



Variation and genetic parameters of axial resin canal features in clones and families of *Pinus radiata*

James Kudjo Govina^{1,2} · Luis A. Apiolaza² · Clemens M. Altaner² 

Received: 14 May 2019 / Accepted: 10 February 2020
© Springer Nature B.V. 2020

Abstract

Resin canal features are associated with significant economic losses to appearance grade *Pinus radiata* timber. This study investigated the variation in resin canal features in young, 2-year-old, *P. radiata*. Axial resin canal size, density and relative cross-sectional area were determined in twenty families and ten clones from images of microtomed sections, scanned with polarised light to highlight resin canals. Axial resin canal size was generally homogeneous with a mean value estimate of 0.02 mm², and a coefficient of variation of ~10%. Estimated mean values for axial resin canal density and relative area were more variable (coefficients of variation ~30%) and lower for clones (0.69 canals/mm² and 1.13%, respectively) than for families (0.90 canals/mm² and 1.53%, respectively). Narrow-sense heritability (h^2) estimates of the studied axial resin canal features in radiata pine at age 2-years-old were ~0.30. Modulus of elasticity and longitudinal shrinkage were moderately correlated with axial resin canal density and relative area, while basic density and volumetric shrinkage were independent of axial resin canal features. The study indicated that there could be potential for breeding *P. radiata* for resin canal features, with the aim to improve the grade yields of appearance grade products.

Keywords Appearance grade · Heritability · Radiata pine · Stiffness · Wood defect

Introduction

Resin canals in softwoods are a complex network of tubular structures, oriented in both radial and axial directions (Baas et al. 2004; Bannan 1936), providing the trees with a defence mechanism against pests and pathogens (Franceschi et al. 2005; Hodge and Dvorak 2000; Moreira et al. 2015). Resin canals in pines are lined by a layer of resin-secreting epithelial cells, filling this network with resin. Resin will flow from the canal network to seal wounds and suffocate intruding organisms. While resin canals are always formed in pines, they can also be induced by traumatic events (Bannan 1936; Wu and Hu 1997). Studies concerning the resin features associated with the resilience of trees against pathogens

✉ Clemens M. Altaner
Clemens.Altaner@canterbury.ac.nz

¹ CSIR-Forestry Research Institute of Ghana, P. O Box UP 63, Kumasi, Ghana

² New Zealand School of Forestry, University of Canterbury, Christchurch, New Zealand

generally concluded that elevated levels of resin features facilitated forest health (Ferrenberg et al. 2014; Franceschi et al. 2005; O'Neill et al. 2002; Rosner and Hannrup 2004).

However, resin features in softwoods have been also investigated for technical reasons. First, resin itself can be a desired resource, for example as a source of turpentine (Fett-Neto and Rodrigues-Correa 2012; Mergen et al. 1955; Neis et al. 2019). Second, especially for appearance grade timber, resin 'blemishes' are the major defect, having been reported to account for up to 58% of downgrades from clear wood in radiata pine (Cown et al. 2011). Two resin features might be distinguished in this regard. Resin pockets, typically of traumatic origin and under environmental control (Woollons et al. 2008) dominating timber downgrades, as well as regularly formed resin canals, which render surfaces unappealing as resin canals are surface indentations, visible even after successful coating. The latter is relevant to this study.

In general, stems with higher resin canal frequencies are associated with higher incidences of resin-related defects (Cown et al. 2011; Yang et al. 2007), but the relationships are not always strong (Ananias et al. 2010). Resin-related defects also influence wood processing, for example resin can increase fouling of saws (Bergstedt and Lyck 2007) and dissolve paint finishes on wood products (Dawson et al. 2002). Contrary, resin canals may be advantageous for preservative treatments and timber drying, as they increase the permeability of the material (Flynn 2007; Keey et al. 2012).

Resin canal features have been reported to vary according to genetic (Hannrup et al. 2004; Li et al. 2017; Mergen et al. 1955) and environmental factors (O'Neill et al. 2002; Rosner and Hannrup 2004). While environmental traits, in particular water stress (Rosner and Hannrup 2004; Woollons et al. 2008) but also nutrient levels (Moreira et al. 2015), were identified to have an effect on resin canal features, genetic control was generally found to be most important in spruce (Hannrup et al. 2004; Rosner and Hannrup 2004).

