Effects of seed origin and site on the amenability of Sitka spruce (*Picea sitchensis* (Bong.) Carr.) grown in Britain to preservative treatment in longitudinal and radial directions

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Summary

Variations in longitudinal and radial permeability were investigated in eight seed origins of Sitka spruce (Alaska (AL), British Columbia (BC), Queen Charlotte Islands (QCI), North Washington (NW), South Washington (SW), North Oregon (NO), South Oregon (SO) and California (CA)) grown at two sites in Britain (Dalby, Eastern England and Rhondda, South Wales). Five trees of each seed origin at each site were sampled at three heights (1, 2 and 3 m above ground level). Permeability of timber grown at the two sites showed an inverse relationship between longitudinal and radial permeability. The general trend showed that, although they were less treated longitudinally, the trees on the Rhondda site were more treated radially as compared with those at Dalby. Results obtained in this study generally show that, of the seed origins, QCI and NW had the greatest permeability in either direction. This is in contrast to NO and SO which had the lowest permeability longitudinally (NO) and radially (SO). Therefore, it is suggested that to optimize the permeability in either flow direction, QCI and NW should be selected for plantation use. The seed origins NO and SO should be avoided in future plantations as they were resistant to treatment with liquid preservative. It appears that there are reasonable explanations for differences in longitudinal permeability and that the differences are linked to wood density which is a selection criterion in current breeding programmes.

Introduction

Density (the dry mass contained in a volume of wood) is directly related to the mechanical properties of wood (Fielding, 1967; Bendtsen, 1978) and, therefore, is important as an index of wood quality (De Zeew, 1965). In addition to its effects on mechanical properties, density has an influence on resistance to biological attack (Nilsson and Daniel, 1992), and higher density may reduce the void volume for preservative treatment. Despite this, increases in density within a species are generally in the lateral direction which is a residual pathway of preservative flow after drying and, hence, density is an important factor with preservative studies (McQuire, 1975). It is therefore most important to recognize and understand both direct and indirect factors which control density and influence its variability within the tree.

It is generally agreed that research into quality improvement should aim at identifying favourable genotypes and also growing conditions which will produce wood of the desired quality (Denne and Dodd, 1980). In this case, the most important area of influence that the forester has in manipulating the quality of the timber is genetic control (e.g. the species, provenance/seed origin and selected genotype), and the second area is the management of growing trees. Therefore, a programme of tree and timber selection is being undertaken by the Forestry Commission in Britain for Sitka spruce in order to recognize and, in due course, to breed from those trees combining high yield and good timber quality (Fletcher, 1976).

In British forestry, Sitka spruce is the most widely planted species (Harding, 1988). According to Lines (1987), it was mostly planted in the north and west of Britain, in some areas comprising 90 per cent of all trees planted. It is likely that Sitka spruce will continue to be planted on a large scale. There are over 600 000 ha of Sitka spruce in the UK, comprising ~27 per cent of the total area under coniferous forest (Locke, 1987).

The success of Sitka spruce in Britain and Ireland can be attributed to its ability to grow on a wide range of sites (often under poor conditions) and to have both a good stem form (where the stems are generally straight and the branching habit of most trees is satisfactory) and a high proportion of vigorous growth, i.e. the yields of Sitka spruce generally exceed those of other species (Brazier, 1967, 1970, 1972; Faulkner, 1987; Gill, 1987; Worrell, 1987; Fletcher, 1992; Thompson, 1992).

Sitka spruce sapwood is generally regarded as being very permeable to fluid before drying (Erickson, 1970; Liese and Bauch, 1977) but after drying it is much less permeable (Phillips, 1933; Bolton and Petty, 1975) and is classed as resistant to preservative treatment (British Standards Institution, 1994). It is generally believed that the cause of loss of permeability is axial tracheid bordered pit aspiration in the earlywood where the pit margo and torus are displaced when air bubbles move past the membrane as would typically occur during drying (Hart and Thomas, 1967; Comstock and Cote, 1968; Petty, 1970a, 1972). In a situation such as pole treatment, longitudinal flow treats the pole ends very well, whereas the region of high risk, the ground line zone, is situated above this well-treated zone (Siau and Shaw, 1971). It is in this context that radial flow into the sapwood is particularly important (Siau, 1984).

Comstock (1970) has shown that, in softwoods, longitudinal and tangential flow are controlled by the same factors but radial permeability is controlled by separate factors. In many softwoods, tracheid pitting is concentrated on radial cell faces which favours flow in the tangential direction via a longitudinal route (i.e. along axial tracheids through tracheid pits, along axial tracheids through tracheid pits, etc.), and thus gives a long path length for tangential flow (Eaton and Hale, 1993). However, there is no real insight in Comstock's models of the mechanism of radial flow.

The major problems in the treatment of spruce relate to the anatomical structure of the material (Petty, 1970b; Baines and Saur, 1985). For instance, the bordered pit is normally considered the most important structure regulating the permeability of softwoods (Gregory and Petty, 1973), but the rays have also been proven influential (Liese and Bauch, 1967). The small ray size and the cross-field pit structure may contribute to the refractory nature of spruce in the radial direction (Liese and Bauch, 1977).

