Comparison of the bordered pits of two species of spruce (*Pinaceae*) in a green and kiln-dried condition and their effects on fluid flow in the stem wood in relation to wood preservation

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Summary

The relationship between bordered pit aspiration, pit sizes and permeability measured as preservative uptake and expressed as porosity was examined in two species of spruce, Sitka spruce (*Picea sitchensis* (Bong.) Carr.) grown in the UK and Eastern spruce (*Picea orientalis* (L.) Link.) grown in Turkey, before (in the freshly felled green condition) and after kiln drying. A 2.5 per cent chromated copper arsenate preservative solution was allowed to flow in either the longitudinal or tangential direction of the stem wood and the uptake was assessed. Bordered pit anatomy was examined by light and scanning electron microscopy and image analysis was used to characterize the samples. The permeability of the wood declined following drying but less so in the Sitka spruce. From an analysis of measurements made on the wood features it appeared that basic density, latewood percentage and degree of pit aspiration were the most important features explaining these results. The structure of the bordered pits varied between the two species and the relative size of the aperture in comparison with the pit chambers was greater in the Eastern spruce. The effects of these and other variables including differences in conventional drying systems and natural tree responses to environmental conditions on pit behaviour affecting permeability are discussed.

Introduction

In the xylem of coniferous trees, water in sapwood moves longitudinally through the tracheid lumina, passing from one tracheid lumen to the next via the bordered pits. The same pathway is also used by preservative liquids penetrating wood from both transverse and lateral faces. With preservation, the longitudinal and tangential flow paths are thus controlled by the bordered

Forestry, Vol. 79, No. 4, 2006. doi:10.1093/forestry/cpl011
Advance Access publication date 28 April 2006

pit, while the horizontally aligned ray cells constitute the principal pathway for radial flow (Comstock, 1970).

Longitudinal flow is much greater than the tangential flow because the flow path is shorter and fluids have to pass through fewer pits (Siau, 1984). Tracheid lumina provide an unobstructed pathway for flow but bordered pits largely control the movement of fluids in conifer wood (Petty, 1970).

In earlywood the cell lumina are wide and bordered pits are both numerous and large; estimates of 50–300 are reported (Stamm, 1970) and observations in *Pinus sylvestris* give a diameter of *c.* 6 µm for the pit aperture. In latewood fewer (10–50) and smaller (aperture diameter of *c.* 2 µm) pits are encountered. In the tree, the earlywood is suited for sap flow while the bordered pits serve as a mechanism to prevent air embolisms disrupting flow by aspirating; however, in dried wood pit aspiration becomes a barrier to flow. In dried wood the latewood is more permeable than earlywood (Petty and Preston, 1969). Pit aspiration closes off the pit; the pit membrane (margo) and torus move across the pit chamber to seal off one of the pit apertures, thus preventing fluid flow through the pit (Petty, 1972). Because the latewood bordered pit membranes are smaller and the thickness of the cell wall is greater, the surface tension of the sap–air interface is insufficient to effectively aspirate the pits and close the longitudinal pathway of flow in the latewood.

The aspiration caused by drying makes many softwoods less permeable to pressure preservative impregnation in the longitudinal direction (Banks, 1970), and many species are described as refractory, i.e. resistant to fluid flow and require a long period of treatment (EN 350, 1994, Part 2). In this case, spruce sapwood is very permeable to fluid before drying (Banks, 1970; Erickson, 1970) but after drying it is much less permeable (Banks, 1970; Siau, 1984; Baines and Saur, 1985). In Norway spruce, the proportion of aspirated pits in earlywood is almost total (97 per cent) while that in the permeable sapwood of Scots pine is marginally lower (93 per cent) (Phillips, 1933). Although the contribution of rays to bridging longitudinal pathways of flow has not been thoroughly examined, it is possible that differences in ray structure and the contribution of ray tissue to longitudinal flow may be considerable in many pines. Thus, in spruces discontinuous or blocked pathways of flow accumulate deeper into the dried wood so that it is essentially refractory.

