Growth-layer-level microfibril angle, lignin and carbohydrate variation with radial direction, earlywood and latewood, and compressionwood content, for bent and straight ramets of a radiata pine clone

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Abstract
The Bent and nominally straight trees were ramets from the same clone. Discs were taken from the second growth unit from the ground and contained 15 or 16 identifiable growth layers. Bark-to-bark strips were taken through the pith and the longest radial dimension of the compressionwood side of the discs. Separate earlywood (EW) and latewood (LW) samples were obtained for most growth layers giving some 95 samples in total. Data analyses took account of the chemical constituent and microfibril angle (and other SilviScan generated fibre properties) variation with radial direction, growth layer number, compressionwood severity, and earlywood and latewood origin.

Notable findings include:
- Lignin and carbohydrate EW and LW differences are large in moderate and small in severe compressionwood.
- MFA increases with increasing compressionwood content but with similar EW/LW differences in moderate and severe compressionwood.
- EW and LW mannan contents are consistently different one from another in both oppositewood and compressionwood.
- Galactose, lignin, glucose and mannose are linearly and strongly correlated one with another, whereas their relationships with xylose and arabinose are non-linear.

Introduction
A research program underway at Scion has the objective to model gene expression in the form of tree morphology, growth-layer-level wood and fibre microstructure and chemistry, and macroscopic wood performance (*1*). To this end, growth-layer-level radial, circumferential and height variation in fibre length, a selected wood colour parameter (L*) and of microfibril angle (MFA), modulus of elasticity (MOE), density, coarseness, and fibre wall thickness and perimeter, have been determined for a nominally straight (Control-tree) and a severely bent (Bent-tree) ramet of the same radiata pine genotype grown on the same site (*2-5*). Growth-layer-level patterns of change with stem height and radial direction were strongly matched (particularly for the Bent-tree) for fibre length, L*, MFA and MOE; with increasing compression wood contents giving progressively shorter fibres, lower L* (darker) and MOE, and higher MFA values respectively. Correlations among the property residuals of length, MFA, MOE, and colour L* were moderate-to-strong for both the Control- and Bent-tree. In contrast, the property residual correlations between the compression wood indicator of colour L* and density, wall thickness and coarseness, were weak for the Control-tree and moderate to strong for the Bent-tree. Hence, fibre length, MFA and MOE growth-layer-level patterns of change with radial-direction and height-position, vary over the compression wood severity range (absent-to-severe). In contrast, density, wall thickness and coarseness are considered poor indicators of mild compression wood.

The presence and anatomical properties of compressionwood, including, anatomy, lignin distribution, and SilviScan generated MFA, density, radial and tangential lumen diameter and cell wall thickness have also been reported for the control and bent trees (*6*).

Interrelationships among lignin and carbohydrate contents, and the SilviScan generated properties of MFA, density, coarseness and fibre perimeter are examined in this conference paper. Chemical constituent and property patterns of change with radial direction, growth-layer number from bark, compressionwood severity, and EW and LW origin are considered. A more detailed account of lignin and carbohydrate contents and distributions in the Control and Bent trees is presented elsewhere (*7*).

Experimental
Sample trees, discs and radial strips
The two 16-year-old trees were from clone 84 in the 266 series, planted 1985 (8 m apart) in the Long-Mile area of the Scion, Rotorua campus. One tree (Tree 113) was bent to the ground at an early age and was highly swept as a result of corrective growth (Bent-tree). The second tree (Tree 112) was of a similar diameter and considered to be nominally straight despite some deviation from straightness (Control-tree). PhotoMARVL stem profiles and sample disc positions in the lower 15 to 20 m of the standing trees is presented elsewhere (*2,3*).

Two adjacent discs were cut from each tree at right angles to stem axis, the uppermost disc being for assessment with SilviScan and the lower disc for chemical composition analyses. For this study they were taken from the second internode from the ground and from the internodal wood located between whorls of branches (*2,3*). A growth unit is defined as a branch cluster and the clear section of stem below that cluster. One bark-to-pith-to-bark direction was assessed for the Control-tree (Northeast and Southwest (NEast and SWest)), and Bent-tree (East and West). These were selected based on standing stem form in space, and visual compression wood within the disc (*2,3*). Visually there was compressionwood throughout rings 13 and 14 from the West strip and rings 1-12 from the East strip of the Bent–tree, suggesting that the direction of lean changed at an early age. There appeared to be compressionwood in some of the latewood samples from the NEast strip from the control tree.

Bark-to-bark strips for chemical assessment were cut from the lower disc from each tree. The two strips, ca. 25 mm in the tangential direction and 40 mm in the longitudinal direction were cut from the air-dried disc immediately below the disc used to collect the SilviScan sample; so as to be centred about the same bark-pith-bark line analysed by SilviScan.