The work described in this paper forms part of a larger study on the influence of genetic and environmental factors on the amenability of Sitka spruce to preservative treatment. The objective of this part of the study was to examine genotype × environment interactions in wood permeability of eight seed origins extending from the north to the south of the natural range of the species when grown at two sites in Britain, one in Eastern England and one in South Wales. Since density may have a direct influence on preservative uptake, and because density is a factor under

Table 1: Geographical locations of the trial seed origins from throughout the natural distribution of Sitka spruce grown from north to south (from Alaska to California)

Region	Seed origin	Code*	Latitude (N)	Longitude (W)	Elevation (m)
Alaska	Duck Creek, Juneau Area	3024	58.37°	134.58°	30
British Columbia	Inverness, Prince Rupert	3044	54.20°	130.25°	0–30
Queen Charlotte Islands	Masset (commercial seedlot)	7111	54.00°	132.00°	0–15
North Washington	Forks, Olympic Rain Forest	3003	48.07°	124.30°	120–140
South Washington	Raymond, Willapa Bay	3009	46.68°	123.87°	15–30
North Oregon	Necanicum	3012	45.82°	123.77°	45
South Oregon	Brookings, Oregon	3018	42.25°	124.38°	90
California	Crescent City, California	3020	41.67°	124.18°	10–15

* IUFRO seed identification numbers (represented in Figure 1).

genetic control, this study also details the effect of seed origin on density. In addition to seed origin, its variability both within and between trees and also between sites is examined. Other factors, including growth ring width and tree size are accounted for. Also, its variability both within and between trees and between sites was examined.

Materials and methods

The seed origins sampled and trial sites

The study was carried out on 80 20-year-old trees from eight seed origins (Alaska (AL), British Columbia (BC), Queen Charlotte Islands (QCI), North Washington (NW), South Washington (SW), North Oregon (NO), South Oregon (SO) and California (CA)) of Sitka spruce grown at two experimental sites in the UK: Dalby in Eastern England and Rhondda in South Wales (Table 1 and Figure 1).

All the trees (a total of 40 trees from each site, i.e. five trees per seed origin) were growing in an IUFRO (International Union of Forest Research Organization) seed origin trial planted in 1975 when plots representing 34 (Rhondda) and 64 (Dalby) seed origins were laid down. According to Lines (1987), the two sites represent extremes of the range of sites on which this species is grown in Britain, and were chosen for this reason. Each site was laid out in a randomized block design with three blocks and nine (3 × 3) trees per square plot. The planting density (spacing) was 2 m × 2 m. The soil type at Dalby is iron pan with soft limestone, whereas at Rhondda it is *Molinia*/*Calluna* bog over carboniferous sandstone. Elevation and rainfall are higher in Rhondda (450 m, 2400 mm a^{-1}) compared with that for Dalby (183 m, 835 mm a^{-1}).

Collection and preparation of experimental samples

The diameter at breast height (1.3 m above ground level according to Philip, 1994) was measured for each tree before felling and prior to conversion. The selected trees were felled at 50 cm above ground level and the lower 3 m of each tree was then cut into 1-m lengths and marked to assist in identification. Three discs 5 cm thick were cut from each tree at heights of 1, 2 and 3 m. The discs were then sampled by means of a 15-mm plug as shown in Figure 2. In this manner, the four cylindrical samples of 15 mm in diameter and 50 mm in length were produced radially (in east–west and north–south directions) and longitudinally (in the stem direction) from each disc using a core-forming drill. Each core was then kiln dried to 12 per cent moisture content by a mild drying schedule (schedule J: 60°C dry bulb, 53°C wet bulb) in accordance with recommended kiln drying schedule for *Picea* (Pratt, 1974).

From one end of each longitudinal core, thin samples 3 mm thick were cut, and the remainder of each longitudinal core was cut to 30 mm in

