plus 2.0 percent sucrose) and on a 10 percent aqueous sucrose medium. Pollen of lodgepole pine and limber pine failed to germinate. Highest germination of blue spruce pollen was obtained from pollen stored at 50 percent relative humidity; culture medium had no significant effect. Highest germination of ponderosa pine pollen was obtained from pollen stored at 25 to 50 percent relative humidity and cultured on the aqueous sucrose medium.

In a second experiment, pollen stored at 50 percent relative humidity and 0 to 4^0 C. for eleven years was cultured on 0, 5, 10, 15, 20, and 25 percent aqueous sucrose solutions. Optimum concentration for germination of blue spruce pollen was 15 percent; 5 percent for ponderosa pine pollen. In 1954, optimum concentration for gerrnination of fresh pollen from the same lots was 10 percent for both species.

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Progeny Test Designs for Pinus patula in Rhodesia[1])

By J. Burley[2]), P. M. Burrows[3]), F. B. Armitage[4]), and R. D. Barnes[5])

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Introduction

Afforestation with exotic pines in Rhodesia had been in progress for 30 years and some 70,000 acres had been established before tree breeding was initiated in 1958. By then well over half the planted area comprised stands of *Pinus patula* while *P. elliottii* and *P. taeda* accounted for most of the remainder. The iinportance of *P. radiata* had diminished because of its susceptibility to disease. It was evident that the growth rate and health of the first three species was satisfactory, provided sites were carefully selected, but that improvements were desirable in other respects. The phenotypic variation in stem, crown and timber characteristics appeared to warrant the establishment of an improvement programme (Hodgson and Barrett, 1962).

Initially, plus trees were selected for the establishment of clonal seed orchards. Forty such trees of *P. patula* have so far been selected from 3,600 acres of local stands more than 12 years old. Their frequency is estimated at 1 in 31,500 trees remaining in stands selectively thinned to an average of one-third of the original density. Plus tree clones have been randomised in suitably isolated seed orchard areas at altitudes between 5,500' and 6,100'. An additional seven clones have been acquired from other countries and most of these have been incorporated in the seed orchards.

It was provisionally intended to assess the general combining abilities of selected clones by a polycross test, to be followed in subsequent years by diallel crosses among the better combiners (Hodgson and Barrett, 1962; Hodgson, 1963). The limited number of progenies planted to date are those derived from early work undertaken to gain practical experience in controlled pollination techniques.

In 1964 it was realised that, particularly in the early stages of the breeding programme, the progeny testing method used should not only identify the brst general and specific combiners, but should also yield information on population genetics. It was therefore decided to review the existing proposals.

The progeny test plan described here is the outcomr of this review in which it was possible for a forest geneticist and a biometrician to participate with local forest research staff.

The Intended Function of Progeny Testing in Rhodesia

The improvement programme must provide for a local seed source that will yield continuous and adequate quantities of seed representing the maximum improvement attainable at the time of supply.

The respective merits of clonal and seedling seed orchards have been much discussed elsewhere (see for example the first issue of *Silvae Genetica* 13, 1954, devoted to this subject). It is necessary here only to record the local reasons for the choice of progeny tested clonal seed orchards as the intended source of improved *P. patula* seed.

The continual acquisition of new plus trees, changing utilisation requirements and different rates of improvement in the various traits, all imply that seed orchards require periodic reconstitution. Routine progeny testing is essential in order to determine the optimum constitution at any given time. Clonal seed orchards have the advantage that

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[1]) Published with the permission of the Directors of the Agricultural Research Council of Central Africa and the Rhodesia Forestry Commission.

[2]) Forest Geneticist, Agricultural Research Council of Central Africa, P. O. Box 1210, Kitwe, Zambia.

[3]) Biometrician, Agricultural Research Council of Central Africa. P. O Box 3397, Salisbury, Rhodesia.

[4]) Conservator of Forests (Management and Research), Rhodesia Forestry Commission, P. O. Box 8111, Causeway, Salisbury, Rhodesia.

[5]) Forest Officer (Research), Rhodesia Forestry Commission. John Meikle Forest Research Station, Private Bag 76 G, Penhalonga, Rhodesia.

seed producers remaining after roguing are proven by progeny tests. The actual seed producers in a seedling seed orchard, although possibly members of families selected by progeny testing, are only phenotypically proven; they are performance tested rather than progeny tested. Clonal orchards have the further advantages of minimal delay in seed production after reconstitution, and of convenience of working.

This intended seed production programme, however, is clearly dependent upon successful vegetative propagation. Some delayed graft incompatability failures have led to the decision to establish a seedling seed orchard as an interim measure to ensure continuity of seed supply until such time as the clonal propagation problems have been solved.