The aim of this study was to determine the variation in resin canals features for clones and families of the New Zealand radiata pine production population at age 2-years-old and to test if the studied variables were under genetic control. Resin canal features were also related to basic density, modulus of elasticity (MoE) and shrinkage of the same samples.

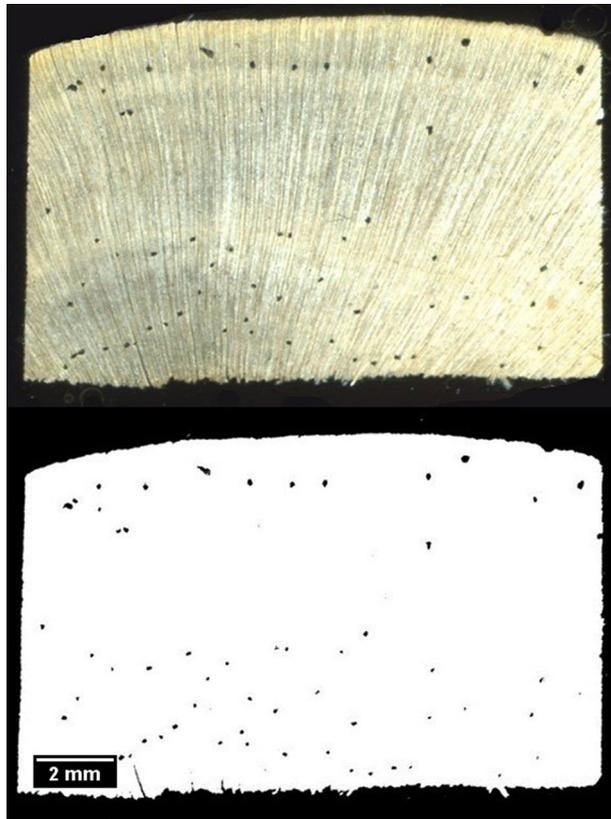
Materials and methods

Trial design

Samples were sourced from 2-year-old radiata pine (*Pinus radiata* D. Don) trees planted in a randomized complete block design with 30 replicates at Harewood, Christchurch. Fifty-nine known genotypes (49 full-sibling families and ten clones) of the New Zealand radiata pine breeding population were grown in 75 L bags filled with potting mix containing slow-release fertilizer and drip irrigated (Apiolaza 2014). The family genotypes had been selected for growth and density, whereas clones were selected for growth and stiffness. Three months after planting, the young plants were leaned and tied at a 15° angle for 21 months to separate compression wood from opposite wood (normal wood) (Chauhan et al. 2013).

Twenty out of 49 full-sibling families were selected by using Ranked Set Sampling (Ridout 2003) to collect observations covering the range of both basic density and wood stiffness, while all ten clones were used in this study. For each of the selected families and clones, 10 out of 30 trees were randomly selected and the normal wood samples were used.

Fig. 1 Scanned wood section in polarized light displaying resin canals as dark dots (top) and after image processing in ImageJ (8-bit, threshold) (bottom)

