DETERMINATION OF OPTIMUM SELECTION AGES: A SIMULATION APPROACH

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ABSTRACT. Prediction models of growth (height and stem volume), phenotypic variation, heritability, and age-to-age correlations provided an integrated framework for predicting optimum selection ages in a breeding program of fixed duration. The risks of early selection were assessed by computing a minimum significant gain ratio of juvenile selection; only gain ratios exceeding this minimum were permissible options for juvenile selections. Optimum selection ages were either very low (usually below one-sixth of the rotation age) or equal to the rotation age itself. Although intermediate selection ages promised more gain per unit time than selection at rotation age, the gain did not outweigh the associated risk. Slow growth (high rotation) made juvenile selection more attractive than it was in the fast growth scenarios. Minor changes in model parameters often had dramatic impacts on the age of optimum gain ratio. The simulation approach to estimation of optimum selection ages provides an useful tool for sensitivity analyses of a gain expression with many interrelated parameters.

Keywords: Early selection, simulation, decicion making, heritability, correlation, genetic gain

INTRODUCTION

Determining the selection age that achieves the highest rate of genetic progress in a tree improvement program requires information on time trends in variances, heritabilities, and age-to-age correlations (Falconer 1981, Lambeth 1980). Sufficient information is rarely available; so the choice of selection age is frequently based on general prediction models (Lambeth 1980), the strength of age-to-age correlations in existing trials (Cotterill and Dean 1988, Foster 1986, Lambeth et al 1983, Magnussen 1988, Riemenschneider 1988, Williams 1987), or eclectic experience. The potential pitfalls of parsimonious

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information is widely recognized (Franklin 1979, Kang 1985, Namkoong et al 1972, Nienstaedt 1984, Rehfeldt 1983).

Simulation of competing hypothetical time-trends within parameters of the genetic gain expression provides a simple tool for sensitivity analysis; it also helps bracket the range of the most likely optimum selection age. Accepted solutions should be robust against moderate changes in the parameters of genetic gain.

The present study illustrates how simulation can assist the breeder in deciding selection age. Within a fixed time horizon, different scenarios of growth, variances, heritability, and age-to-age correlation are formalized mathematically and the optimum selection age found by computing the predicted gain per unit time for all possible outcomes. The risk of early selection is considered by requiring that the prospective reward of early selection outweighs the potential risk.

MODEL PARAMETERS

Under consideration is mass selection for tree height or stem volume in a progeny trial. Genetic gains are attained at harvest of improved seed whereas commercial gain is realized by harvest of stands grown from improved stock. Improvement in economically mature traits is, therefore, the objective of breeding efforts. The expected gain (G) in a mature trait (m) arising from selection on trait (j) is equal to:

$$[1] \quad G_{m:j} = i*h_j*h_m*r_{jm}*\sigma_m$$

(Falconer 1981)

where i = selection intensity
h_j, h_m = square root of heritability
r_{jm} = correlation between j and m
σ_m = phenotypic standard deviation of trait m

Henceforth j and m signifies the juvenile and mature expression of the same trait at time T_j and time T_m, repectively.

In a continuous breeding program the cumulated total genetic gain produced per year (CG) in a given total time (TT) equals:

$$[2] \quad CG_{m:j} = \sum_{q=1}^{C-1}\{\sum_{n=1}^{N_C}(q*G_{m:j})/((q*T_j+d)+s*(n-1))+$$
$$\sum_{n=0}^{N_F-1} c*G_{m:j}/(c*(T_j+d)+s*n)\}$$

where

c = number of breeding cycles in a given total time TT,
c = TT/(Tj+d)
d = delay between selection and production of improved seed
s = years between seed harvests
N =number of seed harvests during a breeding cycle
N^{c}= (Tj+d)/s
N_F = number of seed harvests after the last breeding cycle

Default values for TT, d, and s were 150, 5, and 3 respectively.

In order to calculate $CG_{m;j}$ we must know the time trends in heritabilities $(h2)$. variances (σ^2). and correlations (r). Models of heritability are depicted in Figure 1. All fourteen models have an average heritability of 0.20 in the interval from one to 40 years, a realistic expectation (Foster 1986, Zobel and Talbert 1984).

