. Die dreijährigen Hybridnachkommenschaften aus diesen Kreuzungen wiesen im Höhenwachstum eine größere Variation auf als die beteiligten Kreuzungsfamilien innerhalb der jeweiligen Art. Heterosiseffekte zeigten sich nur dort, wo die Standortsbedingungen für beide Arten weniger günstig waren.

Introduction

Many successful hybrids have been made amoag pines. Most species are heterozygous but heterosis in growth rate has been the exception rather than the rule. Heterosis in fitness occurs more frequently and a few interspecific crosses exhibiting this type of hybrid vigour are used commercially. Although the expected potential of hybridization in the genus has not been realised, most pine hybrids do tend to be viable and fertile and there are still prospects that further experimentation will lead to the production of valuable material.

Pinus elliottii Engelm. var. elliottii and P. taeda L. are both important afforestation exotics in Rhodesia. Although their optimum environmental requirements are similar, each species has adaptive and morphological attributes which make it more suitable than the other in certain circumstances. P. elliottii is more drought resistant and also more tolerant of poor drainage than P. taeda. It is less severely affected by the group dying fungus, Rhizina inflata (Schaff.) Karst., and less susceptible ta damage by fire. P. elliottii tends to have better stem and branch characteristics, allows more flexibility in management, its timber is generally favoured by the trade and it is a high yielder of oleoresin. P. taeda on the other hand is more resistant to the pine woolly aphid, Pineus pini (L.), and to the honey fungus, Armillaria mellea (Vahl ex Fr.) Kummer. It captures the site more rapidly, is more tolerant of cold conditions and is much more resistant to windthrow and wind breakage at higher altitudes. P. taeda generally yields more timber than P. elliottii.

Breeding Programmes far P. elliottii and P. taeda were started in Rhodesia in 1960. Populations of plus trees (superior phenotypes) were built up and controlled crosses were made for progeny tests. Both the incentive and the conditions were therefore present for experimentation with hybrids between these two closely related species and

Table 1. — Analysis of variance, ranked means and Duncan Multiple Range test of three-year height (m) for four half-sib P. *elliottii* (E), five half-sib P. taeda (T) and 20 full-sib hybrid families at three localities.

Source of variation	d.f.	Mean square	Variance component value	Variance component percent
Localities (L)	2	842.045***	0.510	27
Families (F)	28	63.867***	0.338	18
F x L	56	6.745***	0.094	5
Replications in L	15	3.782**	0.009	<1
Error (pooled)	420	1.445***	0.060	3
Trees in plots	4,364	0.884	0.885	47

Repeatability of family performance over localities = 78%

Family ♀	Parents ♂	Rank	Mean height (m) and D.M.R.T.
8(T)	mixed T	1	4.58
162(T)	mixed T	2	4.32
10(T)	mixed T	3	4.28
13(T)	mixed T	4	4.21
49(E)	8(T)	5	4.21
49(E)	10(T)	6	4.03
9(E)	10(T)	7	3.98
49(E)	162(T)	8	3.89
49(E)	13(T)	9	3.83
9(E)	13(T)	10	3.83
171(T)	mixed T	11	3.81
129(E)	8(T)	12	3.79
9(E)	162(T)	13	3.70
177(E)	10(T)	14	3.66
177(E)	13(T)	15	3.59
129(E)	10(T)	16	3.56
9(E)	8(T)	17	3.54
49(E)	mixed E	18	3.50
177(E)	162(T)	19	3.36
9(E)	mixed E	20	3.35
129(E)	mixed E	21	3.33
129(E)	13(T)	22	3.24
177(E)	8(T)	23	3.23
177(E)	mixed E	24	3.20
49(E)	171(T)	25	2.76
129(E)	162(T)	26	2.59
9(E)	171(T)	27	2.52
177(E)	171(T)	28	2.29
129(E)	171(T)	29	2.12
Overall mean			3.53
Standard error			0.0925

