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# SILVA FENNICA

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**Editorial Office** Unioninkatu 40 A, FIN-00170 Helsinki, Finland  
Phone +358 9 857 051, Fax +358 9 625 308, E-mail [silva.fennica@metla.fi](mailto:silva.fennica@metla.fi),  
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Progeny Trial Estimates of Genetic Parameters for Growth and Quality Traits in Scots Pine

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Matti Haapponen, Pekko Velling & Marjo-Leena Annila

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Estimates of individual heritability and genetic correlation are presented for a set of 10 growth and quality traits based on data from 16 Scots pine (*Pinus sylvestris* L.) progeny trials in Finland. Seven of the traits (tree height, stem diameter, crown width, Pilodyn value, branch diameter, branch angle and branch number) were objectively measured, whereas three traits (stem straightness, branching score and overall score) were assessed visually. The genetic correlations were mostly moderate or low, and favorable from the tree breeder's point of view. All variables related to tree size correlated relatively strongly and positively. Tree height exhibited a more favorable genetic relationship with the crown form traits than diameter, the latter showing positive correlation with branch diameter. Except for the slight negative correlation between branch angle and branch diameter, the branching traits were not notably correlated. The pilodyn value was positively correlated with stem diameter, reflecting negative correlation between diameter growth and wood density. The highest genetic correlations occurred among the two visually evaluated quality scores and branch diameter. All of the heritabilities were less than 0.4. Overall score, Pilodyn, branch angle, branching score and tree height showed the highest heritability.

**Keywords:** heritability, genetic correlation, progeny testing, Scots pine, wood quality  
**Author's address:** Finnish Forest Research Institute, Vantaa Research Centre, Bldg 118, FIN-01391 Vantaa, Finland. Fax +358 9 4570 5711. E-mail matti.haapponen@metla.fi  
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## Introduction

Together with total yield, wood quality is one of the most important targets of genetic selection in tree species used commercially in sawn-wood production. The greatest attention in breeding efforts, such as Scots pine (*Pinus sylvestris* L.), has been given to determining the value

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**Keywords** heritability, genetic correlation, progeny testing, Scots pine, wood quality

**Authors' address** Finnish Forest Research Institute, Vantaa Research Centre, Box 18, FIN-01301 Vantaa, Finland **Fax** +358 9 8570 5711 **E-mail** matti.haapanen@metla.fi

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## 1 Introduction

Together with total yield, wood quality is considered an important target of genetic improvement in tree species used commercially as sawn timber, such as Scots pine (*Pinus sylvestris* L.).

In Scandinavia, the number, size and quality of knots are the key factors determining the value of sawn goods (Nordic timber... 1995). Consequently, crown form and branch characteristics have received the greatest attention in breeding for quality in Scots pine. The first-generation

plus trees in Finland, for instance, were selected giving a strong emphasis on branch diameter and form of the living crown (Sarvas 1953). In progeny testing, the evaluation of form traits is usually postponed to the age of 10–20 years. At this age, trees are assumed to express a sufficient degree of genetic variation in traits affecting the final product value, for instance in branch diameter and angle, number of branches and wood density.

Selection for multiple goals is normally based on a linear model which combines genetic and economic information on a number of traits into an optimal index value (e.g. Hazel 1943, Falconer 1981, Adams and Morgenstern 1991). The construction of selection indices requires estimates of heritability and genetic correlation. However, genetic parameters are often not known or poorly estimated. In Scots pine, genetic parameter estimates for various traits have been reported in a number of studies, e.g. Ehrenberg (1963), Werner and Ericsson (1980), Pöykkö (1982), Velling (1982), Velling and Tigerstedt (1984), Andersson (1986), Eriksson et al. (1987), Velling (1988) and Haapanen and Pöykkö (1993). In the majority of studies, however, the estimates originate from just one or at the most only a few of experiments. This easily results in poor precision; estimates of genetic correlation especially are sensitive to a small number of genetic entries included in the analysis (Klein et al. 1973, Namkoong and Roberds 1974, Hodge and White 1992). Secondly, single-site heritabilities are usually biased (overestimated) due to the confounding of variance components for genotype-by-site interaction and the additive genetic variance (Zobel and Talbert 1984). Finally, applying the estimates obtained in one study to other situations is usually difficult since the same traits are often assessed in slightly different ways, and the reference populations examined may also not be the same. To address these problems, the aim of this study was to obtain reliable estimates of genetic parameters for the normal growth and quality traits utilising comprehensive experimental data from 16 progeny trials of Scots pine. The main emphasis was placed on between-trait genetic correlations as they are much less well known in Scots pine than the heritabilities of individual traits.