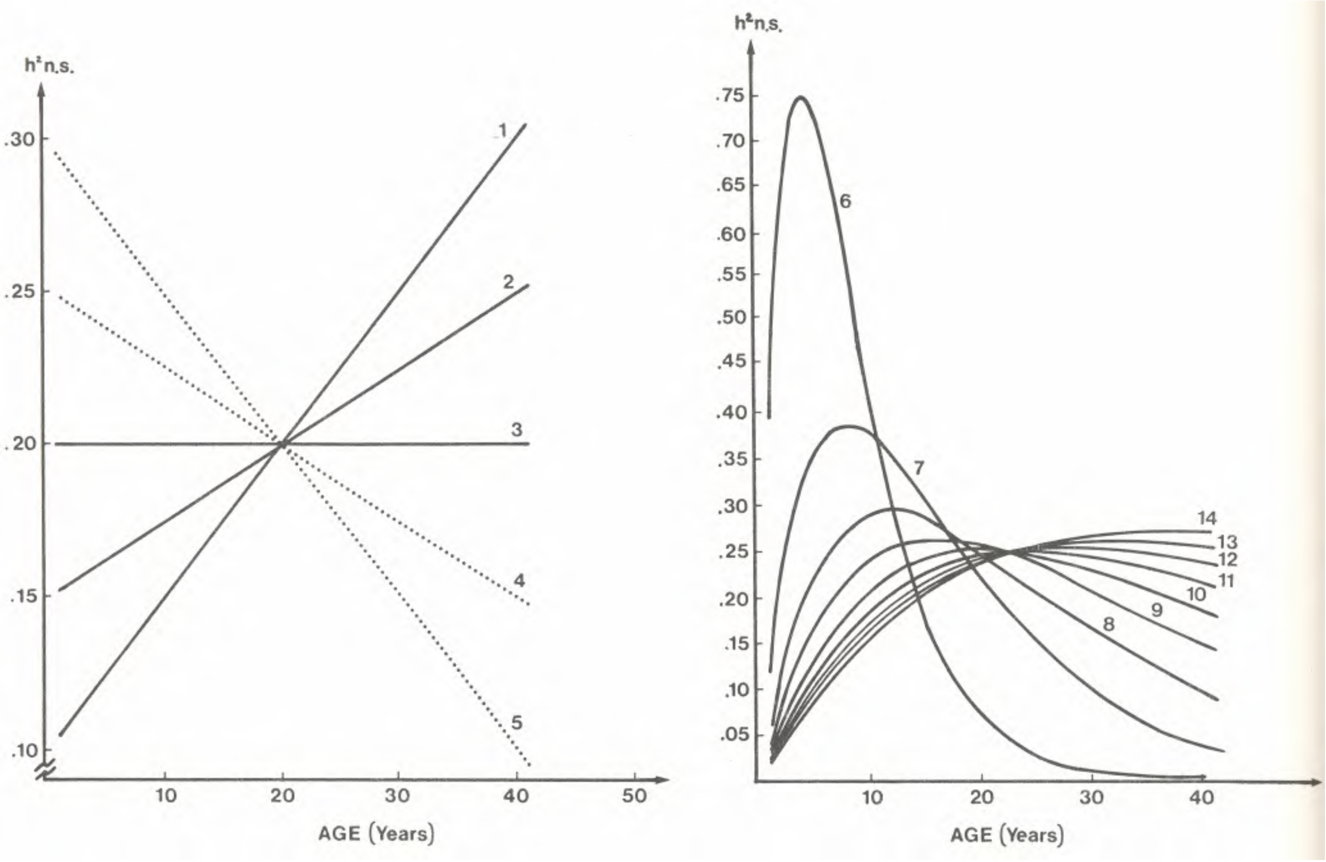


Figure 1. Fourteen models of age trends in heritability.

Time trends in variances were derived by combining the models of tree growth (height and stem volume) in Figure 2 with the trend models of coefficient of variation in Figure 3. It is assumed that actual growth figures will fall within the outlined limits.

