Despite the reduced number of parents in the diallel, in experiment 2, specific combining effects seem small compared with additive effects. Low specific combining effects were also found in large hardwood cutting experiments of *E. globulus* (LEMOS *et al.,* 1998) and *E. nitens* (TIBBITS *et al.,* 1997). The low specific combining effects ensures that the performance of an untested cross should fall close to the mean genetic merit of both parents. Providing selection accuracy of the parents is good, crosses between outstanding rooters should therefore produce families of outstanding rooting ability for deployment. The statistically significant levels of additive genetic variation detected within *(Table 1)* and between (WYLLIAMS *et al.,* 1992) populations indicates that there is potential for improving rooting ability in *Eucalyptus globulus.* Genetic gains could be rapidly made for this trait by crossing high rooting genets already growing in clonal trials or clonal plantations. However, the low heritability of this trait would strongly argue for the utilisation of information on the performance of relatives (through index or BLUP selection) to increase the accuracy of individual selection.

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Heartwood and Sapwood Variation in Mature Provenance Trials of *Pinus sylvestris*

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Abstract

In two Swedish provenance test series of Scots pine *(Pinus sylvestris* L.) from 1911 and 1955, only limited provenance differences were found in number of heartwood and sapwood annual rings and in the width of heartwood and sapwood. Variance components were smaller than for tree size traits. Correlations between heartwood and sapwood annual rings were negative and significant, while weak correlations were indicated between heartwood and sapwood width. Correlations with tree size traits were weaker in the young test series than in the older series. The results indicate that stand characteristics (such as stand density) have stronger influence than provenance and latitudinal transfer on heartwood and sapwood traits. This was pronounced for sapwood width and for mature field tests as compared to younger tests. No differences due to provenance origin or latitudinal transfer were detected, possibly since the within provenance variation was large due to other effects (e.g. family effects).

Key words: heartwood, sapwood, annual ring, *Pinus sylvestris* L., provenance, latitudinal transfer, crown size, environmental variation.

FDC: 811.5; 232.12; 181.6; 165.52; 174.7 *Pinus sylvestris;* (485).

Introduction

The aim of the present study was to investigate whether there are provenance differences and transfer effects on heartwood and sapwood traits in Scots pine *(Pinus sylvestris* L.) in Sweden, and to study the relationship between those wood traits and growth traits. There has been an increasing interest in wood traits in recent years. The reason has been the desire to utilize the wood and wood-based chemicals more effectively. In Scots pine, heartwood has distinct properties compared to sapwood which makes it less favourable for pulping, but very attractive for construction and carpentry. The reason for this is the wood extractives that occur in the heartwood of pines (Higuchi, 1985), and that they, by being fungitoxic (Rudman, 1966; Hart, 1981; Hillis, 1987) contribute significantly to the quality of the wood. In addition, those wood extractives give valuable by-products after pulping, such as talloil and turpentine, which are used as cleaning agents and raw materials for chemical processes (Sjöström, 1993; Anon., 1995). Due to the considerable differences in properties between heartwood and sapwood, it is clearly desirable to improve our understanding of factors that influence their relative abundance.

In north Sweden, the official recommendation is that Scots pine should be transferred southwards to maximise the production per unit area SKSFS (1993). According to Ståhl (1998), a southern transfer should reduce the percentage of heartwood due to an increase in annual ring width. Whether the actual amount of heartwood (and not only in relation to the amount of sapwood) would decrease has, however, not been stated. It has, furthermore, not been shown that the current Scots pine breeding program, emphasising adaptation, production, and certain wood property traits (Wilhelmsson and Andersson, 1993), will lead to any unexpected, and possibly undesired, impact on the heartwood and sapwood relationship. The latitudinal transfer of Scots pine in Sweden implies both a change in adaptation to the temperature climate (Eriksson *et al.,* 1980), and to the photoperiod, which is important for the growth cessation (Persson, 1994). The latter may influence the relation between earlywood and latewood (Larson, 1962), with possible effect on the heartwood formation. The actual transfer of a certain provenance in one test site may, thus, have another influence on the wood formation processes than for the same provenance in another test site, and, thus, cause additional provenance differences in number of heartwood annual rings and heartwood width. In addition, effects of local growth conditions on the onset of heartwood formation have been noted (Nepveu and Velling, 1986; Velling and Nepveu, 1986).

To investigate whether there are provenance differences and transfer effects on heartwood and sapwood traits in Scots pine in Sweden, two provenance test series were analysed for the width of the heartwood and sapwood sections and their number of annual rings (or fractions of annual rings). In addition, tree size traits (height, stem diameter at breast height, crown limit and crown length) were analysed. One test series was at approximately middle-rotation age (50 years from seeding) and one was mature (87 to 88 years from seeding). It may be regarded as a complement to earlier analyses of one 25-year-old and one 44-year-old full-sib progeny test recorded in Fries and Ericsson (1998) and Ericsson and Fries (1998). These studies showed that the amount of heartwood had a higher heritability and stronger genetic correlation than the total stem diameter.

