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Transfer effects and variations in basic density and tracheid length of *Pinus sylvestris* L. populations

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Abstract

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Basic density and tracheid length were assessed in 67 provenances from one or more of 18 provenance trials at the age of 30 years. From each provenance and trial 10 trees were sampled from a 1.25 metre spacing and 10 trees from a 2.0 metre spacing whenever possible. Assessments were made at growth rings five and ten respectively from the bark for basic density and at growth ring five from the bark for tracheid length.

Provenance variation was significant for basic density and tracheid length in 50% of the trials. A narrow spacing increased basic density but tracheid length was not changed. Basic density was low in trees with large diameter or wide growth rings and in assessments made close to the pith. Tracheid length was short in short trees and assessments made close to the pith. Contour plots of basic density and tracheid length indicate that low values are obtained for northern latitudes and high altitudes. Tracheid length was also reduced at coastal sites. Transfer functions indicate in general that a southward and upward transfer increases basic density and fibre length.

The study indicates that changes in forest management and forest tree breeding are needed in order to increase basic density and fibre length.

Key words: Pinus sylvestris L., provenance, basic density, tracheid length, variation, transfer, spacing.

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Introduction

Wood density and tracheid properties significantly affect both the quality and yield of pulp and paper, and the strength and utility of sawn products. The control of wood density and tracheid properties should therefore form part of the silvicultural planning and forest tree improvement programme.

In the Nordic countries, there have been numerous studies of variation and control of wood density and tracheid dimensions. A summary of older literature is given by Ericson (1966), while Zobel & Talbert (1984) summarize more recent knowledge of this subject.

Basically, there are three ways of controlling the quality of the raw material: changing wood quality by silvicultural methods (Ericson, 1966; Uusvaara, 1974; 1985; Persson, 1976, 1977), utilization of the geographical variation in quality (Nylinder & Hägglund, 1954; Ericson, 1966; Hakkila & Panhelainen, 1970; Ericson, Johnsson & Persson, 1973; Uusvaara, 1974; Björklund, 1984), and manipulation of wood quality by provenance transfer or in forest tree improvement programmes (Ericson, 1960; Persson, 1972; Remröd, 1976).

Geographical variation in wood density and tracheid length in Sweden is fairly well known. There are, however, few results which describe the magnitude and sources of provenance variation or the effect of provenance transfer on wood density and tracheid length.

The aim of this study is to describe the magnitude and sources of provenance variation in wood density and tracheid length in Sweden.

Material and methods

Material

In the years 1951–53, a large-scale Scots pine *(Pinus sylvestris L.)* population series was planted in Sweden (Eiche, 1966). The series comprises 29 trial locations, covering latitudes 59°–68°N and altitudes between 5–765 metres above sea level.

Figure 1 shows both the origin of the populations and the location of each trial. Each site includes 7 or 14 provenances. The experiments are incomplete Latin squares, (Youden squares; Cochran & Cox, 1957), with seven treatments and four replications. The trials which comprise 14 provenances are not true Youden squares, although the randomization and restrictions included are based on the same assumptions. In each trial, two of the four replications have a 1.25×1.25 m spacing, the others 2.0×2.0 m spacing. Each plot contains 80 or 50 trees at the narrow and the wide spacing, respectively.

The series was inventoried when the age of the trees from planting was between 29 and 31 years, and at the same time, each trial was thinned. The material in this study is a sample of the trees removed by thinning.

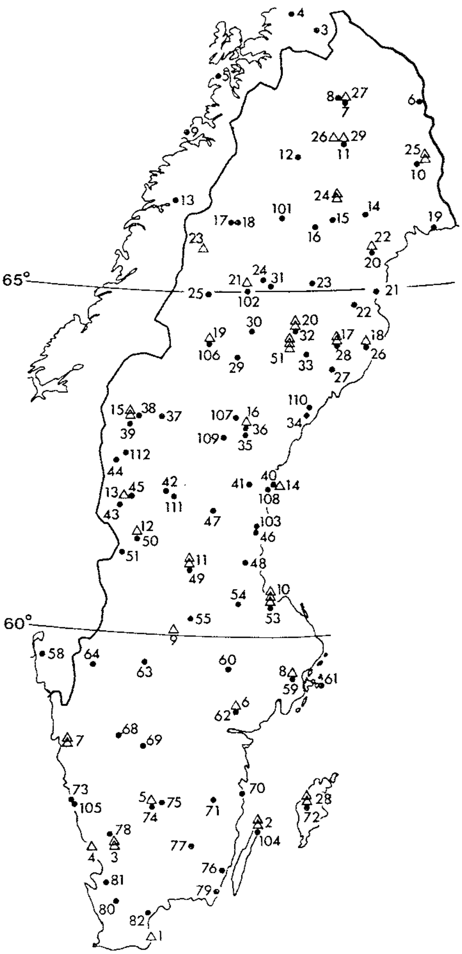
Table 1 shows both the trials included and the provenances sampled in each trial. In all 67 provenances were sampled in 18 provenance trials.

For each population and replication in each trial, five of the trees removed were sampled where possible. The following categories were selected: The tree with the largest diameter, a tree with a diameter corresponding to the mean for the standing trees and three trees with intermediate diameters. From each of these trees a 200 mm thick disc was cut at a height of three metres.

The three metre height for assessment was necessary, since close to 2,000 logs were used and these belonged to the landowners. The logs were therefore intended for use as pulpwood in three-metre standard lengths.

The sampled trees were measured in the same way as other trees in the series, i.e. they were assessed for height, diameter, bark thickness, height to first live branch, stem straightness and number of spike knots.

The discs were treated in the following way for trees removed in 1981. For assessment of tracheid length, a sample of latewood with an approximate diameter of 4.5 mm was extracted with an increment borer from the fifth growth ring from bark. For assessing density, an increment core was bored straight through the disc and two samples were taken from growth rings 4–6 (D_1), two from growth rings 9–11



Experimental plantations nos. 1–29 and 51

△ = 7 populations tested

△△ = 14 populations tested

△△△ = 20 populations tested

● = localities of populations nos. 1–112

Populations not shown on the map originating from:

Provenance no.	*Lat. N*	*Long. E*
Norway		
1	69°48′	23°20′
2	69°55′	23°15′
56	59°35′	07°50′
57	60°12′	05°23′
Germany		
84	52°40′	10°42′
85	50°10′	12°07′
86	49°45′	11°33′
87	49°22′	11°38′
88	49°17′	12°18′
89	49°12′	12°17′
90	47°38′	13°00′
91	50°45′	09°28′
92	50°02′	08°58′
Holland		
93	51°25′	04°45′

Fig. 1. Origin of populations and location of trials in the Scots pine population series established in the years 1951–1953.

