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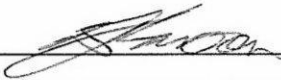Divisional Records   Plot Folder

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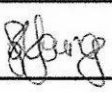**AUTHOR'S PROPOSAL FOR FUTURE PUBLICATION:**

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KEYWORDS: EARLY SELECTION, JUVENILE–MATURE CORRELATION, GAIN PER YEAR

ABSTRACT[*]

A review of the relevant literature on early selection, along with a simulation exercise on discounted genetic gain found that there should be no change in the current practise of selecting *Pinus radiata* families and individuals within families for growth rate at 7 years in the field. It is possible that the recent use of improved progeny test site selection and design may have further reduced this recommended selection age. Recent literature indicates the potential of early selection using Farm Field Testing and glasshouse studies. It is proposed that the feasibility of these new techniques be investigated for *Pinus radiata* in New Zealand using remnant seed in retrospective progeny tests.

[*] Note: This material is unpublished and must not be cited as a literature reference

FRI/INDUSTRY RESEARCH CO-OPERATIVES

MANAGEMENT OF IMPROVED RADIATA BREED
CO-OPERATIVE

EXECUTIVE SUMMARY

REVIEW OF EARLY SELECTION

S.J. LEE AND P. JEFFERSON

REPORT NO.   APRIL 1991

Breeders try to maximise the use of genetic testing resources and the rate of realisation of genetic gain by identifying as soon after planting as possible those genotypes that will be most superior at rotation age. Current practice for multi-trait selection within forest based *Pinus radiata* progeny tests in New Zealand is to select at age 7 years. This report documents information from elsewhere in the world that suggests the age of selection for growth-rate may be reduced further by selecting within tests established on more uniform environments (such as Farm Field Sites) or within a glasshouse.

It is recommended in this report that the feasibility of early selection based on Farm Field Testing and testing in the glasshouse be investigated for radiata pine. Two experiments (each to be established within each of a Farm Field and glasshouse testing environment) are recommended. The first involves use of remnant seed from families already being tested on several forest sites to determine the efficiency of early selection; the second involves testing the importance of maternal effects in early selection.

INTRODUCTION

In an attempt to maximise the use of resources and the rate of genetic gain tree breeders are striving to identify the most superior genotypes in progeny tests as soon after planting as possible. Progeny tests designed to run for a full rotation would yield the most complete information with regards to both selection for a mature trait and achieving maximum genetic gain within a generation. However, gain per year and optimum financial return may well be greater when selection is made at a younger age.

Progeny tests retained beyond the optimum juvenile age require undesirable further maintenance and additional costly assessments while delaying the return on invested resources. Recent advances of flower induction in juvenile trees by applying growth hormones, fertilizers and drought stress are such that trees can be brought to flower at earlier ages, allowing the next cycle of breeding and selection to commence.

Breeders investigate the possibility of making selections at younger ages by calculating correlations (either phenotypic or genetic) between the younger and older material. These are referred to as age:age correlations. Ideally breeders would like the age of the mature trait to be end-of-rotation. Since few progeny tests of sufficient age exist the 'mature' ages used in correlation of juvenile and mature data are often well short of rotation age and represent simply the oldest available data.

Current practice in the N.Z. *Pinus radiata* breeding programme is to make initial forward selections at 5 years with final multi-trait selections for the breeding population at age 7-10 years (Carson *et al.*, 1990). Seed orchard parent clones used in production populations are usually selected 'backwards' on General Combining Ability (GCA) estimates from tests aged 7-15 years. Early selection is also likely to be of critical importance to clonal forestry programmes for which candidate clones need to be maintained in a juvenile state during a clonal testing phase.

The purpose of this literature review is to investigate existing knowledge with regard to early selection and testing procedures and make recommendations where necessary on possible changes in practice.

EVALUATION OF EARLY SELECTION

In order to fully appreciate the effects of mathematical relationships operating on gain expectations when early selections are made it is necessary to be familiar with some

basic equations for expression of genetic gain. Gain is usually expressed either in terms of total gain within the generation, or in gains per unit of time.

1. Gain per generation:

1.1 Gain from direct selection:

Tree breeders are usually interested in end-of-rotation gain as the selection objective. The expression of this gain is referred to as the 'mature' trait. Gain resulting from direct selection on the mature trait can be expressed as:

$$G_m = i_m h_m^2 \sigma_{Pm} \quad (1) \quad \text{(Falconer, 1983)}$$

where: 'm' refers to parameters at maturity

G_m =   Genetic gain

i_m =   selection intensity

σ_{Pm} =   phenotypic standard deviation

h_m^2 =   heritability $= \dfrac{\sigma_{Gm}^2}{\sigma_{Pm}^2}$

σ_{Pm}^2 =   phenotypic variance

σ_{Gm}^2 =   additive genetic variance

1.2 Correlated response:

Gain in the mature trait based on selection for a juvenile trait is effectively indirect selection and equation (1) becomes modified as follows:

$$CG_m = i_j h_m h_j r_{Gjm} \sigma_{Pm} \quad (2) \quad \text{(Falconer, 1983)}$$

where: 'j' refers to parameters at the juvenile age

CG_m =   Correlated gain at maturity

h =   square root of the heritability

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

The efficiency of selection based on the juvenile trait relative to selection based on the mature trait can be expressed as the ratio of correlated to direct response:

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

$$= \frac{(i_j\, h_j\, h_m\, r_{Gjm}\, \sigma_{Pm})}{(i_m\, h_m^2\, \sigma_{Pm})}$$

This simplifies to:

$$= r_{Gjm} \cdot \frac{i_j\, h_j}{i_m\, h_m} \qquad (3) \qquad \text{(Falconer, 1983)}$$

This ratio was referred to as 'Generation Efficiency' (Q_{gen}) by Cotterill and Dean (1988).

