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Selection for an Optimum Tree Growth Curve

By S. MAGNUSSEN and A. KREMER



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Selection for an Optimum Tree Growth Curve

By S. MAGNUSSEN¹⁾ and A. KREMER²⁾

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Abstract

Height growth trajectories of 100 half-sib families of *Pinus pinaster* Arr. were subject to selection that aimed at a constant improvement (here 20%) for all ages or a

gradual improvement of $p \cdot \log(\text{age}) \cdot 100\%$ (here $p=0.05$). Height growth was under strong additive genetic control and prospects of genetic gain were promising. A 2nd degree polynomial on a log-log scale was successfully used to describe the height-age relationship in all trees. Classical SMITH-HAZEL selection indices, growth curve parameter indices, and continuous selection indices were also computed for the 2 improvement objectives. The continuous selection index was a second degree polynomial on a log

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transformed time scale derived from stochastic integration of covariance kernels. Results suggest that selection on the growth curve continuum is more efficient for both mass selection and family selection because it utilized more information than selection at discrete ages. The latter had to be restricted to 3 distinct ages in order to avoid singularity of covariance matrices. Selection on growth curve parameters was intermediate in efficiency.

Key words: Selection index, continuous index, restricted index, *Pinus pinaster*, heritability, gain.

Introduction

Genetic improvement of quantitative traits in forest tree species is generally initiated by selection directly on the trait expression at a given age or through an index of trait expressions at several ages (WHITE and HODGE, 1989). Selections can be restricted or aimed at predefined changes in trait expression (CUNNINGHAM et al., 1970; LIN, 1978) under a given set of economic weights (GIBSON and KENNEDY, 1990). Instead of selection exercised at discrete ages one might alternately consider changes in the entire growth trajectory of size versus age as the breeding objective. A growth curve is often more directly related to economic management decisions about value and rotation than is trait size at a given age. Selection on growth curves promises greater flexibility and better maintenance of growth rates than pointwise selections. Breeders can, therefore, affect management by creating a shift of the whole curve.

Given sufficient data to construct individual growth trajectories, a functional analysis of growth as a stochastic process would furnish the necessary parameters for construction of a selection index and estimation of genetic progress. Two approaches of this nature have been suggested: (i) the parameters of the growth trajectory are considered to be the 'traits' under selection, and (ii) the growth curve continuum is the 'trait' under selection. Examples of the first approach are given by BROWN and DONELLY (1988), KACHMAN et al. (1988), NAMKOONG and MATZINGER (1975). The 2nd approach, which requires the definition of a desirable optimum growth curve, provides the breeder with a selection index that is continuous in time. Repeated application of this index in a recurrent selection and breeding programme should change the growth trajectory of the breeding population to the desired goal (KIRKPATRICK and HECKMAN, 1989; TALLIS, 1968). Despite the claimed advantages of the latter approach (more complete description of the trait, greater accuracy in predicting changes due to selection, and increased efficiency in estimating genetic parameters), examples with real data are still wanted.

In this study we define 2 competing 'optimum' height-age curves for maritime pine (*Pinus pinaster* Arr.) and computes the expected response to mass and family selection (BULMER, 1985) from alternate selection indices aimed at changing the current growth pattern towards the 'optimum' in the shortest possible number of generations. For the sake of demonstration we defined an improvement of 20% in height at all ages, and a gradual improvement of 0.05·log(age)·100% as the 2 'optimum' strategies. The selection indices were based on either classical SMITH-HAZEL selection indices (HAZEL, 1943; SMITH, 1936), selection on growth curve parameters, or selection on the growth curve

continuum (function). The information used in the classical selection indices had to be limited in order to avoid singularity of covariance matrices caused by the strong age-to-age correlation of tree height in the data. Improvement in the growth performance of maritime pine, a species that dominates one of the largest forest complexes in Europe (Les Landes), is a priority in France (BARADAT, 1986).

Material and Methods

Data

Data for this study came from a progeny test of 100 maritime pine open pollinated families (assumed to be maternal half-sibs). The test site, located in the Landes near Cestas (France), was a semihumid sandy podzol (BONNEAU et al., 1968) with a well developed B-horizon. The vegetation cover of the nutrient poor sands was dominated by *Molina coerulea* MOENCH., *Erica scoparia* L., and *Ulex* spp. The test design was triple 10x10 lattice replicated three times with 10-tree plots (2 rows of 5 trees) planted in 1965 with 1 year-old-seedlings at a 3m x 1m spacing (KREMER, 1981). A first thinning was done at age 11 (1976) systematically removing every 2. tree in each row. A second thinning in 1986 (age 22) removed every 2. row leaving 2 to 3 trees per plot. A complete height-age chronology (age 2 to 22) was established for all felled trees and used for analysis.

Linear model

All variables of interest (heights and regression parameters) were subject to an analysis of variance (ANOVA/MANOVA) of the following linear model:

$$[1] \Psi_{ijkl} = \mu + \lambda_i + \rho_{j(i)} + \phi_k + \gamma_{ik} + \eta_{jk(i)} + \varepsilon_{ijkl}$$

where:

Ψ_{ijkl} = Observation(s) or estimate(s) on l'th tree of family k in replicate j of lattice i $l=\{1,2,3\}$, $k=\{1,2,...,100\}$, $j=\{1,2,3\}$, $i=\{1,2,3\}$.

μ = total mean(s) of all trees

λ_i = effect attributed to lattice i

$\rho_{j(i)}$ = effect attributed to replicate j in lattice i

ϕ_k = effect attributed to family k

γ_{ik} = effect attributed to family k in lattice i

$\eta_{jk(i)}$ = effect attributed to family k in replicate j of lattice i

ε_{ijkl} = residual part of observation (estimate) not accounted for by the above effects

Variance components, heritability, and genetic correlation

All model effects except μ were considered random with mean 0 and a variance σ^2 . Variance components were estimated by equating the expected mean squares (EMS) in the ANOVA/MANOVA analyses with the observed mean squares (MS). The expected mean squares (type III, MILLIKEN and JOHNSON (1984), ch. 10) for this particular study were:

source of variation	df	MS	Expected mean square (EMS)
Lattice	2	MS _l	$\sigma^2_{\epsilon} + 1.53\sigma^2_{\eta} + 4.38\sigma^2_{\gamma} + 145.9\sigma^2_{\rho} + 437.7\sigma^2_{\lambda}$
Replicate (lattice)	6	MS _r	$\sigma^2_{\epsilon} + 1.53\sigma^2_{\eta} + 145.7\sigma^2_{\rho}$
Family	99	MS _f	$\sigma^2_{\epsilon} + 1.56\sigma^2_{\eta} + 4.50\sigma^2_{\gamma} + 13.48\sigma^2_{\phi}$
Family x lattice	198	MS _{fl}	$\sigma^2_{\epsilon} + 1.58\sigma^2_{\eta} + 4.57\sigma^2_{\gamma}$
Family x rep (lattice)	566	MS _{fil}	$\sigma^2_{\epsilon} + 1.68\sigma^2_{\eta}$
Error	658	MS _e	σ^2_{ϵ}

Variances of the estimated variance components were estimated from (BECKER, 1984, p. 36 section D, ignoring minor discrepancies in the coefficients of corresponding variance components caused by data imbalance, and any distinction between true and estimated sample values):

$$[2] \quad \text{var}(\sigma_x^2) = \frac{2}{c_x^2} \times \sum \frac{MS_x^2}{(df_x + 2)}$$

where c_x is the coefficient to the variance component 'x' in the above table of EMS and summation is over the

[4]

$$h_f^2 = \frac{\sigma_{\phi}^2}{(\sigma_{\phi}^2 + \sigma_{\gamma}^2/3 + \sigma_{\lambda}^2/3 + \sigma_{\eta}^2/9 + \sigma_{\rho}^2/9 + \sigma_{\epsilon}^2/(1.6 \times 9))}$$

Conservative estimates of the standard errors of these heritabilities and repeatabilities were obtained as the standard error of the numerator of the heritability expression divided by the denominator of the heritability expression (HALLAUER and MIRANDA, 1981). Genetic correlations were computed as:

$$[5] \quad \rho(x, y) = \frac{\sigma(x, y)_{\phi}}{\sigma(x)_{\phi} \times \sigma(y)_{\phi}}$$

where x and y denotes 2 traits (heights or regression parameters). Standard errors of genetic correlations were derived using a TAYLOR Series expansion (BULMER, 1985, p. 82 to 83).

