

TIME TRENDS IN GENETIC PARAMETER ESTIMATES AND SELECTION EFFICIENCY FOR SCOTS PINE IN RELATION TO FIELD TESTING METHOD

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ABSTRACT

Multiple assessments of cumulative tree height in 26 *Pinus sylvestris* L. progeny trials in Finland, ranging between 5 and 18 years of age, were analysed to determine time trends in variance components, heritability, coefficient of additive genetic variation, age-age and site-site genetic correlations, and to estimate the impact of test characteristics on these parameters. Two distinctive methods of field progeny testing were investigated, conventional 'forestry trials' and intensively managed test orchard (farm-field) trials. The effects of contrasting stand densities (2,500 vs. 8,888 trees planted per ha) and site quality (forest vs. field sites) on the levels and trends of variance components and genetic parameter estimates were quantified by means of repeated-measures mixed models. Responses to parental and within-family selection were computed using parameters derived from these models. The trials, which were arranged in groups by spacing and site quality, showed markedly different levels of heritability. The highest estimates occurred on the fast-growing test orchard sites. On average, additive genetic variances and heritabilities from single-site analyses were inflated by 60% due to the family-by-site interaction. No systematic time trends were detected for heritability and type-b correlation. Furthermore, the relative magnitude of the family-by-site interaction was independent of the degree of heterogeneity among the trial sites. Age-age correlations were positive and moderately high, and showed a moderate fit to the log of the age ratio. Selection efficiencies were examined using tree height at age 20 as the target trait. The correlated responses per year to early parental (backward) selection peaked at the age of around 5 to 7 years and were always greater than the gains from direct selection for tree height at the age of 20 years. In within-family (forward) selection, the annual responses were initially low, increasing toward the target age. The optimum age of within-family selection occurred later (at the age of 8, ..., 16 years) than in parental selection. The highest selection efficiencies were consistently associated with the densely spaced test orchard scenarios. Correspondingly, widely spaced trials on sites of poor quality produced the least responses to early selection.

Keywords: early selection, genetic correlation, genetic parameters, heritability, *Pinus sylvestris*, progeny testing, testing method, time trends, type-B correlation.

INTRODUCTION

In forest tree breeding, mature performance is customarily predicted using attributes measured in juvenile field trials. The advantages of pre-rotation selection comprise easier measurement and lower costs per tree, and there is also a quicker incorporation of genetically improved materials into forestry. Above all, however, selection at early ages can be expected to yield higher genetic gain per unit of time than direct selection for harvest-age performance (LAMBETH 1980, LINDGREN 1984). In principle, the use of early testing as an effective screening tool requires sufficient knowledge of the quantitative genetic parameters. The outcome of indirect selection depends on the genetic control in selected traits (heritability), their genetic associations with mature traits (age-age genetic correlation), and the

magnitude of genotype-by-environment interaction (site-site correlation). These parameters are thus key ingredients in the planning of efficient breeding, testing and selection strategies, and their estimation is normally a regular part of the analysis of field-testing data.

Genetic parameters may markedly change as trees grow and develop (NAMKOONG & CONKLE 1976, FOSTER 1986, FRANKLIN 1979, BALOCCHI *et al.* 1993, DIETERS *et al.* 1995). To effectively implement a tree improvement programme, there must be a sufficient understanding of the underlying reasons for these changes. There is some evidence suggesting that the genetic control of tree growth is closely related to periodic shifts in the ontogenetic stand development (FRANKLIN 1979, VASQUEZ & DVORAK 1996). FRANKLIN (1979) interpreted sharp changes in genetic variance and heritability as responses to the onset and termina-

tion of intense inter-genotypic competition. However, more recent attempts to verify FRANKLIN's (1979) hypotheses have not always been successful (LAMBETH *et al.* 1983, BOUVET & VIGNERON 1995, FOSTER 1986, GILL 1987, SATO 1994, DANJON 1994) and the issue has not been resolved. This owes much to the fact that the time series of genetic parameters for forest trees are typically sparse and cover only a small part of the rotation. It seems clear that without data from old field trials, any hypotheses about the patterns of genetic parameters are likely to remain controversial. Regrettably, these important mature data are nearly always scarce for long-lived tree species, which have a short history of genetic improvement by comparison to their commercial rotations.

Trends in genetic parameters are in many situations difficult to detect. This is not only because of a deficiency of data, but also because of large variability among genetic parameter estimates at any age. Precise genetic parameter estimates are difficult to obtain from small experiments (HODGE & WHITE 1992). Furthermore, genetic parameter estimates reflect a number of non-genetic factors such as the magnitude and pattern of microsite variability, experimental design, spacing, silvicultural management, and the occurrence of environmental stresses (RINK & CLAUSEN 1989, MAGNUSSEN 1993, XIE & YING 1996). In fact, the common inconsistency of parameter estimates may be seen to be perfectly in line with the fact that population parameters attributed as 'genetic', also reflect the environmental circumstances under which they are estimated (Falconer 1981). Tree breeding trials typically represent diverse environmental conditions and cultural practices since the multiple objectives of genetic testing cannot be optimally met by a single approach (LOO-DINKINS 1992). The accelerated methods adopted by many tree improvement programmes for progeny testing (MIKOLA 1985), add their share to this diversity. It would obviously be important to quantify the effects that the various approaches to field testing may have on the genetic control of traits. This information would be valuable in ensuring the best use of data gathered from different types of field trial, and also when considering the amendment of characteristics of future trials. As yet, however, not too many studies have addressed the effects that test characteristics may have on the patterns of genetic parameters and selection efficiency (FALKENHAGEN 1989, MAGNUSSEN 1991, HODGE & WHITE 1992, WHITE & HODGE 1992, ADAMS *et al.* 1994, WOODS *et al.* 1995, JANSSON *et al.* 1998).

The accelerated field trials used in the progeny testing of Scots pine (*Pinus sylvestris* L.) in Finland are called 'test orchards' (synonymous to 'farm-field trials'). The features of the test orchard method include uniform

and often fertile sites, high planting density (up to 10,000 trees per ha), fencing, and intensive site manipulation to minimise weed competition and edaphic heterogeneity. Hence, test orchard conditions often differ markedly from those prevailing at conventional 'forestry trials', which more resemble managed stands with respect to initial spacing (2,000–2,500 trees per ha), site quality (mostly on typical forest soils) and silvicultural management (MIKOLA 1985). In addition, test orchard trials are intended for fairly rapid screening at the age of 10–15 years, whereas forestry trials can sometimes be assessed up until the end of the commercial rotation, to estimate the productivity of genetic entries over several thinnings to final harvest (MIKOLA 1985).

To my knowledge, only four studies have compared these two approaches to field testing using the same set of genetic entries, namely MAGNUSSEN and YEATMAN (1986) with jack pine (*Pinus banksiana* Lamb.), CARLSON (1990) with lodgepole pine (*Pinus contorta* Douglas ex Loudon), WOODS *et al.* (1995) with Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), and HAAPANEN (1996) with Scots pine. While these studies consistently report higher efficiency of selection for test-orchard-like conditions, the findings are based on rather meager data with respect to the number of trials included for comparison or the range of ages observed. To avoid these limitations, this study exploited the large database of routine measurements accumulated from the Scots pine progeny-testing programme in Finland. The objectives of this study were: to determine and model time trends in the genetic parameters of importance to the Scots pine progeny testing, and to find out how these parameters, their tendencies over time and the efficiency of early selection are affected by the distinctive features of the two testing methods.

MATERIAL AND METHODS

Experimental material and measurements

The data were from 9 independent series of Scots pine progeny trials located between 60th and 64th N in southern Finland. Each of the series comprised 2 to 4 parallel trials (at least one forestry trial and one test orchard). Overall, 15 forestry trials and 11 test orchard trials contributed data to this study (Table 1). The 26 trials were sampled from among the nearly 1,300 Scots pine progeny trials established in Finland since the early 1960's.

The trials comprised 4 to 10 (median = 6) blocks laid out in a randomized complete block design. The plots were usually formed of 5 × 5 trees planted at 2 m × 2 m (the forestry trials) or 0.75 m × 1.5 m (the test

Table 1. Description of the progeny trials used in the analyses.