Table 1. *Trials included in study and provenances sampled in each trial*

Trial no.	Latitude, °N	Longitude, °E	Altitude, m	Provenances included in study
1	55°37′	14°15′	55	42, 74, 79, 81, 82, 85, 93
2	57°19′	17°07′	10	23, 40, 42, 57, 68, 71, 74, 78, 84, 93, 104, 105
4	56°52′	12°35′	15	42, 61, 74, 78, 84, 93, 105
6	56°58′	16°24′	50	40, 42, 61, 62, 74, 76, 91
7	58°27′	11°46′	130	42, 46, 48, 55, 59, 63, 68, 69, 74, 77, 78, 80, 93, 105
8	59°25′	18°12′	25	21, 42, 56, 57, 59, 74, 84
9	60°04′	14°33′	325	35, 40, 42, 51, 55, 70, 74
10:1	60°33′	17°28′	20	29, 40, 42, 53, 54, 56, 64, 71, 72, 74, 105
10:2	60°33′	17°28′	20	53, 85, 86, 87, 89, 93
11	61°05′	14°58′	365	21, 33, 40, 42, 49, 51, 53, 56, 58, 74, 82
14	62°12′	17°42′	15	21, 23, 40, 42, 56, 61, 74
15	63°11′	13°06′	525	10, 23, 25, 34, 36, 37, 38, 39, 42, 50, 107
18	64°10′	20°52′	40	10, 23, 26, 42, 102, 103
19	64°19′	15°20′	350	4, 10, 23, 26, 42, 50, 106
20	64°34′	18°15′	455	10, 11, 13, 19, 23, 28, 32, 101
22	65°39′	21°07′	60	10, 11, 20, 23, 34
25	65°56′	23°12′	200	4, 10, 11, 13, 19, 101
28	57°39′	18°22′	55	72, 74, 84, 86, 88, 89, 91, 92, 93

(D_2) and where possible, two from growth rings 14–16 (D_3) from the bark.

For trees removed in 1982, the same procedure was followed, but samples were taken from growth ring 6 for assessing tracheids and from growth rings 5–7 (D_1), 10–12 (D_2) and 15–17 (D_3) for density assessments.

For trees removed in 1983, samples were taken from growth ring 7 for assessing tracheids and from growth rings 6–8 (D_1), 11–13 (D_2) and 16–18 (D_3) for density assessments.

The following procedure was used for assessing tracheid length: from each sample, thin slices of latewood were placed in test tubes and treated with equal volumes of hydrogen peroxide and acetic acid for 24 hours at 60°C. The sample was washed and rinsed. The test tube was half-filled with distilled water, and shaken to separate fibres. Water was suctioned off and the sample stained with fuchsin. The sample was rinsed and washed once more. Finally, the test tube was half-filled with distilled water and three drops of formaldehyde added, to preserve the sample. Twenty-five unbroken tracheids were measured in a microscope equipped with a measuring micrometer.

For assessing density, the mercury immersion method described by Ericson (1959) was used.

The arguments for the use of latewood from growth rings 5, 6 and 7 for tracheid length assessments were three. The wood sample analysed should be produced in the same year in all trees; the sample should be extracted close to the bark to avoid juvenile wood; latewood was assessed in all samples to reduce the variation within each sample.

The choice of samples for basic density assessment was the same as above, but here larger wood samples made the determination of basic density more reliable. By including wood samples closer to the pith, the gradual change from juvenile to adult wood could be detected.

Statistical methods

Mean values, standard deviations, analyses of variance, analyses of regression, correlation coefficients and partial correlation coefficients were calculated with a standard programme for statistical analysis, SISS (Öberg, S. 1985, SISS—Swedish Interactive Statistical System). The method used for graphical presentation of the regression analyses is the same as that described by Kung & Clausen (1984) and by Prescher (1986), but was modified to suit the ND 520 computer at Garpenberg.

In this study the following notations are used to indicate significance levels:

ns	not significant at 5 per cent level
*	significant at 5 per cent level
**	significant at 1 per cent level
***	significant at 0.1 per cent level.

In order to describe basic density and tracheid length at different trials, and furthermore to formulate general models and transfer functions, a three-step procedure was used.

The first step was to calculate the basic density (BD_1) and tracheid length (TRL) of the zero-transfer at each trial (Figs. 3 and 4). This zero transfer value was estimated by regression analyses at each trial using BD_1 and TRL as dependent variables. Transfer in latitude (ΔLAT) and altitude (ΔALT), the transfers squared (ΔLAT^2, ΔALT^2) and the transfer product ($\Delta LAT \times \Delta ALT$) were used as independent variables. The values obtained for zero transfer in the transfer function were then used as the estimated value of the local population.

There are three reasons for using a calculated value (zero transfer) to estimate the value of the local provenance at different trials. In some of the trials there is no local provenance included, i.e. an adjacent provenance would have to be used instead; by using a calculated value for the local provenance (zero transfer), we avoid the effect of an individual provenance being genetically good or poor when in fact we wish to calculate the value of the site; and by using the whole material instead of a single provenance value, we increase the reliability of the estimate. Eriksson et al. (1980) discuss the advantages of this method when used in calculations of mortality rates.

The second step was to calculate the model for basic density (BD_1) variation and tracheid length (TRL) variation (Figs. 5 and 6). The estimated value for the local provenance was used as dependent variable. Latitude, altitude, their square and their product were used as independent variables.

The third step was to calculate the transfer function. The independent variables used in the regressions analyses were the same as in the first step. The dependent variables used were relative basic density (RBD_1) and relative tracheid length ($RTRL$), i.e. actual provenance value divided by the calculated value for the local provenance. Using these values, the results from the different trials could be merged into different groups. Through an iterative test of different groups, the final transfer models were formed. The aim was to find groups of adjacent trials with similar patterns of variation.

The abbreviations and units used in the study are presented in Table 2.

