THE NUCLEUS BREEDING SYSTEM

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Abstract. -- A description is given of nucleus breeding as a system where the traditional breeding population is divided into a small elite "nucleus" and a large "main" population. The nucleus population is regenerated each generation by control-pollinations involving assortative mating. This assortative mating, together with intensive combined index selection, is intended to maximise short term genetic gains in the nucleus. These rapid early gains can be transferred into plantations using clonal forestry or seed orchards. Selection and mating in the large main population is less intensive in order to ensure continuing genetic gains in the longer term.

A fundamental feature of nucleus breeding is transfer of genes between main population and nucleus. The nucleus is "open" in the sense that it is replenished each generation by transfer of highly productive breeding individuals from the main population. This transfer from main to nucleus allows genetic improvement made in the main population to be incorporated into the nucleus, thus improving the potential nucleus gain beyond what could be expected in a "closed" structure (with no transfer). Transfer from main to nucleus allows inbreeding in the nucleus to be maintained at acceptable levels.

The transfer of genetic material in the opposite direction, from nucleus to main, allows genetic improvements made by mating outstanding individuals in

in tree breeding in terms of optimising the proportion of resources devoted to the nucleus versus the main population.

INTRODUCTION

This gaper describes the system of "nucleus breeding" which was first proposed for tree improven ent by Cotterill *et al.* (1988). The fundamental feature of nucleus breeding is that breeding effort and investment are concentrated on the best (nucleus) material in the breeding population. The nucleus strategy fits very well with clonal forestry. Nucleus breeding has been a relatively recent innovation in sheep improvement cooperatives in Australia and New Zealand (fames 1977, Rae 1979).

CYCLIC IMPROVEMENT

The breeding population is improved each generation by selecting superior trees and then mating these select individuals to produce improved progeny. These progeny are planted in the field to become the next generation breeding population for future selection. Every one (or maybe two) generations the gains made in the breeding population are exploited by taking the very best individuals from the breeding population and using them in seed orchards or clonal forestry (as depicted in Figure 1).

This well known cyclic improvement of the breeding population is the foundation stone of tree breeding. If good gains are not produced from each cycle (generation) of improvement in the breeding population the tree breeding enterprise will eventually fail. The importance of gains in the breeding population is well illustrated by Cotterill and Jackson (1989) in their investigation of alternative seed orchard strategies. These authors demonstrate that over three-quarters of the genetic gain expected from culled second-generation clonal orchards is due to the two cycles of improvement in the breeding population. The other one-quarter of the gain is due to selecting a few outstanding individuals from the second-generation breeding population

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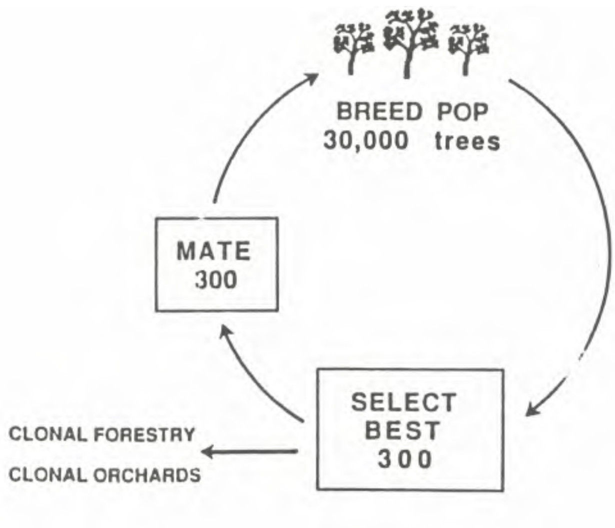
to establish the orchard, a I then subsequently culling the orchard on the basis of progeny test results. Under clonal fort try the I rogress made in the breeding population also has a major influence on the overall superiority of mass propagated clones.

Figure 1. Cyclic improvement in the breeding population.



POPULATION STRUCTURE

Nucleus breeding involves reorganising the traditional breeding population used in tree improvement to create a two-tier structure including: large "main" breeding population, arid elite nucleus population. Following case studies given in Cotterill *et al.* (1988) the main breeding population may be a constant 300 parents each generation which are mated to generate say 30,000 progeny. Cotterill *et al.* (1988) argue that open-pollinated mating may be used to regenerate the main each generation (discussed later).