Material and Methods

Provenance tests

The study analysed two provenance test series, the Schotte series from 1911 to 1912 and the Stefansson series from 1950 to 1951 (Schotte, 1923; Remröd, 1976) *(Table 1).* In the Schotte series, samples were taken from seven field tests during July to September 1997. The field tests were located on normal forest soils suitable for Scots pine, between latitude 60°45'N and latitude 65°47'N. The design was provenance blocks without replications. In each field test, only provenances from the south or the local provenance were planted *(Table 2).* Planting was undertaken in spring 1911, with 2-year-old plants (except at site 7, which was planted with 3-year-old plants in 1912). The stands were thinned in 1960 to 1963 (when 10% to 30% of the stems were removed) and, again, at site nos. 1 and 3 to 6 in 1968 to 1978 (20% to 30% removed). At around 55 years of age, 30% to 80% of the trees remained in the provenance plots, except for a few plots on poorer parts of the site for which just 5% to 30% remained.

The localization of the three field tests in the Stefansson series and the studied provenances are given in *tables 1* and *3.* The same eleven provenances were sampled in all sites (plus the local provenance in Laxå). They were all located on suitable sites for Scots pine, i.e. dwarf-shrub type (mesic at Bratten and Björkvattnet and dry at Laxå), and site indices T19 to T20 (Hägglund and Lundmark, 1982). The provenances, in 4 to 5 replications, were planted in spring 1951 (autumn 1950 in Björkvattnet) with 3-year-old plants in 11 x 11 plants (12 x 12 plants in Björkvattnet). The spacing was 1.5 m x 1.5 m (1.2 m x 1.2 m in Laxå). Broadleaves were cleaned from the sites after between 4 and 6 growing seasons. At thinning in 1969, i.e. 18 years after planting, survival at Brattfors was 47% to 85% for all but one provenance (23%); at Björkvattnet survival was 40% to 88%; and at Laxå 78% to 90%. For both the Stefansson and Schotte series, the sampling was restricted to provenances for which the growth habit of most of the remaining trees (ca. 2/3) appeared to be undisturbed. Since wood traits should be studied, variation in growth conditions had to be minimized, and sampling was, thus, allocated to one part of the experiment. In each experiment, 5 to 6 trees were generally sampled per provenance *(Table 1).*

Increment cores to be used for heartwood measurements were taken at breast height from the south. Care was taken to assure that the pith was included in the cross-section, but to avoid too large damage on the trees, the last part of the end section of the sapwood was not bored. The increment cores were stained with sulfanilic acid saturated with sodium nitrite (Cummins, 1972), to permanently distinguish the heartwood. They were subsequently placed in paper tubes for drying at room temperature until the next day, when the exact borders between heartwood and sapwood, which may occur in the middle of an annual ring, were marked with a pen. The cores were kept chilled (+8 °C) in open tubes until ready for measurement, when the number of heartwood annual rings on each side of the pith was counted. One figure of number of sapwood annual rings was also obtained, but since the total number of annual rings on each side of the pith is equal, the number of sapwood annual rings that were missing at the end of the

Table 1. – Provenance tests in the study, and height, stem diameter, heartwood and sapwood averages, *a)* the SCHOTTE series, *b)* the STEFANSSON series.