EW, LW and WR sample preparation

The junction between the earlywood and latewood within each growth ring was taken as the point where the SilviScan density profile starts to climb steeply (*8*). This density-assigned EW/LW boundary generally corresponded to that seen visually, except for some of the inner rings where LW bands were wider than observed. Where there was insufficient material, whole rings or multiple rings were taken.

- For each sample, the positions for cutting were marked (EW/LW or between-ring boundaries) to the nearest 0.5 mm along the line corresponding to the SilviScan sample. These positions were then marked to the edges of the strips using the visual latewood bands and then through to the bottom side of the sample.
- The strips were carefully cut up using a fine bandsaw, so that the cut was centred about the line dividing the samples. The resulting wood blocks were then ground in a small Wiley mill to pass a 2 mm screen and conditioned at 23°C and 50% rh and extracted with dichloromethane.
- The extracted samples were reground in the same Wiley mill to pass an 0.25 mm discharge screen.

Chemical analyses

Ground samples were extracted with dichloromethane in a Soxhlet apparatus using a boiling time of 1 hour and a rinsing time of 1 hour.

Klason and acid-soluble lignin were determined using Tappi Standards T222 om-88 and UM 250 respectively. Klason and acid soluble lignin values were combined to give the values used in this paper. Carbohydrates in the filtrates from Klason lignin determinations were analysed by ion chromatography (*9*). All carbohydrate results are expressed based on anhydrosugar units and all carbohydrate and lignin results are expressed as grams/ 100 grams oven-dried extracted wood.

SilviScan wood density and tracheid properties

Transverse wood tracheid dimensions and microfibril angle were determined on SilviScan using image analysis, and X-ray densitometry and diffractometry (*8,10*). A single diameter was cut from each disc, then solvent-exchanged in ethanol and dried. Thin pith-to-bark strips (2mm wide x 7mm high) were cut from each dried diameter. Wood density, and tracheid radial and tangential diameters were measured at 50 µm intervals along the strip. Tracheid coarseness, outer perimeter (from radial and tangential diameters) and average wall thickness were generated from these primary measures. All SilviScan samples were conditioned to 20°C and 40% relative humidity.

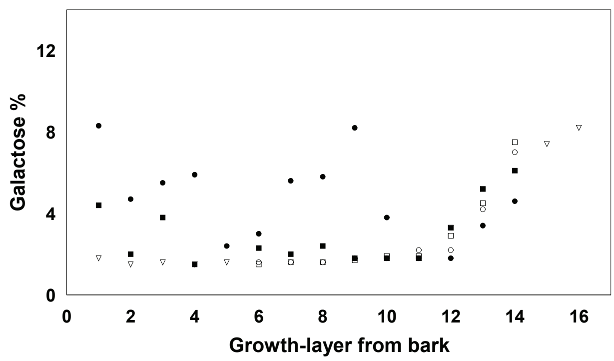
RESULTS

Galactose, lignin, glucose and mannose

The Control- and Bent-trees are ramets from the same clone and, therefore, had identical genetic drivers. Furthermore, the bark-to-bark strips were taken through the pith and the longest radial dimension of the compressionwood side of each disc. Each disc was taken from the second growth unit from the ground and contained 15 or 16 identifiable growth layers (rings). Hence, this analysis takes account of the chemical constituent growth-layer level variation with radial direction, compressionwood severity, and EW and LW origin.

Using galactose as the example against which other constituents are compared, the radial strips from the Control- and Bent-tree can be separated into two roughly similar growth-layer sets numbered from the bark, rings 1-11 and 12-15 (Bent-tree), and 1-10 and 11-16 (Control-tree) (Figure 1). Separation of the EW and LW compressionwood (NE strip) of the Control- but not the Bent-tree is noteworthy. Also noteworthy are the marked differences between the compressionwood and oppositewood radial strips from both trees.

Control-tree



Bent-tree

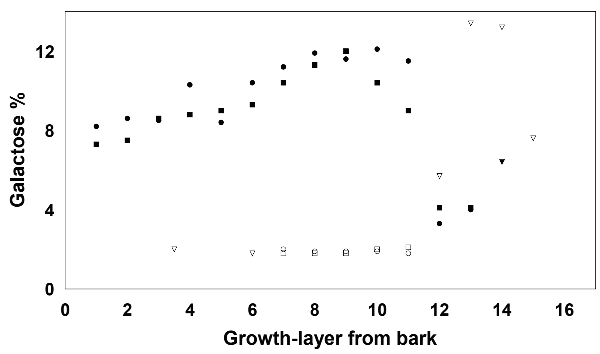


Figure 1: Galactose % versus growth-layer numbered from bark for the Control- and Bent-tree. Filled symbols refer to LW, EW and WR (whole-ring) values from the compressionwood side of a disc, while unfilled symbols refer to corresponding values from the oppositewood of a disc: ■ EW ● LW ▼WR NEast or East, □ EW ○ LW ▽ WR SWest or West.