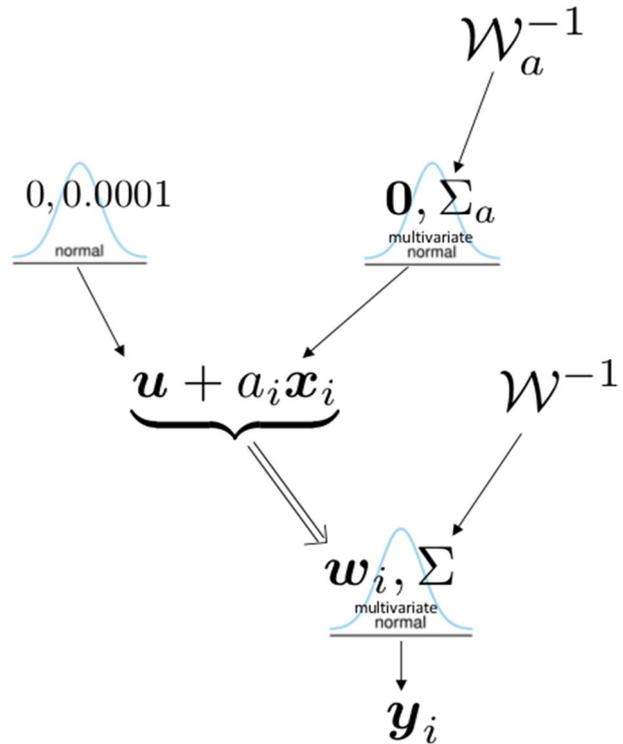


Twenty families and ten clones were included in this study, with 10 replicates each, for a total of 300 trees.

Measurement of resin canal features

Normal wood samples, ~2 cm in all dimensions and containing the outermost wood were softened at 60 °C for 24 h in distilled water. After cooling the water was replaced with a 1:1 solution of glycerol and ethanol to preserve the wood cubes (Thomas and Collings 2017). Sections ranging from 20 to 60 μm were cut from the cross-sectional surface of the softened wood using a sledge microtome (HM 400, Microm, Walldorf, Germany) and temporarily mounted on a specimen slide in glycerol. One section per tree was scanned with linear polarised light in colour at 2400 dpi resolution using a flatbed scanner (Epson Perfection V700) (Thomas and Collings 2017). Images (Fig. 1) were processed and analysed in ImageJ (Abràmoff et al. 2004). The area (mm^2) of the wood sections, the number of resin canals within the section and the size of each resin canal (mm^2) within the section were extracted automatically from each of the 300 images with ImageJ macros. The data collected were used to calculate the axial resin canal density, defined as resin canal count divided by the area of the section and the relative resin canal area, defined as the average canal size multiplied by the number of canals divided by the area of the section.

Fig. 2 Directed acyclical graph modified following Kruschke (2010) representing the multivariate hierarchical model for estimating genetic parameters



Density, modulus of elasticity (MoE), and shrinkage data

All wood samples had been previously assessed for basic density, MoE, longitudinal and volumetric shrinkage following the methods described by Chauhan et al. (2013). Mean basic density, MoE, longitudinal and volumetric shrinkage of opposite wood in the samples were 295 kg/m^3 , 2.63 GPa , 0.79% and 18.21% , with coefficients of variation of 6.05% , 14.84% , 39.03% and 24.90% , respectively (Apiolaza 2014). The trial showed large variability in wood properties at young age with moderate to high genetic control.

Statistical analysis

The dataset was analysed using the R statistical software (R Core Team 2016). The genetic analysis adopted a hierarchical-bayesian approach to estimate the posterior distributions for the heritabilities and additive genetic correlations between the assessed traits. The statistical model included an overall intercept and additive genetic effects for each of the traits (Fig. 2). Replicate effects were negligible and eliminated from the model. The vector \mathbf{y}_i stacks the assessments for each tree sample, so \mathbf{y}_i follows a multivariate normal distribution (\mathbf{w}_i, Σ) with expected value \mathbf{w}_i and a multivariate residual Σ . Σ was given a vague inverse Wishart prior (W^{-1}). As the data comprised a mix of clonal and controlled pollination individuals, the analysis uses a multivariate, individual tree (animal) model. The predicted values for the traits of the i th tree sample was represented as a function of an overall intercept for each trait and the additive genetic effect for each trait ($a_i x_i$). The relatedness

between individuals was accounted for via a numerator relationship matrix derived from the parental relationships between families and clones. Non-additive genetic effects were ignored, as the opportunistic mating design and sample size were inappropriate to properly estimate them.

The model was fitted using Markov Chain Monte Carlo methods implemented in the R software package MCMCglmm (Hadfield 2010). The model was run for 510,000 iterations, with a burn-in period of 10,000. The chain was thinned keeping one every 500 samples for the genetic parameters. Posterior distributions of heritability (h^2) and genetic correlations between two traits (r_{12}) were estimated using the standard formulas:

$$h^2 = \frac{\sigma_a^2}{\sigma_a^2 + \sigma_e^2} \quad \text{and} \quad r_{12} = \frac{\sigma_{a12}}{\sqrt{\sigma_{a1}^2 \sigma_{a2}^2}}$$

where σ_a^2 corresponds to the additive genetic variance, σ_{a12} to additive genetic covariance between two traits, and σ_e^2 to the residual variance.