The long term arrangements envisaged for seed production have been described above in general terms, but detailed planning of their implementation is dependent on knowledge of the following: –

(1) the genotypic variance/covariance structure – used to evaluate selection procedures including predictions of the expected improvements;

(2) the phenotypic variance/covariance structure – required together with (1) for the derivation of the progeny testing routines (knowledge of juvenile-mature correlations is included here);

(3) the genotype-environment interactions – to indicate the extent to which specific genotypes must be bred for specific localities.

With some exceptions in (2) this knowledge is not at present available.

It is accordingly proposed at this stage to expand the original plan for testing the existing plus trees to provide this required information. The interim requirement of a seedling seed orchard will be fulfilled by the eventual use of one of the progeny test plantings for this purpose. The siting of this particular planting will be affected, but the primary function as a progeny test will not be compromised.

Choice of Genotypic Material and Test Sites

The objects of progeny testing are considerably easier to define than are the populations of genotypes and sites on which it is to be performed.

Genotypic material

It has always been assumed *a priori* in the selective breeding of forest trees that selection of superior phenotypes (plus trees) is the correct initial procedure.

Estimates of genetic parameters yielded by progeny tests of plus tree populations do not refer directly to the original forest population; but knowledge of the genetic structure of the original forest population is required for a comprehensive evaluation of the improvement expected through the several phases of the selection programme. Therefore a choice exists between raising progenies from a random sample or from a phenotypically superior sample of the forest population. In our case, progeny testing of plus trees is to be used for the provision of genetic information *and* the determination of the optimum constitution of existing clonal seed orchards. Consequently, genotypic variances in the original forest population will be inferred from those of the plus tree progeny population, rather than estimated directly.

Test sites

A decrease in the within site environmental contribution to phenotypic variation leads to an increase in the precision of clonal comparisons. Uniformity is therefore a consideration in the choice of test sites. If there is a negligible interaction of genotype with site uniformity, choice of atypically uniform sites will not contribute to selection errors in seed orchard reconstitution. However, as no information on genotype-site interactions is available, a small test series is included in the overall plan to study the repeatability of progeny test results over several sites. Subsequently, the resulting information will be used to indicate the importance of within-site uniformity when choosing sites for routine testing.

In the interim, it has been decided to avoid atypically uniform sites for the main test series of this current proposal but to include sufficient replications to maintain adequate precision. Furthermore, the resultant estimates of environmental variation may be more reliably extrapolated to the original forest population.

P. patula is grown on a variety of site types in several localities in the Eastern Districts of Rhodesia. With existing resources it is only possible to plant the main test series at one site in each of two major localities which differ considerably both in macroclimate and in geological history. The planting sites will be some 70 miles apart in the Stapleford (5,200–6,600 ft.) and Martin (3,500–5,500 ft.) Forest Reserves.

Methods of Progeny Testing

Various mating designs are available for naturally outcrossing crops and many are suitable for forest trees although several have not been used in forestry to date. They differ largely in the degree of control over the male parent and hence both in their value for progeny testing and in the quantity of genetic information they yield.

Open and polycross tests

The simplest form is the open pollinated test in which the source of pollen is unknown and the progeny indicate the average value of the female when mated at random (Fabricius, 1922).

In the topcross test, commonly used in agricultural crop breeding, the inbred lines are crossed as males with a uniform population of females. A refinement of this is the polycross test (Tysdal, Kisselbach and Westover, 1942) which may be carried out in two ways, each adaptable for forest crops:

either, interpollination is permitted among all the randomly placed clones in a seed orchard so that the bulked seed from each clone is theoretically the product of random mating between the selected clones as females and all others as males,

or, each clone is pollinated artifically with a mixture of pollens from other clones in the seed orchard, e. g. all the clones; the best phenotypes; the first to produce pollen; those that produce abundant pollen; a random selection (Gustafsson, 1949).

These methods are relatively easy to perform and allow large numbers of phenotypes to be tested economically. However, they yield information only on general female combining ability with no indication of specific combining ability or reciprocal effects. Furthermore, the assumption has to be made that the males in a seed orchard or pollen mix contribute equally to all families. When clones differ in flowering periodicity or pollen productivity, viability and compatibility, this assumption is invalid. Moreover genetic variation amongst the males may increase the variability within families to the extent that differences between families are obscured.

Finally, the lack of control over the male parent in polycross tests renders them inadequate for the additional objective of estimating population genetic parameters.

Two-parent tests

Many of the objections to open and polycross tests are accounted for when some form of systematic controlled two-parent crossing is undertaken.

Estimates of specific combining ability and reciprocal effects are dependent on the design used, as is the partition of genetic variance into the additive, dominance and epistatic portions (Hayman 1954, 1958 a, 1958 b, 1960).