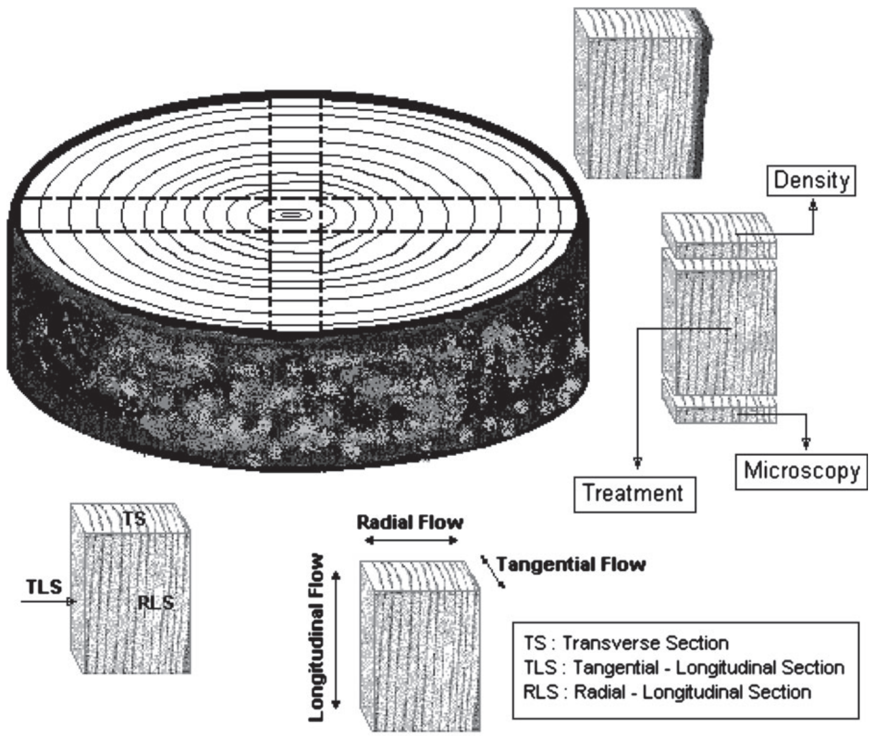
Thus, the difficulty of obtaining satisfactory preservative treatment of refractory species is a problem reducing the effective utilization of many rapidly growing plantation softwoods, where an understanding of various factors controlling fluid flow and their variations is necessary. The present investigation has therefore selected two species of spruce grown in different geographic locations to elucidate the influence of bordered pits and their behaviour at drying on the longitudinal and tangential flow on permeability in stem wood.

Materials and methods

Block preparation

Wood samples, of Sitka spruce (*Picea sitchensis* (Bong.) Carr.) grown in the UK and Eastern spruce (*Picea orientalis* (L.) Link.) grown in Turkey, were collected as being representative of the major commercial plantation spruce species within these two countries. Sitka spruce is the most widely planted species in the UK (Savill, 1991). It was introduced from the western North American seaboard, while Eastern spruce is an important softwood species indigenous to Turkey which covers 286 658 ha of the total forested area (Konukcu, 1998). According to Eraslan (1947), many of the plantations for Eastern spruce have proved successful in Trabzon (North-eastern Black Sea region). The Sitka spruce was of South Oregon (USA) origin raised at Dalby in North East England (53°N, 0°W, 183 m) and the Eastern spruce was collected from the plantation at Meryemana in Trabzon, Turkey (40°N, 39°E, 1050 m). The trees collected were of a similar age class (20–25 years).

Freshly cut logs of the two species, 120 cm long and with their bark still attached, were obtained from 1.3 m above ground level. Once back at the laboratory, the central 40 cm of the each log was taken and converted (Figure 1). Four stakes of 20 × 20 mm were taken from the outer sapwood zone, each was cut into six specimens (producing 24 specimens each 50 mm long) and each specimen was then further divided along its length



flow direction	surface					
	transverse		tangential-longitudinal		radial-longitudinal	
	TS 1	TS 2	TLS 1	TLS 2	RLS 1	RLS 2
longitudinal	unsealed	unsealed	sealed	sealed	sealed	sealed
radial	sealed	sealed	unsealed	unsealed	sealed	sealed
tangential	sealed	sealed	sealed	sealed	unsealed	unsealed

■ sealed surface □ unsealed surface

Figure 1. Collection and preparation of the experimental samples for density and porosity (top, 5 mm long), treatment (centre piece, 40 mm long) and microscopy (bottom, 5 mm long).

into three blocks, a 5-mm block for wood density determination, a 40-mm block for treatment studies and another 5-mm block for microscopy.

The maximum moisture content (MC) method (Olesen, 1971) was used to determine basic density (g cm^{-3}). The green volume is measured by the water displacement method and the oven dry weight is then divided by the green volume as reported earlier (Usta and Hale, 2003).