Trial	Type	Lat.	Lon.	Alt., m	Site type	Establ. year	Area, ha	Families	Blocks	Trees/plot	Planting density, trees/ha	Measurement ages	Mean height at age 12, dm
572/1	Test orchard	61°48'	29°18'	87	Field, mould	1978	0.64	39	7	15	8888	6, 7, 9, 11, 15	50.0
572/2	Forestry trial	60°36'	23°22'	75	Field, clayish	1978	0.97	35	4	16	2500	6, 11, 16	28.9
572/3	Forestry trial	62°32'	24°27'	195	Dryish heath	1978	2.88	39	10	16	2500	7, 11, 17	23.5
572/4	Forestry trial	63°19'	28°50'	185	Moist forest land	1978	2.80	39	10	16	2500	6, 11, 16	27.5
698/1	Test orchard	61°48'	29°17'	83	Field, mould	1980	0.32	23	4	25	8888	5, 7, 8, 11, 14	48.1
698/2	Forestry trial	61°36'	26°18'	110	Moist forest land	1980	1.20	21	4	25	2500	7, 11, 16	24.7
739/1	Test orchard	62°46'	25°42'	140	Dryish heath	1981	1.38	74	6	25	8888	5, 7, 12	20.4
739/2	Test orchard	61°48'	29°17'	81	Field	1980	1.49	78	6	25	8888	5, 7, 9, 12	49.1
739/5	Forestry trial	62°59'	31°13'	178	Dryish heath	1980	2.76	42	6	25	8888	7, 12, 18	26.1
739/6	Forestry trial	60°41'	23°59'	120	Moist forest land	1981	2.70	41	6	25	8888	8, 12, 18	22.9
757/1	Test orchard	60°58'	22°43'	93	Dryish heath	1980	0.76	30	6	25	6944	7, 9, 13, 18	28.2
757/2	Forestry trial	62°00'	25°11'	155	Moist forest land	1981	1.00	30	3	25	2500	7, 12, 18	26.8
803/1	Test orchard	62°44'	25°41'	140	Dryish heath	1982	0.68	50	4	25	8888	7, 10, 12	22.0
803/2	Test orchard	61°48'	29°17'	79	Field	1982	0.66	50	4	25	8888	5, 7, 10, 12, 16	48.8
803/3	Forestry trial	60°21'	25°01'	57	Dryish heath	1982	1.00	21	4	25	2500	7, 12, 18	29.3
861/1	Forestry trial	62°16'	26°55'	122	Dryish heath	1983	2.13	31	6	25	2500	12, 17	24.4
861/2	Forestry trial	62°03'	25°27'	200	Moist forest land	1983	2.16	31	6	25	2500	12, 17	23.4
861/3	Test orchard	62°45'	25°41'	140	Dryish heath	1983	0.41	31	4	25	8888	5, 10, 12, 17	24.3
862/1	Forestry trial	61°35'	28°55'	110	Dryish heath	1983	1.80	25	6	25	2500	12, 17	22.6
862/3	Test orchard	61°49'	27°13'	117	Dryish heath	1983	0.33	25	4	25	8888	5, 10, 13, 17	19.9
864/1	Forestry trial	62°54'	31°33'	190	Dryish heath	1983	2.10	30	6	25	2500	12	20.8
864/2	Forestry trial	62°03'	25°27'	200	Moist forest land	1983	2.10	30	6	25	2500	12, 17	24.8
864/3	Test orchard	62°54'	25°41'	140	Dryish heath	1983	0.39	30	4	25	8888	5, 10, 12, 17	23.4
865/1	Forestry trial	61°35'	28°55'	110	Dryish heath	1983	2.21	32	6	25	2500	12, 17	24.5
865/2	Forestry trial	62°16'	26°55'	132	Dryish heath	1983	2.19	32	6	25	2500	12, 17	24.1
865/3	Test orchard	61°49'	27°13'	117	Moist forest land	1983	0.142	32	4	25	8888	5, 9, 13, 17	19.5

orchards) spacing. The initial spacing varied considerably with the type of trial. The test orchards were planted at a density of 8,888 trees per ha, which is up to 3.5 times higher than that used in the forestry trials (2,500 trees per ha). Differences in site qualities were also large, although not as closely linked to the testing method as the differences in spacing. Most of the trial sites (8 forestry trials, 6 test orchards) were classified as dryish forest land (*Vaccinium* type). Seven trials (6 forestry trials, 1 test orchard) were situated on moderately dry forest sites (*Myrtillus* type). One forestry trial and 4 test orchards were planted on former agricultural land. Apart from these farmland sites, the Podzol soils were typical to the Scots pine dominated natural stands of the region. No thinnings had taken place in any of the trials prior to the measurement.

The families were open-pollinated offspring of first-generation 'plus trees' selected from natural stands of southern Finland. The seed for the progeny trials were collected either from the original plus trees or, most commonly, from their grafts in young seed orchards that had a negligible amount of internal pollen production at the time of collection. In both cases, the pollen parents were presumed to be a random sample of genotypes from the surrounding wild population, and thus share the same origin with the plus trees.

The number of half-sib families in a trial ranged from 25 to 78 (Table 1). As a rule, the parallel trials within any one series consisted of a common set of families. The two exceptions to the rule were the series No. 739 and 803, in which half of the families planted in the test orchard trials were not present in the parallel forestry trials. Altogether the 26 trials consisted of 338 unique half-sib families and approximately 122,000 planted seedlings. In addition, each trial accommodated a few standard check-lots which were omitted in the analyses.

The data comprised measurements of cumulative tree height (to the nearest 1 dm) carried out at inconsistent intervals from age 5 (age from seed) through age 18. In total, the 26 trials provided 82 data sets for analyses (Table 1).

Analyses

Single-site and across-site partitioning of variance

In the first stage, the total variance in each of the 82 data sets was decomposed into additive components due to random family, plot and within-plot effects. Effects due to differences among blocks were interpreted as fixed since they are not relevant to genetic parameter estimation. The single-site analysis was

based on the following linear model:

$$y_{jkl} = \mu + B_j + f_k + fB_{jk} + w_{jkl} \quad [1]$$

where: y_{jkl} = height of l^{th} tree in j^{th} block and k^{th} family, $E(y_{jkl}) = \mu + B_j$, $\text{var}(y_{jkl}) = \sigma_{f(1)}^2 + \sigma_{fB(1)}^2 + \sigma_{w(1)}^2$; μ = a general mean; B_j = fixed effect of j^{th} block; f_k = random effect of k^{th} half-sib family; $E(f_k) = 0$, $\text{Var}(f_k) = \sigma_{f(1)}^2$; fB_{jk} = random plot error due to interaction between j^{th} block and k^{th} family; $E(fB_{jk}) = 0$, $\text{Var}(fB_{jk}) = \sigma_{fB(1)}^2$; w_{jkl} = random tree error of l^{th} tree in jk^{th} plot; $E(w_{jkl}) = 0$, $\text{Var}(w_{jkl}) = \sigma_{w(1)}^2$.

The variance components were estimated using the method of restricted maximum likelihood (REML), available in the MIXED procedure of the SAS/STAT package (SAS 1992, LITTELL *et al.* 1996). The single-site estimates of family variance ($\sigma_{f(1)}^2$) are biased, comprising a variance component that estimates the varying relative performance of families from one site to another. To obtain unbiased estimates of genetic variance and heritability, data from multiple environments are mandatory (ZOBEL & TALBERT 1984). In this study, the measurements made at equal ages were combined over parallel trials within each series (one year difference between the measurement ages was tolerated in order to ensure enough data for each analysis). Before the analysis, the data from each parallel trial were transformed to equal additive genetic variance by multiplying all the observations by a factor $\sigma_{A_i}/\sigma_{A_i}$, where σ_{A_i} denotes a single-site estimate of the additive genetic standard deviation for the i^{th} parallel trial and σ_{A_i} is some constant (DANELL 1988, SONESSON & ERIKSSON 2000). In this study, σ_{A_i} was set equal to the mean of the additive genetic standard deviations for the n parallel trials included in an analysis. The total number of independent across-trial analyses performed was 22, representing ages 5, 6, 7, 10, 11, 12, 16, 17 and 18 (Table 2). The additive model used to estimate variance components across trials was:

$$y_{ijkl} = \mu + S_i + B_{ij} + f_k + fS_{ik} + fB_{ijk} + w_{ijkl} \quad [2]$$

where: y_{ijkl} = height of l^{th} tree in k^{th} family and j^{th} block in i^{th} trial; $E(y_{ijkl}) = \mu + S_i + B_{ij}$, $\text{Var}(y_{ijkl}) = \sigma_f^2 + \sigma_{fS}^2 + \sigma_{fB}^2 + \sigma_w^2$; μ = a general mean; S_i = fixed effect of i^{th} trial; B_{ij} = fixed effect of j^{th} block in i^{th} trial; f_k = random effect of k^{th} half-sib family; $E(f_k) = 0$, $\text{Var}(f_k) = \sigma_f^2$; fS_{ik} = random interaction effect of k^{th} family in i^{th} trial; $E(fS_{ik}) = 0$, $\text{Var}(fS_{ik}) = \sigma_{fS}^2$; fB_{ijk} = random plot effect due to interaction between k^{th} family and j^{th} block in i^{th} trial; $E(fB_{ijk}) = 0$, $\text{Var}(fB_{ijk}) = \sigma_{fB}^2$; w_{ijkl} = random tree error of l^{th} tree in ijk^{th} plot; $E(w_{ijkl}) = 0$, $\text{Var}(w_{ijkl}) = \sigma_w^2$.

