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High heritability for heartwood in north Swedish Scots pine

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Abstract In 44-year-old full-sibs of north Swedish Scots pine (*Pinus sylvestris* L.), the estimated heritability of heartwood diameter was 0.5 despite the influence of environmental changes (caused by an earlier thinning) which apparently had reduced the heritabilities of height and diameter to around zero. The heritability of bole straightness was estimated to be 0.6. The coefficient of additive genetic variation of heartwood diameter was estimated at 0.2. If a reliable 'heartwood-meter' becomes available that allows nondestructive measurements to be rapidly made in the field it should be possible to breed for or against heartwood formation with less effort compared with that required in breeding aimed at improving regular production traits.

Key words Bole straightness · Heartwood diameter · Increment core · *Pinus sylvestris* L. · REML estimation

Introduction

The properties of pine heartwood differ distinctly from those of sapwood, the former being less suitable for pulping but more suitable for use in construction and carpentry. Despite these important differences, however, the genetics of heartwood formation in Scots pine (*Pinus sylvestris* L.) has received little attention. By contrast, the genetic background of heartwood content and other wood properties in *Pinus radiata* D. Don (e.g. Cown et al. 1992) have been studied in greater detail.

Our aim in the study presented here was to estimate genetic parameters related to heartwood content and to compare them with certain other growth traits in a Scots pine progeny test about midway through the rotation (44 years). The results complement those obtained in a younger (25 year) full-sib progeny test and provide a basis for comparison (Fries and Ericsson 1998). These previous results suggested, among other things, that being less modified by the environment heartwood diameter has a higher heritability than total stem diameter. In terms of heritability, heartwood diameter and tree height were found to be quite similar.

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Materials and methods

The full-sib progeny test plantation and the data collection

The experimental plantation on former farm land was a progeny test[1] carried out with 11 full-sib families and two full-sib family mixtures. The parents and their progenies are described in Table 1. The controlled crossings were carried out in 1951. The resulting seeds were collected in autumn 1952 and sown in spring 1953, and seedlings were outplanted 1955. The irregular crossing-scheme derives its origin from the eagerness to instantly plant experiments with seedlings from early successful controlled crossings. This experimental plantation is one of the very first ones established in north Sweden with controlled crosses of Scots pine suited for genetic evaluation.

Each progeny was represented by 7×7 seedling plots with a 2×2-m spacing arranged as randomized blocks with three replicates. In late 1991, when the trial was assessed and marked for thinning, 27 original trees/plot remained, on average. The high

[1] 'S23F551153 Storbränna' at 63°07′N, 17°E on 150 m elevation, testing a few parent trees from the earliest Swedish selections

Table 1 Parental data and design matrix entries revealing known parents of full-sib families as well as probabilities of parentships in mixes of full-sib families estimated from available records of seedling numbers ('parent weights'). Dots represent zeroes

Parent number	Label	Latitudinal origin (N)	Family identity number[a]												
			1	2	4	5	6	7	8	9	10	17	25	43	44
Mother tree															
1	W4007	61°19′	·	·	·	·	·	·	·	·	·	1	·	·	·
2	AC1012	64°56′	1	·	·	·	·	·	·	·	·	·	·	·	·
3	Y487	62°26′	·	1	·	·	·	·	·	·	·	·	·	·	·
4	Y3064	62°26′	·	·	·	1	·	·	1	·	·	·	·	·	·
5	Z160	62°57′	·	·	·	·	·	1	·	1	1	·	·	·	·
6	Z3008	64°12′	·	·	1	·	·	·	·	·	·	·	·	·	·
7	Z18	64°16′	·	·	·	·	1	·	·	·	·	·	·	·	·
8	Bg123	61°34′	·	·	·	·	·	·	·	·	·	·	1	·	·
9	Bg120	61°34′	·	·	·	·	·	·	·	·	·	·	·	·	1/3
10	W3202	61°35′	·	·	·	·	·	·	·	·	·	·	·	·	1/3
11	Bg122	61°34′	·	·	·	·	·	·	·	·	·	·	·	2/5	1/3
12	Bg44	61°08′	·	·	·	·	·	·	·	·	·	·	·	1/5	·
13	Bg45	61°08′	·	·	·	·	·	·	·	·	·	·	·	2/5	·
Father tree															
14	Y273	63°30′	·	·	1	·	1	·	·	·	1	·	1	·	1
15	Y3004	63°35′	1	1	·	·	·	·	1	1	·	1	·	·	·
16	BD139	67°10′	·	·	·	1	·	1	·	·	·	·	·	1	·

