GENETIC CORRELATIONS OF HEARTWOOD EXTRACTIVES IN *PINUS SYLVESTRIS* PROGENY TESTS

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ABSTRACT

Estimates of additive genetic correlations (r_A) between wood extractive concentrations in heartwood of Scots pine (*Pinus sylvestris* L.) at two sites in northern Sweden were found to be high, on average, while their genetic correlations with tree growth were less clear. In a full-sib 25-year-old progeny test, r_A was estimated to be about 0.7 between pinosylvins and resin acid contents, and about 0.9 between specific compounds within the pinosylvin and resin acid groups. The saturated fatty acid contents were also correlated with pinosylvins and resin acid contents (r_A = 0.4 to 0.8), while genetic correlations involving unsaturated fatty acids were lower, and less distinctly expressed. Concentrations of sterols were negatively correlated ($r_A \approx -0.6$) with those of other wood extractives. Similar patterns were found, confirming these trends, in another, 44-year old, full-sib progeny test. The generally high heritabilities recorded for production of fungitoxic substances (pinosylvins and resin acids), and the apparent absence of negative genetic correlations with tree growth or heartwood formation, suggest that each of the studied traits could be considered for inclusion in commercial tree breeding programs.

Keywords: fatty acid, genetic correlation, heartwood, heritability, pinosylvin, *Pinus sylvestris*, resin acid, Scots pine, sterol, wood extractive, wood durability

INTRODUCTION

This is the second part of a study concerning wood extractives in two full-sib Scots pine (*Pinus sylvestris* L.) progeny tests located in northern Sweden. The first part (FRIES *et al.* 2000) concentrated largely on heritabilities, while this paper deals primarily with genetic correlations between the amounts of pinosylvins, resin acids, fatty acids and sterols.

Wood extractives in the heartwood of pines (*Pinus spp.*) are of great importance for the natural durability of their wood, since many of these compounds have fungitoxic and water repellent effects (HART 1981, KENNEDY *et al.* 1995, GREF *et al.* 2000). Due to changes in environmental regulations, which have increased restrictions against the use of artificial wood preservatives, interest in natural fungitoxic substances has increased within the wood industry and forest research community. Scots pine, one of the most important tree species in Sweden, is widely used for construction and external woodwork. Thus, high contents of any wood extractives that increase resistance against pathogens should be advantageous. Once such compounds have been identified, breeding programs could be devised for producing higher quality wood for external timbers, and other programs to generate wood more suited to pulping. However, such plans require detailed knowledge of the genetic parameters that influence the contents of fungitoxic compounds in specific trees – as reported here. An earlier study on these progeny trials described key genetic parameters related to amounts of heartwood and growth traits (FRIES & ERICSSON 1998, ERICSSON & FRIES 1999). The variation of heartwood formation in Scots pine of different provenances has also been examined (FRIES 1999).

MATERIAL AND METHODS

The study examined full-sib progenies of plus trees selected for the Swedish Scots pine breeding program, intended for use in the central part of northern Swe-

den. Two field planted progeny tests were investigated: 'T25'[1], 25 growing seasons after seeding and 'T44' [2] after 44 growing seasons (corresponding to roughly one fourth, and half the rotation, respectively). The crossing scheme layouts and progeny tests (with randomised designs) have already been described in detail (FRIES & ERICSSON 1998, ERICSSON & FRIES 1999). For T25 (with a circulant partial diallel crossing scheme involving 50 parents), one tree from each of 160 full-sib families were sampled, while for T44 (with factorial crosses involving 8 mother and 3 father trees), four trees from each of 11 full-sib families were sampled. The sampling procedure, details concerning heartwood measurements, grinding of samples, extraction with acetone, and the gas chromatographic analyses of wood extractives, are described in our previous paper based on the same data (FRIES *et al.* 2000).

The abietic and pimaric resin acids include many chemotypes and isomers, and the different abietic acids are especially liable to interconversion during preparation of the wood samples. In contact with air, further oxidation may also occur (HEMINGWAY *et al.* 1971, ENOKI 1976). Therefore, standardised procedures and schedules were rigorously applied in preparing all the samples. Since the samples were collected within three weeks at site T25, and 2 days at site T44, any possible seasonal fluctuations were minimised. The wood extractive data were grouped and pooled as shown in Table 1.