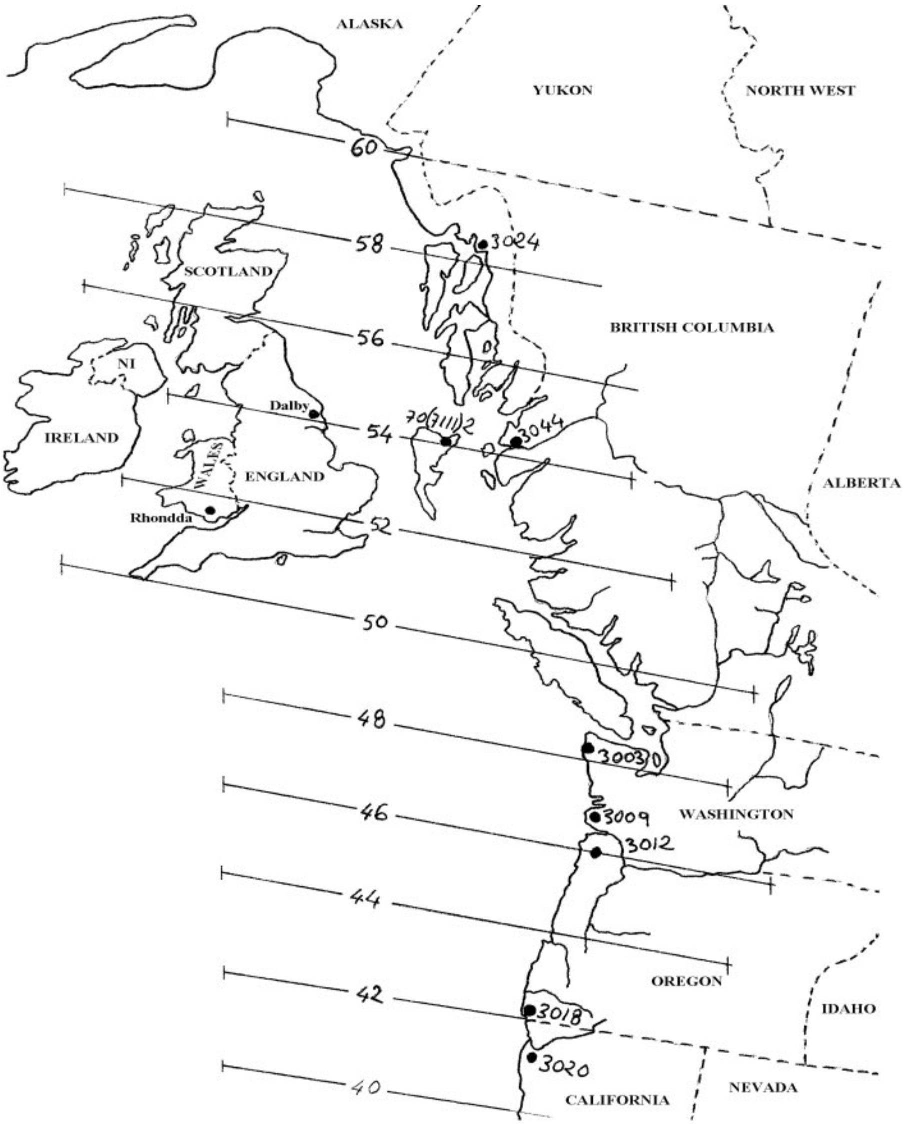

Figure 1. The geographical locations of the selected seed origins (shown as IUFRO seed identification numbers; Table 1) on natural distribution of Sitka spruce (*Picea sitchensis* (Bong.) Carr.) from southern Alaska to northern California, and the locations of trial sites in Britain: Dalby (national grid reference SE882849; Eastern England), Rhondda (national grid reference SN940019; South Wales).

length, likewise the radial plug samples. The small samples (3 × 15 mm diameter), referred to as 'density samples', were taken for density determinations using the maximum moisture content method. All longitudinal and radial samples (30 × 15 mm diameter), referred to as 'treatment samples', were used in the treatment experiment with CCA-tanalith C via a mild schedule of full-cell impregnation process using a lab scale (30 l) pressure treatment plant.

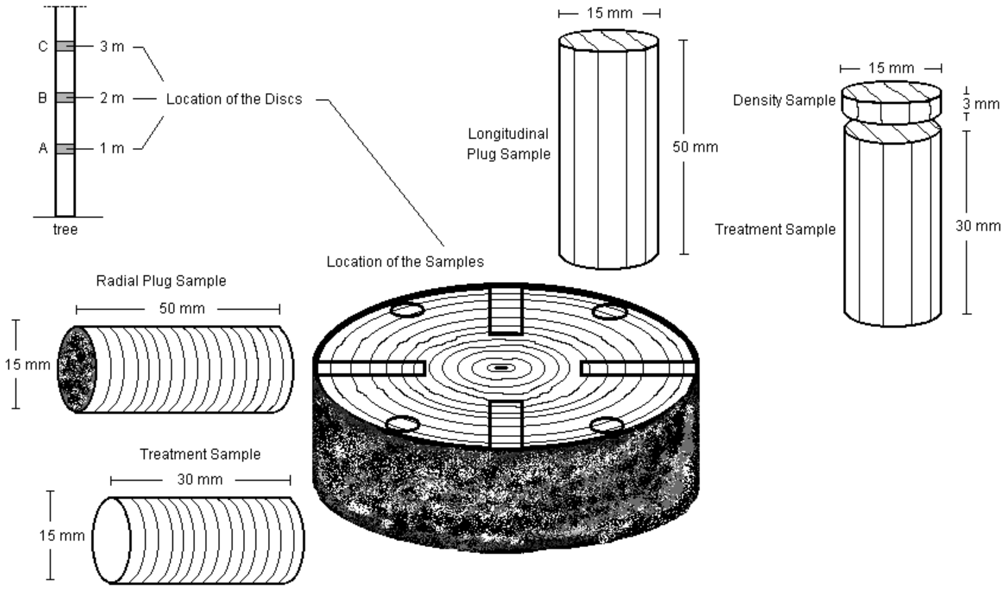

Figure 2. Initial locations of the plug experimental samples on the transverse section of the selected discs.

Determination of wood density

Wood density was calculated from the weight after drying until constant weight (at 103 ± 2°C) divided by the green volume (measured by the water displacement method; Oleson, 1971). To obtain the green volume, experimental samples were firstly saturated with deionized water by evacuating them at –80 kPa (600 mmHg) for 12 h, and soaking for 10 days. The volume was then determined from the amount of liquid which it displaced. After having performed this procedure, density of the samples was calculated from the following equation:

$$d = \frac{M_o}{\frac{M_o}{G} + \left(M_s - M_o\right)} \times 1000$$

where d is density (k gm^{-3}), M_o is an oven dry mass of sample (g), M_s is the mass of sample saturated with deionized water (g), G is specific gravity of cell wall substance (taken to be 1.53 g cm^{-3}).

Plugs of various trees of the same seed origin that have grown in different sites vary in density; this is an important factor influencing the amount of liquid that can be absorbed in a given block volume, hence the way preservative penetration is expressed. Therefore, the maximum theoretical uptake of each plug based on void volume was also assessed. The space available in each plug, allowing for density, was calculated as an estimation of the maximum volume of preservative which could be absorbed by wood (McQuire, 1970).