Results and discussion

Variability in resin canal features

The axial resin canal features considered in this study were size, density and relative cross-sectional resin canal area (Table 1). Axial resin canal size in 2-year-old *P. radiata* was similar for clones (0.0165 mm²) and families (0.0170 mm²). The estimated mean axial resin canal cross-sectional area of 0.017 mm² (Table 1), equating to a diameter of approximately 150 μm, fell into the reported diameter range of 100–200 μm for axial resin canals of this species (Cown et al. 2011). However, the size was smaller than the reported average resin canal size of 0.028–0.036 mm² for harvest-sized *P. radiata* trees (Ananias et al. 2010; Yang et al. 2007). The reported increase in axial resin canal size with cambial age in young trees could account for this difference (Ananias et al. 2010; Boschiero Ferreira and Tomazello-Filho 2012; Reid and Watson 1966; Yang et al. 2007). Axial resin canal sizes have also been reported for other pines. For example, reported values were ~0.018 mm² for 7-year-old *P. taeda* (Westbrook et al. 2015), 0.024–0.044 mm² for 18-year-old *P. elliottii* (Neis et al. 2019), 0.012–0.018 mm² (122–150 μm in diameter) for 35-year-old *P. caribaea*

Table 1 Summary statistic for axial resin canal features in xylem of 2-year-old *P. radiata* clones and families

Variable	Plant type	Mean	95% confidence interval		<i>p</i> value of the difference between means	Coefficient of variation
			Lower	Upper		
Resin canal density (number/mm ²)	Clone	0.69	0.65	0.73	4.73e–12	31.4
	Family	0.90	0.87	0.94		27.8
% Resin canal area	Clone	1.13	1.06	1.20	1.95e–14	30.7
	Family	1.53	1.47	1.59		28.3
Resin canal size (mm ²)	Clone	0.0165	0.0161	0.0169	0.0186	11.9
	Family	0.0170	0.0168	0.0173		10.1

var. *hondurensis* (Boschiero Ferreira and Tomazello-Filho 2012), 0.035–0.045 mm² for 75-year-old *P. pinaster* (Rodríguez-García et al. 2014) or 0.003–0.020 mm² for *P. contorta* (Ferrenberg et al. 2014; Reid and Watson 1966).

The estimated mean axial resin canal density of 0.69 and 0.90 canals/mm² (Table 1) agreed with estimates for 14-year-old *P. radiata* of 0.5–1.5 canals/mm² (Ananias et al., 2010). While these authors did not observe a radial pattern, a more intensive study of resin canals in *P. radiata* found a clear increase in axial resin canal density with annual ring number (Yang et al. 2007); a result also reported for *P. caribaea* var. *hondurensis* (Boschiero Ferreira and Tomazello-Filho 2012). This radial trend could contribute to the slightly lower axial resin canal density in this dataset, which was based on young 2-year-old trees. Reported values for other pines were ~0.4 canals/mm² for *P. taeda* (Westbrook et al. 2015), 0.52 canals/mm² for *P. caribaea* var. *hondurensis* (Boschiero Ferreira and Tomazello-Filho 2012), 0.51–0.76 canals/mm² for *P. pinaster* (Rodríguez-García et al. 2014), 0.13–0.30 canals/mm² for *P. elliottii* (Neis et al. 2019) or ~1 canals/mm² for *P. contorta* and *P. flexilis* (Ferrenberg et al. 2014).

The relative area covered by axial resin canals was 1.13% and 1.53% for clones and families, respectively (Table 1). This was comparable to the ~1 to 3% of relative axial resin canal area in *P. pinaster* (Moreira et al. 2015; Rodríguez-García et al. 2014) or the 0.2–0.9% in *Picea abies* xylem (Luostarinen et al. 2017).

