growth rhythm traits are measured under photoperiodic and temperature conditions different from those in the production stand.

Similar strong relationships between wood density and growth rhythm do not generally seem to be present for families. Indirect selection for wood density based on such traits may therefore not be efficient and it will be necessary to measure the density directly. This will delay the selection until reliable wood density predictions can be made (HYLEN, 1999). However, this offers opportunities to select for different combinations of growth, growth rhythm and wood density.

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The Effect of Pedigree Error by Misidentification of Individual Trees on Genetic Evaluation of a Full-sib Experiment

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Abstract

A simulation based on real data shows how increasing rates of individual tree misidentification result in increasing underestimation of additive genetic variance and narrow-sense heritability as well as increasing overestimation of the dominance variance. The data used came from a *Pinus sylvestris* L. progeny trial with 202 full-sib families from 52 unrelated parents at about one-third of the rotation. When 1% of 4970 individual trees were misidentified, the estimates of additive variance and heritability decreased by an order of magnitude that corresponded to the standard errors. The estimate of dominance variance approached that of additive variance when the error rate increased to 2%, after which further misidentification made the estimates diverge beyond the expected parameter space of the genetic model. The error effect was less pronounced when selecting the best parents using approximate best linear unbiased predictors, but their predicted performance was increasingly underestimated as the error rate increased.

Key words: additive variance, BLUP, breeding value, dominance variance, genetic parameter, heritability, pedigree error, mixed model equations, *Pinus sylvestris,* REML.

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Introduction

A simplified genetic model that is often used to evaluate fullsib progenies of monoecious, crossbreeding forest trees assumes that the genotype is composed of an additive part and a dominance part. The additive element is most important for traditional breeding with recurrent selection, while the dominance part may be useful in cases where vegetative propagation for reforestation is an option.

The dominance variance is unlikely to exceed the additive variance since it is improbable that a lot of genes on average express such a high concurrent dominance for polygenic controlled traits (Falconer, 1985; Lynch and Walsh, 1998), and by experience it seems reasonable that the dominance variance for growth traits normally should come to around a quarter to a half of the additive variance (Li et al., 1996; Yanchuk, 1996; Yeh and Heaman, 1987; Wellendorf, 1983). These two variance components are regularly estimated in full sib progeny tests. However, the estimates sometimes show irregularities such as dominance variance greater than additive variance. The reason for this is either that there is insufficient data, causing large sampling errors, or that the model does not adequately describe the real world. The latter problem may be caused by, for example, misidentification of individual trees in the test plantation causing pedigree errors by wrong family code. On sites with what are known as single-tree plots, numerous trees may be erroneous identified because of a simple accidental displacement of one row of trees.

Most earlier studies concern consequences of pedigree errors in animal breeding (e.g. Geldermann et al., 1986; van Vleck, 1970a, b) and attention has been put on available methods for pedigree verification (e.g. Ron et al., 1996; Beechinor and Kelly, 1987; Wellendorf, 1983). Pedigree errors bias parameter estimates and reduce genetic gain. Long et al. (1990) suggest that in spite of being much affected by pedigree errors, BLUPs will give better selection response than other predictors (phenotype values, family average values) even with 20% of the pedigrees in error. This study, carried out in a real full-sib progeny test of trees, will show the influence of varying degrees of family misidentification on the estimates of genetic parameters and breeding values. We will assume that the basic genetic model is adequate, and that the data set available for pedigree error simulation is initially without such errors and large enough to support a useful estimation of genetic parameters and breeding values.

Material and Methods

Crossing scheme and field layout

The study was based on 26-year-old Scots pine *(Pinus sylvestris* L.) progeny of $n = 52$ unrelated parent trees, mated in a circulant partial diallel scheme according to Kempthorne and Curnow (1961). Each parent was basically involved in $s = 8$ crosses where 202 out of 212 planned were successful; the scheme was 'approximate' since n and s should strictly not both be odd.

The progeny test plantation[2]) was established in 1971 at latitude 64°18' N, longitude 19°34' E, and 300 m elevation in north Sweden. With about 40 sibs per family, a total of 8160 seedlings were planted randomly as single-tree plots in a single large unit with two metre square spacing. At the most recent measurement in September 1997, 5251 living trees (64%) remained. In this study, the heights of 4960 healthy trees were considered.