Parameter estimation

In biological terms, a phenotypic value (P) of an individual was assumed to consist of $P = A + E$, where A is the additive genetic effect (breeding value), and E is the independent environment effect, which also includes a genetic residual. The phenotypic variance was thus assumed to be divisible into $\sigma_P^2 = \sigma_A^2 + \sigma_E^2$. We assumed that any non-additive genetic variance, thus included in the environmental variance σ_E^2, was negligible. Similarly, the phenotypic covariance between two traits is subdivided into additive genetic and environmental covariance: $\sigma_{P_1P_2} = \sigma_{A_1A_2} + \sigma_{E_1E_2}$.

The statistical analyses were carried out for all pairs of traits, which were assumed to follow the two-trait mixed model

$$\begin{bmatrix}\mathbf{y}_1\\ \mathbf{y}_2\end{bmatrix} = \begin{bmatrix}\mathbf{1} & \mathbf{0}\\ \mathbf{0} & \mathbf{1}\end{bmatrix}\begin{bmatrix}\mu_1\\ \mu_2\end{bmatrix} + \begin{bmatrix}\mathbf{Z} & \mathbf{0}\\ \mathbf{0} & \mathbf{Z}\end{bmatrix}\begin{bmatrix}\mathbf{u}_1\\ \mathbf{u}_2\end{bmatrix} + \begin{bmatrix}\mathbf{e}_1\\ \mathbf{e}_2\end{bmatrix}$$

where an observation vector $\mathbf{y}_i$ (i = 1 or 2 for the two traits) had one tree value per family (160 in T25) or four tree values per family (11 families in T44). Since there was no basis for inclusion of fixed effects besides general means (μ_i) in the model, the **1** vectors represent the fixed-effect part. The **Z** design matrix for random effects, equal for any trait, had rows indicating the parents for each tree in $\mathbf{y}_i$ according to the analysed crossing plan. The random parent effects of $\mathbf{u}_i$ (with element u_{ip} for trait i, parent p) and the random residual effects of $\mathbf{e}_i$ were assumed to have independent bivariate normal distributions with zero means and common variances/covariances according to

$$\text{Var}\begin{bmatrix}\mathbf{u}\\ \mathbf{e}\end{bmatrix} = \begin{bmatrix}\mathbf{G}\otimes\mathbf{I} & \mathbf{0}\\ \mathbf{0} & \mathbf{R}\otimes\mathbf{I}\end{bmatrix}$$

where $\mathbf{u}' = [\mathbf{u}'_1 \quad \mathbf{u}'_2]$, $\mathbf{e}' = [\mathbf{e}'_1 \quad \mathbf{e}'_2]$,

$$\mathbf{G} = \begin{bmatrix}\sigma^2_{u_1} & \sigma_{u_1u_2}\\ \sigma_{u_1u_2} & \sigma^2_{u_2}\end{bmatrix}, \text{ and } \quad \mathbf{R} = \begin{bmatrix}\sigma^2_{e_1} & \sigma_{e_1e_2}\\ \sigma_{e_1e_2} & \sigma^2_{e_2}\end{bmatrix}$$

Estimates of $\sigma^2_{u_1}$, $\sigma^2_{u_2}$, $\sigma^2_{e_1}$, $\sigma^2_{e_2}$, $\sigma_{u_1u_2}$, and $\sigma_{e_1e_2}$ were computed using the restricted maximum likelihood (REML) technique (e.g. SEARLE *et al.* 1992) with the computer program ASREML (GILMOUR *et al.* 1999). The data did not allow estimation of parameters for more than two traits simultaneously.

