Wood structure and properties of clonal plantlets and seedlings of *Pinus radiata*

A thesis

submitted in fulfillment of the requirements for the Degree

of

Doctor of Philosophy

at the

Department of Plant and Microbial Sciences
University of Canterbury

by

Guizhen Li



IK 194,5 1966 16928 2000

ABSTRACT

The ontogeny of vascular cambium and the wood formation in the 8 month-old *Pinus radiata* have been examined. The results showed that the procambium develops from the subapical meristem parenchyma, which is converted to procambial cells by periclinal division about 0.5 mm from the shoot tip. The interfascicular cambium originates from the interfascicular parenchyma, which is also derived from the subapical meristem. Transverse sections show that the interfascicular parenchyma convert to interfascicular cambial cells requires activation by the fascicular cambium. The vascular cambium was established by the fascicular cambium connecting with the interfascicular cambium.

Compression wood formation is related to the plantlet's response to stress. The magnitude and distribution of compression wood is related to whether the stem is free-growing, staked vertically, or tied to an inclined stake, the three situations generating 27%, 14% and 49% compression wood as assessed by image analysis of thin sections.

Stiffness, density, tracheid length, cell numbers/mm², and percent cell wall area were tested for plantlets of clones 8 and 31 grown under three treatments. Compared to the free grown plantlets, the angled plantlets were shorter, thinner, contained more compression wood with thicker cell walls and more cells/mm², and had shorter denser tracheids to formed weaker wood. By contrast the tied plantlets were taller and thinner, having fewer cells/mm² with each tracheid being longer and less dense (thinner cell walls), but of similar stiffness to the free grown ones. Compression wood was stiffer than opposite wood because of its higher density, and the angled plantlets were weaker than the free and tied plantlets due to their shorter tracheids. Stiffness is related to density in angled plantlets, and related to tracheid length in the free and tied plantlets. Tracheid length is negatively related to density, cells /mm², and percent cell wall. Density is related to percent cell wall and cells /mm², and the percent cell wall and cells/mm² related each other.

Stiffness, microfibril angle, density, and maximum crushing strength have been studied for 1 and 2 year-old seedlings from seedlots 10 and 28. The results indicated that stiffness increased and microfibril angle decreased from one year-old to two year-old material. A relationship between maximum crushing strength and density and a negative relationship between stiffness and microfibril angle existed in two years old plantlets. Stiffness and maximum crushing strength related each other in both one and two years old plantlets.

Overall, this work proved to be a scoping trial. While the results could have been anticipated in general terms they do provide a useful description of very young wood. The extent of compression wood varied greatly between treatments, but even in the best case (tied) it takes up a significant proportion of the stem cross-section. However, the technical challenges, especially in the measurement of mechanical properties in such small samples remains a formidable challenge.

ACKNOWLEDGEMENTS

First I would like to sincerely thank my supervisor, Dr. Brian G. Butterfield, Professor in the Department of Plant and Microbial Science, for his supervision and positive criticism, which have always been carried out in a thoughtful and constructive way. I greatly appreciate his encouragement, patient help, valuable guidance, and useful advice.

I would like to sincerely thank my associate supervisor, Dr. John C. F. Walker, Professor in the School of Forestry, for his associate supervision, helpful assistance, and useful advice.

I would like to thank the technical staff in the Department of Plant and Microbial Sciences for their help throughout this study, especially Matt Walters, Reijel Gardiner, Manfred Ingerfeld, Graeme Young, Vera Pal. Also, thanks to Dr. Brian A. Fineran, Associate Professor in the Department of Plant and Microbial Science, for his helpful suggestions on the tissue differentiation. Thanks to Dr. Richard C. Woollons for his advice in data analysis. Thanks to Dr. Addis Tsehaye and Mr. Paul Fuller for their help in using the Instron equipment for wood stiffness testing.

I am also greatly indebted to the School of Forestry, University of Canterbury and the Fletcher Challenge Forestry Limited for providing seedlings and clonal plantlets.

I would like to acknowledge the financial support received for this research in the form of a doctoral scholarship from Canterbury University Scholarship Committee.

Also, I appreciate the scientific advice and/or assistance given by my friends and colleagues

Finally, I would like to thank my parents for their support and encouragement; my husband, Zhang Jianlu, and my son, Zhang Han, for their support, understanding and help over my study.

CONTENTS

ABSTRA	ACT		i
ACKNO	WLEI	OGMENTS	iii
CONTE	NTS		iv
LIST OF	TAB	ELES	xi
LIST OF	FIGU	JRES	xiv
LIST OF	PLA?	ΓES	xvii
		IONS	
СНАРТ	ER 1	AN INTRODUCTION TO CAMBIUM ONTOGEN	1Y
AND W	OOD	PROPERTIES IN JUVENILE AND COMPRESSIO	N
WOOD	IN P	INUS RADIATA	1
1.1	Gener	al introduction	1
	1.1.1	Radiata pine	1
	1.1.2	Wood	1
	1.1.3	Vascular cambium	2
	1.1.4	Wood properties and quality	2
1.2	Lows	stiffness in radiata pine corewood (juvenile wood)	2
1.3		of the research programme	
1.4	Organ	nization of research programme	4
	1.4.1	Observations on cambium ontogeny and wood formation	4
	1.4.2	Studies of young clonal plantlets grown for 8 months	
		in a regulated glasshouse	4
	1.4.3	Studies of young seedlings (1 and 2 year-old) grown out of door	rs
		in Canterbury	5
1.5	Clon	al plantlets and seedlings	5
1.6	Thes	is outline	6

	CHAPTE	CR 2	LITER	ATURE REVIEW - An over view on	
	cambium	devel	lopment	, juvenile wood properties, and compre	ssion
	wood pro	pertie			
	Part one:	An o	ver view	on vascular cambium development	7
	2.1	Proca	ımbium, 1	fascicular cambium, and interfascicular camb	ium8
		2.1.1	Origin o	f the procambium	8
		2.1.2	Origin of	f the interfascicular cambium	9
		2.1.3	Ontogen	y and development of the vascular cambium	10
	2.2	Wood	l formatio	on	12
	2.3	Vascu	lar camb	ium activity	12
	2.4	Camb	ium qual	ity and its wood cells	15
	Part two	: Rev	view of l	iterature on juvenile wood properties	17
	2.5	Juven	ile wood.		17
ş. Ş.	2.6	Juver	nile wood	features	17
	2.7	Juver	nile wood	quality/properties	18
		2.7.1	Wood qu	nality variation	19
		2.7.2	General		19
		2.7.3	Stiffness	and strength	20
			2.7.3.1	Stiffness	20
			2.7.3.2	Strength	21
			2.7.3.3	Inferior quality of radiata pine corewood	22
	2.8	Anat	omical ch	aracteristics	23
		2.8.1	Microfil	oril angle	23
			2.8.1.1	Microfibril angle measurement	25
			2.8.1.2	Microfibril angle variation	26
			2.8.1.3	Microfibril angle effect on wood stiffness	29
		2.8.2	Trachei	l length	31
			2.8.2.1	Tracheid length variation	32
			2.8.2.2	Influence of tracheid length on wood stiffness	
				and strength	33
			2.8.2.3	Tracheid length and microfibril angle	34

		A A	35
	2.9.	1 Density	35
	2.9.2	2 Density variation	35
	2.9.	density effects on wood stiffness and strength	39
2	2.10 Med	chanical properties	41
	2.10	0.1 Variation of mechanical properties	41
	2.10	0.2 Relationship between stiffness and strength	44
Part th	iree: C	Compression wood properties	45
	2.11 Co	mpression wood in soft woods	45
	2.12 Co	mpression wood formation	46
2	2.13 Va	riation of compression wood	46
4	2.14 Co	mpression wood properties	47
	2.14	4.1 Microfibril angle and tracheid length of compression woo	od47
	2.14	1.2 Density of compression wood	49
	2.14	3.3 Stiffness and strength of compression wood	50
4	2.15 Pro	perties of wood type (compression and opposite wood)	52
CHAP	TER.3	ONTOGENY OF THE VESCULAR CAMBIUM	[
		ONTOGENY OF THE VESCULAR CAMBIUM FORMATION	
	VOOD		56
AND V	VOOD Induc	FORMATION	56
AND V 3.1 3.2	VOOD Induc	FORMATIONtiontion methods	56
AND V 3.1 3.2	WOOD Induc	FORMATIONtiontion methods	56 56 57
AND V 3.1 3.2	WOOD Induc Mater Resul	FORMATIONtiontion methodsts.	56 57 58
AND V 3.1 3.2	VOOD Induc Mater Resul 3.3.1	FORMATION tion rials and methods ts The plantlet growth.	56 57 58 58
AND V 3.1 3.2	VOOD Induc Mater Resul 3.3.1	FORMATION tion rials and methods ts The plantlet growth Differentiation and development of the vascular tissues	56 57 58 58 60
AND V 3.1 3.2	VOOD Induc Mater Resul 3.3.1	FORMATION	56 57 58 60 60
AND V 3.1 3.2	VOOD Induc Mater Resul 3.3.1	FORMATION	56 57 58 60 60
AND V 3.1 3.2	VOOD Induc Mater Resul 3.3.1	tion	56 57 58 60 60 60
AND V 3.1 3.2	VOOD Induc Mater Resul 3.3.1	tion	56 57 58 60 60 61
AND V 3.1 3.2	VOOD Induc Mater Resul 3.3.1	tion	56575860606161

		3.3.3	Wood formation	71
			Primary xylem and secondary xylem	71
			Percent pith and wood	71
			Normal wood and compression wood	73
			Distribution of the compression wood	73
			Percent compression wood	73
			Percent cell wall area in normal and compression wood	75
			Cell numbers/mm ² in normal and compression wood areas.	76
			The Growing characteristics of the plantlets	79
	3.4	Discu	ıssion	85
			Secondary growth	87
			Compression wood formation	87
			Wood structure	87
			Percent cell wall area and cell numbers/mm ²	87
	3.5	Conc	lusion	88
CLO	ONA	LPL	ANTLETS	89
	4.1	Intro	duction	89
	4.2	Mate	rials and methods	90
		4.2.1	Materials	90
		4.2.2	Methods	91
			4.2.2.1 Preparation of samples from the free, tied and	
i			angled plantlets	91
			4.2.2.2 Equipment and testing procedure	92
			4.2.2.3 data analysis	94
	4.3	Resul	lts for the angled plantlets	96
		4.3.1	Test samples	96
		4.3.2	Wood properties of the four wood types	97
				//
			4.3.2.1 Variations in stiffness between wood types	
			4.3.2.1 Variations in stiffness between wood types	99
			••	99 100

4.3.2.5 Variation in percent cell wall area between wood types1	Э1
4.3.3 Influence of angled clones on wood properties1)5
4.3.4 Statistical relationships between wood properties of wood types1	Э7
4.3.5 Discussion	9
4.3.6 Conclusions1	11
4.4 Results of clonal wood properties1	12
4.4.1 Teat samples1	12
4.4.2 Comparison of wood properties between clones, treatments,	
and stem positions1	12
4.4.2.1 Stiffness	13
4.4.2.2 Density1	15
4.4.2.3 Tracheid length	18
4.4.2.4 Cell numbers/mm ² 1	20
4.4.2.5 Percent cell wall area	21
4.4.3 Discussion	24
4.4.4 Conclusions	24
4.4.5 Results of the relationships between wood properties	26
4.4.5.1 Relationships between wood properties of	
the angled plantlets1	29
4.4.5.2 Relationships between wood properties of	
the free and tied plantlets1	31
4.4.5.3 Altered relationships between wood properties1	34
4.4.5.4 The relationships between wood properties of 6 plantlets1	35
4.4.6 Conclusions	40
CHAPTER 5 PROPERTIES OF ONE AND TWO YEAR-OLD	
SEEDLING WOOD14	,1
5.1 Introduction	41
5.2 Materials and methods1	41
5.3 Results of wood properties of seedlings	45
5.3.1 Variations in wood properties between seedlings1	45
5.3.2 Effect of stem position on the wood properties of seedlings1	50
5.3.3 Variations in wood properties of seedlings between seedlots1	53

