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Wood structure and quality in natural stands of *Salix caprea* L. and *Salix pentandra* L.

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Studia Forestalia Suecica
No. 182 · 1989

ISSN 0039-3150
ISBN 91-576-3711-3

Abstract

Sennerby-Forsse, L. 1988. *Wood structure and quality in natural stands of* Salix caprea *L. and* Salix pentandra *L.* Studia Forestalia Suecia 182. 17pp. ISSN 0039-3150, ISBN 91-576-3711-3.

Wood anatomy and physical properties in *Salix caprea* and *S pentandra* growing at different sites in Sweden were investigated. The mean length of fibres was 0.8 mm and of vessels 0.4 mm in both species. The length of the tracheary elements increased in a gradient from the pith towards the cambium in the transverse section of the wood. Longitudinally, the cell length increased from the base to breast-height (1.3 m) followed by a decrease towards the top of the tree. No significant differences were found between the two species in this respect. Mean width of fibres was 21 μm in both species, vessel width was significantly greater in *S. caprea* (82 μm) than in *S. pentandra* (74 μm). Type and distribution of cells and cell wall thickness was similar in both species. Cell dimensions within the annual ring were investigated. The mean specific gravity of stem wood (0.48 $g.cm^{-3}$), branches (0.46 $g.cm^{-3}$) an also in the bark (0.40 $g.cm^{-3}$) in *Salix caprea* was significantly higher than in *S. pentandra,* which species had a significantly higher moisture content in the stem wood and branches. Bark percentage was higher in *S. pentandra* than in *Salix caprea.*

Key words: Willow, specific gravity, moisture content, bark amount, fibres.

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MS. received 20 March 1987
MS. accepted 6 September 1987

016.76 Tofters tryckeri ab, Östervåla 1989

Introduction

Interest in biomass plantations in Sweden has concentrated on the growing of shrubby willows, mainly *Salix viminalis* L. and *Salix dasyclados* Wim. as fuel (Sennerby-Forsse, 1986; Siren, Sennerby-Forsse & Ledin, 1987). Other willow species have not hitherto been of economic importance to the forest industry in Sweden. In several countries, tree-formed willows such as *Salix alba* and *Salix fragilis* are used in the forest industry and their quality and utilization have been described (FAO 1979). The corresponding knowledge on native tree-formed willows in Sweden seems to be limited. However, as the demand for high-quality forest products exceeds supply, tree species other than those traditionally used may be considered as a resource for the production of pulp, board and other products.

The potential of willows as a resource depends on their properties as a raw material. Studies on clonal variation of wood quality in short rotation coppicing systems with selected willows and poplars have suggested that large genetic gains may be achievable through selection and breeding (Marton, Stairs & Schreiner, 1968; Flower-Ellis & Olsson, 1981; Anderson & Zsuffa, 1982; Sennerby-Forsse, Siren & Lestander, 1983; Sennerby-Forsse, 1985). When selecting phenotypes for breeding, it is desirable to know more about the wood characteristics and quality of abundant willow species from natural stands in Sweden. The extensive variation which exists in the quality of biomass in natural forest is considered to originate in environmental effects on growth, and from inherent variation in basic wood structure and composition (Anderson & Zsuffa, 1982). It is also known that wood structure varies within the tree, in relation to the distribution of leaf in the crown (Denne, 1979) and is modified by environmental factors acting directly or indirectly on cambial differentation (Larsson, 1969). Willows, which have a wide ecological distribution, and which grow on different soils and under various climatic conditions throughout Sweden, might be expected to show extensive variation in important traits.

The purpose of the present investigation was to determine specified wood characteristics in two native willow species, *Salix caprea* L. and *Salix pentandra* L., and to study their variation, both within the stem and between stands from different parts of Sweden.

Material and methods

In all, 58 trees of *S. caprea* and *S. pentandra* were studied. Of these trees, 31 were *S. caprea* and 27 *S. pentandra*. The twelve sampled sites were all located at low altitudes in Sweden (Fig. 1., Table 1).

Trees of medium height in each stand (Table 1), without serious visible damage, were randomly selected at each site. Samplings were made during late autumn and early winter, i.e. October-December. Transverse segments, 5–10 cm long, were cut at 0, 10, 30, 50, 70 and 90% of the stem height and at breast-height (1.3 m). On a randomly selected branch at 25% of the crown length (measured from below), segments were cut at 0, 25, 50 and 75% of branch length (Fig. 2a). The approximate age of the trees was 25 years.

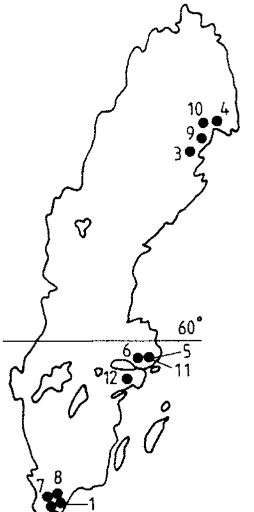


Fig. 1. Location of the 12 different sampling sites. Stands 1 to 6 were sampled for *S. caprea* and stands 7 to 12 were sampled for *S. pentandra*.

Measurements

The following observations were made on each sampled segment: diameter on and under bark was measured using calipers in two directions at 90° to each

Table 1. *Description of the felling areas and stands. Stand Nos. 1 to 6 refer to S caprea test trees and stand Nos. 7 to 12 to S pentandra trees. + = presence*

Stand No.	Sample area	Latitude N	Alt.* m a.s.l.	Site cond.	Tree mix, prop. by %	Mean height of willows, m
1	Mullsbjär	55.5	<50	Dry	Conif 90 Willows 10	10.9
2	Kullaröd	55.5	<50	Dry	Conif 90 Willows 10	14.1
3	Norrfjärd	65.0	<10	Dry	Conif + Birch 10 Willows 90	7.9
4	Boden	65.8	<50	Dry	Conif 90 Birch + Willows 10	10.6
5	Bogesund	59.7	<20	Dry	Birch + Willows 100	11.6
6	Hägernäs	59.7	<30	Dry	Birch + Willows 100	10.6
7	Björkesåkra	55.5	<50	Wet	Willows 100	6.6
8	Björnstorp	55.5	<50	Moist	Birch 40 Alder 30 Willows 30	6.5
9	Alvik	65.5	<10	Moist	Birch + Willows 100	10.5
10	Udden	65.8	<50	Moist	Conif + Birch 20 Alder 10 Willows 70	11.7
11	Bogesund	59.7	<20	Dry	Birch + Willows 100	7.9
12	Studsvik	58.8	<10	Wet	Birch + Willows 100	12.4

* metres above sea level.

