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Characterisation of within-tree and within-ring resin-pocket density in *Pinus radiata* across an environmental range in New Zealand.

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Abstract

Resin pockets are found in the xylem of conifers belonging to four main genera and can generally be classified into two types. Type 1 are radially narrow discontinuities in the wood while type 2 are radially flattened, contain less callus tissue, and are open to the external environment at early stages in their development. Although resin pockets are a major cause of degrade for appearance grade timber little is known about how the frequency of type-1 and type-2 resin pockets varies within trees and within rings.

In this study, we collected data from 15- to 18-year-old *Pinus radiata* D.Don stands at four sites covering a wide environmental gradient. Resin pocket frequency was determined by cutting the lower 5 m of six trees at each site into 50-mm sections. Each of these sections was then imaged. Resin pockets were identified as type 1 or type 2 and the location of the resin pockets in three dimensions was recorded. Using these detailed measurements, the objectives of this study were to characterise: (i) three-dimensional variation in type-1 and type-2 resin pocket frequency within trees; and (ii) the position of type-1 and type-2 resin pockets within rings.

The frequency of type-2 resin pockets was double that of type-1 resin pockets, and this ratio did not vary significantly between sites. Within trees, resin pocket density varied markedly in the radial but not the longitudinal or circumferential dimensions. At all four sites, variation in the radial dimension was characterised by an absence of resin pockets in the inner rings and fluctuating resin pocket densities in the outer rings. The age at which substantial resin pocket formation began ranged from 4 years on the fastest growing site to 8 years on the slowest growing site. On the driest sites, resin pocket incidence consistently peaked in the latter part of the growth ring in all trees, but on the windiest and wettest site the distribution was more irregular and varied between trees. The distribution of type-1 and type-2 resin pockets was highly segregated within the growth ring with mean positions occurring respectively at ca. the 30th and 80th percentile of the growth ring width.

Keywords: *Pinus radiata*; resin pockets

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Introduction

Resin production in the stems of softwood trees is a defence mechanism that helps to prevent infection of wounds to the cambium, protects the stem against decay, and limits the effects of insect and fungal attack. Resin pockets are the most common defect of a range of resin blemishes (Woollons et al., 2008; Cown et al., 2011) and are found as a regular feature of four timber producing genera of the *Pinaceae* that have resin ducts (*Larix*, *Pinus*, *Picea* and *Pseudotsuga*). In these genera, long-lived secretory epithelial cells synthesise resin that is dispersed through interconnecting vertical (axial) and horizontal (radial) resin canals (Harris, 1991).

Although resin pockets serve an important biological function they are also a major cause of degrade in trees grown for appearance-grade timber (Beauregard et al., 1999; Gazo et al., 2000). Species in which resin pockets form are widely distributed, both in natural forests (predominantly in the northern hemisphere) and in plantations (of which the greatest area is in the southern hemisphere). *Pinus radiata* D.Don is the most widely planted plantation species in the southern hemisphere and New Zealand in particular (Lewis & Ferguson, 1993). In New Zealand, resin pockets are a major cause of degrade in the clearwood zone of pruned *P. radiata* logs (Park, 2004; Park, 2005). Resin pockets are found in nearly all exotic forests throughout New Zealand (Cown, 1973), and reach epidemic levels in regions that are dry and windy.

Three types of resin pockets were described by Somerville (1980). Type-1 resin pockets are radially narrow discontinuities in the wood that are oval in the tangential-radial plane and filled with oleoresin and callus tissue, leaving no external signs on the stem (Figure 1A). Type-2 resin pockets are similar to type 1 but are radially flattened, contain less callus tissue, and are open to the external environment at early stages in their development (Figure 1B). They later become occluded by cambial overgrowth with the formation of an occlusion scar that may be retained across several subsequent growth rings. Type-3 resin pockets originate as lesions in the cambial zone. Surrounding healthy cambium occludes causing an occlusion scar similar to that of type-2 resin pockets. Generally, no distinction is made between type-2 and type-3 resin pockets.

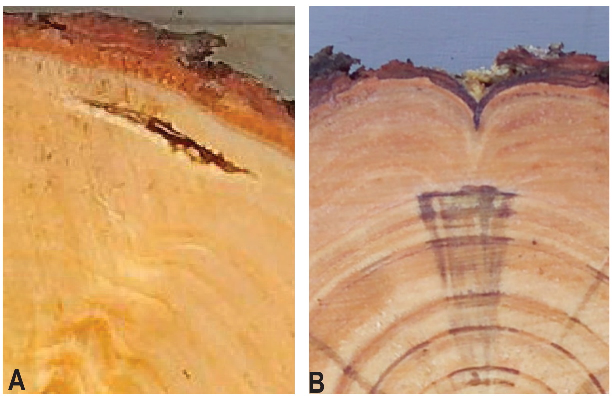

FIGURE 1: Photograph of typical classic type-1 (A) and type-2 (B) resin pockets.