Samples of various wood species grown in different sites vary in wood density. This is an important factor which influences the theoretical maximum amount of preservative liquid that can be absorbed in a given block volume and this is taken account of here in the way preservative uptakes are expressed. Therefore, the gross pore space or porosity, which is referred to here as the void volume of each sample, was assessed. This takes into account the nominal density as follows: void volume (porosity) = [1 − (density of wood sample/1.53)]. Thus, the amount of space available in each sample was calculated as an estimation of the maximum volume of preservative, which could be absorbed by wood (McQuire, 1970).

Prior to treatment, half of the number of wood specimens were kiln dried to nominal 12 per cent MC using a spruce schedule (schedule J, 60°C dry bulb, 53°C wet bulb, Pratt, 1986) to minimize any drying degrade (Smith, 1986). After drying they were conditioned to equilibrium MC of 12 per cent in a constant temperature and relative humidity (20°C and 65 per cent). The remainder were treated (and analysed) in green condition, i.e. in its original MC level.

Samples for treatment were sealed leaving their ends or radial faces open, allowing either longitudinal or tangential flow (Figure 1). The samples were then full cell treated with 2.5 per cent chromated copper arsenate solution (Tanalith C). The treating schedule was 5 min vacuum at −0.84 bar, 5 min pressure at 1 bar and no final vacuum. Retentions were assessed by uptake. After the process, the maximum possible preservative uptake was calculated as a percentage of void volume filled (VVF per cent) on an individual block basis, as follows: VVF per cent = [((treated weight (g) − sealed weight (g))/block volume (cm^3))/porosity] × 100. Block volume is calculated by multiplying measured dimensions.

Microscopy

Microscopic examinations were made on green and kiln-dried specimens to examine the proportions of aspirated bordered pits and to measure the size of the pit apertures. For light microscopy, radial longitudinal sections 15 µm thick and 20 mm in width of the outer sapwood were cut on a sledge microtome from blocks immersed in formalin–acetic acid–alcohol for some 72 h (O'Brien and McCully, 1981). Transverse sections were also taken to determine the proportions of early- and latewood following the Mork/Denne definition (Denne, 1988). Latewood cells were distinguished from earlywood cells when twice the cell wall thickness (i.e. 2× that of the wall pair including the middle lamella) was greater than the radial diameter of the lumen. Images were captured digitally and pit sizes were measured using a Seescan Image Analysis System (SIA), as reported in Usta and Hale (2003).

Images of the pits seen on the radial faces were also captured digitally in a scanning electron microscope (SEM) and were measured by SIA. The specimens wood were split along the radial plane, razor cut, dried, adhered onto SEM stubs and sputter coated with gold prior to examination in the SEM (Usta and Hale, 2003).

The treatment preservative uptake data and the pit size data were analysed using Minitab v10 statistical software. Mean values were compared by analysis of variance and then by Duncan's multiple range comparison test at 5 per cent significance level (Steel and Torrie, 1960).

Results

Gross anatomy and basic density

The growth rate (based on growth ring features) and basic density of the Sitka spruce grown at a low altitude (183 m) were greater than that of the Eastern spruce grown at a higher altitude (1050 m) (Table 1). In addition there was a higher

Table 1: Physical properties of Sitka and Eastern spruce

	Growth ring feature				Density		
Species	GRW (mm)	Ew (mm)	Lw (mm)	*L* (%)	*R* (g cm^{-3})	*K* (%)	*P* (%)
Sitka spruce	3.4 ± 0.42	2.1	1.3	38.2	0.403 ± 0.012	26.9	73.1
Eastern spruce	2.2 ± 0.61	1.7	0.6	25.9	0.357 ± 0.024	23.8	76.2

Each value is the mean ± SD of 24 replicates. SD is only indicated for the (GRW) and (*R*) GRW = growth ring width; Ew = earlywood width; Lw = latewood width; *L* = the proportion (%) of latewood in a growth ring; *R* = basic density; *K* = the proportion (%) cell wall within a given volume; *P* = porosity (fractional void volume), i.e. data were shown as a percentage for comparison. According to Studentized Range Test, *P* = 0.021 for GRW at the 1% level (**) and *P* = 0.039 for *R* at the 5% level (*).

proportion of latewood in the Sitka spruce (Table 1). As a result of a lower density, the corresponding fractional void volume of the Eastern spruce was higher (Table 1).