	5.3.4	Relation	ships between wood properties of seedlings154
		5.3.4.1	Relationships between wood properties
			in one year-old seedlings155
		5.3.4.2	Relationships of wood properties of
			two year-old seedlings156
		5.3.4.3	Effect of age on relationships between wood properties159
5.4	Discu	ssion	162
5.5	Conc	lusion	164
CHAPTE	ER 6	GENE	RAL DISCUSSION165
6.1	The v	ascular c	ambium development and wood formation165
6.2	Comp	ression v	vood167
6.3	Comp	pression v	wood samples and the angled plantlets168
6.4	Stiffn	ess (MOI	E) influenced by several factors168
6.5	Alter	ed relatio	nships of wood properties in different treatments170
6.6]	Micro	fibril ang	gle to stiffness in young wood170
6.7	Variat	tion of sti	ffness in young wood171
6.8 I	Effect	of age an	d development stages on wood properties172
6.9]	Effect	of enviro	onmental factors on wood properties172
6.10	Geneti	ic factors	and preselection173
6.11	Proble	ems	173
6.12	Furth	er work	174
Adde	endui	n	1749
REFI	EREI	VCES	
APPE	ENDI	CES	
Appen	dix 1	The hei	ght and the stem lengths of the 8 year-old
		plantlet	s of clones 8 and 31195
Appen	dix 2	Variabi	lity in tracheid length between clones 8 and 31,
		three tre	eatments and stem positions197
Appen	dix 3	The rela	ntionships between wood properties of
		clonal p	lantlets205

Appendix 4	The wood property weighted-means according to
	four quadrant area percentage on stem cross area206
Appendix 5	The influence of compression wood, clone, treatment, stem
	position and other factors (tracheid length and microfibril angle)
	on young wood stiffness207
Appendix 6	The results of correlation analysis between stiffness and
	tracheid length for clones 8 and 31212

LIST OF TABLES

Table 2.1	Variations of wood density in loblolly pine grown in the southeastern coastal plain of the United States	20
Table 2.2	Clearwood stiffness (MOE) and wood characteristics of radiata pine (<i>Pinus radiata</i>) logs from a stand in Canterbury, New Zealand	23
Table 2.3	Mean tracheid length (mm) for radiata pine trees	32
Table 2.4	A comparison of strength and stiffness by tension with the design code	42
Table 2.5	The mechanical property means of 2-year-old radiata pine seedlings	44
Table 2.6	Properties of normal and compression wood	49
Table 2.7	Comparison of specific gravity (air-dry) between compression and normal wood in radiata pine	50
Table 2.8	Properties of single fibres from side and compression woods of <i>Picea sitchensis</i>	54
Table 2.9	A comparison of properties between compression and opposite wood	54
Table 3.1	The mean height and diameter of the 12 plantlets	59
Table 3.2	The onset of the secondary growth in free, tied, and angled radiata clones 8 and 31	63
Table 3.3	Comparison of variable means between clones, treatments, and stem positions	79
Table 3.4	The growth characteristics in the stems of the plantlets	80
Table 4.1	The means of wood properties for compression wood, opposite wood, mixed wood, and normal wood by stem position	98
Table 4.2	Means of modulus of elasticity, density, tracheid length, cell numbers/mm ² , and percent cell wall area by wood type and position in the angled plantlets	99
Table 4.3	Property means for compression wood, opposite wood, normal wood and mixed wood according to stem position in the angled clone 8	.106

Table 4.4	The property means for compression wood, opposite wood, normal wood and mixed wood according to stem position in the angled clone 31	106
Table 4.5	Wood properties, weighted average for cross section, at all heights up the stem for 4 angled plantlets	107
Table 4.6	Correlation analyses for stiffness, density, and tracheid length in angled clonal plantlets	107
Table 4 7	weighted-means of stiffness, density, tracheid length, cells/mm ² , and percent cell wall area for clones, treatments, and stem positions at all height up the stems for all treatment plantlets.	113
Table 4.8	The mean values of stiffness (GPa) of the stems of	
Table 4.9	free (F), tied (T) and angled (A) clones 8 and 31 The mean values of density (kg/m³) of the stems of	
	free (F), tied (T) and angled (A) clones 8 and 31	115
Table 4.10	The mean values for tracheid length (mm) in the stems of free (F), tied (T) and angled (A) plantlets of clones 8 and 31	118
Table 4.11	The mean number of cells/mm ² at various positions up the stem for the free (F), tied (T) and angled (A) plantlets of clones 8 and 31	121
Table 4.12	Mean percent cell wall area up the stems of the free (F), tied (T) and angled (A) plantlets for clones 8 and 31	122
Table 4.13	The results of correlations between stiffness, density, and tracheid length of clonal plantlet wood	126
Table 4.14	Correlations between modulus of elasticity, density and tracheid length for the angled plantlets	129
Table 4.15	Correlations between modulus of elasticity, density, and tracheid length for the free and tied plantlets	131
Table 4.16	Relationships between stiffness, density, tracheid length and cell numbers/mm ² , percent cell wall area of plantlets	135
Table 5.1	The means of maximum crushing strength, stiffness, microfibril angle, and density of 32 seedlings	146
Table 5.2	The means of wood properties in the upper two and lower two positions for 2 year-old seedlings	150

Table 5.3	The means of wood properties for GF10 and GF28 at ages 1 and 2 years: standard errors are shown in parenthesis
Table 5.4	The means of wood properties for two GF groups
Table 5.5	The means of wood properties between 1-and 2 year-old seedlots154
Table 5.6	The results of correlations between wood properties of seedlings (r values)
Table 5.7	The ratio of MOE/MCS in one and two year-old seedlings

LIST OF FIGURES

Figure 2.1	The procambial strands develop from the sub-apical meristem (left) and the procambium originates and develops into a procambial strands in <i>Ricinus Communis</i> (right)
Figure 2.2	Transverse sections of the <i>Ricinus communis</i> showing a sequence of the interfascicular cambium origins from interprocambial residual meristem
Figure 2.3	A region of the vascular cambium (VC) in <i>Hoheria angustifolia</i> 11
Figure 2.4	Seasonal change in the number of mitosis per increment core in the fifth internode of five <i>Pinus strobus</i> trees14
Figure 2.5	Eccentric root growth of <i>Cissampelos pareira</i> (A) and stem of <i>Tilia heterophylla</i> (B) in transverse sections
Figure 2.6	Transverse section of compression wood of radiata pine16
Figure 2.7	Wood quality is different in the corewood and in the outerwood
Figure 2.8	A diagram shows when a material is under load, at first the relation between load and extension is linear and reversible
Figure 2.9	The structure of a wood cell wall24
Figure 2.10	Changes in microfibril angle with ring number
Figure 2.11	Microfibril angle varied with cambial age and height in the tree (above), and varied between trees
Figure 2.12	Relationship between stiffness and microfibril angle30
Figure 2.13	A plot of breaking load against tracheid length length34
Figure 2.14	Density distribution within a tree showing a low density in the corewood which increases on going outward from the centre in the tree
Figure 2.15	Wood density distribution in New Zealand radiata pine plantation forests
_	Modulus of elasticity at 12% moisture content vs. basic density from all samples except butt logs

Figure 2.17	Microfibril angle in normal and compression wood areas of <i>Picea abies</i> 48
Figure 2.18	A reinterpretation of Wardrop's data (wood quality confines the breaking load within an envelope bounded by the lower juvenile wood/ compression wood line and the upper outwood line52
Figure 2.19	The variation in longitudinal and tangential shrinkage, average tracheid length, microfibril angle and basic density of the side-wood, compression-wood and opposite-wood sectors of a disk from the butt of tree 52
Figure 3.1	The height of the eight month-old <i>Pinus radiata</i> clonal plantlets59
Figure 3.2	The pattern of percent pith from base to tip72
Figure 3.3	The percent wood from the base to tip
Figure 3.4	Percent compression wood in clones 8 and 31 with height74
	Percent compression wood in the free, tied and angled plantlets with height
Figure 3.6	Percent cell wall area of the free, tied, and angled plantlets in the normal wood
Figure 3.7	Percent cell wall area of the free, tied, and angled plantlets in the compression wood
Figure 3.8	Cell numbers/mm ² of the free, tied, and angled plantlets in the normal wood
Figure 3.9	Cell numbers/mm ² of the free, tied, and angled plantlets in the compression wood
Figure 4.1	Sampling from the 8-month-old clonal plantlets95
Figure 4.2	Splitting the angled stem made isolation of the wood types possible97
Figure 4.3	Modulus of elasticity for compression, opposite, normal, and mixed wood
Figure 4.4	The density of compression, opposite, normal, and mixed wood103
Figure 4.5	Tracheid length of compression and opposite wood
Figure 4.6	Cell numbers/mm ² in compression and opposite wood104

Figure 4.7	Percent cell wall area of compression wood and opposite wood	.105
Figure 4.8	Relationship between MOE and density for various wood types	.108
Figure 4.9	Stiffness of wood up the stem	.117
Figure 4.10	Density variations up the stem	.117
Figure 4.11	Tracheid length variations up the stem	.120
Figure 4.12	Variations in cell numbers/mm² up the stem	.123
Figure 4.13	Percent cell wall area of treatments	.123
Figure 4.14	Relationship between stiffness and tracheid length in plantlets	.128
Figure 4.15	Relationship between density and tracheid length in plantlets	.128
Figure 4.16	Relationship between stiffness and density for the angled plantlets	.130
	Relationship between modulus of elasticity and tracheid length of the free and tied clones only	.133
	Relationship between density and tracheid length of the free and tied treatments.	.133
Figure 4.19	Relationship between density and cells/mm ²	.138
Figure 4.20	Relationship between air-dry density and percent cell wall area	.138
Figure 4.21	Relationship between tracheid length and cells/mm ²	.139
Figure 4.22	Relationship between tracheid length and percent cell wall area	.139
Figure 4.23	Relationship between cells /mm² and percent cell wall area	.140
Figure 5.1	Sampling from one and two year-old seedlings	.144
Figure 5.2	Maximum crushing strength of one and two year-old seedlings	.148
Figure 5.3	Stiffness of one and two year-old seedlings	.148
Figure 5.4	Microfibril angle of one and two year-old seedlings	.149
Figure 5.5	Density of one and two year-old seedlings	.149
Figure 5.6	Microfibril angle at the upper two and lower two stem positions	.152

Figure 5.7	Density of stem at the upper two and lower two stem positions	152
Figure 5.8	Relationship between stiffness and maximum crushing strength in 1 year-old seedlings	156
Figure 5.9	Relationship between stiffness and microfibril angle in 2 year-old seedlings.	.158
Figure 5.10	Relationship between maximum crushing strength and density in 2 year-old seedlings	158
Figure 5.11	Relationship between stiffness and maximum crushing strength in 2 year-old seedlings	159
Figure 5.12	Comparison of relationships between stiffness and microfibril angle in 1 and 2- year-old seedlings.	160
Figure 5.13	Relationships between stiffness and maximum crushing strength in 1 and 2 year-old seedlings	.161

LIST OF PLATES

3.1	The early development of the procambial strands – shoot tip down to 1.7 mm6	5
3.2	The closure of the interfascicular sectors 2.5 m from the shoot tip6	6
3.3	The onset of secondary growth – 11 mm from the shoot tip	7
3.4	The radially expanding vascular cambium – 16-30 mm from the shoot tip6	8
3.5	An origin and developmental sequence of the procambium6	9
3.6	A developmental sequence of the interfascicular cells	0
3.7	A primary xylem tracheid in low magnification (1) and in detail (2)8	1
3.8	Primary xylem tracheids showing helical secondary thickening and intertracheid pit-pairs	2
3.9	Transverse sections from the base of angled plantlet. No. 1 Opposite wood; No. 2 compression wood	3
3.10	Cross sections through eight month-old <i>Pinus radiata</i> clonal plantlets. Showing the distribution of compression wood in the free, tied, and angled plantlets	4