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Source of variation	d.f.	Mean square	Variance component value	Variance component percent
Localities (L)	2	452.706***	0.382	18
P. taeda parents (T)	4	208.378***	0.281	14
P. elliottii parents (E)	3	76.032	0.059	3
T x E	12	10.453**	0.048	2
T x L	8	14.154***	0.053	3
E x L	6	19.268***	0.061	3
T x E x L	24	2.516	0.014	1
Replications in L	15	3.356*	0.009	<1
Error (pooled)	285	1.736***	0.070	3
Trees in plots	2 962	1.090	1.090	53

Repeatability of full-sib families over localities = 75%
Repeatability of P. taeda parents over P. elliottii parents = 85%
Repeatability of P. elliottii parents over P. taeda parents = 55%

Parent		Rank	Mean height (m) and D.M.R.T.
P. taeda	10	1	3.81
	8	2	3.69
	13	3	3.62
	162	4	3.38
	171	5	2.42
Overall mean			3.38
Standard error			0.0512
P. elliottii	49	1	3.74
	9	2	3.51
	177	3	3.23
	129	4	3.06
Overall mean			3.38
Standard error			0.0458

Source of variation	d.f.	Mean square	Variance component value	Variance component percent
Localities (L)	2	4.429***	0.025	15
Families (F)	28	1.084***	0.052	31
F x L	56	0.144***	0.011	7
Replications in L	15	0.048	0.000	0
Error (pooled)	420	0.078	0.078	47

Family Parents ♀	♂	Rank	Transformed mean within plot variance ($\log_{10}(s^2 \times 10)$) m
49(E)	171(T)	1	2.212
177(E)	8(T)	2	2.130
9(E)	171(T)	3	2.114
9(E)	8(T)	4	2.114
49(E)	8(T)	5	1.984
129(E)	8(T)	6	1.932
129(E)	162(T)	7	1.909
129(E)	13(T)	8	1.887
129(E)	171(T)	9	1.869
49(E)	13(T)	10	1.813
177(E)	171(T)	11	1.792
49(E)	162(T)	12	1.746
129(E)	10(T)	13	1.625
171(E)	mixed T	14	1.624
177(E)	10(T)	15	1.623
177(E)	13(T)	16	1.612
9(E)	mixed E	17	1.574
9(E)	162(T)	18	1.556
9(E)	10(T)	19	1.547
177(E)	162(T)	20	1.508
177(E)	mixed E	21	1.497
13(T)	mixed T	22	1.492
49(E)	10(T)	23	1.492
8(T)	mixed T	24	1.488
162(T)	mixed T	25	1.478
10(T)	mixed T	26	1.470
49(E)	mixed E	27	1.453
129(E)	mixed E	28	1.426
9(E)	13(T)	29	1.387
Overall mean			1.702
Standard error			0.0660

this paper describes the production of, and early results with, some of these hybrid families.

The controlled pollinations

Eight P. elliottii and eight P. taeda seed orchard clones were used to make the hybrid crosses. The clones were a sample from the breeding populations of these two species and were not selected for any particular attributes except that they produced sufficient pollen and cones for the experiment.

In Rhodesia P. elliottii reaches its flowering peak in late July or early August whereas P. taeda flowers almost exactly a month later. Therefore the P. taeda pollen for the controlled pollination of P. elliottii had to be collected and stored for eleven months before use while the P. elliottii pollen for the reciprocal cross was collected and stored for only one month. The standard controlled pollination techniques were employed (BARNES and MULLIN, 1974) using casein sausage casing isolation bags.

In 1969, totals of 40 P. elliottii × P. taeda and 48 P. taeda × P. elliottii controlled crosses were made out of the possible 64 for each reciprocal set. There were marked differences in the numbers of cones and seeds produced by reciprocal crosses. Cone recovery from the controlled pollinations was 94% for P. elliottii × P. taeda and 65% for P. taeda × P. elliottii; the overall proportions of filled seed were 24% and <4% respectively. Where P. elliottii was used as the pollen parent, an average of less than one viable seed (range of cross averages — 0 to 10) was produced per controlled pollinated cone collected, whereas P. taeda pollen on P. elliottii yielded an average of 25 (0 to 74) viable seeds per cone.