When tracheid lengths were examined, Sitka spruce had wider, longer tracheids and latewood tracheids were longer than the earlywood tracheids in both species (Table 2). The wall thickness was also slightly less in Eastern spruce which in combination with the lower latewood percentage explains its lower wood density.

Ultrastructure

Expectedly, the latewood showed fewer and smaller bordered pits on the radial surfaces of the axial tracheids than earlywood in both species. Bordered pits are scattered on the radial walls along the length of the tracheids but are mainly concentrated at the cell ends where the longitudinal flow paths of two tracheids overlap at the ends. An estimated number of earlywood bordered pits in this region of overlap ranges from 4 to 21 in both species but was generally lower in Eastern spruce.

The pits themselves showed major differences in their features (Table 3). The general appearance of the aspirated pits in Sitka spruce showed relatively prominent torus and margo structures but those of the Eastern spruce were less obvious and encrusted (Figure 2); possibly the degree of adhesion of torus to the pit border was different as well. Although the pit chamber diameters (μm) were greater in Sitka spruce, the apertures in earlywood were smaller than those of Eastern spruce. In latewood both the chambers and apertures were larger in Sitka spruce.

Table 2: Dimensions of the axial tracheids in both earlywood and latewood zones

		Length (mm)	Total diameter (μm)	Wall thickness (μm)	Lumen (μm)
Measured tangentially (across the growth rings)					
Sitka spruce	Earlywood	3.0	32.4 ± 0.006	3.6	25.2
	Latewood	3.4	25.8 ± 0.009	4.3	17.2
Eastern spruce	Earlywood	2.6	29.5 ± 0.008	2.8	23.9
	Latewood	3.2	17.7 ± 0.005	3.8	10.1
Measured radially (in the ray direction)					
Sitka spruce	Earlywood	—	34.5 ± 0.004	3.4	27.7
	Latewood	—	18.3 ± 0.006	4.5	9.3
Eastern spruce	Earlywood	—	31.8 ± 0.008	2.9	26.0
	Latewood	—	12.4 ± 0.005	3.6	5.2

All the measurements were made from the transverse section, except the tracheid length, which was measured from macerates. Each value is the mean ± SD of 32 replicates for earlywood, and of 28 for latewood in either varieties. SD is only indicated for the total diameter of the axial tracheid.
Total diameter = (2 × wall thickness) + lumen.

Table 3: Dimensions of the axial tracheid bordered pits (surface view, on the radial longitudinal face)

Location in growth ring	Species	Pit chamber dia.* (μm)	Pit aperture dia.* (μm)	Shape
Earlywood	Sitka spruce	19.6 ± 0.014 a	6.5 ± 0.0023 a	Circular
	Eastern spruce	17.5 ± 0.011 b	7.3 ± 0.0018 b	Circular
Latewood	Sitka spruce	6.2 ± 0.008 c	2.3 ± 0.0012 c	Slit-like
	Eastern spruce	3.9 ± 0.009 d	1.8 ± 0.0016 d	Blurred

Each value is the mean ± SD of 20 replicates for earlywood, and of 10 for latewood in either varieties. Means with a common letter in a given column are not significantly different at $P < 0.05$ level (Studentized Range Test).
*dia. = diameter.