[a] 1–25, 11 full-sib families; 43, 44, mixtures of full-sib families

mortality (44%) was caused mainly by vole damage to young seedlings. The thinning, which was carried out in the subsequent winter, resulted in an average density of 17.4 trees per 14 × 14-m plot.

In October 1996, at a tree age of 44 years[2], increment cores to be used for heartwood measurements were extracted at 130 cm above the ground from 4 sample trees from each of the progenies (for two of them 5 and 8 trees, respectively, were used). Basically 2 sample trees per plot were chosen more or less at random from two of the replications (57 sampled trees in total).

Trees with visible growth disturbances manifested as forking, severe trunk crooks, etc. were rejected. The cores were taken from an invariable direction; care was taken to assure that the pith and most of the sapwood on the opposite side was included in the cross-section. If the extracted increment core revealed any degree of growth disturbance at a lower age, another sample tree was chosen.

Total tree height (m) as well as clear bole height (m) and bole diameter at 130 cm above ground (mm) were also recorded. The bole was straight or slightly bent. None of the sample trees was severely curved. The frequency of straight trees was 0.62 (16/26) in block 1 and 0.65 (20/31) in block 2.

The increment cores were stained with sulfanilic acid saturated with sodium nitrite (Cummins 1972) in order to distinguish the heartwood from the sapwood. They were subsequently placed in paper tubes and dried at room temperature for about a day, whereupon the exact borders between the heartwood and sapwood were marked with a pen. Cores were kept chilled (+ 8°C) in open tubes prior to measurement, when the lengths of the sections of sapwood and heartwood were measured with an accuracy of ± 0.1 mm. The 'heartwood diameter', that is, the sum of the opposite heartwood sections on each side of the pith, was further analyzed for this study. It varied between 23 and 113 mm and averaged 70.5 mm.

The 1991 diameter (mm) and height (dm) assessments were used for comparison. Diameters of all trees were recorded, whereas heights were only registered for sample trees. The same number of trees was sampled in each of the three blocks.

[2] Growing seasons from seeding

Parameter estimation

In biological terms, a phenotypic value (P) was assumed to consist of $P = A + E$, where A is the additive genetic effect (breeding value), and E is an independent environmental effect. Dominance deviations and other genetic effects were assumed to be negligible since pilot analyses indicated that our data were insufficient to support a more detailed model. The phenotypic variance was assumed to split up correspondingly into $\sigma_P^2 = \sigma_A^2 + \sigma_E^2$ where σ_E^2 represents both environmental and non-additive genetic variation.

The statistical analyses for individual traits were carried out according to the mixed model equation $\mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{e}$. In all but two cases $\mathbf{y}$, the observation vector, had four entries per family that had been assessed in 1996 (more trees in the 1991 data; cf. Table 2). $\mathbf{X}$ is the design matrix corresponding to the fixed block effects $\mathbf{b}$, and $\mathbf{Z}$ is the design matrix with rows according to the corresponding parentship columns in Table 1. The random parent effects of $\mathbf{u}$ (with element u_p for parent p) and the random residual effects of $\mathbf{e}$ were assumed to have independent normal distributions with zero means and common variances of σ_u^2 and σ_e^2, respectively. Estimates of σ_u^2 and σ_e^2 were computed using a restricted maximum likelihood (REML) procedure (Searle et al. 1992).