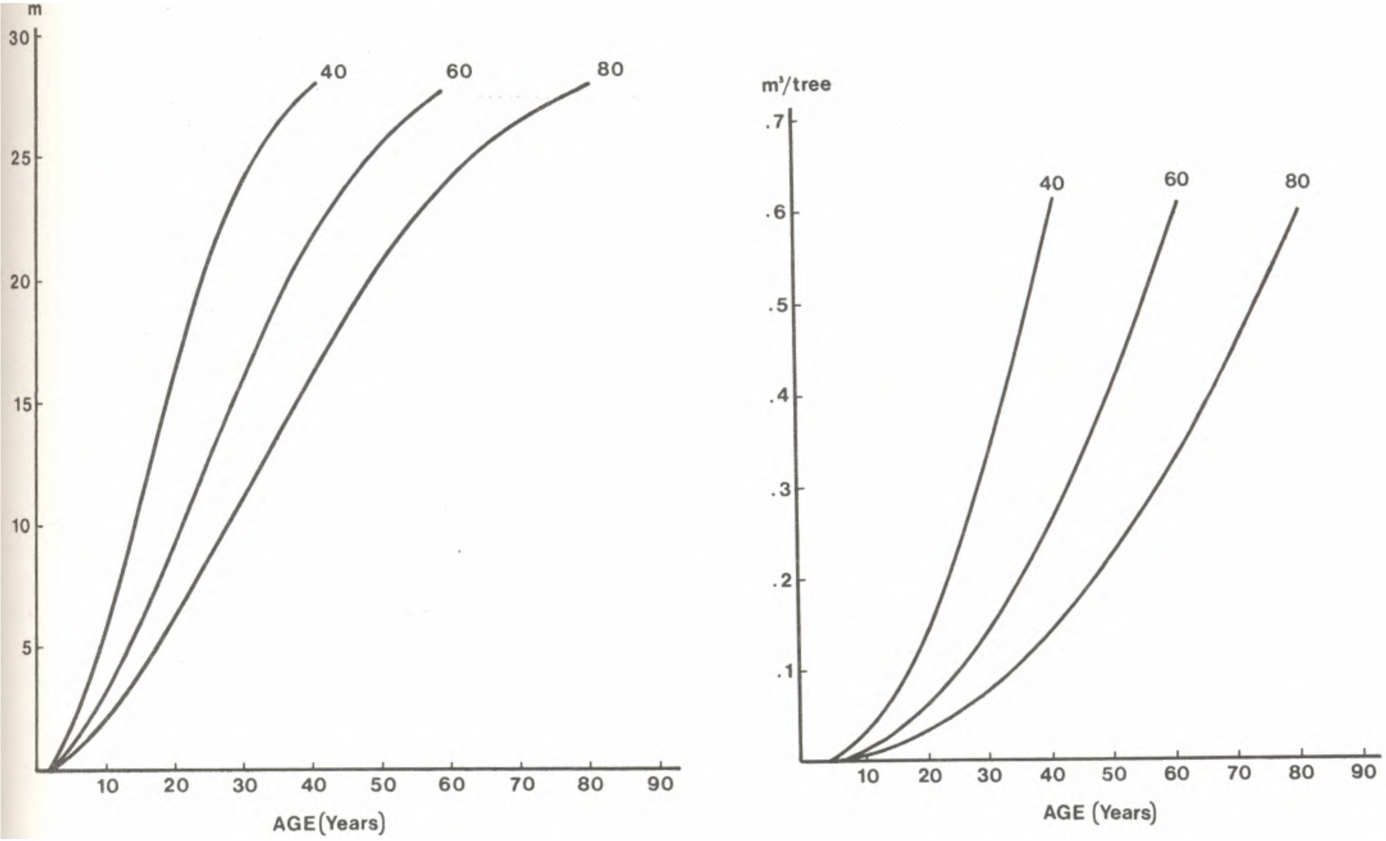


Figure 2. Height (left) and stem volume (right) over age. Rotation length in years is indicated at each curve.