Table 2. *Traits analysed; their abbreviation and units used*

Trait	Abbreviation	Unit
Basic density of growth ring 4 to 6 counted from bark	BD_1	g/cm^3
Width of growth ring 4 to 6 counted from bark	L_1	mm
Basic density of growth ring 9 to 11 counted from bark	BD_2	g/cm^3
Width of growth ring 9 to 11 counted from bark	L_2	mm
Basic density of growth ring 14 to 16 counted from bark	BD_3	g/cm^3
Width of growth ring 14 to 16 counted from bark	L_3	mm
Tracheid length from sample at growth ring 5 counted from bark	*TRL*	mm
Diameter at breast height	*DBH*	cm
Height	*H*	m
Volume/stem	*VST*	dm^3
Number of growth rings from pith to point of assessment	*AGE*	
Basic density in relation to calculated basic density for the local provenance at each trial	RBD_1	
Tracheid length in relation to the calculated tracheid length for the local provenance at each trial	*RTRL*	

Results

Mean values and standard deviations for basic density and tracheid length are presented in Table 3, together with a test of significance for population variation. Note that all populations and both spacings are included in these values.

The relation between the values of sampled trees in the two spacings is presented in Figure 2. The comparison is limited to populations and trials where sampling was done at both spacings.

Partial correlation coefficients are used to eliminate site differences and facilitate understanding of the results. The partial correlation coefficients, which indicate the relationship between different characters, are presented for individual trees (Table 4) and for population mean values (Table 5).

The calculated basic density values for the local population in each trial are presented in Figure 3 ($S_{y \cdot x}$<0.02). Corresponding values for tracheid length are presented in Figure 4 ($S_{y \cdot x}$<0.25). Based on these values, a model for basic density variation in Sweden is presented in Figure 5. (The values from trial 25 are excluded from this model.) A corresponding model for variation in tracheid length is presented in Figure 6. The calculations were based on samples taken from the 1.25 m spacing.

The effect of population transfer on basic density (BD_1) is presented in Figures 7 to 9 for southern, central and northern Sweden, respectively. In Figure 10, the optimum transfer is given for these three regions.

The effect of population transfer on tracheid length is presented in Figures 11 to 13 for low altitude in southern Sweden and northern Sweden and for high altitude in northern Sweden, respectively. The optimum transfer for the three regions is presented in Figure 14.

The variation in basic density (BD_1) for populations when tested at different sites is indicated in Figure 15 for population 42 and in Figure 16 for population 74. Variation in tracheid length for population 42 is presented in Figure 17 and for population 74 in Figure 18.

The difference in height between the mean sample value and the total mean value for each population in the 1.25 metre spacing is presented in Figure 19.

Table 3. *Mean values ($\bar{x}$) and standard deviation of mean values (s) for basic density and tracheid length in different trials. Significant variation between populations is shown by asterisks*

Trial no.	BD_1		BD_2		*TRL*	
	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s
1	0.327	0.028	0.309	0.038	2.44	0.25
2	0.343	0.037	0.311*	0.030	2.77**	0.23
4	0.369**	0.040	0.340**	0.044	1.98	0.23
6	0.356**	0.036	0.343**	0.033	2.63*	0.28
7	0.358*	0.032	0.332**	0.031	2.64*	0.21
8	0.362	0.034	0.330	0.032	2.46**	0.27
9	0.318	0.027	0.308*	0.022	–	–
10.1	0.365	0.032	0.339	0.037	2.58**	0.25
10.2	0.329**	0.033	0.308**	0.034	2.76	0.24
11	0.311*	0.027	0.303*	0.026	2.44**	0.29
14	0.320	0.027	0.298	0.029	1.94	0.14
15	0.327**	0.025	–	–	1.66	0.24
18	0.314	0.028	0.309	0.026	2.11	0.16
19	0.320*	0.024	0.314	0.023	2.12	0.22
20	0.320**	0.030	–	–	1.99	0.24
22	0.320	0.023	0.317	0.028	–	–
25	0.352	0.028	0.338	0.029	1.97	0.18
28	0.322**	0.028	0.317**	0.032	–	–

Table 4. *Partial correlation coefficients (site differences eliminated). Single-tree values (df>1,500)*

	BD_2	TRL	DBH	H	VST	AGE	L_1	L_2
BD_1	0.599***	−0.001^{ns}	−0.134***	0.064*	−0.105***	0.133***	−0.200***	−0.254***
BD_2		−0.036^{ns}	−0.162***	−0.020^{ns}	−0.164***	0.117***	−0.187***	−0.306***
TRL			0.204***	0.280***	0.182***	0.326***	−0.085***	−0.075**

Table 5. *Partial correlation coefficients (site differences eliminated). Provenance mean values (df>200)*

	BD_2	TRL	DBH	H	VST	AGE	L_1	L_2
BD_1	0.591***	0.150*	−0.258***	−0.144*	−0.197**	0.152*	−0.408***	−0.346***
BD_2		0.109^{ns}	−0.263***	−0.244***	−0.299***	0.159*	−0.378***	−0.390***
TRL			0.171*	0.230***	0.088^{ns}	0.518***	−0.228**	−0.155*

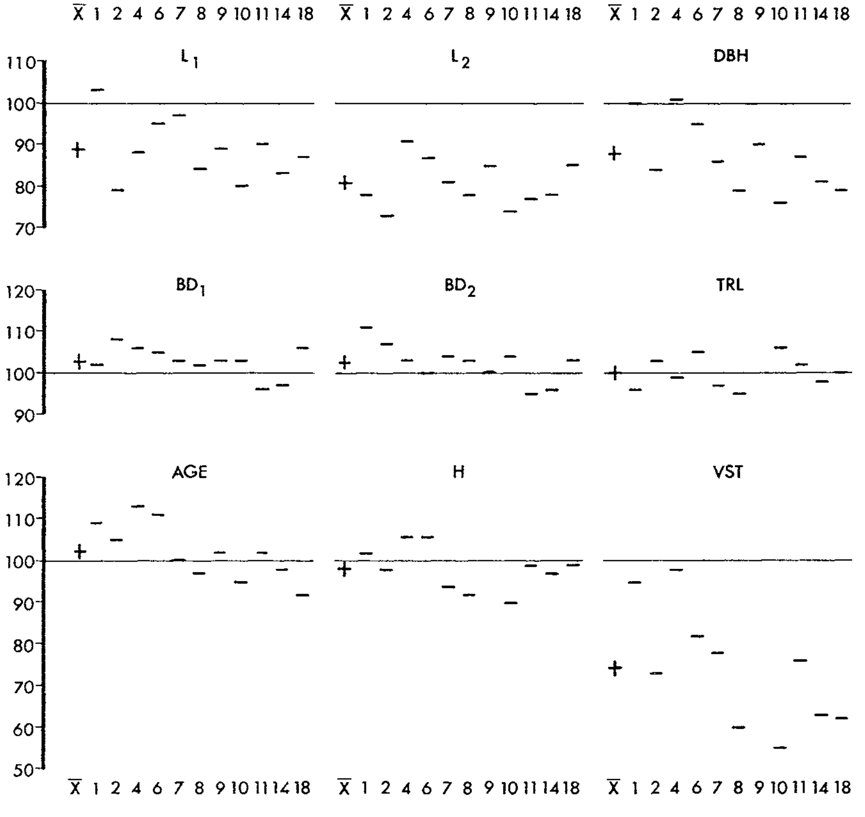


Fig. 2. Total mean (+) and trial mean values (−) for different traits in the 1.25 m spacing in relation to the 2.0 m spacing (1.25 m spacing value × 100/2.0 m spacing value).