Field test Number, name and county code	Latitude (N)	Longitude (E)	Altitude (m)	No. of analysed prove-nances	 trees per provenance	Total no. of planted trees per provenance	Site mean values[1] Height (m)	 D1.3[2] (cm)	 Heartwood annual rings	 Heartwood width (mm)	 Sapwood annual rings	 Sapwood width (mm)
a)												
1 Alträsk, BD	65°47'	21°19'	120	9	5[3]	330	17.4 (0.18)	20.5 (0.44)	27.1 (0.49)	54.8 (1.54)	47.6 (0.54)	37.1 (1.12)
2 Bocken, AC	64°35'	18°45'	280	5	5-6	600 (ca)	18.5 (0.38)	21.9 (0.44)	27.9 (0.60)	60.4 (1.77)	46.8 (0.60)	39.5 (1.34)
3 Svartberget, AC	64°14'	19°40'	175	9	6-7	400 (ca)	21.1 (0.20)	25.6 (0.47)	30.0 (0.55)	67.3 (1.77)	45.2 (0.65)	46.5 (1.13)
4 Hårkaskogen, Z	63°22'	14°52'	270	7	6	420 (ca)	20.5 (0.33)	25.6 (0.43)	30.9 (0.66)	61.9 (1.31)	44.4 (0.63)	48.6 (1.13)
5 Frösön, Z	63°13'	14°28'	325	12	6	300 (ca)	20.4 (0.15)	25.6 (0.32)	32.3 (0.56)	62.4 (1.00)	45.9 (0.53)	47.5 (0.90)
6 Bunkris, W	61°26'	13°29'	590	8	5	480 (ca)	17.4 (0.26)	25.2 (0.58)	25.8 (1.04)	65.0 (2.45)	44.7 (0.84)	47.5 (2.01)
7 Ovansjö, X	60°45'	16°23'	285	8	5[4]	500	21.6 (0.33)	30.4 (0.76)	30.0 (0.72)	85.2 (2.33)	47.4 (0.75)	52.8 (2.00)
b)												
1 Brattfors, AC	64°31'	18°24'	310	11	6	484	16.1 (0.27)	18.0 (0.23)	11.5 (0.25)	35.8 (0.46)	26.3 (0.20)	45.9 (0.89)
2 Björkvattnet, Y	63°26'	16°02'	460	11	5[3]	605	13.6 (0.19)	28.3 (0.41)	13.5 (0.26)	39.1 (0.76)	25.3 (0.19)	46.0 (1.11)
3 Laxå, N	59°00'	14°30'	100	11	8[5]	576	12.5 (0.28)	14.5 (0.26)	11.0 (0.26)	21.1 (0.77)	28.9 (0.24)	42.8 (0.86)
3 Laxå, N[6]				12			12.5 (0.26)	14.5 (0.24)	10.8 (0.28)	21.0 (0.71)	29.2 (0.34)	43.2 (0.88)

[1] Based on provenance means. Within parantheses: standard error.
[2] Stem diameter at breast height.
[3] Six trees were analysed for one provenance.
[4] Three trees from one and four from another provenance analysed.
[5] Nine trees from one provenance. Height and stem diameter measured on five trees (on six for one provenance).
[6] Including the local provenance.

Table 2. – Provenances studied in the SCHOTTE series. Their origin and test sites in which they were studied.

No.	Name	Latitude (N)	Longitude[1] (E)	Alt (m)	Used in field test number[2] 1	2	3	4	5	6	7
5	Hässleby, F	57°38'	15.6°	199					x	x	
6	Ö. Holaveden, F	58°06'	15°	150			x		x	x	x
8	Björkvik, E	58°50'	16.5°	48					x		x
11	Karlsby, E	58°39'	15.3°	119					x		x
12	Rekarne, D	59°13'	16.5°	59					x		x
13	Bjurfors, U	60°07'	16°	145	x		x	x	x	x	x
14	Fagerberg, W	60°59'	14.9°	260	x	x	x	x	x	x	x
15	Hillevik, X	60°48'	17.2°	20			x	x	x	x	x
16	Svärdsjö, W	60°48'	15.8°	170	x	x	x	x	x	x	x
17	Voxna, X	61°21'	15.5°	200	x	x	x	x	x	x	
18	Haverö, Y	62°21'	15.2°	265	x	x	x	x	x	x	
19	Fors, Z	63°01'	16.5°	120	x		x	x	x		
20	Skatan, AC	64°21'	19.5°	185	x	x	x				
21	Fagerheden, BD	65°20'	20.9°	200-220	x						
23	Torneå, BD	66°01'	23.5°	50	x						

[1] Approximate from the map.
[2] For the test site names, see *table 1*.

Table 3. – Provenances studied in the STEFANSSON series.

No.	Name	Latitude (N)	Longitude (E)	Alt (m)
BD116	Lainio	67°41'	22°10'	325
BD117	Kompelusvaara	67°03'	22°20'	300
BD118	Björkfors	65°55'	23°29'	30
AC316	Norrsele	65°36'	17°30'	360
BD119	Brännberg	65°48'	21°15'	100
BD120	Nordanås	65°45'	18°35'	420
BD121	Moskosel	65°52'	19°28'	340
BD122	Kolerträsk	65°34'	20°28'	275
AC318	Svanmyren	64°37'	18°10'	350
Y48	Söråker	63°34'	17°32'	75
Z270	Hede	62°25'	13°32'	410
Bg31	Laxå	59°02'	14°35'	90

increment core could be calculated. The length of this missing sector was obtained from the length of the same annual rings at the beginning of the core. The 'heartwood width' *(Hw.w)* and 'sapwood width' *(Sw.w)*, measured to one tenth of a mm, were defined as the averages of the total length of the wood sections on each side of the pith.

Statistical analyses

In each test series, two-way analyses of variance were used for studying interaction effects between sites and provenances, and one-way analyses for analysing provenance within site differences. Due to the unbalanced design in the analysis of all test sites together, the analyses of variance and estimations of variance components were made with the REML method of the SAS Varcomp-procedure (SAS, 1992) and model (1) below. Sampling within each test site followed a balanced design, and the separate analyses of variance and estimations of variance components for them were, thus, made with the SAS GLM-procedure (2).