The nucleus is initiated by screening the main breeding population for outstanding trees. Cotterill *et al.* (1988) suggested that the nucleus population may have around 40 parents each generation which are control-pollinated to produce 10,000 full-sib progeny. However, this population size does not represent a strict rule but merely a guideline for establishing the initial nucleus.

It will become evident that the innovation and fundamental feature of the nucleus system is concentration and mating of elite parents in *a distinct* and separate population. The nucleus provides a formal population structure for cumulatively capturing gains made from intensive selection and assortative mating from one generation to the next.

TWO-WAY GENE TRANSFER

The nucleus may be "closed" in the sense that transfer of genetic material from main population to nucleus occurs only at the initial screening to establish the nucleus. In subsequent generations there would be no further flow of genes from main to nucleus. The closed nucleus is regenerated after each generation by mating superior individuals selected only from within the nucleus itself.

An "open" nucleus would continue to be replenished each generation by transfer of highly productive breeding individuals from the main population (or from other breeding programs). Outstanding selections from both the nucleus and main would, therefore, be mated to regenerate the nucleus in successive generations. Likewise, there would be a transfer of genetic material in the opposite direction and parents from the nucleus and main are used to regenerate the main.

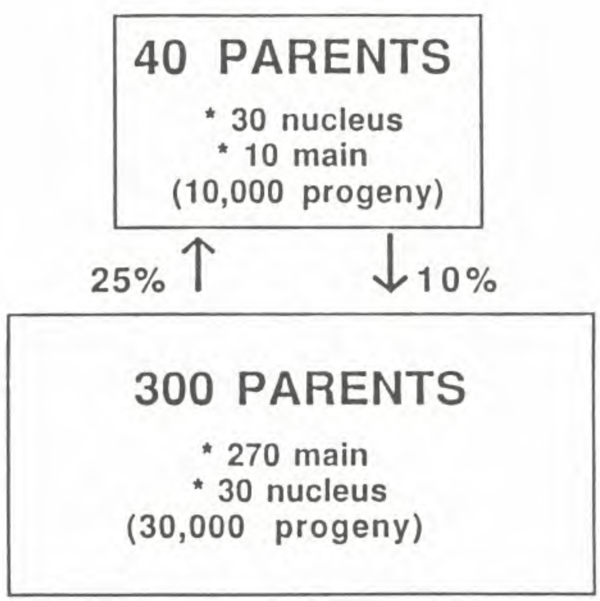
Transfer from Main to Nucleus

Cotterill *et al.* (1988) suggested that the best 30 individuals may be selected (using combined indices) from the 10,000 full-sib nucleus progeny. These 30 individuals, together with 10 of the best new generation selections from the main population, are control-crossed in 100 combinations to produce 10,000 progeny to regenerate the nucleus population (Figure 2). Of the 40 parents used to regenerate the nucleus each generation, 25% (or 10 parents out of 40) are therefore selected in the main population and the remaining 75% (30 parents) are selected in the nucleus. Research into nucleus breeding in animals and trees suggests that when 25 to 50% of the nucleus parents are selected in the main the rate of increase of inbreeding in the nucleus is minimised and longer-term gains are maximised (James 1977, 1978, Cotterill 1990).

The 10 selections from the main population can be transferred to the nucleus as pollen and consequently serve as male parents in the control-crossing. Cotterill (1990) showed how this procedure can lead to the same generation time in the nucleus as in the main population.

This transfer of genetic material from main to nucleus allows genetic improvement made in the main population to be incorporated into the nucleus, thus improving the potential nucleus gains beyond what could be expected in a closed population (James 1977). As already mentioned, transfer from main to nucleus may also allow inbreeding in the nucleus to be maintained at acceptable levels over successive generations (James 1978).

Figure 2. Main and nucleus population structure with two-way transfer of genes.



Transfer from Nucleus to Main

Following the case studies given in Cotterill *et al.* (1988) the 30 individuals selected in the nucleus population are used as parents in the main as well as the nucleus. Of the 300 female parents used to regenerate the main, 10% (or 30 parents) are therefore selected in the nucleus population and the remaining 90% (or 270 parents) are selected in the main (Figure 2). This transfer of genetic material from nucleus to main allows genetic improvement made in the nucleus to be incorporated into the main. We will see later that the genetic gains expected in the main population are enhanced by this scheme.

