



Phenotyping a *Pinus radiata* breeding population for resin canal traits

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Abstract

Resin defects can substantially decrease timber value in *Pinus radiata*, a commercial forest plantation species known for its good machinability. Tree breeding is a common approach to improve economic viability and product quality in commercial forestry. This study evaluated resin canal features in a *P. radiata* breeding population at two sites. Phenotypic resin canal features close to the pith differed significantly between the sites. The study estimated heritabilities for resin canal size, area, and density in 2-year-old trees as $h^2=0.25, 0.42$ and 0.23 , respectively. The corresponding coefficients of genetic variations were 7.7%, 22.6% and 15.2%. Furthermore, resin canal features were assessed along radial cores of 6-year-old trees. Resin canal size increased with cambial age, while resin canal density and area showed minima 4 cm from the pith. Radial changes were accompanied with increased variation between families. While heritability and genetic variation would allow for selection at age 2-year-old, increased variation further from the pith could allow more accurate selections when trees are older. Genetic correlations between resin canal traits indicate that genotypes with larger resin canals tended to have fewer canals, larger trees having bigger but fewer resin canals and stiffer trees having less resin canal area.

Keywords Cambial age · Heritability · Radiata pine · Resin canal density · Resin canal size

Introduction

Numerous conifers produce resin in a tubular three-dimensional network (Ma et al. 2023; Peter 2018) called resin canals or ducts. This provides defence against pathogens and positively impacts tree and forest health (Franceschi et al. 2005; Howe et al. 2024); however, their implications extend beyond biological functions. On one hand, conifer resins are a commercial product and their occurrence in trees is actively promoted (López-Álvarez et

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al. 2023; Peter 2018). On the other hand, resin canals are associated with economic losses in appearance grade *Pinus radiata* timber. For appearance grade timber, resin ‘blemishes’ are a major defect, accounting for up to 58% of downgrades from clear wood in radiata pine (Cown et al. 2011; Jones et al. 2022). Two resin features might be distinguished in this regard, resin pockets which are typically of traumatic origin and under environmental control (Woollons et al. 2008) and regularly formed resin canals. The latter are relevant to this study as they render surfaces unappealing (Fig. 1) and are visible even after successful coating as surface indentations.

Several measures have been developed to quantify features of resin canals. Among them are canal size, expressed as area or diameter, canal density, expressed as the number of resin canals per unit area and canal area, expressed as the proportion of the surface area comprised of resin canals.

Environment and genetics affect resin canal features. Among the environmental variables, water stress (Rosner and Hannrup 2004; Woollons et al. 2008) and nutrient levels (Moreira et al. 2015) affect resin canal features. Genetic control of resin canal features has been reported for several species, including the pines *P. radiata* (Govina et al. 2021; Li et al. 2017), *P. oocarpa* (Fabián-Plesníková et al. 2021), *P. elliottii* (Mergen et al. 1955), *P. taeda* (Westbrook et al. 2015) and the spruce *Picea abies* (Hannrup et al. 2004; Rosner and Hannrup 2004).



Fig. 1 Low (left) and prevalent (right) resin canals features (dark spots) in appearance grade radiata pine. Photo credit: SWI (Solid Wood Initiative), New Zealand

Pinus radiata dominates 90% of New Zealand's commercial forest plantations, which is supported by an advanced breeding programme (Paget 2022). Resin canal features are currently not a selection criteria, but could be of interest to reduce downgrades through resin defects (Jones et al. 2022). This study utilised available samples from a previous very early screening study, which contained 92 families and 10 clones. This material was evaluated for wood stiffness (dynamic MoE – Modulus of Elasticity), basic density and longitudinal shrinkage when trees were 2-years-old (Apiolaza and Sharma 2023). A sister trial, consisting of the same families, was evaluated at age 6-years-old for growth and standing tree acoustic velocity, when in addition, a 14 mm diameter increment core was taken.

The objectives of this study were (1) to investigate the site effect on the expression of resin features, (2) to estimate genetic parameters for resin features at age 2-years-old, and (3) to explore the effect of cambial age on resin features by assessing resin features along cores of 6-year-old *P. radiata* trees.