Carbohydrate and lignin content statistical differences with radial direction for the Control-tree (ring-sets 6-10 and 11-14) and Bent-tree (ring-set 7-11), are presented in Table 1. Each of these three data sets are complete (balanced with no missing data). For the carbohydrate and lignin content statistical differences with EW and LW origin, on the other hand, an increased number of growth layers was able to be included in the analyses for both the Control- and Bent-tree NEast and East strips respectively (Table 2). Unfortunately, the innermost growth layers of the Bent-tree oppositewood (rings 12-15) were highly compressed and unable to be separated into their EW and LW components and hence, inappropriate for inclusion in the analyses of Tables 1 and 2. For similar reasons, the oppositewood data of growth layers 1-5 (Control-tree) and 1-6 (Bent-tree) were also excluded from the analyses of Tables 1 and 2.

Table 1: Chemical constituent variation through comparing radial direction for each tree / ring subset / wood-type.

Tree and ring subset	Woodtype	Response	East mean	West mean	p-value*
Bent-tree Rings07to11	EW	Arabanose	1.09	1.55	.0006
		Galactose	10.6	1.9	.0001
		Glucose	32.4	45.9	.0006
		Xylose	4.28	5.34	.0027
		Mannose	6.45	10.71	.0008
		Lignin	39.6	27.8	.0005
	LW	Arabanose	1.18	1.58	.0012
		Galactose	11.7	1.9	.0001
		Glucose	31.6	47.5	.0001
		Xylose	4.38	5.07	.04
		Mannose	6.83	12.24	.0001
		Lignin	38.0	26.2	.0001
			NEast mean	SWest mean	
Control-tree Rings06to10	EW	Arabanose	1.34	1.42	.35
		Galactose	2.1	1.7	.09
		Glucose	45.4	45.9	.18
		Xylose	4.79	4.99	.19
		Mannose	11.1	10.8	.33
		Lignin	29.3	28.4	.03
	LW	Arabanose	1.18	1.33	.03
		Galactose	5.3	1.7	0.016
		Glucose	42.8	47.3	.05
		Xylose	4.28	4.85	.017
		Mannose	9.7	12.2	.020
		Lignin	31.5	27.2	.04
			NEast mean	SWest mean	
Control-tree Rings11to14	EW	Arabanose	1.69	1.61	.07
		Galactose	4.1	4.2	.85
		Glucose	43.2	42.1	.11
		Xylose	5.68	5.50	.41
		Mannose	9.8	9.6	.11
		Lignin	28.7	30.7	.01
	LW	Arabanose	1.56	1.61	.47
		Galactose	2.87	3.90	.12
		Glucose	44.5	42.2	.003
		Xylose	5.44	5.08	.12
		Mannose	11.1	11.0	.58
		Lignin	27.9	29.7	.002

* General linear model with direction and ring number as classification variables.

An interpretation of the galactose content trends for all growth layers covered in Figure 1 follows, with levels of statistical significance being based on a limited number of growth layers as specified in Tables 1 and 2 as discussed above:

1. Control-tree (rings 1-10): NEast LW galactose contents are greater than corresponding EW contents ($P<0.001$ (Table 2)), and greater than those of the closely matched SWest LW, EW and whole-ring values.
2. Control-tree (rings 11-16): NEast and SWest LW, EW and WR galactose contents increase with increasing ring number from bark. Furthermore, galactose values for the three wood-types are generally similar one to another in this juvenile wood zone. NEast EW galactose contents are, however, greater than corresponding LW values ($P=0.05$ (Table 2)). Note that the EW compared to LW galactose difference is reversed for the inner rings of the control tree.
3. Bent-tree (rings 1-11): Galactose contents are extremely high for the compressionwood (East-strip) and low for the oppositewood (West-strip) ($P=0.0001$ (rings 7-11, Table 1)). East-strip galactose contents are higher for LW than EW but differences are non-significant, as are those for the closely matched West EW, LW and WR values ($P>0.05$ (Table 2)).
4. Bent-tree (rings 12-15): Rings 13 and 14 from the West strip contained compressionwood and have higher values of galatose than the corresponding samples from the East strip.

Table 2: Chemical constituent variation through comparing wood-types for each tree / ring subset / direction.

