Influence of Wood's Anatomical and Resin Traits on the Radial Permeability of the Hybrid Pine (*Pinus elliottii* × *Pinus caribaea*) Wood in Australia

William Leggate,[a,b,]* Maryam Shirmohammadi,[b] Robert L. McGavin,[b] Kerri Chandra,[c] Mark Knackstedt,[a] Lydia Knuefing,[a] and Michael Turner [a]

Wood permeability has a major effect on industrial wood processing and utilization. Wood anatomy and resin influence the permeability of wood. Understanding and manipulating these influences is important to optimize the manufacture and use of forest products. This study investigated the relationships between wood anatomical traits, radial permeability, and resin content of samples collected from 19-year-old hybrid pines (*Pinus elliottii* var. *elliottii* × *Pinus caribaea* var. *hondurensis*) from Queensland, Australia. The earlywood tracheid tangential lumen diameter and axial resin canal diameter were statistically positively correlated with radial permeability. The heartwood proportion and the frequency of axial resin canals were statistically negatively correlated with radial permeability and positively correlated with resin content. The axial resin canal diameter, sapwood proportion, latewood content, ray frequency, and earlywood tracheid lumen diameter increased from pith to bark, whereas the axial resin canal frequency decreased. Resin was found distributed throughout the wood microstructure, from pith to bark in many samples, and in both heartwood and sapwood. However, there was a much greater quantity of resin in heartwood and wood from the middle (inner radius) of the tree, with widespread occurrence of resin impregnation in the axial tracheids.

Keywords: Wood anatomy; Wood permeability; Resin content; Pinus elliottii; Pinus caribaea

*Contact information: a: Research School of Physics and Engineering, The Australian National University, Canberra, ACT 0200, Australia; b: Queensland Department of Agriculture and Fisheries, Horticulture and Forestry Science, Salisbury Research Facility, 50 Evans Rd, Salisbury, Qld 4107, Australia; c: Queensland Department of Agriculture and Fisheries, Eco Sciences Precinct, 41 Boggo Rd, Dutton Park, Qld 4102, Australia; *Corresponding author: william.leggate@daf.qld.gov.au*

INTRODUCTION

Permeability is a measure of the ease with which liquids and gases flow through a porous substance under the influence of a pressure gradient (Comstock 1968; Tesoro 1973; Milota *et al.* 1994). The permeability of wood influences many of its important processing and utilization properties, such as drying, preserving, wood modification systems, pulping, gluing, finishing, and even durability (Fogg 1968; Tesoro 1973; Hansmann *et al*. 2002; Zimmer *et al*. 2014). Generally, less permeable wood types are more difficult to dry and to treat with chemical preservatives (Milota *et al.* 1994). Wood permeability is also one of the main controlling factors influencing the depth of adhesive penetration (Kumar and Pizzi 2019). Lower wood permeability has also been linked to higher durability in some cases (Nicholas *et al.* 2005; Sandberg and Salin 2012).

Wood microstructure and wood extractives have been shown to exert a major influence on permeability (and the treatability of wood), contributing to the problems that arise when treating refractory heartwood and sapwood. The wood anatomical characteristics and phenomena that have been shown to affect wood permeability in softwoods include heartwood content, pit aspiration, latewood proportion, cellular dimensions, tylosoids (outgrowths in resin canals), the presence of interstitial spaces, and the frequency of longitudinal tracheids, longitudinal parenchyma, ray parenchyma, ray tracheids, and resin canals (Stamm 1931; Fogg 1968; Tesoro 1973; Hansmann *et al*. 2002; Martín *et al*. 2010; Leggate *et al.* 2019). Permeability is also influenced by wood chemistry, in particular extractives, including resins that can block liquid flow (Ellwood and Ecklund 1961; Fogg 1968; Olsson *et al*. 2001; Baraúna *et al.* 2014). The migratory characteristics of resins (*e.g.* during high temperature drying) also influence the penetration of preservative liquids including penetration depth and uniformity (Ahmed *et al.* 2012). Resins are produced as a natural tree defense mechanism against pests, diseases, and mechanical damage. A key function of resin, apart from some fungicidal and insecticidal effects, is to seal wood tissue to prevent the invasion of microbes (such as fungal hyphae) and to fill air spaces (Back and Allen 2000). The resin seal is water resistant, therefore creating impermeable barriers to liquid movement (Back and Allen 2000).

The hybrid pine, (*Pinus elliottii* var. *elliottii* [PEE] × *Pinus caribaea* var. *hondurensis* [PCH]) now dominates exotic softwood plantations and log supply in Queensland, Australia, with approximately 94,100 ha planted and an annual log production soon to exceed 1 million cubic meters per year (Leggate *et al*. 2019). This important resource supports a diverse processing sector that includes sawn timber, engineered wood products, reconstituted panels, landscaping, and lower-grade end uses (Lee 2015).

Leggate *et al.* (2019) reported a study on the radial gas and liquid permeability and resin content of 19-year-old PEE × PCH plantation-grown hybrid pine trees from Queensland, Australia, which were represented by various genotypes and tree stocking rates (stems per hectare). The key findings from this study were that there was no important effect of genotype or stocking rate on radial permeability; both gas and liquid radial permeability increased significantly from pith to bark positions within the tree. Conversely, resin content decreased from pith to bark. Gas and liquid permeability were significantly correlated and a highly significant negative relationship was found between permeability (gas and liquid) and resin content. However, the Leggate *et al.* (2019) study did not investigate the relationships between wood anatomical traits and these factors. Understanding and manipulating (*e.g.* genetically, silviculturally, or *via* wood product manufacturing techniques) these relationships is important for optimizing the manufacture and use of forest products. This paper reports on a study that investigated the influence of wood anatomical and resin traits on radial permeability.

EXPERIMENTAL

Wood Samples

The wood samples used for this study were derived from a previous study reported by Leggate *et al.* (2019) on the radial permeability and resin content of 19-year-old PEE × PCH trees. These trees were represented by three commercially relevant genotypes: the F_1 seedling, which was selected as a routine plantation seedlot (a single cross family); Clone 887, which was selected for good growth and flat, fine branches; and Clone 625, which was selected for heavy branches to contrast with clone 887. Five plantation tree-stocking rates (200, 333, 500, 666, and 1000 stems per hectare [spha]) represented a low to high range of stocking rates. A set of 30 trees was harvested from Experiment 622NC, an F_1 (first filial hybrid of PEE × PCH) taxon (clones and F_1 family) spacing trial planted during March of 1997 within compartment 202 Donnybrook LA (26° 58’ 30” S; 152° 59’ 00” E), SF 611 Beerburrum, north of Brisbane, Queensland, Australia. Experiment 622NC was established for wood production research purposes and not for resin production – therefore no trees in Experiment 622NC were tapped for resin collection. The trees were 19 years old at the time of harvest in October 2016. As per Table 1, two trees from each stocking rate and genotype combination were harvested to provide samples for wood property analysis.

Table 1. Tree Sampling Criteria (Number of Trees Sampled for Each Genotype and Stocking Rate Combination) (Leggate *et al.* 2019)

Genotype	Stocking Rates					Total (Number of Trees Sampled)
	200 spha	333 spha	500 spha	666 spha	1000 spha	
F_1 Seedling	2	2	2	2	2	10
Clone 887	2	2	2	2	2	10
Clone 625	2	2	2	2	2	10
Total	6	6	6	6	6	30

Wood samples were obtained from one transverse disc (35-mm thickness) that was taken from each tree at 2.34 m height. From each disc, samples for radial permeability and resin content determination were taken at three radial locations from pith to bark as per Fig. 1 (from Leggate *et al.* 2019). Further description of the methodology used for tree sampling, permeability (gas and liquid [water]), and resin content measurement is provided in Leggate *et al.* (2019).

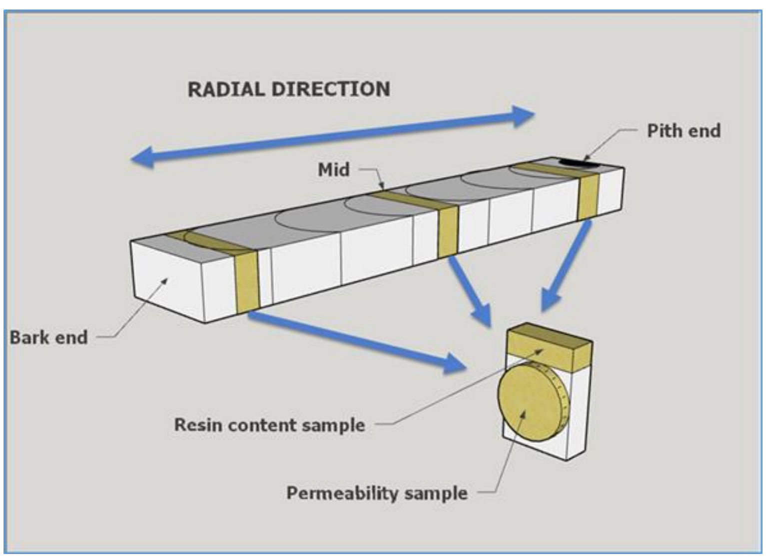


Fig. 1. Permeability and resin content samples cut from discs at three radial locations from pith to bark (Leggate *et al.* 2019)

A subset of permeability samples was selected from the study undertaken by Leggate *et al*. (2019) to facilitate anatomical analysis that formed the basis for the present study (Table 2).