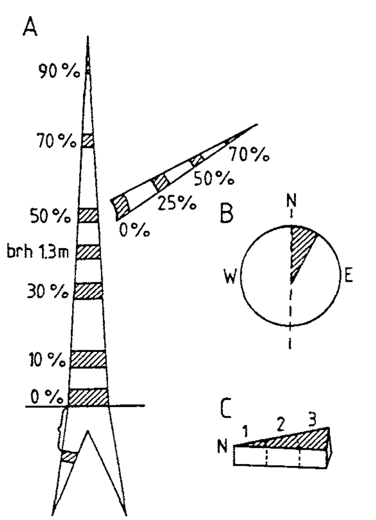


Fig. 2. A. Position of specimens in stem and branch
B. Position of specimens in the cross-section
C. Position of specimens in the north-east section.

other. The green weight of the samples with and without bark was determined; specimens were then cut into an eastern (E) and a western (W) half (Fig. 2b). The green weight of the western half was determined, and its green volume estimated by xylometry. After drying in an oven at 104°C for five days, the samples were weighed. All weights and displacement volumes were measured to the nearest 0.01 g. From the eastern half of the specimen, the northernmost segment was cut out and divided into three pieces with the same radial length (Fig. 2c). The green weight, green volume and dry weight of each piece were measured. The remainder of the eastern half was frozen for anatomical studies. The specific gravity of wood and bark was calculated from green volume and oven dry weight. The moisture quotient of wood and bark was expressed in per cent of its oven-dry weight. The bark percentage by weight was calculated as the green weight of bark (Bg_w) as a percentage of the green weight on bark of the tree ($Wood_{o.b.}$),

$$\left(\frac{Bg_{w}}{Wood_{o.b}} \cdot 100\right)$$

The volume of the bark was calculated by displacement in water at 20°C as a percentage of the volume of bark (B_v) over the volume of wood (W_v) plus the volume of bark,

$$\left(\frac{B_v}{W_v+B_v} \cdot 100\right)$$

All weight and volume displacements were measured to the nearest 0.001 g.

Anatomical studies

In the breast-height segments (1.3 m) taken from 10 trees each of *S. caprea* and *S. pentandra*, the distribution of vessels, fibres and parenchyma cells was investigated in every fifth annual ring. Where the term fibres is used in what follows, tracheids, fibre tracheids and libriform fibres are included, if nothing else is stated.

Transverse sections (TS), about 20 μm thick, of the thawed stem segments were cut on a sledge microtome and stained with pale green (lichtgrün) or a saturated solution of saffranin in ethanol. An ocular with a grid graticule was used to place a sample grid (5×5 mm), selected with the help of a randomization table, over the specimen within every fifth annual ring. The different cell types were counted in a light microscope (LM) at a magnification of ×25. Cell wall thickness was also measured on 10 fibres in every fifth annual ring.

For scanning electron microscope (SEM) examination, cubes of stem segments (5 mm) were cut and dried in an oven at 104° for 48 h, coated with Au/Pd in a Polaron E 5100 cool sputter coater and investigated in a JEOL JSM P 15 scanning electron microscope at 20 kV.

The length and width of fibres and vessels were measured in every fifth ring, and always in the first and last annual ring in the breast-height specimens. In every third annual ring from the cambium, fibre and vessel lengths and widths were measured in all stem segments from one tree each of *S. caprea* and *S. pentandra*, i.e. at 0, 10, 30, 50, 70, 90% of relative stem height and at breast-height. The measurements were made with a LM at ×40 (length) and ×400 (width) on exposed cells. Samples were treated with maceration liquid (Triethylene-P-toluensulphonic acid) to dissolve the lignin of the middle lamella. The cells exposed were mounted in glycerine on a microscope slide. Measurements were made on 20 fibres and 20 vessels from each annual ring on a projection of the cells beside the LM.

To investigate variation within the annual ring, lumen size, cell wall thickness, length and width of 20 randomly selected fibres and vessels were measured in the latewood, and 20 in the earlywood zone, in the tenth annual ring of the breast-height segment from 10 trees of *S. caprea* and *S. pentandra*, respectively.

The measurements were statistically analysed using ANOVA procedures for means and anlyses of variance. Duncan's multiple-range test was used to compare more than two samples with each other. Levels of significance: NS = not significant ($p>0.05$); ★ $\doteq$ $p<0.05$; ★★ = $p<0.01$; ★★★ = $p<0.001$.

Results

Wood structure

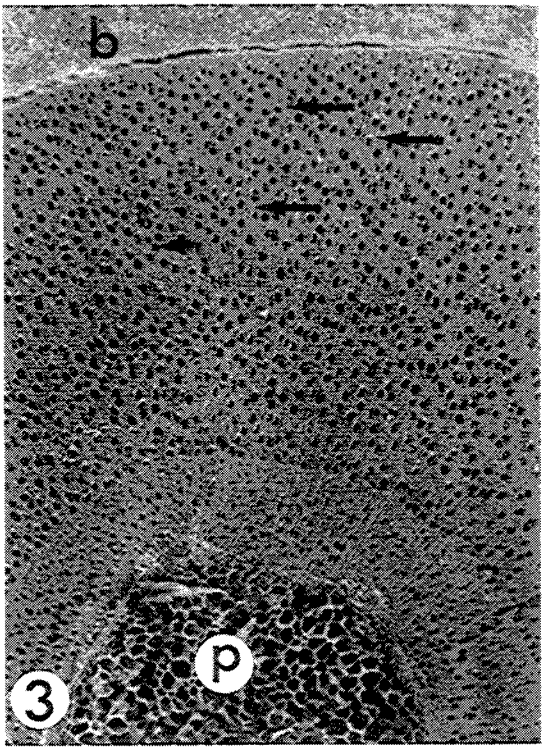
The secondary wood in *S. caprea* and *S. pentandra* is of the diffuse-porous type. The vessels (arrow-head), are evenly distributed over the entire annual ring with small differences between the early and late wood (Fig. 3). The vessels are frequently linked in groups of two or three (Fig. 4) and communicate with each other through bordered pits in the common walls (Figs. 5, 6). The vessel members are also characterized by simple perforation, i.e. the terminal walls are completely dissolved (Fig. 7).

The bulk of the wood was made up of thick-walled fibres (Fig. 4), and tracheids with bordered pits and libriform fibres with stacked pits were recognized in both *S. caprea* and *S. pentandra* (Fig. 7). Although no attempt was made to estimate the amounts of different fibre types, the libriform fibres seemed to dominate in the breast-height samples investigated.

The numerous rays are uniseriate, i.e. one cell row wide, and heterocellular, consisting of two kinds of parenchyma cells (Figs. 8, 9). The pits are simple in the common cell walls between the ray cells (Figs. 9, 10), but appear as half-bordered pit pairs when communicating with a tracheid-like element or a vessel, (Fig. 8). Except for ray cells, xylem parenchyma cells occurred to a minor extent only at breast-height in *S. caprea* and *S. pentandra*.