ABBREVIATIONS

°C degrees Celsius

A (angled) tied plantlets to an angle of 45°

ANOVA analysis of variance

CW compression wood

 ∂L change in length of stick sample

F free growth

F.A.A. Formalin acetic acid alcohol

FC fascicular cambium

GPa gigapascal

Ht helical thickening

IC interfascicular cambium

IR interfascicular residual meristem

IS interprocambial sector(s)

kg kilogram(s)

M meristem

M.C. moisture content

MCS maximum crushing strength

MFA microfibril angle

ML middle lamella

 $\mu \mathbf{m}$ micrometre

mm millimetre

MOE modulus of elasticity

MOR modulus of rupture

MPa megapascalMW mixed woodNW normal wood

OpW opposite wood

P value value of probability

PP primary phloem

PS procambial strands

PX primary xylem

r value correlation coefficient

R ray cell(s)

RLS radial longitudinal section

S1 first layer of secondary wall

secondary layer of secondary wall

\$3 third layer of secondary wall

 Σ sum

SX secondary xylem

T tied plantlet to a stake vertically

T.B.A tertiary butyl alcohol

TLS tangential longitudinal section

Tracheid L. tracheid length

VC vascular cambium

CHAPTER 1

AN INTRODUCTION TO CAMBIUM ONTOGENY AND WOOD PROPERTIES IN JUVENILE AND COMPRESSION WOOD IN PINUS RADIATA

1.1 General introduction

1.1.1 Radiata pine

Pinus radiata D.Don (Syn. P. insignis Douglas), usually called radiata or, previously Monterey pine, is one of the most important plantation tree species grown extensively in several southern-hemisphere countries, such as New Zealand, Australia, Chile, and South Africa (Bamber and Burley, 1983). Radiata pine is the major species in New Zealand forestry plantations due to its impressive growth throughout the country. No other species grows as fast, with the possible exception of certain eucalyptus. However, because these young, fast grown pines achieve millable size in a relatively short space of time (≤ 30 years), the poor quality of the wood reflects this relative immaturity.

1.1.2 Wood

Wood is the common term for the xylem cells and comprises the fibrous material between the bark and pith in the tree. Wood comprises mainly cellulose, hemicelluloses, lignin, and numerous minor extractives (Webster and Mckechnie, 1980). In conifers, wood is made up of tracheids, horizontal ray tissue, and sometimes vertical parenchyma cells. Radiata pine wood, like that of other conifers, comprises about 95% tracheids (Higuchi, 1997). Radiata pine is a medium-density wood that is excellent for general purpose uses, such as construction, plywood, particleboard, furniture, and paper production.

1.1.3 Vascular cambium

The vascular cambium, sometimes, called the secondary meristem, is a cylinder, at most a few cells wide, between the bark (phloem) and wood (xylem). The cambium has two types of dividing cells. The fusiform initials that divide longitudinally to form the axial system of the secondary vascular tissues are long and thin, the ray initials that divide forming the horizontally oriented ray cells comprising the radial system in the wood are rounded in tangential view. The vascular cambium develops in a number of ways (Butterfield, 1976). In some plants it originates from the residue of the apical meristem, while in other plants it is derived from subapical meristem parenchyma cells (Soh *et al.*, 1989). Cambial initials and wood cells can be modified by internal and external stress to form compression (in softwoods) or tension wood (in hardwoods) that has different wood structures and properties (Wardrop, 1948; Lim and Soh, 1997).

1.1.4 Wood properties and quality

Wood properties are determined by the cellular, anatomical, chemical, and physical characteristics of the wood, such as cell wall thickness, tracheid length, microfibril angle, lignin content, and density. These characters are influenced by tree age, species, and geography. Therefore, the wood properties vary from growth ring to ring, from the base of the tree to its top, from tree to tree, from species to species at same site, and between sites (Larson, 1969). Wood quality determines the wood utilisation value of a tree (Zobel and Buijtenen, 1989). For many purposes wood scientists measure stiffness and strength. Wood density, microfibril angle, tracheid length, cell wall thickness all effect these two properties (Cave and Walker, 1994; Walker and Butterfield, 1996; Mishiro and Eiji, 1997).

1.2 Low stiffness in radiata pine corewood (juvenile wood)

Low stiffness is recognised to be a general problem in fast-grown, short-rotation softwoods. It is therefore very desirable to improve corewood quality by increasing wood stiffness and strength. Radiata pine has been commonly regarded as a rather poor timber (Welch, 1927; Bamber and Burley, 1983). It also has a low stiffness to strength ratio (Addis Tsehaye, 1995). Previous studies indicate that radiata pine had a low stiffness due to its corewood (Cown, 1992). The corewood zone contains a number of undesirable features including low density, thin cell walls, high moisture content,

5 .

significant amounts of compression wood, short fibres and high shrinkage values (Senft et al., 1985). Addis Tsehaye (1989) and Hadi (1992) reported that radiata pine grown on dry, stoney, windy sites in central Canterbury of New Zealand had especially low stiffness corewood. An analysis of the corewood of radiata pine from such a location on the Canterbury Plains showed that this Canterbury timber had 60 percent of the tensile strength and only 40 percent of the stiffness of comparable Nelson material (Addis Tsehaye, 1995).

This thesis aims to examine those wood properties important for improving corewood quality but by focussing on young seedlings and clonal plantlets, rather than by studying older trees. The first part of the work examines the development of the cambium and describes the formation of xylem tissue in young radiata pine plantlets. Later, the thesis examines how properties vary within trees of different genetic origin when grown under different conditions, and seeks to find correlations between wood properties to predict wood quality at an early stage.

1.3 Goals of the research programme

The overall goals of the research program are:

- (a) To investigate tissue differentiation and wood formation in *Pinus radiata* and to study compression wood formation and distribution in clonal radiata pine plantlets grown under different treatments.
- (b) To determine differences in wood properties between clones, treatments, and location within the stem, and so to explain the genetic, environmental, and developmental factors influencing wood properties.
- (c) To measure properties of compression, opposite and normal wood in the young clonal plantlets grown at an angle to deliberately induce compression wood, and to characterise the modified wood formation.
- (d) To study wood properties of young seedlings from different seedlots to find seedlings with stiffer wood.

(e) To explore the interplay between wood characteristics and properties in determining wood quality. To determine the relationships between stiffness and wood properties (microfibril angle, cell number /mm², percent cell wall area, tracheid length, percent compression wood, density, stiffness in compression, stiffness in tension, and maximum crush strength).

1.4 Organization of research program

The thesis falls into three parts, a study of cambium ontogeny, a study of the properties of clonal material, and of seedlings.

1.4.1 Observations on cambium ontogeny and wood formation

In this experiment the top parts of clonal plantlets are sectioned and observed for tissue differentiation and wood formation. The percent pith, percent wood, percent compression wood, cell numbers/mm² and percent cell wall area in both normal wood and compression wood will be measured. The aims of this experiment are:

- (a) To observe how the vascular cambium develops, when secondary growth starts, how is wood formed, and the formation of compression wood and distribution in the stems of the plantlets.
- (b) To measure differences in percent pith, percent wood, percent compression wood, cell number /mm², and percent cell wall area between clones, treatments, and with relative height up the stem.

1.4.2 Studies of young clonal plantlets grown for 8 months in a regulated glasshouse

In this experiment the stiffness in tension, the microfibril angle, density, tracheid length, cell wall percentage, cell number /mm² for wood cut from different parts of the stem in young plantlets will be determined. The wood properties of the samples of compression wood, opposite wood, normal wood, and mixed wood of the angled trees will be examined. The aims of this experiment are:

- (a) To analysis differences in wood properties between clones, treatments and position up the stem; to find genetic, developmental, and environmental factors acting on wood properties.
- (b) To determine differences in wood properties between compression, opposite, normal, and mixed wood samples.
- (c) To determine if there are correlations between wood properties and the stiffness of wood.

1.4.3 Studies of young seedlings (1 and 2 year-old) grown out of doors in Canterbury

In this experiment the stiffness in compression, the maximum crushing strength, density, and microfibril angle of clear wood samples from seedlings will be determined. The aims of this experiment are:

- (a) To analysis differences in wood properties for existing seedlots, and to observe the effect on wood properties of seedling age.
- (b) To determine relationships between wood properties.
- (c) To find superior seedlots and seedlings having above average stiffness.

1.5 Clonal plantlets and seedlings

Seedlings were planted on Selwyn Plantation Board Land at Dalethorpe in the Canterbury foothills and at Burnham on the Canterbury plains in 1993. A further trial site was planted at Port Levy in late 1994. These trials were planted primarily to measure tree growth and form over the next 15 years and are subject to other research at the School of Forestry, University of Canterbury. However, a small area of land was planted with additional material to allow for destructive sampling of both clones and seedlings for wood quality. The trial block at Port Levy provided the GF seedling material used in Chapter 5. Subsequent concerns about the variability in the resource material suggested that more reproducible data would be obtained if future work was

done on clonal material grown in a glasshouse under controlled conditions. Two clones supplied by Fletcher Challenge Forestry were grown in planter bags in a glasshouse of Plant and Microbial Sciences at the University of Canterbury in July 1996. Clonal plantlets taken from the glasshouse provided material for work reported in Chapters 3 and 4 of this thesis.

1.6 Thesis outline

This thesis has the following format:

- An introduction to the thesis topics in Chapter 1;
- An overview of the literature on tissue differentiation, wood structure, compression wood, and mechanical properties in Chapter 2;
- A study of ontogeny and development of the vascular cambium and wood formation in Chapter 3;
- A study of clonal plantlet stemwood properties and wood types (compression, opposite, normal, and mixed wood) in Chapter 4;
- A study of the variability found in young trees, in Chapter 5;
- A general discussion in Chapter 6.

CHAPTER 2

LITERATURE REVIEW

An over view on cambium development, juvenile wood properties, and compression wood properties

This literature review is broken into three parts. The first part concerns **cambial** development and is relevant to the experimental work in Chapter 3 of this thesis. Part two and three concern juvenile wood and compression wood properties (microfibril angle, tracheid length, density, stiffness, and strength) and relate to work in Chapter 4 and 5 respectively.

Part one: An overview on vascular cambium development

The vascular cambium is of importance in the practical fields of forestry, and timber production and utilisation, many of the wood properties depend on the length of its cells. Relationship of tracheid length to activity of cambium has not been well understood. A consideration of the processes of division and elongation of the cambium initials is essential for a more understanding of wood formation and wood properties. Therefore, the cambium ontogeny, development, activity, and quality will be reviewed in this part.

The vascular cambium is called the secondary meristem and is a thin layer cylinder between the bark and wood in the tree. It contains actively or potentially actively dividing cells and responding to secondary growth, or, thickening growth for the trees. The vascular cambium develops from the procambium, fascicular, and interfascicular cambium (Philipson *et al.*, 1971; Butterfield, 1973, 1974).

2.1 Procambium, fascicular cambium, and interfascicular cambium

The apical meristem is the growing point of the shoot of seed plants. Its cells divided into two main regions: one is the promeristem which comprises the apical initials and neighbouring cells, and behind it is another one called the meristematic zone in which there are three basic meristems (the protoderm, procambium, and ground meristem) of the tissue systems can be distinguished (Fahn, 1990, p.52). In gymnosperms and dicotyledons, it is common to first appear as a system of discrete procambial strands in the sub-apical meristem region, and these procambial strands are separated by the interfascicular areas called the interfascicular sectors. Procambium is a cambium located in procambial strands which cells were differentiated from sub-apical meristem. With the development, the procambial strands develop to the fascicular bundles. The cambium in fascicular bundles is called the fascicular cambium. The cambium develops from the interfascicular sector cells called the interfascicular cambium (Soh and Young, 1992). These three cambia are essential tissues for establishing a complete vascular cambial cylinder.

2.1.1 Origin of the procambium

The procambium has its origin in the actively dividing and enlarging shoot apex and is the source of the primary vascular tissues. The procambium originates from the subapical meristem, where cells converted by periclinal division form radial files forming the procambium. Figure 2.1 shows a procambium is initially forming in the centre of the procambial strands in *Ricinus Communis*. Note the procambial cells in the centre of a procambial strand are well developed through periclinal division to form radial row that is presenting procambium characteristics (after Fahn, 1990).