Table 2. Sub-sampling for Anatomical Studies (number of wood samples)

Radial Position	Genotype	Stocking Rate (spha)					Total	Radial Total
		200	333	500	666	1000		
Pith Zone	C625	2	1	2	1	1	7	21
	C887	1	0	2	2	2	7	
	F_1 Seedling	1	1	2	1	2	7	
Mid-radius Zone	C625	2	2	2	1	2	9	24
	C887	2	2	2	1	0	7	
	F_1 Seedling	1	2	2	1	2	8	
Bark Zone (Wood Only; Does Not Include Bark)	C625	2	1	1	2	1	7	23
	C887	2	1	2	2	0	7	
	F_1 Seedling	2	2	2	2	1	9	
							Overall	68

These permeability samples (24 mm in diameter and 8 mm in thickness) were cut into three sections as per Fig. 2.

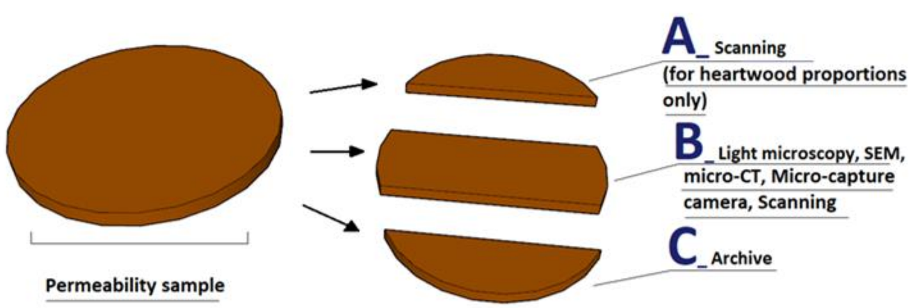


Fig. 2. Sectioning of the permeability samples for wood anatomical studies

Light Microscopy

Section B shown in Fig. 2 was used for light microscopy studies. The top and bottom transverse surfaces of section B were prepared using a Reichert sliding microtome (Model Number 338188; Reichert, Vienna, Austria) with steel blades to provide a clean, smooth surface. Images from both surfaces were captured using a Nikon Eclipse LV100ND microscope (Tokyo, Japan) at 50x magnification. Image J (IJ 1.46r) (U.S. National Institutes of Health, Maryland, USA) was used to measure:

- The cell lumen diameter in both the tangential and radial directions of the earlywood [first-formed wood within an annual growth ring that has a high proportion of relatively large diameter thin-walled cells (Zobel and Sprague 1998)] and latewood [later formed wood within an annual growth ring that has thicker cell walls (Zobel and Sprague 1998)] tracheids;

- The diameter and area of individual axial resin canals (a tubular intercellular duct lined by an epithelium, conducting secondary plant products secreted by the epithelial cells and that is surrounded by subsidiary cells [Richter *et al.* 2004]); resin canal diameter was determined as the average of tangential and radial diameters, and resin canal area was measured as the surface area occupied by the resin canal on the transverse surface. Resin canal diameter and area measurements included all components of the resin canal complex (includes epithelial, parenchyma and other subsidiary cells).

Scanning

The same middle section (Section B) used for light microscopy studies was also scanned on the transverse surface using an Epson Perfection Dual Lens System V850 Scanner (EPSON, Suwa, Japan) at high resolution (9600 dpi). Image J (IJ 1.46r) was used to process the scanned images to measure the following features:

- The earlywood and latewood proportions (based on surface area);
- The total number of axial resin canals per mm^2;
- The percentage of axial resin canals in both earlywood and latewood; and
- The percentage of resin-filled/closed axial resin canals in both earlywood and latewood.

Section A shown in Fig. 2 was used to determine the heartwood and sapwood proportions on the transverse surface. Heartwood is defined as the inner layers of the wood in a growing tree that no longer contain living cells, and in which the reserve materials (*e.g.*, starch) have been removed or converted into heartwood substances (International Association of Wood Anatomists 1957). It is usually notably darker than the surrounding sapwood. Sapwood is defined as the outer layers of wood in a living tree containing living cells and reserve materials (*e.g.*, starch) (International Association of Wood Anatomists 1957). Sapwood is usually markedly paler in color than the surrounding heartwood.

A chemical spot test method for differentiating heartwood and sapwood in *Pinus* species (QDPI 2003) was applied. After chemical application, the samples were scanned using an Epson Perfection Dual Lens System V850 Scanner at high resolution (9600 dpi). After scanning, the heartwood and sapwood proportions were measured using Image J (IJ 1.46r)

Image Capture Using a Micro-capture Camera

Section B (shown in Fig. 2) used for light microscopy studies and scanning as discussed above, was photographed using a USB Micro Capture Plus camera at a magnification of 10x (Model Number QC 3199; DIGITECH Industries, Hong Kong, SAR, China). The camera used was equipped with eight LED lights with adjustable brightness and had an image resolution of 2592 × 1944 pixels. The images were then assessed using Image J (IJ 1.46r) to determine the number of rays per mm^2 on the transverse surface. A ray is defined as a ribbon-like aggregate of cells extending radially in the xylem and phloem (International Association of Wood Anatomists 1957).

Micro-computer Tomography

To examine the micro-distribution of resin within the wood structure, eighteen permeability samples with dimensions (24 mm diameter and 8 mm thickness) representing three radial positions (from pith to bark) and from low to high permeability were scanned at the National Laboratory for X-ray Micro Computed Tomography (CTLab) based at the

Australian National University (ANU, Canberra, Australia). A HeliScan MicroCT system with an optimized space-filling trajectory (ANU, Canberra, Australia) (Kingston *et al.* 2018) was used to yield sharp images (Latham *et al.* 2008; Myers *et al.* 2011) at a resolution of 10.9 μm. A subset of these samples (seven) was also scanned at a smaller dimension (of 8 mm or 6 mm diameter × 8 mm thickness) to achieve a higher resolution image of 4.6 μm. These images were then assessed using the open-source scientific visualization software DRISHTI (Version v2.6.6; ANU, Canberra, Australia) (Limaye 2012).

Scanning Electron Microscopy

For detailed observations of the wood's anatomical features, six samples with dimensions of 8 mm (radial) × 12 mm (tangential) × 8 mm (longitudinal) representing different radial positions and permeability values were used for scanning electron microscopy (SEM). Prior to imaging, samples were kept in an oven at 50 °C for 7 days to reduce the sample's moisture content. To increase the contrast of samples, transverse and tangential surfaces of oven-dried samples were platinum coated using a Leica EM-SCD005 sputter coater (Leica, Wetzlar, Germany). A Zeiss Sigma VP field emission SEM (Zeiss, Oberkochen, Germany) was used to capture images of transverse and tangential surfaces. Images were taken in different magnifications (200x, 500x, and 1.5kx) to visualize the cell size and types in each plane.

Statistical Analysis

Gas and liquid permeability, resin content, and other wood anatomical features and their relationships were initially explored using a graphical compilation of scatterplots, histograms and Pearson correlation values (Fig. 3) from a data matrix using the pysch package (v1.9.12; Northwestern University, Evanston, IL, USA) (Revelle 2019) in R (R Foundation for Statistical computing, Vienna, Austria) (R Core Team 2019). A data matrix of the most significant variables, as chosen in the statistical analysis detailed below, was created to compile the graphical output showing the individual relationships and their correlation.

Statistical analyses were performed in GenStat v19 (VSN International 2018, Hemel Hempstead, UK). The wood anatomical features were each analyzed with a general linear regression. However, the heartwood proportion did not have a wide enough range to analyze *via* linear regression and was thus converted into proportional categories of All (samples with100% Heartwood), Intermediate (samples with 1 to 99% Heartwood), and None (samples with 0% Heartwood). The heartwood was subsequently analyzed using a multinomial regression. Stocking rate, genotype, position, and their interactions were fitted as explanatory variables/factors and any interactions that were found to be non-significant were dropped from the model *via* backwards selection.

Gas and liquid permeability as well as resin content were analyzed using general linear regressions. Rather than using the design factors of stocking rate, genotype, and position as explanatory variables (as per Leggate *et al.* 2019), the wood anatomical features were considered as potential explanatory variables to determine the underlying biological relationship brought on by the experimental design. To determine the most significant variables, multiple all-subset regressions were performed on groups of variables. The most influential variables were selected, and interactions between them were also tested. The final model was chosen as the model that included all significant interactions and their individual effects, as well as any other significant variables. For all models, the means and standard errors were calculated and, where relevant, pairwise comparisons were performed using Fishers Protected Least Significant Difference at a 5% significance level.

RESULTS AND DISCUSSION

Summary of Statistical Relationships between Wood Anatomical Traits, Permeability, and Resin Content

Using only the wood anatomical features (heartwood proportion, earlywood proportion, ray frequency, resin canal characteristics and dimensions, and tracheid dimensions) the linear regressions were able to account for 78.6%, 74%, and 63.2% of the variation in gas permeability, liquid permeability, and resin content, respectively. For each of these models, the individual contributions from the wood anatomical features are discussed below. Figure 3 shows a graphical matrix for the direct relationships between key variables independent of interaction with other variables.