Genetic evaluation

The phenotypic value *(P)* of an individual tree was assumed to be described by the biological model equation $P = A + D + E$, where A is the additive genetic value, D is the genetic dominance deviation, and E is the residual deviation where environmental effects dominate. Epistatic, maternal, reciprocal, and all other effects were assumed to be small and/or negligible and included in E. The corresponding variances were accordingly written $\sigma_P^2 = \sigma_A^2 + \sigma_D^2 + \sigma_E^2$. The equations $h^2 = \frac{\sigma_A^2}{\sigma_P^2}$ and $H^2 = \frac{\sigma_A^2 + \sigma_D^2}{\sigma_P^2}$ were assumed to express narrow-sense and broad-sense heritabilities, respectively.

In order to minimise environmental disturbance in the subsequent evaluation, the experimental area was subdivided into 70 blocks with on average 75 living trees per block, using previous experience from similar situations (Ericsson, 1997). By analogy with the biological model, the phenotypic values were approximated to the linear model equation $y_{ijkl} = b_i + a_j + a_k + f_{jk} + e_{ijkl}$, where y_{ijkl} is the phenotypic value of an individual tree, b_i the fixed effect of block i ($i = 1, \ldots 70$), a_j the random effect of mother j ($j = 1, \ldots 30$), a_k the random effect of father k ($k = 24, \ldots 52$), f_{jk} the random effect of the full-sib family with mother j and father k, and e_{ijkl} the residual effect of an individual tree, including environmental and residual genetic effects (l varied from 1 to 40). All model terms were assumed to be independent and their variances were expressed as $\sigma_y^2 = 2\sigma_a^2 + \sigma_f^2 + \sigma_e^2$. The parent variance ($\sigma_a^2$, assumed to be equal for mothers and fathers), the family variance (σ_f^2), and the residual variance (σ_e^2) were estimated using the restricted maximum likelihood (REML) method as provided by the SAS Mixed procedure (Littell et al., 1996). Corresponding to the phenotypic values of individual trees (y_{ijkl}), the phenotypic variance was estimated assuming $\sigma_P^2 = \sigma_y^2$. Since the additive genetic value (breeding value) of parent i is $A_i = 2a_i$, the additive variance was estimated according to $\sigma_A^2 = 4\sigma_a^2$. The dominance variance was similarly estimated using $\sigma_D^2 = 4\sigma_f^2$ according to Lynch and Walsh (1998).

Estimated BLUP breeding values (BVs) for the parents were computed using the SAS Mixed procedure by resolving the Henderson mixed model equations (McLean et al., 1991) corresponding to the linear model and assuming diagonal variance matrices with non-zero elements in accordance with the REML estimates.

Simulation of family misidentification

Each input record for analysis showed the block and family identity as well as the height of the tree. The misidentification simulation was repeatedly carried out through a procedure that involved substituting the family identity of individual trees randomly selected at a certain probability levels or error rates (0.5%, 1%, 2%, 3%, or 4%). The erroneous identity was drawn with equal probability from all existing family identities. Subsequently, each tree was assigned parent identities according to its assumed family membership.

After the single analysis with original family identities, the genetic parameter and breeding value estimation was repeated 25 times with modified data on each error rate level and mean values were computed. The empirical average standard errors of the parameters after the 25 simulations are shown in *table 1* (these are not the precisions of the variance estimates)[3]). The empirical standard errors are based on error variances derived for each actual function of the basic estimates $\hat{\sigma}_a^2$, $\hat{\sigma}_f^2$, and $\hat{\sigma}_e^2$, using series expansion of the functions (e.g. Bulmer, 1985).

For each set of parent BVs at 1%, 2%, 3%, and 4% error rate, the parents were ranked and the best 5, 10, 15, and 20 were selected. Their average merit was computed in each case according to the BVs using the correct pedigree information, as well as with

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[2]) Identification at SkogForsk: S23F7110264 Vindeln

[3]) The average precision of the $\hat{\sigma}_a^2$ and $\hat{\sigma}_f^2$ means was around 2% at 0.5% misidentification, increasing up to 5.7% at higher error rates.

BVs resulting from data with pedigree errors. The means and standard deviations are based on 25 simulation runs.

Results

The main results regarding parameter estimates are summarised in *table 1* and *figure 1*. An error rate of 0.5 %, corresponding to about 25 trees with misidentified pedigree, already had a detectable impact on the genetic parameter estimation with decreasing additive variance as well as heritability. At 2%, or 100 trees, the dominance variance estimate increased to the same level as the simultaneously decreasing estimate of additive variance, which is an explicit mark of incorrectness as the assumptions of the genetic model are violated. The further course of the variance and heritability curves is only of technical interest. These curves will approach zero if tree identification becomes 100% random.