Methods

Material

The analysed *P. radiata* breeding population contained 102 pedigreed genetic entries of which 92 were controlled-pollinated families and 10 were clones. Out of the 92 families, 49 were obtained from the operational seed orchard, and 43 were new selections from a breeding programme focusing on growth and form. The material was the offspring of 143 distinct parent trees. Two trials were established from the same material; one at Harewood in Christchurch and one at Tarawera, southeast of Rotorua.

The Harewood trial was established on a flat site in Christchurch (43° 28' 1.92" S, 172° 35' 15.86" E), using a randomised complete block design with 30 replicates; each family or clone was represented by a single tree in a replicate. Trees were grown in controlled conditions on a lean to separate compression wood from opposite wood. Previously a ~10 cm long stem section was harvested at the tree base, ripped in half and assessed for opposite and compression wood properties as reported by Apiolaza and Sharma (2023). Basic density, volumetric shrinkage, longitudinal shrinkage and dynamic MoE were calculated from measurements of green mass, dry and green volume (assessed by water displacement), dry and green length as well as dry acoustic velocity (assessed by resonance). For this study, a random selection of at least 10 individuals per genetic entry of opposite wood samples were phenotyped for resin canals features, resulting in a total of 1,185 trees.

At Tarawera, seedlings of the 92 families and 2 controls were planted directly into the ground on a flat site (38° 13' 26.93" S, 176° 34' 49.12" E) at a stocking of 806 stems per hectare, and a spacing of 4 m by 3.1 m resulting in a total of 3,240 trees. The trial site is set up as an incomplete-block experimental design containing 30 replications and 3 incomplete-blocks per replication. From the surviving trees a full stem diameter core was taken at breast height (1.4 m) in 2017 and measured for acoustic velocity, basic density, and volumetric shrinkage. For this study resin canal features within 2 cm of the pith were assessed in 5 randomly chosen cores of 30 chosen families, i.e. for a total of 150 cores. The 30 chosen families were a stratified sample based on resin canal density in the Harewood trial. Furthermore, resin canal features were assessed in 2 cm intervals along 5 cores of four

families totalling 20 trees. Based on resin canal density within 2 cm of the pith, two families with high (families 133 and 144) and two families with low (families 105 and 165) were chosen. Data for each position on the two radii of a core were averaged.

Assessing resin canals

Axial resin canal features were measured according to Govina et al. (2021). In brief, 20 to 60 μm thick cross sections were placed between 2 sheets of perpendicularly arranged linear polarizing films (Edmund Optics) and scanned at 2,400 dpi. The number of resin canals per unit area, the average size of the resin canals, and area percentage of resin canals were extracted from the digital images with ImageJ (Schneider et al. 2012).

The selected increment cores from the Tarawera trial were sanded on the cross section to expose a flat surface and subsequently split into 2 cm radial section, from which sections were cut with a microtome as described above.

Data analysis

Data was analysed with the open software R (R Core Team 2022). Tukey's HSD (honestly significant difference) tests utilised the multcompView package (Graves et al. 2024).

Phenotypic analyses in Tarawera used the following linear mixed model implemented in the nlme package (Pinheiro et al. 2023):

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}_1\mathbf{t} + \mathbf{Z}_2\mathbf{c} + \mathbf{e}$$

where \mathbf{y} is the vector for the response, \mathbf{b} is the vector of fixed effects containing the overall mean, Position, Family and Position:Family interaction, \mathbf{t} and \mathbf{c} are the random nested effects of tree and core radii within tree, and \mathbf{e} are the random residuals. \mathbf{X} , \mathbf{Z}_1 and \mathbf{Z}_2 are incidence matrices linking the observations to their respective effects. The expected value of the response was $E[\mathbf{y}] = \mathbf{X}\mathbf{b}$; the expected value for all random effects was zero and their variances were σ_t^2 , σ_c^2 and σ_e^2 . The model assumed 0 covariance between random effects. The residuals were assumed to be uniformly and normally distributed. As the measurements were ordered along the cores, we compared models that accounted for autocorrelation (using an AR1 process) versus assuming independent residuals.