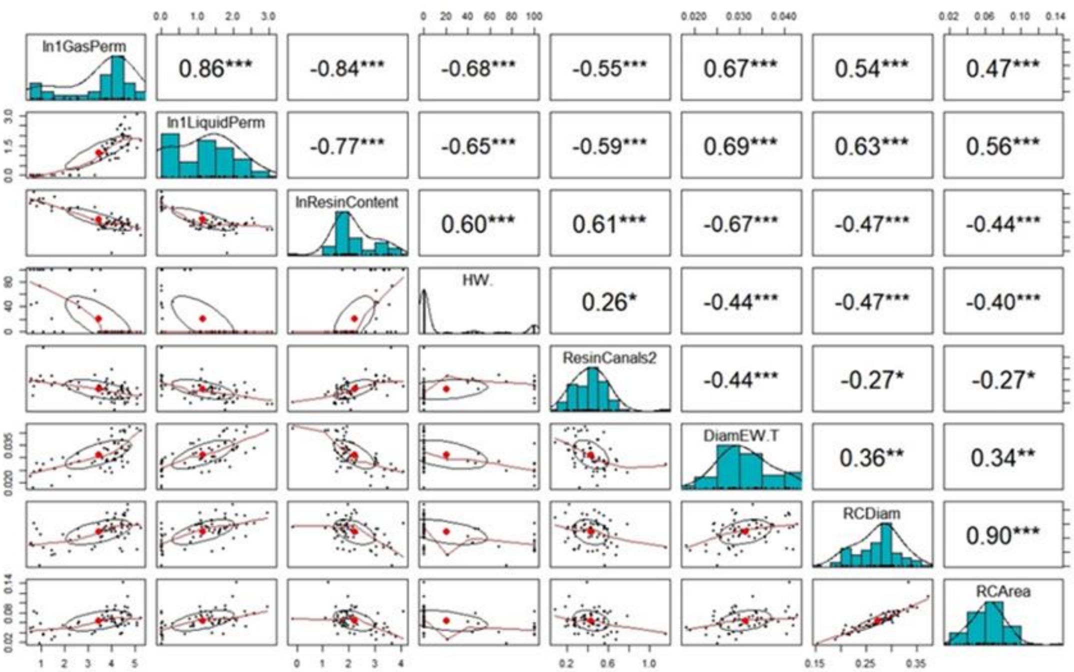


Fig. 3. Graphical representation showing direct relationships between key variables (where significant Pearson correlation values are shown as: * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$). In1Gasperm = gas permeability; In1Liquidperm = liquid permeability; In1ResinContent = resin content; HW = heartwood; ResinCanals2 = axial resin canal frequency; DiamEW.T – tangential diameter of earlywood tracheids; RCDiam = resin canal diameter; RCArea = resin canal area.

Heartwood Proportions

The statistical analyses of heartwood proportion split into categories of All (samples with 100% Heartwood), Intermediate (samples with 1 to 99% Heartwood), and None (samples with 0% Heartwood), showed a significant difference for radial positions ($p < 0.001$) with the pith zone having significantly more heartwood compared with the mid-radius and bark positions (Table 3). The bark and mid-radius positions were not significantly different in any heartwood category, and had none or almost none in the All and Intermediate categories. Neither genotype nor stocking rate had a significant relationship with the heartwood proportion categories.

The heartwood proportion category and resin canal area (for individual resin canals) had a significant interaction ($p < 0.001$) for gas permeability; permeability did not significantly change with increasing resin canal area for those with no heartwood (None category). However, for those samples with some/all heartwood (Intermediate and All categories), as the resin canal area increased, the gas permeability decreased. The decrease appeared more pronounced in samples consisting of only heartwood. The heartwood proportion category had a significant effect ($p < 0.001$) on liquid permeability in those with no heartwood, which had a significantly higher liquid permeability than those with some/all heartwood. The analysis of resin content showed that samples with no heartwood had significantly lower ($p < 0.001$) resin content than those with some/all heartwood.

Heartwood is much less permeable compared with sapwood, which is one major factor explaining the lower permeability of the wood from the middle of the tree (on the horizontal axis of the tree) (Leggate *et al*. 2019). The heartwood of the *Pinus* genus is less permeable compared with sapwood due to factors, such as higher extractives (resin) content, greater pit aspiration, pit encrustation, reduced size and frequency of pits, and the presence of tylosoids (Fig. 4). Heartwood formation also entails a shift in the mean pore size toward smaller radii (Schneider and Wagner 1974).

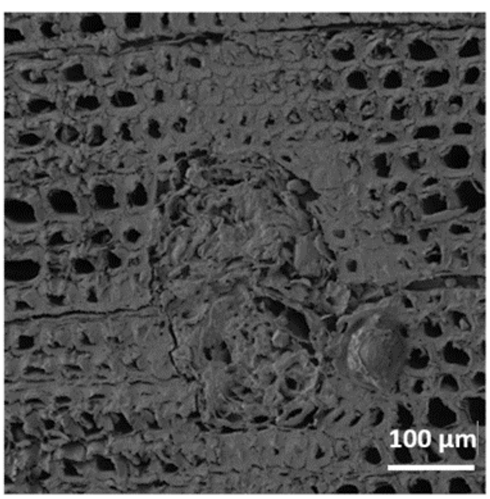


Fig. 4. An SEM image of a tylosoid in an axial resin canal from a heartwood sample at magnification of 500x

Koch (1972) defines the southern pines as those species whose major natural range is in the United States south of the Mason-Dixon line (39 °43´ N.) and east of the Great Plains. The southern pine group of species includes PEE. *Pinus caribaea* is not strictly a southern pine species according to Koch's definition, but it is viewed as closely related, and has been crossed with other southern pine species to yield hybrids. Koch (1972) reports considerably higher extractives content in the heartwood of southern pines compared with sapwood. Other studies on similar species within the southern pine group have shown that the permeability of sapwood can be up to 12,000 times more permeable than heartwood (Stamm 1931; Fogg 1968; Tesoro 1973). However, even in the absence of heartwood, permeability has been shown to decrease in the sapwood from the outer to the inner in all three anatomical directions (Hansmann *et al*. 2002), a tendency also observed in the present study. Juvenile wood has also been shown to have lower permeability than mature wood (Milota *et al*. 1994).

The extent of heartwood formation in the *Pinus* species varies by age. Koch (1972) commented that until 50 years of age southern pines have minimal heartwood, with most of the wood volume comprising light-colored sapwood. Benson (1930) reported an examination of stumps and cross-sections of several hundred southern pine trees, ranging in age from 10 to 300 years and in size from saplings to old forest veterans. His observations indicated that heartwood formation in southern pines usually began when the trees were between 20 and 30 years of age. In trees under 20 years of age, regardless of size, little or no heartwood was found (Benson 1930). However, this study by Benson (1930) examined heartwood proportions in southern pines in the United States, and not in trees grown in Australian conditions. The wood samples in the present study were sourced from 19-year-old plantation-grown trees in Queensland, Australia, and were already showing heartwood development at the time of sampling. The age that heartwood formation begins has been shown to be influenced by various climatic conditions—for example, in Scots pine (*Pinus sylvestris*), heartwood is formed after approximately 20 years in Alsace, France, compared with 70 years in northern Sweden (Back and Allen 2000).

Earlywood and Latewood Proportions

Overall, this study revealed a much greater proportion of earlywood (the average across all samples was 86%) compared with latewood (the average across all samples was 14%) (Table 3). The earlywood proportion decreased and the latewood proportion significantly increased from pith to bark ($p < 0.001$), with the average earlywood proportion for both regions 100% and 71%, respectively (Table 3). This pattern has been a typical trend in southern pines, where the percentage of latewood and the wood density increases from the pith toward the bark until the maximum is reached (Hakkila 1989). There was no statistically significant relationship between the proportion of earlywood or latewood and tree stocking rates or genotype.

When considered independently of other variables, the earlywood/latewood proportion accounted for approximately 25 to 30% of the variability in both gas and liquid permeability and resin content. However, once other more statistically significant wood anatomical variables were accounted for, the earlywood/latewood proportion did not significantly add to the model. In dried softwood, latewood has been shown to have greater permeability compared with earlywood (Hansmann *et al*. 2002). As such, the decreased proportion of latewood in samples taken from near the radial center of the log may be an additional factor that explains the lower permeability of wood from this zone. Latewood (in dried wood) is usually more permeable than earlywood because of its higher resistance to pit aspiration (Phillips 1933; Liese and Bauch 1967; Siau 1984, 1995; Richter and Sell 1992; Hansmann *et al*. 2002). In latewood, the higher resistance to pit aspiration is usually attributed to the greater rigidity of pit membranes and thicker cell walls (Comstock and

Côté 1968). However, in some cases, such as with wood at higher moisture content, the earlywood has been shown to be more permeable than latewood (Erickson 1970).

Ray Frequency

Ray frequency (Fig. 5, Table 3), as number per mm^2, was found to significantly decrease as tree stocking rate increased ($p = 0.035$). Genotype was also found to be significant ($p = 0.034$), with the F_1 seedling having a significantly lower ray frequency than C887. C625 had a ray frequency in the middle that was not significantly different from either of the other genotypes. There did appear to be an increasing trend in ray frequency toward the outer wood, but it was not significant ($p = 0.06$). While rays have been shown to act as important flow paths for liquids (Côté 1963; Liese and Bauch 1967; McQuire 1970; Olsson *et al*. 2001), in this study there was no significant relationship between ray frequency and radial permeability.