The effect on BVs is summarised in *table 2* and *figure 2*. The errors make the greatest impact on the apparent BVs. However, selected trees will have an average real BV that is considerably higher than what is estimated, and hence the disadvantage is reduced.

Table 1. – The variance and heritability estimates for tree height ($\hat{\mu}$ = 70.3 dm) and their change at different misidentification error rates. The estimates where correct identification is assumed are given with standard errors.

Average error rate	$\hat{\sigma}_P^2$	$\hat{\sigma}_A^2$	$\hat{\sigma}_D^2$	$\hat{h}^2$	$\hat{H}^2$
0%	151.1 ± 4.5	30.2 ± 7.2	16.1 ± 4.4	0.200 ± 0.043	0.307 ± 0.047
0.5%	+0.3	–2.6	+1.4	–0.018	–0.009
1%	+0.5	–5.2	+2.0	–0.035	–0.022
2%	+0.5	–10.8	+3.6	–0.072	–0.048
3%	+0.6	–13.7	+4.4	–0.091	–0.062
4%	+0.4	–17.8	+7.8	–0.118	–0.067

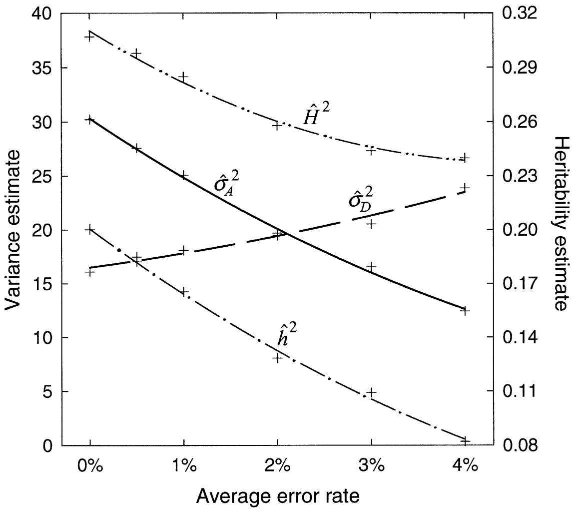

Fig. 1. – The additive variance, dominance variance, and heritability estimates for tree height at different misidentification error rates. The sample point trends are elucidated by means of second-degree, least-square-fit polynomials.

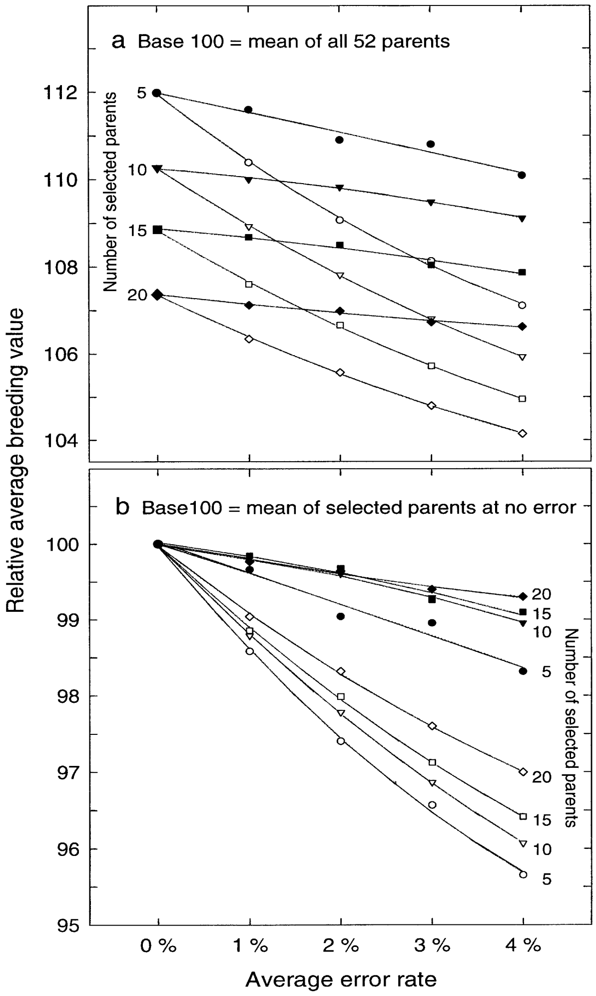

Fig. 2a and b. – Selection based on ranking for tree height breeding value estimates (BVs) at different misidentification error rates. Selection of the 5, 10, 15, or 20 best trees from 52 is shown. Filled symbols indicate zero-error BVs for the best ranked trees at the varied error rates. Open symbols are apparent BVs at the varied error rates. The sample point trends are elucidated by means of second-degree least-square-fit polynomials.