Selection Intensity and Heritability:

It follows from equation (3) that an increase in total gain for the mature trait whilst selecting for the juvenile trait, will only occur if ($r_{Gjm}\, i_j\, h_j$) is greater than ($i_m\, h_m$). Since r_{Gjm} is likely to be less than 1, either the selection intensity and/or the square root of the heritability at the juvenile age will have to be larger by a commensurate amount if Q_{gen} is to exceed 1. In practise, the selection intensities at the juvenile and mature age are usually the same (although Cotterill and Dean (1988) argue that i_m can often be less than i_j owing to effects of mortality and silvicultural thinnings).

It is difficult to find a consistent trend for changes in heritability with increasing age for traits expressing vigour. Examples from the literature of how family heritabilities can vary with age are given in Table I. Lambeth *et al.* (1983) found that heritability trends can vary from one experiment to another but that on average they remained constant. It is quite possible that variables such as test design and competition will have varying effects on the expression of heritabilities.

In one of the more comprehensive investigations into changes in heritability with time, Franklin (1979) divided the development into three phases; juvenile, mature/genotypic, and codominance/supression. He investigated four different conifer species and found roughly similar trends in that the heritability starts high and then falls in the first phase, rises to a maximum in the second, and then gradually falls off in the third. He concluded the changes between these three phases were so marked that selection at conventional spacing should be deferred until at least half-rotation.

Table I: Variation of family heritability with time.

The following is not intended as a comprehensive list, merely examples taken from the literature to illustrate the possible directional change with time effecting family heritability across species and traits.

Stays (roughly) the same:

King and Burdon (1991):   *Pinus radiata*

h^2_f: Diameter 5 years = 0.59
Diameter 10 years = 0.57
Diameter 17 years = 0.55

Rises:

Cotterill and Dean (1988):   *Pinus radiata*

h^2_f: Basal area 2.5 years = 0.34
Basal area 6.5 years = 0.41
Basal area 10.5 years = 0.63
Height 2.5 years = 0.55
Height 6.5 years = 0.71

Foster* (1986):   *Pinus taeda*

h^2_f: Volume 3 years = 0.58
Volume 7 years = 0.69
Volume 15 years = 0.75

Gill* (1987):   *Picea sitchensis*

h^2_f: Diameter 10 years = 0.71
Diameter 15 years = 0.75

* See 'Falls' also

Falls:

Foster (1986):   *Pinus taeda*

h^2_f: Diameter 3 years = 0.54
Diameter 6 years = 0.39
Diameter 15 years = 0.28

Gill (1987):   *Picea sitchensis*

h^2_f: Height at planting = 0.91
Height 3 years = 0.83
Height 6 years = 0.82
Height 10 year = 0.75

Estimated heritabilities at rotation age are unlikely to be known and will be an extrapolation of the oldest available assessment data. If actual heritabilities are known they can only increase the precision of the models. Given the errors associated with heritability estimates and the variation in published trends over time breeders often choose to assume that they are similar at the juvenile and mature ages and then test the sensitivity of that assumption.

Assuming $i_j = i_m$ and $h_j = h_m$ then equation (3) reduces to:

$$Q_{gen} = r_G \quad (4)$$

Choice of genetic or family age:age correlations:

The choice has to be made between using genetic (r_{Gjm}) or phenotypic correlations (r_{Pjm}) in any model employed to calculate an optimum selection age. Phenotypic correlations are simply the correlations between the measured values for two ages or traits; genetic correlations represent the correlation between breeding values for those same traits and indicate the degree to which genes are influencing more than one trait.

In the equations presented thus far, r_{Gjm} has been used. However, one of the better-known models for calculating age:age correlations, proposed by Lambeth (1980) used r_{Pjm}, having made the assumption that $r_{Gjm} = r_{Pjm}$. In a later study (Lambeth, 1983) the same author reported that on average, r_{Gjm} exceeds r_{Pjm}. Lambeth (1980) acknowledges that if $r_{Gjm} > r_{Pjm}$ the optimum selection age calculated using r_{Pjm} would be over-estimated.

When King and Burdon (1991) employed the Lambeth relationship for early selection in radiata pine they initially investigated the similarity between r_{Pjm} and r_{Gjm} and found r_{Gjm} consistently higher than r_{Pjm}. They chose to use r_{Gjm} in subsequent calibration of the model since elimination of any environmental component incorporated in the estimate of r_{Pjm} was felt to be more technically correct.