## 2 Material and Methods

### 2.1 Material

Sixteen Scots pine progeny trials located in southern Finland were assessed for a varying number of growth and quality traits. Most of the assessments were made late in the 1980's. The age of the trees ranged from 11 to 24 years at the time of assessment (Table 1). The main body of the material consisted of open-pollinated families of first-generation Scots pine plus trees. The family structure was unique in each progeny trial, except in the two pairs of replicated trials (329/1–2, and 428/1–2). A few parent trees were represented in more than one trial. All the trials were laid out using a randomized complete block design. The typical plot configuration was a plot with 25 trees arranged in 5 × 5 contiguous plots.

The selection of trees for assessment was carried out systematically. The sampling practice and the number of trees selected per plot varied in the different trials but a couple of main rules were followed. If the trees had been planted in easily identifiable rows, trees were sampled along the diagonal axis of the plot (i.e. 5 trees on 25-tree square plots); otherwise, every fifth tree on a plot was assessed. Damaged or exceptionally small trees were disregarded as potential outliers.

### 2.2 Traits

Table 1 lists the traits assessed in each trial. Of the traits, only tree height, stem diameter, branch diameter, branch angle, branch number and Pilodyn value were assessed in almost all of the trials. Branch diameter and angle were recorded on the thickest branch in two whorls that located approx. at height of 1.3 m. The branch number was counted on the same two whorls. Wood density was assessed on the northern and southern sides of the stem at breast height, using Pilodyn Wood Tester. The two observations obtained for each of the branching traits and the Pilodyn value, were averaged and treated as a single observation.

Stem straightness, branching and overall quality were assessed visually in 3–6 trials (Table 1).



**Table 1.** Summary of the progeny trials and the assessed traits. The number of blocks is given as the harmonic mean per entry. The codes for the traits are as follows: H = Tree height (dm), D = Stem diameter (mm), CW = Maximum crown width (dm), BD = Branch diameter (mm), BA = Branch diameter (mm), BA = Branch angle (degrees), NB = Number of branches in a whorl, BR = Branching (1–5 score), ST = Straightness (1–5 score), OS = Overall score (1–10 score). PV = Pilodyn value (mm).

Trial	Planted, year	Assessed, years	Entries	Blocks	Type of trial	Spacing	H	D	CW	Overall means of the traits assessed									
										BD	BA	NB	BR	ST	OS	PV			
277/1	1969	17	12	12.0	Forestry trial	2 × 2	58.3	83.0	-	20.8	64.4	6.2	-	-	-	-	22.3		
329/1	1970	16	47	3.0	Forestry trial	2 × 2	51.1	83.7	-	20.4	62.5	5.8	-	-	-	-	20.1		
329/2	1970	16	47	3.0	Forestry trial	2 × 2	58.0	87.7	-	19.5	61.4	6.1	-	-	-	-	20.1		
347/1	1969	24	23	13.5	Forestry trial	2.5 × 2.5	-	145.0	-	19.3	68.6	-	-	-	-	-	18.7		
349/1	1970	20	32	4.0	Forestry trial	2 × 2	59.7	85.4	-	18.5	75.0	5.5	-	1.1	-	-	20.8		
369/1	1970	16	21	3.9	Forestry trial	2 × 2	63.5	99.8	-	20.0	68.5	5.6	-	-	-	-	21.3		
377/1	1969	17	17	5.8	Forestry trial	2 × 2	59.4	89.9	-	18.3	72.0	6.1	-	-	-	-	21.0		
392/1	1972	20	32	4.0	Forestry trial	2 × 2	62.4	86.9	-	16.9	72.7	5.3	-	1.1	-	-	19.9		
418/1	1973	13	25	4.0	Forestry trial	2 × 2	43.9	76.0	-	21.7	67.2	5.7	-	-	-	-	21.6		
423/1	1973	17	28	4.0	Forestry trial	2 × 2	48.6	78.0	21.5	17.2	67.3	3.7	-	-	-	-	-		
428/1	1973	16	25	3.9	Forestry trial	2 × 2	57.6	94.0	-	22.1	73.3	5.4	3.2	1.3	-	3.2	21.1		
428/2	1973	16	25	5.0	Forestry trial	2 × 2	65.3	101.1	-	19.4	76.5	5.4	3.2	1.5	-	3.1	21.4		
429/1	1973	17	19	3.2	Forestry trial	2 × 2	56.6	97.6	-	19.7	68.2	5.2	3.5	1.5	-	3.4	21.8		
553/1	1976	14	30	6.0	Test orchard	0.9 × 0.9	55.0	52.0	-	12.6	58.9	6.0	-	-	-	-	28.8		
572/1	1978	11	39	6.0	Test orchard	0.75 × 1.5	46.8	64.0	13.2	19.3	72.5	7.1	-	-	-	-	-		
594/1	1977	12	106	3.9	Test orchard	1 × 1	31.2	31.6	-	10.9	73.7	5.0	-	1.4	-	-	-		