In order to quantify the parameters in terms of the biological model, the additive genetic variance was estimated using $\hat{\sigma}_{A_i} = 4\hat{\sigma}^2_{u_i}$, where $A = \mu + 2u$ is the additive breeding value of a parent tree, and $\hat{\sigma}^2_{P_i} = 2\hat{\sigma}^2_{u_i} + \hat{\sigma}^2_{u_i}$ since each entry in $\mathbf{y}_i$ is a phenotypic value of an individual tree with two unrelated parents. An estimate of environmental variance is obtained from $\hat{\sigma}_{E_i} = \hat{\sigma}^2_{P_i} - \hat{\sigma}^2_{A_i}$. The corresponding equations

[1] 'S23F731280 Vännäsby' (designated 'T25'), located at 64°01' N, 19°51' E and at 200 m elevation, testing unrelated clones from the Scots pine seed orchard 411 Domsjöänget. The clones originated from various locations in the latitudinal range of approximately 62.5-64.5°N, and at 150-300 m elevations in Sweden.

[2] 'S23F551153 Storbränna' (designated 'T44'), located at 63°07'N, 17°E and at 150 m elevation, testing a few unrelated parent trees from the earliest selections from northern Sweden.

Table 1. Grouping and pooling of wood extractive analytical data.

Groups of substances analysed in heartwood		Substances quantified in the group
Abbreviation	Full name	
PS	pinosylvin	pinosylvin
PSME	pinosylvin- monomethylether	pinosylvin-monomethylether
PSS	PS + PSME (pinosylvin sum)	
PiRA	pimaric resin acid	pimaric acid, sandara-copimaric acid, isopimaric acid
AbRA	abietic resin acid	abietic acid, neoabietic acid, dehydroabietic acid, palustric acid, 7-oxo-dehydroabietic acid
RAS	PiRA + AbRA (resin acid sum)	
FAsat	saturated fatty acids	C_{16}, C_{17}, C_{18}, C_{20}, C_{22}
FAun	unsaturated fatty acids	$C_{16:1}$, $C_{18:2}$, $C_{18:3}$, $C_{20:3}$, $C_{9\text{-}18:1}$, $C_{11\text{-}18:1}$
FAS	FAsat + FAun (fatty acid sum)	
STE	sitosterol	sitosterol, kampesterol
STA	sitostanol	sitostanol
STS	STE + STA (sterol sum)	

for covariances are

$\sigma_{A_1A_2} = 4\hat{\sigma}_{u_iu_2}$, $\hat{\sigma}_{P_1P_2} = 2\hat{\sigma}_{u_1u_2} + \hat{\sigma}_{e_1e_2}$, and
$\sigma_{E_1E_2} = \hat{\sigma}_{P_1P_2} + \hat{\sigma}_{A_1A_2}$, respectively.

Correlations were estimated using

$$\hat{r}_{E_{ij}} = \frac{\hat{\sigma}_{E_iE_j}}{\sqrt{\hat{\sigma}^2_{E_i}\hat{\sigma}^2_{E_j}}} \text{ for environmental, and } \hat{r}_{A_{ij}} = \frac{\hat{\sigma}_{A_iA_j}}{\sqrt{\hat{\sigma}^2_{A_i}\hat{\sigma}^2_{A_j}}}$$

for additive genetic correlations. These estimates were computed for each pair (i, j) of traits using a post-processing module of ASREML, which also provided estimates of parameter standard errors. Parameters involving individual traits were, initially, estimated in single-trait analyses (FRIES *et al.* 2000). Here, heritability estimates, that is $\hat{h}^2 = \hat{\sigma}^2_A/\hat{\sigma}^2_P$, were calculated as means of the estimates obtained from the two-trait analyses.

Estimation of variance components was usually straightforward, although many estimates showed low precision in terms of standard errors. Further, whenever tree height was included as one of the traits, the estimates of variance components were very imperfect or impossible to calculate, since the data provided insufficient information. Thus, tree height was not analysed in this study. For the same reasons, fatty acid contents could not be meaningfully evaluated from the T44 data. Regarding sterols, only the sum of sterol contents could be evaluated for the T44 sample, while sitostanol was the only sterol that produced meaningful correlations, with a few other traits, in T25. A few estimates of correlations linking extractive contents to heartwood diameter (FRIES *et al.* 2000) were also obtained.