Magnussen (1988) preferred use of r_{Pjm} to r_{Gjm}, considering the former to provided a form of 'safety margin'. He argued that due to the numerous errors associated with the calculation of genetic correlations it is better to use phenotypic correlations and err on the side of caution with prediction of optimum juvenile selection age. Most of the progeny tests established for the breeding of radiata pine in NZ involve large numbers of families which tends to reduce errors associated with calculation of genetic correlations. Falconer (1983), suggests that whilst phenotypic correlations could be used when calculating the association

between two traits, it is more correct if environmental (and non-additive) components are removed by utilizing the genetic correlation.

Models for calculating age:age correlations:

The main restriction to calculating the ratio of gain from juvenile and mature selection ages is often the lack of known age-age (juvenile-mature) correlation co-efficients. Very few progeny tests have been measured at regular intervals until end-of-rotation age.

One of the better-known models was proposed by Lambeth (1980). Using matrices of age-age correlations and vectors from eight published studies concerning eight different species he derived a generalised regression model for r_{Pjm} concerning tree height in Pinaceae:

$$r_{Pjm} = 1.02 + 0.308 \log_e (T_j / T_m) \qquad (5) \qquad \text{(Lambeth, 1980)}$$

where: $\quad T_j \quad = \quad$ Juvenile selection age

$\quad\quad\quad\quad T_m \quad = \quad$ Mature selection age

Lambeth (1980) concluded that early selection for growth is most efficient around years 6 and 8 regardless of species (but certainly not before trees are 2 m tall).

Burdon (1989), whilst accepting that radiata pine would not conform exactly to this model considered it to be the best available method of extrapolating known age:age correlations to project gains from selection to rotation age.

Magnussen and Yeatman (1987) also considered the Lambeth equation as a useful first approximation of age:age correlations but list three main concerns:

(i)   it predicts equal correlations for similar age:age ratios with a markedly different biological basis.(for example, $r_{10,50} = r_{4,20}$);

(ii)   its predictive power decreases with younger ages (which are often the ages of interest);

(iii) the logarithmic model concept is more appropriate in the exponential growth-phase of younger plantations (T_j) than in older plantations (T_m) in which growth is declining.

Magnussen (1989), also developed a method for estimating r_{Pjm}. It is based on the concept that since growth rates, experimental design, spacing and competition can all affect the variances used in the calculation of correlation co-efficients, time itself is a poor scale

for comparing and predicting correlations. Correlations are expressed in terms of a fixed intrinsic maximum growth rate (which is assumed constant for a given population) and a random component which is assigned to individual trees to express the amount of growth lost to extraneous growth factors. Thus:

$$r_{Pjm} = \frac{(1 + k.l).\ \sigma_j}{\sigma_m}$$

where: k   =   intrinsic maximum growth rate

l   =   the mean growth loss due to extraneous factors

The model is much more complex than that of Lambeth and involves a number of assumptions; consequently it has been largely ignored in the literature.

2.   Gain per year:

Gain per year is an alternative way of interpreting gain which is more commonly used by tree breeders; the optimum selection age being the one that yields the greatest gain per year. Gain per year can be expressed in either absolute terms or an absolute gain discounted to a standard age (such as when breeding commenced).

2.1   Absolute gain per year:

$$\text{Gain per year}\quad =\quad \frac{\text{Gain per generation}}{\text{Generation interval}}$$

$$=\quad \frac{CG_m}{T_j + d} \tag{6}$$

where: $(T_j + d)$ =   Generation interval

T_j =   selection age (which may be at maturity)

d   =   delay between selection and seed production.

Similarly, the efficiency of correlated response relative to direct gain can be expressed in terms of gain per year:

$$Q_{year} = r_{Gjm} \frac{(i_j\ h_j\ h_m\ \sigma\ pm)}{(i_m\ h_m^2\ \sigma_{pm})} \cdot \frac{(T_m + d)}{(T_j + d)} \tag{7}$$

Making the same assumptions (as earlier) of equal heritabilities and selection intensities at the juvenile and mature ages, this reduces to :

$$= \quad r_{Gjm} \cdot \frac{(T_m + d)}{(T_j + d)} \qquad (8) \qquad (Lambeth, 1980)$$

If $h_j > h_m$ or $i_j > i_m$ then maximising equation (8) leads to over-estimates of the optimum age.

Magnussen (1989) states that equation (8) allows ready calculation of what must be the minimum correlation between traits across ages in order to obtain the same gain per year. Examples of minimum r_{Gjm} are given in Appendix II. For example, based on a 25 year rotation and 5 year delay between selection and seed production (typical for *Pinus radiata*), the same gain per year is achieved in year 2 with a minimum $r_{Gjm} = 0.23$ as is achieved in year 10 with a minimum $r_{Gjm} = 0.50$. Gain per year will be improved if r_{Gjm} can be found to be greater than the minimum stated.