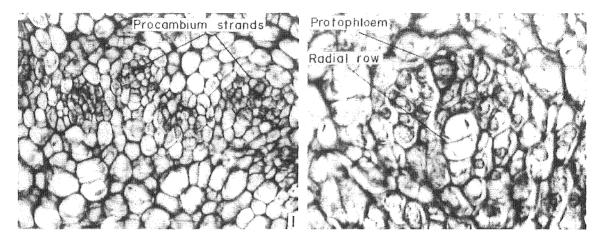


Figure 2.1 The procambial strands develop from the sub-apical meristem (left) and the procambium originates and develops in a procambial strands in *Ricinus Communis* (right) (from Fahn, 1990).

Note the procambial cells in the centre of a procambial strand are well developed through periclinal division to form radial row that is presenting procambium characteristics.

2.1.2 Origin of the interfasciuclar cambium

There are contradictory views on the origin of interfascicular cambium. One view is that, the interfascicular cambium has an ontogenetic continuity from the residual meristem (Siebers, 1971 a, b, 1972; Soh *et al.*, 1989; Soh, 1991; Soh and Young, 1992). In the second view, the interfascicular cambium does not have an ontogenetic continuity from the residual meristem, but differentiates from interfascicular parenchyma (Esau, 1977; Cutter, 1978; Little and Jones, 1980; Buval, 1989; Fahn, 1990).

Soh and Young (1992) reported that in *Ricinus communis*, the interfascicular cambium origins from the residual meristem. There is a structural distinction between the interprocambial and interfascicular residual meristem and adjacent parenchyma in both the transverse and tangential view. The residual meristem does not convert into parenchyma, but becomes interfascicular cambium. Therefore, the interfascicular cambium has a direct ontogenetic continuity with the residual meristem, and does not have its secondary origin from differentiated parenchyma. Furthermore, the ontogenetic pattern of the interfascicular cambium is almost the same as that of fascicular cambium. Figure 2.2 shows the interfascicular cambium origins from the residual meristem in *Ricinus communis*.

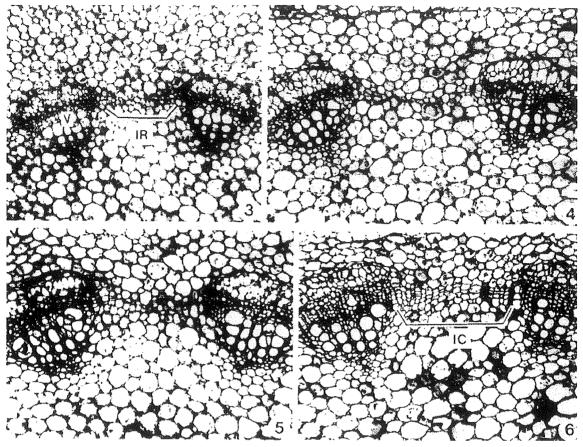


Figure 2.2 Transverse sections of the *Ricinus communis* showing a sequence of the interfascicular cambium origins from interprocambial residual meristem (from Soh and Young, 1992).

Note that there is no information about metaphloem and metaxylem differentiation before occurring initiation of the interfascicular cambium by periclinal division.

2.1.3 Ontogeny and development of the vascular cambium

The ontogeny of the vascular cambium has been investigated by a number of anatomists (Butterfield, 1976; Cutter, 1978; Soh, 1991; Soh and Young, 1992). In general, a complete vascular cambium cylinder is established when the fascicular cambium and interfascicular cambium connect. Larson (1976) studied *Populus deltoides* seedlings, his results demonstrated that progressive development of the vascular cambium occurs from procambial strands to procambial trace to initiation layer to metacambium to cambium.

Butterfield (1976) investigated the ontogeny of the vascular cambium in *Hoheria* angustifolia and found that the complete vascular cambium cylinder is established from procambium developed to metacambium to cambium. And the transition from procambium to cambium is a gradual one with the meristem acquiring some cambial

characteristics before and some after internodal elongation has ceased. Figure 2.3 shows a region of the vascular cambium cylinder in *Hoheria angustifolia*.

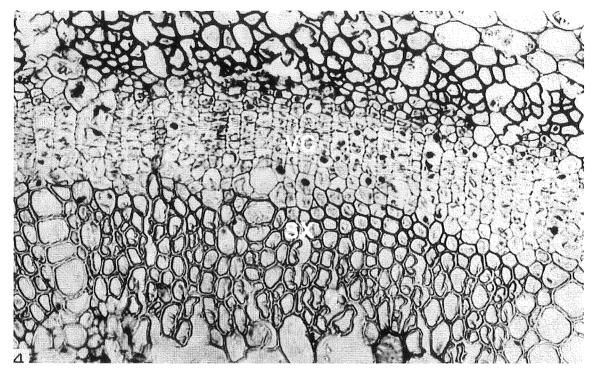


Figure 2.3 A region of the vascular cambium in *Hoheria angustifolia* (from Butterfield, 1976).

Note the secondary xylem cells (SX) were well differentiated from cambial initials and form a complete secondary xylem cylinder (VC).

The development of the vascular cambium varies in different species. This makes the ontogeny of the vascular cambium complex. There are different criteria used for defining secondary growth, and considerable variation between plants, in the transition from procambium to cambium. The precise time of origin of the vascular cambium is difficult to determine both theoretically and practically. It is usually impossible to distinguish sharply between primary and secondary tissues (Butterfield, 1976). Therefore, Esau (1965) suggested that the procambium and the cambium are best regarded as two developmental stages of the same meristem.

Albert and Shah (1998) reported observations on the structural changes in the procambium and its subsequent transformation into the secondary vascular meristem in the developing petiole of *G. Arborea* and *T. rosea*. During the procambial stage, the cells have a homogeneous structure and are short with transverse end walls. With the onset of metaxylem development, procambium in *G. arborea* shows polygonal and

rectangular cells in transverse sections. In longitudinal sections the polygonal cells are shorter and denser than the rectangular ones. In *T. rosea* an intermediate stage of metacambium is traceable between procambium and cambium. Metacambium is characterised by regular periclinal divisions resulting in radial flattened cells arranged in radial files. Tangentially the metacambium shows structurally two separate cell types, long and short cells. In *G. arborea* the secondary vascular meristem cells do not show typical fusiform appearance and hence are termed transit cells. In *T. rosea* the cambium shows both fusiform and ray cell systems.

Stages in the transition from procambium to cambium must become known in a greater number and variety of plants before many of the fundamental problems associated with the onset of secondary growth can be resolved. The cambium can be modified by growth stress to give rise to secondary tissues with specialised characteristics.

2.2 Wood formation

The vascular cambial initials undergo periclinal division and each initial therefore forms radial rows, new cells are added to the secondary xylem, and as a result of the secondary thickening the circumference of the xylem cylinder increases (Fahn, 1990, p.317).

In softwood, the tracheids, ray cells, and parenchyma cells are the principal cells. Wood structure and ultrastructure have been studied and well described in several papers and books (Butterfield, 1993, Butterfield et al, 1997, 2000; Butterfield and Meylan, 1980; Meylan and Butterfield, 1972, 1978; Patel, 1971; Donaldson *et al*, 1995; Kininmonth and Whitehouse, 1992). A block of wood shows three dimensions: cross, tangential, and radial. These three views have different structure faces and properties. Wood structure can be modified by tree growing conditions to form tension wood and compression wood whose cells are quite different compared with cells in normal wood.

2.3 Vascular cambium activity

Cambium activity is important to wood formation. The pattern of radial growth is related to the rate of the cambial activity. The process of division is faster than differentiation when the cambium first becomes active, as a result, the cambial zone

increases in width. When the rate of division reduces and the differentiation proceeds faster than division, the cambial zone becomes narrower (Fahn, 1990, p.321). The vascular cambium shows great variation in the period and intensity of activity. These variations are the results of many internal and external factors, such as apical meristem, season, temperature, and climate, etc.

Cambial activity influencing by the apical meristem is reported by Farrar and Fan in 1969. The cut surface of decapitated seedlings was treated with an auxin (IAA) or gibberellin or both. Examination 35 days after treatment showed that removal of the active shoot caused the cambial cells to stop dividing and the immature xylem cells to stop their differentiation. Auxin treatment resulted in continuation of cambial cell division and differentiation, but most of the xylem cells that matured were characterised by compression-wood features. The results supported the theory that cell division in the cambium is controlled by auxin emanating from the apical region, and that the subsequent differentiation of cambial derivatives is affected by both auxin and gibberellin, and probably other growth regulators.

Seasonal variation influence on cambial activity and wood differentiation was investigated in 20 chir pines (*Pinus roxburgin*) growing under natural conditions near Paniola Chowk, Rawalakot Forest Division, Azad Kashmir from March to December 1988. Samples were collected at 15-day intervals and studied for cambial activity and xylem cell formation. Cambial activity started in the middle of March, reached a peak at the end of July to mid-August and then declined and ceased at the end of November. The cambial zone showed marked periodical changes and became 3-4 layered during the dormant period and 7-10 layered during the active period. The rate of addition of new xylem cells dropped from the end of October onwards until the end of the growing season (Khattak and Majeed, 1993).

Mitotic activity in the cambial zone of 20-yr-old *Pinuse strobus* trees was analysed quantitatively by Wilson (1966). Mitotic counts were made on serial tangential sections cut from 1620 increment cores collected at different positions on the stems. Seasonally, the number of mitosis increased rapidly with the initiation of cambial activity in the spring and summer and then declined (Figure 2.4).

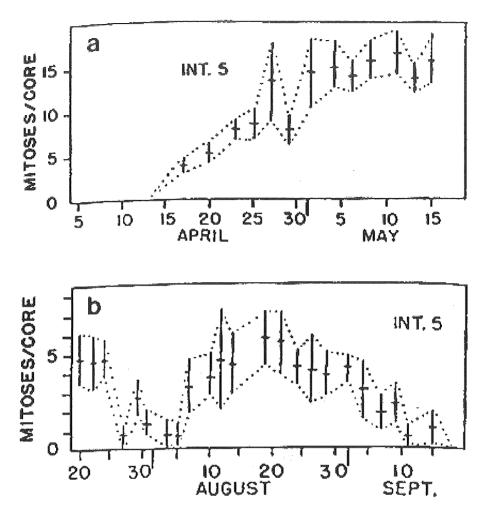


Figure 2.4 Seasonal change in the number of mitosis per increment core in the fifth internode of five *Pinus strobus* trees.

a) is at the initiation of cambial activity in spring. b) is at the cessation of cambial activity in the fall. Dotted lines indicate the range of sampling error (from Larson, 1994, p. 147).

Tree growth stress influenced on cambium activity reported by Larson in 1994. The cambium in compression wood side had a more active division than opposite one; as a result, the tree has an eccentricity growth. The characteristics of the compression wood side are having wider growth rings and the opposite wood having narrow growth rings (Figure 2.5).

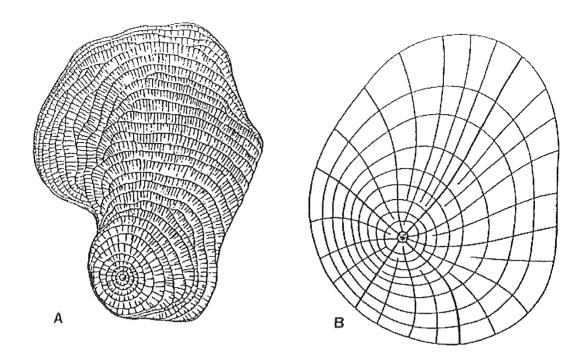


Figure 2.5 Eccentric root growth of *Cissampelos pareira* (A) and stem of *Tilia heterophylla* (B) in transverse sections.

Note the wider growth rings of the compression wood side (upper) and the narrow growth rings of the opposite wood side (lower). (from Larson, 1994, p.445).

2.4 Cambium quality and its wood cells

Cambium quality can influence on its wood cell quality, that is, higher quality cambium produces higher quality wood cells, and the juvenile cambium produce shorter tracheids and the mature cambium produce longer tracheids.

