Early selection in tree breeding programme: a review

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Early selection consists of the selection of genetically superior trees in the breeding programme, long before they have reached the rotation age. It is based on the theoretical assumption that early performance of trees or families is a predictor of later performance. The important parameters required for early selection are high juvenile-mature correlation, higher selection intensities at the early stage and higher heritability of early traits. Many experiments conducted elsewhere in the world also reported that early selection increases the efficiency of the breeding programmes. The possibility of co-ancestry problems associated with early selection through very quick turn-over of generation is the subject of some concern among the tree breeders.

Keywords: Early selection, heritability, juvenile-mature correlation, breeding programme, progeny test

Time is a critical factor in tree breeding programmes. Tree breeders have to wait a long time for results from tests and selections. They generally aim to identify the most superior genotypes in progeny tests as soon after planting as possible; this will significantly reduce the generation interval and the cost of the progeny testing programme. Tree breeders are constantly trying to develop reliable testing techniques that enable them to predict adult tree performance by studying young trees i.e. early selection.

The forest genetics literature shows no consistent usage of early selection. It is often referred to as **early test** (Nanson 1968; Eriksson 1980), **rapid test** (Schmidt 1979), **juvenile test** (Dietrichson 1969), **early selection** (Lambeth 1980), **early evaluation** (Rockwood 1983), or **juvenile selection**. All the terms used in the literature imply making selections in genetic tests long before trees have reached rotation age (Zobel and Talbert 1984).

This paper presents the scope of early selection in both short and long term breeding programmes; discusses the theoretical concepts of early selection and presents the results of an early selection experiment of different species conducted elsewhere in the world.

Scope of early selection in breeding programmes

Early testing is a form of "supportive research" (Figure 1). It functions to generate information necessary to carry out various breeding activities. A successful technique of early testing could then benefit both long-and short-term breeding activities (Jiang 1987).

Long term benefit

In advanced generation breeding, acceleration of generation turnover is the main concern because the overall goal is to maximise genetic gain per unit time (Van Buijtenen 1982). The generation interval can be shortened by inducing earlier flowering. Another way of shortening the generation interval is reliable early selection. The combination of inducing earlier flowering and early selection could substantially accelerate breeding cycles.

Short-term benefit

The function of short-term activities is to generate the maximum possible genetic gain and multiply the selected stock (Gullberg and Kang 1985). Franklin and Squillace (1973) pointed out two disadvantages

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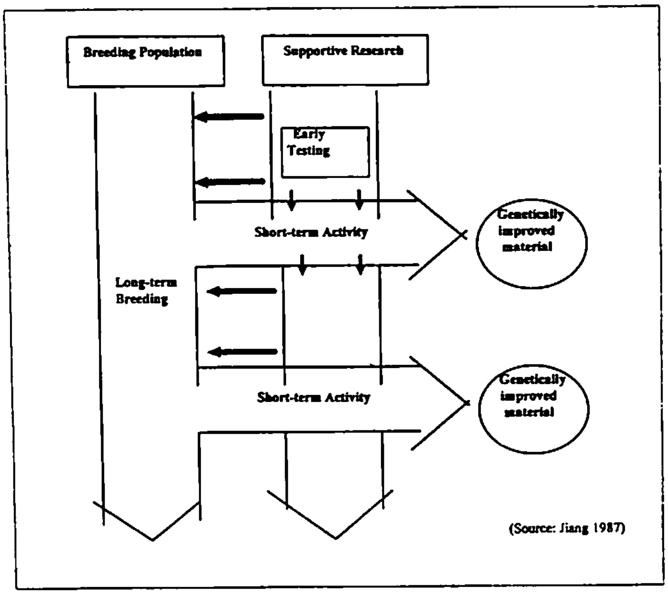
Figure 1 : A tree breeding model showing the relationship between long-term breeding, short-term activity and supportive research.



of conventional progeny tests. Firstly, owing to the high costs of controlled pollination and intensive field testing, the number of parents included in the field test is often severely limited. Secondly, the length of time needed to get results is long. Early testing could eliminate or reduce the impact of these two disadvantages.