Axial resin canal density and percentage area in 2-year-old *P. radiata* xylem had similar variability with coefficients of variation of approximately 30% (Table 1). Similar coefficients of variation were reported for axial resin canal density in equally young *P. radiata* (coefficient of variation 22–29%) (Thomas and Collings 2017) and for 19-year-old *Picea abies* clones (coefficient of variation ~26%) (Hannrup et al. 2004). The size of the axial resin canals were, with a coefficient of variation of approximately 10%, more homogeneous than their occurrence (Table 1). While larger in magnitude, in agreement to this study, the variation in axial resin canal size was found to be three to four times lower than for resin canal density and relative resin canal area in *Picea abies* (Luostarinen et al. 2017).

For all variables, the full-sibling families had higher estimated mean values than the clones (Table 1). These differences were less significant ($p=0.0186$) for canal size. However, for all the variables, more variability was present among clones than families, indicating that the clones were more different from each other than the families. As a consequence larger genetic gain can be achieved by selection from the clones compared to the families.

Heritability and genetic correlations

The estimated narrow-sense heritabilities (h^2) for axial resin canal density ($h^2=0.33$), relative area ($h^2=0.31$) and size ($h^2=0.31$) in 2-year-old *P. radiata* (Table 2) were comparable to estimated heritabilities for other wood properties in similarly aged *P. radiata*, including

Table 2 Median and 95% credible intervals, in parenthesis, for posterior distributions for heritability (diagonal) and genetic correlations (off diagonal) of axial resin canal features in *P. radiata*

Parameter	Canal size	Canal density	% canal area
Canal size	0.31 (0.25, 0.38)		
Canal density	0.00 (−0.26, 0.24)	0.33 (0.22, 0.46)	
% Canal area	0.00 (−0.27, 0.24)	0.69 (0.51, 0.83)	0.31 (0.18, 0.46)

density and shrinkage (Apiolaza et al. 2011). These narrow-sense heritability values also fell close to the, typically higher, broad-sense heritabilities (H^2) for resin canal features in *Picea abies*. Broad-sense heritabilities of $H^2=0.41$ and 0.46 were reported for axial resin canal density at age 19-years-old (Hannrup et al. 2004), while broad-sense heritabilities for radial resin canal density, relative area and size at age 17-years-old were $H^2=0.21-0.81$, $H^2=0.45-0.66$ and $H^2=0.46-0.75$, respectively (Rosner and Hannrup 2004). However, lower H^2 values were reported for resin canal density (~ 0.2) and size (< 0.05) in 7-year-old *P. teada* (Westbrook et al. 2015).

Another resin canal related trait, which has been investigated for genetic control in *P. radiata*, was external resin bleeding with a reported narrow-sense heritability of 0.3 (Kumar 2004; Li et al. 2017)

Axial resin canal density correlated strongly and positively ($r_g=0.69$) to the cross-sectional relative axial resin canal area with a narrow (0.51, 0.83) 95% credible interval (Table 2). On the contrary, axial resin canal size was not correlated to the other measured resin canal features. This matched the observation in 17-year-old *Picea abies*, where a strong and consistent genetic correlation was found among clonal trials between radial resin canal density and their relative area, while no consistent genetic correlation was found between radial resin canal size and the other traits (Rosner and Hannrup 2004).

These results suggest that breeding to reduce resin canal density would automatically reduce the relative axial resin canal area. This was not surprising given the homogeneous size of the resin canals. Resin canal size would need to be independently addressed in a breeding programme. However, the low variability of the trait limits the achievable change.

Basic density, MoE, volumetric and longitudinal shrinkage are important physical properties which influence wood utilization. Mean values for the clones and families from the same samples (Apiolaza 2014), were correlated with means of axial resin canals features estimated in this study (Table 3). Axial resin canal size was independent of the other measured wood properties. This was probably attributed to the relatively homogeneous size of the axial resin canals (Table 1). Basic density and volumetric shrinkage were independent of the axial resin canal features for the 2-year-old radiata pine trees, suggesting that breeding to influence resin canal features should not affect basic density or volumetric shrinkage. No direct causality between the resin and basic density would be expected, considering the small volume proportion of axial resin canals of less than 2% (Table 1) combined with a typically low (approximately 1.5% dry weight) resin content in *P. radiata* sapwood (Bamber and Burley 1983; Moore et al. 2014). The results also matched those reported for *Picea abies* (age 19), where no correlation between density and axial resin canal density was found (Hannrup et al. 2004).