As the sampling at Tarawera included only 1 or, at most, 2 blocks per replicate, we chose to ignore incomplete block when fitting the model.

The effects of position along the core were estimated and compared using the emmeans package (Lenth 2023), using Tukey effects adjusted by multiple comparisons.

The asreml package was used to fit linear mixed models with a pedigree, to estimate (co)variance components to estimate genetic parameters in the Harewood trial (Butler et al. 2009).

The initial genetic analysis used an animal model for a single trait:

$$\mathbf{y}_i = \mathbf{X}_i\mathbf{b}_i + \mathbf{Z}_{1i}\mathbf{r}_i + \mathbf{Z}_{2i}\mathbf{a}_i + \mathbf{Z}_{3i}\mathbf{f}_i + \mathbf{Z}_{4i}\mathbf{c}_i + \mathbf{e}_i$$

Where \mathbf{y}_i is the vector for the response of the i^{th} trait, and \mathbf{b}_i is the vector of fixed effect for the overall mean and population deviations (Clonal, New selections and Seed Orchard).

The model equation also included the following vectors of random effects: r_i for replicate, a_i for random additive genetic, f_i for family (partial estimate of dominance), c_i for clonal (dominance and epistasis, only fitted to clonal material), and e_i for residuals. $X_i, Z_{1i}, Z_{2i}, Z_{3i}$ and Z_{4i} are incidence matrices linking the observations to their respective effects. The expected value of the response was $E[y_i] = X_i b_i$; the expected value for all random effects was zero and their variances were $\sigma_{r_i}^2, \sigma_{a_i}^2, \sigma_{f_i}^2, \sigma_{c_i}^2$ and $\sigma_{e_i}^2$. The model assumed 0 covariance between random effects.

Initial analysis showed that family and clonal effects were not statistically significant and complicated model convergence. Therefore, they were eliminated from successive analyses.

The model was later expanded to a multivariate version, expanding y to groups of stacked vectors, which for a bivariate example the variances become $V[r] = R_0 \otimes Z_1, V[a] = G_0 \otimes A, V[e] = E_0 \otimes I$ where

$$R_0 = \begin{bmatrix} \sigma_{r1}^2 & \sigma_{r12} \\ \sigma_{r12} & \sigma_{r2}^2 \end{bmatrix}, G_0 = \begin{bmatrix} \sigma_{a1}^2 & \sigma_{a12} \\ \sigma_{a12} & \sigma_{a2}^2 \end{bmatrix}, E_0 = \begin{bmatrix} \sigma_{e1}^2 & \sigma_{e12} \\ \sigma_{e12} & \sigma_{e2}^2 \end{bmatrix} \text{ and}$$

A is the numerator relationship matrix, which reflects the relatedness from the pedigree.

Heritabilities for each trait i (h_i^2) were estimated as the ratio of additive variance to total phenotypic variance:

$$h_i^2 = \frac{\sigma_{a_i}^2}{\sigma_{a_i}^2 + \sigma_{r_i}^2 + \sigma_{e_i}^2}$$

where $\sigma_{a_i}^2, \sigma_{r_i}^2$, and $\sigma_{e_i}^2$ are defined as before. The standard error of the variance ratio was estimated by a first-order Taylor series approximation.

Additive genetic correlations were estimated as:

$$r_{g_{ij}} = \frac{\sigma_{a_{ij}}}{\sqrt{\sigma_{a_i}^2 \times \sigma_{a_j}^2}}$$

where $\sigma_{a_{ij}}$ is the additive genetic covariance between traits i and j , and $\sigma_{a_i}^2$ and $\sigma_{a_j}^2$ are the additive genetic variances for traits i and j respectively. The standard errors of the genetic correlations were directly provided by asreml-R.

