# FORWARD SELECTION PLOTS IN BREEDING PROGRAMMES WITH INSECT-POLLINATED TREE SPECIES

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## ABSTRACT

For trees which are naturally insect-pollinated and have effective pollination ranges of less than 40 m, the Forward Selection Plot (FSP) design provides an open-pollinated breeding population layout that is effective for ranking families, for within-family selection, and, subsequently, for collection of seed for the breeding population of the next generation. It therefore provides a basic field resource for breeding which will give near-optimal genetic gain at low cost. It can be used with a sublined breeding population and can also be used to provide improved seed in commercial quantities. The use of the computer programme "NO INCEST" to help layout FSPs minimises the chances of inbreeding in the seed collected after evaluation and roguing of the test.

**Keywords**: forwards selection; breeding programme; tree breeding; insect-pollinated trees.

## BACKGROUND

Selecting the best trees in the best families ("forwards selection") for cloning in a seed orchard and selection of new breeding-population parents are often the main objectives of a progeny trial. Selecting the parents of the best families on the basis of open-pollinated progeny performance in such trials ("backwards selection") for planting in clonal seed orchards will also give good genetic gains, particularly if heritabilities are low. Designs may involve various plot sizes, with higher precision usually achieved by single-tree-plot designs with 20 to 30 replications (i.e., trees) per family (Loo-Dinkins & Tauer 1987). Alternatively, randomised row-plot tests (e.g., six replications of 6-tree row-plots—36 trees per family) will give somewhat less precise family rankings (Loo-Dinkins & Tauer 1987).

When clones are being selected for seed orchards, intensive selection both between and within families is appropriate, whereas the selection of breeding population parents requires much less-intensive selection between families, so as not to overly reduce the effective population size. The optimal number of trees per family for within-family selection can be inferred from the relationship between selection intensity (in standard deviation units) and

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the number of trees screened per select tree (Fig. 1). Selection ratios from the best tree in 30 to the best tree in 50 appear to give optimal gains for a single trait given finite financial resources. (Note: this assumes a normal distribution for the trait under consideration, be it a simple trait or a multi-variate function).

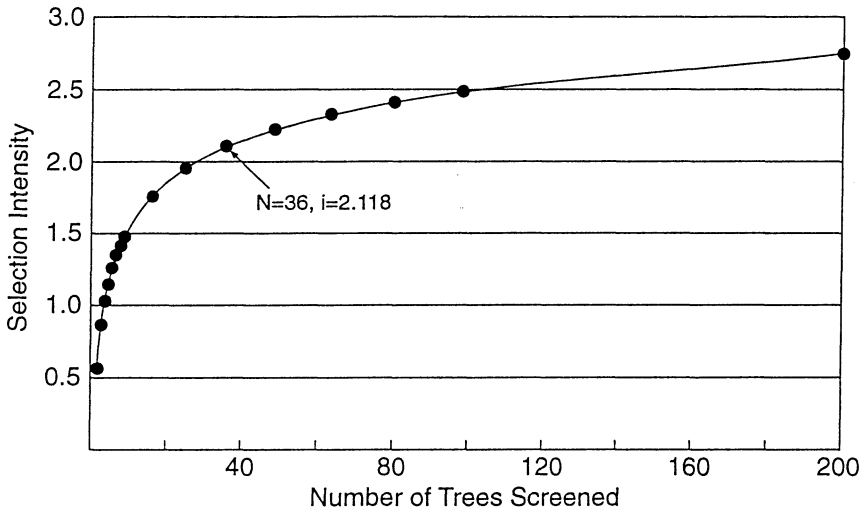


FIG. 1–Relationship between selection intensity (standardised selection differential) and number of trees screened per select tree (from Burdon & Shelbourne 1971).

Open-pollinated seed is required from trees selected in the breeding population trial to provide families with which to plant the next breeding population. Also, trials may be required to yield commercial seed, to be collected either from the whole trial or from selected trees within it. The number of genotypes involved may vary when producing seed for these different purposes but one concern, that of minimising chances of inbreeding, remains throughout.

Breeding programmes can employ different trial designs and different numbers of trials to achieve their objectives. The approach for genetic improvement of *Pinus radiata* D.Don in New Zealand has involved using (1) a control-pollinated factorial design with single-tree-plots on three sites to provide estimates of general combining ability of parents (and thence of the additive genetic values of pair-cross means), and (2) pair-crosses (say in a disconnected factorial design) with plots of 50 trees to provide for within-family phenotypic selection. After within-family selections, grafts of the best trees of the very best families have been made and then planted in a seed orchard for production of commercial seed. To produce seed for the future breeding population, grafts of the best trees from the better families have been made and planted in clonal archives and, after these flowered, desired crosses have been made by controlled pollination. This approach to genetic improvement has provided good results for *P. radiata* (Shelbourne *et al.* 1989), which has been planted on 1 200 000 ha of land in New Zealand to date, but it is too costly for species that are likely to be planted less extensively. For such species, a simpler and less expensive approach, which still gives good gains from selection between and among families, is desirable.