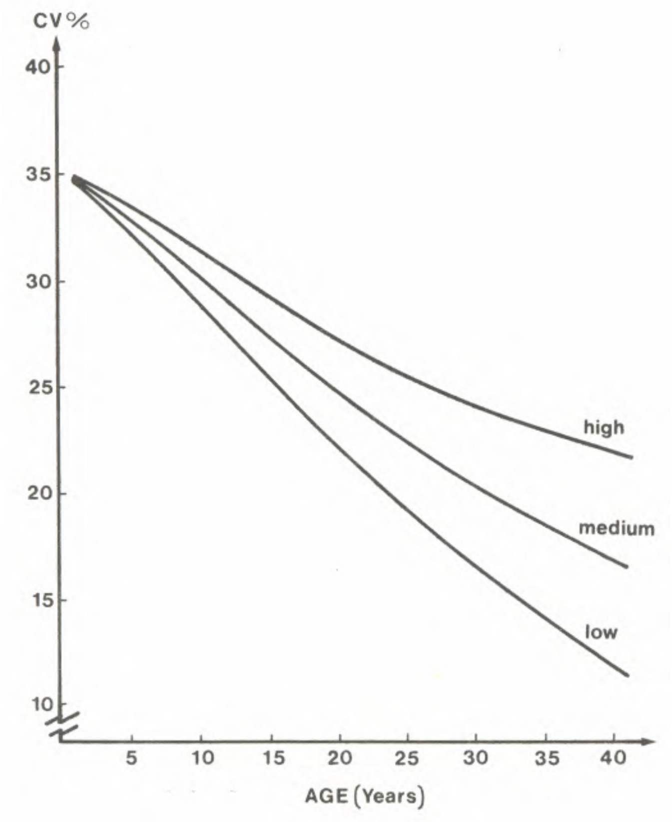
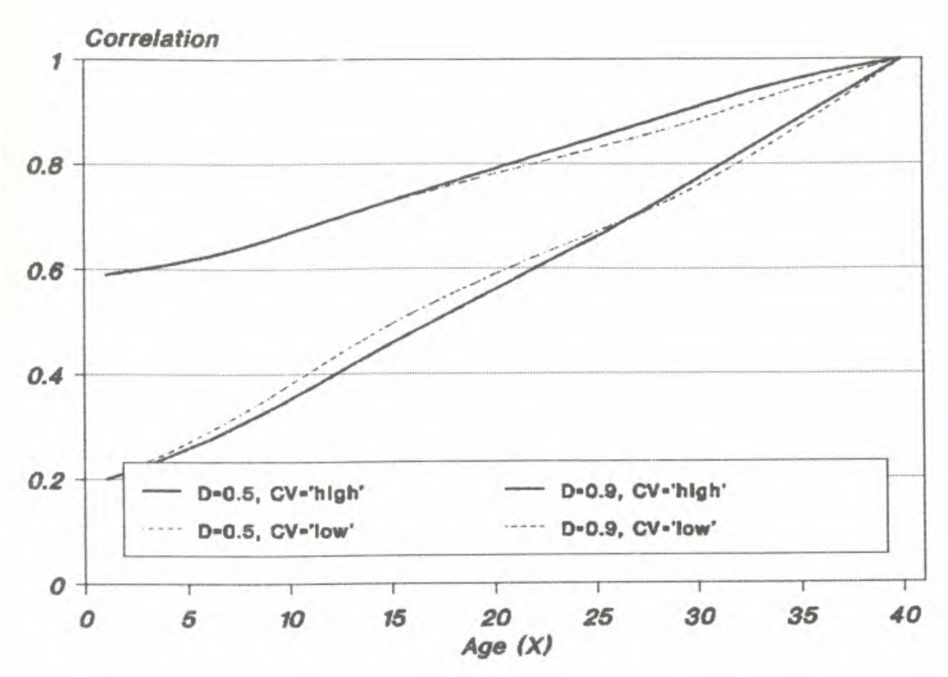


Figure 3. Time trends in the coefficient of variation of tree height and stem volume.

Correlations of trait values at time T_j and time T_m were computed from the ratio of the associated variances (VR= $\sigma^2(T_j)/\sigma^2(T_m)$), the fraction (D) of size dependent growth (0<D<1) and an intrinsic growth rate (k_{jm}) during time T_m-T_j. More specifically:

[3] $r = (1+k_{jm}*D)*\sqrt{(VR)}$ (Magnussen 1989)

D-values were selected between 0.5 and 0.9 in steps of 0.1, which should bracket realistic expectations (Magnussen 1989). The intrinsic growth rate is obtained indirectly from growth models. Figure 4 illustrates the significance of D and the level of variability ('high', 'medium', or 'low') on the expected age-to-age correlations of height and stem volume.