2.2 Discounted gain per year:

The concept of introducing economic analysis into defining the efficiency of early selection was suggested by Lambeth (1983) and developed into a model by Magnussen and Yeatman (1987). They speculate that in a continuous breeding cycle the ultimate objective will be to optimise cumulated gain per year, i.e. total gain discounted back to a standard age (usually zero). Since genetic gain is realized at each harvest of improved seed (or harvest of stands grown from improved seed), the total gain from each generation of breeding depends on the number and frequency of seed harvests. Gain from each harvest should increase as generations progress although the magnitude of that gain will depend on age of selection and correlation with the mature trait. The gain over a fixed period of time could therefore be investigated by adjusting variables such as selection age, interest rate, delay between selection of individuals and collection of seed from seed orchards and when the gain is considered realized. Thus net present value of the cumulated gain is given by:

$$CG_{NO}(m/j) =$$

$$\sum_{c=1}^{c} \sum_{n=1}^{Nc} c.G(m/j).(1+p)^{-(C.Tj+D)+S(n-1))} + \sum_{n=0}^{N_F - 1} C.G(m/j).(1+p)^{-(C.(Tj+D)+D)+S.n)}$$

(9)   Magnussen and Yeatman, (1987)

where: T_j = age of selection

D = delay between selection and gain realization,(this age could be either when the trees are felled or when the seed is sold)

C = number of breeding cycles in a given total time(TT), $= \frac{TT}{Tj+d}$

d = delay between selection and first seed harvest of improved seed

G = gain from each seed harvest

S   =   years between seed harvests

N_C =   total number of seed harvests during a breeding cycle, $\dfrac{(T_j + d)}{S}$

N_F =   number of seed harvests after the last breeding cycle

n   =   number of seed harvests

c   =   breeding cycle

p   =   interest rate $(0 < p < 1)$.

In a worked example Magnussen and Yeatman (1987) calculated optimum selection ages over 1 to 3 generations assuming a 40 year rotation. They found that if gain was not realized before the harvest of trees grown from improved seed, the optimum age was 11 years (1 cycle of breeding) to 15 years (3 cycles of breeding), but that this reduced to 6 years, regardless of number of breeding cycles or interest rate if gain is considered realized when improved seed is sold.

A similar approach was adopted by McKeand (1988). He calculates present value of gains in Loblolly pine (*Pinus taeda*) using the equation:

$$P_0 = \frac{P_n}{(1 + p)^n} \qquad (10) \quad \text{(McKeand, 1988)}$$

where: P_0 =   the present value

P_n =   future value at year n

p   =   interest rate

n   =   year in which gain would be realised.

Little actual detail on the working of the model is presented by McKeand, who concludes that assuming a 25 year rotation and 10 year delay in establishing and obtaining seed from seed orchards the optimum age for selection is 4 years regardless of interest rate. In the same study the optimum age in terms of gain per year (without discounting) was 6 years. The latter was chosen as the optimum age overall owing to uncertainties connected with the economic calculation.

APPLICATION OF EARLY SELECTION MODELS TO PINUS RADIATA IN NEW ZEALAND:

(a)   Absolute Gain:

King and Burdon (1991), used data from the *Pinus radiata* '268' series to calculate the slope and intercept for the Lambeth relationship as follows:

$r_{Gjm} = 1.13 + 0.40 \log_e (T_j / T_m)$

This enabled them to estimate r_{Gjm} for a wide range of different ages and, using equation (7), the optimum age of selection. They concluded that the maximum genetic gain per annum for diameter of *Pinus radiata* in N.Z. was achieved at 7-8 years for family (backwards) selection and slightly earlier for individual within-family (forwards) selection based on rotations of 25-30 years.

Since the '268' series was established, various improvements have been made to progeny test selection and design including use of single tree plots and selection of more uniform, fertile sites. Collectively, these effect could result in an increase in h_j and r_{Gjm} (see S Carson, 1990) and may reduce the optimum age of selection further.

(b)   Discounted Gain:

Using the Lambeth relationship as fitted by King and Burdon (1991) to calculate r_{Gjm}, typical *Pinus radiata* progeny test data has been run through the Magnussen and Yeatman (1987) equation. The model was run to cover three separate breeding periods; 75, 150 and 300 years and detailed results are given in Appendix I. The optimum age was found to be around 7 or 8 years which confirms the work of King and Burdon (1991), but is probably only to be expected considering the overlap of '268' data and Lambeth equation as calibrated by King and Burdon (1991). The limitations of the data used in this simulation are unfortunate since the concept of such a model combined with accurate data appears attractive in influencing policy decisions.

EXPERIENCES FROM ELSEWHERE IN THE WORLD

Cotterill and Dean (1988) looked at *Pinus radiata* in South Australia. Using equation (7) and assuming $i_j = i_m$ they found that selecting individual trees based on height at 6.5 years would produce 60% more gain per year in volume than selection based directly on 16 year volume. Selection at just 1 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 seen as a steady decline of the effects of preplanting factors such as nursery environment and seed weight. The authors also stated that the site was not weed-free in the early years and a repeat of the experiment on a better maintained site may result in a slight reduction of this optimum age.

Lambeth *et al.* (1983) working with loblolly pine identified the best one-third of families for height and volume at age 5, 10, 15 and 20 years and then tracked their progress to later measurement ages. They were able to compare actual correlated gains across a number of ages and by using equation (6), calculate gain per year. They found that 5-year

family mean height gave the greatest gains per year for 20-year volume. However, individuals within families could not be confidently selected until year 10 due mainly to poorer correlation coefficients. Also at the within-family level, height gave much poorer r_{Gjm} for a given age than diameter or volume.

Foster (1986), also working with loblolly pine investigated the generation efficiency Q_{gen} in family mean volume at age 15 based on the use of various indexes for height, survival and volume at a number of different ages. He recommended selection based on a combination of height and survival at age 3 as the optimum selection age for 15-year volume since the decrease in relative efficiency was only 19% compared to direct selection for 15-year volume.