Breeding of *Eucalyptus nitens* (Deane et Maiden) Maiden, *E. regnans* F.Mueller, and *E. fastigata* Deane et Maiden, is currently being undertaken by the New Zealand Eucalypt Breeding Cooperative (Cannon & Shelbourne 1991). However, the anticipated planted area of any of these species is minor compared to that of *P. radiata*, and, as a result, funding for the breeding of these species is more modest. Furthermore, controlled pollination of the tiny flowers of these eucalypts for an entire breeding population would be costly and difficult. One way of containing costs and avoiding the need for controlled pollination is to rely on open-pollinated mating for progeny tests of the breeding populations. The main sacrifice entailed is loss of full pedigree information and thus future control of inbreeding. Another way to contain costs is to reduce the number of trials needed for ranking families and for making between-family and within-family selections. To these ends, a combination of two test types has been adopted. The first, a single-tree-plot (STP) trial, is used to give precise family rankings at one site. The second type of trial has been dubbed a Forward Selection Plot (FSP) trial, the design and advantages of which are the focus of this paper.

## CHARACTERISTICS OF THE FORWARD SELECTION PLOT TRIAL

The FSP trial should be able to:

(1) Accommodate the breeding population;

(2) Obtain family means and thereby estimate breeding values at one site (rankings from another site coming from an STP trial); testing of families at more than one site is needed to select for families with a stable high performance (testing at three or four sites would be desirable but would be too expensive);

(3) Provide opportunities for within-family selection with a selection ratio of 1:30 to 1:50;

(4) Minimise the chances of mating between members of the same family in adjacent blocks after thinning reduces family row-plots to one tree per block;

(5) Produce seed through open-pollination of selections from the breeding population after selective thinning (this seed would be formed from crosses between the better individual trees from most families);

(6) Where sublines are used, control future build-up of co-ancestry in seed orchards by doing mainly within-family selection and maintaining reproductive isolation between sublines.

Sublining is the division of the breeding population into unrelated groups of genotypes. Criteria for deciding how to divide families into sublines have been discussed by Burdon & Namkoong (1983). The main purpose of sublining is to ensure that there is no inbreeding in future seed orchards; this is achieved by allowing only one selected clone from each subline to be represented in the open-pollinated seed orchard. Crosses to produce seed for the next breeding generation can take place only between trees in the same subline and the same subline groupings will be maintained in future generations.

In selection for the breeding population, within-family selection is paramount. If too much emphasis is placed on between-family selections, the effective population size of the breeding population sublines will be reduced and this leads to inbreeding. Crossing between close relatives must also be avoided to minimise inbreeding. Where sublining is used with an open-pollinated species, special care is needed to ensure that the trial is planted in such a way that chances for crossing between half-sibs are minimised.

All of these considerations impose several constraints on the FSP design. In order to ensure that distance between selected half-sib individuals exceeds the effective pollination range (EPR*) at the conclusion of the test, there must be a certain minimum number of families in each subline replicate. The requirement of between 30 to 50 individuals per family for selection (Fig. 1), the need to compare these family members visually, and the need for at least six replications of randomised multi-tree plots to obtain sufficiently precise estimates of family means are other factors that determine the design parameters of the FSP. From six to 15 replications of eight to three trees per family row-plot would be acceptable for estimating family means and for allowing sufficiently intense within-family selection.

Four factors, therefore, control the FSP design: the EPR of the species, the number of trees to be planted in each family-row-plot, the spacing between trees within row-plots, and the spacing between rows.

Some eucalypts and several other insect-pollinated trees have an approximate EPR of 40 m (Pryor 1976; A.R. Griffin pers. comm.). With such an EPR, eight-tree row-plots, a spacing of 2.7 m within rows, and 4 m spacing between rows, it was found, using a specially designed computer program called NO INCEST (Cannon & Low in prep.), that 30 was the minimum number of families needed per replicate to reduce risks of sib-mating (30 row-plots per replicate). More families would be needed if a greater EPR was to be accommodated (i.e., > 40 m), or if row plots were smaller, or if spacing was reduced. Generally, however, the number of families tested in any row-plot progeny test, subline, or set must be kept small (i.e., less than 50) or each replication will become too large and will encompass too much environmental variation.

Several features of the FSP design are shown schematically in Fig. 2. After the growth potential and form of the trees have become apparent (perhaps 4 to 8 years from planting, depending on the growth rate), all trees in the test can be measured and the family rankings determined. Then, the best tree in each family plot in each replicate can be selected phenotypically and the best tree over all replicates for each family can be selected using block adjustment techniques (adjusting for the performance of all members of a family).

The trial is then thinned by removing every tree except the selected tree in each plot. It is important that this thinning precedes collection of open-pollinated seed by at least 18 months so that the offspring of the most recently produced seed are predominantly crosses between unrelated selected genotypes in the trial. Remaining trees of the same family will be separated by the EPR (40 m) or greater. If the test's primary purpose is to advance the breeding population, then only a few of the families (perhaps 20%) can be removed entirely since heavier culling would unduly narrow the genetic base. After seedlots from breeding population selections are collected, a much more rigorous culling of entire families (the more poorly ranked families) can be carried out to give maximum genetic gain from commercial seed collected in the residual stand. If seed production were the only objective, closer initial stocking would be desirable to maximise selection intensity. It should be noted that with advancing generations, seed collected from the thinned breeding population will become progressively more inbred.