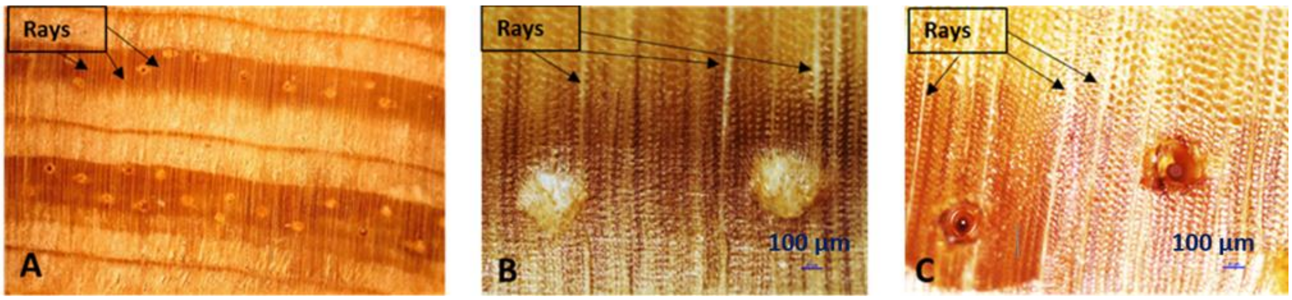


Fig. 5. Transverse surface images of a mid-radial section showing numerous rays in (A) at 10x, and (B) and (C) at 50x magnification

Resin Canals

There was a much higher frequency of axial resin canals (Fig. 6) in the wood from the pith zone (inner-radius) compared with outer wood (mid-radius and outer radial positions [bark]), and this radial trend was significant ($p < 0.001$) (Table 4). This was consistent with the findings from a study by Mergen and Echols (1955) on radial resin canals in slash pine (*P. elliottii*). The findings showed that the number of resin canals formed per unit area was highest during early age (*i.e.*, in rings near the pith) and decreased rapidly until approximately the twentieth year, after which the number was relatively constant. In the present study, the average overall frequency of axial resin canals measured (0.4 per mm^2) (Table 4) was within the range reported for slash pine by Hobert (1932), who found 200 axial resin canals per square inch (0.33 per mm^2) in rings 0.22 inches wide, and 300 canals per square inch (0.47 per mm^2) when rings were twice as wide.

The analysis of resin content showed that as axial resin canal frequency increased, the resin content significantly increased ($p = 0.002$). There was also a much higher resin content in the wood from the inner section of the log (radially) compared with outer wood (Leggate *et al.* 2019). Axial resin canal frequency significantly decreased both gas ($p = 0.013$) and liquid ($p = 0.006$) permeability. Some other studies have shown a positive correlation between resin canal frequency and permeability, but the positive relationship usually only occurs if the resin canals are not blocked with resin (Matsumura *et al.* 1995, 1996, 1998, and 1999; Lee *et al.* 2008; Ahmed *et al*. 2012).

Table 3. Summary of Results (Mean (Minimum to Maximum) for Permeability, Resin Content, Earlywood Proportion, Heartwood Proportion, and Ray Frequency

	Gas Permeability (mD [millidarcy])	Liquid Permeability (mD)	Resin Content (%)	Earlywood Proportion (%)	Heartwood Proportion (%)	Ray Frequency (Number/mm^2)
Overall	55.5 (0.7 to 189.1)	3.5 (0 to 20.5)	12.5 (0.8 to 59.2)	85.8 (50.7 to 100)	20 (0 to 100)	0.8 (0.5 to 1.2)
Position						
Pith	8.1 (0.7 to 54.3)	0.2 (0 to 2)	27.4 (9.2 to 59.2)	100 (100 to 100)	59.2 (0 to100)	0.8 (0.5 to 1)
Middle	66.6 (32.1 to 109.9)	3.4 (1.2 to 6.9)	6.8 (4.2 to 10.1)	87.9 (54.3 to 100)	4.2 (0 to 100)	0.8 (0.7 to 1)
Bark	88.6 (30.6-189.1)	6.8 (1.4-20.5)	5.6 (0.8-9.5)	70.8 (50.7-97.5)	0 (0)	0.9 (0.7-1.2)
Genotype						
F_1 Seedling	63 (0.8 to 189.1)	4.9 (0 to 20.5)	11.7 (0.8 to 59.2)	82.6 (54.3 to 100)	27 (0 to 100)	0.8 (0.5 to 0.9)
C625	52.2 (0.7 to 162.4)	2.6 (0 to 9.7)	13.3 (4.7 to 38.1)	90.4 (63.5 to 100)	17.2 (0 to 100)	0.8 (0.6 to 1)
C887	50.1 (0.7 to 163.4)	2.9 (0 to 12.1)	12.7 (4.6 to 43.8)	84.6 (50.7 to 100)	14.9 (0 to 100)	0.9 (0.7 to 1.2)
Stocking Rate (spha)						
200	63 (0.7 to 108.9)	4.7 (0 to 17.8)	12.4 (4.5 to 32.5)	85 (55.9 to 100)	21.4 (0 to 100)	0.9 (0.7 to1.1)
333	58 (1.2 to 109.9)	2.8 (0 to 6.4)	10.4 (0.8 to 34.4)	79.4 (54.3 to 100)	16.7 (0 to 100)	0.9 (0.7 to 1.2)
500	49.3 (0.7 to 160.4)	3.9 (0 to 20.5)	11.8 (3.3 to 38.1)	88.4 (62 to 100)	21.5 (0 to 100)	0.8 (0.6 to 1)
666	58.4 (3.1 to 189.1)	2.8 (0 to 9.7)	11.8 (3 to 43.8)	84.2 (50.7 to 100)	17 (0 to 100)	0.8 (0.5 to 0.9)
1000	48.7 (0.9 to 162.4)	2.9 (0 to 9.4)	17.4 (5.3 to 59.2)	92 (68 to 100)	23.3 (0 to 100)	0.8 (0.7 to 0.9)

Axial resin canals were distributed throughout the earlywood and latewood (Table 4 and Fig. 6). However, because of the much higher percentage of earlywood, on average the proportion of axial resin canals in the earlywood (76%) was much higher than in latewood (Table 4). In the outerwood, from the bark radial position, there was a higher proportion of axial resin canals in the latewood (55%) compared with the earlywood (45%) (Table 4). This result concurred with Koch (1972), who reported that in the mature normal wood of southern pines (therefore, in the outer radial positions) the resin canals are most prominent in the latewood.

Analysis of the axial resin canal frequency data showed a significant three-way interaction ($p = 0.009$), where genotypes C887 and F_1 seedling showed similar trends of increasing mildly as the stocking rate increased. However, genotype C625 showed a pronounced increase in the pith zone, no trend in the mid-radius, and a decrease in the bark radial position as the stocking rate increased.

Overall, there was a greater frequency of resin-filled axial resin canals (Fig. 6) in the wood from the pith and bark zones of the log compared with wood from the mid-radius zone ($p < 0.001$). Overall, the proportion of canals that were resin-filled averaged 47% (Table 4). Resin-filled axial resin canals were also distributed throughout the earlywood and latewood (Table 4). There were no significant effects of genotype or stocking rates on proportion of resin-filled resin canals. Additionally, there was no significant relationship between the proportion of resin-filled axial resin canals and gas or liquid permeability.

Axial resin canal diameter and area increased radially ($p < 0.001$); however, there was no significant difference between mid-radius and bark positions in this feature (Table 4). It has been previously shown that in southern pines, the size of axial canals increases outward from the pith (Back and Allen 2000).

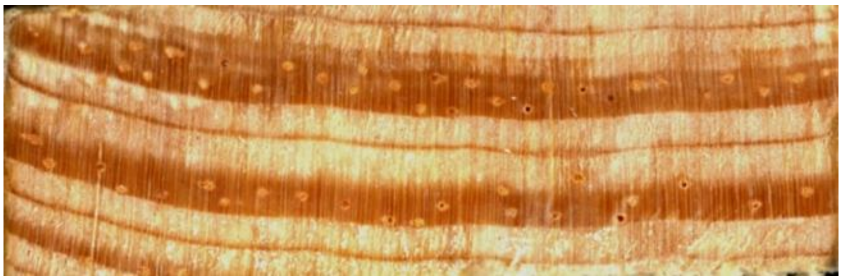
There was a significant positive relationship between axial resin canal diameter and liquid permeability ($p < 0.001$). Concerning gas permeability, axial resin canal diameter was found to interact with the tangential lumen diameter of the earlywood tracheids ($p < 0.001$). The interaction showed that, as did liquid permeability, the gas permeability increased with an increase of the axial resin canal diameter, but only for samples with a low tangential lumen diameter in earlywood tracheids. As the tangential lumen diameter of earlywood tracheids increased, the positive relationship lessened. This result showed that an increase in the size of axial resin canals increased permeability for both gas and liquid, although the relationship weakened for gas permeability when the tangential lumen diameter of earlywood tracheids increased. Axial and radial resin canals have been shown to play a major and active role (when not filled with resin) in the deep penetration of liquid into softwoods (Booker 1990; Matsumura *et al.* 1996; Ahmed *et al.* 2012).