A brownish heartwood was present in most trees investigated.

The distribution of different cell types differed in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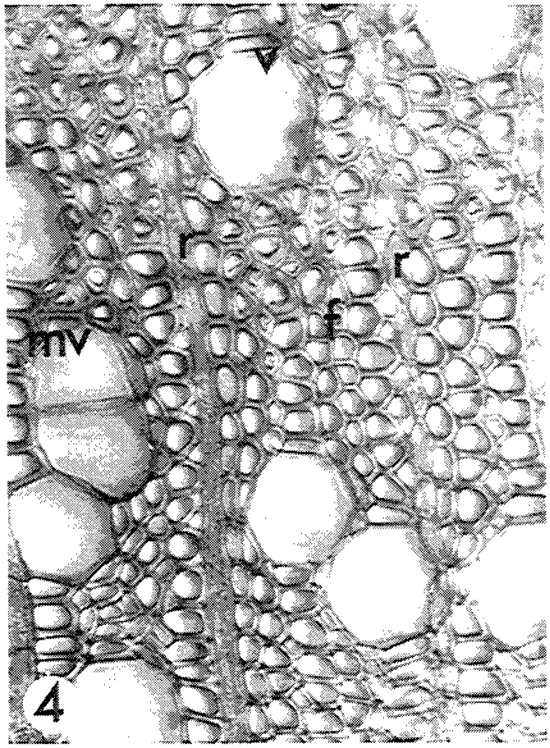
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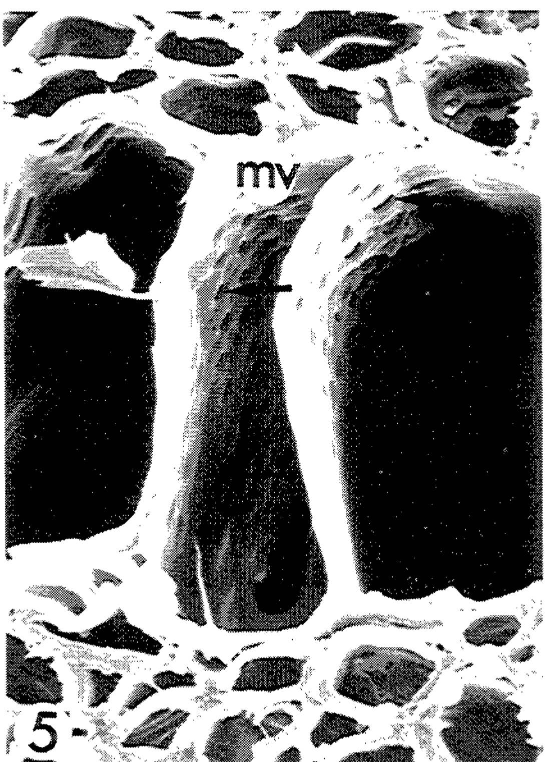
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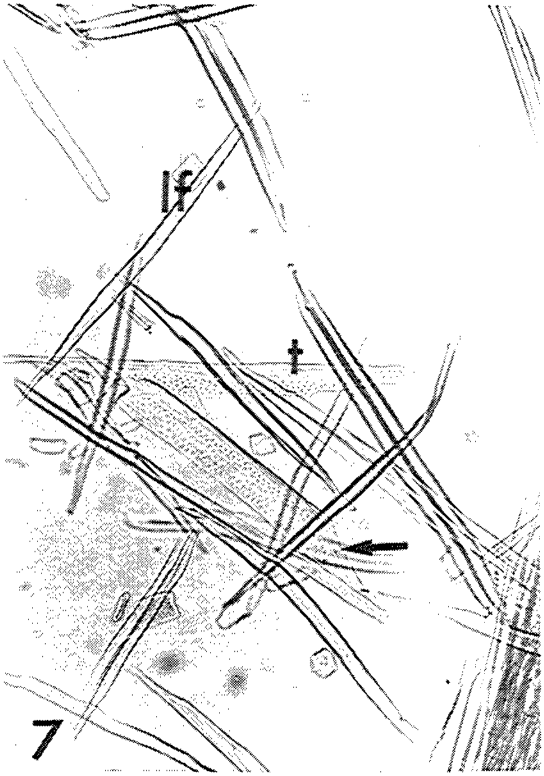
Fig. 3. S. caprea. Transverse section of secondary xylem in a two-year-old stem. Diffuse porous wood with vessels (arrow-head) distributed all over the surface. Rays are abundant (arrows). Thin-walled pith cells (p) and bark (b) can be seen. SEM × 50.

Fig. 4. S. pentandra. Transverse section of secondary xylem. Multiple vessels (mv) in clusters of two or three, thick walled fibres (f) and ray parenchyma cells (r). LM × 175.

Fig. 5. S. caprea. Transverse section of secondary xylem. Multiple vessels with bordered pits in the common cell wall (arrow). SEM × 1 000.