Although there has been considerable literature published on resin pockets, this research rarely distinguishes between different morphological types. The majority of studies that do distinguish type-1 and type-2 resin pockets have been undertaken in New Zealand, where resinous defects have significant commercial implications due to their impact on a well-developed appearance-grade timber manufacturing-sector.

Characterisation of within-tree variation in resin pocket frequency is a very important initial step to understanding patterns of formation. While previous studies examined three dimensional variation in resin pocket frequency within *Picea abies* (L.) Karst. (Wernsdörfer et al., 2002; Gjerdrum & Bernabei, 2007), no segregation between resin pocket type was made. Although research has mapped resin pocket distribution in *P. radiata* at a single site (Watt et al., 2009), we are unaware of any analyses that have examined resin pocket variation in this species across more than one site, or expressed this on a volumetric basis. Describing the three-dimensional variation in resin pocket frequency at a fine scale resolution provides context for further studies and could possibly provide insights into stand and environmental factors likely to affect formation of type-1 and type-2 resin pockets.

Using detailed measurements taken from four sites, we characterise: (i) three-dimensional variation in resin pocket frequency within trees; and (ii) the position of type-1 and type-2 resin pockets within rings. A particular focus of this study was to examine how generalisable the described patterns were between sites.

Materials and methods

Site location

Four sites with *Pinus radiata* plantations that exhibited high levels of external resin bleeding and covered a wide range in rainfall and wind speed were selected for measurements. One of these sites was located at Ohurakura in the North Island (lat. 39.22° S, long. 176.73° E; elevation 375 m above sea level (asl)), while the remaining three were located on the east coast of the South Island at Balmoral (lat. 42.83° S, long. 172.80° E; elevation 180 m asl), Ashley (lat. 43.19° S,

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long. 172.59 E; elevation 210 m asl) and McLeans Island (lat. 43.47° S, long. 172.39° E; elevation 90 m asl). The stand age at the time of sampling (2006) was 15 years at Ashley and McLeans Island, 16 years at Balmoral and 18 years at Ohurakura.

Daily meteorological data were obtained from the Virtual Climate Station Network (VCSN) administered by NIWA (National Institute of Water and Atmospheric Research Ltd.). Environmental conditions at the four sites exhibited a considerable range in mean annual wind speed and total annual rainfall (Table 1). Across the four sites mean annual rainfall ranged three-fold from 529 mm year^{-1} at Balmoral to 1449 mm year^{-1} at Ohurakura (Table 1). These two sites also exhibited the extremes in wind speed with mean annual wind speed ranging two-fold between Balmoral and Ohurakura (Table 1).

Measurements of resin defects

Six trees within each plantation that exhibited moderate to severe external resin bleeding were selected for detailed measurements. Each tree was felled and the lower 5 m of stem cut into 50-mm-thick discs. The height of the tree at each disc position was recorded. The upper surface of each disc was cleaned, and imaged using a high resolution colour camera. From the images, all visible resin pockets were identified. All the visible resin pockets were visually classified as either type 1 or type 2 and allocated to a year of occurrence based on the closest ring number. The radial distances from the inner and outer edges of each resin pocket to the disc pith were measured, along with the angles to the pith of the tangential edges with reference to the original north facing direction of the tree. The precise location of each resin pocket within its growth ring was obtained by estimating the proportion of the ring width of the inner and outer edge of the resin pocket. The midpoint of the radial distance, angle and position within ring as a proportion of ring width were calculated from the inner and outer edge measurements for each resin pocket. Frequent false rings made this a difficult process. To minimise the effects of random variance, all images were processed by a single operator, with much discussion with other authors, to correctly allocate resin pockets to the correct year of formation.

Data analysis

All statistical analyses were performed using SAS Version 9.2. The volume of wood in each growth ring was calculated for each disc from information on disc thickness and the mean inner and outer ring radii. Resin-pocket volumetric densities were calculated by summing the resin-pocket counts by growth ring in 1-m height classes, and dividing by the wood volume. Mixed models were then used to analyse resin pocket volumetric density. Because the distribution of resin pocket density was highly skewed, the transformation *log*(density+1) was used.

Site differences in resin pocket density were compared using one-way analysis of variance (ANOVA) of tree means. Within-tree patterns in volumetric density were tested firstly using quadratic response functions for radial distance from pith and height fitted separately for each site. These response functions were fitted using PROC MIXED as random coefficient models with 'tree' as the subject, and with both radial distance and height standardised by subtracting the mean. By fitting these as random coefficient models, consistent patterns across all trees at each site could be identified. Secondly, to further investigate radial trends in volumetric density, a two-way ANOVA was fitted for each site including tree as a random effect and ring year as a fixed effect, and testing ring against the tree × ring interaction effect. For assessing circumferential direction effects, mean densities were calculated for each tree in 8 equal sized azimuth classes, and two-way ANOVA with factors for tree and azimuth were fitted for each site.