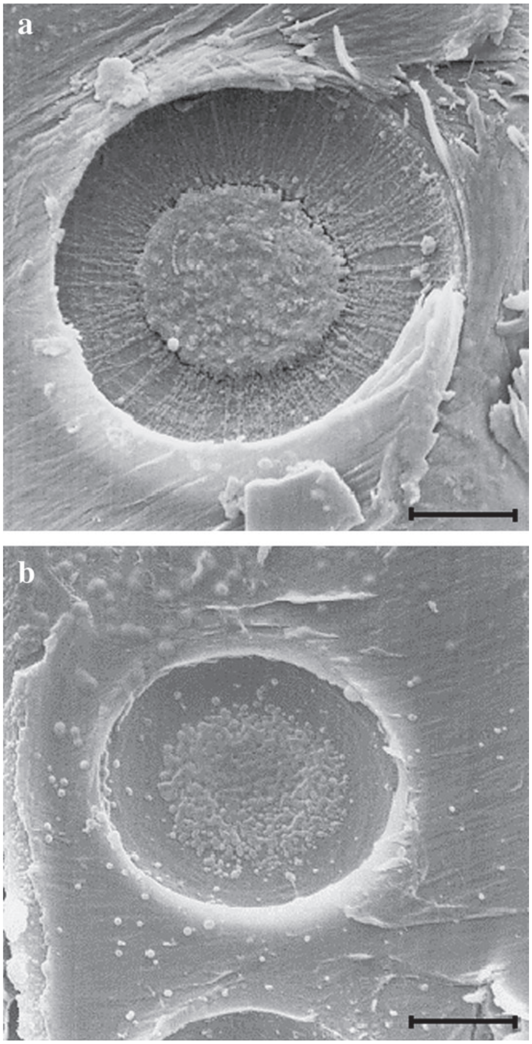


Figure 2. SEM pictures showing the typical appearance (radial face, surface view) of the inside of bordered pits from the earlywood of (a) Sitka spruce and (b) Eastern spruce. 1 bar = 4 μm.

Aspiration and permeability

Both species were better treated either longitudinally or tangentially in the green condition (Table 4), and although there were little differences between the species longitudinally, tangential permeability (not significant, $P < 0.05$) was greater in the Eastern spruce. Kiln drying caused the expected reduction in permeability, being widely attributed to aspiration, and this reduction was greater in Eastern spruce ($P < 0.05$) for both flow directions.

The extent of pit aspiration in the green wood of both species was similar and low (Table 4) and increased markedly on drying. Greater aspiration occurred in the Eastern spruce, consistent with the lower observed permeability.

Discussion

Bordered pit aspiration is well understood as a major factor in the reduction in softwood permeability on drying and this is clearly reaffirmed here. In the green condition both spruce species showed the same permeability but differences in the dry state, which were explained by the degree of pit aspiration, occurred between the two species. What is not clear is what factors affect the different degrees of pit aspiration in different circumstances (among species in this instance). Indeed the extent of aspiration in the dried wood is somewhat lower than the 97 per cent reported for spruces (Phillips, 1933). It is possible that the small block sizes used in this study or kiln drying have reduced the overall extent of pit aspiration. The lower extent of aspiration has had a noticeable effect on preservative uptake; values around 30 per cent VVF are normally reported for Sitka spruce rather than the 70 per cent seen in this study. Further work on the influence of conventional kiln-drying conditions could result in a better understanding of pit behaviour and allow better control of permeability.

Comstock and Cote (1968) stated that rigidity or stiffness of the pit membrane and adhesion of the torus to the pit border also are regarded as important factors affecting aspiration. Due to differences in the diameter of the chamber in relation to the distance of the membrane and torus from the aperture (Liese and Bauch, 1966, 1967), the forces necessary to aspirate the pit membranes are higher in latewood bordered pits, so that even the forces at air–water interfaces as air bubbles move past pit apertures or the cavitation effects which occur during drying are not sufficient to bring about their aspiration. Accordingly, the aspects, which relate to pit dimensions

Table 4: Permeability (as VVF%) in the longitudinal and tangential flow directions and condition of bordered pits in earlywood before and after wood drying

		Permeability (as VVF%)		State of bordered pits (%)	
Varieties	Condition	Longitudinal	Tangential	Open	Aspirated
Sitka spruce	Green	95.8 ± 1.34 a	83.2 ± 1.21 a	93.4	6.6
	Kiln dried	71.4 ± 1.71 b	69.3 ± 1.55 b	49.3	50.7
Eastern spruce	Green	97.4 ± 1.66 a	88.4 ± 1.82 a	93.9	6.1
	Kiln dried	63.5 ± 1.25 c	56.7 ± 1.49 c	40.8	59.2

Each value is the mean ± SD of 24 replicates in either flow direction, and of 78 for the overall of the axial tracheid bordered pits in each variety. SD is only indicated for VVF%. Means with a common letter in a given column are not significantly different at $P < 0.05$ level (Studentized Range Test).

and to the amount of latewood are also likely to be of importance.

When the percentage latewood was examined, it was clear that Sitka spruce has a higher proportion than Eastern spruce (Table 1), which had a significant contribution to the overall permeability in the kiln-dried wood. This is also related to timber basic density. If the relationship between density and permeability either longitudinally or tangentially are examined they appear to be related; Eastern spruce is 88.5 per cent of the density of the Sitka spruce, while its longitudinal permeability is 88.9 per cent of the Sitka spruce. The tangential permeability is less and shows less of a relationship (81.9 per cent), presumably as a result of the longer path length taken for the flow in the tangential direction.