Axial resin canals were observed to be directly connected to horizontal canals in many cases (Fig. 6). This relationship was consistent with the conclusions of Howard and Manwiller (1968), who reported that the radial and longitudinal resin ducts interconnect to form a continuous system in southern pines in the United States.

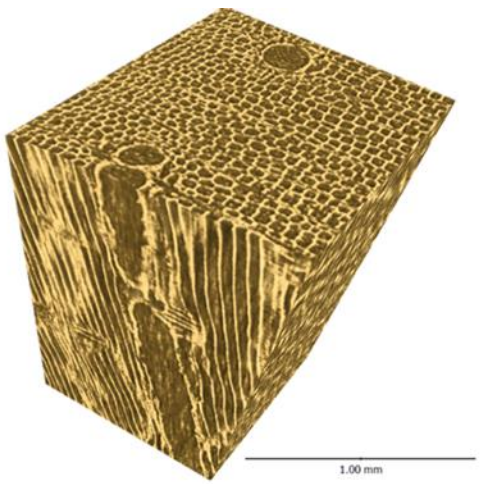
Table 4. Summary of Results (Mean (Minimum to Maximum) for Resin Canal Characteristics

	Axial Resin Canal Frequency (Number/mm^2)	Proportion of Resin-filled Axial Resin Canals (%)	Proportion of Axial Resin Canals in Earlywood (%)	Proportion of Resin-filled Axial Resin Canals in Earlywood (%)	Proportion of Resin-filled Axial Resin Canals in Latewood (%)	Axial Resin Canal Diameter (mm)	Axial Resin Canal Area (mm^2)
Overall	0.4 (0.1 to 1.2)	47.3 (24.7 to 75.8)	76 (9.2 to 100)	45.5 (20 to 80)	50.2 (22.2 to 80)	0.27 (0.15 to 0.37)	0.064 (0.019 to 0.143)
Position							
Pith	0.6 (0.3 to 1.2)	52.5 (32 to 71.6)	100 (100 to 100)	52.5 (32 to 71.6)	0	0.23 (0.15 to 0.30)	0.049 (0.019 to 0.083)
Middle	0.4 (0.1 to 0.6)	40.5 (24.7 to 59.4)	83.1 (37 to 100)	40.3 (24.7 to 65.2)	44.1 (22.2 to 64.3)	0.29 (0.20 to 0.37)	0.071 (0.038 to 0.114)
Bark	0.4 (0.2 to 0.6)	49.7 (34.4 to 75.8)	45.3 (9.2 to 97.7)	44.6 (20 to 80)	53.6 (25 to 80)	0.29 (0.21 to 0.34)	0.072 (0.054 to 0.143)
Genotype							
F_1 Seedling	0.3 (0.1 to 0.6)	48.4 (25.3 to 71.6)	74.5 (27 to 100)	46.1 (25.1 to 71.6)	48.5 (25 to 64.7)	0.28 (0.2 to 0.37)	0.067 (0.035 to 0.143)
C625	0.5 (0.3 to 1.2)	44.1 (24.7 to 64.7)	81.3 (16.4 to 100)	44.1 (24.7 to 80)	47.8 (22.2 to 73.9)	0.27 (0.15 to 0.35)	0.061 (0.019 to 0.091)
C887	0.5 (0.3 to 0.7)	49.7 (30.6 to 75.8)	71.7 (9.2 to 100)	46.5 (20 to 69.7)	55.7 (29.2 to 80)	0.27 (0.19 to 0.34)	0.065 (0.031 to 0.095)
Stocking Rate (spha)							
200	0.4 (0.2 to 0.7)	47.8 (24.7 to 75.8)	75.8 (16.4 to 100)	46.3 (24.7 to 62.5)	53.1 (25 to 80)	0.28 (0.20 to 0.37)	0.068 (0.040 to 0.114)
333	0.4 (0.1 to 0.6)	47.1 (33.3 to 59.4)	72.5 (27 to 100)	46.3 (30 to 65.2)	48.1 (33.3 to 59.3)	0.29 (0.22 to 0.34)	0.068 (0.036 to 0.093)
500	0.4 (0.2 to 0.8)	47.1 (25.3 to 71.6)	73.2 (9.2 to 100)	46.3 (25.1 to 80)	46.8 (25.8 to 64.3)	0.27 (0.15 to 0.34)	0.065 (0.019 to 0.143)
666	0.4 (0.2 to 0.7)	49.2 (36.9 to 63.3)	72.7 (27.7 to 100)	44 (20 to 63.3)	51.8 (22.2 to 73.9)	0.26 (0.19 to 0.30)	0.060 (0.027 to 0.084)
1000	0.5 (0.3 to 1.2)	44.9 (29.6 to 69.7)	88.2 (37 to 100)	44.3 (29.6 to 69.7)	55.7 (43.8 to 64.7)	0.26 (0.21 to 0.30)	0.060 (0.038 to 0.083)

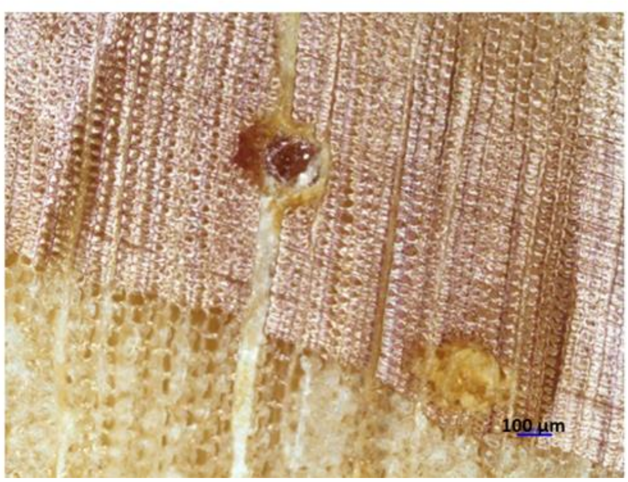
a)



b)



c)



d)

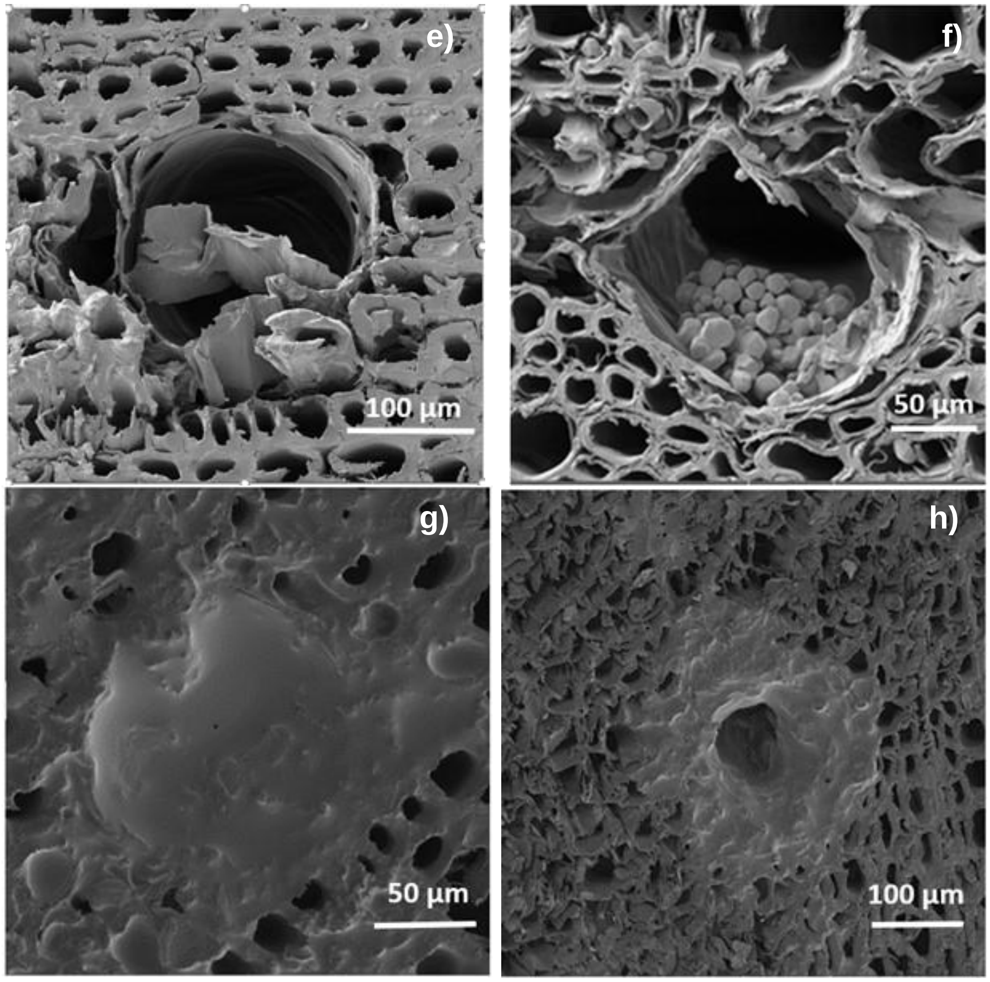


Fig. 6. a) Scanned transverse section showing numerous open axial resin canals; b) Scanned transverse section showing numerous closed/filled axial resin canals; c) Micro-CT image of transverse and longitudinal-radial surfaces showing axial resin canals and other wood structural features; d) Transverse section showing interconnection between an axial and horizontal resin canal; e) SEM image of an open axial resin canal (at magnification of 739x); f) SEM image of an axial resin canal filled with starch granules and/or resin (at magnification of 1000x); g) SEM image of an axial resin canal sealed with resin (at magnification of 1120x); h) SEM image of an axial resin canal surrounded by resin (at magnification of 500x)