A wide range of two-parent mating designs have been developed and several of these have been described by Cockerham (1963) and Wearden (1964). In order of increasing provision of genetic information, one of possible application here are: —

1. *Bi-parental progenies:* A total of n parents are paired at random to yield ½n families. Genetic information is restricted to the between- and the within-family variances.
2. *Nested mating design:* This corresponds to the North Carolina model I (NCM I) mating design of Comstock and Robinson (1948, 1952). The n (= mf + m) parents are crossed in such a way that to each of the m males there is a group of f females, yielding mf families in all. No female occurs in more than one group. Here, variance among the progeny may be partitioned into three sources: males, females in males, and that within families.
3. *Factorial mating design:* This corresponds to the North Carolina model II (NCM II) design of Comstock and Robinson (1948, 1952). Of the n (= m + f) parents each of the m males is crossed with every one of the f females yielding mf families. This is the approach recommended by Zobel and Kellison (1963) in their 4-tester plan for the North Carolina State-Industry Tree Improvement Programme. Here, variance among progeny may be partitioned into four sources: males, females, the interaction males × females, and that within families.
4. *Diallel mating design:* The n parents are crossed in all possible combinations, including selfs, yielding n^2 families (Schmidt, 1919; Yates, 1947; Jinks and Hayman, 1953; Hayman, 1954, 1958 a, 1958 b, 1960; Griffing, 1956 a, 1956 b). With this design variance among the progeny may be partitioned into four sources: the n parents as males and as females, the interaction males × females (which can be subdivided into selfs and the remainder), the reciprocal differences, and the variance within families.

The n^2 families in the last design comprise three groups: the n selfs, a group of ½n (n-1) crosses and the ½n (n-1) reciprocals of these. Griffing (1956 b) indicated three incomplete methods of performing the diallel: one set of ½n (n-1) crosses alone, one set of ½n (n-1) crosses together with the selfs, the set of ½n (n-1) crosses and their reciprocals but omitting the selfs.

When there are some n = 40 clones to be tested however, these designs would be excessively expensive to perform and even less complete forms of the diallel must therefore be considered. The chain block mating design of Cockerham (1963), the partial diallel cross (Matzinger and Kempthorne, 1956; Kempthorne and Curnow, 1961; Fyfe and Gilbert, 1963), sampling of the n^2 possible crosses (Hinkelmann and Stern, 1960; Curnow, 1963; Stern, 1964) are examples of such restricted forms. Although these alternatives may provide sufficient genetic information they are, in varying degrees, of reduced value as methods of progeny testing. This is particularly so when sampling of the parent population excludes some of the plus trees to be tested. Conversely the NCM II design, which is also a sampling of the crosses in the complete diallel, is satisfactory as a progeny test method but does not include reciprocals and is, in this respect, limited as a source of genetic information.

Comparative ratios: families planted per parent tested

When the number of parents tested is fixed, resources required by various designs can be compared on the basis of the number of families planted. Alternatively, when the number of families planted is fixed, the number of parents tested can be compared. Three test designs are compared in this way in *Table 1*. They represent the extreme and intermediate positions with respect to the amount of genetic information provided by two-parent tests.

Table 1. — Comparisons of numbers of parents tested and families planted with three 2-parent designs.

Number of planted families when number of tested parents (n) is fixed.

n	Bi-parental Progenies	North Carolina Model II			Complete Diallel
		f = m	f = 2 m	f = 5 m	
6	3	9	8	5	36
12	6	36	32	20	144
18	9	81	72	45	324
24	12	144	128	80	576
30	15	225	200	125	900
36	18	324	288	180	1296

Number of parents tested when number of planted families (p) is fixed.

p	Bi-parental Progenies	North Carolina Model II			Complete Diallel
		f = m	f = 4 m	f = 9 m	
16	32	8	10	—	4
36	72	12	15	20	6
64	128	16	20	—	8
100	200	20	25	—	10
144	288	24	30	40	12
196	392	28	35	—	14
256	512	32	40	—	16
324	648	36	45	60	18

The versatility of the NCM II design is apparent. The ratio f/m can be manipulated until available resources are deployed over the parents to be tested, subject to the constraint that the number of males is greater than a predetermined minimum.

The Test Plan Proposed

The theoretical and practical requirements presented above have resulted in the choice of a test plan for the existing plus trees, which comprises four separate though complementary designs — a polycross test, an NCM II series, and two sets of incomplete diallel crosses.

The polycross test

In accordance with the original proposals (Hodgson, 1963) a pollen mixture representing 20 plus trees has been applied to 28 of the 47 clones to be tested.

This test will no longer constitute the only or the major progeny test in view of the limitations of the method already noted. It will, however, be completed to provide direct practical and theoretical comparisons of the polycross with two-parent tests.

The NCM II series

Of the four designs included this is the most important in respect of both the amount of genetic information yielded and the number of clones tested.