Height-age relationship

The height-age relationship was described by the following regression model:

$$[6] \quad h_t = e^{(a + b \times \log(t) + c \times \log^2 t)}$$

$$[7] \quad \Gamma_{\omega}(t, s) = \begin{bmatrix} \frac{\partial h_t}{\partial a} & \frac{\partial h_t}{\partial b} & \frac{\partial h_t}{\partial c} \end{bmatrix} \times \Omega(\omega) \times \begin{bmatrix} \frac{\partial h_s}{\partial a} \\ \frac{\partial h_s}{\partial b} \\ \frac{\partial h_s}{\partial c} \end{bmatrix}, \quad \Omega(\omega) = \begin{bmatrix} c_1 & c_2 & c_3 \\ c_2 & c_4 & c_5 \\ c_3 & c_5 & c_6 \end{bmatrix}_{\omega}$$

where $\Gamma_{\omega}(t, s)$ denotes the covariance kernel of height effects attributed to the random effect 'ω' at ages t and s (ω = family, lattice, replicates in lattice, family x lattice, family x repl. (lattice), residual) and $\Omega(\omega)$ represents the variance-covariance matrix of the regression parameters

mean-squares used to determine σ_x^2 ; df_x are the degrees of freedom of the x-th mean square.

Narrow sense single tree heritabilities were computed as:

$$[3] \quad h_{n,t}^2 = \frac{4 \times \sigma_{\phi}^2}{\sigma_{\phi}^2 + \sigma_{\gamma}^2 + \sigma_{\lambda}^2 + \sigma_{\eta}^2 + \sigma_{\rho}^2 + \sigma_{\epsilon}^2}$$

and the family mean repeatability (accuracy of progeny means) as the ratio of the family variance to the variance of phenotypic family means:

where h_t is the tree height at age 't'. The regression parameter a estimates the log of tree height at age 1 whereas b and c estimate the linear and curvilinear trends in the relative growth rate, respectively. (Relative growth rate is growth per unit size, HUNT (1982)). After estimating the 3 regression parameters for each tree in the data set they were subjected to the ANOVA/MANOVA outlined above (eq. 1) and estimation of variances and covariances attributed to the effects listed in [1] was done as outlined for the height data. The separability of genetic and environmental effects (GREGORIUS and NAMKOONG, 1987) in this linear model (on a log transformed time scale) ensured the appropriateness of the procedures.

Variance-covariance kernels

A functional approximation of the variances and covariances of estimated heights (via [6]) at age t (h_t) and age s (h_s) is estimable for each of the random effects in the linear model ([1]) via ordinary double differentials (SERLING, 1980):

attributed to 'ω' ($c_1 = \text{var}(a_{\omega})$, $c_2 = \text{cov}(a_{\omega}, b_{\omega})$, $c_3 = \text{cov}(a_{\omega}, c_{\omega})$, $c_4 = \text{var}(b_{\omega})$, $c_5 = \text{cov}(b_{\omega}, c_{\omega})$, $c_6 = \text{var}(c_{\omega})$). The kernel Γ and the differentials were estimated at the genetic ($\omega = g$) and the phenotypic level ($\omega = p$).

Selection indices

For the sake of demonstration we chose to define a 20% improvement in height of all ages and a relative improvement that followed the formula $0.05 \cdot \log(\text{age})$ as two competing 'optimal' improvement strategies for both mass and family selection. The chosen improvement goals and selection methods (mass and family are two extremes) are believed to demonstrate, in a sufficiently general way, both the principle and efficiency of selection for an optimum tree growth curve. Our results are applicable to all situations where a 'lift' (proportional or gradual) of a growth curve is deemed desirable and for all combinations of family and within family selection schemes.

Restricted selection indices using height at discrete ages

A stepwise procedure (LIN, 1985) was used to derive mass and family selection indices with restrictions on desired gain in height at specified ages. In the following we make no explicit distinction between the two types of selection indices (mass and family), only the general formulae are provided. The conditional indices satisfy the same optimality criterion as the classical SMITH-HAZEL type of selection indices (SMITH, 1936; HAZEL, 1943).

The number of heights included in any index using height at discrete ages was limited to 3 equally spaced ages in order to avoid negative eigenvalues of matrices entering the computations (BAKER, 1986). Any larger number of heights (equally spaced) would result in singular variance-covariance matrices. No attempts were made to 'bend' the sample variance-covariance matrices of heights (HAYES and HILL, 1980) or to obtain maximum likelihood estimates restricted to yield positive definite variance-covariance matrices (GEARY, 1989). The indices using height

$$[12] \quad \left(\Omega(b) \approx \frac{m^2}{r^2} \times G^{-1} \times ((B \times \vartheta \times B + B \times \text{Trace}(B \vartheta)) / df_f + (W \times \vartheta \times W + W \times \text{Trace}(W \vartheta)) / df_{fl}) \times G^{-1} \right)$$

where r is the number of trees per family (here 15.6), $m=4$ (for half-sibs), W is the matrix of family \times lattice mean-square products, $B = W + (r/m)G$, and $\vartheta = bb'$. df_f and df_{fl} denotes the degrees of freedom for families and family \times lattice effects, respectively. Sampling errors in the estimates of P and G will make the true genetic progress slower than estimated from σ^2_I . An estimate of the index variance which includes the effects of sampling errors was derived as:

$$[13] \quad \sigma^2_I = b' \times P \times b + \text{trace}(\Omega b \times P)$$

Selection indices for both family selection and phenotypic mass selection of individual trees were calculated using the above equations with the appropriate phenotypic and additive genetic variance components.

Restricted selection indices for selection on height-age regression parameters

When indices were constructed for selection on the three regression parameters (a , b , and c in [6]) we first quantified the expected direct and correlated height response arising from imposing a unit change in either of the 3 parameters. The functional form of the expected height response are listed in [14], where $A(t)$ gives the change in height at age ' t ' due to a one unit change in a , and $B(t)$ and $C(t)$ express height changes (at age ' t ') caused by a unit change in b and c , respectively.

at discrete ages are, therefore, merely the 'best' possible use of the information from the MANOVA analysis.

From a vector of desired gains (Δ) and an estimate of the genetic (additive) variance-covariance matrix G we derived the index coefficients (b) as:

$$[8] \quad b_{n \times 1} = G_{n \times n}^{-1} \times \Delta_{n \times 1}$$

where n is the number of traits in the index. The variance of the index (I) values (assuming a known P matrix) was estimated as:

$$[9] \quad \sigma^2_I = b'_{n \times 1} \times P_{n \times n} \times b_{n \times 1}$$

where P is the phenotypic variance covariance matrix. Transposed matrices/vectors are identified with an apostrophe. The expected response ($r_{n \times 1}$) per unit selection intensity and per generation of selection and breeding was calculated from:

$$[10] \quad r_{n \times 1} = \Delta_{n \times 1} / \sigma_I$$

Correlations (ρ) between the index value (I) and its genetic merit (H) was obtained via:

$$[11]$$

$$\rho(I, H) = (b' \times G \times \alpha) / \sqrt{(b' \times P \times b) \times (\alpha' \times G \times \alpha)}$$

where α is the vector of economic weights in retrospect (i.e. the economic weights that would have produced the same index coefficients in an unrestricted index, GIBSON and KENNEDY, 1990). An estimate of the variances and covariances of the index coefficients ($\Omega(b)$) were computed as (TALLIS, 1968, eq. 2):

$$[14] \quad A(t) = h_t \times \left(1 + \frac{\partial b}{\partial a} \times \log t + \frac{\partial c}{\partial a} \times \log^2 t \right)$$

$$B(t) = h_t \times \left(\frac{\partial a}{\partial b} + \log t + \frac{\partial c}{\partial b} \times \log^2 t \right)$$

$$C(t) = h_t \times \left(\frac{\partial a}{\partial c} + \frac{\partial b}{\partial c} \times \log t + \log^2 t \right)$$

Estimates of the differentials in expression (14) were obtained from the estimated height-age regression coefficients. Provided with estimates of $A(t)$, $B(t)$, and $C(t)$ we constructed a linear combination thereof ($\pi_1 \cdot A(t) + \pi_2 \cdot B(t) + \pi_3 \cdot C(t)$) which would produce the desired change in height at all ages (π_1 , π_2 , and π_3 were found as solution to the regression of sample estimates of $A(t)$, $B(t)$, and $C(t)$ for $t=1, 2, \dots, 22$ on the desired height gain at the corresponding ages).