Tree and ring subset	Direction	Response	EW mean	LW mean	p-value*
Bent tree Rings01to10	East	Arabanose	1.01	1.09	.02
		Galactose	9.4	10.1	.02
		Glucose	34.1	34.4	.40
		Xylose	3.95	4.13	.007
		Mannose	6.80	7.65	.0008
		Lignin	38.9	36.7	.0001
Bent tree Rings07to11	West	Arabanose	1.55	1.58	.62
		Galactose	1.88	1.91	.76
		Glucose	45.9	47.5	.02
		Xylose	5.35	5.07	.03
		Mannose	10.7	12.2	.005
		Lignin	27.8	26.2	.002
Control-tree Rings01to10	NEast	Arabanose	1.26	1.15	.06
		Galactose	2.13	5.33	.0004
		Glucose	45.9	43.0	.02
		Xylose	4.62	4.30	.02
		Mannose	11.2	9.8	.01
		Lignin	29.3	31.0	.05
Control-tree Rings06to10	SWest	Arabanose	1.42	1.33	.15
		Galactose	1.68	1.68	.85
		Glucose	45.9	47.3	.04
		Xylose	4.99	4.83	.11
		Mannose	10.8	12.2	.002
		Lignin	28.4	27.2	.07
Control-tree Rings11to14	NEast	Arabanose	1.69	1.56	.07
		Galactose	4.08	2.87	.05
		Glucose	43.1	44.5	.02
		Xylose	5.68	5.44	.16
		Mannose	9.82	11.05	.002
		Lignin	28.7	27.9	.003
	SWest	Arabanose	1.61	1.61	.96
		Galactose	4.18	3.90	.27
		Glucose	42.1	42.2	.66
		Xylose	5.50	5.08	.006
		Mannose	9.55	11.02	.002
		Lignin	30.7	29.7	.12

* General linear model with wood-type and ring number as classification variables.

Notable features are the high LW galactose contents where there was visual compressionwood. There were large differences between LW and EW for the Control tree where compressionwood was only visible in the latewood bands. The differences were smaller for the Bent tree where compressionwood was visible throughout the ring. This suggests that LW galactose contents increase before EW as the wood within a growth-layer responds to factors which initiate compressionwood formation. Furthermore, as compressionwood levels increase from moderate to severe, LW and EW galactose content differences progressively decrease.

Control- and Bent-tree, LW/EW and compressionwood/oppositewood patterns of change for lignin content are generally similar to those for galactose content (Figure 1). One notable difference is the somewhat higher lignin content of the EW relative to LW for the Bent-tree when compared to that of galactose; highly significant for both East (P=0.0001) and West (P=0.002) (Table 2).

Glucose and mannose contents show similar patterns of change except that these decrease rather than increase with increasing compressionwood severity (*7*). A notable feature of the Control-tree (NEast-strip) is that LW is higher than EW for galactose and lignin, and lower for glucose and mannose. These differences are highly significant for galactose (P<0.001) and significant for lignin, glucose and mannose (P<0.05) (Table 2). Corresponding LW/EW differences for the Bent-tree (East-strip) are highly significant for mannose and lignin, significant for galactose, and non-significant for glucose (Table 2).

Further comment is warranted concerning EW and LW mannose content. EW and LW mannose contents are consistently different one from another for all radial directions for both the Control- and Bent-tree (Table 2). Furthermore, LW contents are consistently higher than EW contents for all radial strips except for those in rings 1-10 of the Control-tree NEast strip of moderate compressionwood severity (*2*) where EW > LW (*7*). For the Control-tree these differences are highly significant (P≤0.01). LW > EW for the SWest strip and rings 11-14 of the NEast strip. In contrast, EW > LW for the compressionwood portion of the NEast strip (rings 1-10) with the trend reversing at ring 10. For the Bent-tree, on the other hand, LW > EW for all radial directions and all rings except ring 11 of the East-strip. Differences are highly significant (P≤0.005). The moderate level of compressionwood in the NEast strip of the Control-tree shows EW > LW (P = 0.01), whereas the severe compressionwood of the East strip of the Bent-tree has LW consistently greater than EW (P=0.0008).

Xylose and arabinose

Growth-layer-level patterns of change for the Control- and Bent-tree, with radial direction, ring number from bark and EW and LW origin, are somewhat different for xylose (and arabinose) (Figure 2) compared to the other constituents (Figure 1):