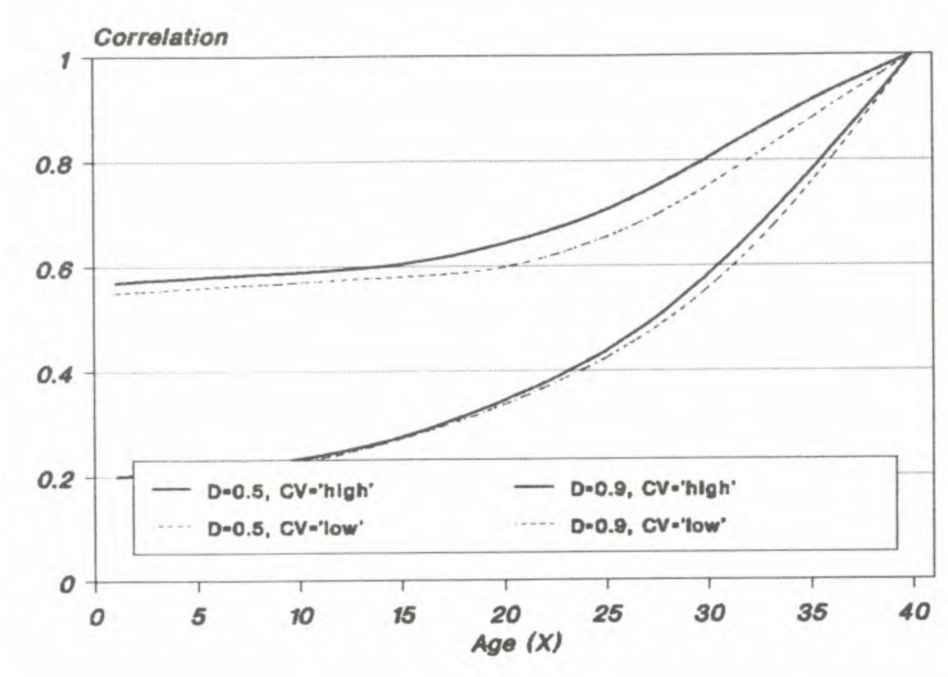


Figure 4. Examples of age 'x' to age 40 correlations. Top: Tree height. Bottom: Stem volume.

Optimum selection age is the age (T_j) that, for a given rotation age (T_m), maximizes the gain ratio $CG_{m:j}/CG_{m:m}$. The standard error of this ratio is cumbersome to estimate (Magnussen 1987). Of the many variables that influence error none is more important than the error of heritabilities (Hallauer and Miranda 1981, Magnussen and Yeatman 1987, Namkoong 1979). Let the standard error of a heritability estimate be 40% (Cotterill and Dean 1988, Dean et al 1983, Foster 1986, Loo et al 1984, Magnussen and Yeatman 1987), the correlation between h_j and hm be 0.7, and ignore the errors of age-to-age correlations and of the phenotypic standard deviation. Thus simplified we obtain the following expression for the relative error of the gain ratio of juvenile to mature gain per unit time (Magnussen and Yeatman 1987, page 59):

$$[4]\ CV_{gain\ ratio} = \sqrt{0.2960*(1-r_{jm})}$$

Selection before rotation age is deemed attractive whenever the predicted gain ratio exceeds 1.0 by a significant margin. By accepting a 10% risk of choosing a selection age that actually will yield less gain per unit time than selection at maturity, the decision rule becomes one of finding the maximum gain ratio that, under assumed normality, satisfies:

$$[5]\ CG_{j:m}/CG_{m:m} > 1/(1-1.29*CV_{gain\ ratio})$$

An example of time trends in the minimum acceptable gain ratio and in the expected gain ratios is provided in Figure 5. Permissible selection ages fall within the cross-hatched area between the two curves.