Wardrop (1948) reported that the application of external radial pressure upon growing conifer stems results in the differentiation of shorter tracheids with a flatter spiral microfibril angle than those differentiated in comparable regions of the stem but not subject to compression. It is suggested that the shorter tracheids arise as the result of an increased number of transverse divisions in the cambium.

Bamber and Burley (1983) illustrated compression cambial initials and compression wood cells in radiata pine. These compression cambial initials and compression wood cells present abnormal shape by transverse view (Figure 2.6).

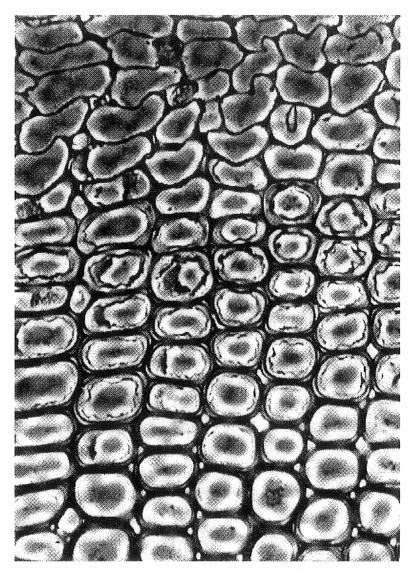


Figure 2.6 Transverse section of compression wood of radiata pine. The upper part of the micrograph shows the cambial region and the lower the fully developed compression wood tracheids. Note the rounded cell shape and the intercellular spaces. x 500. (from Bamber and Burley, 1983, p.45).

From a comparison of cambial cells and their derivatives between naturally occurring dwarf pine trees and normal ones, growing in Chonbak Province, Korea, the results showed that tracheids in the annual rings of dwarf trees are shorter, narrower and fewer than those of normal trees. The frequency of anticlinal division and loss of cambial initials is low during differentiation of xylem cells from cambial initials in dwarf pines. Thus, it is concluded that the shortening of tracheids in dwarf trees is due to the fact that cambial initials are themselves shortened (Lim and Soh, 1997).

Part two: Review of literature on juvenile Wood properties

2.5 Juvenile wood

Wood near the pith is commonly referred to as "juvenile" or "corewood". Juvenile wood is a cylindrical column surrounding the pith of the tree. Its cells do not reach the length found in mature cells (Smith and Briggs, 1986) and most wood characteristics and properties are considered inferior to those found in mature wood or outerwood.

The occurrence and importance of corewood in *P. radiata* in fast-grown plantations in New Zealand has been highlighted in a number of wood quality studies (Walker and Woollons, 1998; Butterfield and Pal, 1998; Cown *et al.*, 1991; Cown, 1999). By convention the inner 10 growth rings are considered corewood, and on this basis corewood density is taken to be between 350 and 400 kg/m³ basic density, tracheid length to be between 1.5 to 2.5 mm long, and microfibril angle to lie between 45 and 25 degrees. In practical terms Harris and Cown (1991) argue that "for sawn timber the most damaging features of corewood will be confined to the first 3-5 annual growth layers from the pith." This statement emphasises an important feature of corewood, namely that wood characteristics and properties are improving very rapidly on moving from the pith outwards, and that the rate of change (the improvement) is greatest near the pith and becomes more gradual as the outerwood region is approached.

However, there is no definite line of demarcation between juvenile and mature wood. The duration of juvenile wood formation is influenced by genetics, environmental factors and the property being considered; and the boundary between juvenile and mature wood is often determined by the subjective judgement of the investigator (Zobel and Talbert, 1984).

2.6 Juvenile wood features

Features characterising juvenile wood include the following: wide growth rings, short tracheids, high spiral grain angle, large microfibril angle, a low percentage of latewood, thin cell walls, low density, high knot incidence, low transverse shrinkage, higher longitudinal shrinkage (Brown, 1971; Austin, 1988; Zobel, 1975). This is in

comparison with mature wood. Figure 2.7 summarises the major contrasts between juvenile (corewood) and mature (outerwood).

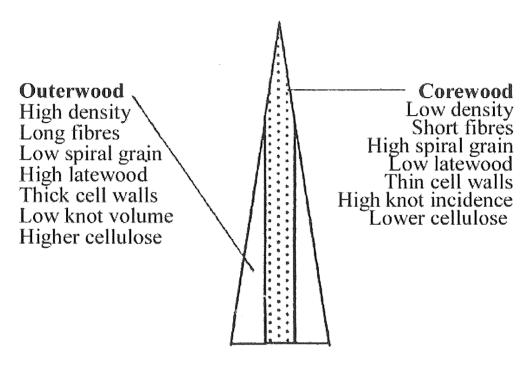


Figure 2.7 Wood quality is different in the corewood and in the outerwood (from Cown, 1992).

The thesis looks at the worst possible corewood – the wood formed in the first 1-2 years of growth in a number of seedlings and in clonal stock.

2.7 Juvenile wood quality/properties

Juvenile wood quality is important in fast-grown softwood species as it occupies such a large proportion of the merchantable stem volume. Owing to its lower density, shorter tracheids, and larger microfibril angle, juvenile wood is recognised as being lower in stiffness (MOE) and strength (MOR) than mature wood. Several studies indicate that juvenile wood has a greater effect on stiffness than on strength (Bendtsen and Senft, 1986; Bendtsen *et al.*, 1988; Addis Tsehaye *et al.*, 1991; Walker and Butterfield, 1996; Butterfield, 1998; Walker and Nakada, 1999).

2.7.1 Wood quality variation

Wood quality relates to the cumulative effect of the wood properties on some specified product or products, and it varies with tree age, species, and growth rate and site. Sometimes, in usage the term wood property and wood quality are used interchangeably.

2.7.2 General

Variations of wood quality can occur within a tree between growth rings and upward along the stems, between trees, and between the same species growing on different sites. Walker (1993), in a review of basic density, observed that the variations of basic density within a tree exemplified by the hard pines and medium- to high-density diffuse porous hardwoods have received particular attention as many important plantation species fall into these groups.

Wood quality variability exists within growth rings and between growth rings of the trees. Preston (1974) explained that in juvenile wood, especially in the first and second growth rings, the secondary walls of cells are significantly thinner and the microfibril angle be significantly larger than of the cells in the mature wood.

Wood quality varies upward along the stem in a tree. Walker (1993) stated that this variation is primarily a function of the proportion of coerwood up the height of the tree. He observed that basic density decreased and moisture contant increased on moving up the stem as the wood further up the stem have more corewood.

Harris (1981) commented on the variations in wood quality between trees. He stated that the large variations between trees may be under genetic control (because the trees have different genotypes), and it is a source for improving wood quality by selective tree breeding. This thesis looks at very young material for evidence of significant genetic variation. Again, Dadswell *et al.* (1961) discussed the variations between radiata pine growing in Australia and New Zealand, noting that these variations result from two factors, that is, heredity and environment. Characteristics such as height, stem type, crown diameter and bark thickness can be improved by genetic selection.

Variations of wood quality also exist between growing sites (environmental effects). Zobel and van Buijetenen (1989) discussed the variations of wood density between populations of the same species (loblolly pine) growing on different sites of the United states showing in Table 2. 1. And then they make an important statement, namely that natural selection does not operate on averages but on extremes, ie. it is extreme frosts rather than the mean annual temperature that matters. Further they conclude that selection can be very effective from a large population, selecting the best trees from the best unrelated families to get trees having superior characteristics.

Table 2.1 Variations of wood density in loblolly pine grown In the southeastern coastal plain of the United States.

Tree grown location	Specific gravity	memoca
Central Florida	0.58	
Middle Georgia	0.54	
South Carolina	0.54	
North Carolina	0.53	
Virginia (South)	0.52	
Virginia (North)	0.47	

For structure timber, most wood scientists would consider stiffness and strength to be among the most important properties. These are concerned with the ability of wood to resist external forces and loads.

2.7.3 Stiffness and strength

2.7.3.1 Stiffness

In order to define the terms stiffness and strength, it is necessary to understand the meaning of stress and strain (Gordon, 1973, p. 26-60).

The stress is simply the load per unit area of material, that is to say:

$$S = P / A$$

Where, S = stress; P = load; A = area.

The strain is the amount of stretch under load per unit length of material, or the fractional change divided by the original length.

e = 1/L

Where, e = strain; I = total amount of stretch; L = original total length.

Stiffness (MOE, or, Young's modulus) in tension describes the elastic extension of the material: when the material is under load. The initial slope of the stress-strain diagram (or the load-extension diagram) is the elastic modulus or stiffness of that material.

The slope is taken to be the initial linear part of the stress-strain curve. In a tension test the elastic modulus is called Young's modulus. The calculation of the modulus of elasticity is more complex in a bending tests (see Walker 1993, p.329 - 336).

The initial stiffness, flexible, or springy nature of a material, whether deflecting under a bending load or resisting buckling under a compressive load, can be related to the modulus of elasticity (Figure 2.8).

2.7.3.2 Strength

Stiffness = Initial stress /Initial strain

Strength is the force/unit area or stress needed to break a sample. That is, strength is defined in terms of the maximum force that the material sustains prior to failure. It expressed in terms of the force per unit area, or the stress.

The strength of wood can be measured by testing in tension, in compression and in bending – as well as in other modes that are not discussed in this thesis. For example, the measurement of the maximum strength of wood in bending is called the modulus of rupture (MOR); and the maximum stress in compression parallel to the grain is called the maximum crushing strength (MCS). A piece of lumber is strong in one respect but weak in another (Gordon, 1973; Walker, 1993; Cown, 1999). Wood is three or four times as strong in tension as it is in compression because the cell walls fold up in compression.

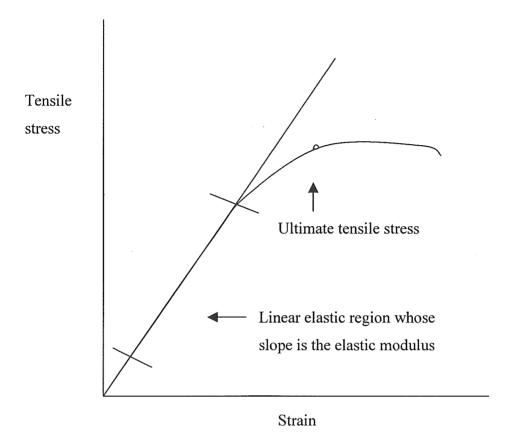


Figure 2.8 A diagram shows when a material is under load, at first the relation between load and extension is linear and reversible.

Under this condition (Figure 2.8) the ratio of stress to strain is modulus of elasticity (MOE). The maximum stress that the material sustains in tension is called the ultimate tensile stress. In a compression test maximum value would be the maximum crushing strength (MCS).

2.7.3.3 Inferior quality of radiata pine corewood

Addis Tsehaye *et al.* (1998) given the results of a study on radiata pine grown in Canterbury, New Zealand. The juvenile wood (corewood) had inferior quality compared with mature wood (outerwood). These results are shown in Table 2.2.

Table 2.2 Clearwood stiffness (MOE) and wood characteristics of radiata pine (*Pinus radiata*) logs from a stand in Canterbury, New Zealand.

(For the high and low stiffness trees, further distinguished according to corewood and outerwood, after Addis *et al.*, 1998).

	Low stiff	ness trees	High stiffness trees		
	Corewood Outerwood		Corewood	outerwood	
MOE (GPa)	4.0	7.8	7.2	12.5	
Air dry density (kg/m ³)	486	506	498	580	
MFA (degrees)	33.9	24.6	23.4	16.2	
Tracheid length (mm)	1.9	3.1	3.0	3.5	
Cellulose (%)	40.0	43.3	43.5	45.0	
Lignin (%)	28.0	26.4	27.6	26.2	

In subsequent sections the literature will be review wood properties including anatomical, physical, and mechanical properties that concerning the juvenile wood especially in radiata pine. The reasons for poor wood quality of corewood are discussed.

2.8 Anatomical characteristics

Anatomical properties to be reviewed include microfibril angle and tracheid length as they play major roles in determining the stiffness of juvenile wood from fast grown pine plantations.