Continuous selection indices for selection on the growth curve continuum

Solutions to the continuous selection index problem were obtained by finding a polynomial (in $\log(\text{age})$, say $\beta(\log t)$) whose value at each age would be an index coefficient (β). Finding $\beta(\log t)$ poses a problem of accounting for direct and correlated responses in much the same way as discussed for selection on the regression coefficients a , b , and c . To assure that the direct and correlated height

responses by application of the index polynomial $\beta(\log t)$ adds up to the desired gain at, say, age t ($\Delta(\log t)$) it

suffices to find a solution ($\beta(\log(\text{age}))$) to the following integral equation (TALLIS 1968):

$$[15] \quad \Delta(\log t) = \int_{s_{\min}}^{s_{\max}} \beta(\log s) \times \Gamma_g(\log t, \log s) \times d(\log s), \text{ for } g = 4 \times \sigma_{\text{family}}^2$$

where integration over the 'dummy' age (s) is done to incorporate all correlated selection responses due to genetic covariances (as per Γ_g) between heights at a fixed age of t and heights at any other age ($s, s \in \{s | s_{\min} \leq s \leq s_{\max}\}$). Note that the age variables s and t are fully interchangeable. Our choice for $\beta(\log s)$ was a second degree polynomial ($\beta(\log s) = \beta_0 + \beta_1 \times \log s + \beta_2 \times \log^2 s$) defined for ages 1 to 22 years. A second degree polynomial was chosen because it allowed more flexibility in the

selection procedure than a purely linear model. The quadratic term in $\beta(\log s)$ will be insignificant whenever the selection objectives can be achieved by a strictly linear model, and a cubic or quartic polynomial would require an inordinate amount of calculus for a marginal reward. To obtain the coefficients β_0, β_1 , and β_2 we solved numerically the following system of three (differential) equations with three unknowns (β_0, β_1 , and β_2):

$$[16] \quad \left. \frac{\partial^n}{\partial \log^n t} (\Delta(\log t)) \right|_{\log t = 0} = \int_{\log 1}^{\log 22} \left[\frac{\partial^n}{\partial \log^n t} \Gamma_g(\log s, \log t) \right]_{\log t = 0} \times \beta(\log s) \times d \log s, \text{ for } n = \{1, 2, 3\}$$

Estimation of the continuous index (I) and its variance (σ_I^2) followed from:

[17]

$$I = \int_{\log 1}^{\log 22} \beta(\log s) \times (h_{\log s} - \mu_{\log s}) \times d \log s$$

[18]

$$\sigma_I^2 = \int_{\log 1}^{\log 22} \int_{\log 1}^{\log 22} \beta(\log s) \times \beta(\log t) \times \Gamma_p(\log s, \log t) \times d \log s \times d \log t$$

where subscript p denotes the phenotypic covariance kernel.

Approximate errors on the continuous selection index

In order to obtain an approximation of the errors of the index polynomial $\beta(\log s)$ we repeatedly (20,000 times) added a random error term δ to the covariance kernel Γ , kept the initial estimate of $\beta(\log s)$, and recalculated the left side of [16]. The δ terms were simulated multivariate random variables with a variance-covariance matrix as determined by the delta technique (BULMER, 1985, p. 82 to 83) applied to the first integrand in [16]. These repeated estimates of the left side of [16] enabled us to compute the approximate variance-covariance of the

terms. Calling this matrix $\Omega(\Delta)$ and casting [16] in the form of

$$[\beta_1 \ \beta_2 \ \beta_3] = Q \times \left[\frac{\partial \Delta}{\partial t} \ \frac{\partial^2 \Delta}{\partial t^2} \ \frac{\partial^3 \Delta}{\partial t^3} \right]_{t=1}$$

we obtained by standard techniques the variance-covariance matrix of the coefficients β_1 - β_3 (Q is now considered a constant). Call this covariance matrix $\Omega(\beta)$ and let the vector $[1 \ \log^2 t \ \log^2 t]$ be denoted by lt and the vector $[1 \ \log s \ \log^2 s]$ be denoted by ls , we then have (TALLIS, 1968, eq 3):

[19]

$$\sigma_I^2 = \sigma_I^2 + \int_{\log 1}^{\log 22} \int_{\log 1}^{\log 22} lt \times \Omega(\beta) \times ls \times \beta(\log s) \times \beta(\log t) \times d \log s \times d \log t.$$

Supplied with the above statistics we first computed the index value and its standard error for all genetic entries (families and trees). Then we computed, for a range of selection intensities, the average index value and its standard error for the selected units (trees or families).

Correlations among index values were ignored in these calculations (HILL, 1976). From these results we obtained an estimate of the error on the genetic gain in relation to the selection intensity (the error on the index variance was equated to the last term of [19]).

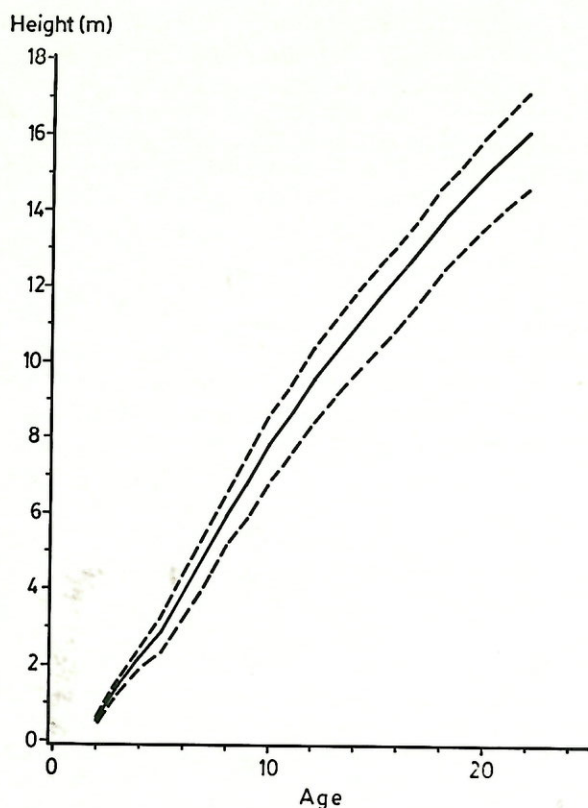


Figure 1. — Height-age relationship for the average, best, and slowest growing family.

Results

The mean family height increased from 0.5m at age 2 years to 16.1m at age 22 (Figure 1). Family mean height differences were statistically significant ($P < 0.05$) from age three onwards. At age 2 years the family differentiation was weaker (F -ratio for families = 1.31, $P = 0.056$). A mul-

Table 1. — Variance components (in cm^2) and heritabilities. Standard errors of estimates are given in brackets below each estimate.

Ages	σ^2_{fam} (s.e.)	σ^2_{tree} (s.e.)	$\sigma^2_{\text{p-fam}}$ (s.e.)	h^2_{tree} (s.e.)	h^2_{fam} (s.e.)
2	4.91 (2.13)	187.8 (10.96)	21.2 (2.76)	0.105 (0.091)	0.232 (0.201)
7	368.10 (58.69)	3747.7 (218.22)	616.04 (66.03)	0.393 (0.125)	0.598 (0.191)
12	957.64 (130.25)	6074.4 (341.69)	1378.38 (186.67)	0.631 (0.172)	0.695 (0.189)
17	1224.38 (166.23)	7509.34 (417.03)	1743.90 (176.77)	0.652 (0.177)	0.702 (0.191)
22	1669.30 (229.17)	7574.22 (582.57)	2365.67 (241.78)	0.641 (0.176)	0.706 (0.194)

σ^2_{fam} = family variance component

σ^2_{tree} = phenotypic variance of trees

$\sigma^2_{\text{p-fam}}$ = family phenotypic variance

h^2_{tree} = narrow sense individual tree heritability

h^2_{fam} = family mean repeatability

Table 2. — Genetic correlation of additive genetic values (standard errors in brackets).