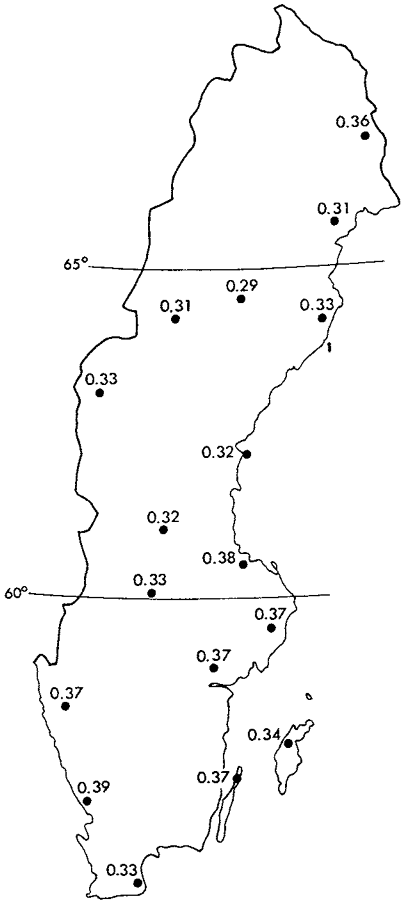


Fig. 3. Calculated basic density values (BD_1) for the local population at each trial ($S_{y \cdot x}<0.02$).

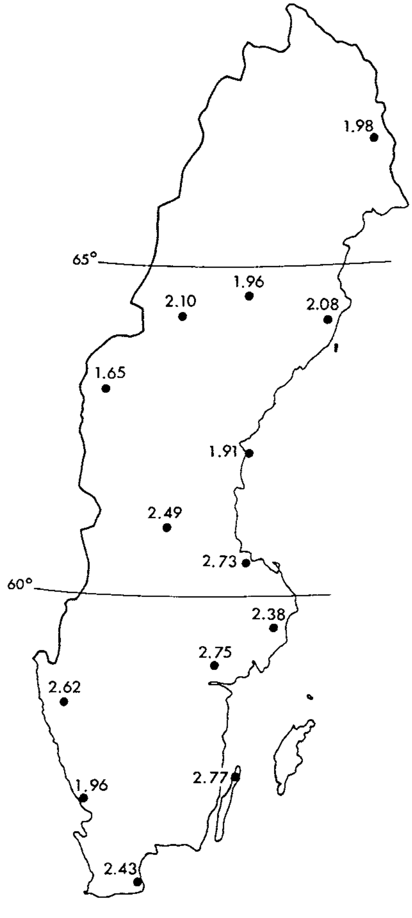


Fig. 4. Calculated fibre length (TRL) for the local population at each trial ($S_{y \cdot x}<0.25$).

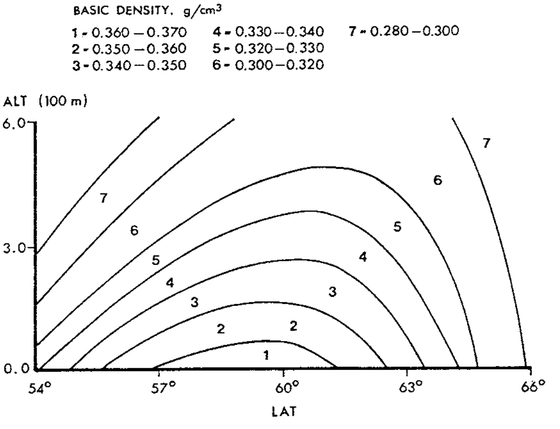


Fig. 5. Model of basic density variation in Sweden.
$BD_1=0.366-0.0026(LAT-60°)-0.0015(LAT-60°)^2$
$-0.0097ALT+0.0012(LAT-60°)ALT$.
$R=0.82$, $F=5.07$, $n=15$ ($S_{y \cdot x}=0.019$).

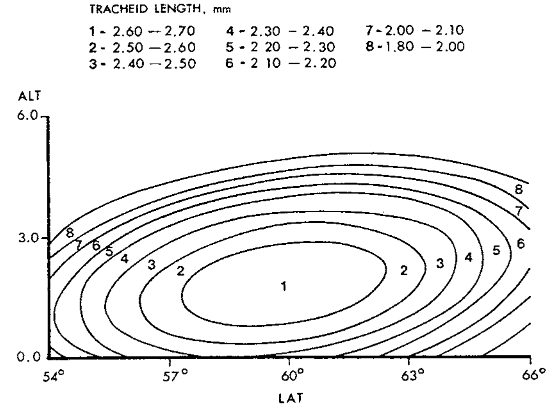


Fig. 6. Model of tracheid length variation in Sweden.
$TRL=2.38+0.023(LAT-60°)ALT-0.017(LAT-60°)^2$
$-0.092ALT^2+0.341ALT-0.048(LAT-60°)$.
$R=0.80$, $F=2.83$, $n=14$ ($S_{y \cdot x}=0.28$).