Straightness and branching were recorded using a five-point subjective (1–5) scoring system in which class 1 represents “straight bole” or “very small number of branches” and class 5 “very crooked bole” or “very many branches”, respectively. The variable ‘overall score’ had 10 classes (1 for excellent and 10 for the most inferior phenotype). The categorical traits were analysed in the same way as the other traits.

### 2.3 Methods

Prior to further data processing, all unimproved check seedlots and full-sib families were deleted. The remaining families raised from open-pollinated seed orchard seed were assumed to have a half-sib structure with a coefficient of relationship of 0.25.

Individual heritabilities were estimated for all trials and traits using the formula

$$h_{ind}^2 = \frac{\sigma_f^2}{0.25(\sigma_f^2 + \sigma_{fb}^2 + \sigma_w^2)} \quad (1)$$

The three variance components denote family ( $\sigma_f^2$ ), family  $\times$  block ( $\sigma_{fb}^2$ ) and within-plot ( $\sigma_w^2$ ) effects. The standard errors of the heritability estimates were calculated using the formula of Becker (1984, page 48).

The formula used for calculating genetic correlations ( $r_G$ ) between all pairs of traits,  $i$  and  $j$ , was:

$$r_{G(ij)} = \frac{0.5(\sigma_{f(i+j)}^2 - \sigma_{f(i)}^2 - \sigma_{f(j)}^2)}{\sigma_{f(i)} \sigma_{f(j)}} \quad (2)$$

where  $\sigma_{f(i+j)}^2$  denotes the family variance component estimated for the sum of the two variables (Williams and Matheson 1994). The MIXED procedure of the SAS statistical package (SAS Institute Inc. 1992) was used to derive REML estimates of all the variance components.

Since single-site estimates of heritability are upward biased, the estimates were pooled in order to obtain a more reliable single estimate. No interdependence was observed between the genetic parameter estimates and the age of the trials. Hence, the pooling was done across the trials irrespective of the age. The varying precision of the

trials was taken into account by weighting each single-site heritability by the inverse of its variance as outlined by Borralho et al. (1992). The genetic correlations were also averaged across the trials. In this case, the inverse of the number of families analysed per trial was used as the weighting factor. Before averaging, individual correlations having a value beyond the theoretical boundaries, were set to either  $-1.00$  or  $+1.00$ . In addition, if the standard error of a single-site family variance component ( $\sigma_{f(i)}^2$  or  $\sigma_{f(j)}^2$ ) exceeded the value of the variance component itself, the variance component was assigned a missing value in order to eliminate its biasing effect on the pooled estimates.