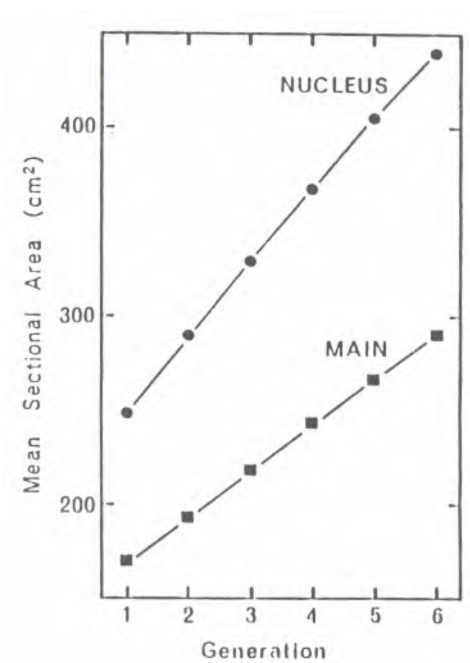
The open nucleus approach with two-way transfer of genetic material represents a fundamental shift away from the strictly one-way flow of genes from bottom to top of the hierarchy of populations (i.e. from breeding population to seed orchards) which is a feature of traditional tree improvement. The seed orchards have been "dead ends" and contributed only to present progress but not to continuing progress. This is because the genetic changes made by mating outstanding parents in orchards are not transferred back into the breeding population.

EXPECTED GENETIC GAINS

Gain Calculations

Figure 3 presents genetic gains expected from selection on sectional area of stem over six generations in the nucleus and main populations. These gain calculations are taken from case studies for *Pinus radiata in* Australia and *Eucalyptus globulus* in Portugal (as taken from Cotterill *et al.* 1988). The sectional area of stem is assumed to be measured at six to eight years after planting and have an individual heritability around h^2=0.2 for both species. The main population is assumed to be regenerated by open-pollinated mating each generation and the nucleus by control-crossing (Cotterill *et a!.* 1988). Theory for determining expected gains under nucleus breeding in forestry is presented in Cotterill (1990).

Figure 3. Cumulative gains expected in sectional area in the nucleus and main populations over six generations of selection.



It is apparent from Figure 3 that the gains expected per generation in the nucleus far exceed corresponding gains expected in the main population. Having provided the most productive parents to initially establish the nucleus an "improvement lag" develops between the nucleus and main populations. The rapid early gains in the nucleus lead to a doubling of this improvement lag over the first six generations. Early financial returns from rapid pre Tress in the nucleus and widening of the improvement lag has been a potent factor in the acceptance of nucleus breeding in the sheep industry (Rae 1979).

If the system is continued as recurrent cycles of selection and transfer (in both directions) the gain in the nucleus will diminish and the gain in the main increase. The main population will eventually make the same rate of genetic progress as the nucleus and the improvement lag becomes constant (James 1977, Rae 1979). However, it may take many generations before this point of stability is reached and it could therefore be of little practical importance in tree breeding.

The gains in sectional area after the first-generation in Figure 3 represent a 14% change in mean of the main population and a 24% change in mean of the nucleus. It is interesting to note that without transfer of genetic material from nucleus to main the expected gain in the main would have been only 11% per generation (Cotterill *et al.* 1988). The transfer from nucleus to main is therefore important in enhancing progress in the main.

Nucleus Gains

The rapid gains in the nucleus population (Figure 3) are due to three factors:

1. Selection Intensity. High selection intensities are used in choosing the 30 nucleus parents out of 10,000 trees within the nucleus itself and, in particular, in choosing the remaining 10 nucleus parents out of 30,000 trees in the main population.

2. Family Information. The combined indices used to select nucleus parents can place far greater emphasis on family information compared with combined indices used to select main parents. This is because the nucleus is open and any build-up in inbreeding will be alleviated by transfer of unrelated (or less related) pollen from the main population. However, in the main population it is essential to avoid rapid increases in inbreeding as a consequence of placing heavy emphasis on family information in combined indices.

3. Assortative Mating. The control-pollinations in the nucleus represent a form of assortative mating of best parents with best parents. These pollinations will not follow a rigid mating pattern such as diallels or factorials. Rather than follow a predetermined pattern, "best mate" indices are used to attempt to predict which of the 40^2 crossing combinations among the 40 nucleus parents should produce the most economically valuable progeny. The 100 combinations which appear to be potentially most valuable would subsequently be completed in the control-pollination program. The potential advantages of assortative mating are highlighted by Cotterill *et al.* (1987), and details of constructing best mate indices are given in Cotterill and Dean (1989).