Generally, the precision of the clonal comparisons increases with the number of tester males. It was foreseen that some 35 of the 47 clones would produce sufficient flowers in the 1965 and 1966 seasons to be incorporated in a tester series and that a maximum of seven tester males could be handled provided the pollination, nursery and planting phases were each spread over two year periods. To ensure that the tester males were representative of the population under test, the clones were stratified into seed origin groups. With the proviso of adequate flowering, one clone was selected at random from each of the first five groups and two from the sixth and largest group.

In the 1965 season these seven clones were used to pollinate just over half of the remaining 28. Thus, theoretically it will be possible to plant seven tester series with the first group of 14 clones as females in 1968 and with the second group of 14 in 1969. However, it is possible that in practice not all the crosses will yield sufficient seed and that fewer than seven tester series, or fewer than 14 females in each year, will be available. Six or even five tester series will be acceptable and the number of females in each year will be balanced.

By distributing the work over two years the groups tested become subject to year effects so that controls must be included. The same controls will be used in later tests of the clones not included in 1968 and 1969 plantings. These control crosses ("genetic checks", ZOBEL and KELLISON, 1963), will be chosen from the incomplete diallel test described next.

The reciprocal test

Neither the polycross test nor the NCM II series provide information on reciprocal effects. Furthermore, the seven clones used as tester males must be tested in comparable fashion to the 28 clones tested as females. A complete diallel cross among the seven testers would meet both these requirements; but because of the generally deleterious effects and poor seed production of self-pollination in conifers, the seven selfs have been omitted from the complete diallel. The 42 families of the resulting incomplete diallel will be planted in both 1968 and 1969 with the main tester series. These plantings will also provide information on 42 specific combining abilities additional to those of the main tester series.

The genotype-site interaction test

Resources limit the planting of the NCM II series and the reciprocal test to one site in each of two localities (see previous section). The site to site repeatability of progeny test results will be examined by smaller progeny tests planted at several sites within the localities. These will take the form of single replicates of the 21 families in the incomplete diallel obtained by omitting the selfs and reciprocals from the complete diallel cross among the seven testers.

This series of test plantings will be repeated within localities as many times as seed resources permit. It is intended to maintain consistency in the choice of which familiy in a reciprocal pair is included. However, to extend the series to as many sites as possible some pooling of seed from reciprocal crosses may be necessary.

Quantitative Models and Statistical Analysis

The following general model has been adopted to represent the phenotypic observation of a quantitative character on a single tree: —

$X_{klpqrs} = M$ (a general mean)
$+ F_k$ (the "genetic" mean effect of the k th family)
$+ Y_l$ (the effect of the l th year of planting)
$+ S_p$ (the effect of the p th site)
$+ R_q$ (the effect of the q th replication at the p th site)
$+ P_r$ (the effect of the r th plot in the q th replication)
$+ T_s$ (the effect of the s th tree in the k th family)
$+$ the 2- and 3-factor interaction effects representing the family-environment interactions,

where X_{klpqrs} is the measure on the s th tree of the k th family planted in the r th plot of the q th replication at the p th site in the l th year. The phenotypic variation is partitioned into the analogous variance components: —

$$\sigma^2_X = \sigma^2_F + \sigma^2_Y + \sigma^2_S + \sigma^2_{FY} + \sigma^2_{FS} + \sigma^2_{FSY} + \sigma^2_R + \sigma^2_P + \sigma^2_T$$

All the additive parameters in this model are assumed "random effects" in the sense of ANDERSON and BANCROFT (1952). The problems associated with the assumption that effects such as years and sites are "random" have been considered by HANSON (1964), whose approach will be adopted in the ultimate summary of this series of estimated variance components.

For the first requirement of reconstituting the clonal seed orchards, analyses are based on the extended model for the genetic mean of the k th family (SPRAGUE and TATUM, 1942): —

$$F_k = g_i + g_j + s_{ij}$$

where g_i is the general combining ability of the i th plus tree as male,
g_j is the general combining ability of the j th plus tree as female,
s_{ij} is the specific combining ability associated with the i × j cross.

The variation among the family means is correspondingly partitioned into the general combining ability variance, the specific combining ability variance and the reciprocal variance.

Not all of the effects in these models are included in each of the four designs of the progeny test plan presented above. For the analysis of any one design, the models must be re-defined accordingly.

With the exception of the polycross test, estimates of the specific combining abilities are available in the form of family means over the replications, taken either within or over all sites according to the magnitude of the genotype-environment interaction variance. Estimates of general combining abilities are available from the polycross and the NCM II series as the clonal means over families and replications, again computed either within or over sites. In the case of the two sets of incomplete diallel plantings, estimating equations for general combining abilities have been derived and are given later.