### 3 Results

The genetic correlations and the individual level heritabilities are presented in Tables 2 and 3, respectively. In general, the heritabilities, as well as most of the averaged correlations, were either moderate or low. The highest genetic correlation was found between the branching and overall scores ( $r_G = 0.90$ ). Both of these traits reflected variation in branch diameter ( $r_G = 0.79$  and  $r_G = 0.83$ , respectively) and tree height ( $r_G = -0.57$  and  $-0.63$ ).

Of the other quality traits, the branch diameter and angle were loosely associated ( $r_G = -0.27$ ). Branch number and stem straightness, in turn, exhibited low genetic correlations with all of the other traits. The Pilodyn value was also rather independent of the other traits, showing notable correlation only with stem ( $r_G = 0.45$ ) and branch diameter ( $r_G = 0.40$ ).

The tree size variables (height, stem diameter, branch diameter and maximum crown diameter) were all positively correlated,  $r_G$  ranging from 0.08 to 0.77. The two standard growth traits assessed in the progeny trials, namely tree height and stem diameter, showed markedly dissimilar genetic relationships with the individual quality traits. For instance, stem and branch diameter showed a fairly high correlation ( $r_G = 0.43$ ), whereas tree height and branch diameter had a genetic correlation of only 0.11. Moreover, contrary to height, diameter was not highly correlat-



ed with the visual branching and overall scores.

The weighted averages of the heritability estimates fell by between 0.06 and 0.33, being consistently smaller than the respective unweighted averages. The variation among the single-site estimates of heritability was considerable (Table 3). The traits with the highest heritabilities were overall score (0.33), Pilodyn value (0.28), branch angle (0.27), branching score (0.26) and tree height (0.24). Stem and branch diameter, branch number and straightness score, in turn, were the least heritable traits. Standard errors of the single-site heritabilities were mostly between 0.10 and 0.20, whereas those for the weighted means were in the range 0.01 to 0.12 (Table 3). Test orchard trial No. 553/1 showed exceptionally high heritabilities for almost all the traits, otherwise there was no sign of any consistent difference in the magnitude of the heritability estimates between the test orchards and the conventional forestry trials.

## 4 Discussion

The additive genetic relationships between the traits were mostly neutral or favorable for tree breeding, suggesting relatively straightforward selection for multiple objectives. The pooled heritability estimates were between 0.1 and 0.3, which is in perfect consistency with the results of Cornelius (1994), who reviewed heritability values from 67 separate studies. Of the growth traits, tree height had a relatively high heritability and was also more advantageously associated with stem quality than diameter. Among the quality traits, the Pilodyn value and branch angle showed the highest heritability, as noted in many earlier studies (Ehrenberg 1963, Velling and Tigerstedt 1984, Velling 1988). Thus, tree height together with a couple of additional traits, such as branching score and Pilodyn value could probably be incorporated to form an effective selection index. Unrestricted selection for stem diameter or volume alone, in turn, would most likely result in severe deterioration of branch quality and consequent loss of economic gain (e.g. King et al. 1992, Haapanen and Pöykkö 1993).

Visual assessment of stem quality has lately

received much attention in Finland as a cost-effective alternative to laborious measurement of a large number of individual branching and form traits (Venäläinen et al. 1995). Visual grading covers many more traits than can easily be measured and incorporated into a selection index. In this study, the overall score and branching score had somewhat higher heritability than the measured traits. Moreover, in spite of their close interrelationship with branch diameter, the score traits showed negative, and thus favorable, correlation with tree height and stem diameter, whereas the respective correlation between branch diameter and growth traits was strongly positive. These results, although based on three trials only, encourage continued study of the use of visual scoring in connection with advanced generation selection.

Stem straightness exhibited notably lower heritability than the other two score traits. Possible reasons for this are low phenotypic variation or an insufficient number of categories used for scoring, a question discussed by Raymond and Cotterill (1990). The former explanation is more probable, since the mean score value in the six trials assessed for straightness varied between 1.1 and 1.5 (Table 1). In other words, the scorers had placed most of the trees in the best two categories. It is important to note that all score traits were assessed using an absolute rather than a site-specific scale. Williams and Lambeth (1989) discussed the pros and cons of both systems, and concluded that an absolute score is more effective than a relative one, when genetic expression of the assessed trait varies widely across test sites. Using a site-specific scale, as supported by Cotterill and Dean (1990), could quite possibly have resulted in higher heritability for stem straightness.