Petty and Puritch (1970) showed that two structural components offered resistance to flow in green wood: tracheid lumina and pit margo pores. Similarly, Bailey and Preston (1970) and Smith and Banks (1971) identified the annulus (margo) and the torus of bordered pits, tracheid lumina and bordered pits. Bolton and Petty (1975) also reported a third structure, the pit aperture, as offering resistance to flow. However, Gregory and Petty (1973) considered that the fractional contribution of lumina to the total flow resistance is less in refractory softwoods.

From a simple consideration of the physics of wood, smaller pore radii, whether they are lumina, apertures or margo pores, will be expected to have a marked influence on permeability. Pit aperture sizes have here been seen to be smaller in the less permeable species but it is impossible to separate out whether this is a significant component of lower permeability. It is interesting, however, to speculate on the influence of aperture size on the effect of aspiration in the earlywood because in this work Eastern spruce has a larger aperture and a greater proportion of aspirated pits. A larger pit aperture size is capable of transferring greater force to a pit membrane by the air interface effects or cavitation effects which cause aspiration.

Whether these differences noted in this paper are typical for each species and whether the different climatic conditions of each locality are also a contributing factor is unknown. It is known that factors like water availability are related to tree growth rate, wood density, the amount of latewood and cell width and length (Chalk, 1951; Larson, 1969; Sperry, 1995). Some of these aspects are directly related to the ability of particular species of trees, under a given set of climatic conditions, to transport water and survive environmental stresses. In this work some of these aspects have been addressed in respect of permeability before and after drying but it is likely that with the range of variability for a particular species, environmental conditions will produce wood which is more tolerant of drought stresses; one of the characteristics of this may be minor modifications in bordered pit structure. The converse of this is that some trees grown in lower stresses will give wood with low resistance to cavitation and pit aspiration and that trees grown under these conditions may be more suitable for preservation. Clearly, there is scope for further work on the permeability of the same or similar softwood species grown under varying conditions.

Conclusions

The questions for differences in the extent of bordered pit aspiration in refractory species remain unresolved, but differences seen in this study between Sitka spruce (grown in the UK) and Eastern spruce (grown in Turkey) deserve more investigation.

As the frequency of aspirated bordered pits, their sizes and location are generally thought to have an influence on the refractory nature of softwood species, the structure of these conducting pathways has therefore been examined both before and after kiln drying. Both longitudinal and tangential permeabilities were much greater in the green than kiln-dried conditions in both species but the permeability in the kiln-dried wood was greater than expected and the permeability of the Sitka spruce was greater than that of the Eastern spruce. Variations in the extent of pit aspiration, pit sizes and amounts of latewood are thought to be the major reasons for the differences, particularly those differences between the two species. It is suggested that further work on pit anatomy and the behaviour of pits during conventional kiln drying will give worthwhile practical improvements in the longitudinal and tangential permeabilities of spruce. Some attention needs to be paid to Eastern spruce to improve wood density, which may also improve its permeability to preservative treatments. Another suggestion may be to consider planting other spruce species (e.g. Sitka spruce) in the Black Sea region.

Acknowledgements

We are grateful to Dr P. Denne and Dr Christine Cahalan (from University of Wales, Bangor) for their valuable discussions, and indebted to Mr M. Jones and Mrs H. Simpson for their expert technical assistance. We also thank Miss P. Bienz for her skilled help.

References

Bailey, P.J. and Preston, R.D. 1970 Some aspects of softwood permeability (II). *Holzforschung* **24** (2), 37–45.

Baines, E.F. and Saur, J.M. 1985 Preservative treatment of spruce and other refractory wood. In *Proceedings, American Wood Preservation Association*, pp. 14–26.

Banks, W.B. 1970 Some factors affecting the permeability of Scots pine and Norway spruce. *J. Inst. Wood Sci.* **5** (1), 10–17.

Bolton, A.J. and Petty, J.A. 1975 Structural components influencing the permeability of ponded and unponded Sitka spruce. *J. Microsc.* **104** (1), 33–46.

Chalk, L. 1951 Water and the growth of wood of Douglas fir. *Q. J. For.* **45**, 237–242.

Comstock, G.L. 1970 Directional permeability of softwoods. *Wood Fiber* **1**, 283–289.