Determination of preservative uptake as the percentage of void volume filled

After kiln drying to a nominal 12 per cent moisture content, the core longitudinal and radial plug samples were conditioned to an equilibrium moisture content of about 12 per cent at 20°C, 65 per cent relative humidity. The plugs were then weighed and sealed with ABS (Durapipe Norton Canes, Staffs, UK) leaving either only one end open (for longitudinal flow) or a tangential face (for radial flow), so that penetration was restricted to one face. The sealing compound for the purpose of handing large numbers of specimens was ABS polymer dissolved in methyl ethyl ketone. The coating was done three times to achieve a good seal. This compound adhered well to the wood (provided the first coat was applied in a fairly dilute, low viscosity condition) and set very quickly. The final seal was strong but elastic enough to withstand liquid pressure of 7 bar and to accommodate lateral swelling. After reconditioning, the sealed plugs were reweighed. A 2 per cent CCA (Commercial Tanalith C; Arch (formerly Hicksons, Castleford, Yorks, UK)) was prepared and checked by hydrometer for concentration (British Standards Institution, 1987); this was used throughout the experimental work. Prepared plugs were cell treated with an initial vacuum of –84 bar (640 mmHg) for 15 min followed by flooding and different pressure applications according to the plug orientations (longitudinal, 3 bar for 6 min; radial, 5 bar for 45 min). No final vacuum was applied. After the treatment was finished, treated specimens were taken out from the cylinder and were put on absorbent paper for a few seconds prior to weighing. Thereafter, the fluid uptake was determined on a whole-block basis. The amount of space available in each plug was calculated as the maximum volume of preservative which could be absorbed by wood:

$$\mathrm{VVF\%} = \frac{\left(\dfrac{T_\mathrm{w} - S_\mathrm{w}}{V}\right)/1000}{P}$$

where VVF per cent is void volume filled (per cent); T_w is treated weight (g); S_w is sealed weight (g); V is block volume (m^3) and calculated by $[\pi(r)^2\, l]$ where r is radius of the sample (m), l is length (m); P is porosity (per cent) as the fractional void volume of wood and determined by $\{[1 - (\text{density}/1530)] \times 100\}$.

Data analysis

All the parameters were compared initially on overall means for both sites and then for each site. The experimental data were then analysed by balanced analysis of variance to examine the relative importance of the factors and their interactions (site (S), seed origin (O), S × O, trees within S and O, height (H), O × H, and H on trees within S and O) on diameter growth, ring width, wood density, percentage of longitudinal void volume filled (LVVF%), and percentage of radial void volume filled (RVVF%). Interactions of permeability data (LVVF%, RVVF%) between seed origins and sites were examined using analysis of variance, rank correlations and regression analysis (Finlay and Wilkinson, 1963; Bland, 1995). Relationships of the variations of both LVVF% and RVVF% at height, tree and seed origin levels were then examined.

Results

The summary results of analysis of variance (according to site (S), seed origin (O), S × O, trees within S and O: T(S O), height (H), O × H, and H on trees within S and O) are shown in Table 2a. Variations in diameter, ring width, density, LVVF%, RVVF% among S, O, S × O, T(S O), and H were very highly significant ($P < 0.01$). The height × site interaction (H × S) and height × seed origin interaction (H × O) was highly significant for diameter and both LVVF% and RVVF%, although it was not significant for ring width. Effect of H × O was also highly significant for density, whereas H × S was not.

Descriptive statistics of the experimental results are given in Table 2b including pairwise differences between seed origins in either site. Means of diameter shown here are at breast height (1.3 m above ground level) from the trial trees ($n = 5$) but that for the growth ring width, wood density, LVVF% and RVVF% are of data from five trees per seed origin and three heights per tree in each trial site ($n = 15$).

The average growth ring widths and densities of sites as well as both LVVF% and RVVF% were significantly different from each other at $P < 0.05$ level, i.e. Rhondda was greater in growth ring width, density and RVVF% than Dalby, whereas LVVF% was greater at Dalby than Rhonda.

Although there were no significant differences between sites, the stem diameter differed significantly ($P \leq 0.05$) among seed origins within the trial sites. The mean tree diameter at breast height varied from 12.2 cm to 17.6 cm in Dalby, and 13.8 cm to 15.9 cm in Rhondda. In both sites, the seed origin AL had the narrowest tree diameter, while the widest was QCI in Dalby and CA in Rhondda.

The seed origin North Washington (NW) showed the narrowest rings, whereas CA showed the widest growth rings. This was therefore

Table 2a: Summary of the results of analysis of variance for permeability trial indicating significant effects ($P \leq 0.050$) for the influencing factors

Source	Diameter at 1.3 m (cm)	Ring width (mm)	Density (kg m^{-3})	LVVF%	RVVF%
S	***	***	***	***	***
O	***	***	***	***	***
S × O	***	***	***	***	***
T(S O)	***	***	***	***	***
H	***	***	***	***	***
H × S	***	n.s.	n.s.	***	***
H × O	***	n.s.	***	***	***
H × S × O	***	**	n.s.	n.s.	***
H × T(S O)	***	*	***	***	***

S = site; O = seed origin; T = tree; T(S O) = trees within S and O; H = height; H × T(S O) = height on trees within S and O; n.s. = not siginificant; * = significant at 95 per cent level; ** = significant at 99 per cent level; *** = significant at 99.9 per cent level.

Table 2b: Means of diameter, growth ring width, density, longitudinal void volume filled (LVVF%) and radial void volume filled (RVVF%) in each seed origin in either site