- Xylose (and arabinose) content ranges are determined by minimum compressionwood (NEast and East strips) and maximum oppositewood (SWest and West strips) values (Figure 2), whereas those of galactose, lignin, glucose and mannose are specified by maximum and minimum oppositewood values only (Figure 1). Furthermore, Bent-tree galactose and lignin contents are markedly higher, and glucose and mannose contents markedly lower, than those in the Control-tree (rings 1-10 only) (*7*).
- For the Control- and Bent-tree compressionwood NEast and East strips (rings 1-10): LW xylose (and arabinose) contents are significantly lower than EW contents for the Control-tree, whereas the converse holds for the Bent-tree with its severe compressionwood (Figure 2). For xylose these reversed EW/LW differences are highly significant for the bent-tree (P=0.007), and significant for the Control-tree (P=0.02) (Table 2). Corresponding levels of significance for arabinose are somewhat lower at P=0.02 & 0.06 respectively. Furthermore, LW, EW and WR oppositewood (SWest and West strips) arabinose and xylose contents are similar, but higher than those in the LW and EW of the corresponding NEast and East strips. For the innermost growth layers (rings 11-16), xylose (and arabinose) contents are generally similar for the EW, LW and WR wood-types, and increase with increasing ring number from bark, in agreement with expected radial distributions and juvenile wood contents (*11,13,14*).

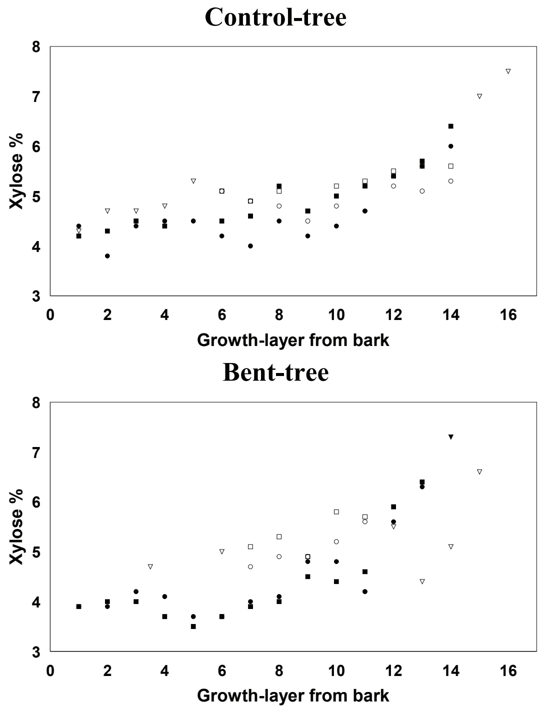


Figure 2: Xylose % versus growth-layer numbered from bark for the Control- and Bent-tree. Filled symbols refer to LW, EW and WR values from the compressionwood side of a disc, while unfilled symbols refer to corresponding values from the oppositewood of a disc: ■ EW ● LW ▼WR NEast or East, □ EW ○ LW ▽ WR SWest or West.

Chemical constituent correlation matrices

Correlations are strong among galactose, glucose, mannose and lignin for the EW, LW and WR samples from the opposite wood and compressionwood sides of the bark-to-bark strips from both the Control- and Bent-trees (Table 3). Correlation coefficients are high (|r |= >0.93) with glucose and mannose being negatively correlated with galactose and lignin content. Xylose and arabinose, on the other hand, are strongly and positively correlated one with another, but poorly correlated with galactose, lignin, glucose and mannose when all data are combined (Table 3). Such correlations are, however, strong within the oppositewood SWest data of the Control-tree, and within the oppositewood West data of the Bent-tree when rings 13 and 14, with their severe compressionwood are excluded (Figures 1, 2) (*7*).

Galactose, lignin, glucose and mannose are strongly correlated one to another (Table 3), with comparable bark-to-pith patterns of change (Figure 1) (*7*). These correlations hold for all data from the Control- and Bent-tree despite wide growth-layer level variation with radial direction, compressionwood severity and EW and LW origin, as indicated by the galactose/glucose relationship (Figure 3). In contrast, xylose and arabinose relationships with the other constituents are non-linear, as indicated for glucose and xylose in Figure 4, in agreement with their weak correlations (Table 3).

Table 3: Chemical constituent correlation coefficients for all Control-tree and Bent-tree earlywood, latewood and whole-growth-layer samples (N = 95).

	Arabinose	**Galactose**	**Glucose**	**Xylose**	**Mannose**	**Lignin**
Arabinose	1.00	-0.28	0.17	0.91	0.26	-0.42
Galactose	-0.28	1.00	-0.97	-0.28	-0.93	0.93
Glucose	0.17	-0.97	1.00	0.17	0.94	-0.94
Xylose	0.91	-0.28	0.17	1.00	0.21	-0.40
Mannose	0.26	-0.93	0.94	0.21	1.00	-0.94
Lignin	-0.42	0.93	-0.94	-0.40	-0.94	1.00

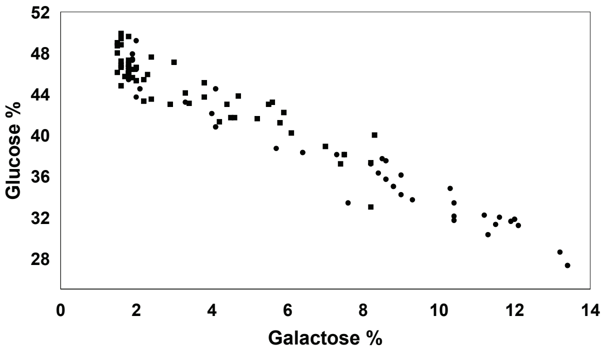


Figure 3: Glucose versus galactose percent for the Control-tree (■) and Bent-tree (●), and all wood types (LW, EW and WR), growth layers and radial directions.