RESULTS

The derived estimates of environmental and genetic correlations amongst the wood extractives (and between the extractives and the amount of heartwood) are given along with estimates of narrow-sense heritability in Table 2 for site T25 and Table 3 for site T44. Generally, the standard errors were larger for site T44 than for T25, reflecting both the smaller sample size from T44, and the fact that the pedigree of the trees at T44 (details in ERICSSON & FRIES 1999) gave less information relevant to the purpose of this study. These factors are also major reasons for the higher frequency of missing entries in Table 3.

The heritability results were fairly consistent with those obtained from the earlier single-trait analyses. The two-trait analyses also provided estimates of heritabilities for AbRA and heartwood diameter at site T25, the latter being fairly consistent with the earlier analysis of a larger data set (ERICSSON & FRIES 1999).

The correlations between the relative amounts of wood extractives were always positive, except for the genetic correlations between the sterols (STA/STS) and the other substances tested, and the genetic correlations were similar at the two test sites, in so far as plausible estimates were obtained. Further, within the groups of pinosylvins (PS, PSME, and PSS) and resin acids (PiRA, AbRA, and RAS), genetic correlations were extremely high. For pinosylvins, the environmental correlations were slightly lower, but for resin acids, the environmental correlations were also

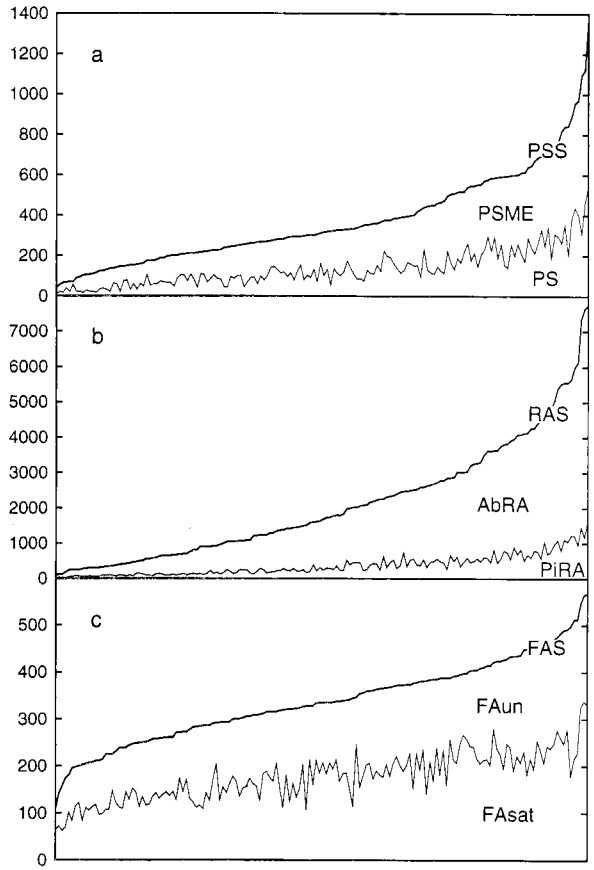

Figure 1. Composition of the total amounts detected of (a) pinosylvins (PSS), (b) resin acids (RAS), and (c) fatty acids (FAS) in the heartwood of 160 trees at the T25 site, in order of increasing total amounts ($\mu g \cdot g^{-1}$ dry weight).