	Diameter at 1.3 m (cm)	Ring width (mm)	Density (k gm^{-3})	LVVF%	RVVF%
Dalby					
AL	12.2 (± 2.19) ad	3.1 (± 0.67) a	449.3 (± 26.1) a	58.6 (± 8) a	17.4 (± 8) ab
BC	15.4 (± 3.39) ab	3.5 (± 0.84) b	391.4 (± 48.1) b	62.9 (± 11) ab	15.9 (± 5) a
QCI	17.6 (± 2.90) be	3.6 (± 0.83) b	400.5 (± 43.6) bc	69.0 (± 14) b	23.8 (± 13) b
NW	15.1 (± 1.06) abc	3.5 (± 0.53) b	421.7 (± 48.7) cd	68.5 (± 10) b	16.5 (± 4) ab
SW	14.6 (± 2.47) ab	3.2 (± 0.54) a	415.0 (± 34.0) bcd	61.1 (± 7) a	12.4 (± 4) a
NO	14.0 (± 4.24) cd	3.3 (± 0.66) a	430.2 (± 33.9) ad	58.6 (± 17) a	17.4 (± 7) ab
SO	14.8 (± 2.69) ace	3.5 (± 0.67) b	393.9 (± 53.5) b	71.0 (± 5) b	13.8 (± 6) a
CA	16.5 (± 1.84) bc	5.6 (± 0.88) c	361.3 (± 11.1) e	60.2 (± 6) a	17.2 (± 2) ab
Rhondda					
AL	13.8 (± 1.98) a	5.4 (± 0.17) a	394.3 (± 28.3) ac	50.9 (± 10) acb	23.9 (± 4) ac
BC	14.7 (± 2.69) a	5.0 (± 0.47) b	382.3 (± 21.6) a	49.7 (± 12) bc	21.9 (± 4) ab
QCI	15.4 (± 3.82) a	4.9 (± 0.88) b	422.3 (± 45.8) bd	58.8 (± 10) a	25.4 (± 8) a
NW	14.4 (± 0.85) a	3.9 (± 0.34) c	446.6 (± 47.8) be	59.4 (± 7) a	22.9 (± 5) ab
SW	14.8 (± 2.62) a	4.1 (± 0.72) c	430.2 (± 39.6) bd	58.8 (± 8) a	19.9 (± 6) ab
NO	15.3 (± 1.13) a	5.1 (± 0.77) b	418.6 (± 30.3) cd	43.2 (± 7) b	18.1 (± 6) ab
SO	14.0 (± 2.05) a	4.2 (± 0.68) b	458.1 (± 30.4) e	52.8 (± 11) ac	15.7 (± 6) b
CA	15.9 (± 4.03) a	6.1 (± 0.45) d	371.2 (± 17.3) a	52.9 (± 8) ac	17.6 (± 5) bc
Dalby	15.0	3.7	407.9	63.7	16.8
Rhondda	14.8	4.8	415.6	53.3	20.7
Overall	14.9	4.3	411.8	58.5	18.8

Means having same letter within each trial site show non-significant differences according to the Tukey Comparison Test at 0.05 level of probability.

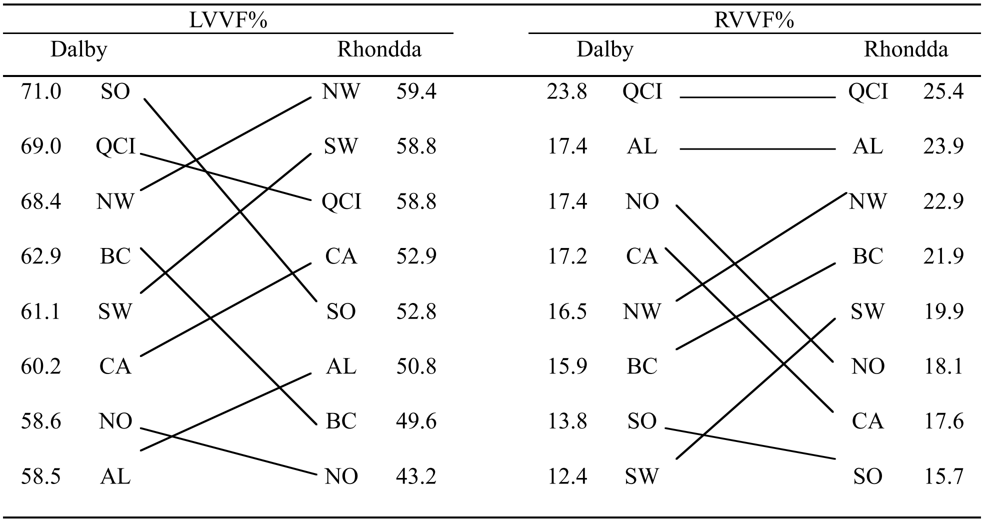

Figure 3. Site × seed origin interactions for both longitudinal void volume (LVVF%) and radial void volume (RVVF%) filled.

reflected in wood density which was the greatest in NW (434 kg m^{-3}), and the lowest in CA (366 kg m^{-3}). Mean growth ring width was largest in seed origin CA in both sites (Dalby, 5.6 mm; Rhondda, 6.1 mm), whereas the narrow growth ring occurred in different seed origins, i.e. the growth ring width was 3.1 mm in AL (Dalby) and 3.9 mm in NW (Rhondda).

The percentage of longitudinal void volume filled (LVVF%) and the percentage of radial void volume filled (RVVF%) range also differed significantly among seed origins ($P \leq 0.05$). The values were most in Queen Charlotte Island (LVVF%, 64; RVVF%, 25) and least in North Oregon (LVVF%, 51) and South Oregon (RVVF%, 15). The seed origin North Oregon (NO) showed the lowest longitudinal permeability in both sites (Dalby, 59 per cent; Rhondda, 43 per cent), whereas NW (59 per cent) in Rhondda and South Oregon (71 per cent) in Dalby were the most permeable ones. For radial permeability, QCI was the most permeable from either site (Dalby, 24 per cent; Rhondda, 25 per cent) while seed origins SO (16 per cent) in Rhondda and South Washington (12 per cent) in Dalby had the lowest permeability. Overall the second most permeable seed origins in terms of LVVF% and RVVF% were QCI and AL, respectively. Both of the two seed origins were second greatest in either Dalby (QCI, 69 per cent; AL, 17 per cent) or Rhondda (QCI, 59 per cent; AL, 24 per cent).

Site × seed origin – interactions

In general, the experimental trees of each seed origin were better treated longitudinally in Dalby and radially in Rhondda, although the percentage of void volume filled in both longitudinal and radial flow directions at each seed origin indicated different behaviour in particular trial sites (Figure 3).