	Age				
	2	7	12	17	22
2	1.00	0.58 (0.48)	0.46 (0.33)	0.31 (0.24)	0.22 (0.18)
7		1.00	0.95 (0.70)	0.81 (0.62)	0.70 (0.56)
12			1.00	0.94 (0.74)	0.96 (0.71)
17				1.00	0.97 (0.82)

tivariate test (WILK's lambda) of equality of family heights at ages 2, 7, 12, 17, and 22 years lead to rejection of the null hypothesis ($F_{495,975} = 1.94$, $P < 0.0001$). The assumption of normal distributed height data was deemed reasonable after it was found that only 146 within-family distributions of heights out of 2100 (100 families times 21 years) deviated significantly ($0.01 < P < 0.05$) from the Gaussian expectations (SHAPIRO and WILK's test, SHAPIRO and WILK (1965)).

Figure 1 also illustrates the spread between the best and the poorest growing family at each age; a difference that grew from 24cm at age two to 2.6m at age 22 years. Relative family performance (in percent of the mean of all families) was quite stable across ages with an average of 0% to 2% change between any 2 ages. Within-family performances, however, changed more rapidly, especially during the first 5 years after outplanting. A tree's change in relative performance after age 5 years was often substantial (20% to 26%). Performance at age 10 was only 10 to 15 percentage points away from its performance at an older age. During the last 5 years (age 17 to 22) the relative performance of a single tree fluctuated by less than 5%.

Variance components and heritabilities of tree height are listed in table 1. Both family and phenotypic variances increased sharply with age. With an initial (ages 2 to 17 years) faster increase in the family variance component than in the phenotypic counterpart heritabilities more than tripled during the same period. A plateau around 0.65 was reached for the individual tree narrow sense heritability at about 17 years of age. The individual tree heritabilities were surprisingly high and almost as strong as the family mean repeatability. A geographic variance component in the family variance is a plausible explanation for this (BARADAT, 1986) although not expected. Standard errors of the listed variance components were, with the exception of the 2-year results, less than 20% of the estimated values. Heritabilities had, as expected, larger relative errors (around 25%) but all estimates (except the 2-year results) were more than 3 times their associated standard errors. Correlation of additive breeding values at ages 2, 7, 12, 17, and 22 years are listed in table 2. Correlations close to 1.00 were computed for lags less than 10 and for ages above 7. Large errors must be attributed to these estimates and the 95% percent confidence intervals of all the listed correlations include negative values.

The chosen regression model for the height growth of individual trees produced satisfactory results for all but a few trees. Overall, the root mean square error of

the regression was 3.1% of the measured height, with 96% of all residuals within 7% of the measured heights. A SHAPIRO-WILK's test of normality of residuals at ages 2, 7, 12, 17, and 22 years led to acceptance of the hypothesis of normal distributed residuals ($W > 0.97$, $P(W > 0.97) > 0.05$).

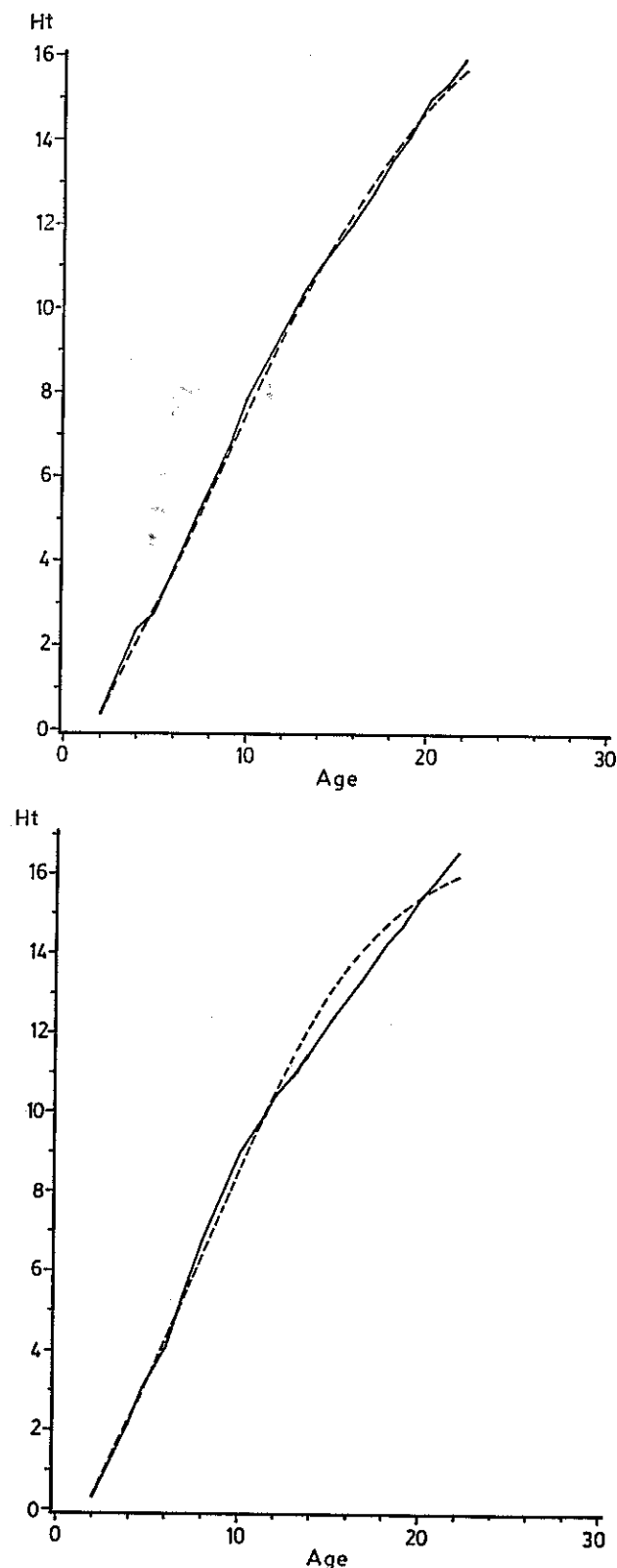


Figure 2. — Examples of observed (full line) and regression estimates of heights (dash line). Top: Good fit (deviations $< 1\%$). Bottom: Poor fit (deviations 1% to 10%).

No systematic bias or trend in the residuals was observed when inspecting plotted values. Examples of 'good' and 'poor' model fit for individual trees are displayed in figure 2. Ten trees had residuals in excess of 1m (avg. 1.09m). Only 4 regressions had a maximum height within the given age interval (2 to 22 years); the rest had a predicted maximum between age 24 and 100 years. The 4 trees with a maximum before age 22 were deleted from further analyses. The excluded trees were the only trees with prediction errors above 12%.

Table 3 lists the summary statistics of the three regression coefficients a , b , and c of the height-age model in [6]. Family effects were most pronounced in the c coefficient and least expressed in the intercept term (a), as expected. A multivariate test (Wilk's lambda) of no family effects in a , b , and c combined led to a rejection of the null hypothesis ($F_{297,589} = 2.439$, $P(>F) = 0.0001$). All 3 parameters were strongly correlated (Table 4) and normally distributed individually ($W > 0.98$, $P > 0.10$) and combined ($W_{(a,b,c)} = 0.965$, $P > 0.06$) in the first principal component (88% of the total variance). The 6 kernel coefficients (c_1 - c_6 , see equation 7 for details) needed to derive the continuous selection index are listed in table 5. Covariances predicted from the kernel functions were strongly correlated ($r^2 > 0.93$, $P < 0.001$) with the covariances obtained by equating the observed mean squares to their expectations (see Material and Methods). Linear regressions with the kernel estimates of the covariances for family, phenotypic family, phenotypic tree, and residuals as the dependent variables and the directly computed covariances as the independent variables indicated that all intercept terms were statistically nonsignificantly different from zero ($P > 0.21$) and that the slope was less than 1.0 ($P < 0.02$). The less than 1.0 slope (actual values: 0.84 to 0.92) is caused, in part, by the omission of the residual variance in the height-age regressions.