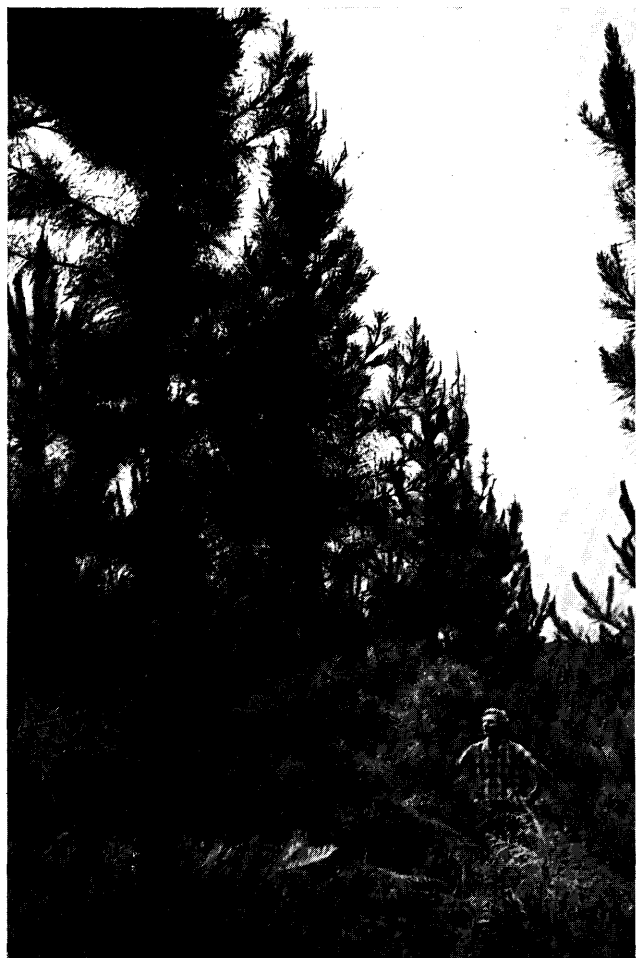Figure 1. — Open pollinated progeny of Pinus elliottii clone 49.

Figure 2. — Open pollinated progeny of *Pinus taeda* clone 8.

The progeny tests

All the controlled pollinated seed produced was sown at the John Meikle Forest Research Station in the Eastern Districts of Rhodesia in June, 1972. There was no formal nursery experiment. In addition to the hybrid families, open-pollinated clonal orchard seed of each parent of both species was sown at the same time. The stock was planted in January, 1973, in tests at the three different localities described below.

Test 14A: Stapleford, altitude 1 750 m, mean annual rainfall, 1 750 mm, thermographic mean monthly temperature *c*. 10 to 17⁰ C.

Test 14B: Martin, altitude 1 280 m, mean annual rainfall 1 015 mm, thermographic mean monthly temperature *c*. 13 to 20⁰ C.

Test 14C: Gonye, altitude 800 m, mean annual rainfall 1 400 mm, thermographic mean monthly temperature *c*. 16 to 23⁰ C.

Despite its relatively high annual rainfall, Gonye has a more severe winter soil moisture deficit (101 mm) than Martin (61 mm) which in turn has a more severe deficit than Stapleford (1 mm). Each test consisted of six replications of 10-tree line plots at 2.5 m square spacing. As many of the *P. elliottii* × *taeda* crosses as possible were planted at each locality; there were insufficient seedlings of any reciprocal *P. taeda* × *P. elliottii* cross for inclusion in the field experiment. Only the complete set of 20 crosses between four *P. elliottii* (female) and five *P. taeda* (male) clones and the nine open-pollinated families of each parent were common to all three localities and the analyses and discussion here are limited to these 29 families. There was no selection in the nursery before planting out. Very few plants failed after germination or pricking out. Total height of each tree was measured in April 1976, three years and three months after planting, by which time 5.8, 5.3 and 12.6 per cent of the trees had died in tests 14A, 14B and 14C respectively.