Position within ring was converted into a class variable by dividing each ring into five equi-length classes (0-<20, 20-<40, 40-<60, 60-<80, 80-<100% of ring width). Firstly, to test whether within-ring patterns of resin pocket incidence repeated consistently within each annual ring, resin pocket counts were summed across all trees at each site by ring number and position class. A two-way ANOVA was then fitted to log-transformed counts with ring number and position as factors. Secondly, to test whether within-ring patterns were consistent between trees at each site, counts were summed across all rings by position and tree. A

TABLE 1. Climatic conditions for the four sampled sites. Values shown are the mean total rainfall and mean annual averages for the other climatic variables determined from the time of plantation establishment to sampling.

	Ashley	Balmoral	McLeans Island	Ohurakura
Rainfall (mm year^{-1})	684	529	612	1449
Temperature (°C)	11.5	12.5	11.5	12.0
Relative humidity (%)	74	72	79	81
Wind speed (m s^{-1})	3.5	1.8	2.7	4.4
Number of years of data averaged	15	16	15	18

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two-way ANOVA was fitted to log-transformed counts with tree and position as factors. Also, to visually inspect within and between ring patterns of resin pocket incidence in each tree, resin pocket counts were obtained in 0.05 ring units for each tree, and smooth curves fitted using PROC LOESS, with count as the dependent variable and fractional ring number as the independent variable.

The percentage of type-2 resin pockets to total (type-1 + type-2) resin pocket count was compared across sites by one-way ANOVA using tree means. Percentages were also calculated by ring and height class and compared using random coefficient regression models. The mean position within ring expressed as a percentage of ring width was calculated for each type by tree and compared across sites using three-way ANOVA with fixed effect factors for site and type, and a random factor for tree within site.

The effects of site, ring number, height and type on resin pocket tangential width was tested using analysis of variance. Because the distribution of tangential width was highly skewed, the log transformation was used in this analysis.

Results

Site variation in resin pocket density

Tree volume over the first five metres of the stem was greatest at the Ohurakura site and significantly exceeded volume at any of the other sites by between two-fold and five-fold (Table 2). The frequency of resin pockets per stem at the McLeans Island site significantly exceeded that of any of the other sites by between two to three-fold. Expressing this resin pocket density on a volumetric basis (Table 2) accentuated these differences with values at the McLeans Island site (1090 resin pockets m^{-3}) significantly exceeding that of any of the other sites by between four-fold for the Balmoral site (242 resin pockets m^{-3}) to nine-fold for the Ohurakura site (117 resin pockets m^{-3}). Overall, 71% of all resin pockets in the dataset were of type 2, and the ratio of type 2 to type 1 did not vary significantly between sites.

Within tree variation in resin pocket density

Within-tree variation in resin pocket density in the radial and longitudinal dimensions (modelled using random coefficient quadratic response functions to describe radial distance from pith and height) revealed strong radial trends but inconsistent longitudinal trends (Table 3). The linear radial term was statistically significant and positive for all sites indicating an increasing trend with radial distance from pith. The quadratic radial term was negative at all sites and was statistically significant at two of the four sites. The linear height term was significantly positive at the Ohurakura site where resin pocket density tended to increase with height, but negative though non-significant at the other three sites. The quadratic height term was significant at Ashley where densities decreased sharply in the upper metre or so of the five-metre measured stem section. There was no significant interaction between radial and longitudinal terms at any site. Age at ring formation was also tested using analysis of variance. In this analysis the stand age at ring formation was highly significant at all sites (Table 3).

The radial trends in resin pocket density are shown for each site plotted against distance from pith (Figure 2) and age of ring formation (Figure 3). The most obvious trend is a near absence of resin pockets near the pith (Figure 2) at all sites. This effect was least apparent in samples from the McLeans Island site although, even there, 95% of resin pockets were more than 37 mm from the stem centre. It was most apparent at the Ohurakura site where 95% of resin pockets were more than 83 mm from the pith. Although the

TABLE 2: Influence of site on resin pocket formation in the lower 5 m of each *Pinus radiata* stem. Site means are given for stem volume, number and density of resin pockets, and the percentage of resin pockets classified as type 2. Standard errors based on six trees at each site are in parentheses. For the analysis of variance, the *F*-ratio (3, 20 d.f.) and *P* category are shown.

Site	Stem volume (m^3)		Resin pocket count (no. $tree^{-1}$)		Resin pocket density (no. m^{-3})		Type 2 resin pockets (%)	
Ashley	0.28 (0.04)	b	38 (10)	b	143 (42)	b	65 (13)	a
Balmoral	0.20 (0.02)	ab	46 (7)	b	242 (45)	b	70 (8)	a
McLeans Island	0.11 (0.02)	a	116 (14)	a	1090 (134)	a	88 (5)	a
Ohurakura	0.60 (0.07)	c	71 (21)	ab	117 (31)	b	63 (14)	a
ANOVA	28.9^{***}		3.94^{*}		10.9^{***}		1.2^{ns}	

Asterisks ***, * indicate significance at *P* = 0.001 and 0.05, respectively, ns = not significant at *P* = 0.05.
Sites followed by the same letter are not significantly different at *P* = 0.05.