The use of clonal propagation in production forestry is an attractive alternative option in short-term activities because it captures a greater proportion of the genetic variation than is possible from the seed orchard approach. The major biological obstacle that blocks the progress of clonal forestry is maturation of the ortets; when reliable results finally come from the clonal test the original clones may be too mature to be mass propagated (Libby 1974). Until methods of rejuvenation or of retarding maturation have been fully developed clonal testing will depend heavily upon early testing (Rauter 1985).

Theory of early selection

Early selection is based on the theoretical assumption that early performance is a predictor of later performance in the selected trees or families. Divided opinions were observed in literatures for and against this assumption.

Some authors have argued that early performance of genotypes is not strongly related to later performance; therefore early selection is ineffective. Cannell (1978) hypothesized that genotypes which perform well in an open grown situation, i.e. before crown closure, may not be well suited for competitive growth conditions following crown closure. In such cases, the genetic correlation between early performance and later performance may be zero or negative if the genotype suited to open grown condition is unable to cope in the competitive environment. Franklin (1979) also argued against early selection. He suggested that heritability of growth-traits may initially be high and then decrease, possible to zero, at about the time of crown closure and then increase as the stand reaches maturity.

Others (Lambeth 1980; Nanson 1970; Squillace and Gansel 1974; Lambeth, et. al. 1983; Foster 1986; Gill 1987; Cotterill and Dean 1987) working with conifers have suggested that the most efficient age for selection is 5-10 years for species with a 40-50 year rotation. They determined the efficient selection age which results in the greatest genetic gain per unit of time in the continuous cycling of breeding, testing, and selection.

The decision to choose early selection to accelerate breeding depends on the cost-benefit analysis of the operation. It is adopted if a fixed early gain outweighs the costs. Lambeth (1980) states that early selection can shorten the breeding generation only at the expense of gain per generation. Genetic gain per generation is less in early selection as compared to later selection, but gain per year is expected to be greater in early selection relative to long-term selection. For example: a 15-year generation interval would permit two cycles of selection and breeding for each single cycle of 30-years. Genetic gain at the end of a single 15-year interval would most likely be less than that at the end of a 30-year cycle, but the genetic gain per year would probably be higher with the 15-year cycle than the 30-year cycle.

Generally, selection efficiency per unit time (i.e. per year and per generation) is used to determine optimum selection age, using indirect selection.

Selection efficiency per generation:

$$(Q_{gen}) = \frac{\text{Gain in mature trait by selecting for the juvenile trait}}{\text{Gain in mature trait by selecting for mature trait}}$$

$$= \frac{i_j h_j h_m r_{Gjm} \sigma_{pm}}{i_m h_m^2 \sigma_{pm}} = r_{Gjm} \times \frac{i_j \times h_j}{i_m \times h_m} \quad \text{(Falconer 1981)}$$

where: j and m refers to parameters at the juvenile and mature age respectiv

h = square root of the heritability

r_{Gjm} = genetic correlation between the mature and juvenile traits

$$= \frac{COV_{j,m}}{\sqrt{Var_j}\sqrt{Var_m}}$$

$COV_{j,m}$ = Covariance of juvenile and mature traits

Var_j = Variance of juvenile trait

Var_m = Variance of mature trait

Selection efficiency per year:

$$(Q_{year}) = r_{Gjm} \times \frac{(i_j h_j h_m \sigma_{pm})}{(i_m h_m^2 \sigma_{pm})} \times \frac{(T_m + d)}{(T_j + d)}$$

$$= r_{Gjm} \times \frac{(i_j \times h_j)}{(i_m \times h_m)} \times \frac{(T_m + d)}{(T_j + d)} \quad \text{(Falconer 1981)}$$

where;

$(T_j + d)$ = generation interval

T = selection age

d = delay between selection and seed production.

Theoretically, the following parameters are required for successful early selection:

i. high juvenile-matur correlation;

ii. higher selection intensity at the early stage than at later stages;

iii. higher heritability of early trait than the mature trait.