Gill (1987) investigated the correlated gains for 15-year diameter based on selection for height and diameter at a number of different ages in Sitka spruce (*Picea sitchensis*). He found that Q_{gen} based on 6-year height was 81% and recommended that there seemed little point in delaying selection to a later age.

TECHNIQUES INVOLVED IN EARLY SELECTION

Forest progeny test sites can turn out to be quite heterogeneous even when rigorous attempts are made to select homogenous sites and establish experiments designed to give maximum precision of family mean estimates. In an attempt to use early selection without the complications associated with heterogenous forest environments, breeders and physiologists are increasingly looking to early selection in more controlled, often non-forest environments.

(a) Early selection based on traits measured in the glasshouse or phytotron

The literature has many examples illustrating attempts of very early selection based on physical and physiological traits in the glasshouse or phytotron. Some are successful, many are not. The traits with which the authors claim success with early selection often vary considerably.

Williams (1987) looking at seedling shoot length of open-pollinated loblolly pine families found that height after the free growth phase (6 months) was the best indicator of 8 year height. The value of r_{jm} continued to increase between 6 to 18 months from germination for height growth. Juvenile-mature correlations based on shoot dry weights, were low and had little value as an indicator of later growth performance. This contrasts with the procedures developed in Texas by Lowe and van Buijtenen (1989) where the poorest

20% of loblolly pine families based on total shoot dry weight after 5 months in the glasshouse are rejected leaving final selection to the field test.

Riitters and Perry (1987) working on Douglas fir in Oregon found good correlation (r=0.54) between 15-year family mean heights in the field and 2-year family mean heights in the glasshouse.

Pharis *et al.* (in press) claim to be able to predict the rankings for growth rate of first generation *Pinus radiata* families from Australia and Black spruce families (*Picea mariana*) from Canada based on 3-6 month total height, height growth, stem volume, and stem dry weight measured in a phytotron. No supportive data were supplied in terms of gain per year or generation efficiency.

In a more physiologically based approach Pharis *et al.* (op.cit.) also suggest that 'rapid growing' families may have higher concentrations of endogenous gibberellins and conversely that some 'slow-growing' families may have lower concentrations. Matheson (pers com.) is cautiously optimistic that the allocation of photosynthate to the stem of *Pinus radiata* trees is a good indicator of later field performance of families. Matheson is dismissive of the use of any physical traits such as height, diameter, or dry weight although admits that further work is required using large sample sizes.

Burdon (1982) listed the criteria which would be needed for successful application of early selection based on very early physical or physiological traits. The concept of avoiding environmental noise through use of glasshouse, phytotron or laboratory appeals but reference to equation (7) would indicate that one or more of the following needs to apply:

(i)   Very high $r_{Gj,m}$
(ii) i_j/i_m is favourable
(iii) h_j/h_m is favourable
(iv)   the genetic relationship, between the juvenile and mature trait, is essentially linear
(v)   the genetic relationship is not dependent upon genetic values for other variables.

Carson and Carson (1989) report good success in early selection for fusiform rust on *Pinus taeda* due to highly favourable values of (i) to (ii) above. Early selection for Dothistroma on *Pinus radiata* however was found to be less successful due to unfavourable values of $r_{Gj,m}$ and juvenile family heritabilities.

(b)   Early screening based on nursery or glasshouse results

Rather than making final selections at a very early age, breeders may choose to screen out a proportion of the poorest families based on glasshouse or nursery performance prior to establishing field tests. This would have the effect of decreasing the cost of the progeny testing programme. Gain per year would only be reduced if the generation interval was extended due to this two stage process.

Fins *et al.* (1990) working with Douglas fir (*Pseudotsuga menziesii*) in Canada, report that their intention is to screen off the poorest 25-50% of families based on first-year height in the glasshouse. Lee *et al.* (1990, unpublished British Forestry Commission (FC) report) also found that 25% of open-pollinated Sitka spruce families could have been culled based on mean 2-year nursery height with only a slight decrease in gain per generation compared to selection at the mature trait of 15-year diameter.

Lowe and van Buijtenen (1989), outline how they propose to incorporate a two-step testing procedure combining independent culling at the end of the first test (glasshouse) with assortative mating for the second test (field) to not only decrease the cost of progeny testing by up to 22%, but also increase generation genetic gain by 0.5%. Their loblolly pine breeding programme involves testing selections for GCA before establishment of seed orchards, and utilisation of the same clones in a disconnected diallel mating programme within which the next breeding population selections will be made. Five-month shoot dry weights measured in the glasshouse are used to screen out the poorest GCA families, reduce the size and cost of field tests, and rank families for assortative matings within the diallels.

A similar approach was adopted by Carter *et al.* (1990). They found that a proportion of open-pollinated jack pine (*Pinus banksiana*) families could be culled based on height at the end of the second growth cycle in the glasshouse. It was suggested that short-term polycross tests could be used with subsequent pair-wise matings employing an assortative mating strategy.