Table 2. Across-site estimates of variance components [2], additive genetic variance (unbiased and biased) [7], type-b correlation [6], the ratio of the between-family and family-by-site variance components, and unbiased individual heritability [4].

Trial series	Age	σ_f^2	σ_{fS}^2	σ_{fB}^2	σ_w^2	σ_A^2	$\sigma_{A(biased)}^2$	r_A	σ_{fS}^2/σ_f^2 %	$h_i^2 \pm$ S. E.
572	6	0.138	0.113	0.397	5.548	0.55	1.00	0.55	82	0.089±0.030
572	11	1.277	0.945	2.058	31.874	5.11	8.89	0.57	74	0.141±0.045
572	16	2.845	1.785	2.384	74.317	11.38	18.52	0.61	63	0.140±0.044
698	7	0.547	0.685	1.311	8.021	2.19	4.93	0.44	125	0.207±0.143
698	11	1.478	2.070	8.385	39.865	5.91	14.19	0.42	140	0.114±0.109
739	7	0.348	0.308	0.993	8.968	1.39	2.63	0.53	89	0.131±0.043
739	12	0.987	1.412	7.642	34.697	3.95	9.60	0.41	143	0.088±0.039
739	18	0.935	2.334	26.021	84.923	3.74	13.08	0.29	250	0.033±0.055
757	7	0.145	0.037	0.785	4.622	0.58	0.73	0.80	25	0.104±0.055
757	12	0.418	0.755	6.291	26.431	1.67	4.69	0.36	181	0.049±0.061
757	18	1.454	3.891	8.135	52.068	5.82	21.38	0.27	268	0.089±0.095
803	7	0.311	0.149	0.381	5.759	1.24	1.84	0.68	48	0.189±0.056
803	12	1.563	0.687	1.486	26.462	6.25	9.00	0.69	44	0.207±0.059
861	12	0.320	0.342	2.494	27.011	1.28	2.65	0.48	107	0.042±0.026
861	17	1.239	0.750	7.075	62.144	4.95	7.95	0.62	61	0.070±0.034
862	12	1.245	1.127	3.531	27.405	4.98	9.48	0.52	91	0.149±0.090
862	17	3.729	3.154	8.316	59.678	14.92	27.53	0.54	85	0.199±0.110
864	12	0.553	0.305	3.275	26.450	2.21	3.43	0.64	55	0.072±0.035
864	16	2.354	0.757	10.627	65.696	9.42	12.45	0.76	32	0.119±0.061
865	12	0.888	0.537	3.511	27.882	3.55	5.70	0.62	60	0.108±0.044
865	17	3.035	1.389	9.018	64.224	12.14	17.70	0.69	46	0.156±0.058

Estimation of genetic parameters

The open-pollinated families were assumed to consist of paternally unrelated siblings. Accordingly, the additive genetic variance on a single-site basis was estimated by multiplying the among-family component of variance by four ($\sigma_{A(1)}^2 = 4 \sigma_{f(1)}^2$), the inverse of the coefficient of genetic relationship for half-sibs (FALCONER 1981). Single-site [3] and across-site [4] estimates of individual heritability and single-site coefficients of additive genetic variation [5] were calculated from the equations:

$$h_{i(1)}^2 = 4 \sigma_{f(1)}^2 / (\sigma_{f(1)}^2 + \sigma_{fB(1)}^2 + \sigma_{w(1)}^2) \quad [3]$$

$$h_i^2 = 4 \sigma_f^2 / (\sigma_f^2 + \sigma_{fS}^2 + \sigma_{fB}^2 + \sigma_w^2) \quad [4]$$

$$CV_{A(1)} = 100 (4 \sigma_{f(1)}^2)^{0.5} / x \quad [5]$$

Standard errors of the heritability estimates were calculated according to an approximation given by DICKERSON (1969).

The influence of the family-by-site component of variance on the single-site additive genetic variance was determined by calculating the ratio of the unbiased and biased estimates of the additive genetic variance, using variance components from the across-site analysis. This ratio [6] estimates the average degree of ‘type-B’ genetic correlation (r_B) between different individuals of the same genetic group when many environments are involved for testing (DICKERSON 1962).

$$r_B = \sigma_f^2 / (\sigma_f^2 + \sigma_{fS}^2) = (1/4 \sigma_A^2) / (1/4 \sigma_{A(1)}^2) \quad [6]$$

The type-B correlation is actually a measure of genotype-by-environment interaction ($G \times E$) which can range from 0 to 1. The higher values indicate less interaction (BURDON 1977). In this study, type-B correlation was mainly used to approximate and adjust for the upward bias in the single-site estimates of heritability [9, 10].

Age-age genetic correlations within each trial (‘type-A’ correlation, r_G) were approximated by Pearson correlation using least-square family means as observational units.

Estimation of time trends

A repeated-measures model was developed [7] and fitted to the time-series data representing single-site estimates of variance components, heritability and coefficient of variation. The aims of the analysis were: (1) to draw statistical inferences on the fixed main effects of testing method (narrow vs. wide spacing) and site quality (forest vs. field site), especially on the interactions of these two main effects with age (modeled as a continuous regression variable), and (2) to set up time-trend functions needed in forecasting the genetic response to early selection. The exponential

Table 3. Parameter estimates of the time-trend model [7] fitted to the natural logarithms of the single-site additive genetic variance, family-by-site variance and residual (within-plot) variance [1], estimates of single-site individual heritability [3], single-site coefficient of additive genetic variation [5], and cumulative mean height. Variances due to the random effects of the model [7] are given in the bottom. Missing estimates (–) denote a statistically non-significant factor which was omitted from the final model.

Factor	Level	Parameter	Parameter estimates and their standard errors					
			$\log_e(\sigma^2_{A(i)})$	$\log_e(\sigma^2_{jB(i)})$	$\log_e(\sigma^2_{w(i)})$	$h^2_{i(i)}$	$CV_{A(i)}$	Cumulative height
Intercept			-4.871±0.340	-4.736±0.643	-3.618±0.297	0.372±0.040	26.539±3.065	-18.505±3.061
Age or $\log_e(\text{age})$ (Continuous)		b_1	3.155±0.072	2.031±0.264	2.974±0.133	0.005±0.002	-1.904±0.474	4.576±0.501
Age (Continuous)		b_2	–	–	–	–	0.044±0.021	0.085±0.022
Method	forestry trial	M_1	-0.493±0.199	2.196±0.767	1.096±0.359	-0.262±0.084	-3.349±1.123	–
	test orchard	M_2	0.000	0.000	0.000	0.000	0.000	–
Site quality	forest	S_1	-1.223±0.240	-3.207±0.782	-0.936±0.362	-0.193±0.046	-7.365±2.977	14.981±2.994
	field	S_2	0.000	0.000	0.000	0.000	0.000	–
Method-by-Site	forestry trial, forest	MS_{11}	–	–	–	0.144±0.091	–	-5.723±2.665
	forestry trial, field	MS_{12}	–	–	–	0.000	–	10.164±5.543
	test orchard, forest	MS_{21}	–	–	–	0.000	–	0.000
	test orchard, field	MS_{22}	–	–	–	0.000	–	0.000
Method-by-Age	forestry trial	b_{11}	–	-0.861±0.298	-0.536±0.170	–	–	-2.419±0.477
	test orchard	b_{12}	–	0.000	0.000	–	–	0.000
Site-by-Age	forest	b_{11}	–	1.623±0.316	0.076±0.160	–	0.644±0.250	-3.437±0.273
	field	b_{11}	–	0.000	0.000	–	0.000	0.000
Method-by-Site-by-Age	forestry trial, forest	b_{111}	–	–	0.227±0.092	–	–	3.159±0.515
	forestry trial, field	b_{112}	–	–	0.000	–	–	0.000
	test orchard, forest	b_{121}	–	–	0.000	–	–	0.000
	test orchard, field	b_{122}	–	–	0.000	–	–	0.000
			Variance components					
Among trials		σ_g^2	0.155	0.342	0.017	0.004	0.857	7.968
Within trials		σ_e^2	0.169	0.197	0.049	0.005	13.279	8.745

relationship between the variance components and age was accounted for by analysing these variables on a natural log-log scale.