Nanson (1976) pointed out that i_j is quite possible larger than i_m because in early test environments (e.g. laboratory, nursery, or young field-trial) it is easy to evaluate a much larger number of genotypes; h_j is also likely to be higher than h_m because environmental factors can be designed to be more homogenous in early tests. The time needed for early selection, T_j, is certainly smaller than T_m, the time needed for the conventional test. The only uncertain factor is the juvenile-mature correlation (r_{Gjm}).

Lambeth (1983) argues that with the assumption of equal selection intensity and heritability between the juvenile and mature trait, if the species of 30 year rotation is selected at 2 years (T_j) with 5 years delay (d) to breed than a juvenile-mature correlation of only 0.20 is required to make a selection efficiency per year equal to unity (E=1). i.e. :

$i_j = i_m$

$h^2_j = h^2_m$

T_j = selection age (2 years) + 5 years to breed = 7 years, and T_m = selection age (30 years) + 5 years to breed = 35 years,

then, $r_{j,m}$ = 0.20 is required to make E=1

Similarly, with a mature selection age of 8 years, a juvenile-mature correlation of 0.54 is needed for unity selection efficiency per year.

Errors in early selection

There are two types of errors in selecting or rejecting families based on early testing data:

i. Type A error

ii. Type B error

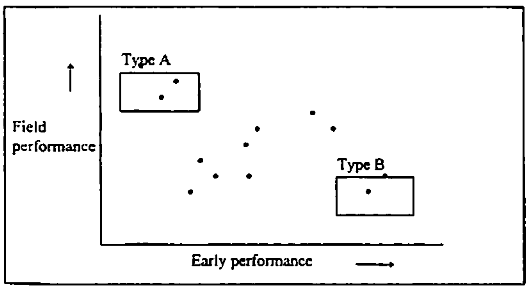
Type A error occurs due to the rejection of families with poor early performance that would later perform very well in field tests. Type B error occurs due to the selection of families with a good early performance that would not perform well in later field tests. Type B errors may not be as important as type A errors because type B error can be revealed in subsequent long-term field tests (NCSU 1997). An illustration of type A and type B errors is shown in Figure 2.

Early selection: experiences with different species and countries

i) Genetic test in 20-year-old Loblolly pine (*Pinus taeda*)

Lambeth *et al* (1983) working with Loblolly pine (*Pinus taeda*) found a strong genetic correlation between 5 years height with family volume of 20 years. They identified the best one third of families for height and volume at age 5, 10, 15 and 20 years and compared actual correlated gains across a number of ages. Early selection based on height at age 5 was only nominally lower in volume at age 20 than direct selection at age 20. They found early selection very effective and concluded that there is no apparent advantage to delay selection beyond age 5 if generations are cycled more rapidly with early selection.

Figure 2 : An illustration of type A and type B errors in early testing studies



(Source:Lowe and Buijtenen 1989)

With the same species in another experiment, Foster (1986) found an excellent correlation between 15-year family mean volume and 3-year height in Loblolly pine. He recommended the selection based on a combination of height and survival at age 3 as the optimum selection age for 15-year volume. It achieves 81% more gain relative to direct selection for 15-years volume.

ii) *Pinus radiata* in South Australia

Cotterill and Dean (1987) working with *Pinus radiata* in South Australia found that selection of individual trees based on height at age 6.5 years would produce 60 percent more gain per year in volume than selection based directly on 16 year volume. Selection at just one year would have given a negative gain due to slightly negative correlation of one year height with 16 year volume. The switch in sign (negative to positive) with time was thought to be due to a steady decline of preplanting factors such as nursery environments and seed weight.

iii) Coastal Douglas-fir (*Pseudosuga menziesi*) in a farm-field test environment

Woods *et al* (1995) reported 162 percent family selection efficiency per year for height and diameter at age 3, relative to direct selection on field volume at age 13 in Coastal Douglas fir (*Pseudosuga menziesi*). In this study, they compared 1-7 years growth and wood density from a farm-field environment with 13 years stem volume and wood density from 11 field sites. The breeding value correlations of farm-field heights with field stem volume at age 13 increased from a low of 0.5 at age 1 and levelled off at about 0.7 by age 3. All selection in the farm-field tests has a higher efficiency per unit time than selection in field tests. The author concluded that correctly established farm-field tests will provide greater gain per year in stem yield and wood density traits than field sites.