Table 2. – BVs[a] of the best trees at no error compared with BV means and standard deviations[b] based on ranking after 25 repeated misidentification simulations. BVs are shown as deviations from the general mean of 52 parent trees at no error = 100.

Average error rate	Best 5 trees		Best 10 trees		Best 15 trees		Best 20 trees	
	Zero-error[c]	Apparent[d]	Zero-error	Apparent	Zero-error	Apparent	Zero-error	Apparent
0%	12.0	12.0	10.3	10.3	8.8	8.8	7.4	7.4
1%	11.6 (0.3)	10.4 (0.7)	10.0 (0.2)	8.9 (0.6)	8.7 (0.2)	7.6 (0.5)	7.1 (0.2)	6.3 (0.4)
2%	10.9 (0.6)	9.1 (0.8)	9.8 (0.4)	7.8 (0.6)	8.5 (0.3)	6.7 (0.5)	7.0 (0.2)	5.6 (0.4)
3%	10.8 (1.0)	8.1 (1.0)	9.5 (0.4)	6.8 (0.8)	8.0 (0.6)	5.7 (0.7)	6.7 (0.4)	4.8 (0.6)
4%	10.1 (1.0)	7.1 (1.1)	9.1 (0.9)	5.9 (0.9)	7.9 (0.5)	5.0 (0.7)	6.6 (0.4)	4.1 (0.6)

[a] Average estimated relative parent tree breeding value of height.

[b] Standard deviations in parentheses.

[c] Calculated from breeding values without error simulation.

[d] Calculated from breeding values after error simulation.

Discussion

Since an apparent effect of the pedigree errors of the kind studied here was a rise in $\hat{\sigma}^2_D$ and a drop in $\hat{\sigma}^2_A$, any surprisingly high estimate of dominance variance indicates that the results should be viewed with some caution. Even small levels of pedigree errors of the kind simulated here could explain abnormally low heritabilities or $\hat{\sigma}^2_A$ / $\hat{\sigma}^2_D$ ratios, but it would take moderate levels of errors to deteriorate the genetic gains from selection.

Cases where expected selection response tends to be unusually low may as well indicate identification errors, but this may well be less serious in the sense that selected trees should perform better than their BVs indicate. The important consequence is that, on average, identification errors will cause underestimation of the selection effect. Additionally, the standard errors in *table 2* indicate that with some unknown positive error rate one will often obtain BVs that deviate substantially from what should be found with correct tree identification.

Identification errors under testing conditions similar to those in this example should not inflate general genetic parameter estimates, except in the case of $\hat{\sigma}^2_D$. A general average identification error rate below 1% to 2% should not seriously affect the success of a breeding program based on additive genetic effects.

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Cloning Strategy for Chinese-fir *(Cunninghamia lanceolata* (LAMB.) HOOK.) Suggested by Early Test Results

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Abstract

Fifteen cuttings from each of 252 donors, originating from seedlings from a seed-orchard of an appropriate provenance were taken and rooted in spring 1991. The stecklings were planted in Hubei in a randomized complete-block design; seedlings from a local source were used as controls. About 15% of the least-desired clones were rogued from the test plantations in each of the third and sixth years.

It was found that: (1) the height, diameter and volume growth of the stecklings were consistently and significantly higher than those of the seedlings over the years; (2) the absolute growth difference between the seedlings and the stecklings increased with age dramatically; however, the gain as a percentage of current size decreased rapidly; (3) there were significant differences among clones and roguing raised the average performance of the steckling population; (4) early-late correlation coefficients in growth were low.

The results indicated that: (1) clonal selection can be done while timber-production plantations are growing, so that increases in later plantation performance and the development of clonal varieties can be achieved incrementally over time by roguing in the cutting orchard; (2) early selection of a very few clones is likely to be less effective than retaining more clones for later selection approaching or at rotation age; (3) a very few clones that have not been well studied should not be used in operational practice.

Key words: Cunninghamia lanceolata, clonal forestry, tree improvement.

Introduction

Chinese-fir (*Cunninghamia lanceolata* (LAMB.) HOOK.) is the most important timber species in southern China. Afforestation and reforestation of Chinese-fir by cuttings has been used for