2.8.1 Microfibril angle

The cellulose microfibrils in the cell wall are laid down during the process of cell wall thickening prior to the deposition of lignin. The cell wall is finally composed of the framework substance (about 42% microfibrils) and matrix substances (about 30% lignin and 28% hemicelluloses, with mannans predominating in conifers) (Preston, 1974, p.276). The cellulose microfibrils are oriented at an angle to the longitudinal axis of the tracheid. Because the S2 layer is thicker than any other layer within the cell wall, its behaviour largely determines the properties of wood. Thus the term microfibril angle is taken to refer to the angle of the microfibrils in the S2 layer. This angle is called the microfibril angle (MFA). It has a major influence on many of the physical and mechanical properties of the cell wall (Fig. 2.9). The microfibril angle is also a useful

indicator of the presence of compression wood in conifers, as compression wood cells have a large microfibril angle in the S2 layer (Cave and Walker, 1994; Walker and Butterfield, 1996; Butterfield, 1998).

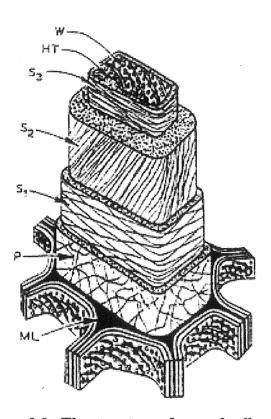


Figure 2.9 The structure of a wood cell wall

ML-middle lamella, P- primary wall, S1- first layer of secondary wall, S2- secondary layer of secondary wall, S3- third layer of secondary wall, Ht- helical thickening, W-warts layer (when present) (from Butterfield and Meylan, 1980).

Figure 2.9 shows schematic representation of the cell wall ultrastructure of a softwood tracheid, showing the orientation of the cellulose microfibrils in the various layers of the cell wall.

Dadswell and Wardrop (1959) emphasised that the microfibril angle is important in determining the strength properties of individual fibres. There is a relationship between microfibril angle and the tensile strength of individual fibres, a small microfibril angle being related the high tensile strength.

Cave (1968, 1969) produced experimental data supported by theoretical analysis demonstrating that the microfibril angle has an enormous effect on wood properties, and in particular very strongly determines the stiffness of wood in the corewood.

A workshop at Westport (Butterfield 1998) produced a large amount of evidence demonstrating that the microfibril angle in the S2 wall layer of the individual wood cells is one of the main determinants of stiffness in wood. A high microfibril angle results in low stiffness as well as resulting in high longitudinal shrinkage. Both effects are particularly relevant for fast grown plantation softwoods.

2.8.1.1 Microfibril angle measurement

Microfibril angle can be measured by a number of techniques:

Direct by electron microscope observation of wall features

Iodine crystal deposition angle (Bailey and Vestal, 1937)

Angle of fibre pit inner aperture (Donaldon, 1991)

Cell wall checking (Marts, 1955)

Micro Raman spectroscopy (Pleasants et al., 1997)

Polarised light extinction (Preston, 1952)

Confocal microscopy (Vebelen and Stickens, 1995)

X-ray diffraction (Cave, 1966; Preston, 1974)

These techniques and their accuracy, reliability and easy of use are compared by Huang et al. (1998). Huang studied southern pine lumber, he estimated microfibril angles by some above methods and found the magnitude of variations can be ranked as Pit Aperture > Ultrasonic Checking > Iodine Staining > Polarised Light. Further he suggested the x-ray method was better than by other methods when measuring large numbers of samples. The X-ray diffraction technique requires that the microfibril angle be measured by iodine staining for calibration, the correlation between them is, as expected, very good (r=0.96).

The x-ray method for measuring microfibril angle was refined by Cave (1966), having being used since the 1930s. The angle measured using this method is called the Cave-T angle or angle T. The angle T is an indicator of microfibril angle and is not the same

thing as microfibril angle measured by iodine and other methods. However calibrations between these methods have carried out by some researchers. For radiata pine, Meylan (1967) calculated that the microfibril angle (iodine) = 0.612T + 0.843. It is now known that this equation does not fit all woods. MeGraw (1998) showed that MFA (iodine) = 0.91T - 10.71 for his loblolly pine samples. He also notes that MFA (iodine) = 0.93T - 12.35 for earlywood and MFA (iodine) = 0.92T - 10.35 for latewood samples in this species.

2.8.1.2 Microfibril angle variation

Microfibril angle is a variable wood property that is influenced by the position in the tree, age of tree, species, growth conditions etc. Juvenile wood has larger microfibril angles than mature wood (Donaldson, 1992, 1993; Butterfield and Pal, 1998; Dupont and Mariaux, 1988; Walker and Nakada, 1999).

Addis Tsehaye *et al.* (1998) reported that the corewood of radiata pine grown in Canterbury of New Zealand had larger microfibril angle (33.9 and 23.4 degrees for low and high stiffness trees respectively) than outerwood (24.6 and 16.2 degrees for low and high stiffness trees respectively). The values are "true" microfibril angles corrected using Meylan's equation discussed in the previous section.

Butterfield (unpublished data) has measured the microfibril angle in radiata pine from a dry, slow-growing stand on the Canterbury Plains. In normal wood (free of compression wood) he found that the mean microfibril angle in the earlywood decreased from 55 degrees in ring 5, to 45 degrees at ring 10, to 25 degrees at ring 15 (these values are derived by the Cave-T method using x-ray diffraction).

Kretschman and Bendtsen (1992) working with loblolly pine suggested that a segmented least-squares regression would best fit the microfibril angle-age relationship. Using their data and earlier work as a guide, a segmented least-squares regression was fitted to the data as shown in Figure 2.10.

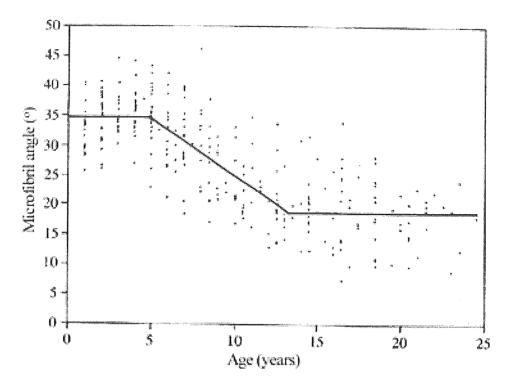


Figure 2.10 Changes in microfibril angle with ring number.

Data derived from loblolly pine trees from the southern United States (after Kretschman and Bendtsen 1992). The plot graph indicates that the juvenile wood (age 1 to 5) has larger microfibril angle than mature wood (age 15 to 25), and microfibril angle decreases rapidly from ring 5 to 15 showing a transition period. Again these values are "true" values.

Donaldson (1993) investigated the microfibril angle in five 22-yr-old *Pinus radiata* trees growing in the Kaingaroa Forest, New Zealand. The microfibril angle was measured for every growth ring at butt, breast height, and at 7, 12, 18, 23, and 30 m height. Mean micrfibril angles varied from 9° to 55° with the highest angles occurring in the juvenile wood of the butt log (Figure 2.5). The microfibril angle in any particular growth ring declined rapidly with height up the trees. As can be seen in Figure 2.5 the corewood has larger microfibril angle (18 to 36 degrees) than does the outerwood (15 to 23 degrees) in all positions of the trees. The angles were measured through pit apertures and approximate to iodine ("true") values

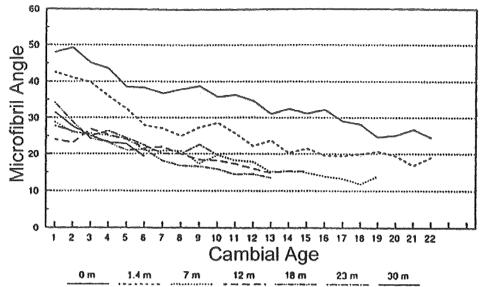


Figure 1: Variation in mean microfibril angle with cambial age and height

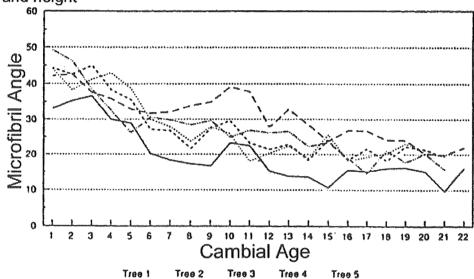


Figure 2: Variation in volume-weighted microfibril angle for corewood (rings 1-10) and outerwood with height

Figure 2.11 Microfibril angle varied with cambial age and height in the tree (above), and varied between trees (after Donaldson 1993).

Note tree 1 had smaller MFA in ring 1 and keep the smaller angle in later growth rings.

This thesis is concerned with very young wood, so it is appropriate to consider the few references that have examined such material.

Butterfield and Pal (1998) studied 3 year-old radiata pine clonal material grown in Canterbury of New Zealand. The results showed that the microfibril angle of these

young trees is large being around 60-80 degrees (Cave-T method) and varied between clones and the growth rings.

Downes *et al.* (1990) measured 4-month-old radiata pine seedlings grown in a glasshouse in Australia. The microfibril angle was large being around 46 degrees (polarised light microscope), and there were no significant differences between treatments (straight and leaning seedlings).

Further work by Downes *et al.* (1993) examined 2-yr-old radiata pine seedlings grown in Australia. The results indicated that these young trees had large microfibril angles being around 43 degrees (polarised light microscope), and the variations in MFA do not reach a statistically significant level between the four genetic sources and treatments (cuttings and seedlings, staked and unstaked).

2.8.1.3 Microfibril angle effect on wood stiffness

Previous work on microfibril angle has demonstrated that the microfibril angle is one of the main determinants of wood stiffness (Cave, 1968; 1969; Meylan and Probine, 1969; Butterfield and Hanna, 1994; Cave and Walker, 1994; Walker and Butterfield, 1996; Butterfield, 1998). In general, the lower the microfibril angle the greater the longitudinal/axial stiffness of the wood. The helical inclination of the cellulose microfibrils within the cell walls is analogous to the spiral inclination of wire in a stretched spring. Thus the stiffness of a piece of wood is determined largely by the microfibril angle and, again by analogy, just as a lazy spring can be easily stretched and fencing wire is very stiff and inextensible, so the stiffness of wood increases greatly (four or five fold) as the microfibril angle decreases from 40° (a lazy spring) to 10° (approximating to a taut fencing wire) (Walker & Nakada 1999). This analogy is not mathematically rigorous but is conceptually valid.

Cave (1969) reported a fivefold increase in the stiffness of cell wall tissue in the earlywood of *Pinus radiata* as the microfibril angle decreased from 40 to 10 degrees (Fig. 2.12). This figure compares Cave's fundamental equation (describing the relationship between microfibril angle and stiffness of the cell wall) and experimental data.

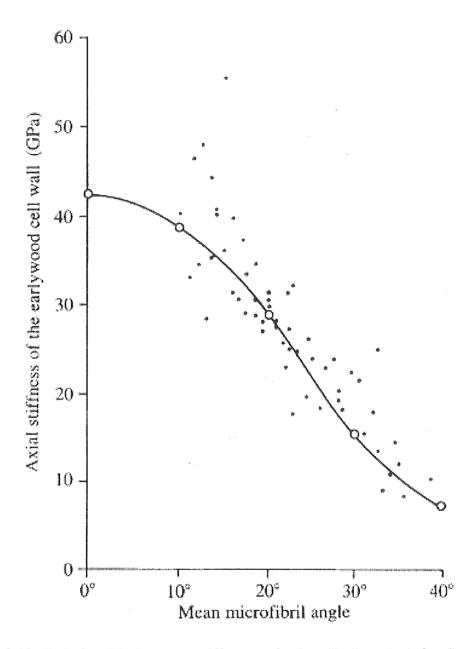


Figure 2.12 Relationship between stiffness and microfibril angle (after Cave 1968).

Similarly, Cowdrey and Preston (1966) observed a six-fold increase in the stiffness in the earlywood of *Picea sitchensis* as the microfibril angle decreased from 40 to 10 degrees.