Summary statistics of the various discrete and continuous selection indices are given in table 6. It should be stressed that without knowledge of the 'correctness' of the implied index model any comparison of the indices can only be indicative. Further, with different amount of information used by different indices we must expect a better performance of the index with the highest demand on information (the continuous index). Remember, only 3 ages could be used in the discrete solutions; more ages would lead to singularities of some of the involved matrices unless special estimating techniques (GEARY, 1989) or a 'bending' (HAYES and HILL, 1980) of estimates were applied.

The continuous single tree index (I_3) under the 20% improvement objective had a lower variance than the discrete index (I_3) based on kernel estimates of variances at age 2, 12, and 22 years which, everything else being equal, translates into a higher gain (3.4% versus 2.9%) per unit selection intensity. Alone, the use of kernel variance estimates in the index calculations (as in I_2) instead of the variances derived from the MANOVA analyses (as in index I_1) introduced a sharp drop (50%) in the index variance. Part of this difference can be explained by the aforementioned inability of the kernel functions to account for all of the variance. Relative genetic gains for the various indices are also listed in table 6. These gains are based on the assumption of "known" variance components. More realistic gain expectations can be obtained by multiplying

Table 3. — Summary statistics of regression coefficients a, b, and c in model [6].

	Mean	Min.	Max.	Std. dev.	F-fam (p>F)	h^2_{tree} (s.e.)	h^2_{fam} (s.e.)	W^1 (Prob)
a	2.19	-2.38	5.39	0.511	1.27 (0.08)	0.093 (0.044)	0.218 (0.104)	0.97 (>0.05)
b	2.70	0.58	5.90	0.444	1.32 (0.05)	0.109 (0.046)	0.248 (0.104)	0.98 (>0.05)
c	-0.33	-0.87	0.19	0.093	1.41 (0.0322)	0.135 (0.045)	0.292 (0.103)	0.99 (>0.05)

¹⁾ Wilks W for testing for normality. Prob= probability under the null hypothesis of normality.

the listed gains by the ratio σ_1/σ_i . Hence, due to sampling errors of variance components, the gain expectations ought to be reduced by 10% to 20%.

Correlation coefficients between index values and their genetic merit were fair (0.63 to 0.81) for the continuous indices but rather weak (0.30 to 0.56) for the indices based on discrete ages. These results indicate that total information via kernels provides a better optimization than a few discrete data points. Much higher (>0.80) correlations

Table 4. — Genetic (above diagonal) and phenotypic correlations of the regression parameters a, b, and c (see model [6]). Standard errors are enclosed in brackets.

	a	b	c
a	•	-0.767 (0.412)	0.550 (0.337)
b	-0.943 (0.071)	•	-0.948 (0.377)
c	0.864 (0.059)	-0.981 (0.064)	•

Table 5. — Coefficients c1 to c6 of the covariance matrix $\Omega(\omega)$ (see [17] for details).

	Family	P-family	P-tree	Residual
c ₁	0.00711	0.03254	0.30471	0.25450
c ₂	-0.00477	-0.02431	-0.23305	-0.19780
c ₃	0.00079	0.00457	0.04452	0.03796
c ₄	0.00545	0.02195	0.20054	0.17200
c ₅	-0.00120	-0.00457	-0.01024	-0.03524
c ₆	0.00029	0.00101	0.00872	0.00749

where $\omega = \{\text{Family, Phenotypic Family (P-fam.), Phenotypic tree (P-tree), Residual}\}$.

were possible for indices with only a single data point under selection.

Individual index coefficients (b_2 , b_{12} , and b_{22}) were estimated with large standard errors. Few of the coefficients listed in table 6 were statistically significant different from 0 at the 5% risk level. Figure 3 depicts, for both the 20% and the 0.05*log(age) gain objective, the estimated continuous selection index coefficients and their 68% confidence interval. The generating 2nd degree polynomial has been provided as well. Negative coefficients were given to height performance between ages of about 6 to 16 years while height at younger ages (<4 years) were given the highest numerical weights. It is, however, height at ages above 20 years that determines the absolute value of the indices. More than 2/3 of the absolute index contributions arose from the height performance during the last 2 years.

Although most individual index coefficients were statistically nonsignificantly different from zero, the errors on the estimated relative genetic gains were acceptable. Figure 4 illustrates the trends in the 95% confidence interval of the predicted gain as a function of the selection intensity. Absolute errors increased with selection intensity (fewer trees selected), as expected. Allowance was made for the sampling errors of the phenotypic and genotypic variance components (or kernels) in these graphs. It is clear that gain in age 2 heights under the objective of a gradual (0.05*log(age)) improvement with age was not significantly different from 0.

Actual and predicted (ages 23 to 50 years) height growth performance of the trees with continuous selection index values in 1 of the top 5 deciles of the population are graphed in figure 5. For the 20% gain objective (topmost diagram in Figure 5) the ranking between index decile and average height was perfect (1.0). However, some rank changes occurred under the alternative selection objective of a gradual improvement (0.05*log(age)), notably between ages 5 and 15 years where the best height performance was found in trees with indices in the second decile and the trees with indices in the 40% to 50% decile had the 3. best height ranking. Selection procedures aimed at a gradual improvement of height with age would in this case have been inefficient if carried out before age 15. The potential importance of finding the best trees is vividly demonstrated by the increasing spread among the extrapolated height-age trajectories. Separation of the growth curves accelerates around age 15. Height data from trees older than 15 years are thus clearly needed for selection aiming at improving mature height.

Table 6. — Selection index statistics for height selection at three distinct ages. Methods for calculating correlations $r_{I,H}$ for the continuous indices are unknown.

Parameter	I ₁	I ₂	I ₃	I ₄	I ₅	I ₆	I ₇
$\sigma^2_{I_1}$	100.3	48.7	35.4	128.3	104.7	13.3	50.6
$\sigma^2_{I_1}$	159.6	64.4	54.5	157.9	175.7	22.2	83.8
$r_{I,H2}$	0.23	0.26	-	0.33	-	-	-
$r_{I,H12}$	0.31	0.41	-	0.51	-	-	-
$r_{I,H22}$	0.39	0.52	-	0.64	-	-	-
$r_{I,H \text{ avg.}}$	0.30	0.34	0.63	0.56	0.73	0.79	0.81
b_2 (s.e.)	0.57 (0.55)	0.29 (0.23)	0.09 (0.03)	1.14 (0.93)	0.39 (0.13)	0.031 (0.02)	1.14 (0.09)
b_{12} (s.e.)	-0.06 (0.05)	-0.02 (0.02)	-0.01 (0.01)	-0.08 (0.09)	-0.03 (0.04)	-0.004 (0.007)	-0.02 (0.03)
b_{22} (s.e.)	0.08 (0.04)	0.05 (0.02)	0.02 (0.02)	0.20 (0.06)	0.07 (0.07)	0.013 (0.011)	0.05 (0.05)
$e\%(2)$	2.0	2.9	3.4	1.8	2.0	1.0	0.5
$e\%(12)$	2.0	2.9	3.4	1.8	2.0	3.4	1.7
$e\%(22)$	2.0	2.9	3.4	1.8	2.0	4.2	2.2

Objective: 0.05 · log (age) improvement of height (age 2 to 22).

I₁ = Single tree index based on variance components (age 2, 12, and 22) derived from MANOVA.

I₂ = Single tree index based on variance components (age 2, 12, and 22) derived from kernel functions.

I₃ = Single tree continuous selection index (age 2 to 22) derived from kernel functions.

I₄ = Family selection index based on variance components (age 2, 12, and 22) derived from kernel functions.

I₅ = Family continuous selection index (age 2 to 22) derived from kernel functions.

Objective: 20% improvement of height (age 2 to 22).

I₆ = Single tree continuous selection index (age 2 to 22) derived from kernel functions.

I₇ = Family continuous selection index (age 2 to 22) derived from kernel functions.

$\sigma^2_{I_1}$ = Estimated variance of selection index, P and G assumed known.

$\sigma^2_{I_1}$ = Estimated variance of selection index with P and G subject to sampling errors.