Results and discussion

Resin canal features at age 2

The resin canal features (Table 1) were in agreement with the earlier study of this *P. radiata* breeding population (Govina et al. 2021) and slightly smaller than the reported 0.028–0.036 mm² for mature *P. radiata* trees (Ananias et al. 2010; Yang et al. 2007). There was a statistically significant difference in clonal and seed orchard material for all three assessed resin canal traits. Clonal material had smaller and fewer resin canals compared to seed orchard material. New selections were indistinguishable from clonal material in terms of resin canal

Table 1 Summary statistics for resin traits in 3 groups of the radiata pine breeding population at age 2-years-old. Superscript letters indicate Tukey's HSD 95% confidence levels

Trait	Population	Phenotypic Mean	Phenotypic CV (r_p) (%)
Resin canal size (mm ²)	All	0.0162	15.2
	Clonal	0.0159 ^a	14.1
	New selections	0.0160 ^a	16.1
	Seed orchard	0.0164 ^b	14.8
Resin canal area (%)	All	1.46	34.2
	Clonal	1.17 ^a	32.9
	New selections	1.50 ^b	35.5
	Seed orchard	1.53 ^b	30.1
Resin canal density (n / mm ²)	All	0.906	31.9
	Clonal	0.750 ^a	37.3
	New selections	0.936 ^b	30.7
	Seed orchard	0.937 ^b	29.6

Table 2 Heritability estimates (h^2) and coefficient of genetic variation (CGV) of resin canal traits of *P. radiata* at age 2-years-old in the diagonal. Phenotypic (r_p) correlations above and genetic correlations (r_g) below the diagonal. se: standard error

Trait	Resin canal size (mm ²)	Resin canal area (%)	Resin canal density (n / mm ²)
Resin canal size (mm ²)	h^2 0.25 (se 0.05) CGV 7.7%	0.36 ($p < 0.001$)	-0.09 ($p < 0.01$)
Resin canal area (%)	0.89 (se 0.05)	h^2 0.42 (se 0.06) CGV 22.6%	0.88 ($p < 0.001$)
Resin canal density (n / mm ²)	-0.26 (se 0.13)	1 (se NA)	h^2 0.23 (se 0.05) CGV 15.2%

size, and were indistinguishable from seed orchard material for the other two resin canal traits. The cause of these differences could not be determined from the available data, but as older trees were reported to have larger resin canals (Ananias et al. 2010; Yang et al. 2007) it is unlikely that it was caused by physiological aging of the clonal material.

Mean resin canal size (0.0162 mm²) and resin canal density (0.906 n/mm²) as well as phenotypic variation (15% and 32%, respectively) were similar to the means (0.0173 mm², 0.860 n/mm²) and coefficients of variation (22% and 33%, respectively) reported for juvenile wood of *P. oocarpa* (Fabián-Plesníková et al. 2021).

Resin canal traits of *P. radiata* at age 2-years-old were under partial genetic control (Table 2). Heritability estimates for resin canal size, resin canal area and resin canal density were $h^2 = 0.25$, 0.42 and 0.23, respectively. These values fell into the 95% confidence intervals found for a subset of the samples investigated in this study (Govina et al. 2021) and were similar to those reported for 17-year-old *P. abies* (Rosner and Hannrup 2004). Fabián-Plesníková et al. (2021) found that resin canal density ($h^2 = 0.35$), but not resin canal size, was under genetic control in *P. oocarpa*.

Genetic correlations between traits indicate that genotypes with larger resin canals tended to have fewer resin canals ($r_g = -0.26$) (Table 2), an observation also made in 17-year-old *P. abies*. Genotypes with a larger area of axial resin canals had more ($r_g = 1$; $r_p = 0.88$) and bigger ($r_g = 0.89$, $r_p = 0.36$) resin canals. The strong correlation between resin canal density and the relative resin canal area (Table 2) matched the earlier study of the *P. radiata* breeding

population (Govina et al. 2021) and 17-year-old *P. abies* (Rosner and Hannrup 2004) and *P. pinaster* branches (Zas et al. 2015).