Comstock, G.L. and Cote, W.A. 1968 Factors affecting permeability and pit aspiration in coniferous wood. *Wood Sci. Technol.* **2**, 279–291.

Denne, M.P. 1988 Definition of latewood according to Mork (1928). *IAWA J.* **10** (1), 59–62.

EN 350. 1994 *Durability of Wood and Wood-Based Products: Natural Durability of Solid Wood. Part 2: Guide to Natural Durability and Treatability of Selected Wood Species of Importance in Europe*. British Standards Institute, London.

Eraslan, I. 1947 *Study on the Technical Quality of Picea orientalis (L.) Link and Its Usage*. Forestry Ministry Press, Ankara, 96 pp.

Erickson, H.D. 1970 Permeability of southern pine wood—a review. *Wood Sci.* **2** (3), 149–158.

Gregory, S.C. and Petty, J.A. 1973 Valve action in bordered pits of conifers. *J. Exp. Bot.* **24**, 763–767.

Konukcu, M. 1998 *Statistical Profile of Turkish Forestry*. State Planning Organisation, Ankara, 43 pp.

Larson, P.R. 1969 Wood formation and the concept of wood quality. *Yale University Press, School of Forestry, Bulletin* 74.

Liese, W. and Bauch, J. 1966 Longitudinal permeability of green silver-fir and Norway spruce sapwood to organic solvents. *Holzforschung* **20** (6), 169–174.

Liese, W. and Bauch, J. 1967 On anatomical causes of the refractory behaviour of spruce and Douglas-fir. *J. Inst. Wood Sci.* **19**, 3–14.

McQuire, A.J. 1970 *Radial permeability of timber*. Ph.D. thesis, University of Leeds, 123 pp.

O'Brien, T.P. and McCully, M. 1981 *The Study of Plant Structure: Principles and Selected Methods*. Termarcarphi Pty Ltd, Australia, 215 pp.

Olesen, P.O. 1971 The water displacement method. A fast and accurate method of determining the green volume of wood samples. *For. Tree Improv.* **3**, 1–23.

Petty, J.A. 1970 Permeability and structure of the wood of Sitka spruce. *Proc. R. Soc. Lond. B Biol. Sci.* **175**, 149–166.

Petty, J.A. 1972 The aspiration of bordered pits in conifer wood. *Proc. R. Soc. Lond. B Biol. Sci.* **181**, 395–406.

Petty, J.A. and Preston, R.D. 1969 The removal of air from wood. *Holzforschung* **23** (1), 9–15.

Petty, J.A. and Puritch, G.S. 1970 The effects of drying on the structures and permeability of the woods of *Abies grandis*. *Wood Sci. Technol.* **4** (2), 140–154.

Phillips, E.W.J. 1933 Movement of the pit membrane in coniferous woods, with special reference to preservative treatment. *Forestry* **7**, 109–120.

Pratt, G.H. 1986 *Timber Drying Manual*. 2nd edn. (revised by CHL Tumun). Building Research Establishment Report, Aylesbury, 152 pp.

Savill, P.S. 1991 *The Silviculture of Trees Used in British Forestry*. CAB International, Wallingford, 143 pp.

Siau, J.F. 1984 *Transport Processes in Wood*. Springer-Verlag, Berlin, 245 pp.

Smith, D.N. and Banks, W.B. 1971 The mechanism of flow of gases through coniferous wood. *Proc. R. Soc. Lond. B Biol. Sci.* **177**, 197–223.

Smith, W.B. 1986 Treatability of several north-eastern species with chromated copper arsenate wood preservative. *For. Prod. J.* **36** (7/8), 63–69.

Sperry, J.S. 1995 Limitations of stem water transport. In *Plant Stems: Physiology and Functional Morphology*. B.L. Gartner (ed.). Academic Press, San Diego, pp. 105–124.

Stamm, A.J. 1970 Maximum effective pit pore radius of the heartwood and sapwood of six softwoods affected by drying and soaking. *Wood Fiber* **1**, 263–269.

Steel, R.G.D. and Torrie, J.H. 1960 *Principles and Procedures of Statistics*. McGraw-Hill, New York, 300 pp.

Usta, I. and Hale, M.D. 2003 Radial permeability of wood as affected by wood structure. Permeability of cross field pits in uniseriate rays. *IAWA J.* **24** (2), 197–204.

Accepted date 15 March 2005