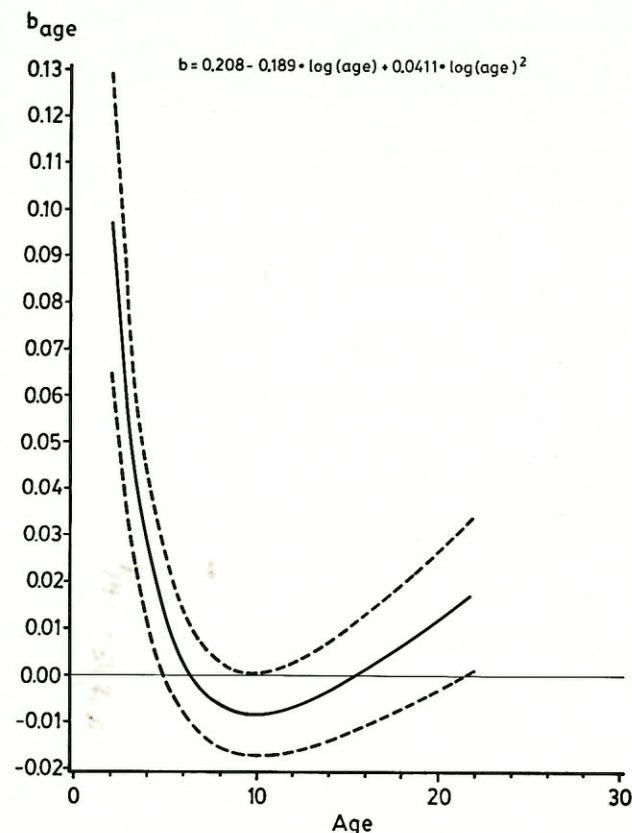
$r_{I,H(t)}$ = Estimated correlation between index value and breeding value of height (H) at age (t).

$b_{(t)}$ (s.e.) = Selection index coefficient to height at age (t) (s.e.)=standard error of estimate.

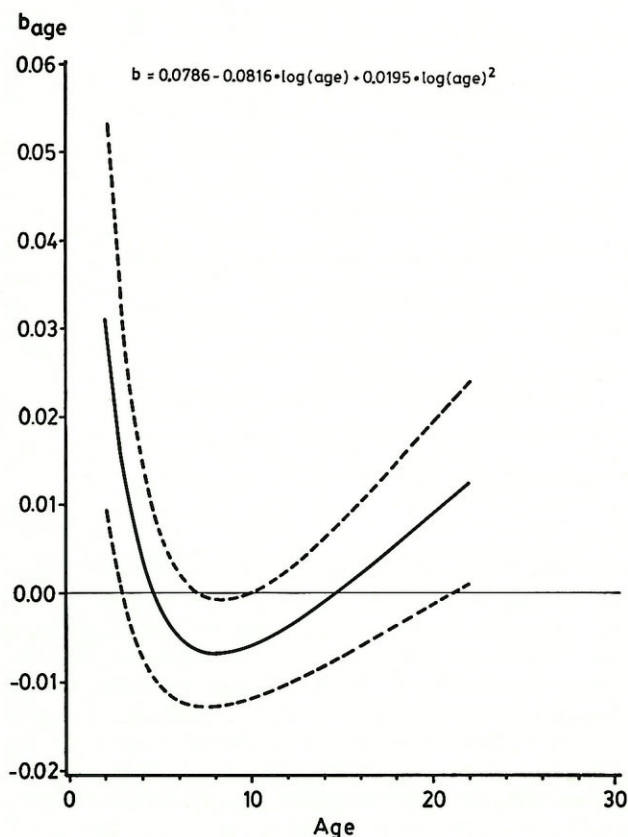
$e\%(t)$ = Expected genetic gain in percent of trait value at age=t prior to selection and breeding (intensity=1.0).

An index selection on the three height-age regression parameters (a, b, and c) can be designed in a way that will satisfy the 2 breeding objectives of either a constant relative improvement for all ages or a more gradual improvement with age, provided that we can establish the relationship between direct and indirect (through correlations) changes in the parameters and their effects on height growth. The first step in finding the desired selection index is visualized in figure 6 where the expected height responses (direct and indirect) per unit change in the parameters a (curve A(t)), b (curve B(t)), or c (curve C(t)). The linear weighting of the 3 curves that provides the desired gain is also provided in figure 6. From linear regression analysis of the relationships that exists among the three parameters (Table 7) we were able to derive

the expected indirect changes in any parameter brought about by an unit change in another parameter. Inspections of scatterplots and residuals convinced us that simple linear relationships among the parameters were an appropriate abstraction. By combining the linear weights for the three single trait strategies A(t), B(t), and C(t) with the partial derivatives obtainable from table 7 (i.e. the slopes), we arrived at the desired gain vector for the 3 parameters a, b, and c. A summary of the selection indices derived from these desired gains are listed in table 8. One notes that the relative gains expected from selections with these indices are similar to those predicted from the continuous selection indices. However, realistic gain expectations may be approximately 50% lower than the gains expected from the continuous solutions due to the



Target: 20% improvement for all ages



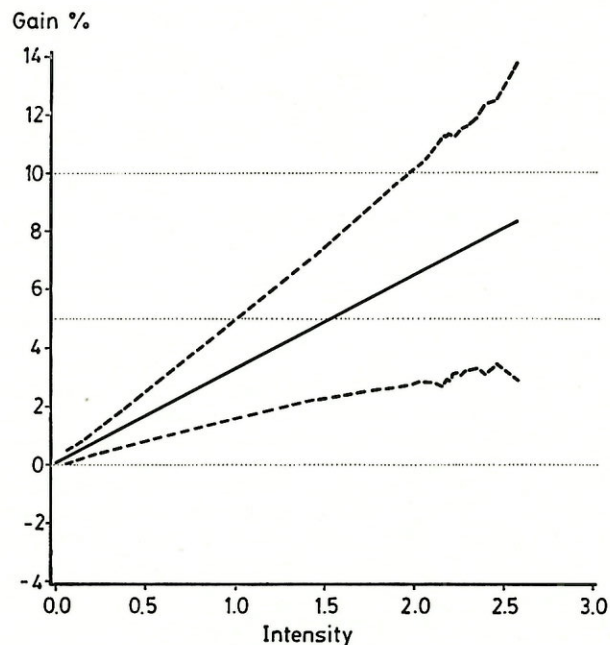
Target: improvement = $0.05 \cdot \log(\text{age})$

Figure 3. — Continuous selection index coefficients (full line). The 68% confidence interval of the index coefficients is indicated by the dashed lines.

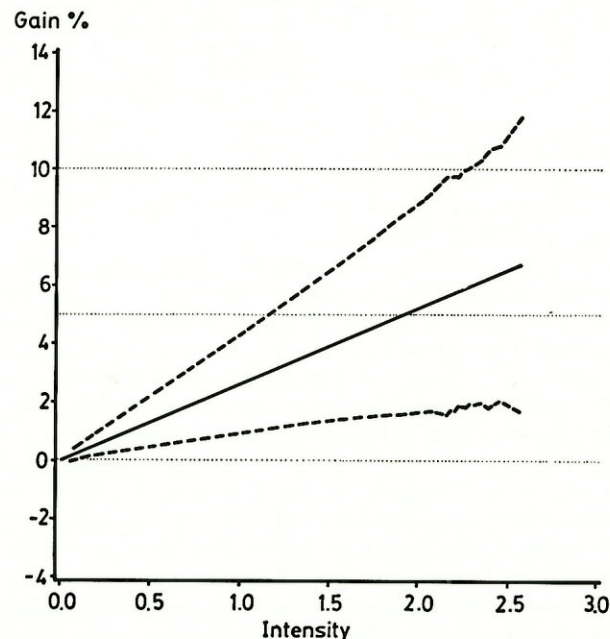
considerable sampling errors associated with the regression parameters (compare σ^2_1 with σ^2_l). Index coefficients associated with either a (b_a), b (b_b), or c (b_c) were individually nonsignificant at the 5% risk level and the correlation between index and genetic merit was only fair (0.35 to 0.70). The growth rate parameter associated with growth rate (b) contributed most to the overall index value followed by the contributions from c and then a.