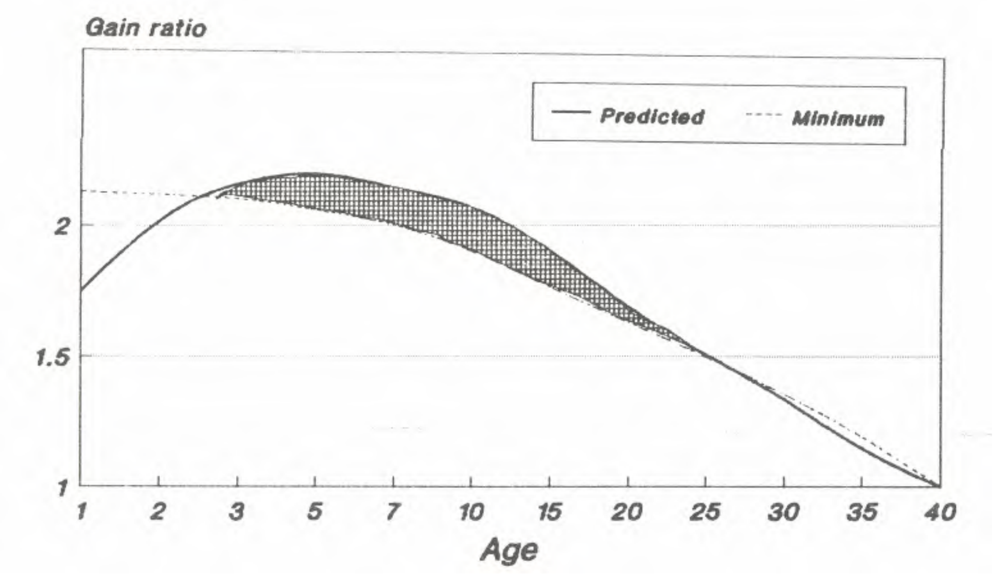


Figure 5. Predicted and minimum significant gain ratio plotted against age. Model: Rotation=40 years, D=0.6, CV%='high', and h2=curve no. 12.

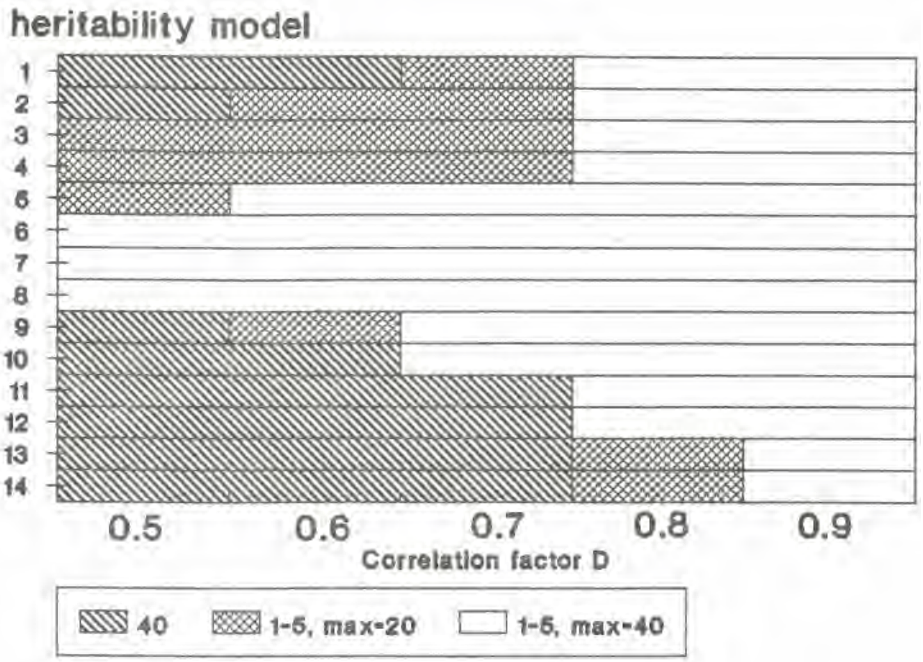
RESULTS

Optimum selection age were either equal to rotation age (T_m) or below five years. A schematic presentation of the most promising selection age for the various combinations of heritability model and level of age-to-age correlations (D-factor) is given in Figure 6 for a rotation age of 40.

It is clear that the combination of low age-to-age correlations (D<0.7) and a heritability rising with age or showing a late culmination (as in models 1,2,10,...,14) leads to postponements of selections until rotation age has been reached. Conversely, the expectation of a falling heritability (model 4 and 5), perhaps after a brief juvenile peak (model 6,7,and 8), justifies selections before age 5. Finally, high age-to-age correlations (D>0.7) support a selection before age 5, regardless of heritability. Such early selections hold the promise of two to 20 times as much gain per unit time (average is about seven times) as selections at rotation age. A delay of five to 10 years beyond the optimum selection age can still be expected to produce about twice the amount of gain per unit time as selection at maturity. However, selections should not be postponed unnecessarily because the involved risk quickly outstrips the diminished reward. This is illustrated in Figure 6 where an upper limit of 20 years is imposed on several solutions. The limit signifies that the additional gain per unit time arising from selection between age 20 and rotation is marginal compared to the associated risk.