The observed genetic variations for the resin canal area and density (Table 2) were similar to those observed for 17-year-old *P. abies* (Rosner and Hannrup 2004). The genetic and phenotypic variation for resin canal size were small, limiting the potential genetic gain by selection of favourable genotypes. However, Rosner and Hannrup (2004) found more variation in resin canal size in older *P. abies* and in combination with the observed increase in resin canal size with cambial age (Ananias et al. 2010; Boschiero Ferreira and Tomazello-Filho 2012; Yang et al. 2007), selection might be feasible. Breeding values for resin canals of the parents of the trees assessed in the *P. radiata* pine breeding population are visualised in Fig. 2.

Correlations between resin canal traits and other stem features

Stem diameter and wood properties, namely basic density, dynamic modulus of elasticity, as well as longitudinal and volumetric shrinkage (Table 3) were available for these samples from an earlier study (Apiolaza and Sharma 2023). Larger trees had bigger ($r_g = 0.13$; $r_p = 0.44$) but fewer ($r_g = -0.42$; $r_p = -0.95$) resin canals (Table 4). A positive phenotypic correlation between resin canal size and stem volume was also reported for 26-year-old radiata pine from a commercial plantation (Jones et al. 2022) and *P. contorta* and *P. flexilis* (Ferrenberg et al. 2014). The previously reported relationship between MoE and resin canal features (Govina et al. 2021) was also found in this data, with stiffer trees having lower measures of resin canal features (Table 4). It is in accordance with the negative correlation of resin blemishes with acoustic velocity, a measure of microfibril angle, of commercial radiata pine logs

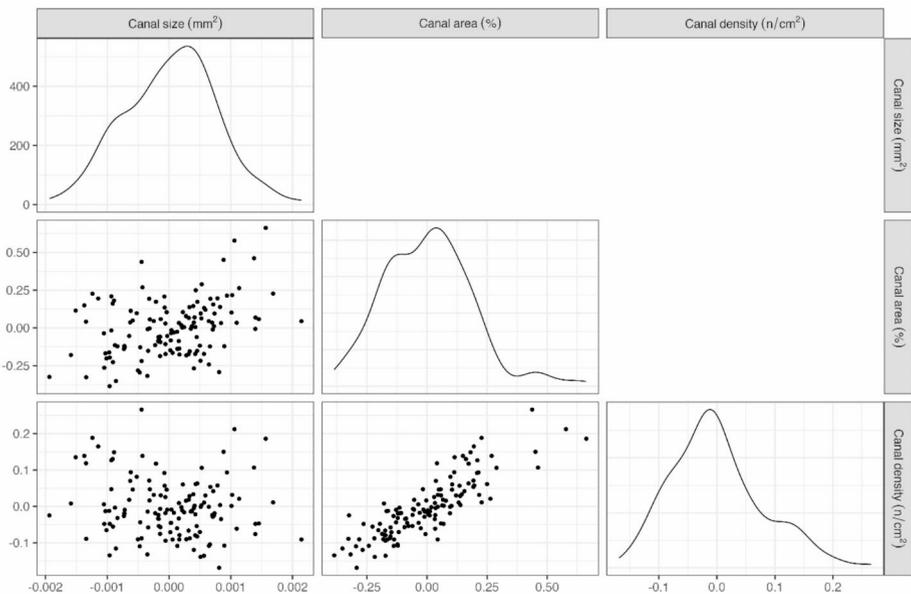


Fig. 2 Diagonal: Density plot for parental breeding values; Off diagonal: scatterplot of parental breeding values for resin canals features for 2-year-old *P. radiata* trees

Table 3 Summary statistics for stem traits in 3 groups of the radiata pine breeding population at age 2-years-old. Superscript letters indicate Tukey's HSD 95% confidence levels