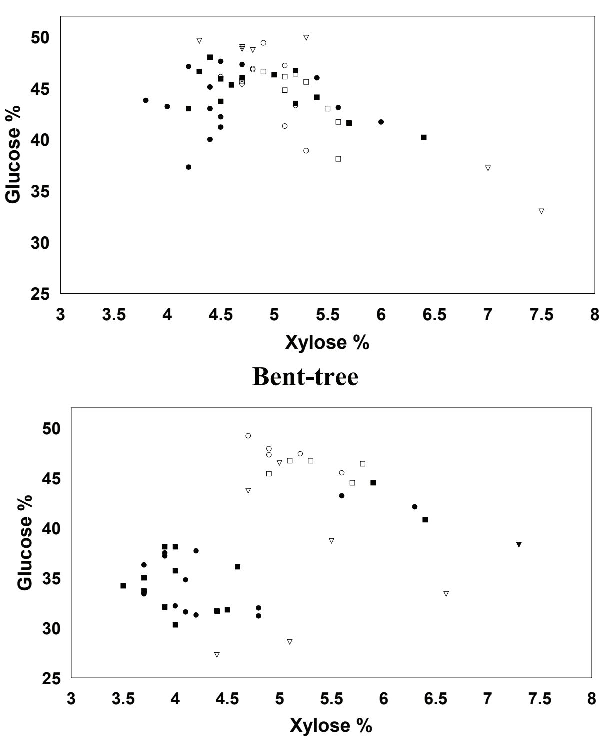


Figure 4: Glucose versus xylose percent for the Control- and Bent-tree. Note that the Control- and Bent-tree data envelopes are closely matched one to another. Filled symbols refer to LW, EW and WR values from the compressionwood side of a disc, while unfilled symbols refer to corresponding values from the oppositewood of a disc: ■ EW ● LW ▼WR NEast or East, □ EW ○ LW ▽ WR SWest or West.

Cellulose, galactan, galactoglucumannan (GGM), and arabinoxylan (xylan)

Cellulose, galactan, GGM, and xylan content patterns of change and their statistical significance are very similar to those of the anhydro sugar units alone. In fact, GGM and xylan patterns of change and levels of significance are identical to those presented since the same numbers of glucose and galactose units per mannose unit, and arabinose units per xylose units, were used in their calculation for all radial directions, ring numbers from bark, and EW and LW origin (*15,16*). Galactan patterns of change are, however, noteworthy since pure galactan occurs within rings 1-10 of the NEast and East strips from the Control- and Bent-trees, and is absent from corresponding oppositewood, indicating a strong correlation with compressionwood severity (*7*).

Interrelationships among chemical constituents and selected wood /fibre properties

The SilviScan generated properties of MFA, density, coarseness and perimeter are considered here together with their correlation with lignin, cellulose, galactan, GGM and xylan contents (Table 4). Correlations are moderate to weak compared to the strong correlations among lignin, glucose, galactose, and mannose, and between xylose and arabinose (Table 3) (*7*).

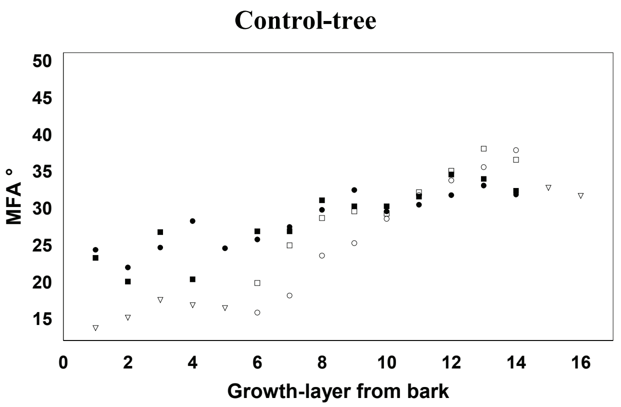
Table 4: Chemical constituent and selected SilviScan generated wood property correlation coefficients for all Control-tree and Bent-tree earlywood, latewood and whole-growth-layer samples (N = 95).