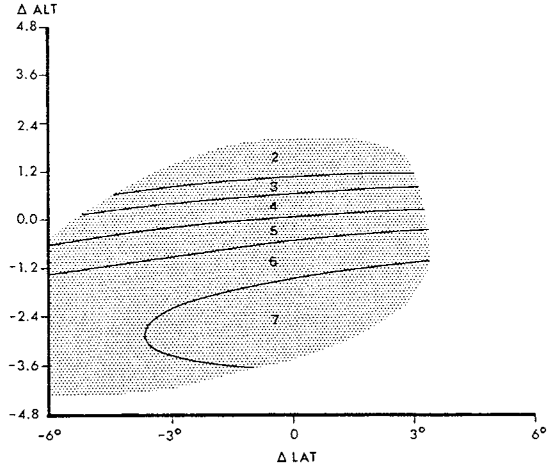


Fig. 7. Transfer effect on relative basic density (RBD_1) in southern Sweden (trial nos. 1. 2, 4, 6, 7 and 8).
$RBD_1 = 1.009 + 0.0360 \triangle ALT + 0.0065 \triangle ALT^2 - 0.0029 \triangle LAT$.
$R = 0.68$, $F = 8.74$, $n = 35$ ($S_{y \cdot x} = 0.028$).
$\triangle ALT+$ Transfer to a higher altitude
$\triangle ALT-$ Transfer to a lower altitude
$\triangle LAT+$ Transfer to a more northern location
$\triangle LAT-$ Transfer to a more southern location

Units in Figure refer to the following classes:

1 = 1.10–1.15	4 = 1.01–1.03	7 = 0.95–0.97
2 = 1.05–1.10	5 = 0.99–1.01	8 = 0.90–0.95
3 = 1.03–1.05	6 = 0.97–0.99	9 = 0.85–0.90

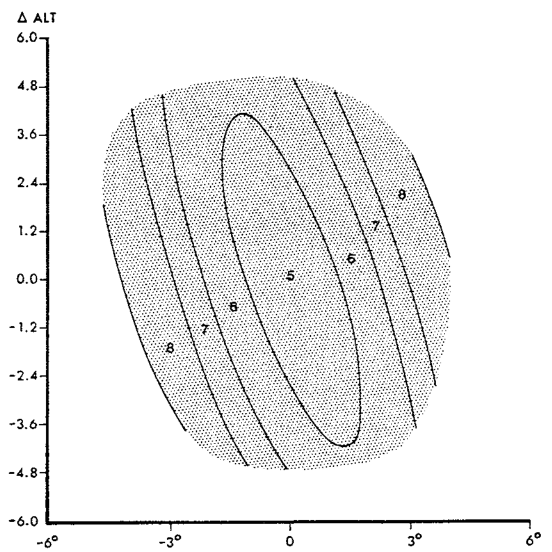


Fig. 8. Transfer effect on relative basic density in central Sweden (trial nos. 9, 10 and 11)
$RBD_1 = 0.997 - 0.0056 \triangle LAT^2 - 0.0036 \triangle LAT \times \triangle ALT - 0.0010 \triangle ALT^2$
$R = 0.60$, $F = 3.68$, $n = 24$ ($S_{y \cdot x} = 0.033$).
$\triangle ALT+$ Transfer to a higher altitude
$\triangle ALT-$ Transfer to a lower altitude
$\triangle LAT+$ Transfer to a more northern location
$\triangle LAT-$ Transfer to a more southern location
Units as in Figure 7.

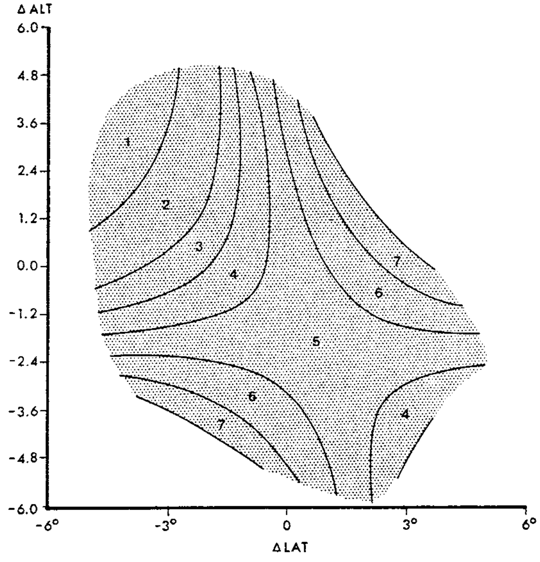


Fig. 9. Transfer effect on relative basic density in northern Sweden (trial nos. 14, 15, 18, 19, 20 and 25).
$RBD_1 = 1.003 + 0.0069 \triangle LAT \times \triangle ALT - 0.0136 \triangle LAT - 0.0015 \triangle ALT^2$
$R = 0.60$, $F = 7.01$, $n = 42$ ($S_{y \cdot x} = 0.046$).
$\triangle ALT+$ Transfer to a higher altitude
$\triangle ALT-$ Transfer to a lower altitude
$\triangle LAT+$ Transfer to a more northern location
$\triangle LAT-$ Transfer to a more southern location
Units as in Figure 7.

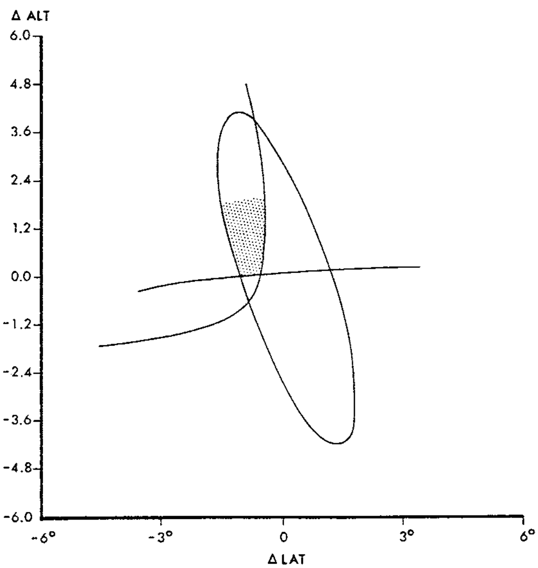


Fig. 10. Mode of transfer which yields basic density equal to or higher than that of the local population. Values greater than or equal to 1.0 in Figures 7–9 shaded.
$\triangle ALT+$ Transfer to a higher altitude
$\triangle ALT-$ Transfer to a lower altitude
$\triangle LAT+$ Transfer to a more northern location
$\triangle LAT-$ Transfer to a more southern location
Units as in Figure 7.

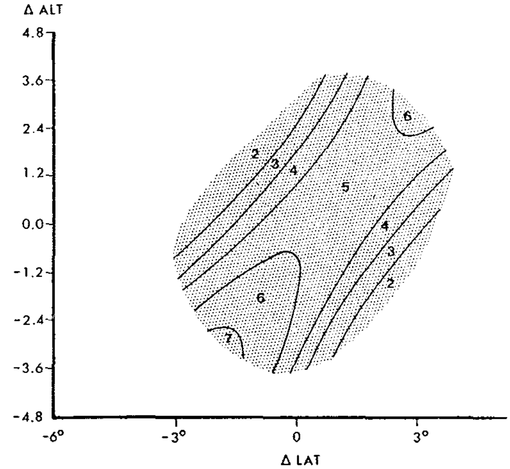


Fig. 11. Transfer effects on relative tracheid length in south and central Sweden (trial nos. 1, 2, 4, 6, 7, 8 and 11),
$RTRL = 0.996 - 0.0145 \triangle LAT \times \triangle ALT + 0.0079 \triangle LAT^2 + 0.0115 \triangle ALT - 0.0045 \triangle ALT^2 - 0.0093 \triangle LAT$
$R = 0.46$, $F = 1.40$, $n = 32$ ($S_{y \cdot x} = 0.046$).
$\triangle ALT+$ Transfer to a higher altitude
$\triangle ALT-$ Transfer to a lower altitude
$\triangle LAT+$ Transfer to a more northern location
$\triangle LAT-$ Transfer to a more southern location
Units as in Figure 7.