Interestingly, axial resin density and relative axial resin canal area were moderately correlated to MoE and longitudinal shrinkage. As the correlations were negative for MoE and positive for longitudinal shrinkage, these axial resin canal features appear to be positively

Table 3 Correlation coefficients (p value in parentheses) for resin canals features against selected physical properties of 2-year-old radiata pine wood

Parameter	Canal density	% Canal area	Canal size
Basic density	0.02 (0.74)	0.03 (0.60)	0.05 (0.36)
MoE	-0.29 (<0.001)	-0.32 (<0.001)	-0.09 (0.11)
Volumetric shrinkage	0.07 (0.23)	0.08 (0.15)	0.01 (0.82)
Longitudinal shrinkage	0.21 (<0.001)	0.25 (<0.001)	0.07 (0.26)

correlated to microfibril angle. The underlying physical causality is unclear. Hannrup et al. (2004) did not observe such a relationship between microfibril angle and axial resin canal density in *Picea abies*, probably due to the older age of the investigated trees, which typically have a low and consistent microfibril angle. Considering a breeding programme, a decrease in axial resin canal density and relative area would result in an increase in mean MoE and a decrease in mean longitudinal shrinkage. In both cases, this is a favourable correlation because a high MoE and low longitudinal shrinkage are the desired traits for *P. radiata* (Apiolaza 2014).

It is worth mentioning that the clones were selected for growth and stiffness, whereas the families were bred for growth and density. Hence, the clones would be expected to have lower resin canal features as the families (Table 1).

These observations were conducted with young, 2-year-old, trees on a single site. Resin canal features were reported to be extremely stable across sites (Hannrup et al. 2004; Rosner and Hannrup 2004), suggesting that making use of a single site is sufficient. The fact that resin canal features are known to increase radially (Ananias et al. 2010; Yang et al. 2007) indicates that resin defects become more critical at older age. Consequently, a strong age–age correlation is needed if early assessment is to lead to a superior crop at harvest age (Apiolaza 2009). It would be prudent to confirm the stability of the rankings calculated at 2-years-old from one site at older age for multiple sites. Furthermore, resin related traits have been associated with the ability of the trees to react to pests (Ferrenberg et al. 2014) and therefore unintended effects on tree health when minimising resin canals for wood quality and vice versa should be considered.

Conclusions

Of the investigated axial resin canal features, density and relative area were highly variable and strongly correlated, while size was more homogenous and not correlated to the other features. As frequency of axial resin canals was variable and heritable in 2-year-old radiata pine (Tables 1, 2), they could be included in a breeding programme. The favourable correlations of resin canal features with wood stiffness and longitudinal shrinkage (Table 3) would make it easier to find superior individuals, which produce high quality appearance-grade timber. This correlation could also explain the overall lower number of resin canal features in the investigated clones compared to the families of the commercial radiata pine breeding population, as the clones had been selected for stiffness.

However, as resin canal features are positively correlated to forest health (Ferrenberg et al. 2014; Franceschi et al. 2005; Westbrook et al. 2015), such radiata pine genotypes selected for lower levels of resin canal features might be more susceptible to pests. Alternatively selecting radiata pine genotypes for higher levels of resin canal features could be an option to improve forest health, with the consequence of reduced appearance quality of the timber.

Authors' contributions JKG conducted the experiments, analysed the data and prepared the manuscript draft; LAA assisted with data analysis and revised the manuscript; CMA conceived the study, provided technical advice and revised the manuscript.

Funding James Govina received a New Zealand Development Scholarship (NZDS). The trial was funded by the New Zealand Radiata Pine Breeding Company. The trial was managed by John C. F. Walker and Monika Sharma (NZ School of Forestry, NZ).

Compliance with ethical standards

Conflict of interest The authors declare no competing interest.