(c)   Farm Field Testing

Numerous studies have found that both the overall accuracy of progeny testing and subsequent calculation of repeatability of family means, genetic variance and genetic gains are improved by optimum choice of planting sites (Burdon, 1977; Burdon and Johnson, 1990; S.Carson, 1990; and others). In addition, and as previously stated some authors (Lambeth *et al.*, 1983; Magnussen and Yeatman, 1989; and McKeand, 1988) consider correlations at development stages more relevant than ages. Further, Magnussen (1989) found that r_{jm}

between 15-year volume and 20-year through to 35-year volume increased with decreasing initial tree spacing from 4.3 m to 1.2 m. A logical extension might be to grow progeny tests at closer spacing on highly homogeneous, weed-free, fertile sites using uniform planting stock. This technique is known as testing on 'Farm Field Sites' (FFS).

Carlson (1990), reports on FFS for open-pollinated families of Lodgepole pine (*Pinus contorta*). FFS's were found to be more productive, gave improved precision for estimates of family means and higher family heritability values than (geographically) corresponding forest sites containing the same families. The family mean correlations (30 or 60 families) between 2 year-height measured in the FFS and 6-year height measured in the forest varied across the 8 sites studied from $r_{2,6} = 0.07$ to 0.70 (mean 0.30). This could partly be a factor of forest site quality since a number of the sites investigated suffered from frost damage. However, the correlations between FFS and the more fertile, homogenous, frost-free forest sites were very good ($r_{2,6} = 0.70$). This latter site is probably more typical in terms of quality of the type used recently for testing radiata pine families in NZ.

Magnussen and Yeatman (1986), found good correlations between 4-year heights of half-sib jack pine family means in the nursery (similar to FFS) and 12 year heights across two forest sites (r=0.61). In a similar experiment, Franklin and Squillace (1973) found a high offspring-parent correlation for height by comparing 3-year-old offspring grown under accelerated, highly intensive culture with heights of their 25-year-old parents grown in a widely spaced plantation.

Woods (pers. com) working with Douglas fir in Canada reports good correlations between 1-year height in a FFS and 12-year volume, across a number of forest sites ($r_{2,12} = 0.60$).

In the UK, there are proposals to plant full-sib Sitka spruce progeny material on a FFS for 3 years prior to culling the poorest 40-50%. The remaining families will be re-sown and planted out to three carefully selected forest sites. (Lee *et al.*, 1990 unpublished FC report). These measures are being taken for reasons of resource limitations (since actual genetic gain per year will be decreased) but the similarity with FFS testing is apparent.

REPEATABILITY OF AGE:AGE CORRELATIONS

Lambeth (1983), ran simulation studies that indicated that large experimental and sampling errors can lead to only moderate family mean rank correlations even when the underlying correlation is r=1.0 . It follows that in glasshouse and phytotron experiments with limited numbers of families, where the underlying correlation is far from r = 1.0,

sampling error will be even greater. A calculated age:age correlation therefore could well be incorrect. It also would seem possible that a 'chance' significant correlation may be identified if large numbers of traits are assessed (both physical and physiological) on a small sample of families and individuals within families. Before accepting calculated r_{Gjm} involving very juvenile selection ages and small sample sizes, the breeder needs to be sure the results are repeatable and based on large sample sizes of families and individuals within families.

Lambeth (1983) speculates that the sampling problems associated with correlation analysis may be the main reason why, after decades of research, there is no general consensus on whether early testing can work. One way of validating the effectiveness of early selection may be to carry out a retrospective test of extremes. Waxler and van Buijtenen (1981) identified five fast-growing and five slow-growing families in 10- to 20-year old field tests and classified their performance based on glasshouse testing. Mean dry weight in the glasshouse correctly identified 4 out of the top 5 families in the field test. This approach helps show whether there is a positive association but is of little value in pinning down the magnitude of that association.

POSSIBLE PROBLEMS OF EARLY SELECTION

(i)   So far discussion has been concerned with early selection for tree growth rate only. However, final selection for the breeding or production population is usually based on their 'Index Value' combining all traits of interest (including form, disease resistance and wood properties) along with information on economic weights and genetic correlations between traits.

If it becomes possible to select families for vigour at a very early age and before information is available for all the other traits of interest it may be possible to adjust breeding strategies to take advantage of this. Organisations may choose to establish the best possible production populations for vigour alone as soon as early test results are available so maximising gain for that trait. Roguing and additions to such populations may follow once information on other traits becomes available.

In addition, success in early selection for one trait stimulates research into finding successful methods of early selection for other traits.

(ii)   When selections are made at early ages, there is an increased tendency for non-genetic starting effects to be confounded with genotypic effects. These can lead to apparent growth rate gains (Burdon and Sweet,1976). Wilcox (1983) found that the influence of

reciprocal differences in seed size in *P.radiata* was still reflected in height growth for several families after 2 years in the field; sufficient he concluded, to make selection at this age unreliable. Carson *et al.* (1986, unpublished Project Record) analysed the same experiments after 5 years and found that significant differences can still persist.

One method of testing for GCA and avoiding non-genetic starting effects due to seed size is to test clones as males to a number of different female testers. This is already operational in breeding of *Pinus radiata* in NZ (Shelbourne *et al.*, 1989). In addition, adjustment of family mean using, for example, seed weight or early seedling height as a covariate could help circumvent this problem.