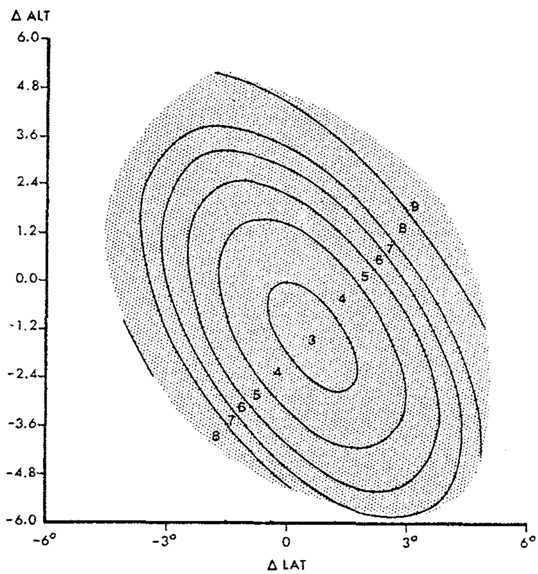


Fig. 12. The effect of population transfer on relative tracheid length on low altitudes in northern Sweden (trial nos. 10:1, 18, 20 and 25).
$RTRL = 1.029 - 0.0046 \triangle ALT^2 - 0.0066 \triangle LAT^2 - 0.0061 \triangle LAT \times \triangle ALT - 0.0087 \triangle ALT$
$R = 0.62$, $F = 2.93$, $n = 24$ ($S_{y \cdot x} = 0.040$).
$\triangle ALT+$ Transfer to a higher altitude
$\triangle ALT-$ Transfer to a lower altitude
$\triangle LAT+$ Transfer to a more northern location
$\triangle LAT-$ Transfer to a more southern location
Units as in Figure 7.

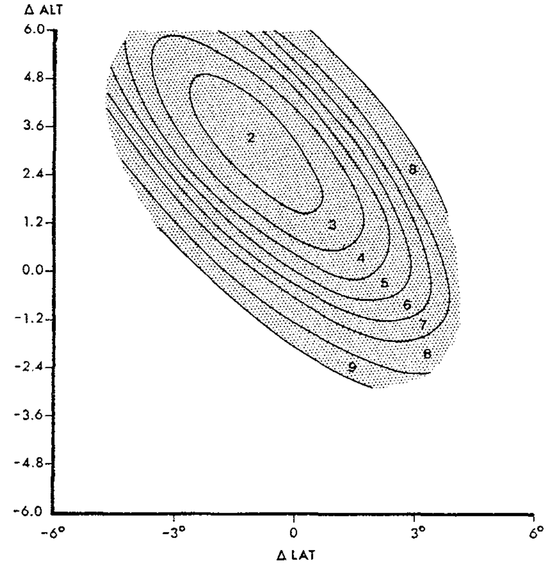


Fig. 13. The effects of population transfer on relative tracheid length at high altitudes in northern Sweden (trial nos. 15 and 19).
$RTRL = 0.991 + 0.0572 \triangle ALT - 0.0118 \triangle ALT^2 + 0.0343 \triangle LAT - 0.0181 \triangle LAT \times \triangle ALT - 0.0120 \triangle LAT^2$
$R = 0.72$, $F = 2.39$, $n = 17$ ($S_{y \cdot x} = 0.060$).
$\triangle ALT+$ Transfer to a higher altitude
$\triangle ALT-$ Transfer to a lower altitude
$\triangle LAT+$ Transfer to a more northern location
$\triangle LAT-$ Transfer to a more southern location
Units as in Figure 7.

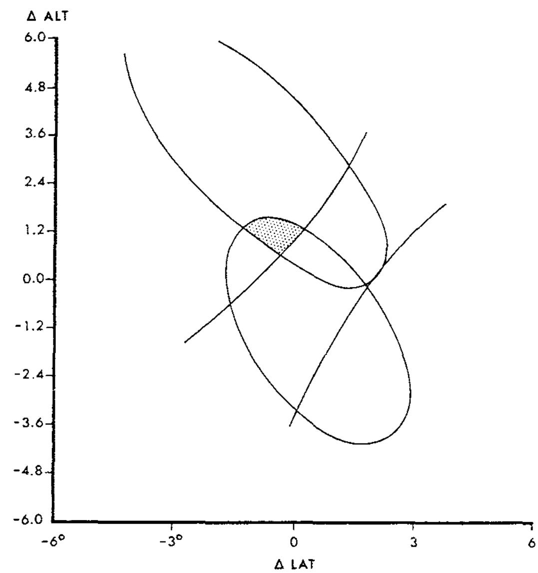


Fig. 14. Mode of transfer which yields increased tracheid length in comparison with the local population. Values greater than 1.0 in Figures 11–13.
$\triangle ALT+$ Transfer to a higher altitude
$\triangle ALT-$ Transfer to a lower altitude
$\triangle LAT+$ Transfer to a more northern location
$\triangle LAT-$ Transfer to a more southern location
Units as in Figure 7.