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* The effective pollination range (EPR) is defined as the range within which 90% of the pollen causing natural fertilisation of a designated tree must originate (Cannon & Low in prep.).

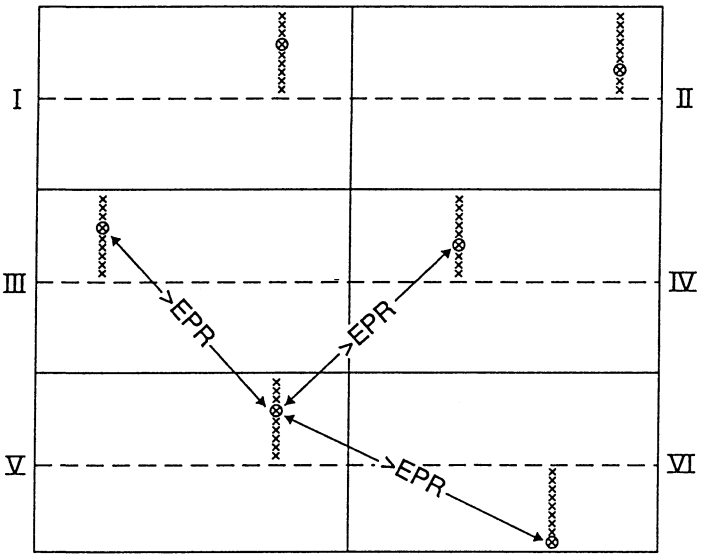


FIG. 2–Operation of the Forward Selection Plot layout. The computer program NO INCEST lays out the family x in randomly assigned row plots after first ensuring that the mid-points of row plots of this family are separated by at least the EPR (Effective Pollination Range). Positions of other families in the test are similarly assigned. Phenotypic selection is used at about one-half rotation age to select the best tree to remain in each row plot (⊗ for family x); all other trees are thinned.

There are other designs for an open-pollinated breeding population which could be opted for in lieu of the FSP; for example, a non-contiguous multi-tree-plot design (where several individuals per family are planted in each replication) or single-tree-plots. Both of these are more efficient for giving family rankings than row-plots such as the FSP (Loo-Dinkins & Tauer 1987). However, the process of selecting the best individual tree per family is more complex and time-consuming and involves additional measurements and analyses since visual phenotypic comparisons cannot be made; additionally, block and nearest-neighbour adjustments would be required. It is also very difficult to achieve the desired spacing of trees at time of thinning with these designs. With small row-plots and the FSP design, a target spacing of say 100 stems/ha with 10 m ± 5 m of distance between final select trees is relatively easy to achieve. All that need to be known are the final objectives of the FSP and whether seed is required for the breeding population alone, or for commercial seed collection as well.

Selection of trees in the very best families, and grafting of scions from these to plant in clonal seed orchards, will give the highest genetic gains. An alternative strategy is to collect open-pollinated seed from these same ortets and to plant out seedling progenies in a design similar to the FSP but with sublines mixed and with plot location controlled by the program NO INCEST. Genetic gains from a seedling orchard of this type are estimated to be very similar to those of the equivalent clonal orchard (Shelbourne 1992).

A practical factor which would tend to favour the use of the clonal seed orchard approach in New Zealand is that for many tree species grown, good growth rates are rarely found in

the same areas where seeding is heavy. Thus the FSP test should be planted in an area conducive to good expression of growth and form characteristics and needs to be able to produce only enough seed for the next breeding population. For commercial seed production, grafts from the best trees of the best families would be outplanted in a clonal orchard on a good seed-producing site.

## APPLICATIONS

The use of the Forward Selection Plot design, in combination with single-tree-plot tests, can accomplish most of the objectives of a tree improvement programme with insect-pollinated species while minimising costs to only a fraction of the amount required to test an equal number of families using a control-pollinated approach such as the one used for improving *P. radiata* in New Zealand. Furthermore, the expected gains from the open-pollinated breeding population are only slightly lower than for the control-pollinated (Shelbourne 1992).

The full pedigree is lost using the open-pollinated approach, but the FSP design, coupled with selective thinning, minimises chances of crossing between members of the same family. The FSP design is particularly appropriate when a breeding population, consisting of perhaps 200–800 open-pollinated families, is divided into sublines. For example, the New Zealand breeding populations of *E. nitens*, *E. regnans,* and *E. fastigata* each consist of 300–450 families which have been divided into 10–15 sublines each containing 30 to 40 families (Cannon & Shelbourne 1991). In the field each subline is planted with a FSP layout and is located at a distance of greater than 40 m (the EPR) from any other subline, with a buffer planting of a non-hybridising species. It is possible to produce commercial seed from thinned FSP progeny tests, although a grafted or seedling seed orchard could give heavier seed crops and should give much higher genetic gains.

The FSP design is also suitable for layout of seedling seed orchards where the top families (say 25 to 35 of these) have already been identified through previous progeny testing. In this situation, mainly within-family selection is appropriate.

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