The pooled estimates of genetic parameters presented here were based on by far the largest number of Scots pine trials and families analysed for this purpose so far. Thus, we believe they are much more precise than the sort of single-site estimates commonly published. Even so, many of the pooled estimates that were based on a small number of observations (trials) are likely to be relatively imprecise. This especially concerns the estimates of genetic correlation that showed much variation among the trials. In ad-

**Table 2.** Genetic correlations between growth and quality traits in 16 Scots pine progeny trials. The means and standard deviations were weighted by the number of families in each trial. Irrational estimates ( $-1 > r_G > 1$ ) were set to  $-1$  ja 1 before averaging. The codes for the traits are the same as in Table 1.

Trial	Age	H-D	H-CW	H-BD	H-BA	H-NB	H-BR	H-ST	H-OS	H-PV	D-CW	D-BD	D-BA	D-NB	D-BR	D-ST	D-OS	D-PV	CW-BD	CW-BA	CW-NB	BD-BA	
277/1	17	0.64		-0.64	-0.16	0.45				-0.32		-0.26	-0.40	0.55				-0.02					-0.07
329/1	16	0.89		0.13	-0.09	0.72				-0.50		0.34	-0.01	0.79				-0.51					-0.55
329/2	16	0.82		0.08	-0.01	0.71				0.20		0.43	0.07	0.58				0.51					-0.39
347/1	24											0.76	-0.43					0.49					-0.16
349/1	20	0.49		-0.56	0.56	-0.34		1.13		-0.21		-0.19	0.16	0.55		1.19		0.28					-0.25
369/1	16	0.76		0.34	0.16	0.79				0.48		0.74	-0.07	0.61				0.58					-0.24
377/1	17	0.79		0.11	0.36	0.51				-0.58		0.46	0.39	0.50				-0.42					0.10
392/1	20	0.26		-0.46	0.55	-0.43		0.31		0.10		0.21	0.02	-0.10		-0.37		0.41					-0.43
418/1	13	1.00		0.48	0.08	-0.70				0.14		0.30	-0.08	-2.36				0.23					-0.16
423/1	17	-0.43	0.10		-0.39	1.44					0.64		0.13	-3.64						0.14			-2.86
428/1	16	0.46		-0.55	-0.06	0.11	-0.81	0.67				-0.14	0.20	-0.02	-0.29	0.66	0.12	0.01					-0.16
428/2	16	0.57		-0.29	0.39	-0.13	-0.30	1.14	-0.43	-0.04		0.56	0.26	-0.03	0.45	0.91	0.29	0.62					0.00
429/1	17	0.86		-0.41	-0.26	0.02	-0.81	-0.84	-0.73	-0.11		-0.24	-0.49	-0.16	-0.72	-0.68	-0.64	0.15					-0.14
553/1	14	1.00		0.93	-0.17	0.58				1.01		0.95	-0.14	0.55				0.99					-0.23
572/1	11	0.88	0.44	0.65	0.03	0.12					0.31	0.77	-0.22	0.14					0.08	0.29			-0.67
594/1	12	0.81		0.34	0.06	0.02		-0.17				0.45	0.04	0.09		-0.22							-0.18
Weighted mean		0.77	0.44	0.11	0.10	0.26	-0.63	0.21	-0.57	0.00	0.45	0.43	-0.02	0.31	-0.14	-0.04	-0.03	0.26	0.08	0.23	-0.08	-0.27	
Weighted std		0.19		0.44	0.23	0.36	0.25	0.57	0.12	0.43	0.16	0.30	0.20	0.30	0.48	0.49	0.39	0.45		0.07			0.19

Table 2 contid.