Two separate analyses of the three-year height data are presented here and each comprises an analysis of variance (fully random model) with F-tests, component estimates and Duncan Multiple Range tests for significance between ranked means. For these analyses the families were grouped as follows: —

1) All 29 families over three sites *(Table 1)*

2) 20 controlled pollinated full-sib hybrid families over three sites *Table 2)*

There were large differences in the variability in plots and these were examined through an analysis of the transformed and scaled within-plot variances ($\log_{10} (s^2 \times 10)$). The results are given in *Table 3*. Within-plot variances were homogeneous within and between the *P. elliottii* and *P. taeda* half-sib families but there were significant differences between them and the hybrid families which generally had larger variances. Among the hybrid families themselves there were significant differences in within-plot variances but these differences were associated with certain parents and were not proportional to the mean. No transformation of the height data was therefore possible and, as there may be heterogeneity in the error term, the Duncan Multiple Range tests in *Table 1* and *2* must be taken as approximations of the significance of differences.

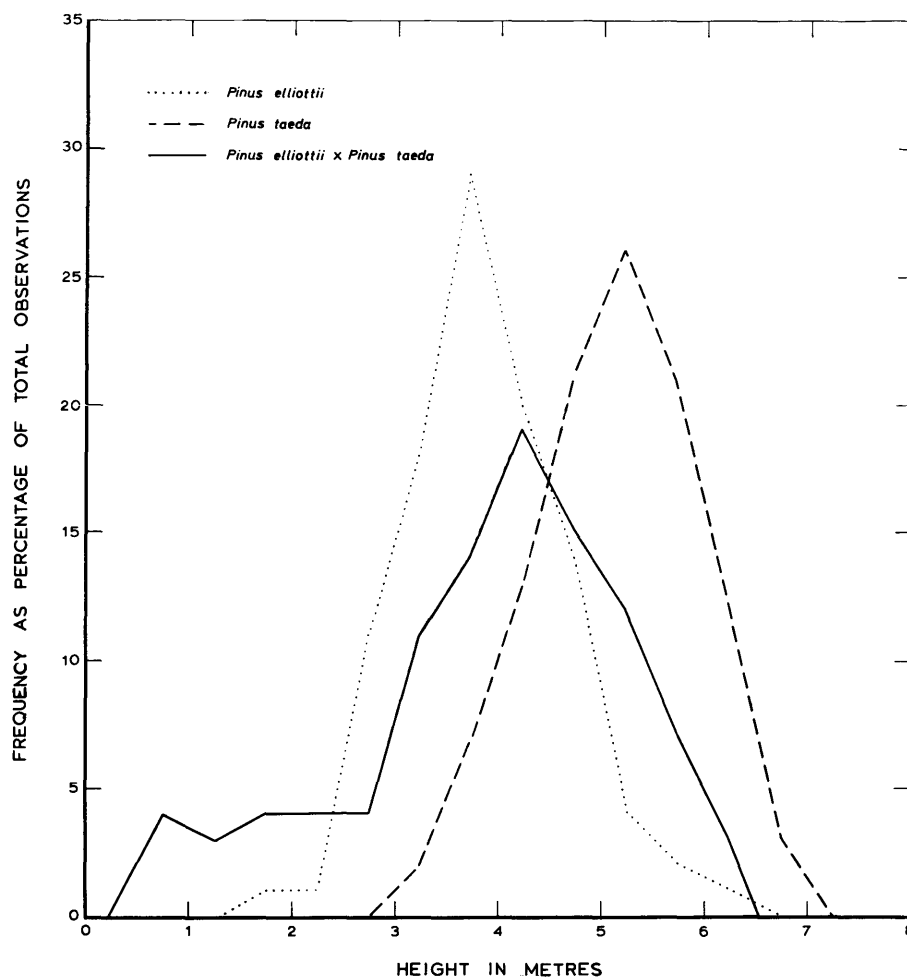Figure 3. — Hybrid progeny of *Pinus elliottii* clone 49 × *P. taeda* clone 8.

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Figure 4. — Frequency distribution of height at three years in *Pinus elliottii, P. taeda* and
hybrid families in Progeny Test 14B at Martin.

Discussion and conclusions

The *P. elliottii* × *P. taeda* cross and its reciprocal have
been reported (e. g. Duffield and Snyder, 1958; Little and
Righter, 1965; Long, 1973). As far as we know it is not
used commercially and no particular attributes have been
claimed for the hybrid except drought resistance (Duffield
and Snyder, 1958).