$$y_{ijkl} = \mu + M_i + S_j + MS_{ij} + (b_{1..} + b_{1i.} + b_{1.j} + b_{1ij})T + b_2T^2 + g_k + e_{ijkl} \quad [7]$$

where: y_{ijkl} = single-site parameter estimate (Table 3) (= $\log_e(y_{ijkl})$, if y is a variance component); M_i = fixed effect of i^{th} testing method ($i = 1 \dots 2$; 1='forestry trial', 2='test orchard'); S_j = fixed effect of j^{th} site quality ($j = 1 \dots 2$; 1='field', 2='forest'); T = age of the trial (= $\log_e(T)$, if y is a variance component); MS_{ij} = interaction between i^{th} testing method and j^{th} site quality; g_k = random subject effect of the k^{th} trial, $E(g_k) = 0$, $\text{var}(g_k) = \sigma_g^2$; e_{ijkl} = residual (within-trial) effect, $E(e_{ijkl}) = 0$, $\text{var}(e_{ijkl}) = \sigma_e^2$; $b_{1..}$, $b_{1i.}$, $b_{1.j}$, b_{1ij} , b_2 = regression coefficients (i and j refer to levels of the main effects)

Non-significant effects were dropped from the model one-by-one, starting from the highest-order interactions. The analysis was then repeated until all the effects in the model appeared statistically significant ($p < 0.05$). However, those of the main effects that were

involved in significant interactions were preserved in the model independently of their own level of significance. These interactions comprised age regressions estimated within subclasses of the main effects, which are considered to provide evidence for the disparity of the linear age trends among the main-effects levels. The time-covariance structure for the residual terms was chosen among four options provided by PROC MIXED, namely compound symmetry (CS), and three spatial structures, SP(POW), SP(SP) and SP(GAU). The structure that gave the best fit, as measured by the Akaike's Information Criterion (LITTELL *et al.* 1996), was used to construct the final model.

The time-trend analysis of the site-site (r_B) and age-age (r_G) correlations consisted of regressing the correlation estimates on age, or the natural logarithm of the age ratio ($LAR = \log_e(\text{younger age/older age})$), respectively. The model for the age-age correlations also accounted for possible interactions between LAR, testing method and site quality. Predictions from these regression equations were subsequently used to estimate genetic gains.

Selection efficiency

Efficiency of early selection was examined by choosing total height at age 20 as the target trait to be improved. The selection schemes considered were: 1) parental (backward) selection (PS), under which parents are chosen based on average performance of their progeny in a single trial, and 2) within-family selection (WFS) among offspring (forward selection), on the basis of deviations of individual phenotypes from family and block averages. Family information is usually combined with individual-level information when trees are selected forward in genetic tests (COTTERILL & DEAN 1990), but this option was not considered here. The correlated responses to early selection (R_{20ij}) were predicted for four groupings of the data (the combinations of two testing methods and two site qualities) as follows (FALCONER 1981):

$$R_{20ij} = q i_j r_{Gj20} h_j h_{20} cv_{20}, \quad [8]$$

where q is a constant (1 for WFS and 2 for PS), i_j is the selection intensity at age j , r_{Gj20} is the genetic correlation between cumulative height assessed at ages j and 20, h is the square root of heritability, and CV_{20} is the target-age phenotypic coefficient of variation ($cv_{20} = 100 s_{20} / \text{age-20 mean height}$). The heritability values appropriate for PS (family heritability, h^2_f) and WFS (within-family heritability, h^2_{wf}) were calculated as in Eq. 9 and 10, on the basis of predictions of single-site variance components from [7].

$$h^2_f = r_B \sigma^2_{f(1)} / (\sigma^2_{f(1)} + \sigma^2_{fb(1)} / n_B + \sigma^2_{w(1)} / (n_B n_p)), \quad [9]$$

$$h^2_{wf} = 3 r_B \sigma^2_{f(1)} / (c_1 \sigma^2_{fb(1)} + c_2 \sigma^2_{w(1)}) \quad [10]$$

The terms n_B and n_p refer to the numbers of blocks per trial, and of trees per plot, respectively. Here, these values were fixed to: $n_B = 6$, and $n_p = 25$. The coefficients c_1 and c_2 were defined as: $c_1 = (n_B - 1) / n_B$ and $c_2 = (n_B n_p - 1) / (n_B n_p)$.

To adjust for the ‘time penalty’ associated with postponed selection, the response to selection [8] is often presented on a per year basis (R^y). This requires dividing the response by the sum of the testing phase (j) plus the time required to mate the selected trees and produce the new generation of progeny (b).

$$R^y_{20ij} = q i_j r_{Gj20} h_j h_{20} cv_{20} / (j + b) \quad [11]$$

The time required to produce a new progeny generation for WFS was defined as the selection age plus 10 years ($b = 10$). For PS, the length of the breeding phase was assumed to be zero since the parents selected backward can usually be mated in existing clonal collections.

Furthermore, the parental information is immediately applicable for roguing inferior clones in seed orchards.

Relative efficiency of indirect selection (RE_{20ij}) was estimated by dividing R^y_{20ij} by the corresponding response to direct selection on the target trait (R^y_{20i20}).

$$RE_{20ij} = q i_j r_{Gj20} h_j h_{20} cv_{20} (20 + b) / \{ q i_{20} h^2_{20} cv_{20} (j + b) \} \quad [12]$$

Assuming equal intensities of selection ($i_j = i_{20}$), the former equation reduces to a simpler form:

$$RE_{20ij} = r_{Gj20} h_j (20 + b) / \{ h_{20} (j + b) \} \quad [13]$$

RESULTS

Height growth exhibited large variation among the individual progeny trials. The growth potential of each site was quantified by estimating the mean cumulative height at a base age of 12 years (H_{12}) by means of a regression analysis. The range of this index was from 19.5 to 50.0 dm (Table 1, Fig. 1). The highly differential growth curves were clearly related to edaphic differences among the trial sites. The trials established on former arable land (‘field sites’) were superior in height growth (mean $H_{12} = 45.0$ dm) to the trials on forest sites (mean $H_{12} = 23.9$ dm). On field sites, growth trajectories were nearly identical excluding the single

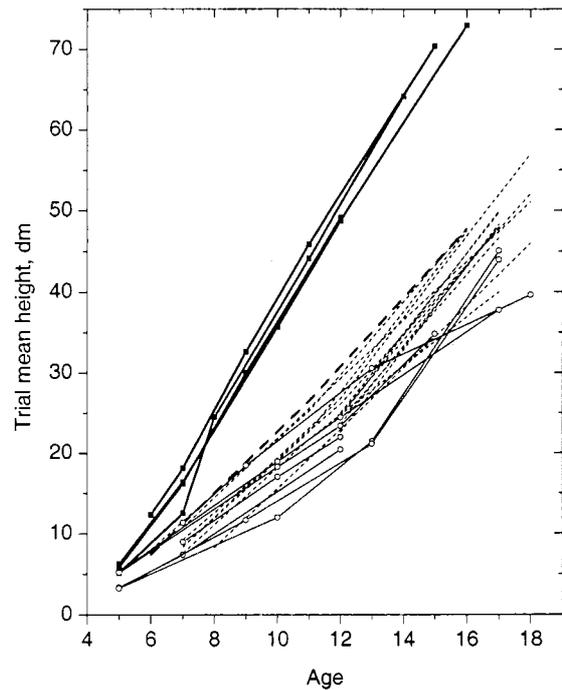


Figure 1. Development of mean height in 26 Scots pine progeny trials representing groups of field – site test orchards (thick solid lines), forest – site test orchards (thin solid lines), field – site forestry trials (thick long-dashed lines), and forest – site forestry trials (thin short-dashed lines).

forestry trial, no. 572/2, which showed markedly slower growth ($H_{12} = 28.9$ dm) than the field-site test orchards. This was probably related to the high clay content of the soil in this trial (Table 1, Fig. 1). The two categories of forest site types, 'dry' and 'moist', appeared to be of similar value from the point of view of tree growth (difference in $H_{12} = 0.55$ dm), so they were combined in the following analyses.