Heritabilities according to $h^2 = \sigma_A^2/\sigma_P^2$ were estimated using $\hat{\sigma}_A^2 = 4\hat{\sigma}_u^2$ where $A_p = \mu + 2u_p$ is the additive breeding value of parent tree p, and $\hat{\sigma}_P^2 = 2\hat{\sigma}_u^2 + \hat{\sigma}_e^2$ since each entry in $\mathbf{y}$ is a phenotypic value of an individual tree with two assumed-to-be-unrelated parents (μ is the general mean). An environmental (including genetic residual) variance estimate can be computed using $\sigma_E^2 = \sigma_P^2 - \sigma_A^2$. Standard errors of the parameter estimates were calculated using variance/covariance estimates for $\hat{\sigma}_u^2$ and $\hat{\sigma}_e^2$ and the delta "technique" (Bulmer 1980), i.e., using series expansion of the functions of $\hat{\sigma}_u^2$ and $\hat{\sigma}_e^2$.

The frequencies of stem straightness classes were used to compute the corresponding class values as 'normal scores', i.e. "optimal

Table 2 Trait mean values ($\bar{y}$) and number of sampled trees (N) along with estimates of phenotypic variances (σ_P^2), additive genetic variances (σ_A^2 with standard errors), heritabilities ($h^2 = \sigma_A^2/\sigma_P^2$, with standard errors), and genetic coefficients of variation ($CV_A = \sigma_A/\bar{y}$)

Trait	N	($\bar{y}$)	σ_P^2	σ_A^2	h^2	CV_A
Heartwood 1996 (mm)	57	70.3	265	145 ± 118	0.54 ± 0.35	0.17
Diameter 1991 (mm)						
• Before thinning[a]	1092	175.5	1565	144 ± 97	0.09 ± 0.06	0.07
• After thinning[a]	690	184.9	1218	178 ± 123	0.15 ± 0.09	0.07
• Of trees sampled in 1996	57	186.2	451	61 ± 84	0.13 ± 0.18	0.04
Diameter 1996 (mm)	57	198.1	408	13 ± 60	0.03 ± 0.15	0.02
Height 1991 (dm)						
• Before thinning[b]	64	127.9	120	31 ± 43	0.26 ± 0.32	0.04
• After thinning[c]	45	128.8	105	46 ± 51	0.44 ± 0.41	0.05
Height 1996 (dm)	57	151.6	124	0[e]	0	0
Clear bole height 1996 (dm)	57	80.4	71	0[e]	0	0
Bole straight/not straight[d]	57	0	0.71	0.45 ± 0.35	0.63 ± 0.36	–

[a] All trees were measured
[b] Measured on trees sampled in 1991
[c] Nineteen of the trees sampled in 1991 were cut
[d] Two classes transformed into 'normal scores'
[e] Impossible to estimate, assumed to be zero

scores" according to Gianola and Norton (1981), before variance estimation.

Results

Table 2 summarizes the parameter estimates from the 44-year (1996) as well as 39-year (1991) data. The results show high heritability estimates for heartwood diameter, and that for stem straightness was even higher. Additionally, the highest coefficients of additive genetic variation were estimated for heartwood. Heritabilities of tree height were substantial at a tree age of 39 years before and after thinning according to estimates based on heights of trees sampled before thinning, but they were seemingly close to zero for tree height as well as clear bole height when based on the sample 5 years later. The diameter heritability estimates also declined substantially from age 39 to age 44. However, the standard errors of the estimated variances and heritabilities indicate that the results should be interpreted with some caution.

Discussion

Due to the great age of this experimental plantation, little information is available regarding the establishment procedures used. There is, however, no reason to question the reliability of the original seedling identifications or the identification correctness in the latest assessments. Orientation within the plots was easy owing to the very regular spacing. The only complication involved the two family mixes outplanted, each with a common father tree. Even though the mother of each individual progeny tree (seedling) was not recorded within 'mixed plots', the number of seedlings per mother was still recorded, providing a base for inclusion of the corresponding fractions as 'motherhood probabilities' in the analysis (Table 1).