The most significant factor in the success of the con-
controlled pollinations between the eight *P. elliottii* and
eight *P. taeda* parents was the contrast between the recip-
rocal crosses. Differences have been found in the propor-
tion of empty seed produced by reciprocal crosses between
individual *P. sylvestris* L. trees (Johnsson, 1976). Where a
parent gave a higher percentage of empty seeds when used
as a male than it did when used as a female, there was
speculation that this individual could have been carrying
a higher number of archegonia than the female parent with
which it was mated. Conversely, if more empty seeds were
produced when the parent functioned as a female, the sug-
gestion was that it could have been carrying gametophyte-
lethal recessives. In our case, the differences between the
reciprocal crosses of *P. elliottii* and *P. taeda* were so great
that the more likely explanation for them was the failure
of the *P. elliottii* pollen tube to function normally in the
nucellar tissue of *P. taeda* (see Mirov, 1967). This inhospit-
ability of the *P. taeda* nucellar tissue may be a character-
istic of the species — in other better known hybrid crosses

such as *P. rigida* Mill. × *P. taeda* and *P. palustris* Mill. ×
P. taeda, the pollen parent is always *P. taeda*. Another ex-
planation might have been that the *P. elliottii* pollens had
a poorer viabiilty, but as they were much fresher than
those of the *P. taeda*, this seems unlikely.

Unfortunately, comparable controlled pollination results
for within-species crosses made during the same year as
the hybrids were not available and therefore crossability
estimates, defined by Critchfield (1973) as the yield of
sound germinable seed expressed as a percentage of seed
yield from within-species crosses, could not be calculated,
but we suspect that the crossability would have been over
50 per cent for *P. elliottii* × *P. taeda* and less than one per
cent for the reciprocal, *P. taeda* × *P. elliottii.*

The conditions under which the hybrid crosses were ma-
de did not entirely preclude the possibility that stray pol-
len could have resulted in within-species rather than hy-
brid crosses. However, as *P. elliottii* was the seed parent,
its contribution was assured and since the hybrid progeny
had a far stronger morphological resemblance to *P. taeda*
than to *P. elliottii* (see *Figures 1, 2* and *3)*, there was little
doubt about their hybrid status.

The flowering times of *P. elliottii* and *P. taeda* do just
overlap in Rhodesia (Barnes and Mullin, 1974) and as
stands of the two species are often grown adjacent to each
other in southern Africa it is almost certain that the oc-
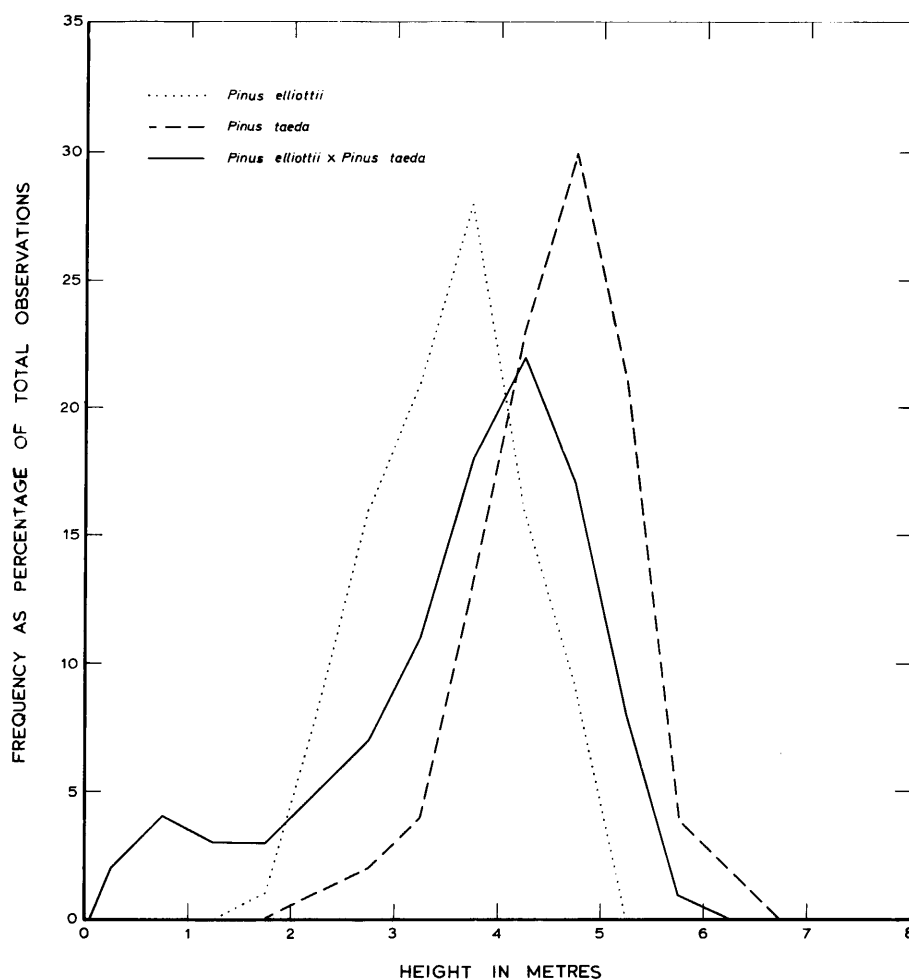casional hybrid occurs naturally. As these are more like