iv) Sitka spruce (*Picea sitchensis*) in Britain

Gill (1987) found strong correlations between 3 or 6 years height and later measures of vigour in Sitka spruce (*Picea sitchensis*). He estimated the correlated gain for 15-years diameter based on selection for height and diameter at a number of different ages. He recommended that selection based on 3 or 6 years height will be more cost effective then progeny testing to 15 years for vigour. Saving in tests cost may well outweigh the slight additional gains achievable by retention to 15 years.

v) Lodgepole pine (*Pinus contarta*) in British Columbia

Carlson (1990) looked at Lodgepole pine (*Pinus contarta*) in British Columbia. He made a comparison of 6-year growth performance rankings of families grown on conventional wild field sites with early growth performance ranking based on 2 through 6 year heights and stem volumes of the same families grown on farm-field sites (FFS). He found quite variable family rankings between early FFS and 6-year heights of progeny sites. The correlation between FFS and the more productive and uniform forest sites were positive and relatively strong but it was much lower between farm-field and forest sites where early frost damages indicated important genotype environment interaction (G×E) effects. He concluded that as the forest site progeny plantations mature, correlations between early growth on farm field sites and ultimate wild site genotypic expression may improve. If so, farm-field sites could be used in advanced generation, at least for productive sites of low frost risk.

vi) Early testing for screening Loblolly pine (*Pinus taeda*)

Lowe and Buijtenen (1989) analysed 11 greenhouse and growth chamber studies to observe the possibility of early screening for loblolly pine. They found that seedling shoot dry weight can be used as an early testing trait to reduce the costs associated with progeny testing programme. They estimated that removal of crosses that contain the parent with the smallest shoot dry weight in each partial diallel will reduce nearly 17 percent of progeny test costs in first generation. Similarly; removal of 30 percent selection with the smallest shoot dry weight based upon the polymix crosses in second generation, will result in a 24 percent cost reduction in establishing the polymix progeny test.

Discussion

The decision to make an early selection is driven by the ratio of juvenile/mature of heritability and genetic correlation. If the heritability on the younger experimental site is greater or equal to the older forest based site and the genetic correlation between them is high, then it may be worthwhile to carry out early selection (Table 2). With a low genetic correlation between the juvenile and mature traits it will not be possible to maximise the genetic gain due to type A and type B error.

Table : Practical guidelines when deciding whether or not to use very early selection

Heritability	Genetic Correlation	Decision on Early Selection
h^2_F of younger site > h^2_F older site	High	Yes
h^2_F of younger site = h^2_F older site	High	Yes
h^2_F of younger site < h^2_F older site	Low	No

Generations are turned over more quickly with early selection; it could possibly increase the rate of inbreeding within sub-lines. The genetic gain per year will initially be at a maximum, but co-ancestry problem could be encounterd earlier. These could effect the total gain per year over a number of generations relative to a more mature selection age. Detail study in this concern is essential to ensure the reliability of early selection.

An alternative approach to the utilisation of early testing procedures would be the elimination of average or below-average performing families based on their performance at a younger age, prior to establishment on a forest based site. This approach would not increase the amount of genetic gain obtained per breeding cycle for a constant-sized breeding population however, it would result in a reduced cost for field testing and field assessment. This would increase the efficiency of an operational programme by decreasing the cost required to obtain a given amount of gain.

Conclusion

The most important genetic parameter for reliable early selection is the higher juvenile-mature correlation. Theoretically, early selection is expected to increase the genetic gain in breeding programme. Experiments conducted elsewhere in the world for different species also showed that early selection increases the efficiency of testing programmes through the shortening of the generation interval and the reduction of cost and size of progeny test. The possibility of co-ancestry problems in the long-term through very quick turnover of generation is the subject of some concern among tree breeders.

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