(1) $y_{ijk} = \mu + \text{Site}_i + \text{Provenance}_j + \text{Site}_i \text{ x } \text{Provenance}_j + e_{ijk}$,
$(i = 1, \ldots, 7; j = 1, \ldots, 15)$
(in the STEFANSSON series, $i = 1, \ldots, 3; j = 1, \ldots, 11$)

(2) $y_{jk} = \mu + \text{Provenance}_j + e_{jk}$,$(j = 1, \ldots, n_i)$ (for site i)
(in the STEFANSSON series, $j = 1, \ldots 12$)

where y_{ijk} and y_{jk} are the phenotypic averages for the test series and the test site, respectively, i the number of test sites, j the number of provenances, and k the number of trees. Since significant provenance differences for wood traits occurred in very few sites, linear regression analyses between traits were made on single tree data. The sapwood constitutes the transport system for the living crown, and since each pipe in the sapwood, according to the LIGNUM model in PERTTUNEN et al. (1996) (originating from SHINOZAKI et al. (1964)), is directly connected to certain branches and leaves, the amount of sapwood at a certain height should be correlated to the size of the living crown above this height. This correlation was also found by KAUFMANN and TROENDLE (1981). To analyse this functional relationship, regression analyses were made between relative sapwood area and relative crown length. These regressions were also made after inclusion of height and stem diameter in a stepwise regression analyses. No such functional relationship could, however, be found, and the relationship was not further analysed. The effect of latitude of origin on wood and tree size traits was analysed using provenance averages. In the analysis of the total effect of latitude in the whole test series, each test site was included as a dummy variable. Both in the analyses of variance and in the regression analyses, significance was assessed at the $p \leq 0.001$, $p \leq 0.01$ and $p \leq 0.05$ levels (denoted ***, ** and * respectively in the tables).

Results

Site means including standard errors for the most important tree size and wood traits are given in *table 1.* Except for Bunkris, which was located at a high altitude, the southern test sites had the highest mean heights in the SCHOTTE series. In the STEFANSSON series, on the other hand, the northern sites were the highest.

Table 4. – Results from analyses of variance of all test and the sites separately, and variance components (VC) (%)
a) the SCHOTTE series, *b)* in the STEFANSSON series. Abbreviations: *Hw.ar* and *Sw.ar,* number of annual rings of heartwood and sapwood, respectively; *Hw.w* and *Sw.w,* total diameter of the heartwood; and sapwood sections on an increment core of a tree (see Material and Methods); *H,* tree height *D1.3,* stem diameter at breast height; *Cr.lim,* height to first living branch; *Cr.l.,* length of the living crown; *df,* degrees of freedom.

a)	df	Hw.ar		Sw.ar		Hw.w		Sw.w		df	H		D1.3		Cr.lim		Cr.l	
		Sign	VC	Sign	VC	Sign	VC	Sign	VC		Sign	VC	Sign	VC	Sign	VC	Sign	VC
All test sites																		
Site	6	***	18.4	*	4.2	***	38.0	***	24.3	6	***	52.3	***	46.2	***	41.4	***	38.3
Provenance	14	ns	1.5	ns	1.2	**	2.7	ns	0.5	14	ns	2.6	**	0	ns	5.4	ns	1.3
Site x Provenance	37	**	11.3	**	11.4	***	12.8	ns	3.2	37	***	7.6	***	10.9	***	17.3	**	8.8
Error	263		68.8		83.2		46.5		72.1	263		37.5		42.9		35.9		51.6
The test sites separately																		
1 Alträsk	8, 37	ns	0	*	19.8	***	40.4	ns	0	8, 37	**	35.4	***	45.0	ns	0	**	32.9
2 Bocken	4, 23	ns	0	**	36.1	ns	0	ns	0	4, 23	***	57.7	ns	0	**	47	**	38.4
3 Svartberget	8, 49	**	27	***	34.1	***	47.2	ns	0	8, 49	***	35.3	***	53.4	***	42	***	20.9
4 Hårkaskogen	6,35	ns	0	ns	0	ns	0	ns	0	6,35	ns	0	ns	0	ns	0	ns	0
5 Frösön	11, 60	ns	0	ns	0	ns	0	ns	0	11, 60	ns	0	ns	0	**	24	ns	0
6 Bunkris	7,32	**	30	ns	0	ns	0	ns	0	7,32	**	42.9	ns	0	***	67	ns	28.0
7 Ovansjö	7,28	ns	0	ns	0	**	41.1	ns	0	7,28	ns	0	ns	0	**	37	ns	0