Solutions were somewhat trait dependent. The juvenile-mature correlations predicted for stem volume were for any given age and D-value lower than the corresponding height correlations (Fig. 4) that raised the optimum selection age for stem volume, especially in models with a decline or a late culmination in heritability (Fig. 6). Also, the ability to select with some advantage between age 1 and rotation age is much more restricted for stem volume than for tree height. Most early selections of stem volume have to be completed in the first half of the rotation.

Optimum selection ages for a rotation age of 80 were, as a rule, well below the corresponding 40-year rotation results. Only the combination of low age-to-age correlations (D=0.5) and rising heritabilities (models 1,2,11,..,14) conditioned selection ages to fall within five years of the rotation age. The advantage of early selection was much higher for this long rotation; when carried out before age five the gain per unit time increased by a factor between 3 and 50. Results for a rotation of 60 years are intermediate to those outlined above.


heritability model
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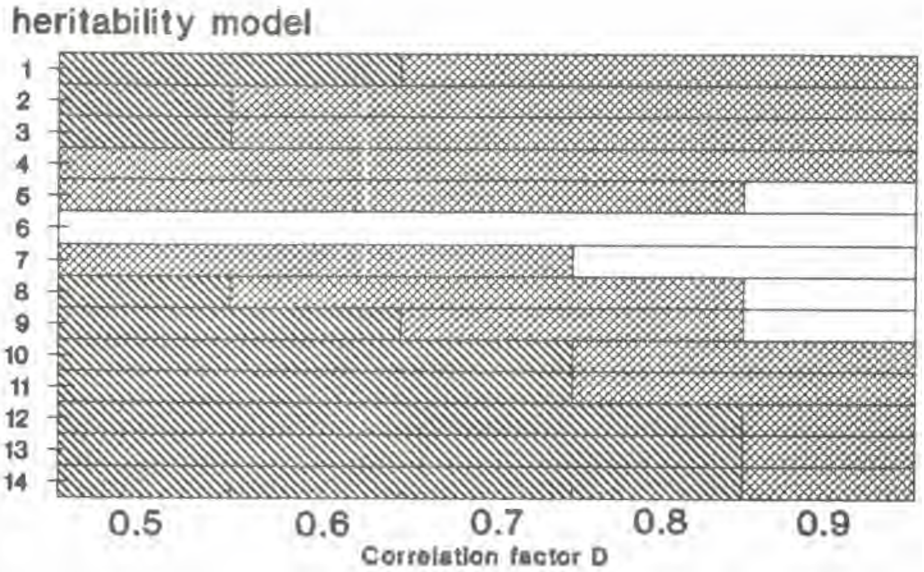
Correlation factor D
40
1-5, max-20
1-5, max-40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0.9
Correlation factor D

A factor of little or no influence was the coefficient of variation. The neglible impact of this parameter on the correlations is illustrated in Figure 4a,b. Optimum selection ages for scenarios that only differed in the level of coefficient of variation were less than one year apart.

It is, of course, of little practical value to consider simultaneously the solutions to all the models included in this study. In practice only a few likely alternatives are enumerated and the optimum selection age is taken as the average solution. Examples are provided in Table 1, where four contrasting choices (A,B,C, and D) of the expected time trends in heritabilities and correlations have been identified along with their average optimum selection ages. Scenario A describes a situation in which heritabilities are expected to increase with time or show a late culmination and where correlations are expected to be below average. Scenario B is identical to A with regard to heritabilities, but correlations are assumed to be strong. The last two scenarios, C and D, reverse the heritability expectations in A and B, respectively.

Solutions for scenarios C and D were identical regardless of trait, rotation age, and the strength of age-to-age correlations. For C and D selection at age two is apparently the optimum strategy under conditions covered by the underlying model assumptions (Table 1). Juvenile selections are not recommended for scenario A unless selection is for height and rotation is about 80 years. Scenario B, which differs from A only with regard to the expected age-to-age correlations, permits optimum selection between ages four (height, rotation=80 years) and 17 (stem volume, rotation=40 years). Optimum solutions for stem volume were as a rule higher than for tree height, and higher for short rotations (40 years) than for longer rotations (80 years).