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Figure 5. — Frequency distribution of height at three years in *Pinus elliottii, P. taeda* and hybrid families in Progeny Test 14A at Stapleford.

P. taeda in appearance, such hybrids might be expected in the selected populations of that species rather than among the P. elliottii. There are, in fact, more flowering periodicity irregularities in the P. taeda breeding population in Rhodesia and these might be due to a P. elliotiti influence. We looked at the possibility of a correlation between crossability and flowering periodicity irregularities among the P. taeda clones used to make the hybrids but found only a tenuous, statistically non-significant relationship. Clones 8 and 162, which yielded most viable seed in hybrid combination, showed asynchronous male strobilus development with pollen shed closer to the P. elliottii period; whereas clones 171 and 164, which were among the poorest producers of viable seed, had flowering periodicity patterns which were normal for P. taeda (BARNES and MULLIN, 1974). What is quite clear is that there are very large differences in compatibility between individual P. elliottii and P. taeda trees and, if hybridization is to be pursued at all seriously, it will be essential to work, at least initially, with a large number of clones.

Quantitative geneticists define heterotic response as a deviation of the mean population hybrid from the midparent value (SCHMITT, 1973). The height data in *Tables 1* and 2 show that, overall, there was a negative heterotic effect but that in some specific crosses the response was positive. Most hybrid families were more variable than the intraspecific crosses and those with lower means tended to have particularly high within-plot variances *(Tables 1* and

3). This was due to an element of undersized trees which showed up in the frequency distribution graphs *(Figures 4—6)*. The proportion of small trees was about 13 per cent over all 20 hybrid families, but only half had distinct groups of small trees in them and the frequency in these was about one in four. There seemed therefore to be two levels of increased variation in the hybrid families. One was probably due to the general genetic diversity of the parents while the other may have been due to a dominance bias which might be expected where genetic differences between the parents were large (STUBER, 1970; NILSSON and ANDERSON, 1970). This appeared to be supported by the significant interaction term in the factorial analysis of the hybrids *(Table 2)* although interpretation of these components may be complex (STUBER and COCKERHAM, 1966).