The largest component of the single-site variance consistently attributed to within-plot residual effects (range 65–95%). The residual variances increased exponentially as the progeny trials became older. The family level sources of variance ($\sigma_{f(i)}^2$ and $\sigma_{fb(i)}^2$) typically remained below 15% of the total variance. The third component in this category, the family-by-site interaction variance from an across-site analysis (σ_{fs}^2), varied from 13 to 295% of the unbiased family variance. The accompanying type-B genetic correlations also showed large variance (range 0.25–0.94). In general, the relative magnitude of the interaction variance did not change much over successive measurements, except for the series No. 757 in which an abrupt decrease in r_B (from 0.86 to 0.25) occurred between ages 7 and 18. When all of the type-B correlation estimates (Table 2) were pooled and regressed on age, no trend was detected [14].

$$r_B = 0.673 - 0.003(\text{age}) \quad (r^2 = 0.01) \quad [14]$$

Because of the flat slope ($p < 0.405$), the intercept of the regression formula, 0.673 (S.E. = 0.118, $p < 0.001$) was used as an age-independent predictor of r_B . Neither was the type-B correlation related to the heterogeneity of the test environments. Three measures of dispersion were calculated to estimate the degree of among-trial heterogeneity: the variance, the natural logarithm of the variance, and the coefficient of variation of the mean heights of the parallel trials. Pearson correlations between these three statistics and the respective estimates of r_B were all small and non-significant ($r = 0.18, 0.13$, and, 0.10 respectively).

The estimated level of type-B correlation suggests that the single-site estimates of heritability were overestimated by roughly 50 % (derived as $100/r_B - 100$) (Table 2). The mean of the biased heritability estimates over all trials and ages was 0.23 (range 0.00–0.65), whereas for the unbiased (across-site) estimates the mean was 0.12 (range 0.03–0.20). The precision of the heritability estimates varied from low to modest: the ratio of the standard error to heritability value ranged from 0.2 to 6.4 (mean = 0.59). Despite the notable temporal fluctuations in some of the trials (Fig. 2), heritability did not show any systematic tendency over the first 18 years of testing. However, the heritabilities

were clearly related to the mean growth rate and, thereby, to the edaphic properties of the test sites. The highest heritability estimates were acquired from the fast-growing test orchards and, conversely, the lowest heritabilities were associated with forest-site forestry trials. Indications of significant testing method-by-site quality interaction were also present (Table 3). For instance, some of the test orchards established on forest soil showed markedly higher levels of heritability as compared to the forestry trials on forest soil (Fig. 2). In general, the effect of the testing method ('high spacing' vs. 'low spacing') on heritability was slightly larger than that of site quality ('forest' vs. 'field') (Table 3).

The coefficient of additive genetic variation, which indicates 'evolvability', the potential for genetic evolution of the mean genotype (HOULE 1992), showed a slightly decreasing tendency over age. The time trends were significantly different for the trials on different type of sites (Fig. 3, Table 3). The most rapid decreases occurred in the fast growing field-site trials. By age 12, most of the CV estimates varied between 5 and 15% of the trial mean height.

The correlations between cumulative heights measured at different ages were all positive and, in most cases, reasonably high. They were also positively and linearly related to the natural log of the age ratio (Fig. 4), decreasing as the time interval between measurement ages increased. The estimated regression slope for the forestry trials indicated slightly slower decrease with increasing age interval, than for the test orchard trials. However, the difference was not statistically significant. The forest vs. field sites also showed nearly identical slopes. Thus, the time trend formula for age-age correlations reduced into a simple regression equation with LAR as the only independent variable:

$$r_G = 1.02 + 0.423 \log_e(\text{younger age/older age}) \quad (r^2 = 0.53) \quad [15]$$

The model [15] was also tested with age difference as the predictor, but this resulted in a somewhat poorer fit ($r^2 = 0.44$) than the LAR model.

The time-trend functions for the variance components (Table 3, Fig. 5) were used to predict heritability and correlated genetic gains from early selection (Fig. 6). The correlated gains improved steadily towards the target age of 20 years (Fig. 5), as a result of increasing age-age correlation. Under the premise of 150 progeny per family, parental selection produced three times more improvement in age-20 height, than forward selection for an individual's own (adjusted) phenotype. Independently of the mode of selection, forestry trials

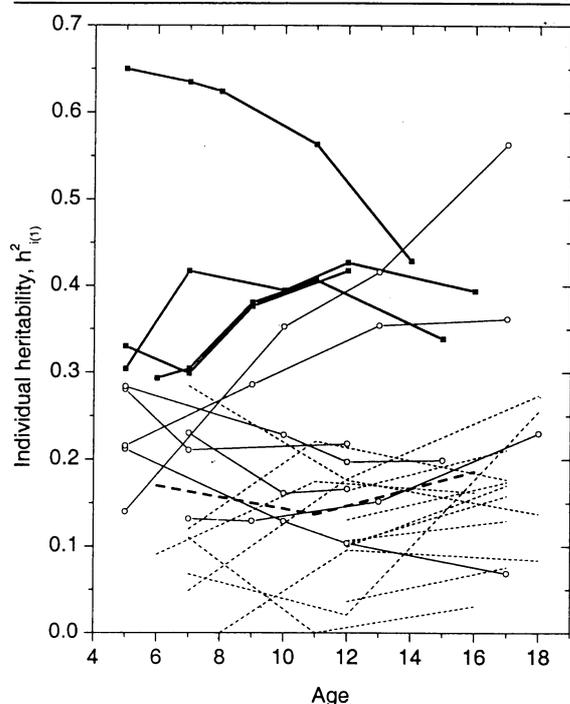


Figure 2. Development of single-site individual-level heritability for tree height in 26 Scots pine progeny trials representing groups of field – site test orchards (thick solid lines), forest – site test orchards (thin solid lines), field – site forestry trials (thick long-dashed lines), and forest – site forestry trials (thin short-dashed lines).

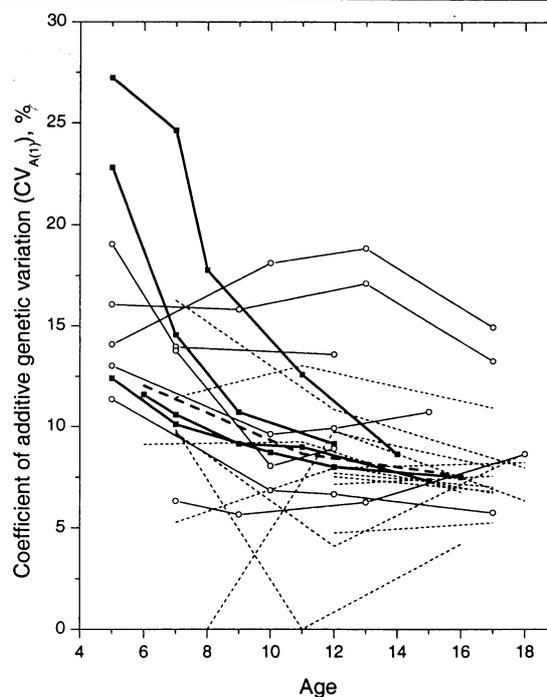


Figure 3. Development of single-site coefficient of variation for tree height in 26 Scots pine progeny trials representing groups of field – site test orchards (thick solid lines), forest – site test orchards (thin solid lines), field – site forestry trials (thick long-dashed lines), and forest – site forestry trials (thin short-dashed lines).

on forest soils were significantly less effective than the other types of trial. The inferiority of this combination of testing method and site quality for field testing was evident in all of the scenarios (Fig. 6, 7, 8).