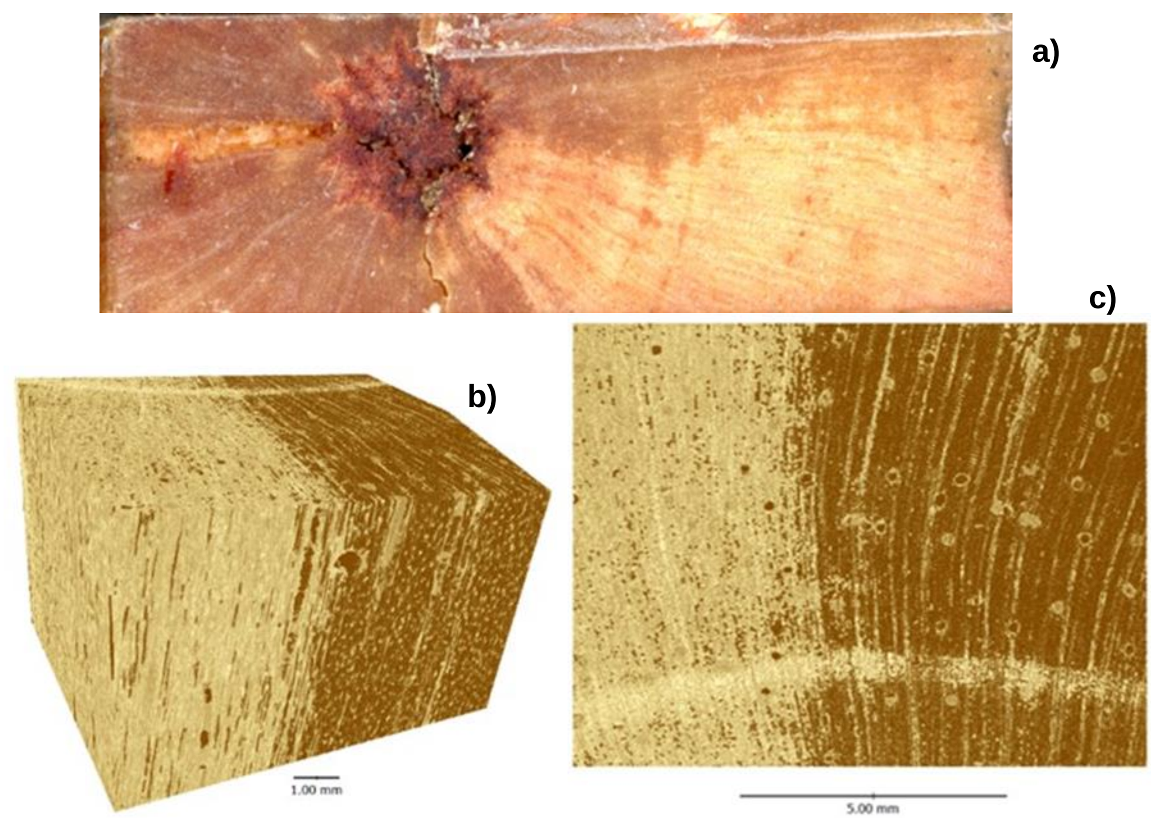
Distribution of Resin

Resin was found distributed throughout the wood from pith to bark radial positions. Therefore, it was not only confined to wood from the pith region, and not only within the heartwood zone. However, there were much higher quantities of resin toward the inside of the log compared with the outerwood. These findings were also reported by Leggate *et al.* (2019).

Resin was found distributed throughout the wood cells and not only confined to resin canals (Fig. 7). It was found in both axial and horizontal resin canals, axial parenchyma cells surrounding resin canals, earlywood and latewood tracheids, and in ray cells. In many cases, particularly in samples from the pith radial zone, there was widespread resin impregnation in tracheids (Fig. 7). In some cases, the extent of tracheid resin impregnation was close to 100%.

Koch (1972) reported that during heartwood formation in southern pines, the rays sometimes secrete resin into adjacent tracheids, forming amorphous deposits, reddish-brown to black in color, that partially or completely fill the cell when viewed in the cross-section. Another source of tracheid resin is the epithelial cells in the resin canals. During heartwood formation, epithelial cells can press out all canal resin into the surrounding wood tissue before they lignify and die (Back and Allen 2000). In longitudinal sections, the deposits appear as transverse plates across the lumen or as lumps on the tracheid wall (Koch 1972). Occurrence of resinous tracheids has been described as sporadic in southern pines (Koch 1972). However, in the present study, resin impregnation of tracheids was widespread and was not confined only to the heartwood zone—it was also observed in sapwood. Resin impregnation of pine wood does not occur only during heartwood formation, but can also occur in wood as a response to wounding or injury (Sehlstedt-Persson 2008).

In many woods of the *Pinus* genus, the resin content of the heartwood is much greater than that of the sapwood. Species such as *Pinus canariensis*, *Pinus rigida*, *Pinus merkusii*, *Pinus ponderosa*, and *Pinus caribaea* have heartwood with high resin content, earning them the name "pitch pine" in commerce (Esteban *et al.* 2005). Esteban *et al.* (2005) attributed the extraordinarily high resin content and resinification of *Pinus canariensis* (Canary Island pine or pitch pine) heartwood to anatomical features, including many subsidiary parenchyma cells surrounding axial resin canals. A high percentage of rays indicates the presence of many parenchyma cells capable of accumulating large amounts of starch, which in turn can be used to synthesize the pitch extractives (resins). The high resin content and resin impregnation observed in the PEE × PCH hybrid pine wood samples in this study may also be linked to the same factors. These results will require further investigation.



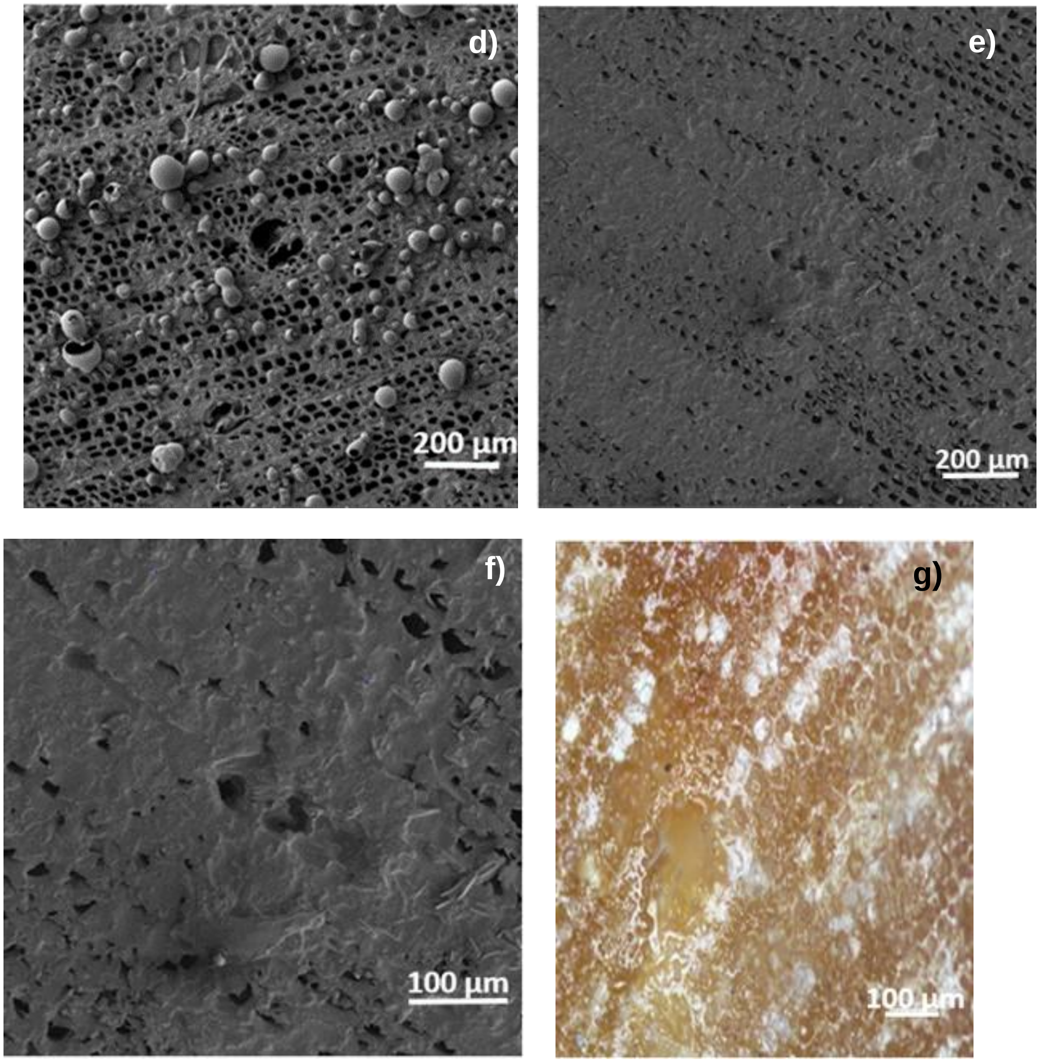


Fig. 7. a) Scanned transverse section showing widespread resin impregnation in wood from the pith zone; b) and c) Micro-CT images of transverse and longitudinal-radial and longitudinal-tangential surfaces, respectively, showing resin impregnation of tracheids and other wood structural features; d) SEM image of widespread resin impregnation in tracheids (at magnification of 200x); e) SEM image of widespread resin impregnation in tracheids (at magnification of 200x); f) SEM image of widespread resin impregnation in tracheids (at magnification of 500x); and g) light microscopy image of a transverse section showing resin impregnation in tracheids (at magnification of 100x)