	MFA	Density	Coarseness	Perimeter
Lignin	0.69	0.55	0.46	-0.05
Cellulose	-0.81	-0.54	-0.33	0.24
Galactan	0.73	0.64	0.49	-0.14
GGM	-0.73	-0.45	-0.33	0.13
Xylan	0.09	-0.41	-0.70	-0.56

Wood/fibre patterns of change with growth-layer number from bark, radial direction, compressionwood severity, and EW and LW origin (Figure 5, Table 5) differ from those of the chemical constituents (Figures 1 and 2).

- MFA increases with increasing compressionwood severity for the NEast and East strips (rings 1-10) but with EW and LW differences essentially unchanged (Figure 5). Oppositewood MFA values are generally lower than those in the corresponding compressionwood NEast and East strips, but also increase with increasing compressionwood severity. Note the very high MFA values for rings 13 and 14 for the Bent-tree (Figure 5) and their corresponding high galactose contents (Figure 1).

- Wood density and fibre coarseness are consistently very much higher, and fibre perimeter lower, for LW than EW (Table 5). These EW/LW differences are generally maintained for the two data sets and levels of compressionwood, except for perimeter where differences can be small or absent for the moderate compressionwood (NEast strip) data-set.



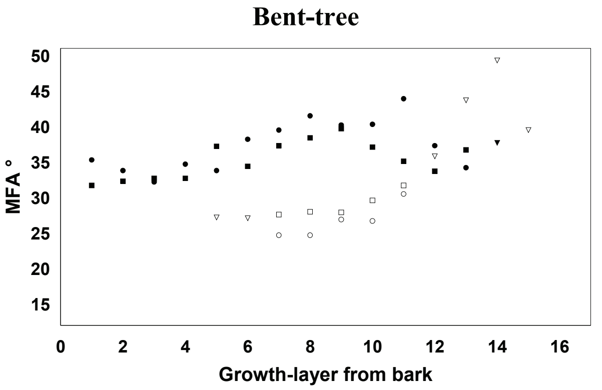


Figure 5: MFA versus growth-layer numbered from bark for the Control- and Bent-tree. Filled symbols refer to LW, EW and WR (whole-ring) values from the compressionwood side of a disc, while unfilled symbols refer to corresponding values from the oppositewood of a disc: ■ EW ● LW ▼WR NEast or East, □ EW ○ LW ▽ WR SWest or West.

DISCUSSION

Chemical constituent patterns of change for the bark-to-bark strips from the Control- and Bent-trees are directly comparable since they are both from the second internode from the ground, and from ramets of the same clone. This has allowed the chemical constituent variation of oppositewood, moderate and severe compressionwood (*2*), and to a lesser extent juvenilewood, to be compared at both the growth-layer and EW and LW levels.

Chemical constituent variation with growth-layer and compressionwood content

The underlying chemical constituent variation with distance from bark is as expected for the oppositewood West and SWest strips with their relatively high juvenilewood content at rings 12-16 (*11-14*). Glucose and mannose contents decrease, while lignin, xylose and arabinose contents increase with increasing growth-layer number from the bark, particularly within the juvenile wood zone (Figures 1, 2).

Oppositewood West (Bent-tree) and SWest (Control-tree) mean-composition values are very similar (Table 1), indicating that oppositewood is chemically unchanged by compressionwood formation elsewhere within a growth-layer, despite gross changes in disc cross-section shape and oppositewood microstructure (*4,6*).

Expected normalwood chemical constituent distributions for the NEast and East strips are obscured because of changes brought about by the respective formation of moderate and severe compressionwood in rings 1-11(Figures 1, 2). Consistent with earlier findings (*7,17,18*), the contents of lignin and galactose increase, while glucose, mannose, xylose and arabinose decrease as levels of compressionwood severity increase (Figures 1, 2, Table 1).

Chemical constituent variation with EW and LW origin and compressionwood content

The very different EW and LW compositions in moderate compressionwood, and their similar compositions in severe compressionwood, are the most noteworthy findings of this study (Figures 1, 2, and Table 2). For moderate levels of compressionwood, LW lignin and galactose contents are higher, and glucose, mannose and xylose contents are lower, than corresponding EW contents. For severe levels of compressionwood, on the other hand, LW and EW content differences are relatively small, but with EW contents now highest for lignin, and lowest for glucose, mannose and xylose. The small compositional differences between EW and LW in severe compression wood, as well as the observed differences between EW and LW in the oppositewood are in agreement with other studies (*17*). It is found that compression wood develops more readily at the middle or end than at the beginning of the growing season (*19*), consistent with our findings that in mild compressionwood, the LW has higher lignin and galactose, but lower glucose and mannose contents than EW.