Early parental selection was always more efficient than selection at age 20 in terms of genetic gain per year. The relative efficiency of PS reached the maximum level between ages 5 and 7 (Fig. 7, 8), producing 40 to 60 % more gain per year than direct PS for height at age 20 (Fig. 8). The efficiency of early WFS was initially low and increased over time. However, in contrast to parental selection, the annual responses to WFS were, at best, only slightly greater than responses to direct selection. The age needed to achieve 95% of the gain from direct WFS varied largely in different type of trials (from 8 to 16 years). The relative selection efficiency was found to be fairly sensitive to changes in the regression formula used to predict age-age correlations. When the model presented by LAMBETH (1980) was applied in place of the empiric model [15], the relative efficiencies of early selection were amplified and the maximum correlated responses occurred slightly earlier.

DISCUSSION

Genetic control of tree height

The test orchard trials and forestry trials were associated with distinctly different levels of heritability, providing firm evidence for a significant impact of test characteristics on the magnitudes of genetic and environmental variation. The higher heritabilities of the test orchard group are probably related to the greater edaphic uniformity of the planting sites and to the closer initial spacing. Spacing contributed to the heritabilities through blocking efficiency; when the number of trees in a plot is constant, block size is coupled with planting density. Thus, the close spacing of the test orchards obviously enabled more efficient control of the environmental variability than the four-fold wider spacing of the forestry trials. The effect of spacing on heritability was, in fact, slightly greater than that of site quality, as quantified by the prediction model (Table 3).

The results suggest that estimates of heritability (or any other genetic parameter) are not very informative if reported without giving sufficient reference to the conditions in which they were obtained. For instance,

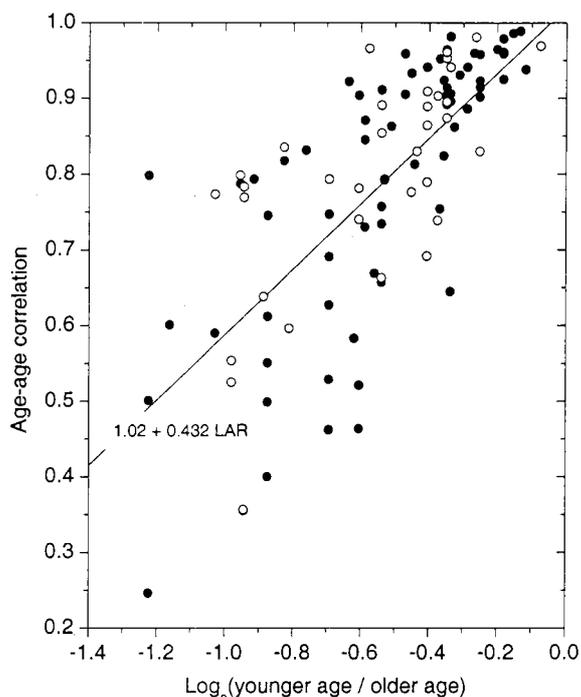


Figure 4. Estimates of age-age correlations vs. the natural logarithm of the ratio of the younger age to the older age (LAR) and the corresponding regression slope (a solid line) from 26 Scots pine progeny trials. The regression slope obtained by LAMBETH (1980) is illustrated by a dashed line. Open and filled dots denote estimates from forestry trials and test orchards, respectively.

in predicting breeding values for trees, the temporal and environmental heterogeneity of genetic parameters is specifically recognized and taken into account in order to improve the accuracy of predictions (WHITE & HODGE 1989). In the context of forest tree breeding, it is obviously more reasonable to consider heritability as an instant measure of experimental efficiency than a stable parameter that pertains to characteristics of some genetic group (or trait). The predictive models developed in this study for the log-transformed variance components apply to the most common situations of Scots pine progeny testing in Finland. Thus, they could facilitate the prediction of additive genetic values of trees and genetic gain, particularly when there are no data available to allow these parameters to be directly estimated. Nevertheless, updating these models with new data would be beneficial, especially in order to balance the insufficient representation of field-site forestry trials in this study. These type of progeny trials are currently rare in Finland. In future, however, Scots pine progeny trials are to be increasingly laid out on uniform and fertile soils, using significantly wider spacing than in currently ongoing test orchards.

Knowledge of temporal changes in heritability is

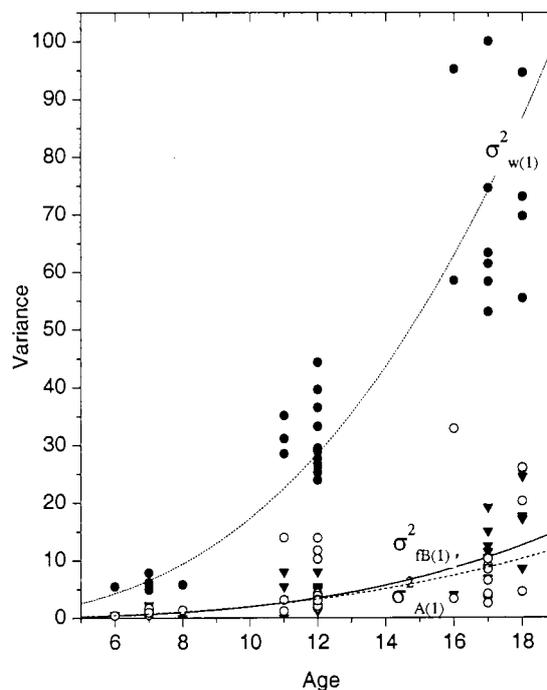


Figure 5. An illustration of single-site variance component estimates [1] and their time-trend models [7] in the group of forest-site forestry trials. Filled triangles, open circles and filled circles denote the single-site estimates of additive genetic variance ($\sigma^2_{A(1)}$), family-by-block variance ($\sigma^2_{fB(1)}$), and residual variance ($\sigma^2_{w(1)}$), respectively. The corresponding estimated time-trends are illustrated with dashed, solid and short-dot lines.

crucial for devising optimized early selection strategies. Studies with conifers in the genus *Pinaceae* (NAMKOONG *et al.* 1972, FRANKLIN 1979, FALKENHAGEN 1989, HODGE & WHITE 1992, BALOCCHI *et al.* 1993, DIETERS *et al.* 1995, COSTA & DUREL 1996, JOHNSON *et al.* 1997) have found individual heritability for height to be initially low, and to increase with age. For Scots pine, information on age trends in heritability is scarce. However, JANSSON *et al.* (1998) found a similar, slightly increasing tendency for heritability of tree height in three Swedish Scots pine trials measured several times from age 9 up to age 29. In the present study, an increasing pattern of heritability was true for a few of the trials whereas some of the others displayed an opposite decreasing tendency (Fig. 2). In the pooled analysis of the single-site estimates of heritability, however, no clear age trend could be detected (the age coefficient of regression was significant but of negligible size). Corresponding to the finding of this study, stable ratios of family to phenotypic variance with advancing stand age have been reported, e.g., by HANNRUP *et al.* (1998) in Scots pine, LAMBETH *et al.* (1983) and Foster (1986) in loblolly pine (*Pinus taeda*), VASQUEZ and DVORAK (1996) in three species of

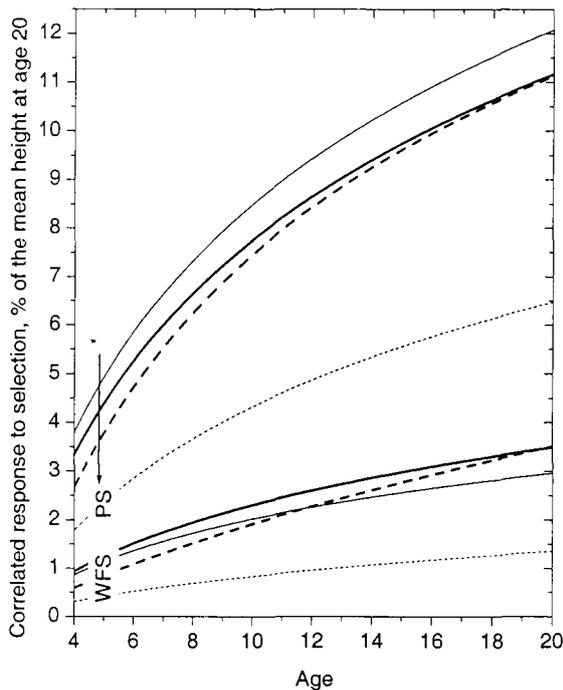


Figure 6. Predicted correlated responses to early parental (PS) and within-family (WFS) selection for field – site test orchards (thick solid lines), forest – site test orchards (thin solid lines), field – site forestry trials (thick long-dashed lines), and forest – site forestry trials (thin short-dashed lines). The responses are given per unit of selection intensity and as percentage of the cumulative height at age 20 [8].

tropical pines, BASTIEN and ROMAN-AMAT (1990) in Douglas fir, XIE and YING (1996) in lodgepole pine (*Pinus contorta* ssp. *latifolia*), and BENTZER *et al.* (1989) in Norway spruce.