(iii)   The question arises as to whether early selection is equally applicable to both forward and backward selection. Lambeth *et al.* (1983) found that genetic correlations were greater at a given age among family means than among individual trees suggesting that more time is required to select the best individual within the best families. However, other authors (e.g. King and Burdon (1991)) found no difference in optimum selection age between families and individuals within families. This could be particularly relevant to selection of the best clones within full-sib families for clonal forestry. For clones, genetic variation within each treatment (clone) will be zero and the only source of variation will be environmental. If test sites are carefully chosen, optimum selection ages could be less for clones than those for family means or individual seedlings within full-sib families in a progeny test.

(iv)   Early selection carries with it the possibility of including maladapted genotypes in breeding and production populations (Carlson, 1990). It is probably wise to investigate any proposed early selection programme with a retrospective analysis of families in long established progeny tests. The possibility of errors from incorrect juvenile selection as a result of long-term maladaption of genotypes, genotype by environment interaction, and early non-genetic effects could then be investigated.

(v)   A possible problem with turning generations over more quickly through use of early selection will be an increase in the rate of inbreeding within sub-lines. Thus genetic gain per year will initially be at a maximum, but (as yet unquantifiable) co-ancestry problems will be encountered earlier. These could effect the total gain per year over a number of generations relative to a more mature selection age. Such problems are restricted to the breeding population rather than the production population (by definition). Also, although early selection is found to be successful and exploitable in a production population, it does not follow that breeding of the next generation needs

to take place immediately. The next stage of breeding could be delayed until a time which is economically justifiable.

(vi) In order to advance to a further breeding cycle once juvenile selections have been made, it is necessary to get selected trees to flower. The earliest age at which radiata pine seedlings could flower is thought to be 4 years old although with further research this could possibly be reduced to 3 or even 2 years from seed (G. Vincent, pers. comm.). Flowering age is not a concern when practising clonal forestry. It becomes relevant however, if it is desired to establish a clonal seed orchard of the best individuals within the best families as soon as possible following early selection or if the objective remains to turn breeding generations over as quickly as possible.

CURRENT PRACTICE WITH *PINUS RADIATA*

Shelbourne *et al.* (1986) outlined the current development plan for radiata pine breeding in New Zealand. Current practice is to carry out selections after 7 years in a forest progeny test based on multi-trait 'Index value', after making preliminary selections at year 5. Is there a need to alter this age? Could genetic gain per year be increased by selection at an earlier age?

The findings of King and Burdon (1991) would tend to confirm the strategy adopted by Shelbourne *et al.* (1986). Results from Cotterill and Dean (1988) also concur with selection in year 7 for radiata pine in South Australia. Ages for optimum selection in species with comparable rotation lengths are also similar e.g Loblolly pine reported by McKeand (1988); although Foster (1986) reports ages as 3 years.

If 7-8 years is the optimum age for juvenile selection it avoids a number of the possible problems of very early selection. Seven to eight years is an age for which the breeding programme has already adapted, and found to be convenient in terms of selection for a number of traits other than vigour (e.g. uni- or multinodal stems, Dothistroma resistance). Trees can also be brought to flower very soon after their selection thus preventing delays in advancing the breeding programme.

PROPOSALS FOR THE FUTURE

The conclusions drawn above with regard to optimum selection ages in *Pinus radiata* in NZ are based very much on the reliability of the Lambeth (1980) equation as calculated by King and Burdon (1991) using data collected from the '268' series. The ideal remains to carry out calculations of optimum genetic gain per year either in absolute or discounted terms

using <u>actual</u> values of r_{jm}, h_j and h_m. Reports from elsewhere suggest that there is potential in attempting the comparison of family performance in both the FFS and glasshouse with well selected, carefully designed field progeny tests.

Since there are no reported studies in NZ on selection of *Pinus radiata* families based on nursery or glasshouse results it is proposed that both Farm Field Trials and glasshouse studies of early selection be established. The following retrospective progeny tests could be established within the FFS and glasshouse using the same families in each environment:

(i)   Remnant seed of at least 90 (up to 120) families (3 or 4 sets) for which there is at least 8 year forest progeny test data. This would allow accurate juvenile/mature correlations to be calculated and estimates of absolute and discounted genetic gain per year. A further objective of the same experiment can be used to investigate the conclusions of Waxler and van Buijtenen (1981) that a large proportion of superior families can be identified in early tests despite a possibly low age:age correlation.

(ii)   Thirty open-pollinated families will be compared with bulked full-sib families of the same thirty clones mated with the female testers. This will allow comparison of accuracy between the two techniques for determining GCA. It is speculated that the female tester method will be more efficient due to the removal of non-genetic starting effects attributable to seed size. This experiment will enable comparisons to be made at the population and family pair-wise level and allow differences over time to be monitored. The magnitude of any differences and how they vary with time should allow an insight into the justification of extra expense associated with the female tester control crossings.

As much as possible, open-pollinated families should be common to (i) and (ii). Field progeny tests will be established in parallel to each of the above experiments established in the FFS and glasshouse. This will allow comparisons to be made between (a) early and later forest field tests and (b) the FFS and the glasshouse with each of the respective forest field sites.

Experimental design and traits to be assessed:

(a)   <u>Farm Field Study:</u>

-    Experiments will be designed to run for at least 4 years.
-    The trial will be on two, fertile, uniform site (0.75 ha each) close to FRI.