Discussion

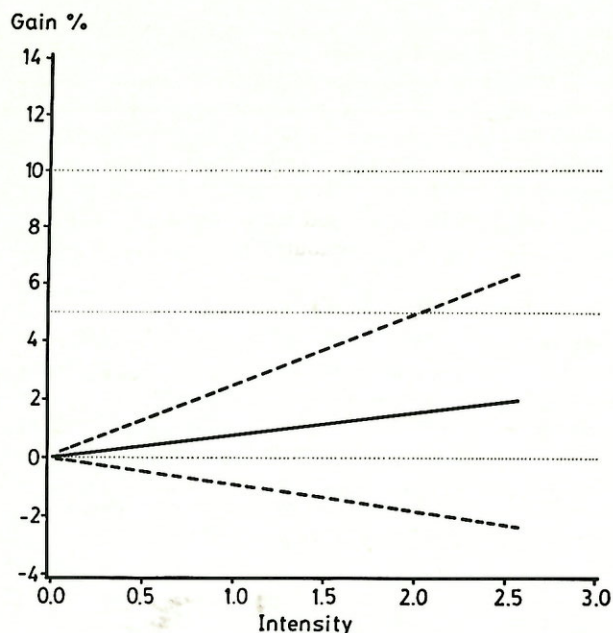
Our results confirmed that the height growth of *Pinus pinaster* Arr. between ages 2 and 22 years was under strong genetic control (see also KREMER, 1981) which could be exploited to produce appreciable gains in the growth performance of advanced generation material. The age trends in the phenotypic and additive genetic variance were



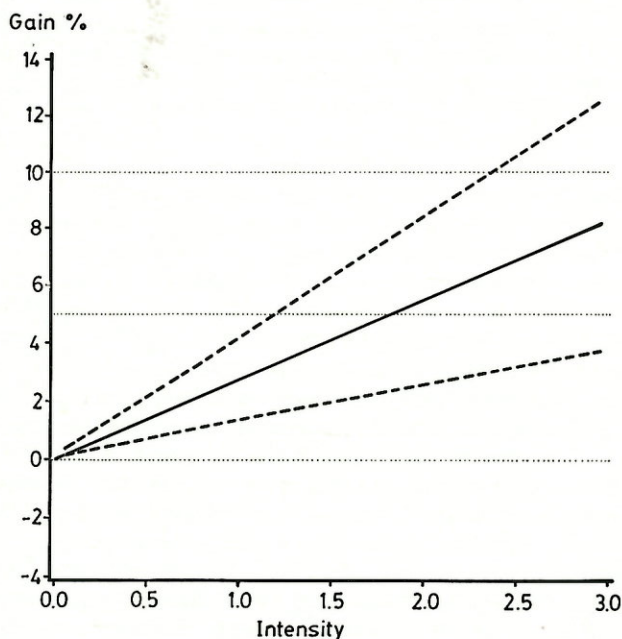
a: Gain objective = $0.05 \cdot \log(\text{age})$; age = 22 years.



b: Gain objective = $0.05 \cdot \log(\text{age})$; age = 12 years.



c: Gain objective = $0.05 \cdot \log(\text{age})$; age = 2 years.



d: Gain objective = 0.20 for all ages. Age = 2 years.

Figure 4. — Expected relative genetic gain in height as a function of selection intensity (full line). The 95% confidence interval of this gain is given by the dashed lines. The erratic patterns for high selection intensities reflect the fluctuations in means and standard deviations caused by small sample sizes

similar to those found in other progeny tests of maritime pine (KREMER, 1981). A possible geographic component in the family variance (BARADAT, 1986), and strong genetic differentiation in the frequency of polycyclic growth are thought to be the major contributors to the increasing heritabilities (KREMER and XU, 1989). The relatively late but pronounced separation of the growth curves at around age 15 indicates that early selection based on expected future performance will be quite efficient once the trees are 15 years or older. Although our results cover only mass and family selection, any results of a combined family and within family selection scheme can be deduced in a fairly straightforward manner by a linear combination (weighting) of the two selection schemes (FALCONER, 1981).

The targets of either a proportional (here 'fixed' as 20%) lift of the average growth curve or a more gradual lift (here 'fixed' as $5\% \cdot \log(\text{age})$) of the tree height-age rela-

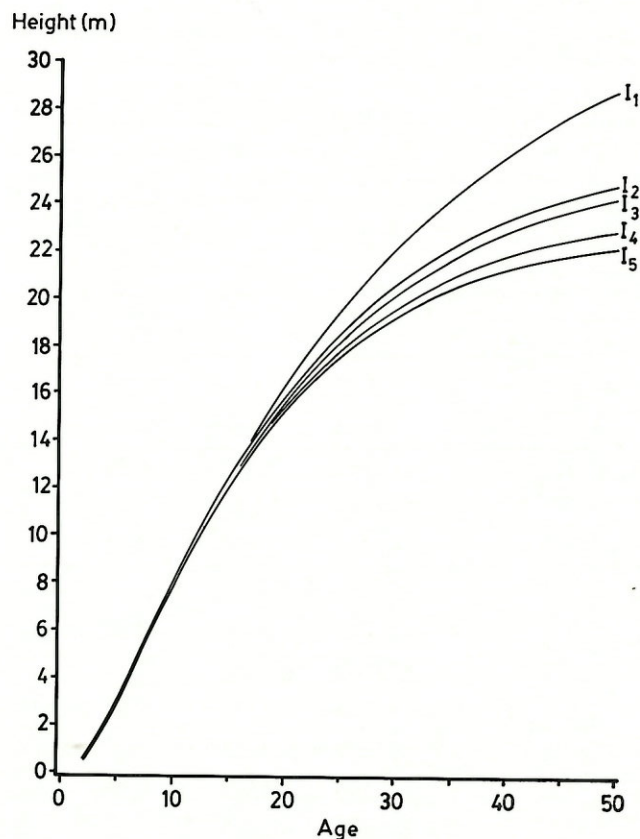
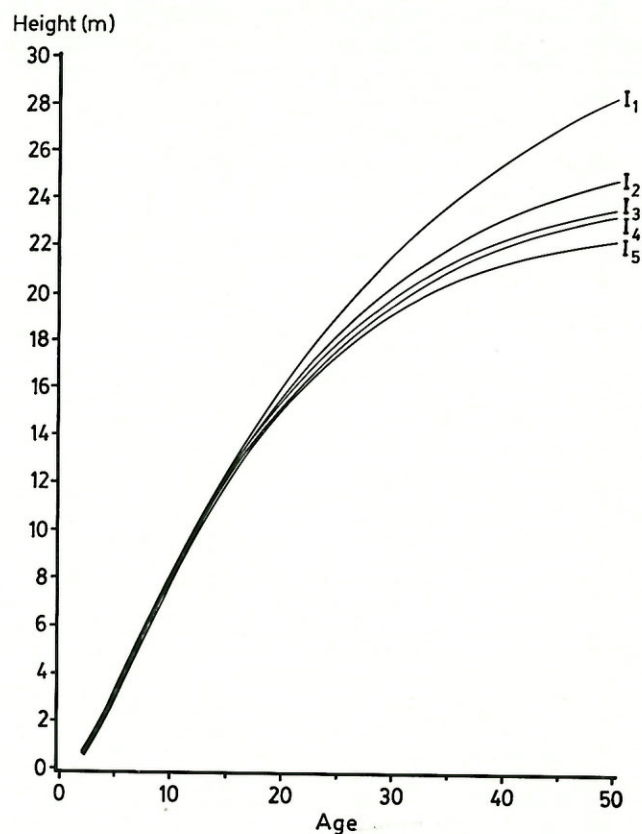


Figure 5. — Height-age curves for the trees with index values in the top 5 deciles (I_1 to I_5).
Top: Gain objective is 20% for all ages.
Bottom: Gain objective is $0.05 \cdot \log(\text{age})$.