It is important to consider both Figures 2.5 and 2.6. In very young wood the microfibril angle is expected to be large and when the microfibril angle is large it has little effect on the axial stiffness of wood. This thesis examines seedlings and young clonal plantlets

and Figures 2. [] and 2. [2] warn that correlations (if any) between microfibril angle and stiffness are likely to be weak.

This warning applies to the study by Downes *et al.* (1993) on 2-yr-old *Pinus radiata* seedlings and cuttings from 4 genetic sources (GSHO, SAXSO, 1164, and 1181) grown on fertilised ex-pasture in New South Wales, Australia in 1990. However, a positive correlation of microfibril angle and stiffness (by 3 points bending of living stem) was evident. Again using glasshouse-grown very young material (Downes and Turvey 1992) stiffness by bending was used in addition to stem lean and no such relationship was found.

However, a study on 3-year-old clonal materials by Butterfield and Paul (1998), clearly identifies the role of microfibril angle to stiffness. The study results showed that the clone 3 was stiffer with smaller microfibril angle (about 60 degrees, Cave T) than clone 9 (about 70 degrees) and clone 10 (about 78 degrees).

A major problem facing the utilisation of New Zealand radiata pine is its low stiffness corewood. Identifying seedlings with a smaller microfibril angle should enable the selection of stock that will produce a superior wood, since microfibril angle plays a major role in wood stiffness and it only gets smaller with increasing distance from the stem centre. With this idea in mind, this thesis examines the microfibril angle in the first and second growth rings of a number of seedlings and clonal material.

2.8.2 Tracheid length

Tracheids are the principal cells of softwood (conifers) and comprise more than 90% of the total wood volume. Juvenile wood has shorter tracheids than does the mature wood. In mature wood, they are very long cells being about 3.5 mm in length and by 0.03 mm in width, and in juvenile wood they are between 0.8 and 2.5 mm long (Bamber and Burley, 1983). Tracheid length is an important property in determining wood quality particularly in tension parallel to the grain (Senft *et al.*, 1985).

2.8.2.1 Tracheid length variation

Tracheid length is a variable property, and juvenile wood had short tracheids and mature wood had longer tracheids.

Addis Tsehaye *et al.* (1998) reported that corewood of radiata pine grown Canterbury New Zealand had shorter tracheids (1.9 and 3.0 mm for low and high stiffness trees respectively) than the mature wood (3.1 and 3.5 mm for low and high stiffness trees respectively).

Cown (1975) and Cown *et al.* (1983) give typical data for New Zealand grown radiata pine. The tracheid length in mature wood is longer than juvenile wood, from 1.5 mm close to the pith (juvenile wood zone), to 3.5 to 4.0 mm at the outer growth layers (mature wood zone), to a little over 4 mm even into the outerwood of very old trees.

Young et al. (1992) examined 25-yr-old radiata pine grown in Kaingaroa Forest in the central North Island of New Zealand. The mean within-tree tracheid length distribution values are given in Table 2.3. Note the very short tracheid length in the second ring at ground level. This is essentially the oldest material that will be examined in this thesis.

Table 2.3 Mean tracheid length (mm) for radiata pine trees (after Young, 1992).

Height	Ring number from the pith					
(m)	2	5	10	15	20	
0	1.6	2.6	2.9	3.4	3.7	
6	2.1	2.8	3.6	4.2		
11	2.5	3.0	3.7	3.8		
16	2.2	3.0	3.8			
21	2.2	3.1	3.5			
26	2.7	3.0				

Tracheid length varies with region, elevation and site. Cown and Kibblewhite (1980) reported that tracheid length in radiata pine varies countrywide. They showed a gradual decrease in fibre length from the North to South of New Zealand. About 3.3mm (ring

15) to 4.1 mm (ring 45) in the North (Auckland) and 2.6 to 3.6 mm at same growth rings in the South (Canterbury).

Tracheid length in other species shows similar variation pattern. In a study on 18 *Pinus contorta* trees from South and Central Finland carried out by Saranpaa (1985) the average tracheid length varied from 1.7 to 3.5 mm (shortest near pith). The diameter and cell wall thickness also increased with increasing distance from the pith.

The tracheids are much shorter in young seedlings (generally less than 1 mm) than are found in even in juvenile wood of mature trees. Moore (1999) studied tracheid length on radiata pine seedlings and clonal plantlets. The results indicated that the tracheid length was highly variable within and between seedlings at all levels in the stem (root collar, and 20, 40 cm from ground). These young tracheids were very short being around 0.85 to 1.0 mm long that is shorter than the juvenile wood in mature trees.

2.8.2.2 Influence of tracheid length on wood stiffness and strength

Addis Tsehaye *et al.* (1998) report their study results on radiata trees that the high stiffness trees had longer tracheids (3.25 mm) and the low stiffness trees had shorter tracheids (2.5 mm). Tracheid length is strongly correlated to stiffness (r = 0.928), the longer the tracheids are the stiffer the wood.

A study on sugi (*Cryptomeria japonica*) trees grown in Tottori Prefecture, western Japan, investigated tracheid length and the modulus of elasticity. The tracheid length was highly correlated with Young's modulus in compression and bending (MOE). The longer the tracheids are the higher the modulus (Furukawa and Ishtt, 1998).

Tracheid length has long been considered an important property determining wood quality. Longer tracheids result in stronger wood (Bamber and Burley, 1983) and the shorter tracheids observed in faster grown conifers implying lower tensile strength (Senft *et al.*, 1985).

Early work by Wardrop (1951) reported on the relationship between the breaking load in tension and tracheid length. The material that Wardrop worked with came from a 12

year-old radiata pine tree that had grown on a lean. This allowed him to collect samples from zones containing either only normal wood or only compression wood. The breaking load increased an increase in tracheid length (Figure 2.13).

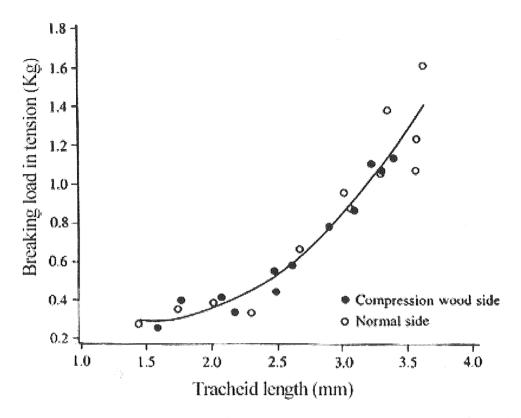


Figure 2.13 A plot of breaking load against tracheid length (after Wardrop 1951)

In Figure 2.13 it is clear that the tracheid length contributes to breaking load. It is significant that in the mature wood, a further increase of 1 mm increases the breaking load by 0.8 kg (a significant increase), but in the juvenile stage, an increase 1 mm only increases the breaking load by 0.3 kg. In paper making a fibre length of at least 2 mm is necessary to provide moderate strength.

2.8.2.3 Tracheid length and microfibril angle

Microfibril angle is observed to be inversely related to tracheid length (Wardrop and Dadswell, 1950; Wardrop, 1951; Addis Tshye *et al.*, 1998; Xu-youming *et al.*, 1999).

Addis Tsehaye *et al.* (1998) reported their study results on radiata pine that the tracheid length well relate to microfibril angle (Cave T). The correlation coefficient is -0.897,

that is, the longer tracheids have smaller microfibril angles and the shorter tracheids have larger microfibril angles.

Microfibril angle was measured in samples of wapa (*Eperua spp.*). Dupont and Mariaux (1988) found the increased microfibril angle corresponded with reduced fibre length.

A study on microfibril angle and tracheid length on slash pine (*Pinus elliottii*) was carried out by Xu-youming *et al.* (1999). Wood samples were taken from 15 trees (17-year-old) grown in 3 sites in Guangdong, China. Results showed that the sites were significantly influence on microfibril angle and tracheid length. The microfibril angle and tracheid length were linearly, negatively, and significantly correlated each other within a tree.

2.9 Physical properties

Of all physical properties of wood, density is a main factor affecting on wood strength and stiffness. Because of its importance, the wood density will be reviewed in this section.

2.9.1 Density

Wood density is a measure of the mass of wood substance per unit volume. It can be expressed in a number of ways which include green density (fresh wood weight/fresh wood volume in kg/m³), basic density (dry wood weight/green wood volume in kg/m³) and air-dry density (measured at 12 percent moisture content in wood). New Zealand radiata pine can be described as a medium density softwood having an overall basic density of around $400 - 420 \text{ kg/m}^3$ (Walker, 1993; Cown *et al.*, 1991; Cown, 1999).

2.9.2 Density variation

Density is a variable wood property affected by several factors, such as tree age, growing conditions, tree genotypes, and is thus subject to much variation (Harris, 1965). The density variations influence wood stiffness and strength, which produces different values at different tree positions, ages, and sites.

The variations of wood density have been extensively reviewed by Cown (1992, 1999). These studies indicated that the distinct difference in wood density across a single growth ring is primarily a response to seasonal climatic variations. The density variation across a growth ring – from earlywood to latewood - far exceeds the density variation between trees.

The density variation from pith to bark is a significant feature in radiata pine. Cown and McConchie (1980) examined wood density variations in an old-crop stand of radiata grown in Kaingaroa Forest, New Zealand. The samples were taken at different heights up the stem for wood properties testing. The wood density increases from the centre of the stem outwards in all cases (Figure 2.14). At breast height the density increases from 386 kg/m³ close the pith to 480 kg/m³ in outerwood. Concerning the low density corewood, Cown and Mcconchie (1980) reports that there is little difference in quality between the corewood in the top parts and the corewood in the butt log which was formed in earlier years.

Density variations up the stem have been investigated by a number of scientists. Cown and McConchie (1983) studied basic density on 12-year-old radiata pine from Kaingaroa Forest. The results showed that a drop in the mean density of 20 kg/m³ between the butt and 3-metres height up the stem followed by a decrease of about 10 kg/m³ for each further 3-metre height increment to the apex.

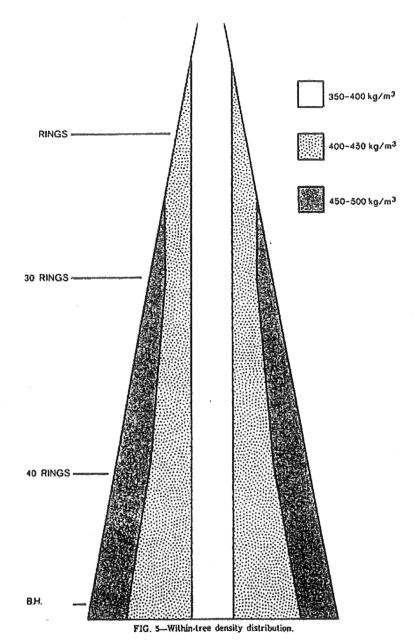


Figure 2.14 Density distribution within a tree showing a low density in the corewood which increases on going outward from the centre in the tree (from Cown and McConchie, 1980).

An extensive survey of radiata pine throughout New Zealand reported by Cown (1974) showed that the wood density decreases with increasing latitude and altitude (Figure 2.15). The figure clearly shows that the density decreases from the North (Auckland) to the South (Canterbury). Further the corewood had lower density than outerwood.

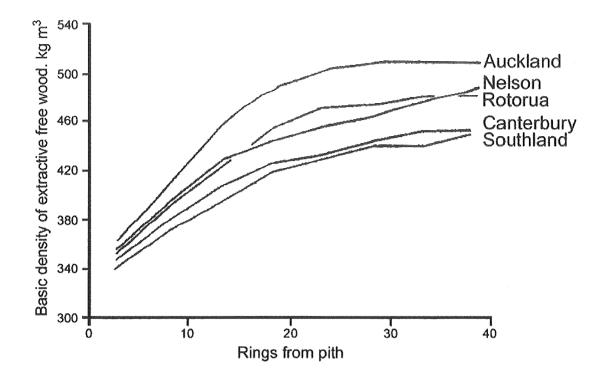


Figure 2.15 Wood density distribution in New Zealand radiata pine plantation forests (from Cown, 1974).

An extensive survey of density in radiata pine (30-35yr) was carried out in New Zealand by Harris (1965). He showed that variations in corewood density were associated with 51% of the variations in outerwood density. The correlation between corewood and outerwood density is not strong (r=0.7) but useful in practice. Again this work points to the opportunity for early selection of wood properties.