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TABLE 3: Analyses of variance from two models describing the radial and longitudinal variation in resin pocket volumetric density. Model (i) is a quadratic response function in height and radial distance fitted using a random coefficient model. Model (ii) is an ANOVA testing stand age at ring formation.Separate analyses of each model were undertaken for each site. Shown are numerator and denominator degrees of freedom, *F*-values and *P*-categories.

Model	Effect	Num. DF	Den. DF	Ashley	Balmoral	McLeans Island	Ohurakura
(i)	Radius (*R*)	1	5	17.3^{**}	10.5^{*}	80.1^{***}	8.3^{*}
	Height (*H*)	1	5	6.0^{ns}	1.1^{ns}	1.1^{ns}	10.2^{*}
	R^2	1	5	3.1^{ns}	9.5^{*}	13.4^{*}	3.9^{ns}
	H^2	1	5	7.2^{*}	0.2^{ns}	2.4^{ns}	0.3^{ns}
	$H \times R$	1	5	1.5^{ns}	6.3^{ns}	3.1^{ns}	0.0^{ns}
(ii)	Age	13-15	61-75	5.2^{***}	4.2^{***}	13.1^{***}	2.6^{**}

Asterisks ***, **, * represent significance at P = 0.001, 0.01 and 0.05 respectively; ns = non-significant at P = 0.05.

low resin-pocket density region extended furthest in terms of radial distance in trees at the Ohurakura site, resin pockets appeared at this site at the earliest age (4 – 5 years) of all four sites tested (Figure 3). Trees also grew most rapidly at this site. Resin pockets were first formed in trees at age 6 years at both the Ashley and McLeans Island sites, and did not appear, in any abundance, until trees reached age 8 years at Balmoral. Note, however, that especially at sites where tree growth was slow, the stand would be several years old before the upper portion of the 5-metre stem section was formed.

In rings formed beyond the low resin-pocket density central portion of the stem, resin pocket densities tended to fluctuate up and down the stem and showed little clear trend. Although there was an apparent reduction in density in the outer part of each of the stems from the McLeans Island site (Figure 2), this was caused by low densities in the rings formed in the 2004 – 05 and 2005 – 06 growing years (Figure 3). This trend was also apparent at the other two South Island sites. The reduction may be due to environmental conditions in these particular growing years rather than reflecting a general reducing trend with radial distance in the outer rings. The oldest stand (that at the Ohurakura site in the North Island) showed no clear trend in resin pocket density with stand age or radial distance in the outer rings.

Site level analyses clearly showed that resin pocket frequency did not vary with circumferential direction at any site (Table 4).

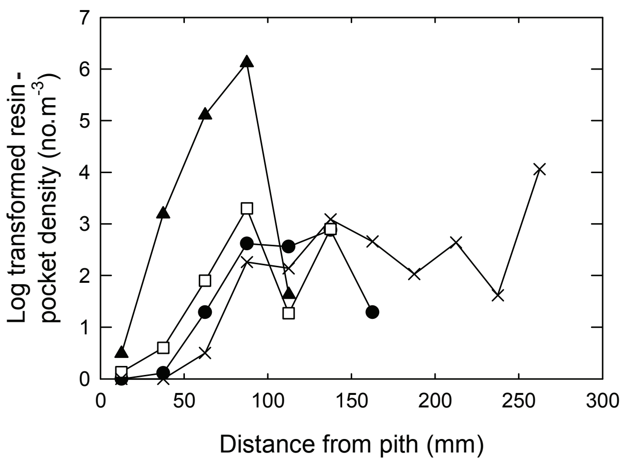

FIGURE 2: Variation in resin-pocket density with distance from pith at four sites: Ashley (circles); Balmoral (squares); McLeans Island (triangles); and Ohurakura (crosses).

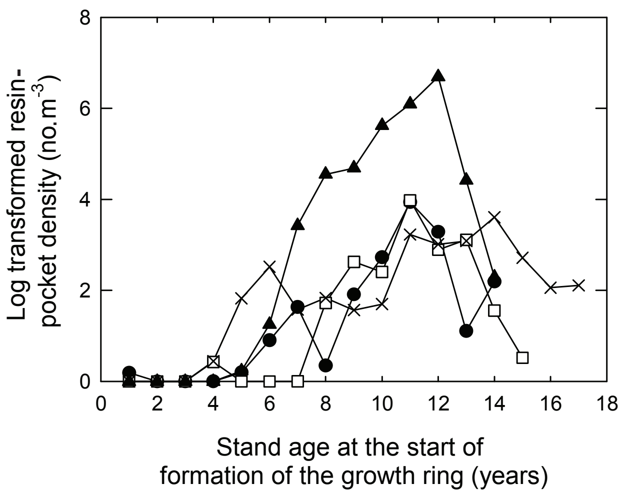

FIGURE 3: Variation in resin-pocket density with year of growth ring formation at four sites: Ashley (circles); Balmoral (squares); McLeans Island (triangles); and Ohurakura (crosses).