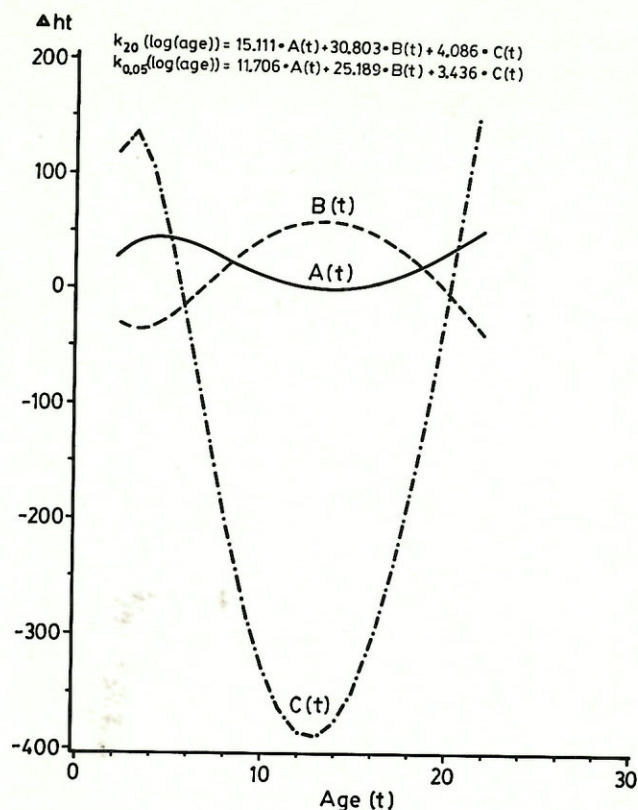


Figure 6. — Height response over age for a unit change in the parameters a , b , and c of the height-age function. $A(t)$ =change in height for a unit change in a . $B(t)$ =change in height for a unit change in b . $C(t)$ =change in height for a unit change in c . $k_{20}(\log(\text{age}))$ = linear combination of $A(t)$, $B(t)$, and $C(t)$ that yields the desired 20% response. $k_{0.05}(\log(\text{age}))$ = linear combination of $A(t)$, $B(t)$, and $C(t)$ that yields the desired 0.05 · log(t) response at age= t .

tionships are intuitively appealing but other objectives not considered here may be as relevant. For example, selection on height at the oldest age only would produce more genetic gain at that age than predicted with the indices in this study. Selection for a maximum simulta-

Table 7. — Regression summary of models $Y = \beta \cdot X + \alpha$ where $Y, X = \{a, b, c\}$.

Y	X	β (s.e.)	α (s.e.)	R^2
a	b	-1.163 (0.010)	5.336 (0.028)	0.89
a	c	5.121 (0.075)	3.889 (0.026)	0.75
b	a	-0.765 (0.007)	4.380 (0.015)	0.89
b	c	-4.708 (0.023)	1.142 (0.008)	0.96
c	a	0.146 (0.002)	-0.652 (0.005)	0.75
c	b	-0.204 (0.001)	0.221 (0.003)	0.96

Table 8. — Summary statistics of selection indices based on selection on a linear combination of regression parameters (a , b , and c). Notation as in table 6.

	I_1	I_2	I_3	I_4
$\sigma^2_{I_1}$	45.33	121.8	14.41	42.44
$\sigma^2_{I_2}$	125.31	293.42	58.19	149.23
$r_{I_1, H}$	0.35	0.56	0.49	0.70
b_a (s.e.)	73.0 (59.4)	292.1 (237.8)	51.3 (45.4)	205.0 (181.7)
b_b (s.e.)	205.0 (181.7)	819.8 (726.8)	166.7 (143.7)	667.6 (574.9)
b_c (s.e.)	639.3 (605.3)	2557.4 (2421.2)	542.9 (479.6)	2171.4 (1918.3)
$e\%$ (2)	3.0	1.8	0.9	0.5
$e\%$ (12)	3.0	1.8	3.3	1.7
$e\%$ (22)	3.0	1.8	4.2	2.2

I_1 = Single tree index. Objective=20% gain in height for all ages.
 I_2 = Family index. Objective=20% gain in height for all ages.
 I_3 = Single tree index. Gain objective=0.05 · log(age).
 I_4 = Family index. Gain objective=0.05 · log(age).

neous progress in height at all ages (MAGNUSSEN, 1990) provides the opportunity of a higher but more unevenly distributed gain. Selection on annual height growth is yet another option (MAGNUSSEN, 1990). By tying the improvement to a growth curve with biologically interpretable parameters we believe the approach is more oriented towards the actual growth process than selection on the trait expression at a few distinct ages.

In addition, selection for an improved (optimum) growth curve appears also more attractive than selection aiming at improving the performance at a few or a single age(s) because forest economics principles and decision making models are based on an integration of the cost-benefits associated with the entire growth process as expressed in a growth curve (CLUTTER et al., 1983). By stating the desired improved growth curve of genetically superior stock the value of genetic breeding can be assessed more accurately than before.

The choice of a growth curve function to represent growth trajectories is crucial for the tractability of the numerical analysis surrounding estimation of continuous selection indices and for quantitative genetics analysis. Our choice was dictated by the numerical aspects and the separability of genetic and environmental effects (GREGORIUS and NAMKOONG, 1987). Several biologically appealing growth models (HUNT, 1982) are, unfortunately, intrinsically nonlinear in the parameters which makes them unsuited for index calculations. By limiting all growth trajectories to a single family of growth curves for the sake of numerical convenience we accepted that the statistical properties of some growth curves would be less than optimal. The prevalence of Gaussian-distributed heights and regression parameters facilitated estimation and inference about covariance kernels and error structures in general. In many situations, however, the covariance kernels will have to be approximated by a subset of the *eigenvalues* and *eigenfunctions* (KIRKPATRICK and HECKMANN, 1989). These

approximations render the calculations of continuous selection indices less transparent and sensitive to the approximation criteria implied.

All selection indices had negative coefficients for height at intermediate ages. This indicated that phenotypic heights between ages 5 and 15 years are inefficient as indicators of overall potential of good height growth. Results of a similar nature was reported by NAMKOONG and MATZINGER (1975) for *Nicotiana tabacum* (L.) They hypothesized physiological constraints on weekly growth as the most likely cause for the midseasonal drop in the index coefficients. Faced with the large standard errors associated with the index coefficients we find it inopportune, at this time, to speculate further on the shape of the index polynomial. Ten more years of growth data will enable us to tell whether these trends will persist.

It appears that gain predictions using the continuous selection index are superior both to those generated by the classical SMITH-HAZEL Index and to those predicted from selection on growth curve parameters. The errors of gain predictions did not challenge these results. Selection on growth curve parameters was apparently less efficient than selection on the growth curve itself but more efficient than direct selection on 3 point estimates of tree heights. Theoretically one might expect that selection on all 21 heights should be as effective as the continuous solution. However, ill conditioned matrices caused by the strong autocorrelation among successive heights prevented us from reaching this result. Selection on growth curve parameters requires a quantification of the interrelationships among the parameters themselves and their effect on the growth curve. Otherwise, the result of the selection may be hard to predict with any confidence (NAMKOONG and MATZINGER, 1975).

Our findings are based on comparisons of sample estimates of selection indices where the 'true' index model remains unknown. Differences in information utilization is considered the main reason for the apparent efficiency differences. A real selection experiment is needed to obtain further evidence on differences in selection efficiencies. It would have been possible to boost the efficiency of the discrete height-age selection by adopting 'bending techniques' (HAYES and HILL, 1980) or by restriction of maximum likelihood variance estimators to those with a positive definite variance covariance matrix (GEARY, 1989). However, these techniques are rather subjective and by no means likely to become a 'standard' approach. Our comparisons of the growth curve selection index with the 'discrete' solution, is therefore, considered the most realistic one of a 'new' alternative procedure versus a more conventional one.

Concluding Remarks

Progress and refinements in the statistical treatment of repeated measures of form and shape (GOODALL, 1991; HOULLIER, 1987; MAGNUSSEN and PARK, 1991; RICE and SILVERMAN, 1991; SANDLAND and MCGILCHRIST, 1979) enable the breeder to perform cogent quantitative genetics analysis of growth. Functional expression of the selection index embody a natural and elegant extension of growth curve analysis. The espoused advantages of selection on a continuum of trait expression rather than at discrete points in time (KIRKPATRICK and HECKMAN, 1989) remains, despite positive indications in this study, largely unsubstantiated. Although the mathematical formulation of the continuous

selection index is deceptively simple, the ensuing numerical algebra needed to obtain descriptive statistics is quite formidable. This may, despite the higher efficiency, limit the practical use of continuous selection indices among practitioners to cases where changing a growth curve is a high priority and associated with large potential benefits.

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