Fig. 6. S. caprea. Transverse section of secondary xylem. Bordered pits (bp) between vessels can be seen from the inside of a vessel. SEM × 2 000.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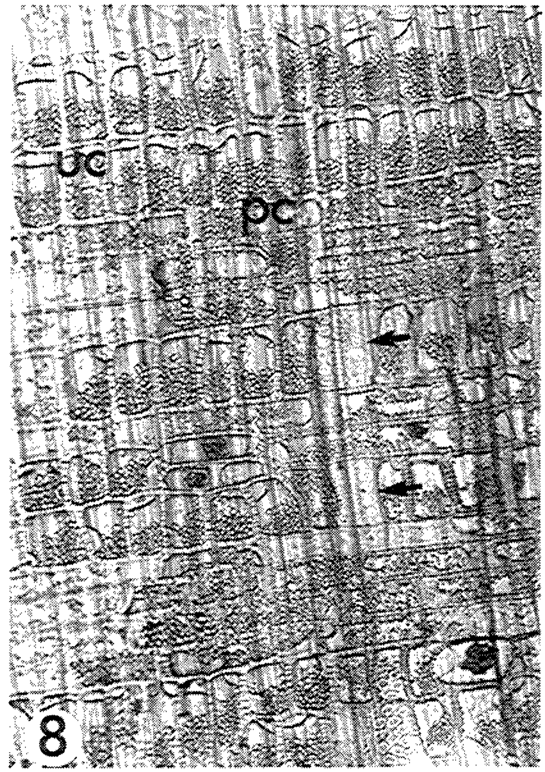
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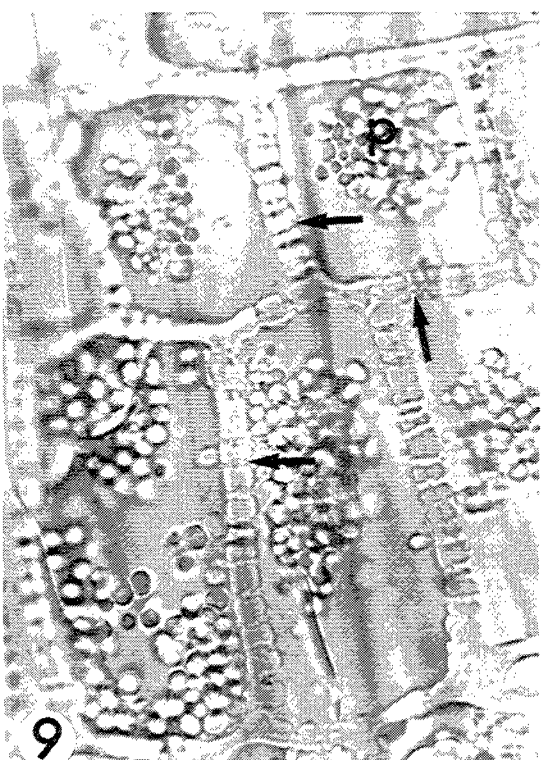
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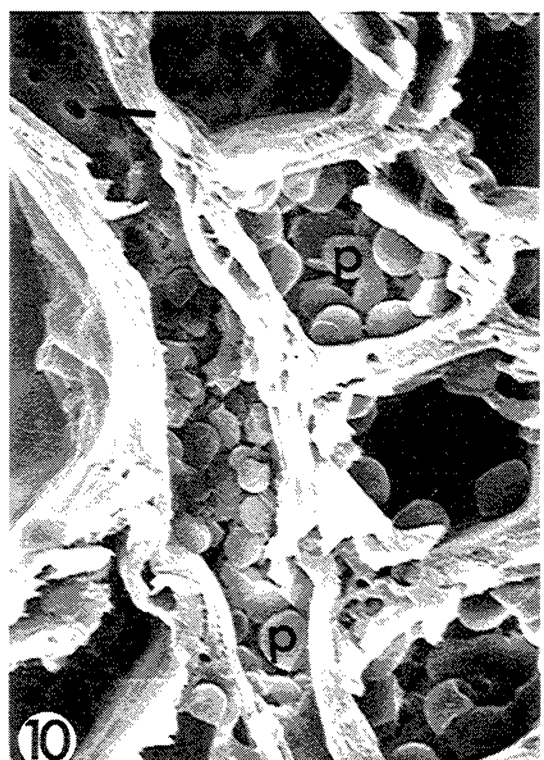
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10

Fig. 7. S. pentandra. Macerated cells of secondary xylem. Vessel with simple perforation (arrow), tracheids (t) and libriform fibres (lf) can be recognized. LM × 60.

Fig. 8. S. caprea. Longitudinal section of secondary xylem. Heterogeneous, uniseriate rays consisting of procumbent (pc) and upright cells (uc). Bordered pits can be seen where ray cells are next to a xylem element (arrow). LM × 480.

Fig. 9. S. caprea. Longitudinal section of secondary xylem. Ray cells with plastids (p). Notice simple pits between the parenchyma cells (arrows). LM × 1 200.

Fig. 10. S. caprea. Longitudinal section of secondary xylem. Ray cells filled with plastids (p). Simple pits visible from the inside of procumbent ray parenchyma cell (arrow). SEM × 2 000.

the two species (Table 2). The proportion of fibres was higher in *S. caprea*. Vessels occurred in similar proportions in both species, while the proportion of parenchyma cells was higher in *S. pentandra*. The number of cells per unit area (i.e. 25 mm^2) expresses the mean over the whole cross-section. The relative variability in fibre content was higher in *S. pentandra* than in *S. caprea*, as shown by the coefficient of variation (Cv).

Length of fibres and vessels

Mean length in a sample of approximately 1,500 fibres and vessels at breast-height in *S. caprea* and *S. pentandra* wood respectively, was 0.8 mm (±0.2) for fibres and 0.4 mm (±0.1) for vessels. The fibre length varied between 0.6–1.0 mm and vessel length between 0.3–0.5 mm in both species (Table 3). Differences between the species were not significant.

The longitudinal variation of fibre and vessel lengths was studied in the third annual ring from the cambium. The pattern of variation was similar in both species. The mean value increased from the base to 10% of relative stem height, then decreased slightly to the top of the tree (Fig. 11).

The length of both fibres and vessels in the stem cross-section at breast-height increased from the pith towards the cambium. The increase was greatest during the first ten years, then declined and appeared finally to stabilize (Fig. 12).

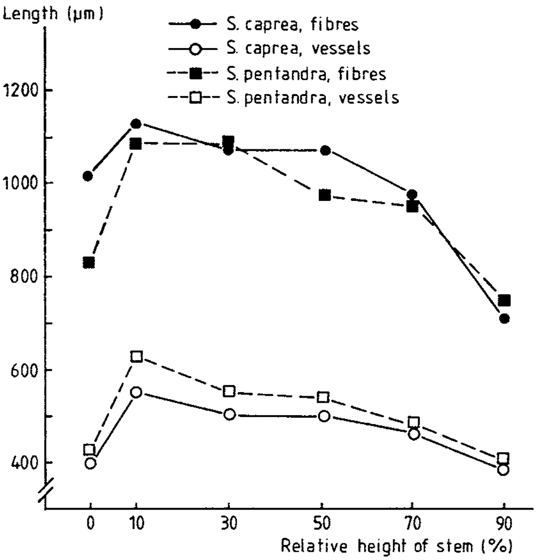

Fig. 11. Variation of fibre and vessel lengths at various relative height of the stem in *S. caprea* and *S. pentandra*.