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TABLE 4: Analysis of variance describing the influence of circumferential azimuth on resin pocket frequency by site. Shown are *F*-values (7, 35 d.f.) followed by *P*-categories.

Site	Type 1	Type 2	Total
Ashley	0.81^{ns}	0.98^{ns}	2.01^{ns}
Balmoral	0.85^{ns}	2.12^{ns}	1.28^{ns}
McLeans Island	0.42^{ns}	2.04^{ns}	1.84^{ns}
Ohurakura	0.30^{ns}	1.37^{ns}	0.99^{ns}

ns = not significant.

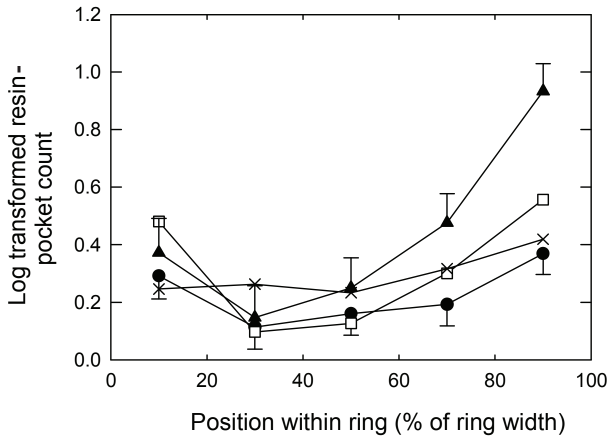

FIGURE 4: Mean resin-pocket count versus position within ring at four sites: Ashley (circles); Balmoral (squares); McLeans Island (triangles); and Ohurakura (crosses). Position within ring is expressed as a percentage of total ring width in five classes: 0-<20, 20-<40, 40-<60, 60-<80, 80-<100%. Error bars are standard errors (for clarity these are only shown for McLeans Island and Ashley).

Location of resin pockets within rings

In general, there was a tendency for resin pocket incidence to increase sharply in the final part of a ring and the start of the following ring, and to be lowest in the centre of the ring (Figure 4). There were clear differences between the four sites in the distribution of resin pockets within the ring. At the McLeans Island site, 67% of resin pockets were in the last 20% of the ring width. At both the Ashley and Balmoral sites, trees also showed a high proportion of resin pockets in the latter part of the growth ring with respectively 44% and 53% being in the last 20% of the growth ring. At these sites about 29% of resin pockets were located in the first 20% of the ring width. All these South Island sites had few resin pockets within the centre part of the growth ring. In contrast, at the North Island site (Ohurakura) the resin pockets were more evenly distributed across the ring although there was a slight increase in frequency towards the end of the ring. At all sites other than Ashley, these within-ring patterns were consistent across rings (Table 5). The patterns were also consistent between trees at all sites except at Ohurakura.

The consistent pronounced peaking of resin pocket incidence late in each growth ring in trees from both the McLeans Island and Balmoral sites, and the lack of such regular peaking at either the Ashley or Ohurakura site can be seen by plotting smoothed resin-pocket count data against radial location for trees at each site (Figure 5). The consistency in location of resin pockets between all six trees examined from McLeans Island is shown in plots of smoothed counts against radial location for each tree (Figure 6). In contrast, the six trees examined from Ohurakura showed no such consistency in resin-pocket location (Figure 7). Of trees from all the sites, those from McLeans Island showed the most regular within-ring pattern between both rings and trees (Table 5). Clear peaks were visible toward the end of each growth ring often carrying into the beginning of the following ring for all rings other than those near the pith, a pattern evident in all trees (Figure 6). Similarly, smoothed resin-pocket count data from trees at the Balmoral and Ashley sites (not shown) also showed consistency in their location between trees. For trees from the Balmoral site, the peak in resin-pocket count was consistently towards the end of each growth ring, but for trees from Ashley there was little consistency in the position of the peak in resin-pocket count within each growth ring.

TABLE 5: Analyses of variance testing for a consistent within-ring pattern of resin-pocket count between: (i) rings; and (ii) trees at each site. Shown are numerator and denominator degrees of freedom, *F*-values and *P*-categories.

Test	Num. DF	Den. DF	Ashley	Balmoral	McLeans Island	Ohurakura
(i)	4	52	2.26^{ns}	7.38^{**}	14.02^{***}	3.58^{*}
(ii)	4	20	5.32^{**}	14.72^{***}	25.95^{***}	1.26^{ns}

Asterisks ***, **, * represent significance at $P = 0.001$, 0.01 and 0.05 respectively; ns = non-significant at $P = 0.05$.