b)	df	Hw.ar		Sw.ar		Hw.w		Sw.w		df	H		D1.3		Cr.lim		Cr.l	
		Sign	VC	Sign	VC	Sign	VC	Sign	VC		Sign	VC	Sign	VC	Sign	VC	Sign	VC
All test sites																		
Site	2	***	26.5	***	47.7	***	68.9	**	5.5	2	***	65.2	***	61.7	***	43.8	***	41.3
Provenance	10	ns	0	ns	0	ns	0	ns	0	10	*	0	ns	0	**	0	ns	0
Site x Provenance	20	ns	2.3	ns	0	ns	0	ns	4.7	20	***	9.1	ns	1.7	***	13.7	**	8.6
Error	178		71.2		52.3		31.1		89.8	178		25.7		36.6		42.5		50.1
The test sites separately																		
1 Brattfors	10, 55	ns	0	ns	0	ns	0	ns	0	10, 55	*	20.9	ns	0	ns	0	**	24.8
2 Björkvattnet	10, 45	ns	0	ns	0	ns	0	*	21.7	10,45	*	22.9	ns	0	ns	0	ns	0
3 Laxå	10, 78	ns	0	ns	0	*	10.6	ns	0	10, 44	***	38.1	ns	0	***	54.4	ns	0
Including provenance 220 in Laxå	11, 85	ns	0	**	16.5	ns	0	ns	0	11, 49	***	36.2	ns	0	***	52.1	ns	0

Significances: ***, $p \leq 0.001$; **, $p \leq 0.01$; *, $p \leq 0.05$; ns, not significant at 5% level

Analyses of variance

Table 4 shows that in the Schotte series, there were significant site differences for all traits, and significant interaction effects for all traits except for sapwood width *(Sw.w)* ($p \leq 0.05$ to 0.001). Provenance differences occurred only for *Hw.w* and stem diameter ($p \leq 0.01$), but the variance components were low for provenance compared to site. When the sites were analysed separately, *Sw.w* showed no significant provenance differences. Significant difference for other wood traits and also for tree size variables occurred non-systematically.

In the Stefansson series, sites differed significantly for all traits, while provenances differed only for tree height and crown limit ($p \leq 0.05$ to 0.01, *Table 4*). In the analyses of the sites separately, wood traits showed on the whole no significant provenance differences, while height among tree size traits differed significantly at all test sites.

Correlation between traits

Table 5 shows that in the Schotte series, *Hw.ar* and *Hw.w* were significantly positively correlated both overall and at all seven test sites ($r = 0.33$ to 0.68), while *Sw.ar* and *Sw.w* showed a weak and varying relationship ($r = -0.38$ and 0.38 at only two sites). Tree height was generally significantly positively correlated with heartwood, but with sapwood, correlations were low

Table 5. – Results from regression analyses between wood traits, and between wood traits and tree size traits on individual trees. The Schotte series, *a)* all sites, *b)* each site separately. Abbreviations and significances: see *table 4.*

a)

		Hw.ar	Sw.ar	Hw.w	Sw.w	H	D1.3	Cr.lim	Cr.l
All test sites	**Hw.ar**	1	-0.57^{***}	0.41^{***}	ns	0.47^{***}	0.30^{***}	0.38^{***}	0.15^{**}
n=322	**Sw.ar**		1	ns	ns	ns	ns	ns	-0.15^{**}
	Hw.w			1	0.21^{***}	0.45^{***}	0.80^{***}	0.11^{*}	0.40^{***}
	Sw.w				1	0.35^{***}	0.67^{***}	ns	0.52^{***}

b)