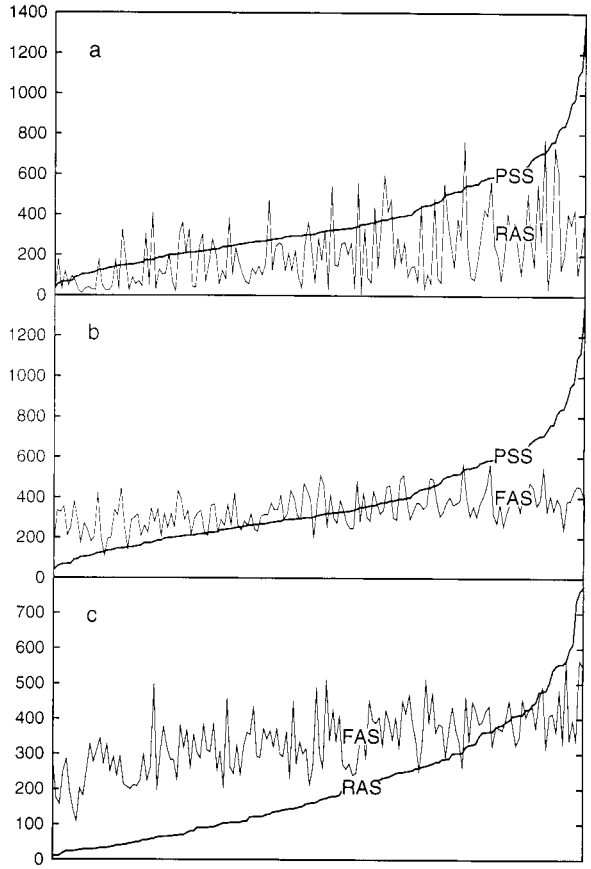

Figure 2. Total amount of detected pinosylvins (PSS,$\mu g \cdot g^{-1}$ dry weight), resin acids (RAS, $\mu g \cdot (0.1\ g)^{-1}$ dry weight), and fatty acids (FAS, $\mu g \cdot g^{-1}$ dry weight) in the heartwood of 160 trees at the T25 site; (a) PSS and RAS in order of increasing PSS, (b) PSS and FAS in order of increasing PSS, (c) RAS and FAS in order of increasing RAS.

close to unity. This indicates that PiRA and AbRA contents, both individually and as their sum (RAS), reflect a common underlying trait. The two main classes of fatty acids (FAsat and FAun) were strongly correlated genetically with the sum of the fatty acids (FAS) at site T25, but their correlations with the other compounds tested were weaker. No reasonable estimate of correlations where fatty acids were involved could be computed for site T44. Figs. 1 and 2 illustrate the tree data used in these evaluations. The different patterns of variation reflect, to a degree, the various correlation estimates.

There were also quite strong genetic and environmental correlations between the contents of the pinosylvin, resin acid, fatty acid and sterol groups, indicating that differences in ability to produce extractives is inherited jointly for many substances, to a degree at least. However, the estimates obtained regarding sterols (STA, STS) showed negative genetic correlations with the other extractive groups without exception, while the corresponding environmental correlations were quite strong and positive.

Concerning heartwood diameter (Heartwood), there is some evidence of positive correlations, both genetic and environmental, with the concentrations of resin acids, while the genetic correlations with fatty acids in T25 and sterols in T44 are negative. There are, however, few consistent results concerning heartwood diameter.

In so far as results are available from both sites, there is a relative uniformity in genetic parameters in the two environments, which is in contrast to the differences in average levels of extractive concentrations at the two sites as shown earlier in FRIES *et al.* (2000).

DISCUSSION

The clear repeatability found between sites in the estimated biological parameters suggests that there is strong genetic control over the formation of extract

Table 2. Estimated environmental correlations (r_E, above the diagonal), heritabilities (h^2, mean values from bivariate runs, in the bold typeface diagonal), and additive genetic correlations (r_A, below the diagonal) ± standard errors (SE) from 160 trees at site T25. Missing entries indicate very weak correlations compared to the experimental error, where SE exceeded the absolute value of the estimate.

	PS	PSME	PSS[a]	PiRA	AbRA	RAS[b]
PS	**0.59±0.17**	0.67±0.11	0.86±0.06	0.34±0.23	0.34±0.23	0.34±0.23
PSME	0.93±0.07	**0.48±0.17**	0.96±0.02	-	-	-
PSS	0.98±0.02	0.99±0.01	**0.55±0.17**	-	-	-
PiRA	0.70±0.16	0.75±0.22	0.73±0.19	**0.54±0.18**	1.00±0.03	1.00±0.02
AbRA	0.76±0.14	0.68±0.23	0.72±0.18	0.88±0.06	**0.58±0.18**	1.00 ± 10^{-3}
RAS	0.77±0.14	0.71±0.23	0.74±0.18	0.92±0.04	1.00 ± 10^{-3}	**0.56±0.18**
FAsat	0.48±0.23	0.51±0.26	0.50±0.24	0.68±0.17	0.82±0.12	0.81±0.12
FAun	0.34±0.27	-	0.31±0.28	-	-	-
FAS	0.47±0.23	0.44±0.26	0.46±0.24	0.32±0.27	0.56±0.21	0.52±0.22
STA	-0.68±0.23	-0.51±0.26	-0.59±0.24	-0.35±0.28	-0.68±0.27	-0.64±0.27
Heartwood	-	-	-	>1[e]	>1[e]	>1[e]