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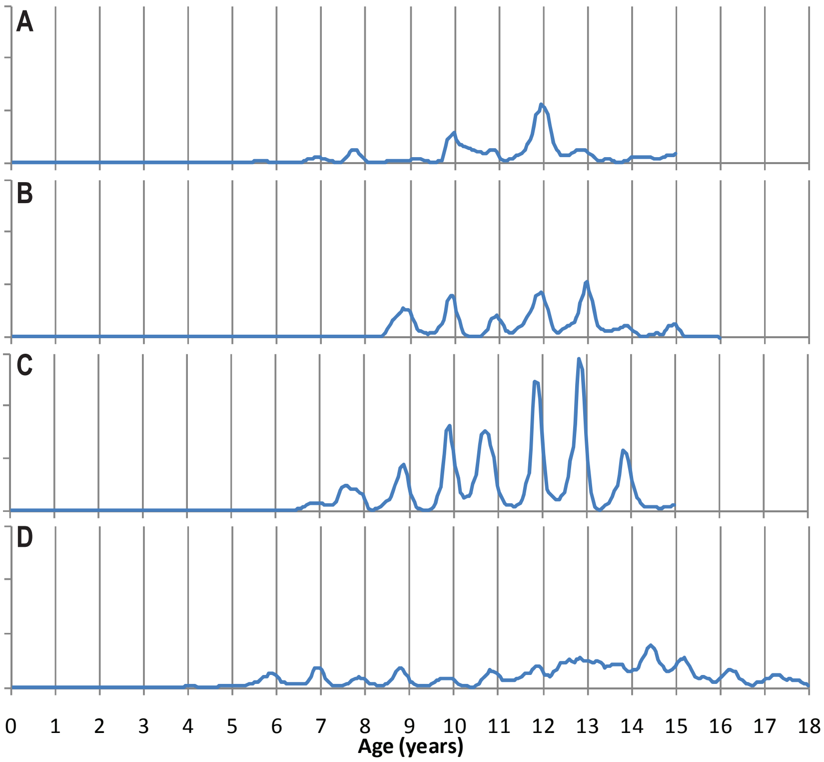

FIGURE 5: Smoothed resin-pocket count versus age at four sites: (A) Ashley; (B) Balmoral; (C) McLeans Island; and (D) Ohurakura.

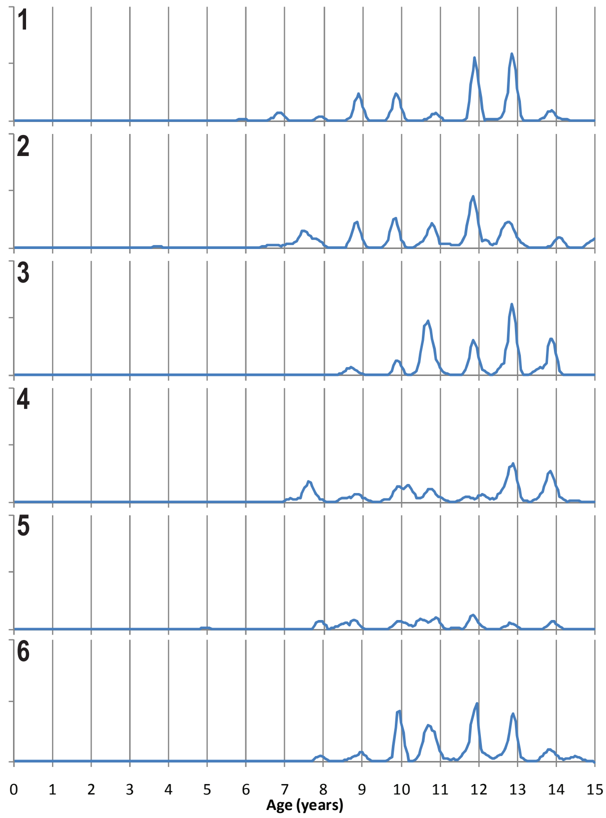

FIGURE 6: Smoothed resin-pocket count versus age for each of the six trees (labelled randomly 1 – 6) studied at the McLeans Island site.

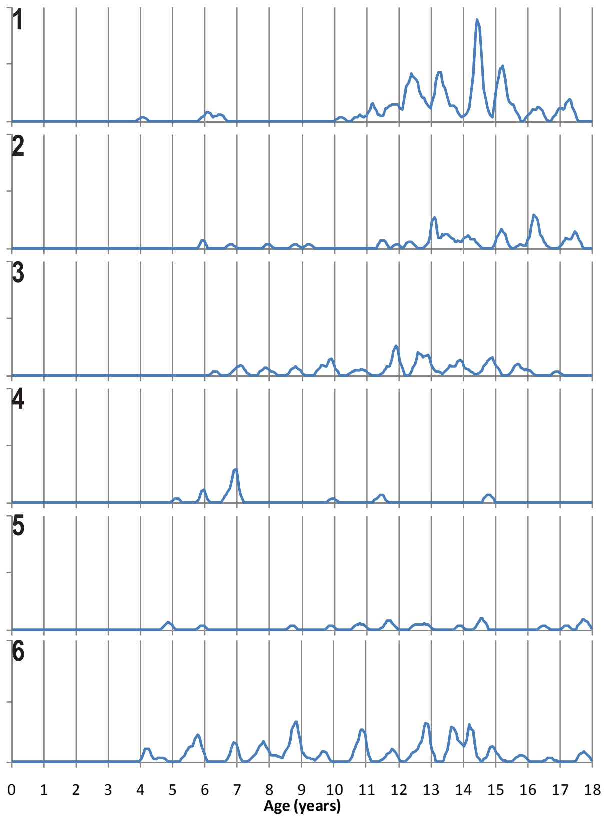

FIGURE 7: Smoothed resin-pocket count versus age for each of the six trees (labelled randomly 1 – 6) studied at the Ohurakura site.