Although the LVVF% was greater in Dalby, values for both NW and QCI were above average and those for both AL and NO below average at both sites. There were, however, inverse changes of LVVF% in the following seed origins SO, SW, BC and CA. Both SO and BC had higher LVVF% in Dalby, whereas each of them had a lower value in Rhondda where both SW and CA had a greater amount of LVVF% at Rhondda. On the other hand, QCI was the most treated radially followed by AL in either site and SO was the least treated radially in Rhondda and was the second lowest in Dalby. The other seed origins (NW, BC, SW, NO and CA) showed an inverse pattern, i.e. NW,

Table 3a: The correlation matrix showing the correlations between the variables of the 240 experimental samples of both sites

Source	Diameter	Density	Ring width	LVVF%
Density	**–0.206**			
Ring width	0.041	**–0.503**		
LVVF%	**0.245**	**0.197**	**–0.330**	
RVVF%	0.029	–0.004	0.094	0.015

The critical value is 0.138 for overall means, and the significant correlations are indicated in bold.

Table 3b: The correlation matrix showing the correlations between the variables of the 120 experimental samples of each site

Source	Diameter	Density	Ring width	LVVF%	RVVF%
Diameter	–	**–0.309**	**0.402**	**0.226**	–0.005
Density	–0.048	–	**–0.582**	**0.303**	–0.071
Ring width	–0.057	**–0.640**	–	**–0.202**	0.119
LVVF%	0.070	**0.197**	–0.162	–	0.011
RVVF%	0.191	0.031	–0.103	0.189	–

Correlations between the variables are given for Dalby in above diagonal, for Rhondda in below diagonal. The critical value is 0.195 for both sites, and the significant correlations are indicated in bold.

BC and SW had greater RVVF% in Rhondda than in Dalby where NO and CA were more treated radially at Dalby.

Relationships at the height level

Correlation analysis for height level for sites (2 sites × 8 seed origins × 5 trees × 3 samples) is shown in Table 3a as a matrix form, and for each site (8 seed origins × 5 trees × 3 samples) is given in Table 3b.

The correlation matrix showed that significant negative correlations were observed between density and both diameter and ring width, and also between ring width and LVVF%. On the other hand, there were significant positive correlations between LVVF% and both diameter and density (Table 3a).

More of the correlations were significant with samples from Dalby than from Rhondda (Table 3b). In Rhondda, there were negative correlations between ring width and density, with positive correlations between density and LVVF%. All these findings of Rhondda also occurred in Dalby. In addition, there were negative correlations between diameter and density, and between ring width and LVVF%. Also in Dalby, positive correlations were noted between diameter and both ring width and LVVF%.

For the combined data of both sites (Table 3c) linear regressions (R^2) between density and ring width were much greater (0.253) than those for density with diameter (0.042), although in either case the correlations are poor. Furthermore, such anatomical patterns showed different variation between LVVF%: R^2 between LVVF% and tree diameter (0.060) was greater than that for LVVF% with density (0.039). However, the most important factor explaining higher longitudinal fluid uptake was the mean growth ring width (0.109).

The growth ring width accounted for more of the variation in density of the wood than tree diameter in both sites: R^2 showed that ring width accounted for much more variation in density between trees in Rhondda (0.410) than in Dalby (0.339), whereas the tree diameter accounted for very little variation in Dalby (0.096). This result

Table 3c: Linear regression equations and coefficient of determinations between the measured variables at height level in both the two trial sites, Dalby and Rhondda

	Equation of the linear regression	R^2
Both sites	Density = 470 – 4.43 (diameter at breast height)	0.042
	Density = 487 – 16 (growth ring width)	0.253
	LVVF% = 38.7 + 1.51 (diameter at breast height)	0.060
	LVVF% = 72.6 – 3.01 (growth ring width)	0.109
	LVVF% = 35.3 + 0.0564 (density)	0.039
Dalby	Density = 497 – 6.51 (diameter at breast height)	0.096
	Density = 491 – 20.8 (growth ring width)	0.339
	LVVF% = 46.7 + 1.24 (diameter at breast height)	0.051
	LVVF% = 71.3 – 1.89 (growth ring width)	0.162
	LVVF% = 31.4 + 0.0793 (density)	0.092
Rhondda	Density = 537 – 22.8 (growth ring width)	0.410
	LVVF% = 31.6 + 0.0524 (density)	0.039

has also been noticed in Rhondda, although the correlations were not statistically significant in that case. Therefore, comparison of the two sites suggests that LVVF% was lower at Rhondda which had the slower growth rate (tree diameter) and higher density, and the LVVF% was greater at Dalby which had a higher growth rate but lower density. Consequently, the slower grown wood of the Rhondda trees had considerably lower LVVF% than that of the faster grown Dalby trees.

Relationships at tree level

Correlation analysis at tree level for both sites (2 sites × 8 seed origins × 5 trees) is shown in Table 4a, and for each site (8 seed origins × 5 trees) in Table 4b. The correlation matrix showed significant correlations between diameter, ring width and density. There were negative correlations between density and both diameter and ring width, and also between ring width and LVVF%. There were positively significant correlations between LVVF% and both diameter and density (Table 4a).

The measured variables were more significantly correlated to each other in Dalby than in Rhondda. As is seen in Table 4b, in Dalby, there were negative correlations between density and both diameter and ring width. Also, there were positive correlations between diameter and ring width, density and LVVF%. In Rhondda, negative correlations were observed between density and diameter. However, density was not significantly correlated with diameter.

Table 4c shows linear regression equations and coefficient of determinations for mean density with diameter and ring width between trees of all sites. Density was inversely correlated with diameter (0.152) but between-tree differences in density were most closely associated with ring width which accounted for more variation in density (0.273). In the same way, the linear regression between LVVF% and ring width (0.151) was closer than that for LVVF% with diameter (0.109).