The sampled trees represent a population after certain selection. First, the thinning operation initiated in 1991, to a certain extent, strived against uniformation of the experimental area like any regular forest stand. On the other hand, the diameter and height results from 1991 (Table 2) indicate the contrary, since heritabilities were increased somewhat by thinning instead of being reduced. Second, the procedure used for selecting sample trees favored normally developed boles of sufficient diameter. That phenotypic evening-out may to some extent reflect genetic parameter estimates. There was, however, no direct selection for or against heartwood formation, and our interest was focused on the unseen variation regarding heartwood revealed in the increment core samples. Thus, we assume that systematic selection only had a minor influence on the results compared with common sampling errors, amplified by the limited sample sizes and experimental circumstances like the irregular crossing-scheme.

The thinning operation carried out naturally altered the environmental conditions substantially for individual trees, apparently concealing the genetically determined differences in growth potential when studied 5 growing seasons later. Thus, diameter heritability was very low 5 growing seasons later. Furthermore, there was no evidence that tree height was heritable in the 1996 sample.

The comparability between the assessments should be given careful consideration while inspecting means and parameter estimates before and after thinning in 1991 as well as in 1996. The fact that only two blocks were sampled in 1996 might have contributed to the change in variation that seemed to occur between 1991 and 1996. The corresponding comparison between heights is harder to make since different trees were sampled at the two points of time.

We believe that any bias in heritability estimates due to the sampling procedure is negligible compared with sampling error. Thus, notwithstanding the inaccurate sampling, the reductions in diameter and height heritabilities over the 5-year-period indicate that the environment has substantial influence on individual-tree growth-related traits. By contrast, the high heartwood heritability estimated in 1996, which exceeded that for tree height in 1991, supports the suggestion that heartwood formation provides less room for environmental modification than is the case for 'ordinary' growth traits. The variation in tree height could have also been influenced by the abundant vole and moose damage sustained by younger seedlings, thereby obscuring the genetic effects on growth, which did not seem to be the case for the heartwood.

In a recent study, Mörling and Valinger (1998) showed that the yield increment over the 12-year period following the thinning and/or fertilization of a 45-year-old Scots pine stand on a north Swedish site was accounted for mainly by sapwood expansion, the contribution of heartwood 'growth' being insignificant. Their findings are in good accordance with the present results.

The fact that heartwood diameter and bole straightness were the only traits that appeared to show substantial heritability in the 1996 data suggests that heartwood formation resembles a quality trait in terms of its genetic control and is not closely associated with growth. Nor do our results contradict the suggestion by Mörling and Valinger (1998) that heartwood is formed as a consequence of aging rather than being actively regulated in accordance with changing growth conditions.

An important conclusion is that if a reliable 'heartwood-meter' becomes available that allows measurements to be rapidly made in the field it should be possible reduce the effort required to breed for or against heartwood formation to a level less than that required in breeding aimed at improving regular production traits. The meter should be hand-held and non-destructively measure the heartwood 'inner diameter' in the same way as, or combined with, an ordinary caliper device used for measuring 'outer diameter'. The need is accentuated by the fact that increment coring interferes with the process of heartwood formation in the nearby wood (e.g. Hillis 1987), which reduces possibilities for resampling. Regular progeny testing experiments within a breeding program cannot be based on a destructive sampling design owing to the high costs and large area required. Resampling is a prerequisite for high accuracy and for monitoring the process of heartwood formation in time and (wood-)space which is still not well understood.

In conclusion, the estimated heritability of heartwood diameter, as measured on 44-year-old Scots pines, was remarkably high. The results were in accordance with our study on 25-year-old trees (Fries and Ericsson 1998) and thus noteworthy despite the small sample sizes and substantial sampling errors.

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