References

- Abràmoff MD, Magalhães PJ, Ram SJ (2004) Image processing with ImageJ. *Biophotonics Int* 11:36–42
- Ananias RA, Lastra J, Salvo L, Contreras H, Barria C, Peredo M (2010) Preliminary study of the resin canals in radiata pine. *Maderas Cienc Tecnol* 12:135–142. <https://doi.org/10.4067/S0718-221x2010000200008>
- Apiolaza LA (2009) Very early selection for solid wood quality: screening for early winners. *Ann For Sci* 66:10. <https://doi.org/10.1051/Forest/2009047>
- Apiolaza LA (2014) Confidential report. An implementation of very early screening for wood properties of radiata pine. New Zealand School of Forestry, Christchurch
- Apiolaza LA, Chauhan SS, Walker JCF (2011) Genetic control of very early compression and opposite wood in *Pinus radiata* and its implications for selection. *Tree Genet Genomes* 7:563–571. <https://doi.org/10.1007/s11295-010-0356-0>
- Baas P et al (2004) IAWA list of microscopic features for softwood identification—preface. *IAWA J* 25:1–1
- Bamber RK, Burley J (1983) The wood properties of radiata pine. Commonwealth Agricultural Bureaux, Slough
- Bannan MW (1936) Vertical resin ducts in the secondary wood of the Abietineae. *New Phytol* 35:11–46. <https://doi.org/10.1111/j.1469-8137.1936.tb06864.x>
- Bergstedt A, Lyck C (2007) Larch wood—a literature review. Forest & Landscape Denmark, Hørsholm
- Boschiero Ferreira AT, Tomazello-Filho M (2012) Anatomical aspects of resin canals and oleoresin production in pine trees. In: Fett-Neto AG, Rodrigues-Correa KCS (eds) Pine resin: biology, chemistry and applications. Research Signpost, Kerala, pp 9–24
- Chauhan SS, Sharma M, Thomas J, Apiolaza LA, Collings DA, Walker JCF (2013) Methods for the very early selection of *Pinus radiata* D. Don. for solid wood products. *Ann For Sci* 70:439–449. <https://doi.org/10.1007/s13595-013-0270-3>
- Cown DJ, Donaldson LA, Downes GM (2011) A review of resin features in radiata pine. *NZ J For Sci* 41:41–60
- Dawson BSW, Kroese HW, Hong SO, Lane GT (2002) Resin bleed after painting from radiata pine boards treated with tributyltin naphthenate (light organic solvent preservative) or copper, chromium and arsenic compounds (water-borne preservative). *Holz Als Roh-und Werkst* 60:18–24. <https://doi.org/10.1007/s00107-001-0255-z>
- Ferrenberg S, Kane JM, Mitten JB (2014) Resin duct characteristics associated with tree resistance to bark beetles across lodgepole and limber pines. *Oecologia* 174:1283–1292. <https://doi.org/10.1007/s00442-013-2841-2>
- Fett-Neto AG, Rodrigues-Correa KCS (2012) Pine Resin: biology, chemistry and applications. Research Signpost, Kerala
- Flynn KA (2007) A review of the permeability, fluid flow, and anatomy of spruce (*Picea* spp.). *Wood Fiber Sci* 27:278–284
- Franceschi VR, Krokene P, Christiansen E, Krokling T (2005) Anatomical and chemical defenses of conifer bark against bark beetles and other pests. *New Phytol* 167:353–375. <https://doi.org/10.1111/j.1469-8137.2005.01436.x>
- Hadfield JD (2010) MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *J Stat Softw* 33:1–22
- Hannrup B et al (2004) Genetic parameters of growth and wood quality traits in *Picea abies*. *Scand J For Res* 19:14–29. <https://doi.org/10.1080/02827580310019536>