The *P. taeda* and *P. elliottii* parents were ranked independently for general combining ability by the performance of their open-pollinated, half-sib families *(Table 1)* and, through the factorial analysis, by the performance of the full-sib hybrid crosses between them *(Table 2)*. The rankings by the two methods were very similar and the small changes in position of clones 8 and 129 were probably due to specific combining ability effects in hybrid combinations. This stability of ranking, and the relatively high general combining ability variance components exhibited in the analysis of the hybrid families, indicate the value of carrying out hybrid work using selected trees, with high general combining ability, from both parent populations.
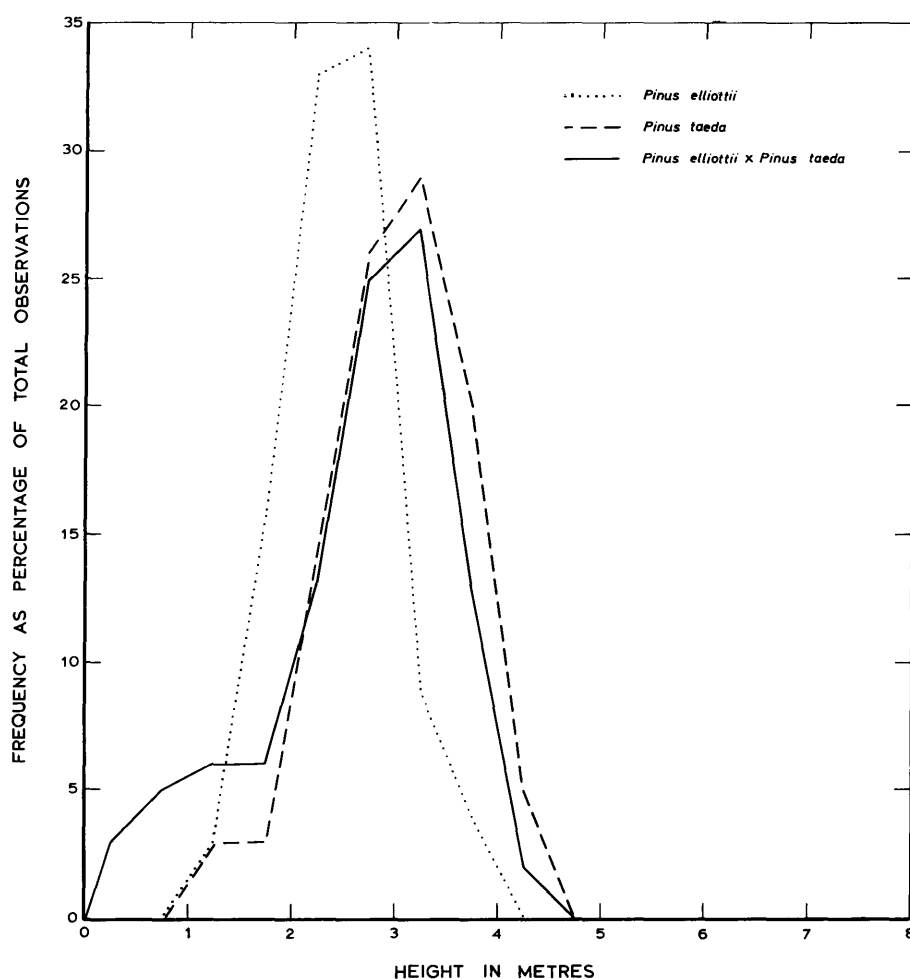
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Figure 6. — Frequency distribution of height at three years in *Pinus elliottii*, *P. taeda* and hybrid families in Progeny Test 14C at Gonye.

Although the genotype-locality interaction term was statistically significant in all three analyses, the component was not large and repeatability of families over localities was not less than 75 per cent in any instance. However, there were interesting differences in the relative performances of the *P. elliottii*, *P. taeda* and hybrid families as groups at the different localities. At Martin where environmental conditions were most favourable for growth, *P. taeda* out-performed *P. elliottii* to the greatest extent and the modal height for the hybrids lay below the midparent value *(Figure 4)*. At Stapleford, environmental conditions were intermediate and although *P. elliottii* performed almost as well as it did at Martin, *P. taeda* did not and the modal height for the hybrid coincided with midparent value *(Figure 5)*. At Gonye where environmental conditions were harsh for both species, particularly for *P. taeda*, the difference between their performances narrowed and the modal height for the hybrids was above midparent value and actually coincided with that for *P. taeda (Figure 6)*. This would seem to be a classic case of positive heterosis being exhibited in a "hybrid habitat" which is marginal for both parents, a phenomenon which has been observed with hybrids between other species of forest trees (WOESSNER, 1973; LESTER, 1973).