Trial	Age	BD-NB	BD-BR	BD-ST	BD-OS	BD-PV	BA-NB	BA-BR	BA-ST	BA-OS	BA-PV	NB-BR	NB-ST	NB-OS	NB-PV	BR-ST	BR-OS	BR-PV	ST-OS	ST-PV	OS-PV
277/1	17	.	.	.	.	0.72	-0.29	.	.	.	-0.51	.	.	.	0.06	.	.	.	.	.	.
329/1	16	.	.	.	.	-0.40	0.33	.	.	.	0.26	.	.	.	-0.18	.	.	.	.	.	.
329/2	16	.	.	.	.	0.43	0.05	.	.	.	0.08	.	.	.	0.29	.	.	.	.	.	.
347/1	24	.	.	.	.	0.01	.	.	.	.	-0.12	.	.	.	.	.	.	.	.	.	.
349/1	20	.	.	0.30	-0.02	-0.22	-0.25	.	0.82	.	0.08	.	-0.24	.	0.35	.	.	.	.	-0.14	.
369/1	16	.	.	.	.	0.58	0.59	.	.	.	0.08	.	.	.	0.22	.	.	.	.	.	.
377/1	17	.	.	.	.	-0.08	0.06	.	.	.	0.33	.	.	.	-0.36	.	.	.	.	.	.
392/1	20	.	.	0.18	0.07	0.39	0.24	.	0.18	.	0.06	.	-0.64	.	-0.23	.	.	.	.	.	-0.12
418/1	13	.	.	.	.	-0.16	-0.05	.	.	.	-0.30	.	.	.	0.42	.	.	.	.	.	.
423/1	17	.	.	.	.	-2.61	-0.03	.	.	.	.	.	.	.	.	.	.	.	.	.	.
428/1	16	0.68	.	-0.19	0.97	0.33	-0.03	-0.06	0.61	0.29	0.12	-0.42	0.05	-0.65	-0.17	-0.34	0.82	0.45	0.00	-0.20	0.78
428/2	16	0.93	.	0.16	0.91	0.45	0.25	-0.27	0.34	-0.40	0.10	0.24	-0.23	0.30	-0.48	-0.19	1.01	0.42	-0.28	-0.09	0.25
429/1	17	0.75	.	0.50	0.55	0.18	0.37	-0.18	-0.04	0.05	0.53	-0.21	0.00	-0.23	0.11	0.82	0.87	-0.04	0.76	0.47	0.38
553/1	14	.	.	.	.	0.93	0.08	.	.	.	-0.04	.	.	.	0.54	.	.	.	.	.	.
572/1	11	.	.	.	.	-0.31	-0.05	.	.	.	.	.	.	.	.	.	.	.	.	.	.
594/1	12	.	.	.	.	-0.05	-0.19	.	0.31	.	.	.	-0.11	.	.	.	.	.	.	.	.
Weighted mean		0.07	0.79	-0.04	0.83	0.21	0.04	-0.17	0.36	-0.02	0.07	-0.12	-0.12	-0.19	0.06	0.04	0.90	0.30	0.11	-0.05	0.48
Weighted std		0.31	0.11	0.20	0.18	0.40	0.23	0.09	0.23	0.30	0.21	0.29	0.09	0.41	0.32	0.49	-	0.22	0.42	0.22	0.24

**Table 3.** Estimates of individual narrow sense heritability and their standard error in the 16 Scots pine progeny trials. Listed on the bottom lines are: Unweighted mean ( $h^2_{\text{unweighted}}$ ) and standard deviation (std) of the single-site heritabilities, weighted mean of the single-site heritabilities ( $h^2_{\text{weighted}}$ ) and its standard error (s.e. ( $h^2$ )).