		Hw.ar	Sw.ar	Hw.w	Sw.w	H	D1.3	Cr.lim	Cr.l
1 Alträsk	**Hw.ar**	1	-0.79^{***}	0.55^{***}	ns	0.30^{*}	0.39^{**}	ns	ns
n=46	**Sw.ar**		1	-0.35^{*}	ns	ns	ns	ns	ns
	Hw.w			1	ns	0.29^{*}	0.79^{***}	ns	ns
	Sw.w				1	0.45^{**}	0.56^{***}	ns	0.50^{***}
2 Bocken	**Hw.ar**	1	-0.74^{***}	0.68^{***}	ns	ns	0.44^{*}	ns	0.51^{**}
n=28	**Sw.ar**		1	-0.38^{*}	ns	ns	ns	ns	-0.50^{**}
	Hw.w			1	ns	0.46^{*}	0.72^{***}	ns	0.59^{***}
	Sw.w				1	ns	0.38^{*}	ns	ns
3 Svartberget	**Hw.ar**	1	-0.36^{**}	0.58^{*}	-0.29^{*}	0.43^{**}	0.38^{**}	ns	0.27^{*}
n=58	**Sw.ar**		1	ns	0.38^{**}	ns	0.36^{**}	ns	ns
	Hw.w			1	ns	0.48^{***}	0.84^{***}	ns	0.30^{*}
	Sw.w				1	ns	0.45^{***}	ns	ns
4 Hårkaskogen	**Hw.ar**	1	-0.90^{***}	0.36^{*}	ns	ns	ns	ns	ns
n=42	**Sw.ar**		1	-0.42^{**}	ns	ns	ns	ns	ns
	Hw.w			1	0.30^{*}	ns	0.81^{***}	ns	ns
	Sw.w				1	ns	0.72^{***}	ns	ns
5 Frösön	**Hw.ar**	1	-0.94^{***}	0.33^{**}	ns	0.31^{**}	ns	ns	ns
n=72	**Sw.ar**		1	-0.30^{**}	ns	-0.29^{*}	ns	ns	ns
	Hw.w			1	ns	0.27^{*}	0.71^{***}	ns	ns
	Sw.w				1	ns	0.61^{***}	-0.25^{*}	0.29^{*}
6 Bunkris	**Hw.ar**	1	ns	0.63^{***}	-0.49^{**}	0.44^{**}	ns	0.47^{**}	ns
n=40	**Sw.ar**		1	ns	ns	0.40^{*}	ns	ns	ns
	Hw.w			1	ns	0.36^{*}	0.70^{***}	ns	ns
	Sw.w				1	ns	0.54^{***}	-0.48^{**}	0.50^{**}
7 Ovansjö	**Hw.ar**	1	-0.86^{***}	0.48^{**}	ns	0.46^{**}	0.46^{**}	ns	ns
n=36	**Sw.ar**		1	ns	-0.38^{*}	-0.42^{*}	-0.44^{*}	ns	-0.32^{*}
	Hw.w			1	ns	0.47^{**}	0.67^{***}	0.37^{*}	ns
	Sw.w				1	0.42^{**}	0.66^{***}	ns	0.46^{**}

Table 6. – Results from regression analyses between wood traits, and between wood traits and tree size traits on individual trees. The STEFANSSON series, *a)* all sites, *b)* each site separately. Abbreviations and significances: see *table 4.*

a)

		Hw.ar	Sw.ar	Hw.w	Sw.w	H	D1.3	Cr.lim	Cr.l
All sites$^{1)}$	**Hw.ar**	1	-0.76***	0.67**	-0.18**	ns	0.52***	0.16*	ns
	Sw.ar		1	-0.73***	0.19***	-0.29***	-0.51***	-0.25***	-0.19**
	Hw.w			1	ns	0.44***	0.79***	0.43***	0.25***
	Sw.w				1	0.26***	0.55***	0.15*	0.23**

b)

		Hw.ar	Sw.ar	Hw.w	Sw.w	H	D1.3	Cr.lim	Cr.l
1 Brattfors	**Hw.ar**	1	-0.79***	0.73***	-0.50***	ns	ns	ns	0.24*
n=66	**Sw.ar**		1	-0.62***	0.64***	ns	ns	ns	ns
	Hw.w			1	-0.31*	ns	0.51***	ns	ns
	Sw.w				1	ns	0.61***	ns	ns
2 Björkvattnet	**Hw.ar**	1	-0.56***	0.76***	ns	ns	0.60***	ns	ns
n=56	**Sw.ar**		1	-0.52***	0.38**	ns	ns	ns	ns
	Hw.w			1	ns	ns	0.61***	ns	ns
	Sw.w				1	ns	0.54***	ns	ns
3 Laxå$^{2)}$	**Hw.ar**	1	-0.77***	0.56***	-0.27**	ns	ns	ns	ns
	Sw.ar		1	-0.35***	0.32**	ns	ns	ns	ns
	Hw.w			1	ns	0.29*	0.42***	0.43***	ns
	Sw.w				1	0.38**	0.71***	ns	0.52***

$^{1)}$ n = 219 for wood traits, n = 183 for tree size traits
$^{2)}$ n = 97 for wood traits, n = 61 for tree size traits

and contradicting: for *Hw.ar,* tree height was positively correlated at five sites (r=0.30 to 0.46), while the relationship between tree height and *Sw.ar* showed no clear positive relationship (r=–0.42 to 0.40 at three sites). Also, tree height was more strongly correlated to *Hw.w* than to *Sw.w* (r=0.27 to 0.48 at six test sites for heartwood, and r=0.42 to 0.45 at two test sites for sapwood). Crown length and crown limit were often weakly correlated to heartwood and sapwood traits.

In the STEFANSSON series, the regressions between *Hw.ar* and *Hw.w* were strongly positively correlated at all test sites (r=0.56 to 0.76), while these regressions for sapwood were somewhat weaker (r=0.32 to 0.64) *(Table 6). Hw.w* and *Sw.w* were, however, weakly correlated. Among tree size traits, the only clear relationship was for stem diameter with *Hw.w* (r=0.42 to 0.61), and *Sw.w* (r=0.54 to 0.71). Neither *Hw.ar* nor *Sw.ar* were, on the other hand, correlated to tree size.