Chemical constituent interrelationships

Comment is required concerning the strong correlation among lignin, galactose, glucose and mannose, and their weak correlation with xylose and arabinose (Table 3, Figures 3, 4). There are clear xylose (and arabinose) content differences between the outer and inner growth-layer sets of the Control- and Bent-tree (Figure 2). For this discussion, the outer growth layer set will consist of rings 1-11 and the inner set of rings 12-16. Arabinose contents are >1.4 % and Xylose contents >5.3 % for rings 12-16, and consistently less than these values for rings 1-11 for the compressionwood strips (NEast and East). Corresponding numbers for the oppositewood SWest and West strips are similar (>1.1 and 5.0% respectively (with one xylose datum exception), for rings 12-16 and similar or slightly lower for rings 1-11. Thus, these arabinose/xylose data naturally separate into two groups accounting for the non-linear relationships between arabinose and xylose, and glucose, galactose, lignin and mannose (Figures 3, 4). One group consists of all oppositewood data plus those from rings 12-16 of the NEast and East strips, while the other consists of data from rings 1-11 of the compressionwood Nstrips.

Note: The innermost growth layers of radiata pine trees can have very different physical properties near the base of a stem (juvenile wood) compared to those in the middle and top stem height positions (*11,12*). In contrast chemical constituent contents vary little with stem height position (*13,14*). Hence, the juvenile wood chemical compositions for the two discs taken from near the base of two ramets of the same clone (rings 12-16), can be expected to be similar throughout the height of each stem.

The relationships of Figures 3 and 4 use glucose as the independent variable. Similar relationships are obtained when glucose is replaced by mannose, while replacement by lignin or galactose gives similar but inverted relationships.

Table 5: Wood/fibre property variation through comparing woodtypes for each tree / ring subset / direction.

Tree and ring subset	Direction	Response	EW Mean	LW Mean	p-value*
Bent- tree	East	MFA	35.3	37.0	0.05
Rings01to10		Density	482	535	0.0003
		Coarseness	542	631	<0.0001
		Perimeter	122	118	0.01
Bent- tree	West	MFA	28.9	26.7	0.01
Rings07to11		Density	406	545	<0.0001
		Coarseness	340	415	0.003
		Perimeter	116	111	0.03
Control-tree	NEast	MFA	25.9	26.8	0.37
Rings01to10		Density	394	533	<0.0001
		Coarseness	416	557	<0.0001
		Perimeter	125	125	0.92
Control-tree	Swest	MFA	26.4	22.2	0.01
Rings06to10		Density	388	513	<0.0001
		Coarseness	383	441	0.02
		Perimeter	127	119	0.03
Control-tree	Neast	MFA	33.0	31.7	0.08
Rings11to14		Density	392	479	0.0002
		Coarseness	344	395	0.02
		Perimeter	120	117	0.09
	Swest	MFA	35.4	34.7	0.41
		Density	384	475	0.001
		Coarseness	337	381	0.006
		Perimeter	120	115	0.0105

* General linear model with wood type and ring number as classification variables.

Wood/fibre property and chemical composition interrelationships

Lignin, cellulose, galactan and GGM content correlation with MFA are moderate, and with density, coarseness and perimeter are weak (Table 4), compared to those among these chemical constituents alone (Table 3). Patterns of change with growth-layer from bark for MFA generally match those for galactose (and galactan) except that EW/LW MFA differences are similar for the Control and Bent trees (Figures 1-5) (*7*). This suggests that had the analyses been made at the growth-layer rather than the EW/LW level, MFA would be strongly correlated with lignin, cellulose, galactan and GGM.

CONCLUSIONS

1. With increasing growth layer number from the bark, lignin, galactose, xylose and arabinose contents increase and glucose and mannose contents decrease, particularly within the innermost growth layers, as expected.
2. With increasing compressionwood severity, lignin and galactose contents increase, glucose and mannose contents decrease. Xylose and arabinose contents also increase but differences between compressionwood and oppositewood are small.
3. Galactose, lignin, glucose and mannose are strongly correlated one with another. Relationships between xylose or arabinose and the other constituents are non-linear with maxima occurring with galactose and lignin, and minima occurring with glucose and mannose, as the dependent variable. Xylose and arabinose content values below the galactose and lignin maxima, or the glucose and mannose minima, indicate the presence of compressionwood.
4. For moderate levels of compressionwood, LW lignin and carbohydrate contents are normally significantly higher or lower than EW contents depending on the chemical constituent. For severe levels of compressionwood, on the other hand, LW and EW compositional differences are small.
5. EW and LW mannose contents are consistently different one from another for all radial directions. Furthermore, LW mannose contents are consistently higher than earlywood contents for all radial strips except for those with moderate levels of compressionwood where EW > LW.
6. MFA increases with increasing compressionwood content but with similar EW/LW differences in moderate and severe compressionwood.

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