	FAsat	FAun	FAS[c]	STA	Heartwood[d]
PS	0.75±0.12	-	0.59±0.15	0.78±0.37	-
PSME	0.38±0.16	-	0.35±0.17	0.50±0.29	-
PSS	0.56±0.14	0.21±0.20	0.48±0.17	0.65±0.33	-
PiRA	0.79±0.10	0.50±0.22	0.79±0.14	0.74±0.31	0.42±0.23
AbRA	0.76±0.10	0.30±0.22	0.66±0.15	0.95±0.38	0.41±0.24
RAS	0.76±0.09	0.34±0.22	0.69±0.14	0.91±0.36	0.42±0.23
FAsat	**0.33±0.16**	0.35±0.15	0.85±0.05	0.64±0.23	-
FA un	0.63±0.27	**0.37±0.17**	0.80±0.06	0.47±0.21	-
FAS	0.91±0.08	0.90±0.09	**0.38±0.17**	0.65±0.22	-
STA	-0.46±0.36	-0.22±0.34	-0.37±0.35	**0.60±0.17**	-
Heartwood	>1[e]	-	-0.85±0.42	-	0.18±0.11

[a] Sum of PS and PSME content (pinosylvin sum)
[b] Sum of PiRA and AbRA content (resin acid sum)
[c] Sum of FAsat and FAun content (fatty acid sum)
[d] Heartwood diameter, 0.8 m above the ground (for details concerning choice of height, see FRIES & ERICSSON 1998)
[e] The REML iterations converged, for Heartwood along with PiRA, AbRA, and RAS, at values notably greater than 1 (cf. r_E).

ives. Thus, heritage generates differences among individual trees, beyond the base levels attributable to various common factors such as environmental influences and the phase of tree development. The results are consistent with those from the first study, where considerably higher heritabilities, especially for pinosylvins and resin acids, were found than are typically observed for growth traits (FRIES *et al.* 2000). Genetic coefficients of variation were also high in the first study.

Pinosylvins and resin acids

Pinosylvin (PS) and pinosylvin-monomethylether (PSME), which are two important (and fairly stable) wood decay-inhibiting substances show strong positive genetic correlations with each other (Tables 2 and 3). Although there is considerable variation between trees, there is no further evidence of specific seasonal influences on differences in their concentrations[3]. For these reasons, our results probably describe fairly general conditions. Furthermore, they indicate weak genetic correlations between the pinosylvin concentrations and the amount of heartwood in a tree.

The resin acids in wood are either of the pimaric (PiRA) or abietic (AbRA) type. These are both quite stable groups of substances, despite the conjugated double bonds of the abietic acids, that are usually degraded by the activity of specific fungi (EBERHARDT *et al.* 1994) or autooxidation (QUINDE & PASZNER

[3] Bergström, B: Chemical and structural changes during heartwood formation in *Pinus sylvestris*. Unpublished manuscript.

Table 3. Estimated environmental correlations (r_E, above the diagonal), heritabilities (h^2, mean values from bivariate runs, in the bold typeface diagonal), and additive genetic correlations (r_A, below the diagonal) ± standard errors (SE) from 44 trees at site T44. Missing entries indicate very weak correlations compared to the experimental error, where SE exceeded the absolute value of the estimate.