The coefficients of determination (Table 4c) between density and ring width were greater with wood from Rhondda site than that from Dalby (0.505 and 0.380, respectively) and ring width accounted for the largest proportion in density variation. In Dalby grown wood, there were also significant coefficients of determination between density and diameter (0.201). Considering between-tree variations within each site, there were no significant differences in LVVF% between the 40 trees sampled from the eight seed origins at Rhondda. At Dalby, however, there were positive and significant correlations between LVVF% and density (0.111).

Relationships at the seed origin level

Correlation analysis at seed origin level for both sites (2 sites × 8 seed origins) is shown in Table 5a,

Table 4a: The correlation matrix showing the correlations between the measured variables at source of the mean data on all the 80 trees of both sites

Source	Diameter	Density	Ring width	LVVF%
Density	**–0.390**			
Ring width	**0.219**	**–0.522**		
LVVF%	**0.330**	**0.220**	**–0.388**	
RVVF%	–0.128	–0.051	0.201	–0.018

The critical value is 0.217 for overall means, and the significant correlations are indicated in bold.

Table 4b: The correlation matrix showing the correlations between the measured variables at source of the mean data on all the 40 trees of each site

Source	Diameter	Density	Ring width	LVVF%	RVVF%
Diameter	–	**–0.448**	**0.653**	0.228	0.060
Density	–0.300	–	**–0.617**	**0.334**	–0.105
Ring width	0.199	**–0.711**	–	–0.228	0.108
LVVF%	0.189	0.253	–0.174	–	0.067
RVVF%	–0.225	–0.049	0.012	0.221	–

Correlations between the variables are given for Dalby above the diagonal, for Rhondda below the diagonal. The critical value is 0.304 for both sites, and the significant correlations are indicated in bold.

Table 4c: Linear regression equations and coefficient of determinations between the measured variables at tree level in both the two trial sites, Dalby and Rhondda

	Equation of the linear regression	R^2
Both sites	Density = 539 – 9.64 (diameter at breast height)	0.152
	Density = 493 – 17.3 (growth ring width)	0.273
	LVVF% = 30.3 + 2.15 (diameter at breast height)	0.109
	LVVF% = 74.4 – 3.4 (growth ring width)	0.151
	LVVF% = 34.6 + 0.0582 (density)	0.049
Dalby	Density = 543 – 9.82 (diameter at breast height)	0.201
	Density = 501 – 23.3 (growth ring width)	0.380
	LVVF% = 31.2 + 0.0797 (density)	0.111
Rhondda	Density = 563 – 27.7 (growth ring width)	0.505

and for each site (8 seed origins) in Table 5b. At this level, none of the measured factors significantly influenced LVVF% or RVVF%. The correlation matrix on overall means of both sites showed no significant correlations between any of the variables. In this case, although the correlations were not statistically significant, density was associated with ring width and diameter (Table 5a). However, the correlations were higher when sites were considered separately (Table 5b).

As seen in Table 5b, in Dalby, there were negative correlations between density and both diameter and ring width. However, in Rhondda, the only significant correlation was observed between density and ring width (negative).

At each site, ring width was significantly correlated with density (Table 5c). Density was more

Table 5a: The correlation matrix showing the correlations between the measured variables at source of the mean data on all the eight seed origins at both sites

Source	Diameter	Density	Ring width	LVVF%
Density	–0.579			
Ring width	0.073	–0.580		
LVVF%	0.507	–0.038	–0.598	
RVVF%	–0.112	0.003	0.381	–0.214

The critical value is 0.666 for overall means, and the significant correlations are indicated in bold.

Table 5b: The correlation matrix showing the correlations between the measured variables at source of the mean data on all the eight seed origins of each site

Source	Diameter	Density	Ring width	LVVF%	RVVF%
Diameter	–	**–0.812**	0.637	0.453	0.463
Density	–0.315	–	**–0.807**	–0.259	–0.019
Ring width	0.374	**–0.897**	–	–0.101	0.169
LVVF%	–0.026	0.372	–0.454	–	0.156
RVVF%	–0.420	–0.140	0.007	0.393	–

Correlations between the variables are given for Dalby above the diagonal, for Rhondda below the diagonal. The critical value is 0.666 for both sites, and the significant correlations are indicated in bold.

Table 5c: Linear regression equations and coefficient of determinations between the measured variables at origin level in Dalby and Rhondda

	Equation of the linear regression	R^2
Dalby	Density = 602 – 14.8 diameter	0.099
	Density = 580 – 30.8 ring width	0.804
Rhondda	Density = 528 – 24.9 ring width	0.781

closely associated with ring width in Dalby (0.804) than in Rhondda (0.781). The significant correlations between seed origin differences also occurred between density and diameter but only in Dalby (0.099).

Discussion

Between tree variation

Wood from the faster-grown Dalby trees was more longitudinally permeable (LVVF%) than the slower-grown Rhondda trees (Figure 4). However, the wood from the Rhondda-grown trees showed higher radial permeability (RVVF%) than the Dalby trees (Figure 5). As all grow well with a good density, the trees of QCI and NW should be selected for more plantations. Individually, the trees of QCI and NW in both sites had higher than average longitudinal and radial permeability; whilst wood from either site of the seed origins NO and SO were, on average, lower. Therefore, it may be suggested that the trees from the seed origins QCI and NW should be particularly planted to produce wood of adequate density and better permeability.