Tracheid Dimensions

The earlywood tracheid cell lumen diameter (in both tangential and radial directions) increased from the pith to bark across all genotypes ($p < 0.001$) (Table 5). Other studies with southern pines have also reported an increase in tracheid lumen diameters with distance from the pith (Taras 1965; Manwiller 1966; McMillin 1968; Barefoot *et al*. 1970). There was a significant positive relationship between tangential earlywood tracheid cell lumen diameter and both gas (although the positive relationship decreased as resin canal diameter increased; interaction of $p < 0.001$) and liquid permeability ($p < 0.001$). Increased permeability and hydraulic conductivity have been shown to be associated with increased tracheid lumen diameters (Fleischer 1950; Shelburne and Hedden 1996; Martín *et al*. 2010).

There were no important relationships between latewood tracheid lumen diameters and permeability, radial position, genotype, or stocking rate. Tracheid lumen diameters, which have considerable variation in species, age, position within the tree, growth rate, site, and climate, were generally within the range reported by Koch (1972) for southern pines. In agreement with other studies on southern pines (Koch 1972), earlywood tracheid radial lumen diameters were generally larger than earlywood tracheid tangential lumen diameters, and the opposite was generally true for latewood tracheid lumen diameters.

Table 5. Summary of Results (Mean (Minimum to Maximum) for Tracheid Lumen Dimensions

	Mean Diameter Earlywood Lumen (mm)		Mean Diameter Latewood Lumen (mm)	
	Tangential	Radial	Tangential	Radial
Overall	0.031 (0.018 to 0.043)	0.036 (0.019 to 0.060)	0.022 (0.013 to 0.032)	0.018 (0.013 to 0.033)
Position				
Pith	0.026 (0.018 to 0.032)	0.031 (0.019 to 0.037)	0.022 (0.022 to 0.022)	0.028 (0.028 to 0.028)
Middle	0.032 (0.026 to 0.041)	0.037 (0.028 to 0.053)	0.023 (0.019 to 0.028)	0.019 (0.013 to 0.033)
Bark	0.036 (0.024 to 0.043)	0.039 (0.028 to 0.060)	0.022 (0.013 to 0.032)	0.018 (0.013 to 0.025)
Genotype				
F_1 Seedling	0.033 (0.018 to 0.042)	0.038 (0.023 to 0.060)	0.025 (0.019 to 0.032)	0.019 (0.013 to 0.025)
C625	0.030 (0.023 to 0.043)	0.035 (0.019 to 0.049)	0.021 (0.015 to 0.027)	0.018 (0.013 to 0.033)
C887	0.030 (0.019 to 0.040)	0.034 (0.029 to 0.044)	0.020 (0.013 to 0.028)	0.018 (0.015 to 0.028)
Stocking Rate (spha)				
200	0.030 (0.018 to 0.041)	0.033 (0.024 to 0.043)	0.023 (0.017 to 0.032)	0.018 (0.014 to 0.023)
333	0.033 (0.029 to 0.042)	0.037 (0.029 to 0.047)	0.024 (0.019 to 0.028)	0.019 (0.013 to 0.023)
500	0.031 (0.023 to 0.041)	0.036 (0.019 to 0.053)	0.022 (0.018 to 0.028)	0.016 (0.014 to 0.021)
666	0.032 (0.024 to 0.043)	0.038 (0.023 to 0.060)	0.021 (0.013 to 0.027)	0.021 (0.013 to 0.033)
1000	0.031 (0.024 to 0.042)	0.036 (0.028 to 0.042)	0.020 (0.020 to 0.021)	0.015 (0.015 to 0.016)

CONCLUSIONS

1. Wood anatomical and resin traits influenced the radial permeability and resin content of 19-year-old hybrid pines [PCH × PEE].
2. Heartwood proportion, earlywood tracheid lumen diameter, and the frequency of resin canals were the key anatomical features that influenced radial permeability and resin content. Resin canal diameter and area each played a part either individually or by interacting with other features for radial permeability.
3. The effects on radial permeability and resin content could generally be summarized as those with no heartwood were significantly different from those with heartwood. An increase in the earlywood tracheid lumen diameter had a positive effect on radial permeability, and the opposite trend was observed for resin canal frequency.
4. Resin canal diameter generally had a positive effect on radial permeability, although the effect decreased for gas permeability as earlywood tracheid lumen diameter increased.
5. Resin was distributed throughout the wood microstructure, from pith to bark and in both heartwood and sapwood. However, there was a much greater quantity of resin in heartwood and wood from the middle (on a horizontal axis) of the tree, with a significant occurrence of resin impregnation in axial tracheids.
6. There were generally limited important influences from genotype and stocking rate on wood anatomical features, although significant radial trends (from pith to bark) in wood anatomical traits were observed.

ACKNOWLEDGMENTS

The authors are particularly grateful for the technical support (laboratory processing and assessments of wood samples) of Mrs. Rica Minnett. Mr. Tomas Leggate is acknowledged for assistance with diagram preparation.

REFERENCES CITED

Ahmed, S. A., Sehlstedt-Persson, M., Karlsson, O., and Morén, T. (2012). "Uneven distribution of preservative in kiln-dried sapwood lumber of Scots pine: Impact of wood structure and resin allocation," *Holzforschung* 66(2), 251-258. DOI: 10.1515/HF.2011.126

Back, E. L., and Allen, L. H. (2000). *Pitch Control, Wood Resin and Deresination*, TAPPI Press, Atlanta, GA, USA.

Baraúna, E. E. P., Lima, J. T., Da Silva Vieira, R., Da Silva, J. R. M., and Monteiro, T. C. (2014). "Effect of anatomical and chemical structure in the permeability of 'Amapá' wood," *CERNE* 20(4), 529-534. DOI: 10.1590/01047760201420041501

Barefoot, A. C., Hitchings, R. G., Ellwood, E. L., and Wilson, E. H. (1970). "The relationship between loblolly pine fiber morphology and kraft paper properties," *Technical Bulletin, North Carolina Agricultural Experiment Station* 202, 1-88.

Benson, H. P. (1930). “Heartwood in second-growth southern pines,” *Savannah Weekly Naval Stores Review and Journal of Trade* 40(29), 28

Booker, R. E. (1990). “Changes in transverse wood permeability during the drying of *Dacrydium cupressinum* and *Pinus radiata*,” *New Zealand Journal of Forestry Science* 20(2), 231-244.

Comstock, G. L. (1968). *Physical and Structural Aspects of the Longitudinal Permeability of Wood*, Ph.D. Dissertation, State University of New York, Syracuse, NY, USA.

Comstock, G. L., and Côté, Jr., W. A. (1968). “Factors affecting permeability and pit aspiration in coniferous softwood,” *Wood Science and Technology* 2(4), 279-291. DOI: 10.1007/BF00350274

Côté, Jr., W. A. (1963). “Structural factors affecting the permeability of wood,” *Journal of Polymer Science: Part C: Polymer Symposia* 2, 231-242. DOI: 10.1002/polc.5070020122

Ellwood, E. L., and Ecklund, B. A. (1961). “Treatment to improve wood permeability as an approach to the drying problem,” in: *Proceedings of the Annual Meeting West Coast Kiln Club*, Medford, OR, USA,

Erickson, H. D. (1970). “Permeability of southern pine wood – A review,” *Wood Science* 2(3), 149-158.

Esteban, L. G., Gasson, P., Climent, J. M., De Palacios, P., and Guindeo, A. (2005). “The wood of *Pinus canariensis* and its resinous heartwood,” *International Association of Wood Anatomists* 26(1), 69-77. DOI: 10.1163/22941932-90001602

Fleischer, H. O. (1950). “An anatomical comparison of refractory and easily treated Douglas-fir heartwood,” in: *Proceedings of the American Wood Preservers Association* 46, 152-156.

Fogg, P. J. (1968). *Longitudinal Air Permeability of Southern Pine Wood*, Ph.D. Dissertation, Louisiana State University, Baton Rouge, LA, USA.

Hakkila, P. (1989). *Utilization of Residual Forest Biomass*, Springer, Berlin, Germany. DOI: 10.1007/978-3-642-74072-5

Hansmann, C., Gindl, W., Wimmer, R., and Teischinger, A. (2002). “Permeability of wood – A review,” *Wood Research* 47(4), 1-16.