	PS	PSME	PSS[a]	PiRA	AbRA	RAS[b]	STS[c]	Heartwood[d]
PS	**0.71±0.37**	0.50±0.38	0.66±0.30	0.78±0.35	0.6±0.3[e]	0.65±0.26	-	-
PSME	0.84±0.25	**0.51±0.39**	0.98±0.02	-	-	-	-	-0.82±0.50
PSS	0.92±0.13	0.98±0.02	**0.59±0.39**	-	-	-	-	-0.78±0.53
PiRA	0.68±0.33	0.58±0.52	0.65±0.44	**0.55±0.36**	1[f]	1[f]	-	-
AbRA	1.0±0.2[e]	0.66±0.59	0.78±0.45	1[f]	**0.32±0.29**	1[f]	-	-
RAS	0.98±0.17	0.64±0.57	0.76±0.44	1[f]	1[f]	**0.36±0.31**	-	-
STS	-0.72±0.36	-	-	-0.95±0.25	-0.95±0.28	-0.95±0.27	**0.87±0.37**	-
Heartwood	-	-	-	0.61±0.44	-	-	-0.55±0.43	**0.42±0.36**

[a] Sum of PS and PSME content (pinosylvin sum)
[b] Sum of PiRA and AbRA content (resin acid sum)
[c] Sum of STE and STA content (sitosterol/stanol sum)
[d] Heartwood diameter, 1.3 m above the ground
[e] Imprecise values from REML convergences that were not fully satisfactory
[f] The attempted analysis indicated that PiRA, AbRA, and RAS reflect the same trait

1991). The near-unity genetic correlations between AbRA, PiRA, and RAS indicate that the proportions of AbRA and PiRA are highly predetermined, with little individual variation from genetic inputs. On the other hand, the high heritabilities indicate that there is a wide individual variation in levels of RAS. This difference in inheritance-of-composition versus inheritance-of-concentration is most clearly expressed for resin acids, but is also evident for pinosylvins, albeit at a slightly weaker level.

Since there do not appear to be any negative genetic correlations between resin acids and heartwood diameter (at least), it should be relatively straightforward to breed trees with more durable wood by increasing both their heartwood content and resin acid concentration. Furthermore, the strong positive genetic correlations between pinosylvins and resin acids (around 0.7) indicate that there would be good general breeding prospects for increasing the amounts of these substances, the two most important classes of wood extractive for protection against microbial degradation (cf. HART 1981, EBERHARDT *et al.* 1994).

Fatty acids and sterols

The unsaturated fatty acids are less stable than their saturated analogues (SJÖSTRÖM 1981). We believe that SARANPÄÄ & NYBERG (1987) illustrated this instability, in a study monitoring changes in the relative abundance of specific fatty acids (both saturated and unsaturated) in sapwood throughout the year. In contrast, they found the total concentration of fatty acids to be fairly constant. Besides describing shifts between different types of fatty acids, they also suggested that interconversions may occur between fatty acids and triacylglycerols. In heartwood, however, they observed more stable concentrations in all categories of fatty acids. The strong correlations on site T25 between FAsat and FAun and their sum suggest that the proportion between FAsat and FAun is fairly constant between trees in the stand. Again, as for pinosylvins and resin acids, inheritance-of-composition appears to be less dependent on the pedigree than inheritance-of-concentration. On the other hand, difficulties in obtaining correlation estimates for fatty acids from the T44 data may to some extent reflect lower substance stability, as well as the other limitations regarding sample size and pedigree in this stand. Nevertheless, very high heritabilities for fatty acids (around 0.7) were derived from the same data in the earlier study (FRIES *et al.* 2000), although these compounds will probably have low priority as breeding traits, since they may serve as fungal substrates (GAO *et al.* 1994). Thus, positive genetic correlations between fatty acids and pinosylvins and/or resin acids might be disadvantageous when selecting for improved durability.

Sterols may also serve as substrates for fungi. However, the estimates of genetic correlations between sterols and the fungitoxic pinosylvins and resin acids are strongly negative, which is advantageous. The fact that the environmental correlations are counteractive in this case should be of minor importance, since the heritability estimates for sterol con-

centrations are amongst the highest found in this study (0.6 for STA in T25 and 0.9 for STS in T44).