Trait	Population	Phenotypic Mean	Phenotypic CV (%)
Basic density (kg / m ³)	All	294.7	5.9
	Clonal	290.7 ^a	6.7
	New selections	291.9 ^a	5.7
	Seed orchard	298.2 ^b	5.6
MoE (GPa)	All	2.55	14.3
	Clonal	2.85 ^a	13.2
	New selections	2.46 ^b	13.9
	Seed orchard	2.51 ^c	12.8
Longitudinal shrinkage (%)	All	0.755	38.9
	Clonal	0.508 ^a	33.0
	New selections	0.803 ^b	37.0
	Seed orchard	0.802 ^b	35.2
Volumetric shrinkage (%)	All	17.79	24.7
	Clonal	15.23 ^a	21.9
	New selections	18.09 ^b	24.3
	Seed orchard	18.46 ^b	23.8
Diameter (mm)	All	36.24	11.1
	Clonal	34.43 ^a	11.4
	New selections	37.21 ^b	10.8
	Seed orchard	36.12 ^c	10.7

Table 4 Phenotypic (r_p) and genetic (r_g) correlations of resin canal traits to other wood property traits of *P. radiata* at age 2-years-old. se: standard error

Trait		Resin canal size (mm ²)	Resin canal area (%)	Resin canal density (n / mm ²)
Basic density (kg / m ³)	r_p	0.04 ($p=0.22$)	0.05 ($p=0.10$)	0.04 ($p=0.18$)
	r_g	0.03 (se 0.09)	0.09 (se 0.11)	0.06 (se 0.10)
MoE (GPa)	r_p	-0.08 ($p=0.45$)	-0.26 ($p<0.001$)	-0.27 ($p<0.001$)
	r_g	-0.16 (se 0.12)	-0.37 (se 0.07)	-0.04 (se 0.09)
Longitudinal shrinkage (%)	r_p	0.00 ($p=0.96$)	0.17 ($p<0.001$)	0.17 ($p<0.001$)
	r_g	-0.06 (se 0.08)	0.17 (se 0.07)	0.22 (se 0.07)
Volumetric shrinkage (%)	r_p	-0.04 ($p=0.17$)	-0.01 ($p=0.66$)	-0.01 ($p=0.77$)
	r_g	-0.22 (se 0.12)	-0.14 (se 0.08)	-0.14 (se 0.11)
Diameter (mm)	r_p	0.13 ($p<0.001$)	-0.32 ($p<0.001$)	-0.42 ($p<0.001$)
	r_g	0.44 (se 0.11)	-0.82 (se 0.05)	-0.95 (se 0.03)

(Jones et al. 2022). The positive correlations between longitudinal shrinkage and resin canal features is consistent with the fact that both, MoE and longitudinal shrinkage are strongly but inversely regulated by the microfibril angle (Ivković et al. 2009). Basic density was independent of resin canal traits, a result also reported for *P. abies* (Hannrup et al., 2004).

The smaller and fewer resin canals (Table 1) in the stiffer (Table 3) clonal material compared to seed orchard material matched the genetic and phenotypic correlations between these traits (Table 4). However, the underlying mechanism for these relationships could not be determined from the available data. Resin canal formation might be related to tree sway. Mechanically, the rigidity of the stem increases with the 4th power of the diameter, the 3rd

power of the stem length (i.e. tree height) and linearly with MoE. Sway of the tree is further linearly dependent on crown weight. As both diameter and MoE were negatively correlated to resin canal features (Table 4), the hypothesis of sway inducing resin canals could be true. However, an experiment with controlled sway would need to be conducted to confirm as neither tree height nor crown weight data was collected.

Site effect

A selection of 30 families was phenotyped at two sites (Tarawera and Harewood) for resin canal features within 2 cm of the pith. For the Harewood site, the means and CVs of the resin features of the 30 selected families (Table 5) were of the same magnitude as those observed for all 92 families in breeding population (Table 1), confirming that the stratified sample did not introduce bias. Resin canal features differed significantly ($p < 0.001$) between the two sites with the Tarawera site featuring larger but fewer resin canals (Table 5). It is unlikely that the difference in size and number of resin canals between the two sites was confounded by the difference in sampling height (stem base in the case of Harewood and breast height in the case of Tarawera). This is because environmental factors such as climate, soil nutrients and insect attack have been identified as factors affecting resin canal size and density and the influence of stem height was reported as unclear (Cown et al. 2011; Yang et al. 2007).