EXPLOITING NUCLEUS MATERIAL

There is no doubt that nucleus breeding fits neatly with clonal forestry. The nucleus acts as a "packaging" population where desirable features of a few outstanding parents are wrapped together in full-sib families. The most highly productive families (or individuals) can be quickly mass vegetatively propagated into plantations. However, nucleus breeding also fits with the more traditional orchard strategies. It is possible to create clonal seed orchards using best unrelated (or least related) material from the nucleus. Alternatively the nucleus population on some sites can be converted into seedling orchards.

REDIRECTING INVESTMENT

It is easily argued that investment in tree improvement should be concentrated on those parts of the breeding program which will give greatest economic returns. Some breeding programs devote large proportions of resources to completing control-pollinations among large numbers of parents in the (main) breeding population. For instance, *P. radiata* breeding operations in Australia have invested up to 40% of their total labour and financial resources in completing extensive control-pollination programs to regenerate big populations.

Cotterill *et al.* (1988) suggested that the main breeding population may be regenerated quickly and at low cost using open-pollinated mating. The idea is that resources saved by implementing open-pollination in the main population can be redirected to pay for intensive control-pollinations in the nucleus. In this way the nucleus provides a focus for financial investment. However, the nucleus system is not dependent on using any particular mating pattern in either the nucleus or main.

ADVANTAGES OF NUCLEUS BREEDING

Genetic Gains

The potential gains in the nucleus population far exceed those which could be expected from traditional strategies of cumulatively improving a single large breeding ., population. This is because the best breeding individuals are concentrated in the nucleus and bred together under assortative mating. The early gains in the nucleus are sustained by intensive selection in the nucleus itself and continued replenishment from highly productive individuals from the main population (and other breeding programs).

Economic Success

The financial investment in traditional tree breeding has often been spread thinly in improving a large, relatively slow moving, breeding population by extensive control-crossing and testing. Under nucleus breeding the investment and breeding effort can be focussed on the smaller nucleus population containing outstanding genetic material. This focussing of investment on a population which is expected to yield rapid gains should ensure good financial success of nucleus breeding. The need to make a commercial success of the breeding enterprise is clearly a critical consideration.

Versatility

The nucleus is a very versatile population in the sense that it is ideal for introducing and testing the best selections from outside breeding programs. These outside introductions may even be from different species and the nucleus would therefore include hybrid material. The nucleus would also be an ideal population for gene engineering research and development.

Breeding Cooperatives

The nucleus strategy may provide a convenient structure for tree improvement cooperatives (as it has for sheep cooperatives). Each partner in the cooperative could have their own nucleus population and be responsible for crossing and testing this commercially valuable material. However, the cost of carrying the large main population necessary to replenish each nucleus could be shared amongst cooperators. Alternatively, the reverse may apply with the nucleus being run by the cooperative and each partner having their own main population contributing to the central nucleus.

LITERATURE CITED

Cotterill, P.P. 1990. Theory and practice of nucleus strategies in tree breeding. *Forest Sci.,* in press.

Cotterill, P.P., and Dean, C.A. 1989. Successful Tree Breeding with Index Selection. 120 pp. CSIRO, Melbourne.

Cotterill, P.P., Dean, C.A., Cameron, J.N., and Brindbergs, M. 1988. Nucleus breeding: a new strategy for rapid improvement under clonal forestry. In Proc. IUFRO Conference on Breeding Tropical Pines. Pattaya, Thailand.

Cotterill, P.P., Dean, C.A., and van Wyk, G. 1987. Additive and dominance genetic effects in *Pinus pinaster, P. radiata* and *P. elliottii* and some implications for breeding strategy. *Silvae Genet.* 36: 221-232.

Cotterill, P.P., and Jackson, N. 1989. Gains expected from clonal orchards under alternative breeding strategies. *Forest Sci.* 35: 183-196.

James, J.W. 1977. Open nucleus breeding systems. *Anim. Prod.* 24: 287-305.

James, J.W. 1978. Effective population size in open nucleus breeding schemes. *Acta Agric. Scand.* 28: 387-392.

Rae, A.L. 1979. Group breeding schemes in New Zealand. Proc. 30th Annual Meet. European Assoc. for Animal Production. Harrogate, England.