- Hodge GR, Dvorak WS (2000) Differential responses of Central American and Mexican pine species and *Pinus radiata* to infection by the pitch canker fungus. *New For* 19:241–258. <https://doi.org/10.1023/a:1006613021996>
- Keey RB, Langrish TA, Walker JC (2012) *Kiln-drying of lumber*. Springer, New York
- Kruschke JK (2010) *Doing Bayesian data analysis—a tutorial with R and BUGS*. Academic Press, New York
- Kumar S (2004) Genetic parameter estimates for wood stiffness, strength, internal checking, and resin bleeding for radiata pine. *Can J For Res* 34:2601–2610. <https://doi.org/10.1139/x04-128>
- Li Y, Dungey H, Yanchuk A, Apiolaza LA (2017) Improvement of non-key traits in radiata pine breeding programme when long-term economic importance is uncertain. *Plos One* 12:e0177806–e0177806. <https://doi.org/10.1371/journal.pone.0177806>
- Luostarinen K, Pikkarainen L, Ikonen V-P, Zubizarreta Gerendiaín A, Pulkkinen P, Peltola H (2017) Relationships of wood anatomy with growth and wood density in three Norway spruce clones of Finnish origin. *Can J For Res* 47:1184–1192. <https://doi.org/10.1139/cjfr-2017-0025>
- Mergen F, Hoekstra PE, Echols RM (1955) Genetic control of oleoresin yield and viscosity in slash pine. *For Sci* 1:19–30. <https://doi.org/10.1093/forestscience/1.1.19>
- Moore JR, Cown DJ, Lee JR, McKinley RB, Brownlie RK, Jones TG, Downes GM (2014) The influence of stem guying on radial growth, stem form and internal resin features in radiata pine. *Trees Struct Funct* 28:1197–1207. <https://doi.org/10.1007/s00468-014-1030-1>
- Moreira X, Zas R, Solla A, Sampedro L (2015) Differentiation of persistent anatomical defensive structures is costly and determined by nutrient availability and genetic growth-defence constraints. *Tree Physiol* 35:112–123. <https://doi.org/10.1093/treephys/tpu106>
- Neis FA, de Costa F, de Almeida MR, Colling LC, de Oliveira Junkes CF, Fett JP, Fett-Neto AG (2019) Resin exudation profile, chemical composition, and secretory canal characterization in contrasting yield phenotypes of *Pinus elliottii* Engelm. *Ind Crop Prod* 132:76–83. <https://doi.org/10.1016/j.indcrop.2019.02.013>
- O’Neill GA, Aitken SN, King JN, Alfaro RI (2002) Geographic variation in resin canal defenses in seedlings from the Sitka spruce x white spruce introgression zone. *Can J For Res* 32:390–400. <https://doi.org/10.1139/X01-206>
- R Core Team (2016) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna
- Reid RW, Watson JA (1966) Sizes, distributions, and numbers of vertical resin ducts in lodgepole pine. *Can J Bot* 44:519–525. <https://doi.org/10.1139/b66-062>
- Ridout MS (2003) On ranked set sampling for multiple characteristics. *Environ Ecol Stat* 10:255–262. <https://doi.org/10.1023/A:1023694729011>
- Rodriguez-Garcia A, Lopez R, Martin JA, Pinillos F, Gil L (2014) Resin yield in *Pinus pinaster* is related to tree dendrometry, stand density and tapping-induced systemic changes in xylem anatomy. *For Ecol Manag* 313:47–54. <https://doi.org/10.1016/j.foreco.2013.10.038>
- Rosner S, Hannrup B (2004) Resin canal traits relevant for constitutive resistance of Norway spruce against bark beetles: environmental and genetic variability. *For Ecol Manag* 200:77–87. <https://doi.org/10.1016/j.foreco.2004.06.025>
- Thomas J, Collings DA (2017) Detection and mapping of resin canals by image analysis in transverse sections of mechanically perturbed, young *Pinus radiata* trees. *Iawa J* 38:170–181. <https://doi.org/10.1163/22941932-20170166>
- Westbrook JW et al (2015) Discovering candidate genes that regulate resin canal number in *Pinus taeda* stems by integrating genetic analysis across environments, ages, and populations. *New Phytol* 205:627–641. <https://doi.org/10.1111/nph.13074>
- Woollons R, Manley B, Park J (2008) Factors influencing the formation of resin pockets in pruned radiata pine butt logs from New Zealand. *N Z J For Sci* 38:323–333
- Wu H, Hu Z (1997) Comparative anatomy of resin ducts of the Pinaceae. *Trees* 11:135–143. <https://doi.org/10.1007/s004680050069>
- Yang J, Downes GM, Chen F, Cown DJ (2007) Investigation of within-tree and between-site resin canal variation in radiata pine. In: IUFRO all-division 5 conference, forest products and environment, Taipei, Taiwan, p 179