For the second requirement of quantifying the structure of genetic variation in the progeny, the variance among the family means is partitioned according to the mating designs and the resulting variance components are interpreted according to the further model (Kempthorne, 1957; Lerner, 1958): —

$$\sigma_G^2 = \sigma_A^2 + \sigma_D^2$$

where σ_G^2 is the genetic variance in the progeny population and σ_A^2 and σ_D^2 are the additive and dominance portions respectively. Epistatic variation is assumed negligible.

Standard formats for the analyses of variance and the expected values of mean squares are given by Griffing (1956 a), Cockerham (1963) and Bohren, McKean and Friars (1965) for the four designs involved in this plan. The variance components in these expected values of mean squares can be expressed in terms of the half- and full-sib covariances. Under the assumptions listed by Kearsey (1965), these contain fractions of σ_A^2 and σ_D^2 as follows: —

half-sib covariance $= \frac{1}{4}\sigma_A^2$

full-sib covariance $= \frac{1}{2}\sigma_A^2 + \frac{1}{4}\sigma_D^2$

With the exception of the polycross design, the variance between trees in plots (denoted by σ_T^2) will contain the full-sibs genotypic variance amongst together with the within-plot environmental variance σ_E^2. For the polycross design, σ_T^2 contains a mixture of half-sib and full-sib covariances in proportions that are unknown unless unwarrantable assumptions are made.

The validity of this model and the assumptions referred to above have been questioned by Gilbert (1958) and Kempthorne (1960), whose comments are especially appropriate here in view of the lack of knowledge in quantitative forest genetics. The adoption of this model implies an obligation to test its validity by comparing the results of future plantings of parentally known material, with the theoretical predictions based on the model and its estimated parameters.

The standard partitions of the between-family variance are well documented in the references listed and they are not repeated here; only the sib-covariances available in each design of the plan are noted. It is necessary, however, to indicate the format of analysis of the family variation as replicated in localities, sites and years as proposed in this project. This is done below for the four designs of the plan separately.

The polycross test

With r replications of f families (corresponding to the f clones tested as females) at each of two sites in the one year, and with t trees per plot, the analysis of variance shown in *Table 2* applies.

The genotypic variance information is limited to σ_F^2. It is necessary to assume that each of the m males in the pollen mix is equally likely to have provided the paternal contribution to each member of each maternally identified family. When this is true, σ_F^2 and σ_I^2 have the following expectations: —

$$\sigma_F^2 = \frac{1}{4}\sigma_A^2 + \frac{1}{4m}\sigma_D^2$$

$$\sigma_I^2 = \frac{1}{4}\left[\left(3-\frac{1}{m}\right)\sigma_A^2 + \left(4-\frac{1}{m}\right)\sigma_D^2\right] + \sigma_E^2$$

As noted previously this assumption is unlikely to be valid and this in turn implies a possible source of bias in clonal comparisons.

The NCM II series

With m testers and two female clonal groups of f plus trees each, resulting in mf families in each of the two years, and with r replications of t trees per plot at both sites, the analysis of variance shown in *Table 3* applies.

Following Kearsey (1965), the between-families variance (σ_F^2) is expressed in terms of the paternal half-sib covariance (between males), the maternal half-sib covariance (between females), and the difference between the full-sib covariance and twice the half-sib covariance (males × females interaction). The two half-sib covariances provide estimates of $\frac{1}{4}\sigma_A^2$, and if these are very different, the presence of maternal effects is usually inferred. The male × female interaction variance component provides a direct estimate of $\frac{1}{4}\sigma_D^2$, and the component σ_T^2 contains σ_E^2 together with the full-sib variance. Thus it is possible to estimate σ_A^2, σ_D^2, σ_E^2.

Table 2. — Analysis of variance for the polycross plantings.

Source of variation	Degrees of freedom	Expectation mean square
Between families	(f—1)	$\sigma_I^2 + t\,\sigma_P^2 + rt\,\sigma_{FS}^2 + 2rt\,\sigma_F^2$
Between sites	1	$\sigma_T^2 + t\,\sigma_P^2 + ft\,\sigma_R^2 + rt\,\sigma_{FS}^2 + frt\,\sigma_S^2$
Families × sites	(f—1)	$\sigma_T^2 + t\,\sigma_P^2 + rt\,\sigma_{FS}^2$
Between replications in sites	2 (r—1)	$\sigma_T^2 + t\,\sigma_P^2 + ft\,\sigma_R^2$
Families × replications in sites	2 (r—1) (f—1)	$\sigma_T^2 + t\,\sigma_P^2$
Between trees within plots	2 rf (t—1)	σ_T^2

Table 3. — Analysis of variance for NCM II series.