Trial	Tree height	Stem diam.	Crown width	Branch diam.	Branch angle	Branch number	Branching	Straightness	Overall score	Pilodyn
277/1	0.37 ± 0.17	0.09 ± 0.06	.	0.10 ± 0.07	0.60 ± 0.24	0.14 ± 0.08	.	.	.	0.11 ± 0.07
329/1	0.73 ± 0.17	0.29 ± 0.11	.	0.15 ± 0.09	0.21 ± 0.09	0.32 ± 0.11	.	.	.	0.51 ± 0.14
329/2	0.47 ± 0.14	0.20 ± 0.09	.	0.38 ± 0.12	0.28 ± 0.11	0.31 ± 0.11	.	.	.	0.59 ± 0.15
347/1	.	0.52 ± 0.21	.	0.15 ± 0.13	0.36 ± 0.18	.	.	.	0.57 ± 0.22	.
349/1	0.57 ± 0.17	0.06 ± 0.07	.	0.18 ± 0.09	0.22 ± 0.10	0.15 ± 0.09	.	0.10 ± 0.07	.	0.44 ± 0.14
369/1	0.35 ± 0.14	0.23 ± 0.11	.	0.45 ± 0.17	0.49 ± 0.17	0.12 ± 0.08	.	.	.	0.30 ± 0.13
377/1	0.54 ± 0.20	0.20 ± 0.11	.	0.20 ± 0.11	0.43 ± 0.18	0.34 ± 0.15	.	.	.	0.31 ± 0.15
392/1	0.34 ± 0.13	0.11 ± 0.08	.	0.11 ± 0.08	0.20 ± 0.10	0.06 ± 0.07	.	0.33 ± 0.12	.	0.18 ± 0.09
418/1	0.54 ± 0.17	0.34 ± 0.13	.	0.18 ± 0.09	0.69 ± 0.20	0.03 ± 0.05	.	.	.	0.23 ± 0.10
423/1	0.06 ± 0.07	0.08 ± 0.08	0.10 ± 0.08	0.00 ± .	0.12 ± 0.09	0.00 ± 0.06	.	.	.	.
428/1	0.64 ± 0.20	0.12 ± 0.09	.	0.18 ± 0.10	0.56 ± 0.19	0.12 ± 0.09	0.24 ± 0.12	0.26 ± 0.13	0.36 ± 0.15	0.40 ± 0.16
428/2	0.41 ± 0.15	0.17 ± 0.09	.	0.26 ± 0.11	0.73 ± 0.21	0.18 ± 0.09	0.31 ± 0.12	0.11 ± 0.08	0.29 ± 0.12	0.54 ± 0.17
429/1	0.52 ± 0.21	0.12 ± 0.11	.	0.27 ± 0.15	0.76 ± 0.26	0.25 ± 0.15	0.23 ± 0.14	0.31 ± 0.16	0.36 ± 0.18	0.38 ± 0.18
553/1	0.77 ± 0.20	0.60 ± 0.18	.	0.80 ± 0.21	0.33 ± 0.13	0.58 ± 0.17	.	.	.	0.90 ± 0.22
572/1	0.45 ± 0.14	0.19 ± 0.09	0.33 ± 0.12	0.17 ± 0.09	0.43 ± 0.13	0.33 ± 0.12	.	.	.	.
594/1	0.38 ± 0.06	0.21 ± 0.04	.	0.10 ± 0.03	0.34 ± 0.05	0.14 ± 0.03	.	0.11 ± 0.03	.	.
$h^2_{\text{unweighted}}$	0.48	0.22	0.22	0.24	0.42	0.21	0.26	0.20	0.34	0.42
std	0.17	0.15	0.16	0.18	0.20	0.15	0.04	0.11	0.04	0.21
$h^2_{\text{weighted}}$	<b>0.24</b>	<b>0.14</b>	<b>0.14</b>	<b>0.14</b>	<b>0.27</b>	<b>0.06</b>	<b>0.26</b>	<b>0.12</b>	<b>0.33</b>	<b>0.28</b>
s.e. ( $h^2$ )	0.03	0.01	0.07	0.02	0.03	0.01	0.07	0.05	0.12	0.03

dition, the fact that the trials were assessed at different ages, may result in some bias. We are not aware of any published results on age trends of genetic parameters for quality traits in Scots pine. However, as no age trends were observed in this study, the bias was assumed to be negligible.

We suggest that these estimates should assist tree breeders in planning a multiple-goal selection strategy for Scots pine in Finland. They can also be used directly to derive the genetic variances and between-trait covariances that are required as input values in traditional selection index matrices (Becker 1984). Computation of specific indices was considered to be beyond the scope of this study, since they commonly depend not only on genetic parameters, but also on the relative contribution of individual juvenile traits to the net economic value of the end product, about which rather little is known.

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