The observed lack of an age trend could be an outcome of two, not mutually exclusive, reasons: (1) the standard errors of the heritability estimates were large enough to conceal possible systematic changes, or (2) inter-family competition had not begun by the time of the latest measurements. According to FRANKLIN's (1979) often-cited hypothesis, heritability can be expected to increase when competition intensifies and begins augmenting differences among families with inherently different growth rates and competitive abilities. The timing of competition is obviously dependent on the mean growth rate (site quality), planting density and changes in spacing due to unplanned mortality. Visual observations made in widely-spaced Scots pine trials suggest that crown closure normally occurs not earlier than 20 to 30 years from planting. Trials with trees at these ages were not represented in this study, and the lack of competition could thus adequately explain the lack of age trend in heritability, at least in the forestry trials. In the dense test orchard stands, canopies typically close much earlier, at around

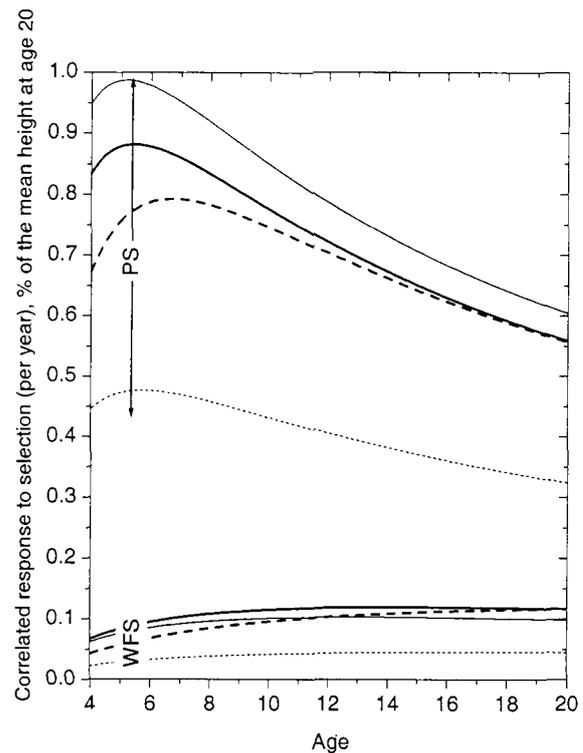


Figure 7. Correlated responses to early parental (PS) and within-family (WFS) selection [11] for field – site test orchards (thick solid lines), forest – site test orchards (thin solid lines), field – site forestry trials (thick long-dashed lines), and forest – site forestry trials (thin short-dashed lines). The responses are presented in terms of gain per year and per unit of selection intensity, given as percentage of the cumulative height at age 20.

10 years of age. However, in trials designed to have multiple-tree family plots, the effects of inter-family competition are likely to require some additional years to actualise, so that they were not properly manifested in this study. Furthermore, tree height is less susceptible to crowding than other routinely recorded growth traits (SAKAI *et al.* 1968, KREMER 1992, PAUL *et al.* 1997). The absence of strong competition effects on genetic and phenotypic variances (HAMBLIN & ROSIELLE 1978, FOSTER 1986) in my data apparently simplified the interpretation of the results. MAGNUSSEN (1995) argued that heritability estimates obtained under heavy competition could be severely distorted and lead to false predictions of selection efficiency.

Individual heritability estimates did not couple with the coefficients of additive genetic variation, which diminished with time, in agreement with the commonly noticed inverse relationship between CVs and trait means (HOULE 1992). The values of the CV_As were mostly below 15%, conforming to earlier results (FOSTER 1986, NAMKOONG & CONKLE 1976, CORNE

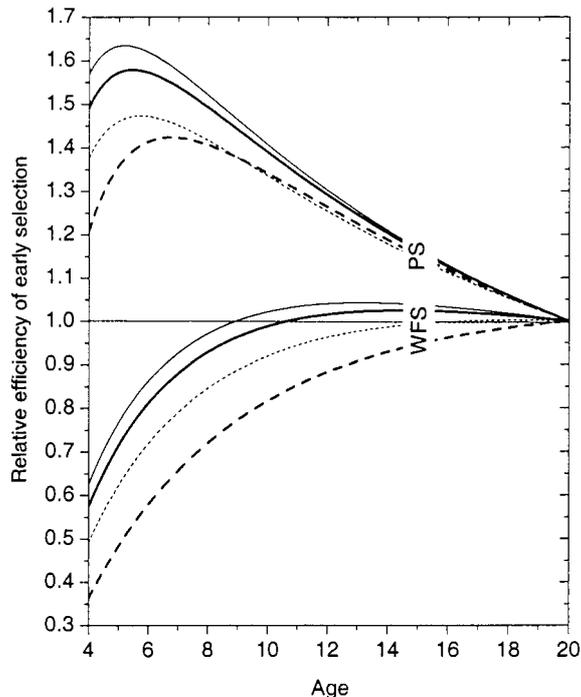


Figure 8. Relative efficiencies of early parental (PS) and within-family (WFS) selection [13] for field – site test orchards (thick solid lines), forest – site test orchards (thin solid lines), field – site forestry trials (thick long-dashed lines), and forest – site forestry trials (thin short-dashed lines).

LIUS 1994, HANNRUP *et al.* 1998).

Impact of family-by-site interaction on genetic parameters and selection

The varying response of the families to the test environments inflated the estimates of the additive genetic variance and heritability by half. As a result, the estimates corrected for the bias were substantially smaller than those usually reported for tree height in conifers. The mean heritability of height in the 67 studies reviewed by CORNELIUS (1994) was 0.28, whereas in this study the mean of the unbiased estimates was less than half of that, 0.12. Type-B correlations were comparable to those found in earlier studies in which the values have mostly fallen between 0.6 and 0.8, corresponding to bias proportions of 66 to 25 %, respectively (ADAMS *et al.* 1994, DIETERS *et al.* 1995, HAAPANEN 1996, JOHNSON *et al.* 1997). DIETERS *et al.* (1995) and JOHNSON *et al.* (1997) found type-B correlations to increase slowly with time, indicating diminishing importance of the G×E. In this study, there was no sign of a time trend for the type-B correlations.

SHELBOURNE (1972) suggested that if family-by-environment interaction variance exceeds the family component of variance by half or more, the interaction can seriously impair selections based on intra-site

information. Although this limit was exceeded in many of the across-site analyses, the biological meaning of the observed interaction is not clear. Consequently, it is difficult to estimate the loss of potential gain, the most important outcome of the genotype-by-environment interaction. However, the loss is likely to be less than what mechanical calculations would suggest, if the statistical family-by-site interaction variance were straightforwardly interpreted to be equivalent with the biologically significant G×E. That would hardly be justified in the field testing of forest trees, where large interactions commonly occur between families and sites within the same region, and even between families and block replications at a single trial (MATHESON & COTTERILL 1990). As environmental variability among trial sites is typically random, also the interactions between families and sites are random and not repeatable (MATHESON & COTTERILL 1990). In this situation, breeders should accept the presence of the interaction rather than try to gain from it. In Scots pine breeding, the goal of genetic testing is to find individuals that perform well over a variety of sites within a climatically determined breeding zone. The fairly low correlations between parallel trials underscore the need to account for site-to-site variation in family performances. First of all, each progeny trial should be replicated at a sufficient number of sites. Five test localities, suggested by LINDGREN (1984) for Scots pine testing in Sweden, is probably adequate. In addition, information on candidate trees and their siblings in other trials should be employed in selection. This especially concerns trees selected forward, as parental (backward) selection is, as a rule, based on results from multiple test sites and is therefore less prone to the possible biasing effects due to the family-by-site interaction.