Table 2. *Number of cells (N) per unit area (25 mm^2) in secondary wood at breast-height in* S. caprea *and* S. pentandra. *Mean ± SD and Cv: 5,000 cells in each species. Proportion (%) was estimated per unit area.*

	S. caprea			*S. pentandra*		
Cell type	Mean ± SD	Cv, %	Prop., %	Mean ± SD	Cv, %	Prop., %
Fibres	86.2±18.7	21.7	60	60.6±24.1	39.7	42
Vessels	2.5±1.5	60.5	26	2.9±1.5	50.4	30
Parenchyma	9.9±4.4	45.0	14	5.2±2.6	50.0	28

Table 3. *Length and width of fibres and vessels in* S. caprea *and* S. pentandra. *Mean ± SD and Cv: 1,500 cells in each species*

	Fibres				Vessels			
	Length, µm		Width, µm		Length, µm		Width, µm	
Species	Mean ± SD	Cv, %	Mean ± SD	Cv, %	Mean ± SD	Cv, %	Mean ± SD	Cv, %
S. caprea	795±210	26.4	21±7	33.0	427±109	26.0	82±43	52.0
S. pentandra	803±203	25.3	21±5	22.0	440±109	25.0	74±20	28.0

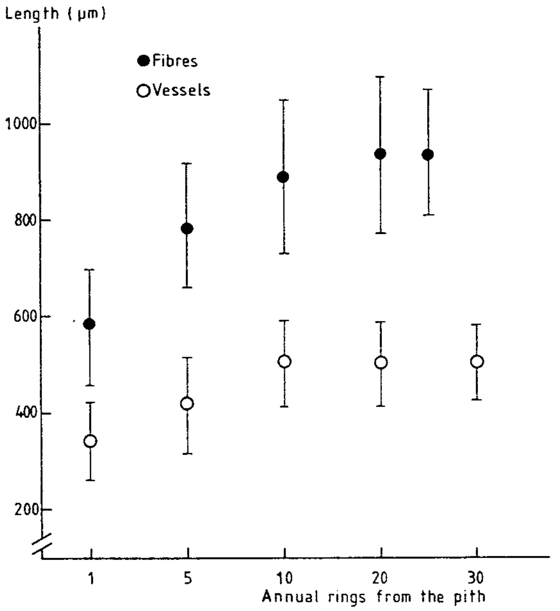

Fig. 12. Variation of fibre and vessel lengths in cross-section at breast-height in *S. caprea* and *S. pentandra*. Means and SD-bars for the two species combined.

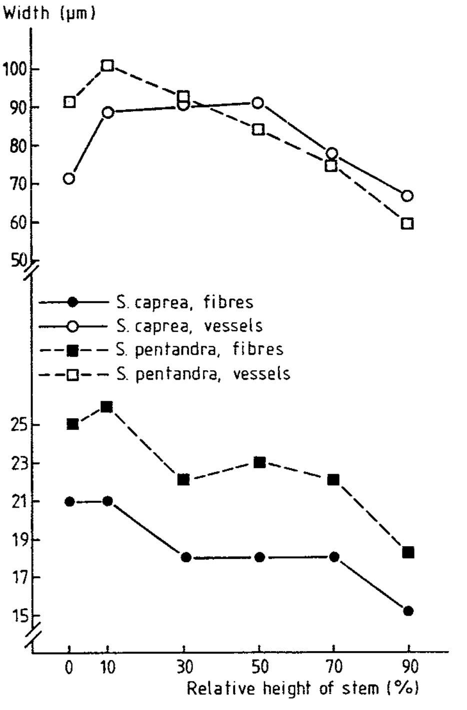

Fig. 13. Variation of fibre and vessel width at various relative height of the stem in *S. caprea* and *S. pentandra*.

Width of fibres and vessels

Mean width of the fibres and vessels investigated was 21 μm and 82 μm in *S. caprea* and 21 and 74 μm, respectively, in *S. pentandra* (Table 3). The range was wider in vessels than in fibres in both species. Analyses of variance revealed that vessel width was significantly greater in *S. caprea* than in *S. pentandra*. The width of the vessels in *S. caprea* showed a considerably higher relative variability than in *S. pentandra*.

Fibre width in the stem was greatest in the interval from the base to 10% of stem height, and then decreased. The width of vessels varied similarly along the stem, being greatest at the base (0–10% of relative stem height), thereafter decreasing towards the top (Fig. 13).

In the breast-height segments, fibre width was almost constant throughout the cross-section, while vessel width increased from the pith to the cambium, with a maximum at 20 years of age (Fig. 14).

Cell wall thickness

Mean fibre wall thickness at breast-height was 2.8 and 3.0 μm in *S. caprea* and *S. pentandra*, respectively (Table 4). The thickness of the fibre wall increased rapidly from the pith towards the cambium (Fig. 15). The increase was more pronounced during the first five to ten years of growth. No significant differences were found between the two species in this respect.

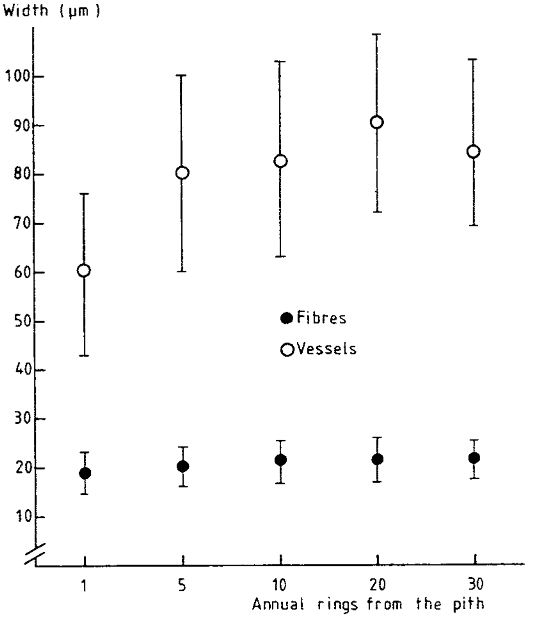

Fig. 14. Variation of fibre and vessel width in cross-section at breast-height in *S. caprea* and *S. pentandra*. Means and SD-bars for the two species combined: n = 400 cells.

Table 4. *Fibre wall thickness at breast-height. Mean ± SD and Cv: 500 cells in* S. caprea *and* S. pentandra *respectively*

Species	Fibre wall thickness, μm Mean ± SD	Cv, %
S. caprea	2.8±6	21.0
S. pentandra	3.0±7	23.0

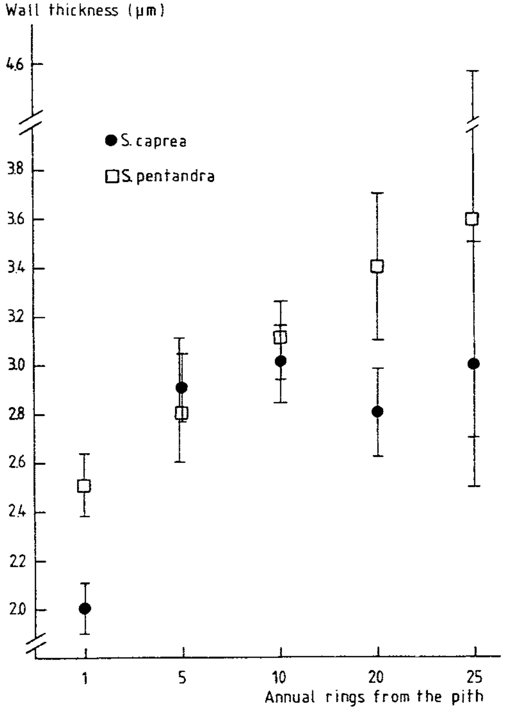

Fig. 15. Variation of fibre wall thickness in cross-section at breast-height in *S. caprea* and *S. pentandra*. Means and SD-bars for each species.