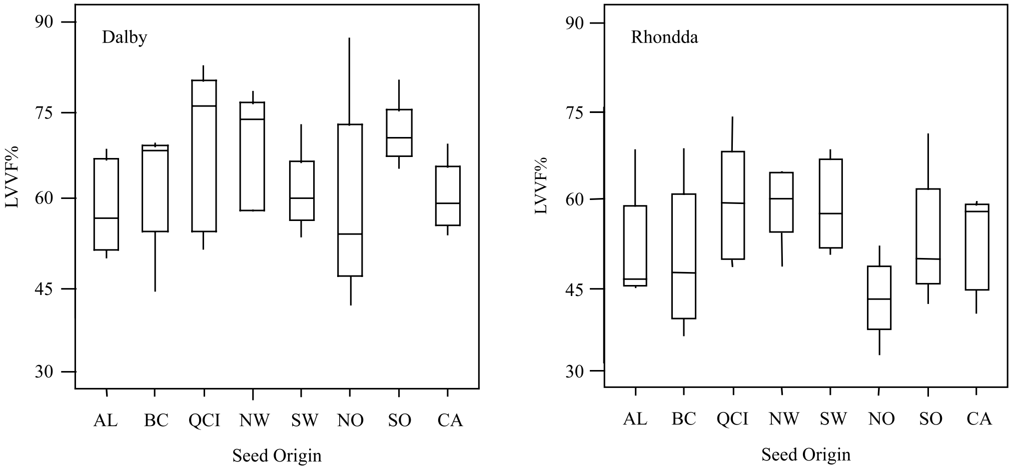

Figure 4. Boxplots showing the distribution of longitudinal permeability values (LVVF%) between trees of each seed origin in trial sites Dalby and Rhondda. [Boxplots are also called box and whisker plots. The box shows the distance between the quartiles, with the median marked as a line, and the whiskers show the extremes (Bland, 1995).]

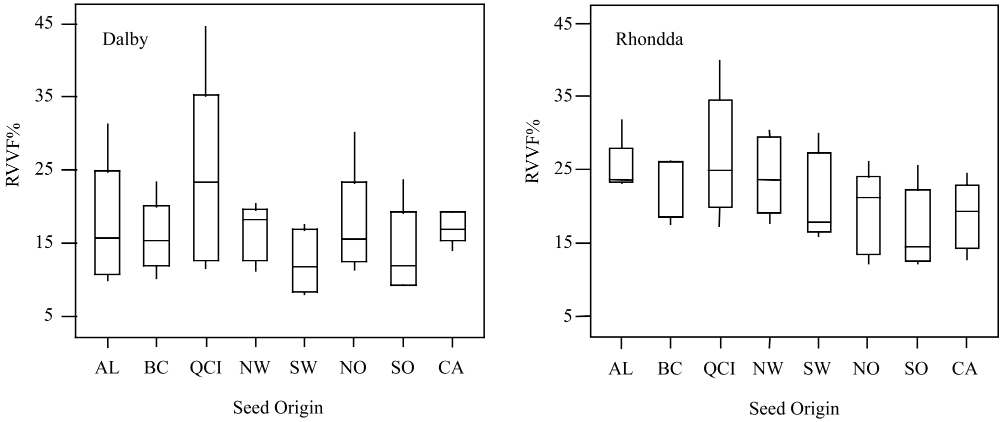

Figure 5. Boxplots showing the distribution of radial permeability values (RVVF%) between trees of each seed origin in trial sites Dalby and Rhondda.

Between seed origin variation

In the discussion of the permeability trial dealing with the correlations between density and the percentage of void volume filled, significant correlations were only found between density and longitudinal permeability (i.e. there were no significant correlations with radial permeability). Since the bulk of the tissue is composed of longitudinal tracheids, latewood percentage is related to density and latewood forms the residual pathway of flow after drying, the correlation between longitudinal permeability and density is not surprising. Furthermore, the lack of correlation between density and RVVF% is not surprising either. However, there are significant differences in LVVF% and RVVF%

between seed origins (Figures 4 and 5). In all cases the seed origins grown at Rhondda show lower LVVF% permeability than those at Dalby but the overall pattern of the seed origins is similar. The overall pattern is again similar between sites for RVVF% permeability but the RVVF% is greater in Rhondda than Dalby.

The results obtained in this study generally show that the longitudinal permeability for seed origins located in the central part of the natural range (Figure 1) of Sitka spruce (average of both sites: QCI, 63.9; NW, 63.9) are greater than NO (50.9) which is situated further south. Moreover, the greatest radial permeability (RVVF%) also occurred in both QCI (24.6) and NW (19.7) in comparison to SO which is located further south (14.8). As shown in Figures 3 and 4, RVVF% values for the southern origins NO, SO and CA are similar at the two sites, although SO showed low RVVF% and high LVVF%. On the other hand, QCI had high radial and longitudinal permeability at both sites. This situation has been shown in some *Pinus* spp. by McQuire (1970) and was explained by the interconnections between the different flow pathways in the different connections. Although Sitka spruce has different anatomical features (extent of aspiration, crossfield pit structure, latewood proportion) compared with *Pinus* spp. further work on the anatomical features of QCI is recommended in future studies. The above comments highlight QCI as an interesting seed origin: in Rhondda it was ranked third LVVF% and second in Dalby. Also, SO highlighted above as having the lowest radial permeability (14.8) had the lowest from the Rhondda wood and second lowest from Dalby.

It appears that there are reasonable explanations for differences in longitudinal permeability and that the differences are linked to density which is now included in British breeding programmes of Sitka spruce. Furthermore, the major aspects of longitudinal permeability that were assessed in this study are affected by post-harvest processing, e.g. drying. It is not surprising that the radial permeability is not correlated with any of the gross features seen or with longitudinal permeability as the features relate more to axial tracheids, i.e. the longitudinal pathway, which account for some 95 per cent of the wood volume (Fengel and Wegener, 1989). Little is known about radial permeability but differences seen in this study between the seed origins QCI and SO deserve greater investigation.

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