Source of variation	Degrees of freedom	Expectation mean square
Between sites in years	2	$\sigma_T^2 + t\,\sigma_P^2 + mft\,\sigma_R^2 + rt\,\sigma_{FS}^2 + mfrt\,\sigma_S^2$
Between replications in years in sites	4 (r—1)	$\sigma_T^2 + t\,\sigma_P^2 + mft\,\sigma_R^2$
Between families in years	2 (mf—1)	$\sigma_T^2 + t\,\sigma_P^2 + rt\,\sigma_{FS}^2 + 2rt\,\sigma_F^2$
Families × sites in years	2 (mf—1)	$\sigma_I^2 + t\,\sigma_P^2 + rt\,\sigma_{FS}^2$
Families × replications in years and sites	4 (r—1) (mf—1)	$\sigma_I^2 + t\,\sigma_P^2$
Between trees within plots	4mfr (t—1)	σ_T^2

Table 4. — Analysis of variance for the reciprocal test.

Source of variation	Degrees of freedom	Expectation mean square
Between sites	1	
Between years	1	
Sites × years	1	
Between m(m-1) families	m (m—1) – 1	$\sigma_T^2 + t\,\sigma_P^2 + rt\,\sigma_{FSY}^2 + 2rt\,(\sigma_{FY}^2 + \sigma_{FS}^2) + 4\,rt\,\sigma_F^2$
Families × sites	m (m—1) – 1	$\sigma_T^2 + t\,\sigma_P^2 + rt\,\sigma_{FSY}^2 + 2rt\,\sigma_{FS}^2$
Families × years	m (m—1) —1	$\sigma_T^2 + t\,\sigma_P^2 + rt\,\sigma_{FSY}^2 + 2rt\,\sigma_{FY}^2$
Families × sites × years	m (m—1) —1	$\sigma_T^2 + t\,\sigma_P^2 + rt\,\sigma_{FSY}^2$
Between replications in sites and years	4 (r—1)	$\sigma_T^2 + t\,\sigma_P^2 + m\,(m-1)\,t\,\sigma_R^2$
Families × replications in sites and years	4 (r—1) [m (m—1) —1]	$\sigma_T^2 + t\,\sigma_P^2$
Between trees in plots	4m (m—1) r (t—1)	σ_T^2

The reciprocal test

With r replications of the ½m (m-1) crosses and their reciprocals amongst the m tester males in each of two years and at each of two sites, the analysis of variance shown in *Table 4* applies.

The between-family variance component (σ_F^2) can be partitioned into half-sib and full-sib covariances similar to the NCM II analysis, together with the reciprocal variance (Griffing, 1956 a). Eisen, Bohren and McKean (1964) have discussed the joint contributions of maternal and sex linkage effects to the interpretation of the reciprocal variation. It is not possible *a priori* to speculate on these effects in this species.

The analysis of these plantings provides the most comprehensive information on genotype-environment interaction variance of the four designs in the overall plan, with estimates of σ_{FSY}^2, σ_{FS}^2, σ_{FY}^2.

The appropriate formula for the within-sites and within-years estimation of the general combining ability of the i th clone, after adjustment for non-orthogonality, is: —

$$\hat{g}_i = \frac{1}{r\,(m-2)}\left\{\frac{1}{2}\sum_j^m (X_{ij} + X_{ji}) - \frac{1}{m}\sum_i^m\sum_j^m (X_{ij})\right\}$$

where X_{ij} denotes the total over the r replications of the means of plots containing the cross between clones i and j. The variance of the difference between the general combining abilities of two clones is then: —

$$\text{var}\,(\hat{g}_i - \hat{g}_j) = \frac{1}{r\,(m-2)}\left\{\frac{\sigma_T^2}{rt} + \frac{\sigma_P^2}{r}\right\}$$

The genotype-site interaction test

With p plantings of the ½m (m-1) crosses in the incomplete diallel (no selfs, no reciprocals) as single replicates of t trees per plot, the analysis of variance shown in *Table 5* applies.

With the absence of replications within sites, there is no strict "error" term in this analysis for the test of families × sites interaction. However, the other three designs in the plan all provide estimates of the plot to plot variation which will be assumed appropriate for this test. The site to site repeatability of the test results will be indicated by the ratio $\sigma_F^2/(\sigma_F^2 + \sigma_{FS}^2)$ which ranges from zero to unity.

The partition of the between-family variance component into the general combining ability variance (half-sib covariance) and the specific combining ability variance (full-sib covariance minus twice the half-sib covariance) is given by Griffing (1956 a). These taken together with σ_T^2 provide estimates of σ_A^2, σ_D^2 and σ_E^2 as was the case with the NCM II series and the reciprocal test.