Differences within the annual ring

Expected differences were found between earlywood and latewood within an annual ring. Cells were longer and had thicker cell walls in the latewood, while the lumen was larger in the earlywood. The pattern of variation was the same in both species (Table 5). The discrepancies in the table between the average width on the one hand, and the average cell wall thickness and lumen size on the other hand, are due to the fact that different cells were measured for these characteristics.

Specific gravity

The mean specific gravity (SG) of both stem wood and branches was significantly higher in *S. caprea* than in *S. pentandra* (Table 6). The longitudinal variation of SG showed the same pattern in both species. It increased from the base to 50% of relative stem height, thereafter decreased towards the top of the tree (Fig. 16). According to Duncan's multiple-range test, the SG of the stem base section was significantly lower than that of all other sections. The SG of the 50% section was significantly higher than that of the others, excluding the 70% section.

The mean SG was lower in the branches than in the stem wood in both species (Table 6). The longitudinal variation of SG in branches was somewhat irregular. In *S. caprea* the highest value was found next to the stem, while in *S. pentandra*, SG was highest at 50% of relative branch length (Fig. 16).

In cross-section, SG in the stem was evenly distributed with no real differences between the three sections (Table 7). The longitudinal variation in the stem differed between the sections. SG in section 1 (close to the pith) decreased from the base to 30% of relative stem height, then increased to 50 or 70% and finally decreased again towards the top. In section 2, SG increased from the base to 50 or 75% of relative stem height and then decreased. In *S. pentandra*, SG in section 3 showed the same longitudinal variability as

Table 5. *Variation of fibre and vessel dimensions within the annual ring. Mean ± SD: 1,250 cells in each species*

Cell type	Dimension, μm	*S. caprea* Earlywood Mean ± SD	*S. caprea* Latewood Mean ± SD	*S. pentandra* Earlywood Mean ± SD	*S. pentandra* Latewood Mean ± SD
Fibres:	Length	650±305	878±160	668±322	882±190
	Width	20± 4	19± 3	21± 4	22± 5
	Wall thickness	2.7±0.8	3.1±0.9	2.8±0.8	3.5±0.8
	Lumen size	10± 2	8± 2	12± 3	10± 3
Vessels:	Length	459±76	467±81	470±87	480±84
	Width	59±50	84±19	77±20	79±21
	Lumen size	58±13	35±11	50± 9	34±11

Table 6. *Specific gravity (SG) and moisture quotient (MQ) in stem wood and branch wood of* S. caprea *and* S. pentandra. *Mean SD and Cv: 325 samples from each species*

Sample	*S. caprea* Mean ± SD	Cv, %	*S. pentandra* Mean ± SD	Cv, %	Diff. between species Level of significance
Stem SG (g. cm^{-3})	0.48±0.03	7.0	0.44±0.06	13.3	★★★
Branch SG	0.46±0.04	8.1	0.41±0.05	13.0	★★★
Stem MQ (%)	82±12	14.1	93±19	20.3	★★★
Branch MQ	79±10	12.0	82±14	17.0	★

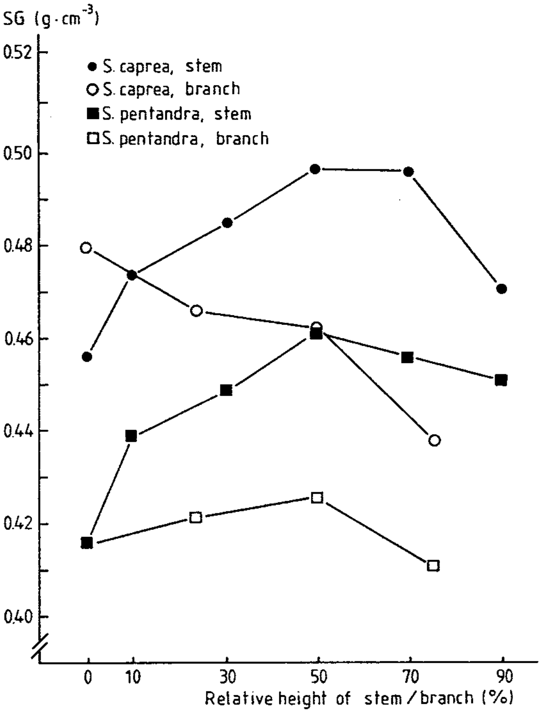

Fig. 16. Variation of specific gravity (SG) in stem and branches at various relative height and length respectively in *S. caprea* and *S. pentandra.*

in section 2. The SG in section 3 in *S. caprea* varied considerably along the stem (Fig. 17).

The mean SG of stem wood varied significantly within stands as well as between stands (Fig. 18). In *S. caprea*, the SG means were equally distributed between the stands from northern, middle and southern Sweden.

In *S. pentandra*, the highest and the lowest mean of SG were found in the stands from southern Sweden. No geographical trend could be traced in this material, since mean SG was significantly different between the two stands in each part of Sweden in both species investigated.

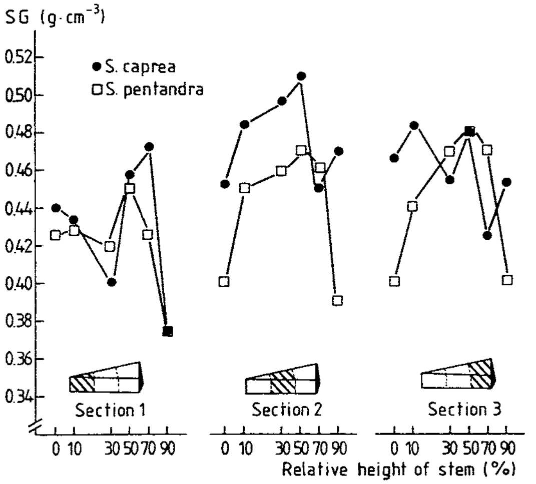

Fig. 17. Variation of stem SG in cross-section at various relative height of the tree in *S. caprea* and *S. pentandra.*

Moisture quotient

The mean moisture quotient (MQ) was significantly higher in *S. pentandra* than in *S. caprea* (Table 6). Moisture quotient increased slightly from the base to

Table 7. *Specific gravity (SG) and moisture quotient (MQ) in cross-section of the stem. Mean ± SD and Cv: 250 samples in each species*