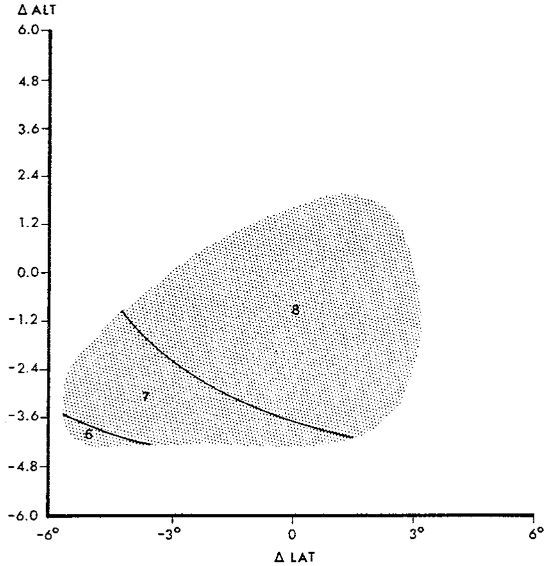


Fig. 15. Variation in relative basic density (RBD_1) for population 42 when tested at different trials (trial nos. 1, 2, 4, 6, 7, 9, 10:1, 11, 14, 15, 18 and 19).
$RBD_1 = 0.933 - 0.0037 \triangle LAT + 0.0013 \triangle ALT^2$
$R = 0.70$, $F = 3.80$, $n = 11$ ($S_{y \cdot x} = 0.018$).
$\triangle ALT+$ Transfer to a higher altitude
$\triangle ALT-$ Transfer to a lower altitude
$\triangle LAT+$ Transfer to a more northern location
$\triangle LAT-$ Transfer to a more southern location
Units as in Figure 7.

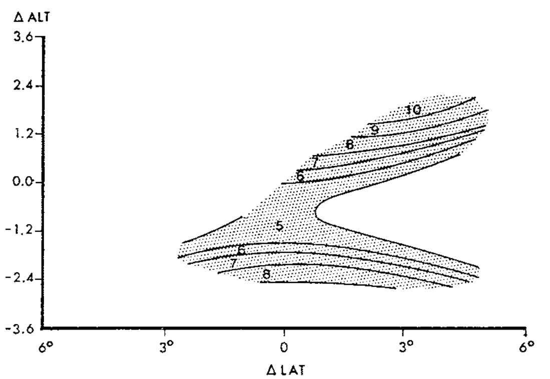


Fig. 16. Variation in relative basic density for population 74 when tested at different trials (trial nos. 1, 2, 4, 6, 7, 8, 9, 10:1, 11 and 14).
$RBD_1 = 0.990 - 0.0510 \triangle ALT - 0.0342 \triangle ALT^2$
$+ 0.0034 \triangle LAT^2$
$R = 0.87$, $F = 6.25$, $n = 10$ ($S_{y \cdot x} = 0.027$).
$\triangle ALT+$ Transfer to a higher altitude
$\triangle ALT-$ Transfer to a lower altitude
$\triangle LAT+$ Transfer to a more northern location
$\triangle LAT-$ Transfer to a more southern location
Units as in Figure 7.

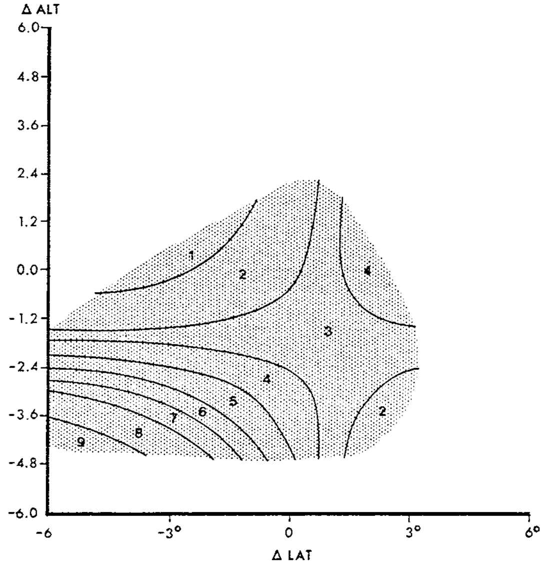


Fig. 17. Variation in relative tracheid length for population 42 when tested at different trials (trial nos. 1, 2, 6, 7, 8, 10:1, 11, 14, 15, 18 and 19).
$RTRL = 1.053 - 0.0101 \triangle LAT \times \triangle ALT + 0.0099 \triangle ALT$
$- 0.0170 \triangle LAT$
$R = 0.82$, $F = 4.02$, $n = 10$ ($S_{y \cdot x} = 0.043$).
$\triangle ALT+$ Transfer to a higher altitude
$\triangle ALT-$ Transfer to a lower altitude
$\triangle LAT+$ Transfer to a more northern location
$\triangle LAT-$ Transfer to a more southern location
Units as in Figure 7.

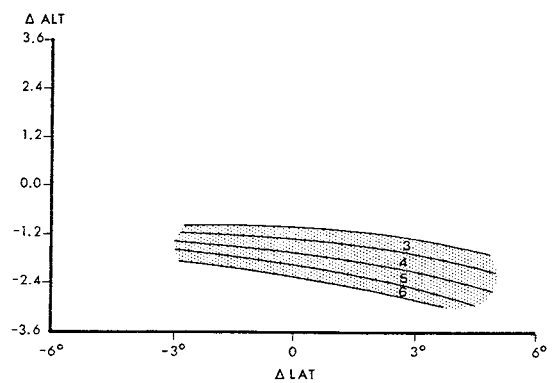


Fig. 18. Variation in relative tracheid length for population 74 when tested at different trials (transfer to lower altitudes only) (trial nos. 1, 2, 4, 6, 7, 8, 10:1 and 14).
$RTRL = 1.124 + 0.0674 \triangle ALT - 0.0048 \triangle LAT \times \triangle ALT$
$R = 0.74$, $F = 3.03$, $n = 8$ ($S_{y \cdot x} = 0.023$).
$\triangle ALT+$ Transfer to a higher altitude
$\triangle ALT-$ Transfer to a lower altitude
$\triangle LAT+$ Transfer to a more northern location
$\triangle LAT-$ Transfer to a more southern location
Units as in Figure 7.

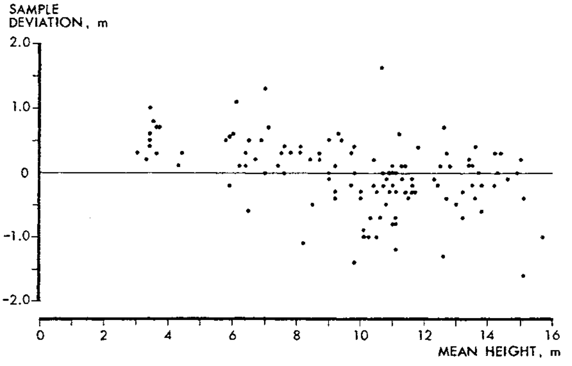


Fig. 19. Sample deviation from population mean height (m) at 1.25 m spacing for all populations and trials in the study.

Discussion

In these 30-year-old trials, the basic density for different trials varied from 0.311 g/cm^3 to 0.369 g/cm^3 for BD_1 and from 0.298 g/cm^3 to 0.343 g/cm^3 for BD_2. Tracheid length varied from 1.66 mm to 2.77 mm (Table 3).