Within-site estimates of the general combining abilities adjusted for non-orthogonality are given by the formula: —

$$\hat{g}_i = \frac{1}{(m-2)}\left\{\sum_j^m (X_{ij} + X_{ji}) - \frac{2}{m}\sum_i^m\sum_j^m X_{ij}\right\}$$

where X_{ij} is the mean of the plot containing the cross between clones i and j. The variance of a clonal comparison of general combining abilities is given by

$$\text{var}\,(\hat{g}_i - \hat{g}_j) = \frac{2}{(m-2)}\left\{\sigma_P^2 + \frac{\sigma_T^2}{t}\right\}$$

Analytical methods

Some general points must be made in respect of all the analyses described. Several terms in these analyses are obtained by pooling variances from sites and years. This is only possible if satisfactory homogeneity of variance prevails. As described, the analyses are appropriate to full stands of t trees in all plots and the blanking operation in

Table 5. — Analysis of variance for the genotype-site interaction test.

Source of variation	Degrees of freedom	Expectation mean square
Between sites	(p—1)	$\sigma_{FS}^2 + {}^1/_2m\,(m-1)\,\sigma_S^2$
Between families	¹/₂m (m—1) —1	$\sigma_{FS}^2 + p\,\sigma_F^2$
Families × sites	(p—1) [¹/₂m (m—1) —1]	σ_{FS}^2
Between trees in plots	¹/₂m (m—1) p (t—1)	

the initial stages ensures that this is so until approximately the eighth year evaluation. When thinning has introduced unequal numbers of trees per plot, non-orthogonal analyses will be performed.

In general, it is proposed that all analyses will be computer processed. General statistical analysis routines capable of dealing with the polycross and the NCM II series already exist for the computer available (A. R. C., 1964 and 1965). Special computer routines will be compiled for the two sets of incomplete diallel series and also to link together all the routines into one coordinated system. The system will be tested at the first opportunity (probably using as test data the observed height in the nursery immediately prior to planting) and will then be operable on a routine basis for each successive evaluation of the planted progenies. By repeating all analyses on sums of the individual variables in pairs, phenotypic and genotypic covariances will be obtained. Additionally, the facility for evaluating juvenile-mature correlations in respect of both the mean and the variance will be included.

Field Plans and Management

When the seed resulting from the 1965 pollinations has been collected, the seed yield of the 1966 pollinations will be predicted. Successive sowings late in 1967 and 1968 will then be arranged so that nursery designs will resemble the field designs of the plantings in 1968 and 1969 respectively. In this way nursery and field replications will be confounded (Wakeley, 1932). The full details of the field plans need not be finalized until early 1968 but in the interim assessment and analysis of existing progenies will be undertaken to indicate optimum dimensions for plots and blocks.

Nevertheless, following a review of the controversy concerning optimum plot size and shape for progeny testing (Wright and Freeland, 1959, 1960; Evans, Barber and Squillace, 1961; Shiue and Pauley, 1961; Conkle, 1963; Johnsson, 1963), it is currently envisaged that the families in the polycross test, the NCM II series, the reciprocal test and their common controls will be arranged as row plots in adjacent sets of randomized complete or incomplete blocks. It is expected that the size of the planting area required will preclude the use of plot surrounds. The year blocks will be adjacent but separate, thus avoiding double-sized replications and one year age differentials between adjacent row plots.

The entire experimental planting for one year will be surrounded by five rows of commercial stock. In the case of the test planting to be used eventually as the temporary seedling seed orchard, this surround will be of a species other than *P. patula.*

The single replicates of the genotype-site interaction test will be planted at a series of sites representing a wide range of site conditions, *e. g.* ridge tops and slopes of varying exposure and the latter at various gradients. The number of such sites at each of the two localities in each of the two years will be determined when the seedling resources are known.

Both nursery and field work will conform to normal afforestation practice but care will be taken to maintain uniformity of treatment throughout. The planting sites will, perforce, be second rotation areas. Planting espacement will be eight feet between and within rows. Extra transplants will be established in the rows so that they can be moved to fill in blanks during the planting season and, if necessary, one year later. Spare plants not required for this purpose will then be removed. The filler plants will be measured and recorded as such during all subsequent assessments.

Normal pruning will be practised but delays in successive stages might be permitted if necessary to ensure adequate assessment of branching characteristics.

There would be some conceptual and analytical advantages if a form of non-silvicultural, systematic thinning were undertaken to maintain equal numbers of trees per plot. However, the family means after silvicultural thinning are more pertinent to selection for normal afforestation. It might be desirable to delay thinning so that assessment is based on means of unthinned plots at the latest stage of development possible, i. e. before stand competition appreciably modifies the true characteristics of the component individuals. Current practice permits the first thinning to be delayed until the eighth or ninth year after planting. The interpretation of the effect of a further delay would be assisted to some extent by Correlated Curve Trend thinning experiments in progress locally (Anon., 1964).

It is intended to carry the main tester series and the reciprocal test through a full commercial rotation of 30 years. Although it is anticipated that comprehensive reconstitution of the existing clonal seed orchards will not be possible before the 15th to 20th year, it is envisaged that earlier roguing, based on stem and crown form characters, will be necessary.