Sample	*S. caprea* SG Mean ± SD	Cv %	MQ Mean ± SD	Cv %	*S. pentandra* SG Mean ± SD	Cv %	MQ Mean ± SD	Cv %
Section 1	0.44±0.07	15.3	79±23	30.0	0.43±0.05	11.1	92±39	42.0
Section 2	0.45±0.06	12.0	74±14	18.3	0.44±0.05	11.2	68±17	26.0
Section 3	0.45±0.09	19.4	80±16	20.4	0.45±0.06	13.0	86±22	26.2

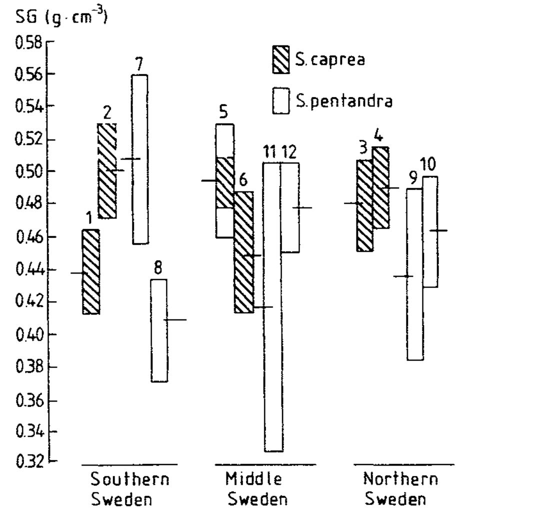

Fig. 18. Geographical distribution of mean SG in *S. caprea* and *S. pentandra*. Variation of stem SG within and between stands. Bars indicating means and SD for each stand.

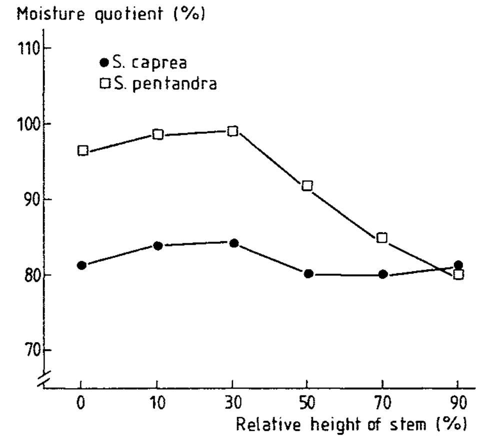

Fig. 19. Variation of moisture quotient (MQ) at various relative height of the stem in *S. caprea* and *S. pentandra.*

30% of relative stem height, and thereafter decreased in both species (Fig. 19).

The mean MQ was significantly lower in section 2 at all levels along stem in *S. pentandra,* and showed the same tendency in *S. caprea,* although differences were not significant in the latter species (Table 7).

Branches had a lower MQ than stem wood, especially in *S. pentandra* (Table 6). In *S. pentandra*, the water content in the branches was significantly higher than that of *S. caprea*. The longitudinal variation of MQ showed the reverse pattern to SG in *S. caprea*, with the lowest value close to the stem. In *S. pentandra* the variation of MQ resembled that of SG, with the highest value at 50% of relative branch length.

A comparison between stands showed that differences were significant both within and between stands. No geographical trend was found in MQ in either species. In general, all *S. pentandra* stands had a higher mean MQ than *S. caprea* stands.

Stem bark characters

The proportion of bark was significantly higher in *S. pentandra* than in *S. caprea* (Table 8). The amount of bark increased slowly from the base to about 70% of the relative stem height and thereafter showed a more rapid increase towards the top of the tree (Fig. 20). This pattern was similar in both species. No geographical variation was found in bark content in either species.

The SG of the stem bark was lower than that of the wood. Bark SG was significantly higher in *S. caprea* than in *S. pentandra* (Table 8).

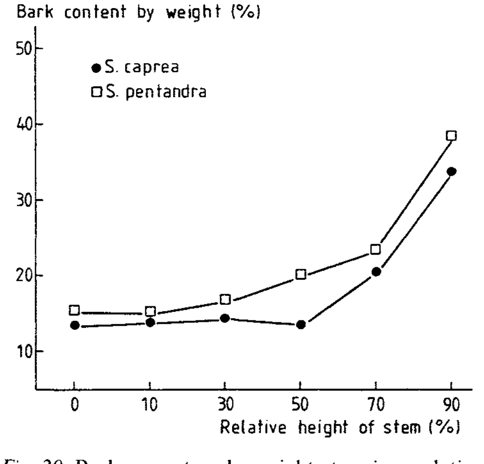

Fig. 20. Bark percentage by weight at various relative height of the stem in *S. caprea* and *S. pentandra*.

Table 8. *Bark proportion and bark properties. Mean ± SD and Cv: 220 samples of* S. caprea *and 190 samples of* S. pentandra

	Bark by weight, %		Bark by volume, %		Bark SG g.cm^{-3}		Bark MQ, %	
Species	Mean ± SD	Cv %	Mean ± SD	Cv %	Mean ± SD	Cv %	Mean ± SD	Cv %
S. caprea	18.2±2.6	15.0	16.0±3.5	22.0	0.40±0.04	8.6	102.4± 9.5	9.3
S. pentandra	20.5±3.5	18.0	19.0±4.4	21.3	0.36±0.10	30.2	101.7±13.0	13.0

Discussion

There was a higher proportion of vessels in *S. pentandra* and the proportion of parenchyma cells was greater, while *S. caprea* had a higher proportion of thick-walled fibres. The described cell type distribution reflected only the situation at breast-height in the investigated trees, and it should be borne in mind that high anatomical variability within trees has been found in other diffuse-porous species. Isebrands (1972) reported that in *Populus deltoides* Bart., vessel percentage inreased with stem height and with age. The decrease of wood SG along the stem in *Salix* indicated a change in the proportion of vessels in the tree, in the same direction as in *Populus deltoides*. The histological differences between the two willow species reflected differences in wood quality, wood of *S. caprea* being denser than that of *S. pentandra*. The proportion of vessels, fibres and parenchyma cells found here was similar to that reported for other diffuse-porous trees such as *Populus* (Isebrands, 1972) and *Betula* (Meyer, 1958).

It is known that fibre length depends upon the length of the cambial initials and on the amount of intrusive growth they undergo during differentiation (Bailey, 1920). Therefore, the length of fibres increases with age until a maximum is reached (Hejnowicz & Hejnowicz, 1958; Denne, 1971). In the two *Salix* species investigated, fibre length increased from the pith towards the cambium, and reached a maximum after about 20 years. The increase was greatest during the first ten years, then declined. Bhat (1980) and Bhat & Kärkkäinen (1981) reported a strong positive correlation between fibre length and age in *Betula pubescens* and *Betula pendula*, with maximum length reached at 75–80 years.

Vessels have little or no intrusive growth, thus the radial gradient of vessel length shows the increase with age of the initials. In *S. caprea* and *S. pentandra*, the cambium initials increased their length until the tenth year of age, and thereafter remained approximately constant.