In this study, assessments were made at a height of three metres and on fairly young trees. When comparing the mean values from this study with higher values on older trees in studies by Ericson et al. (1973) and Persson (1976), the effect of the age at the assessment point seems to be strong. This is further strengthened by the increase in basic density from BD_2 to BD_1 in all trials.

There was significant variation between populations in about half on the trials (Table 3). It is interesting to note that while significant variation was found for tracheid length and BD_2 mainly in southern trials, BD_1 also shows significant variation for northern trials. This could be explained as an effect related to the age and dimensions of the tree. Basic density increases from pith to bark, depending on age and growth rate, up to a value at which the effect levels off (Zobel & Talbert, 1984).

The effect of spacing on basic density and tracheid length may be seen in Figure 2, and appeared to be small. Basic density was in general lower in trees at the 2.0 m spacing than in those at 1.25 m spacing, while fibre length showed no clear trend. Diameter, volume per stem, and width of three growth rings were larger in trees at the 2.0 m spacing, while the height of the sampled trees was similar.

The partial correlations within sites, based on single-tree values (Table 4) and provenance mean values (Table 5), indicate that different traits are related to tracheid length and basic density. Basic density is mainly related to diameter, width of growth rings and number of growth rings from the pith. Low basic density was observed in trees with wide growth rings, as well as in growth rings close to the pith. Tracheid length was positively correlated with the number of growth rings from the pith, as well as with the height of the assessed tree. The relationship between height and tracheid length may be an artifact. Since samples were taken at a height of three metres, assessments made on growth rings in a tall tree will be far from the pith. The negative relationship between tracheid length and width of growth rings found in this study has previously been found for the *Sequoia* species by Resch & Arganbright (1968), and a reasonable explanation was given by Atmer & Thörnqvist (1982).

A regression analysis of provenance values was used to obtain a value for basic density (BD_1) and tracheid length in each trial. The value for zero transfer in the regression was used to estimate the value for the local provenance (Figs. 3 and 4).

The two models for variation in basic density and tracheid length were calculated on the basis of the values given in Figures 3 and 4. It should be noted that sites from high altitudes in southern Sweden could not be included, and that site 25 Korpilombolo was not used in the basic density model.

The model for geographical variation in basic density throughout Sweden (Fig. 5) indicates that basic density is low at high altitudes and at northern latitudes. Similar results were found by Ericson (1960, 1966) and Ericson et al. (1973). Site 25, Korpilombolo, was not included in this model. Basic density at this site was higher than at the surrounding sites (compare Fig. 3). This positive deviation from the general trend in the basic density model has also been reported for other sites in the area (A. Persson, pers. comm.).

The model for geographical variation in tracheid length is described in Figure 6. In this model too, high altitudes and northern latitudes exhibited shorter tracheid length. In addition, coastal sites tended to have reduced tracheid length. Unfortunately, the optimum tracheid length indicated in the model for intermediate latitudes and altitudes is based on results from a few sites only (compare Fig. 4).

When the two models (Figs. 5 and 6) are compared with the calculated value for the local provenances (Figs. 3 and 4), the large residual variance should be noted. There is a large site-to-site variation which is not explained by latitudinal and altitudinal differences.

The results from the calculated transfer functions are presented in Figures 7 to 14. The effect of provenance transfer on basic density is summarized in Figure 10. Although differences exist between regions, a moderate southward and upward transfer may generally be recommended as regards basic density. It is also worth noting that a southward transfer combined with a downward transfer exceeding 100 metres, is not to be recommended in Sweden.

The effect of provenance transfer on tracheid length is summarized in Figure 14. A moderate southward and upward transfer may generally be recommended for tracheid length. At low altitudes in northern Sweden, a downward transfer may also be utilized.

The two provenances 74 Eckersholm and 42 Sveg, which have been studied over a wide range of environments, indicate that basic density depends more on provenance and less on the transfer (Figs. 15 and 16). Provenance 74 had a basic density equal to or below that of the local provenance on all sites tested. Similarly, provenance 42 had a basic density below that of the local provenance on all sites tested. Tracheid length appears to depend more on environment and less on provenance (Figs. 17 and 18). The results indicate that it may be possible to identify provenances or regions from which a good base population for a future quality breeding programme, including high density, may be obtained.

The results from Table 5 show that provenances with the largest dimensions, i.e. diameter, height and volume, also had the lowest basic density and the longest tracheids. Therefore, deviations between sample mean values and mean values for provenances might lead to incorrect conclusions. In this material, the trees sampled are good estimates of the provenances at different sites (Fig. 19). In most cases the sample height deviated less than one metre from the mean of the provenance. The mean height of the sample tended to be too high when the mean height was less than five metres. The reason for this bias is probably that the test disks were cut at a height of three metres; therefore, trees shorter than three metres would be not included in the sample.

The transfer effect on basic density and tracheid length in this material could be described in terms of a photograph of a 400-metre race when the first curve is passed. The inside track could be compared to provenances with slow growth, where measurements are made in juvenile wood and close to the pith. The outside track could be compared to provenances with fast growth, where measurements are made in adult wood and far from the pith. Any adjustment made, i.e. change in the angle from which the photograph is taken, could change the results. This study could be regarded as a photograph taken at right-angles to the track, i.e. no adjustments have been made for differences in diameter, tree height or age. It might be questioned whether this is the most accurate way of describing the material or the race. Any conclusions drawn are subject to this limitation.

Implications for forest management and forest tree breeding

The results of this study have implications for forest management as well as for forest tree breeding.

A denser spacing appears to increase basic density, while tracheid length is not systematically affected.

The combined effect of environmental factors and genetic adaptation to environment, results in the existence of a region suitable for the production of timber with high density and long tracheids. This region consists of the intermediate altitudes from latitude 58°N to latitude 62°N. This is also the region where conditions are best for a breeding programme aiming at high-quality trees.

The results of this study indicate that the density and the tracheid length of wood harvested in thinnings are dependent on the origin of the planting stock used. It is important, when choosing planting stock, to evaluate not only the volume yield but also the technical properties of the wood produced.

It is difficult to estimate the future basic density or tracheid length for a site, spacing or planting stock. The effect of a change in site or material may, however, be predicted.

The implications for forest tree improvement are substantial. Density and fibre length may be increased by modifying the present rules for provenance transfer in northern Sweden. Probably, the same conclusions could be made for the transfer rules for seeds from northern seed orchard zones.

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