Transfer effects

With just a few exceptions, there was no latitudinal influence on wood and tree size traits *(Table 7).* In the joint analysis of the sites in the SCHOTTE series, however, latitude of provenance origin was strongly negatively correlated with both *Hw.w* and *Sw.w* (r=–0.61 and –0.78, respectively), and positively correlated with number of sapwood annual rings (r=0.41), while nearly all correlations were weak in the STEFANSSON series. For tree size data, in the SCHOTTE series, stem diameter and crown length were negatively correlated to latitude of origin (r=–0.86 and r=–0.85, respectively).

Discussion

When analysing provenance differences in the two test series, it is necessary to consider the pattern of provenance origin. The SCHOTTE series includes, in addition to the local

Table 7. – Correlation coefficients *(r)* and significances of regressions between wood traits and tree size traits, and latitude of provenance origin. All sites and each site separately, *a)* the SCHOTTE series, *b)* the STEFANSSON series. Only significant regressions are given. Abbreviations and significances: see *table 4.*

	Test site	Wood traits Trait	 r	Tree size traits Trait	 r
a)	All test sites	Sw a.r.	0.41**	D1.3	-0.86*
		Hw w.	-0.61***	Cr. l.	-0.85***
		Sw w.	-0.78**	–	
	1 Alträsk, BD	Hw a.r.	-0.67*	Cr. l.	-0.74*
		Sw a.r.	0.67*		
	2 Bocken, AC	–		D1.3	-0.93*
				Cr. lim.	-0.90*
	3 Svartberget, AC	–		–	
	4 Hårkaskogen, Z	Hw w.		-0.87*	
	5 Frösön, Z	–		–	
	6 Bunkris, W	Hw a.r.	0.91**	H.	0.87**
		Sw w.	-0.85**	Cr. lim.	0.95***
				Cr. l.	-0.81*
	7 Ovansjö, X	–		–	
b)	All test sites	–		–	
	1 Brattfors, AC	–		–	
	2 Björkvattnet, Y	Sw w.	0.66**	D1.3	0.39*
	3 Laxå, N	–		–	

provenance, provenances from latitude 57.6°N to 66.0°N, which were transferred northwards *(Table 2)*. In the Stefansson series, on the other hand, the choice of provenances represent a narrow clinal transect of 64.6°N to 67.7°N, and the provenances were transferred southwards, apart from three provenances of local or more southerly origin *(Table 3)*. Because of these differences in provenance origin, and the age difference of ca 40 years between the test series, different patterns of provenance variation was possible. One observed difference was that, although significant site differences for wood traits in both series (*Table 4),* there were interaction effects between site and provenance-within-site in the Schotte series but not in the Stefansson series (with the exception of *Sw.w*). The reason may be that the larger latitudinal interval covered in the Schotte series would modify the performance of those traits to a larger extent in this series compared to the Stefansson series. For tree size traits, interaction effects were, however, general. With the exception of *Sw.w,* only site 3 in the Schotte series (Svartberget) differed significantly between provenances for all wood traits. Otherwise, height, crown limit and crown length in the Schotte series showed more frequent provenance differences than wood traits. In the Stefansson series, provenance differences in height occurred in all test sites. With the exception of totally three test sites among the two test series, stem diameter and *Sw.w* did not differ significantly in any site *(Table 4)*. Stem diameter and *Sw.w* showed at the same time strong correlation *(Tables 5* and *6)*, and a reasonable conclusion is that they are under stronger environmental influence than the other traits. Mörling and Valinger (1998) showed that the yield increment over a 12-year period following thinning and/or fertilization of a 45-year-old Scots pine stand in northern Sweden was accounted for mainly by sapwood expansion, the contribution of heartwood expansion being insignificant. This observation agrees with the model proposing that a sudden growth in stem diameter (for any reason) is due to expansion of the sapwood and not the heartwood. In our material, however, *Hw.w* was also correlated to stem diameter, and we can not exclude the possibility that a sudden growth in stem diameter also induces a corresponding expansion in heartwood. It should however be kept in mind that some fraction of the correlation between stem diameter and *Hw.w* or *Sw.w* with necessity should be attributed to autocorrelation.

Correlation between traits

When discussing correlation coefficients including wood traits and between wood traits and tree size traits, it should be noted that they may be overestimated due to autocorrelation, especially since the regression analyses were derived using individual tree data. Although both *Sw.w* and *Hw.w* were correlated to stem diameter in both test series, there was no relationship between *Sw.w* and *Hw.w.* This lack of correlation between *Sw.w* and *Hw.w*, together with the non-common significant differences for both *Sw.w* and stem diameter, and the findings in Mörling and Valinger (1998), support the model advocating that sapwood, but not heartwood expands as a result of stem diameter growth at mature age.