CONCLUSIONS

The main result from the present study is that there are generally very high positive genetic correlations between the concentrations of the main groups of fungitoxic wood extractives, pinosylvins and resin acids, in heartwood of Scots pine. Also, there were clearly no negative genetic correlations between the amount of heartwood and the concentrations of these fungitoxic compounds. Although data were collected from two quite dissimilar stands in north central Sweden with respective tree ages of roughly one fourth and half the rotation, the results are consistent as regards genetic parameters.

Negative genetic correlations were found between sterols, which may serve as fungal substrates, and both pinosylvins and resin acids, which may be advantageous. However, potentially disadvantageous positive correlations between the fungitoxic extractives and fatty acids were also found. Nevertheless, the results indicate that there are very promising possibilities for breeding trees with higher amounts of heartwood and high concentrations of fungitoxic wood extractives.

Although this report has emphasized the potential for breeding to increase the levels of fungitoxic wood extractives in Scots pine, the results would be equally relevant to breeding for decreasing concentrations of the studied substances. The prospects for breeding in either direction should be practically equivalent.

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REFERENCES

EBERHARDT, T. L., HAN, J. S., MICALES, J. A. & YOUNG, R. A. 1994: Decay resistance in conifer seed cones: role of resin acids as inhibitors of decomposition by white-rot fungi. *Holzforschung* **48**: 278–284.

ENOKI, A. 1976: Isomerization and autoxidation of resin acids. *Wood Research* **59/60**: 49–57.

ERICSSON, T. & FRIES, A. 1999: High heritability for heartood in north Swedish Scots pine. *Theor. Appl. Genet.* **98**: 732–735.

FRIES, A. 1999: Heartwood and sapwood variation in mature provenance trials of *Pinus sylvestris*. *Silvae Genet.* **48**: 7–14.

FRIES, A. & ERICSSON, T. 1998: Genetic parameters in diallel-crossed Scots pine favor heartwood formation breeding objectives. *Can. J. For. Res.* **28**: 937–941.

FRIES, A., ERICSSON, T. & GREF, R. 2000: High heritability of wood extractives in *Pinus sylvestris* progeny tests. *Can. J. For. Res.* **30**: 1707–1713.

GAO, Y., BREUIL, C. & CHEN, T. 1994: Utilization of triglycerides, fatty acids and resin acids in lodgepole pine wood by a sapstaining fungus *Ophiostoma piceae*. *Material Org.* **28**: 105–118.

GILMOUR, A.R., CULLIS, B.R., WELHAM, S.J. & THOMPSON, R. 1999: ASREML Reference Manual. NSW Agriculture, Orange, 210 pp.

GREF, R., HÅKANSSON, C., HENNINGSSON, B. & HEMMING, J. 2000: Influence of wood extractives on brown and white rot decay in Scots pine heart-, light- and sapwood. *Material Org.* **33**: 119–128.

HART, J. H. 1981: Role of phytostilbenes in decay and disease resistance. *Ann. Rev. Phytopathol.* **19**: 437–458.

HEMINGWAY, R. W., NELSON, P. J. & HILLIS, W. E. 1971: Rapid oxidation of the fats and resins in *Pinus radiata* chips for pitch control. *Tappi* **54**: 95–98.

KENNEDY, M. J., DRYSDALE, J. A. & BROWN, J. 1995: Efficacy of some extractives from *Pinus* heartwood for protection of *Pinus radiata* sapwood against biodeterioation; 1. Fungal decay. Paper no. 95-30072 presented at the 26th annual meeting of the International Research Group on Wood Preservation. IRG Secretariat, Stockholm, 10 pp.

QUINDE, A. A. & PASZNER, L. 1991: Isomerization of slash pine resin acids during seasoning. *Appita* **44**: 379–384.

SARANPÄÄ, P. & NYBERG, H. 1987: Seasonal variation of neutral lipids in *Pinus sylvestris* L. sapwood and heartwood. *Trees* **1**: 139–144.

SEARLE, S. R., CASELLA, G. & MCCULLOCH, C. E. 1992: Variance Components. Wiley, New York, 510 pp.

SJÖSTRÖM, E. 1981: Wood Chemistry. Fundamentals and Applications. Academic Press, New York, 223 pp.