Howard, E. T., and Manwiller, F. G. (1968). “Anatomical characteristics of southern pine stemwood,” *Wood Science* 2(2), 77-86.

International Association of Wood Anatomists (1957). “International glossary of terms used in wood anatomy,” *Tropical Woods* 107, 1-36.

Kingston, A. M., Myers, G. R., Latham, S. J., Recur, B., Li, H., and Sheppard, A. P. (2018). “Space-filling X-ray source trajectories for efficient scanning in large-angle, cone-beam computed tomography,” *IEEE Transactions on Computational Imaging* 4(3), 447-458, DOI: 10.1109/TCI.2018.2841202

Koch, P. (1972). *Utilization of the Southern Pines – Volume 1 (Agricultural Handbook SFES-AH-420),* U.S. Department of Agriculture Forest Service, Southern Forest Experiment Station, Asheville, NC, USA.

Kumar, R. N., and Pizzi, A. (2019). *Adhesives for Wood and Lignocellulosic Materials*, Scrivener Publishing, Beverly, MA, USA. DOI: 10.1002/9781119605584

Latham, S. J., Varslot, T., and Sheppard, A. (2008). “Automated registration for augmenting micro-CT 3D images,” *ANZIAM Journal* 50, C534-C548. DOI: 10.21914/anziamj.v50i0.1389

Lee, M., Lu, J., and Kang, H. (2008). "Effect of drying methods on longitudinal liquid permeability of Korean pine (*Pinus koraiensis* Sieb. Et Zucc.)," *Mokchae Konghak* 36(5), 49-55.

Lee, D. (2015). *Improving Returns from Southern Pine Plantations through Innovative Resource Characterization*, Project Proposal, Forest and Wood Products Australia, Melbourne, Australia.

Leggate, W., Redman, A., Wood, J., Bailleres, H., and Lee, D. J. (2019). "Radial permeability of the hybrid pine (*Pinus elliottii* x *Pinus caribaea*) in Australia," *BioResources* 14(2), 4358-4372. DOI: 10.15376/biores.14.2.4358-4372

Liese, W., and Bauch, J. (1967). "On the closure of bordered pits in conifers," *Wood Science and Technology* 1(1), 1-13. DOI: 10.1007/BF00592252

Limaye, A. (2012). "*Drishti*: A volume exploration and presentation tool," in: *Proceedings SPIE, Developments in X-Ray Tomography* VIII 8506, San Diego, CA, USA, pp. 85060X-1-85060X-9. DOI: 10.1117/12.935640

Manwiller, F. G. (1966). "Southern pine cell walls and shrinkage," *Southern Lumberman* 213(2656), 184-186.

Martín, J. A., Esteban, L. G., De Palacios, P., and García Fernández, F. (2010). "Variation in wood anatomical traits of *Pinus sylvestris* L. between Spanish regions of provenance," *Trees* 24, 1017-1028. DOI: 10.1007/s00468-010-0471-4

Matsumura, J., Booker, R. E., Donaldson, L. A., and Ridoutt, B. G. (1998). "Impregnation of radiata pine wood by vacuum treatment: Identification of flow paths using fluorescent dye and confocal microscopy," *International Association of Wood Anatomists Journal* 19(1), 25-33. DOI: 10.1163/22941932-90000649

Matsumura, J., Booker, R. E., Ridoutt, B. G., Donaldson, L. A., Mikajiri, N., Matsunaga, H., and Oda, K. (1999). "Impregnation of radiata pine wood by vacuum treatment II: Effect of pre-steaming on wood structure and resin content," *Journal of Wood Science* 45, 456-462. DOI: 10.1007/BF00538953

Matsumura, J., Tsutsumi, J., and Oda, K. (1995). "Effect of ethanol-exchange drying and ethanol treatment after natural drying on longitudinal gas permeability of softwood," *Mokuzai Gakkaishi* 41, 863-869.

Matsumura, J., Tsutsumi, J., and Oda, K. (1996). "Effect of water storage and methanol extraction on longitudinal gas permeability of karamatsu heartwood," *Mokuzai Gakkaishi* 42, 115-121.

McMillin, C. W. (1968). "Morphological characteristics of loblolly pine wood as related to specific gravity, growth rate, and distance from the pith," *Wood Science and Technology* 2(3), 166-176.

McQuire, A. J. (1970). *Radial Permeability of Timber*, Ph.D. Dissertation, University of Leeds, Leeds, UK.

Mergen, F., and Echols, R. M. (1955). "Number and size of radial resin ducts in slash pine," *Science* 121(3139), 306-307. DOI: 10.1126/science.121.3139.306

Milota, M., Tschernitz, J. L., Verrill, S. P., and Mianowski, T. (1994). "Gas permeability of plantation loblolly pine," *Wood and Fiber Science* 27(1), 34-40.

Myers, G. R., Kingston, A. M., Varslot, T. K., and Sheppard, A. P. (2011). "Extending reference scan drift correction to high-magnification high-cone-angle tomography," *Optics Letters* 36(24), 4809-4811. DOI: 10.1364/OL.36.004809

Nicholas, D. D., Schultz, T. P., Sites, L., and Buckner, D. (2005). "Effect of permeability and extractives on the decay rate of southern pine sapwood in above ground exposure," in: *International Research Group on Wood Protection*, Bangalore, India, pp. 1-8.

Olsson, T., Megnis, M., Varna, J., and Lindberg, H. (2001). "Study of the transverse liquid flow paths in pine and spruce using scanning electron microscopy," *Journal of Wood Science* 47(4), 282-288. DOI: 10.1007/BF00766714

Phillips, E. W. J. (1933). "Movement of the pit membrane in coniferous woods, with special reference to preservative treatment," *Forestry* 7(2), 109-120. DOI: 10.1093/oxfordjournals.forestry.a063340

Queensland Department of Primary Industries (QDPI). (2003). *Test Method: Spot test for differentiating sapwood and heartwood in Pinus species*. Internal publication. Queensland Department of Primary Industries, Brisbane, Queensland, Australia.

R Core Team (2019). *R: A Language and Environment for Statistical Computing*, R Foundation for Statistical Computing, Vienna, Austria.

Revelle, W. (2019). *Psych: Procedures for Psychological, Psychometric, and Personality Research*, Northwestern University, Evanston, IL, USA.

Richter, H. G., Grosser, D., Heinz, I., and Gasson, P. E. (2004). "IAWA list of microscopic features for softwood identification," *IAWA Journal* 25(1), 1-70.

Richter, K., and Sell, J. (1992). "Studies on impregnation pathways in white fir (*Abies alba*)," *Holz als Roh- und Werkstoff* 50, 329-336. DOI: 10.1007/BF02628636

Sandberg, K., and Salin, J. G. (2012). "Liquid water absorption in dried Norway spruce timber measured with CT scanning and viewed as a percolation process," *Wood Science and Technology* 46(1-3), 207-219. DOI: 10.1007/s00226-010-0371-1

Schneider, A., and Wagner, L. (1974). "Bestimmung der Porengrößenverteilung in Holz mit dem Quecksilber-Porosimeter [Determination of pore size distribution in wood with a mercury porosimeter]," *Holz als Roh- und Werkstoff* 32(6), 216-224. DOI: 10.1007/BF02607257

Sehlstedt-Persson, M. (2008). *Impact of Drying and Heat Treatment on Physical Properties and Durability of Solid Wood*, Ph.D. Dissertation, Luleå University of Technology, Skellefteå, Sweden.

Shelburne, V. B., and Hedden, R. L. (1996). "Effect of stem height, dominance class, and site quality on sapwood permeability in loblolly pine, (*Pinus taeda* L.)," *Forest Ecology and Management* 83(3), 163-169. DOI: 10.1016/0378-1127(96)03727-9

Siau, J. F. (1984). *Transport Processes in Wood*, Springer, Berlin, Germany. DOI: 10.1007/978-3-642-69213-0

Siau, J. F. (1995). *Wood: Influence of Moisture on Physical Properties*, Virginia Polytechnic Institute and State University, Blacksburg, VA, USA.

Stamm, A. J. (1931). "Three methods of studying capillary structure as applied to wood," *Physics* 1(2), 116-128. DOI: 10.1063/1.1744989

Taras, M. A. (1965). *Some Wood Properties of Slash Pine (Pinus elliottii Engelm.) and Their Relationship to Age and Height within the Stem*, Ph.D. Dissertation, North Carolina State University, Raleigh, NC, USA.

Tesoro, F. O. (1973). *Factors Affecting the Flow of Gas and Liquid through Softwoods and Hardwoods*, Ph.D. Dissertation, Louisiana State University, Baton Rouge, LA, USA.

Zimmer, K. P., Høibø, O. A., Vestøl, G. I., and Larnøy, E. (2014). "Variation in treatability of Scots pine sapwood: A survey of 25 different northern European locations," *Wood Science and Technology* 48(5), 1049-1068. DOI: 10.1007/s00226-014-0660-1

Zobel, B. J., and Sprague, J. R. (1998). *Juvenile Wood in Forest Trees*, Springer-Verlag, Berlin, Germany. DOI: 10.1007/978-3-642-72126-7

Article submitted: April 23, 2020; Peer review completed: June 28, 2020; Revised version received and accepted: June 29, 2020; Published: July 20, 2020.
DOI: 10.15376/biores.15.3.6851-6873