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Analysis of type-1 and type-2 resin pockets

Overall, type-2 resin pockets were more than twice as common as type 1 (Table 2). Random coefficient regression models were used to test whether the percentage of type-2 resin pockets varied with radial distance or height but the results showed no consistency between sites. The percentage of type-2 pockets decreased significantly with radial distance for trees from Balmoral ($F_{1,5}$=19.84, P=0.0067) but no significant radial effect was evident at the other three sites. There was a significant trend for the percentage of type-2 resin pockets to decrease with height in trees from the McLeans Island site ($F_{1,5}$=9.71, P=0.026) but no such height trend occurred at the other sites.

The distribution of types-1 and 2 resin pockets was highly segregated within growth rings (Figure 8). The great majority of resin pockets located in the first half of the growth ring were type 1 with an equally great majority in the second half of the ring being type 2. The mean positions of resin pockets (types 1 and 2) occurred at respectively ca. the 30th and 80th percentile of the growth ring width. This strong segregation between resin-pocket types on the basis of position within the growth ring was clearly apparent at all sites (Table 6).

Distributional properties of resin-pocket dimensions

The distribution of resin pocket tangential widths was positively skewed and well approximated by a lognormal distribution. Mean pocket widths were 4.78 and 2.00 mm for types 1 and 2 respectively, and standard deviations were 2.65 and 2.04 mm. The 90th percentiles of the pocket-width distribution were 8.26 and 4.71 mm, respectively. Analysis of variance of log-transformed widths indicated that tangential widths of type-1 resin pockets were significantly greater on average than those of type-2 resin pockets (P<0.0001) but that there were no significant differences in widths between sites, nor any consistent within-tree variation with either height or ring.

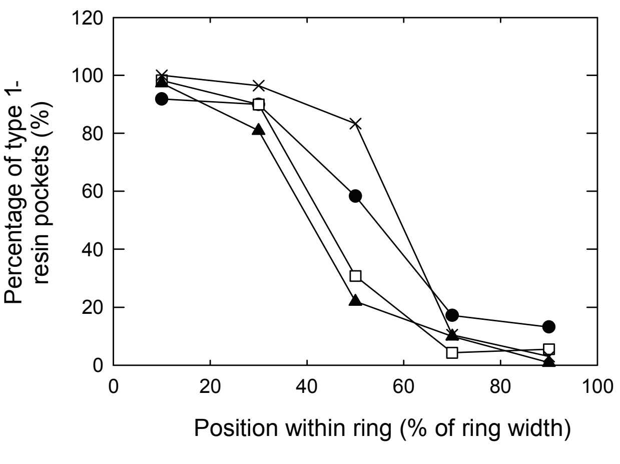

FIGURE 8: Mean type-1 resin-pocket count as a percentage of total resin-pocket count versus position within ring at four sites: Ashley (circles); Balmoral (squares); McLeans Island (triangles); and Ohurakura (crosses). Position within ring is expressed as a percentage of total ring width in five classes: 0-<20, 20-<40, 40-<60, 60-<80, 80-<100%.

TABLE 6: Mean within-ring position expressed as percentage of ring width for type-1 and type-2 resin pockets at each site.

Site	Type 1	Type 2
Ashley	27	78
Balmoral	20	82
McLeans Island	29	81
Ohurakura	31	78
All sites	28	80

The 50 mm spacing between disc surfaces was too wide to make it possible to accurately characterise the distribution of resin pocket length in the longitudinal dimension. There were 27 pairs of measured resin pockets (24 of type 1, and 3 of type 2) in adjacent discs that were separated horizontally by less than 5 mm and 4 sets of resin pockets in close proximity that extended over 3 discs. As measurements accounted for resin pocket occurrences that spanned more than one disc it is likely that these were adjacent but separate resin pockets. There is a small chance these could have been the same defect. However, given that there were 477 type-1 resin pockets and 1 164 type-2 resin pockets in the dataset, it is unlikely that double counted resin pockets spanning more than one disc had a large influence on the results. It is possible that resin pockets less than 50 mm that were entirely included within the disc, with no outside edge, were undetected.

Discussion

In this study, high resolution longitudinal sampling was combined with fine scale intra-ring disc mapping of resin pocket position to accurately characterise the position of resin pockets in three dimensions. Data obtained from these measurements highlighted the importance of radial variation on resin pocket density within stems, and the strong segregation between the positions of type-1 and type-2 resin pockets, within rings. Both of these systematic patterns were consistent between the four sites studied here.