Radial patterns (cambial age effect)

Resin canal features were assessed in 2 cm intervals on the two radii of the full stem diameter cores of 6-year-old *P. radiata*. Average resin canal size increased significantly from pith to bark almost doubling from 0.025 to 0.047 mm² (Fig. 3). A radial increase in axial resin canal size was reported for pines (Ananias et al. 2010; Neis et al. 2019; Reid and Watson 1966; Yang et al. 2007).

Radial profiles of resin canal area and resin canal density were more complex, showing statistically significant minima 4 to 6 cm from the pith (Fig. 3). Two studies providing data on the radial variation of resin canal density in pines did not report statistical significance (Boschiero Ferreira and Tomazello-Filho 2012; Reid and Watson 1966).

Figure 4 displays the resin canal measurements for four families at 2 cm intervals from pith to bark. Although the four families were selected for low and high resin canal density at age 2-years-old, the difference was not statistically significant. Not all trees reached a diameter at breast height of 12 cm, resulting in incomplete data for distances further from

Table 5 Summary statistics for resin canal features within 2 cm from the pith of *P. radiata* trees from the same 30 families grown at Tarawera ($n=150$) and Harewood ($n=341$). All resin canal features were significantly ($p < 0.001$) different between the sites

Trait	Site	Mean	Phenotypic CV (r_p) (%)
Resin canal size (mm ²)	Tarawera	0.0253	17.7
	Harewood	0.0162	16.5
Resin canal area (%)	Tarawera	0.84	36.7
	Harewood	1.48	33.2
Resin canal density (n / mm ²)	Tarawera	0.331	33.2
	Harewood	0.920	30.7

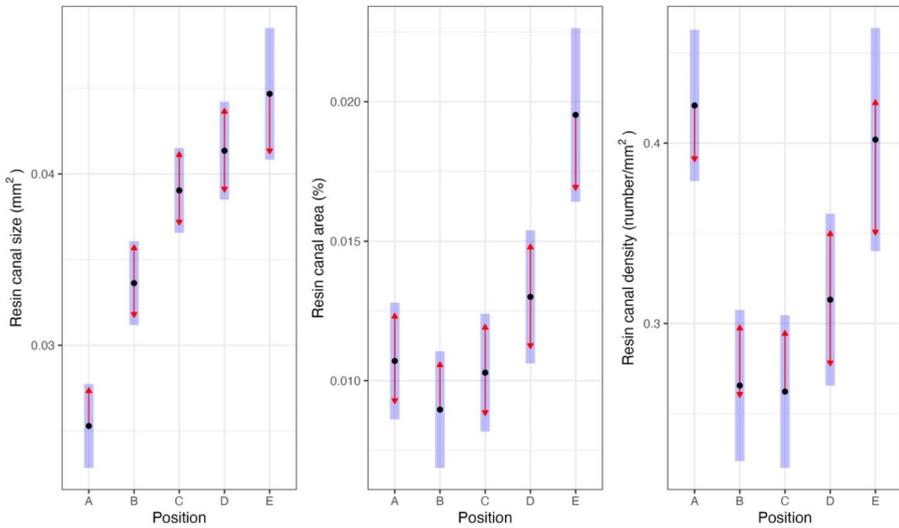


Fig. 3 Resin canal size, resin canal area and resin canal density depending on radial distance from the pith for 6-year-old *P. radiata* trees. Black circles are estimated marginal means, blue bars indicate their 95% confidence intervals and red arrows are for comparisons between radial positions. Overlapping arrows mean not statistically significant ($p=0.05$) differences between positions

the pith. However, families with larger resin canals close to the pith also had larger resin canals further away.

Variation of the traits increased with radial distance (Fig. 4), a phenomenon also reported for resin canal size and density in *P. oocarpa* (Fabián-Plesníková et al. 2021). Selection at older age could therefore be more precise.