Fibre and vessel length increased along the stem from the base to about 10% of relative stem height, then slowly decreased towards the top of the tree in both *S. caprea* and *S. pentandra*. The pattern was similar to that reported for other hardwoods such as shagbark hickory (*Carya ovata*; Spurr & Hyvärinen, 1954). In birch, fibre length was found to be negatively related to height from the ground (Bhat, 1980).

The width of vessels increased from the pith towards the cambium, while fibre width showed minor variation in the cross-section. Thus, the cambial initials seemed to produce not only longer, but also wider, vessels with age. Similar traits have been reported from *Populus deltoides* (Isebrands, 1972). In the oldest trees in the present study, a decrease in vessel width was observed in the outermost annual rings. While maximum vessel length was reached after ten years, maximum width occurred after twenty years in the same trees.

Fibre and vessel width in the stem showed longitudinal variation, with an increase from the base to a maximum at 10% of relative stem height, followed by a decrease towards the top of the tree. A similar pattern of variation was found in sycamore (*Acer pseudoplatanus*; Denne & Dodd, 1980).

In *S. pentandra*, fibre wall thickness increased radially from the innermost rings towards the cambium. The same pattern was evident in *S. caprea*, although the maximum thickness was reached in the tenth annual ring in the latter species.

Since *Salix* belongs to the group of diffuse-porous trees, less variation is to be expected across the growth ring than in ring-porous trees. However, in this study it was clear in both species that the fibres of the latewood were longer, had thicker cell walls and a smaller lumen, than fibres in the earlywood. In sycamore (*Acer pseudoplatanus*), Denne & Dodd (1980) found little variation in cell dimensions across the growth ring, although they observed a tendency for fibre wall thickness to increase from the earlywood to a maximum in the middle of the growth ring, and thereafter to remain constant to the end of the ring.

The specific gravity (SG) of the wood was in general higher in *S. caprea* than in *S. pentandra* in both stems and branches. The pattern of variation of SG along the stems agrees well with that in other reports on diffuse-porous hardwoods (Taylor, 1968; Manwiller, 1979). There was an increase from the base towards the middle of the stem and thereafter a decrease towards the top. A similar pattern of variation in SG was also found in *Alnus incana* (Hakkila, 1970). However, in alder wood, density decreased from the base to 1 m above ground, then increased to the mid-stem and decreased again towards the top of the tree. The pattern of longitudinal variation of SG in *Salix* is notably different in young trees, as one- to five-year-old stems of *S. caprea*, *S. viminalis* and *S. fragilis* showed a linear decrease of wood density from the base towards the top of the stems (Sennerby-Forsse, in preparation). Variation across the stem showed a tendency of increasing SG towards the cambium, but differences were too small to be significant. The variation of SG along the stem, when followed for each of the three sections, was highest in section 1 (close to the pith). The variability pattern was similar in sections 2 and 3, although section 3 in *S. caprea* was somewhat irregular.

The mean wood SG in both *S. caprea* and *S. pentandra* varied significantly among stands. However, no geographical pattern was evident, as both high and low SG were found in the same climatic area in both species. Taylor (1977), in a study of eight important hardwoods throughout the mid-South of the USA, found no general patterns of geographical variation of wood properties. According to Hakkila (1970), the most important cause of variability in wood density is genetic. Further evidence that specific gravity is under genetic control has been provided for poplar by Kennedy & Smith (1959), Herpka (1973) and by Anderson & Zsuffa (1982). Significant clonal variations in wood specific gravity have been demonstrated for *Salix* spp by Flower-Ellis & Olsson (1981), Sennerby-Forsse et al. (1983) and Sennerby-Forsse (1985). Variation within and among stands was higher in *S. pentandra* than in *S. caprea*. Site characteristics, tree age and stand composition must largely have influenced growth and quality in stands in the present study. Stands with *S. pentandra* were more heterogeneous as regards tree height, the sites were wet or moist, and the stands were composed of different hardwoods. The *S. caprea* stands, on the other hand, were generally mixed with conifers, the willows were more homogeneous in height and the site conditions were dry.

The moisture content of the wood varies with season and it should be emphasised that the trees in the present study were sampled in dormant condition during late autumn and early winter, when moisture content is at its lower level (Tamminen, 1970). The moisture content was higher in *S. pentandra* than in *S. caprea*, both in stem wood and in branches. The relative moisture quotient increased from the base to 30% of relative tree height and then decreased towards the top of the tree in both species. In birch (*Betula pubescens*) moisture increased from the base to the top (Tamminen, 1970). The higher moisture content in *S. pentandra* probably reflected the wetness of the sites. However, genetic control may exist in this respect, since in a study of moisture content in current shoots of different willow clones, significant variations were found between clones grown under identical conditions (Sennerby-Forsse, 1985). These differences may be inherited, although differences in the phenological stage of the shoots at the time of sampling, which would most probably affect water content, cannot be excluded. The variation in relative moisture content in the stem cross-section showed the lowest water content in section 2 (the midsection) while sections 1 and 3 were similar. Differences between the three sections were more pronounced in *S. pentandra* than in *S. caprea*. No geographical trend was found in either species with respect to moisture content.

The variation in moisture quotient in branches was irregular and differed between the two species. Some irregularity was also found in branches as regards the SG of the wood, and was probably due to the sampling methods.

Trees were of different age and height. The different developmental stages of the crowns probably also influenced the branches, even though each branch was sampled at the same relative position in the crown.

The bark proportion was higher in *S. pentandra* than in *S. caprea*, probably due to the smaller diameter of *S. pentandra* trees. Bark specific gravity was lower than that of the wood in both species, and bark moisture quotient was higher than that of the wood. Conversely, bark specific gravity was significantly higher than that of the wood in one- to five-year-old stems of willow (Sennerby-Forsse, in preparation). *S. caprea* bark had a higher mean SG than bark from *S. pentandra*, which coincides with the overall higher wood SG in *S. caprea*.

Concluding remarks

The wood quality of the two willow species investigated was similar as regards fibre dimensions and within-stem variation of important traits. However, in general the mean SG of the wood was higher in *S. caprea*. The variation, both within-stem and among-stand was always wider with *S. pentandra* trees. No geographical trend regarding wood characteristics could be detected in this material.

The stands from which the test trees were sampled had not been subject to silvicultural treatments and were in a relatively poor condition. Considering the fact that the trees included in this study represent a totally un-manipulated material, the general wood quality was relatively high compared with other hardwood species used in forest industry, such as birch and aspen. The high level of variation observed in wood properties suggests that the selection potential for wood quality in naturally growing stands of *Salix* may be high.

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Acknowledgement. This work was carried out with the help of funds from the National Energy Administration.