- In order to reduce environmental variation to a minimum, planting stock should be raised to very high standards.
- Highly intensive silviculture will be practised to ensure the site is weed and pest free at all times.
- Spacing between trees will be 1.5 m x 1.5 m (4,400 trees per hectare).
- Single-tree plots will be employed with 16-20 replicates.

Traits to be assessed will include:

(i)   seed weight at time of sowing,

(ii)   height and root collar diameter at time of planting in the field,

(iii)   height at six months followed by annual height assessment,

(iv)   annual assessment of diameter at a standardised height (which may be breast height in years 2,3, and 4).

(b)   Glasshouse:

- Uniform, containerised planting stock.
- Single-tree plots employed over 15 blocks.
- Blocks will be moved to different random positions at regular intervals to avoid any possible positional effects.
- Experiments will run for 8-12 months.

Traits to be assessed will include:

(i)   seed weight at sowing,

(ii)   monthly height,

(iii)   monthly root collar diameter,

(iv)   stem dry weight at harvest,

(v)   total dry weight at harvest,

(vi)   stem volume,

(vii) if possible, other traits assessing distribution of photosynthate.

(c)   Forest field site

- Standard progeny test site selection and design.
- Normal spacing and silviculture.

Traits to be assessed:

(i)   seed weight,
(ii) height after one growing season,
(iii) biennial height assessments,
(iv) biennial diameter assessments after year 3.

All traits assessed in both the glasshouse and FFS trials will be correlated with older field family performance from existing tests in both the unadjusted an also adjusted form, using seed weight and possibly other earlier assessments as co-variates. Data from the new field trials could similarly be interrogated with and without adjustment by seed weight and/or 1-year height as covariates.

CONCLUSIONS

The current selection age for *Pinus radiata* families and individuals within families appears to be optimum in terms of absolute and discounted genetic gain per year. It is therefore proposed there is no change to the age at which selections are currently made.

Calculations to determine optimum ages have, however, incurred certain assumptions and limited data to investigate age:age correlations. More recent improvements in selection and design of progeny tests may act to reduce the optimum selection age.

Experiences elsewhere suggest that very early selection in the field, glasshouse or nursery may be possible. It is therefore proposed that experiments employing Farm Field Sites and glasshouse tests are established using remnant seed for retrospective progeny tests. These should initially be considered as pilot trials with future implementation being dependent on preliminary results.

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APPENDIX I : Worked example using the Magnussen equation

Optimum selection ages in terms of discounted cumulated genetic gain from a continuous breeding programme of *Pinus radiata*. Assuming 25 year rotation, and calculated values of r_{Gjm} using the Lambeth equation as calculated by King and Burdon (1991).

Interest Rate		Total duration of breeding effort		
		75 yrs	150 yrs	300 yrs
(1)				
D = 5	5%	7	6	6
d = 5	10%	5	5	5
(2)				
D= 30	5%	13	14-15	14-15
d = 5	10%	8-10	7-11	7-11
(3)				
D = 10	5%	8	7-8	
d = 10	10%	6	6	
(4)				
D = 35	5%	12-14	15-16	15-16
d = 5	10%	7-11	6-13	6-13
(5)				
D = 3	5%	5	5-6	
d = 3	10%	5	5	

Where: S = years between seed harvests = 1 year

C = Number of breeding cycles in a given total time

$$= \frac{\text{Total Time (75, 150 or 300 years)}}{\text{Selection age} + d}$$

D = Delay between selection and gain realisation

d = delay between selection and first seed harvest.

The model was run to cover 75, 150 and 300 years of breeding. The most sensitive elements were found to be interest rates and the age at which gain is realized. Selection intensity and whether selection was for families or individual offspring seemed to have no marked effect. The latter is not too surprising considering the over-lap of data with King and Burdon (1991) who found only a slight difference in optimum age of selection between family and individual within family.

If gain is considered realized when improved seed is collected and then sold (D = 5 years) and it takes just 5 years to get seed once the orchard has been established (d = 5) then

the optimum age of selection in terms of discounted cumulated gain is 7 years over a 75 year period at a 5% discount rate. This falls to 6 years over 150 and 300 years, and 5 years over all three time spans at 10% interest rate.

If gain is not considered realized until the crop raised from the improved seed is felled and sold (say D = 30), then the optimum selection age is 13 years over a 75 year period and a 5% interest if the first seed is collected 5 years after orchard establishment (d = 5). This figure again falls as interest rates increase.

The most optimistic situation would be D and d both equal to just 3 years. The optimum age of selection now becomes 5 years regardless of interest rate or breeding period.

APPENDIX II :

Minimum values of r_{Gjm} required from ages 1 to 20 years and still yield the same genetic gain per year assuming heritabilities and selection differentials remain constant across ages.

T_j	r_{Gjm}	T_j	r_{Gjm}
1	0.20	11	0.53
2	0.23	12	0.57
3	0.26	13	0.60
4	0.30	14	0.63
5	0.33	15	0.67
6	0.37	16	0.70
7	0.40	17	0.73
8	0.43	18	0.77
9	0.47	19	0.80
10	0.50	20	0.83

The above was calculated by substituting in the following equation.

$$r_{Gjm} = \frac{(T_j + d)}{(T_m + d)}$$

where: T_m =   25 years (rotation length)

T_j =   juvenile selection age

d   =   5 years (delay between selection and seed collection)