This experiment has shown that *P. elliottii* and *P. taeda* have a high unidirectional crossability; that the F_1 progeny are viable and variable; that the hybrid can exhibit positive heterosis in height growth; and that general combining ability variance remains high. Both *P. elliottii* and *P. taeda* have specific, desirable attributes and therefore the 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. We believe that the potential for improvement may be particularly good where the species are grown as exotics in plantations because it is in these conditions that "hybrid habitats" are most likely to occur.

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Computer organised orchard layouts (COOL) based on the permutated neighbourhood design concept

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Summary

COOL is a computer program which produces seed orchard layouts based on the permutated neighbourhood design concept. The program is flexible, coping with irregular areas, up to 100 clones, varying numbers of ramets per clone, and hybrid orchards. It is easy to use, being controlled by a set of English command words, and can be operated without specialised statistical or computing knowledge. The use of COOL should eliminate much of the hard work involved in designing seed orchards.

Key words: seed production, seed orchard design, tree breeding.

Zusammenfassung

Für die Planung und Anlage von Samenplantagen wird ein Computerprogramm (COOL) vorgestellt, mit dem viele Schwierigkeiten bei der Erstellung von Samenplantagen behoben werden können. COOL ist einfach zu handhaben und vielseitig anwendbar. Anlagepläne können auch für unregelmäßig geformte Flächen und für unterschiedlich große Klongruppen konstruiert werden.

Introduction

The first clonal seed orchard in Britain was planted in 1952. Several orchards of various species have been planted since then using a range of designs (Faulkner 1965). In this early period clonal components of the orchards had not been properly tested and the area of individual orchards was generally less than one hectare. Breeding Programmes for the main commercial species have now developed to the stage where most selected trees are in half-sib progeny tests an a nurnber of sites. Selection of clones is based on a full consideration of data from these tests including a detailed analysis of any family X site interaction (Johnstone and Samuel 1978).

New clonal seed orchards of the 1.5 generation type (Weir and Zobel 1975) are being established and before embarking on this programme of orchards a set of basic rules was established.

1. On the basis of past experience, and, to keep the breeding population at an acceptable size in order to minimise problems of relatednoss, the number of clones in any orchard should be between 30 and 50. This number can be reduced by thinning as more information becomes available general and specific combining ability, proportions of male and female flowers, dates of flowering and self-fertility levels.

2. The minimum area of an orchard should be four hectares (Koski 1975) to ensure satisfactory cross-pollination within the orchard.

3. Spacing should be related to the expected shape and development of the crowns for the species and the expected year of the first commercial cone crops.

4. Risk of self-pollinaticm should be minimised.

5. Theoretically all possible crosses should occur with similar frequency to obtain panmixis.

6. For ease of layout, management and the use of machinery for ground cover coatrol, planting should be based on a square or rectangular grid system.

Several types of design have been suggested in the past such as, shifting-clone design (Malac 1962) or a modification of it as used in the southern states of Arnerica; cyclic balanced incomplete block designs (Freeman 1967; Dyson and Freeman 1968); most orchards however use simple randomised designs (Giertych 1975).

Giertych (1975) considered a range of orchard designs and concluded that most tree breeders require minimal self-pollination and good panmixis from their designs. Several designs fulfill these two objectives to a greater or lesser degree but when other factors are considered a permutated neighbourhood design is the most suitable. In commercial orchards factors such as, compariscm of clones or the division of an orchard into replicates for experimentation, are unimportant. The permutated neighbourhood design has not been widely used because it is difficult to coastruct without the aid of a computer, particularly when orchards are extensive and/or have mixtures of clones which are not evenly represented.

La Bastide (1967) developed a computer program for permutated neighbourhood designs which allows all cross-combinations to occur with approximately equal frequency and minimal selfing. However, the program is too rigid and requires the orchard to be rectangular and have equal numbers of ramets per clone.

Experience in Britain shows that prime seed orchard sites are difficult to obtain and are often irregular in shape. In addition the number of ramets available for each clone may not be constant due to varied grafting success, though in some cases varying numbers of ramets may be desirable due to imbalance in flower production between clones. An orchard design was required to take these factors into account and La Bastide having demonstrated the possibility of producing permutated neighbourhood designs by computer, it was decided to develop a similar but more flexible program.