Expressing resin pocket frequency on a volumetric basis represents a methodological advance. As both trees and rings vary in volume, expressing resin

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pocket frequency on these bases is not ideal and could potentially misrepresent actual spatial patterns. For instance, on a per tree basis resin pockets varied three-fold between the four sites, from 38 resin pockets tree^{-1} at Ashley to 116 resin pockets tree^{-1} at McLeans Island. However, as trees at McLeans Island had the smallest volume, conversion to a volumetric basis, amplified this site variation to eight-fold (1090 vs. 143 resin pockets m^{-3}).

Within the lower 5 m of the tree stem, variation in resin pocket frequency was most significant in the radial direction. The radial pattern described here is broadly consistent with previous research in *Pinus radiata* (Watt et al., 2009). All sites showed little or no resin pocket formation in the first few years of growth. The age at which substantial resin pocket formation began ranged from 4 years on the fastest growing site (Ohurakura) to 8 years on the slowest growing site (Balmoral). In wood formed beyond this age, average volumetric resin pocket density showed little obvious radial trend up to the mid-rotation measurement age, although there was considerable fluctuation between growth years. The insignificant radial x longitudinal interaction indicates radial variation in resin-pocket frequency to be very similar over the 5-m height range.

The lack of consistent variation in resin-pocket frequency in the longitudinal and circumferential direction is an important finding. The low and insignificant circumferential variation in resin pocket frequency is consistent with previous research on both *Pinus radiata* (Clifton, 1969) and *Picea abies* (Wernsdörfer et al., 2002). The low variation in resin pocket frequency between azimuths may suggest that directionally related environmental variables, such as wind, have a relatively small influence on resin pocket formation at these sites. Although there was no consistent trend in resin pocket density with tree height, it should be emphasised that this result only applies to the lower 5 m of the stem. There may be significant variation in resin pocket frequency above this height. For instance, Clifton (1969) found a 50% increase in the number of resin pockets in the second log of *Pinus radiata*, compared to the first log, on a dryland site at Ashley Forest, Canterbury.

A new discovery is that resin pocket morphology is strongly associated with location within the growth ring. The clear segregation between type-1 resin pockets in the first half of the ring and type 2 in the second half provides insight into the likely conditions under which the two types develop. Observations made during data collection suggest a possible continuum between type-1 and type-2 resin pockets, with the continuum related to the degree of exposure to some internally experienced stress, affecting cell development. A classic type-1 resin pocket probably results from the localised death of cells in the cambial zone, most likely in the region between cells that are transitioning between meristematic and enlarging stages. The continuity of the cambial surface is not disrupted and there is no deformation of the annual ring structure. Type-1 resin pockets have a very consistent morphology in early wood. This consistency is possibly related to timing, with the damage occurring in a vigorously growing cambium that is able to absorb or respond to damage. This would be likely to occur at a time of year when environmental stresses (such as soil water) are less likely to be severe. As the severity of the stress, or sensitivity to it, increases, the damage to cambial zone cells extends into the meristematic region, eventually resulting in the death of the cambial initials. At that point, some occlusion of adjacent cambial initials is required to seal the wound and the growth ring boundary becomes deformed, characteristic of a type-2 resin pocket.

The within-ring position of a resin pocket may provide clues to the environmental factors associated with its formation. The regular peaking of resin-pocket incidence in the latter part of growth rings from trees at both the McLeans Island and Balmoral sites (Figure 5) is suggestive of a regular environmental driver operating late in the growing season each year. As these two sites were the driest of those studied (Table 1), the most obvious environmental driver for these sites is water stress, which would be expected to peak late in the growing season. In contrast, the overall more random distribution of resin pockets within rings for trees from Ohurakura is suggestive of a more irregular causal environmental factor, such as wind. Indeed, Ohurakura is the windiest of the four site studied. Ohurakura is also the wettest site (Table 1) so regular peaking of resin pocket incidence in the latter part of the growth ring from trees at this site would not be expected. However, there does appear to be some regularity of peaking towards the end of inner growth rings at this site (Figure 5). The Ashley site has more rainfall and a higher average wind speed than either the Balmoral or McLeans Island sites but still less than at Ohurakura. Trees from Ashley also showed little within-ring regularity in resin pocket occurrence.

In conclusion, this study clearly showed that resin-pocket density varied markedly in the radial but not the longitudinal or circumferential dimensions. At all four sites, variation in the radial dimension was characterised by an absence of resin pockets in the inner rings and fluctuating densities in the outer rings. The age at which substantial resin pocket formation began ranged from 4 years on the fastest growing site to 8 years on the slowest growing site. Within rings, type-1 and type-2 resin pockets showed clear segregation and were respectively confined to the first and second half of the growth ring. On the driest sites, resin pocket frequency consistently peaked in the latter part of the growth ring but the distribution was more irregular and varied between trees at the windiest and wettest site.

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