DISCUSSION

The main purpose of this study was to introduce the simulationapproach to determine selection age; realistic values of the parameters in the gain equation are desirable, but not necessary. Simulation is attractive because it brackets unforseeable fluctations in the actual parameters caused by transient technical factors, delayed trait expressions, environmental changes, or ontogenetic phases (Bongarten and Hanover 1985, Dietrichson and Kierulf 1982, Nanson 1969, Nienstaedt 1984, Roulund et al 1986, Skröppa and Dietrichson 1986, Ununger et al 1988, Williams 1988). To limit the scope of this study only single stage selections for a single trait were modelled, with several parameters treated as constants instead of variables. Added realism

Table 1. Optimum selection ages for tree height and stem volume in four hypothetical scenarios of expected time trends in heritabilities and age-to-age correlations.

Scenario	Heritability models	Correlations, D=
A	1,2,11,12,13,14	0.5,0.6,0.7
B	1,2,11,12,13,14	0.7,0.8,0.9
C	4,5,6,7	0.5,0.6,0.7
D	4,5,6,7	0.7,0.8,0.9

Scenario	Height (a)	Volume (a)
	Rotation = 40 years	
A	34 (3)	34 (4)
B	12 (4)	17 (5)
C	2 (1)	2 (1)
D	2 (1)	2 (1)
	Rotation = 80 years	
A	9 (4)	24 (8)
B	4 (1)	5 (1)
C	2 (1)	2 (1)
D	2 (1)	2 (1)

could have been achieved by stochastic simulation (Harris 1964, Karlin and Taylor 1975, Ripley 1987, Sales and Hill 1976) or by implementing Bayesian forecasting principles (Harvey 1984, Magnussen 1988). Techniques to enhance gain by multistage selections or by index selections have been dealt with elsewhere (Baradat 1976, Bridgwater and Williams 1987, Cotterill and Dean 1988, Hühn 1987, Magnussen 1987, Young 1964).

Integration of the age-to-age correlation model with models of growth and variability (Magnussen 1989) furnished a better framework for simulations than correlation models with time as the only independent variable (Lambeth 1980). Rotation age was treated as a variable within fixed time limits on the breeding activities and not as a variable that determines the duration of a breeding program (Lambeth 1980, Kang 1985, Porterfield et al 1975, Squillace et al 1967). This distinction is important because the optimum selection age actually decreases with increasing rotation age when the overall time is fixed, whereas it increases with rotation age when no distinction is made between rotation age and total breeding time.

Quantification of risk was another important aspect of the simulation approach. Although risks of juvenile selections are widely recognized (Dietrichson 1964, Loehle and Namkoong 1987, Nanson 1969, Rehfeldt 1983, Steinhoff 1974, Wakeley 1971), few attempts have been made to quantify and incorporate such risks in the context of finding the optimum selection age (Kang 1985, Namkoong et al 1972, Robinson and van Buijtenen 1979,). Time trends in risk and in genetic gain were frequently related in a way that promoted either early selections at a time when the expected benefits outweighed the risk or at rotation age when the recognized risk was at a minimum. Without the risk virtually all selection ages would have been fallen in the interval between one and five years.

The level of variability exercised little or no influence on the optimum selection age. This somewhat surprising result was due to the particular formulation of the correlation model, in which variances and growth rates were determining parameters. A time dependent correlation model would have isolated the significance of the coefficient of variation more explicitly.

A high sensitivity of selection ages to parameters in the gain equations was amply demonstrated. Minor changes in either the correlation function or the heritability model resulted occasionally in a dramatic shift in the optimum selection age. This indicates very flat vertices in several of the analysed models. Also, the effect of heritability depends on the strength of correlations and vice versa, which confirmed results published by Kang (1985). Optimum could have been achieved by stochastic simulation (Harris 1964, Karlin and Taylor 1975, Ripley 1987, Sales and Hill 1976) or by implementing Bayesian forecasting principles (Harvey 1984, Magnussen 1988). Techniques to enhance gain by multistage selections or by index selections have been dealt with elsewhere (Baradat 1976, Bridgwater and Williams 1987, Cotterill and Dean 1988, Hühn 1987, Magnussen 1987, Young 1964).

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