Conclusion

The size and number of resin canals in *P. radiata* are heritable. It is possible to assess these traits at an early age in less than 2-year-old plants. However, data suggested that the assessment could be more precise further from the pith as variability between genotypes for the traits increased radially with cambial age. Site influenced the magnitude of the resin canal measures. For appearance grade timber, the investigated resin canal traits had favourable correlations to the commercial selection criteria tree diameter and stiffness. The calculated breeding values for resin canal features could be used to cull genotypes with unfavourable resin canal features. In the future, work on genetic control of resin canal features relevant for timber appearance should be expanded to include traumatic resin pockets.

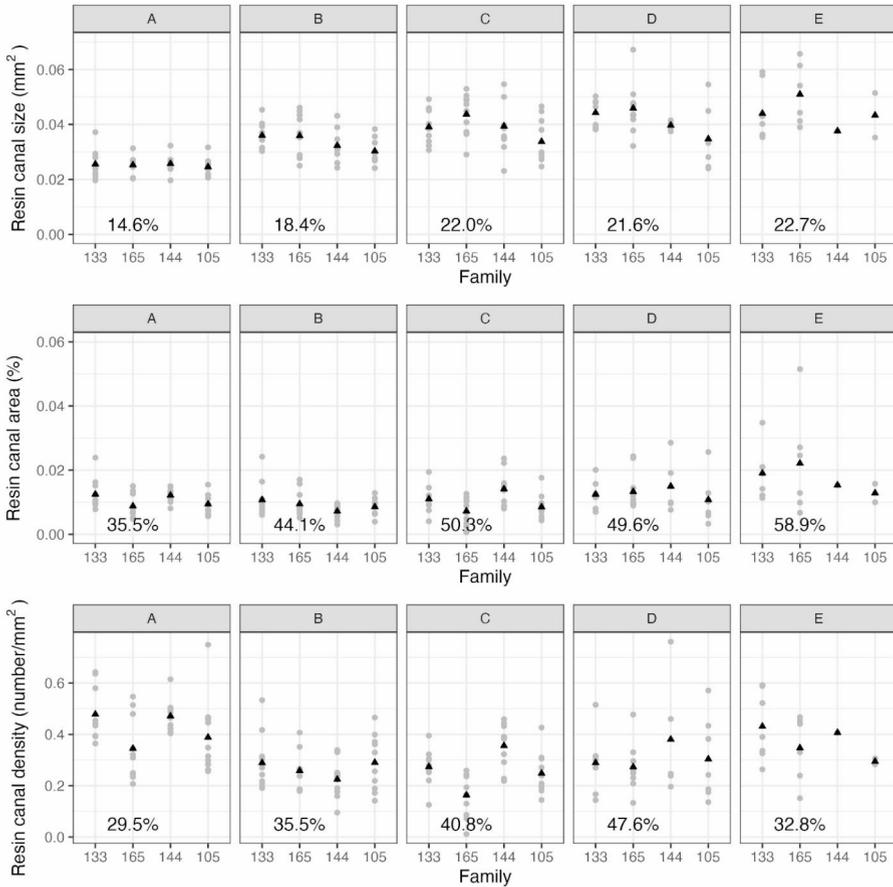


Fig. 4 Resin canal size (top), area (middle) and density (bottom) for four 6-year-old *P. radiata* families at increasing distance from the pith (A-E 2 cm radial increments). Families 133 and 144 were chosen for high and families 105 and 165 for low resin canal density 2 cm from the pith. Triangles depict mean values; percentages are the coefficient of variation of the trait at each radial position

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Author contributions CMA and LAA planned and designed the research. MS and AJG conducted and supervised resin canal measurements. Statistical analysis was conducted by CMA, LAA and MS. The manuscript was drafted by CMA and AJG. All authors edited and approved the final version of the manuscript.

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Data availability Anonymized data will be made available by the corresponding author upon reasonable request.

Declarations

Competing interests The authors declare no competing interests.

Conflict of interest The authors have no relevant financial interests to disclose.

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