Summary

Since 1958 forty plus trees of *Pinus patula* have been selected in Rhodesia and establised in clonal seed orchards. The original proposals for progeny testing are being replaced by the plan presented here. The change is necessary to provide information on population genotypic and phenotypic variances and covariances, genotype-environment interactions and routine methods of progeny testing, in addition to indicating the optimum reconstitution of seed orchards.

Emphasis is placed on the distinction between the genotypic structure of the original forest population and that of the plus tree population. Similarly, the difference between typical and highly uniform sites is stressed in relation to the interpretation of the progeny test results.

A review of possibly applicable progeny test methods is presented. This has led to the choice of three designs to supplement the existing polycross proposal: a factorial mating design and two incomplete diallel cross designs. One-half of the required pollinations have been performed and the tests will be planted in 1968 and 1969.

A general quantitative model of phenotypic variation has been adopted and provides the basis for analyses of variance appropriate to the four designs.

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Zuwachs und Entwicklung junger Lärchenbestände verschiedener Herkunft

Von MIROSLAV VYSKOT[1]

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Die Lärchenprovenienzforschung steht wegen der großen Bedeutung dieser Holzart im Vordergrund unserer Arbeiten. Dabei wecken Lärchenprovenienzen aus dem Gebiet des Gebirges Nízký Jeseník in Mähren, die im Ausland als Sudetenlärchen bekannt sind, ein verstärktes Interesse. Dies veranlaßte auch die Anlage von Vergleichsversuchen mit Lärchen mährischer, tschechischer, slowakischer und österreichischer Herkunft. Dieser Arbeit nahm sich im Jahre 1937 G. VINCENT an, der in Kontakt mit wissenschaftlichen Instituten und der Praxis in der ČSSR und in Österreich Samen von repräsentativen Lärchenökotypen aus verschiedenen Höhenstufen in den erwähnten Gebieten sammelte. Die Samen wurden aus Lärchenpopulationen gewonnen, so daß die Absaaten bestimmte Bestände auf bestimmten Standorten repräsentieren. Das Samenmaterial wurde sorgfältig in Baumschulen ausgesät und das angezogene Pflanzenmaterial im Jahre 1938 auf einer größeren Versuchsflächenserie ausgepflanzt.

In unserer Arbeit werden wir eine von diesen angelegten und schon 25 Jahre hindurch beobachteten Versuchsflächen auswerten, und zwar die Versuchsfläche im Forstrevier Jezírko, Abteilung 61 a, auf dem Gebiet des Forstlichen Schulbetriebs der Hochschule für Land- und Forstwirtschaft in Brno. Auf dieser Versuchsfläche werden insgesamt 8 Provenienzen verglichen; 2 davon stammen aus Mähren (Adamov und Ruda nad Moravou), 1 ist tschechischer (Kuří Vody), 2 slowakischer (Sabinov und Vysoké Tatry), und 3 sind österreichischer (Wienerwald, Semmering [Steiermark] und Deutsch Griffen [Steiermark]) Herkunft. Die Mutterbestände dieser Provenienzen repräsentieren Höhenlagen von 400 m bis 1300 m ü. N. N., wobei die meisten von ihnen aus Höhen von 400—500 m stammen (Adamov, Sabinov, Kuří Vody, Wienerwald und Ruda n. Mor.). Die Provenienz Semmering kommt aus einer Höhe von 800 m ü. N. N., die Provenienz Vysoké Tatry aus 1200 m ü. N. N. und Deutsch Griffen aus 1300 m ü. N. N.

Über die Mutterbestände existieren folgende Angaben:

Adamov: Alter des Mutterbestandes 80 Jahre. Der Bestand wird aus Lärchenüberhältern gebildet. Er stockt auf einem mittleren Podsolboden des Ergußgesteines von Brno (Granit).

Ruda nad Moravou: Der Samen wurde in einem 85jährigen Bestand gesammelt, in dem Lärchen mit sehr guter Form 50% Anteil hatten. Der Bestand befindet sich auf Gneis in einer südöstlichen Exposition.

Sabinov: Der Samen wurde in einem 70jährigen Bestand gesammelt. Weitere Angaben fehlen.

Vysoké Tatry: Der Samen stammt aus einem 90jährigen Bestand, der konische, tief beästete Stämme auswies.

Kuří Vody: Hier stammt der Samen aus einem 60jährigen Bestand. Von den Provenienzen *Wienerwald, Semmering* und *Deutsch Griffen* liegen keine genaueren Herkunftsangaben vor.

Die Provenienzversuchsfläche im Forstrevier Jezírko, die die 8 oben beschriebenen Provenienzen umfaßt, besteht da-

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[1] Verfasser ist Direktor des Instituts für Waldbau der Forstlichen Faktultät der Landwirtschaftlichen Hochschule in Brno, ČSSR.