The fact that *Hw.w* and bole straightness were the only traits that showed substantial heritability in data presented in Fries and Ericsson (1998) and Ericsson and Fries (1998) suggests less strong environmental influence on those traits than on growth traits and *Sw.w.* According to those studies, and the present, heartwood seems to resemble a quality trait in terms of its regulation, and this do not contradict the suggestion by Mörling and Valinger (1998) that heartwood not is actively regulated in accordance with changing growth conditions.

Perttunen et al. (1996) suggest that certain pipes in the sapwood, transporting water and photosynthates, continue to certain branches and leaves in the crown. This mechanistic model should give a functional relationship between amount of sapwood at a certain height and size of the green crown above this height (here estimated by crown length). The amount of the sapwood in terms of its area depends not only on the width of the sapwood, but also on the width of the heartwood section inside the sapwood. The above relationship should, thus, be determined by the area of the sapwood rather than its width, and the correlations between crown length and *Sw.w* shown in *tables 5* and *6* do, therefore, not necessarily depend on the above functional relationship. As shown by the positive correlation between *Hw.ar* and height in the mature test series (the Schotte series), and between *Hw.ar* and stem diameter in both series, it seems possible to combine heartwood formation and mature volume production in breeding programs. In the younger test series, the Stefansson series, there was a positive correlation between *Hw.w* and height, while there was no correlation between *Hw.ar* and height. This indicates that the time for onset of heartwood formation may be a limiting factor for high heartwood production. Knowledge on which factors that triggers the onset of heartwood formation is thus needed for developing methods for intentionally inducing heartwood formation at low age. Combining onset of heartwood formation at low age, and rapid early stem diameter expansion, should in theory produce large amount of heartwood later thanks to wider annual rings at low age. Many factors influence, however, growth rate and growth pattern, and one potentially misleading factor is that by boring at breast height, we have measured the number of heartwood annual rings that has formed after reaching breast height. This may certainly be connected to the growth capacity over the whole rotation, but also to e.g. the rate of establishment and early growth rate.

These studies on the influence of provenance origin on heartwood and sapwood traits do not demonstrate any significant provenance or transfer effects. Testing provenances in Sweden imply a latitudinal transfer and use of material under conditions to which they are not adapted. Provenance differences and transfer effects become, thus, confounded and require large systematic provenance test series that are followed to high age to be possible to separate and prove with significance. From these data, it seems, however, probable that the amount of sapwood, i.e. sapwood width, is mostly dependent on those factors that allow for volume growth also at high age, e.g. good adaptation and wide spacing. Heartwood formation, on the other hand, may be genetically influenced not only by being strongly inherited, i.e. having high heritability (Fries and Ericsson, 1998; Ericsson and Fries, 1998), but possibly also genetically influenced by provenance origin or latitudinal transfer. One conclusion from this study is, however, that there is no risk to loose any heartwood formation capacity by transferring Scots pine according to the Swedish transfer recommendations.

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Root Induction in Microshoots of *Simarouba glauca* L. In Vitro: Peroxidase as a Marker for Rooting

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Abstract

Induction of rooting in microshoots of *Simarouba glauca* L. was achieved within 12 to 15 days of culture on Murashige and Skoog's (1962) medium supplemented with 1.0 mg/l IBA and 3% (w/v) sucrose. There was no spontaneous rooting observed without the application of auxins. Peroxidase activity was the minimum at the induction phase and maximum at the initiation and expression phase grown on medium containing 1.0 mg/l IBA. Rooting was associated with selective expression or repression of isoforms of peroxidase during induction, initiation and expression phase. This study indicates a key role of peroxidase in rooting of microshoots of *Simarouba glauca in vitro*.

Key words: biochemical marker, *in vitro*, peroxidase activity, rooting, *Simarouba glauca*, tree.

FDC: 165.44; 161.4; 181.36; 176.1 *Simarouba glauca*.

Abbreviations: IBA, indole-3-butyric acid; MS, Murashige and Skoog's (1962); PVP, Polyvinyl-pyrrolidone; BA, 6-benzyladenine; NAA, a-naphthaleneacetic acid.

Introduction

Simarouba glauca L. (Simaroubaceae), a fast growing multipurpose tree, grows even on marginal lands under water stress conditions and yields edible oil to the extent of about 60 % of kernels (Rout and Das, 1994). *In vitro* micropropagation of *Simarouba glauca* was reported by Rout and Das (1995). Rooting of microshoots is critical in plant production systems *in vitro*. Induction of rooting for a long time has been considered as a single-phase process but successively there were several reports where the adventitious rooting depended on a series of interdependent phases (induction, initiation and expression) (Moncousin *et al.*, 1988; Gaspar *et al.*, 1992, 1994). Various studies on adventitious root formation in microshoots have shown the fundamental role played by peroxidases in controlling rooting *in vitro* (Quoirin *et al.,* 1974; Van Hoof and Gaspar, 1976; Moncousin and Gaspar, 1983; Berthon *et al.,* 1987; Hausman,

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