BARNES *et al.* (1984) concluded that explaining and using G×E in breeding is realistic only when a single environmental factor affects an economically important trait in a predictable manner. When a growth trait is considered, large differences in family performances from one site to another could be assumed to be related to overall differences in site productivity. Indeed, HODGE & WHITE (1992) were able to demonstrate that type-B genetic correlations were linked to differences in site quality in slash pine (*Pinus elliottii*). However, no sign of this kind of association was found in this study, even though the trial sites were markedly different in terms of height growth. Most of the variation among the across-site correlations remained unexplained, suggesting that while the magnitude of the family-by-site interaction in young progeny trials is not negligible, its nature is highly random and unpredictable and thus of little use for common breeding purposes. It must be stressed, however, that these trials

were designed with the estimation of GCA values as the primary objective, and are not optimal for the study of G×E. A thorough investigation of this issue would require a large sample of families replicated over several well-defined sites.

Age-age correlations

Sufficiently strong genetic correlation between the selection and the target age is a prerequisite for successful early selection. Considering the importance of age-age correlations to all kinds of predictions of future gain, there is a surprising gap in knowledge with regard to the magnitudes of age-age correlations in Scots pine progeny testing. Encouragingly strong age-age correlations have been reported for performances of full-sib families grown in a growth chamber and in older field trials (JONSSON 2000), and also for some other important Scots pine traits such as wood density (HANNRUP & EKBERG 1998). However, the patterns of field-trial correlations are less well known. This study utilized correlations between least-square family means to approximate genetic correlations (LAMBETH *et al.* 1983, NEWMAN & WILLIAMS 1991). These estimates are contaminated by environmental (co)variances, and are thus potentially biased (JANSSON 2000). However, the effect of the bias diminishes with sample size and is likely to be of small importance when the family size exceeds 20 individuals (ROFF & PREZIOSI 1994). As family sizes in Finnish progeny trials are typically large (> 100), family-mean correlations may be expected to be of good accuracy. Furthermore, simulations have shown that true genetic correlations are in many situations estimated with worse precision by direct estimates of genetic correlation than by phenotypic correlations (ROFF 1995), as the former estimates are highly sensitive to the number of families in the sample (KLEIN *et al.* 1973, NAMKOONG 1979, HODGE & WHITE 1992).

As a rule, age-age correlations in growth traits decline with increasing age interval. LAMBETH (1980) reanalysed phenotypic age-age correlations from a number of studies, and found that they could be reliably predicted by means of a linear regression, using the logarithmic ratio of the two ages as the explanatory variable. This same approach has since been frequently used to project age-age correlations (MCKEAND 1988, KING & BURDON 1991, JOHNSON *et al.* 1997). In the present study, the regression method worked acceptably. The slopes were not significantly different between trials on forest vs. field sites. The same was true for the comparison between the forestry and test orchard trials, although the assumption of homogeneity was not quite as clear in this case. Interestingly, the coefficient of regression obtained in this study (0.423)

was very close to that reported by GWAZE *et al.* (2000) for young fast-growing *Pinus taeda* L. genetic tests (0.447). Both of these slopes are markedly steeper than that of Lambeth's 'universal equation' (0.308). The discrepancy may be partly due to the fact that the range of the LARs was only half of that in the study of LAMBETH (1980). Family-mean correlations may also more accurately reflect changes in the genetic mechanism controlling the development of tree height than individual-tree phenotypic correlations, which apparently comprised most of the data in LAMBETH's (1980) investigation. Furthermore, many other studies indicate that the function relating age-age correlations to the log of the age ratio is not invariant, in contrast to LAMBETH (1980) who suggested that a single predictive model given in his study would be valid for a wide range of experiments and species. For instance, JOHNSON *et al.* (1997) and GWAZE *et al.* (2000) reported the regression slope to significantly vary depending on the breeding zone. To obtain a realistic view of the true nature of the LAR relationship in various types of Scots pine progeny trials, they should obviously be followed for a longer period of time, probably at least till half-rotation.

Progeny testing methods and selection efficiency

All the scenarios indicated that the highest responses to selection were associated with the test orchard trials. This is consistent with earlier views advocating close-spaced field trials, established on high quality sites, for progeny testing (FRANKLIN 1979, MIKOLA 1985, CAMPBELL *et al.* 1986, MAGNUSSEN & YEATMAN 1986, WOODS *et al.* 1995, MAGNUSSEN 1995, HAAPANEN 1996, BRIDGWATER & MCKEAND 1997). The superiority of the test orchard method was clearly associated with the high average levels of heritability because the age-age correlations in the fast-growing test orchards were not significantly different from the other types of trials. In an investigation of a number of 10-year-old Scots pine progeny trials (HAAPANEN 1996), test orchard trials laid out on agricultural land discriminated genetic differences considerably better than parallel forestry trials. WOODS *et al.* (1995), who compared the corresponding testing methods in Douglas fir, found that selection in 'farm-field' conditions in all cases provided greater genetic gains in stem yield and wood density than selection in 'field trials' (forestry trials). Similarly, CARLSON (1990), in lodgepole pine, found single-tree plot farm-field trials to be more productive and have greater family heritability values than parallel 'wild field sites'. Hence, although the value of long-term data accumulating from traditional forestry trials is indisputable, they appear not to be the optimal choice when the primary goal is the precise and cost-efficient

ranking of genotypes. This especially concerns widely-spaced trials on forestland, which performed inferiorly in comparison to the other combinations of spacing and site quality.

In Finland, ages from 10 to 15 have been suggested sufficient for selection for growth traits in test orchard conditions (MIKOLA 1985). Similar estimates have been presented for other conifers (NAMKOONG *et al.* 1972, SQUILLACE & GANSEL 1974, FRANKLIN 1979). In general, the optimal selection ages reported for various species in the tree breeding literature show a lack of consistency, which, in view of the present results, is likely to owe much to the variable circumstances under which genetic parameters are estimated. The results obtained here suggest that the optimal age for selection occurs later for slow growing than for fast-growing trials. This especially concerning forward selections (Fig. 8). Moreover, the optimal age for WFS and PS was different. The earlier optimum for PS conforms to a number of earlier findings (LAMBETH *et al.* 1983, MCKEAND 1988, BALOCCHI *et al.* 1994, JOHNSON *et al.* 1997) and was, in fact, expected since PS is based on more information than WFS. The form of the relative efficiency function (for PS) was close to that reported by JOHNSON *et al.* (1997) for Douglas-fir. Unlike the relative efficiencies, the absolute responses to early selection kept raising steadily over age. Therefore, if juvenile selection is not urgent, there is nothing to lose if selection is deferred some years later than the optimum (ignoring the loss due to the lower efficiency per year). On the contrary, this may be reasonable considering the possible changes in the ranking of genotypes that can occur between the selection and true economic rotation ages.

The selection efficiencies predicted here are associated with a number of simplifications and uncertainties, and they should therefore be evaluated with prudence. Most importantly, the target age was set at 20 years, which can hardly be considered as a mature age, since it is equivalent to only one-fourth to one-sixth of the commercial rotation of Scots pine in Finnish conditions. Regrettably, there was no alternative for setting the goal age other than at 20 years because of the scarcity of older assessment information. The use of the LAR regression function to extrapolate selection efficiencies to later ages not covered by the data was not considered as a viable option; the results would have been speculative at best, and highly misleading at worst. However, there may be some justifications for choosing an early target. Firstly, prolonging the progeny testing much beyond 20 years is not likely to be very profitable since many important traits in Scots pine are already established by this age. Secondly, measurement of height and, consequently, estimation of bole

volume, becomes more laborious and imprecise with the increasing physical size of trees. Finally, earlier studies consistently suggest that genetic gains per unit time peak at a relatively early stage of stand development (LAMBETH 1980, LAMBETH *et al.* 1983, MCKEAND 1988). The importance of the obviously imperfect genetic association between age-20 and rotation age (roughly 80 years in southern Finland) performances is difficult to evaluate, but the bias is likely to be tolerable. For instance, studies with other pines (with notably shorter rotations, though) have promisingly indicated that early height could be a good predictor of rotation-age volume and vigour (LAMBETH *et al.* 1983, FOSTER 1986, COSTA & DUREL 1996). However, tree height is seldom the only selection criterion in the context of teenaged Scots pine trials. Other traits, especially those related to the branching quality of the butt log, become increasingly more important in determining the end-product value as the trees mature. Considering the importance of multi-trait selection, the genetic determinism of these traits should also be explored to assure efficient operation of the Scots pine breeding programme.

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