The density is very low in young radiata pine seedlings. Downes *et al.* (1993) tested the density on 2-year-old radiata pine seedlings grown in Australia. The results showed these very young seedlings have very low densities being between 240 to 270 kg/m³. The statistical differences in density were not found between seedling sources (267, 276, 237, and 257 kg/m³ for each family respectively) and between treatments (254, 267, 248, and 270 kg/m³ for unstaked, staked, cutting, and seedling respectively).

2.9.3 Density effects on wood stiffness and strength

The literature dealing with the density of conifers shows density to be a major factor to determine wood quality (Walker, 1993; Mishiro and Eiji, 1997).

Wood density and strength properties of radiata pine, grown on different sites in New Zealand, have been studied. A strong correlation was found between density of airdried wood and strength properties. Thus, wood density appears to be a good index of wood quality in radiata pine (Mishiro, 1984).

Mishiro and Eiji (1997) reported on sample logs (from *Cryptomeria japonica* trees aged over 35 years old) that were collected from four sites in Honshu, Japan. A high linear correlation was found between air-dried density and stiffness in both mature and juvenile wood.

Small samples of Caribbean pine (*Pinus caribaea* var. *hondurensis*) wood grown in Trinidad were measured for specific gravity, modulus of elasticity, and modulus of rupture in bending. Linear relations between specific gravity and mechanical properties were better for the outerwood than for the corewood. Corewood had weaker relationship between MOR and MOE (r = 0.22) than outerwood (r = 0.78) (Schneider *et al.*, 1991).

Pearson and Gilmore (1971) studied loblolly pine, the results for bolt log material indicated that modulus of rupture and modulus of elasticity were very strongly correlated with basic specific gravity, the correlation coefficients being 0.93 and 0.89 respectively (Figure 2.16).

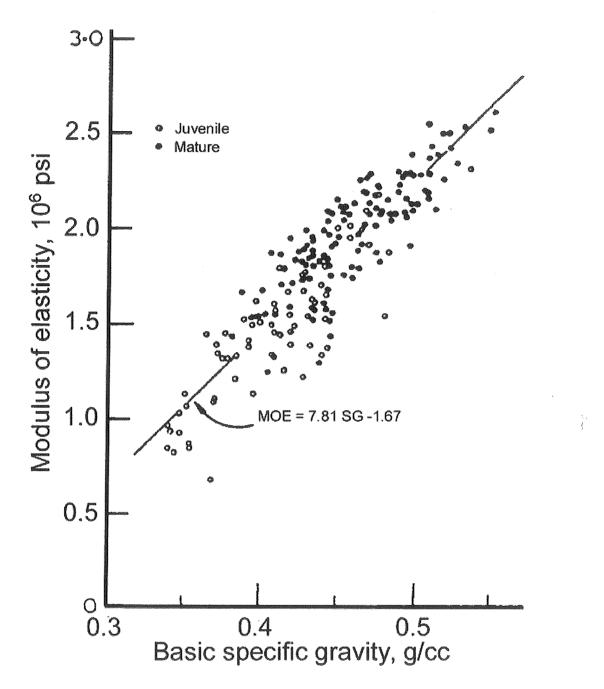


Figure 2.16 Modulus of elasticity at 12% moisture content vs. basic density from all samples except butt logs (from Pearson and Gilmore, 1971).

Note that the MOE and density well related each other in both of juvenile and mature wood samples.

2.10 Mechanical properties

The mechanical properties are important for assessment wood quality. For structure timber, the mechanical properties to measure might include stiffness (MOE), maximum strength (MOR), and maximum crushing stress (MCS) etc.

2.10.1 Variation of mechanical properties

The mechanical properties, like other wood properties, are variable properties as they affected by tree age, species, growing conditions, and as well as by wood characteristics, such as MFA, density, tracheid length that have been reviewed above. Juvenile wood is softer and weaker, whereas the mature wood is stiffer and stronger when compared to each other.

Vertical variations of the mechanical properties in radiata pine were studied by Langlands (1938). The samples (20 x 20 mm clearwood) taken from different height (divided into five 2.4 m sections) of 33-year-old radiata pine trees. The results showed that bending strength was reduced by 2 to 5% from the 2.4 to 4.8 m section, and by 5% moving up from the 2.4 m to the 7.2 m section, and by 10% moving up to the 9.6 m the height of the tree. And the compression strength reduced about 19 to 22% up the tree.

Tree growing location effecting on mechanical properties was examined by McAlister and Clark (1991). The bending properties of clearwood samples from juvenile and mature wood of loblolly pine (*P.taeda*) in USA were measured. Samples were collected from three geographic locations (Dooly, Spadling, and Clark Country). The results indicated that the growth location was a significant factor effecting specific gravity, modulus of elasticity, and bending strength for both juvenile wood and mature wood. The samples from Dooly Country location were 50 to 80 % higher in stiffness and 15 to 20% higher in bending strength than the samples from the other two geographic locations.

Mechanical properties significantly varied with age. Koch (1966) first observed the poorer mechanical properties of juvenile wood in structural lumber. He observed that

with southern pine the veneer core studs had lower bending strength and stiffness than that expected for southern pine stud grade in general.

Juvenile wood has a lower stiffness than mature wood. Addis Tsehaye *et al.* (1991) focussed on the properties of the poorest wood in the tree, ie boxed-pith lumber. They measured the bending and tensile strength of radiata pine from Nelson province, New Zealand. This with-pith juvenile wood was stronger but less stiff than expected when compared with the values in the design code (Table 2.4).

Table 2.4 A comparison of strength and stiffness by tension with the design code (Standard Association of Australia, 1998) (after Addis Tsehaye *et al.*, 1991).

Grade	Tension strength	Stiffness	Tension strength*	Stiffness*
	(MPa)	(GPa)	(MPa)	(GPa)
F8	4.7	8.6	5.2	9.1
F5	3.5	6.7	3.3	6.9
F4	2.9	5.7	2.6	6.1

^{*} is the value of the design code.

Walker and Nakada (1999) report on results for radiata pine grown in Canterbury (New Zealand) and on sugi (*Cryptomeria japonica*) trees grown in Japan respectively. Radiata pine corewood had lower stiffness (5.6 GPa) than the outerwood (10.2 GPa). And the corewood in sugi trees had lower stiffness (4.8 GPa) than outerwood (5.3 GPa).

The poor mechanical properties of the southern pines, noted by Koch (1966), are a general feature of many species, particularly of pines. In the United States, several studies have been conducted on the properties of Douglas-fir and southern pine dimension lumber cut from plantations. In lumber cut from a 75-year-old Douglas-fir plantation, ultimate tensile strength (UTS) and modulus of elasticity (MOE) of 2 by 4s, (50 x 100 mm) composed entirely of juvenile wood were about 60 and 72%, respectively, of those properties of 2 by 4s lumber cut entirely from outerwood (Bendtsen 1988).

David and Bendtsen (1992) reported the studied results on 28-year-old loblolly pine grown in the North Carolina, USA. The stiffness and strength decreased with

increasing amounts of juvenile wood. Average ultimate tensile stress and stiffness values of samples composed entirely of juvenile wood were from 45 to 63% of those samples composed entirely of mature wood.

The study by Bendtsen and Senft (1986) is often quoted in the literature, partly because the article brought the issue of poor wood quality in corewood to the attention of American foresters. This article is discussed later in more detail as it contains important data on the relationship between microfibril angle and stiffness. Here, it provides a useful brief footnote that the problem of corewood is also observed in hardwoods, but the problem is far less acute. Their study was of plantation cottonwood (*Populus deltoides*) as well as of loblolly pine. Average mechanical properties of juvenile wood ranged from 47 to 63% of those for mature wood in pine and from 62 to 79% in cottonwood.

Early juvenile wood has distinctly poorer properties than juvenile wood that is formed a few years later. In a study on 8-years-old plantation Caribbean pine from Puerto Rico (Boone and Chudnoff, 1972), the specific gravity (density), bending stiffness, and strength of small clear specimens of plantation grown wood were less than 50% of the published values for virgin timber (largely outerwood) of the same species. In this study, differences between juvenile and mature wood were probably accented because the trees were very young.

Concerning age influencing mechanical properties, Bendtsen and Senft (1986) concluded that the large change in mechanical properties with age apparently reflected the composite effect of increasing specific gravity, cell length, and microfibril angle.

Downes *et al.* (1992) determined the mechanical properties on 2-year-old radiata pine seedlings grown in Australia and found both of stiffness (MOE) and strength (MOR) were low in these very young seedlings. No significant differences in stiffness and strength were found between seedling families and treatments (Table 2.5).

Seedling family Treatment Variable **GSHO** SAXSO 1164 1181 Unstaked Staked Cutting Seed MOE (GPa) 0.60 0.51 0.44 0.57 0.59 0.40 0.50 0.55 MOR (MPa) 16 16 15 14 12 16 14 16

Table 2.5 The mechanical property means of 2-year-old radiata pine seedlings (after Downes et al. 1992).

Bendtsen (1985) indicated that all research has demonstrated that juvenile wood is substantially lower in mechanical properties than is mature wood. Ratios of modulus of rupture (MOR) and stiffness (MOE) values for juvenile wood compared to those for mature wood ranged from 0.62 to 0.97, depending upon wood property, grade, and size. A large proportion of corewood in a member and its corresponding low stiffness and strength values may explain why the plantation wood generally does not meet the recommended design values.

2.10.2 Relationship between stiffness and strength

The relationships between stiffness and strength have been reported in a number of papers. Addis Tsehaye (1995) studied mechanical properties on 25-year-old radiata pine grown in Canterbury Plain, New Zealand. A linear correlation was found the modulus of elasticity (by bending) and tensile strength (r = 0.57).

Pearson and Gilmore (1971) studied on loblolly pine trees (bolts 5 feet long) grown North Carolina and found that the modulus of elasticity well correlated with the modulus of rupture (r = 0.91).

Mishiro and Eiji (1997) reported that sample logs (from *Cryptomeria japonica* trees aged over 35 years old) were collected from four sites in Honshu, Japan. A high linear correlation was found between MOE and MOR, somewhat higher, than previously reported wood properties of sugi grown in Niigata.

Butterfield and Pal (1998) studied on 3-year-old radiata pine clonal trees grown Canterbury, New Zealand. The modulus of elasticity (MOE) by compression and maximum crushing stress (MCS) were tested using 1x1x4 mm clear wood samples with straight grain. The MOE was significantly related to MCS (r = 0.604).

Part three: Compression wood properties

2.11 Compression wood in soft woods

The meristematic zone of leaning stems reacts to the resulting stress by producing abnormal wood known as reaction wood. In conifers this abnormal wood occurs on the lower side and is known as compression wood. Compression wood is a vital tissue in the gymnosperms (Timell, 1983), and has probably existed throughout the evolution of the conifers.

Compression wood can be recognised visually by its darker colour. In its severest form compression wood is characterised by short tracheids of round shape, the loss of S3 layer and thickening S2 layer with a large microfibril angle – relative to normal wood – and intercellular spaces at the corners between cells (Huhrjanskaja, 1953; Fujita *et al.*, 1979). Other features include a higher lignin content (30% lignin in normal wood, and 39% in compression wood) and lower cellulose content (50% in normal and 30% in compression wood), higher density, and high longitudinal and low transverse shrinkage when compared with normal wood (Senft *et al.*, 1985; Chang and Duh, 1988). These characters greatly influence wood quality. The severity of the abnormalities is a function of the degree of lean (Boyd and Foster, 1974), but compression wood can be found when the lean is only a degree or so.

Timell (1986) emphasised that many of the properties of compression wood are undesirable for both pulpwood and lumber. When lumber contains normal and compression wood, the high longitudinal shrinkage of compression wood causes severe warping, distortion and cross checking. This is the most serious problem in the utilisation of such sawn timber.

Compression wood varies from mild to severe and varies greatly with growth conditions, tree species, tree age, and individual tree. Most of the adverse characteristics of this type of compression wood are related to the more severe forms (Zobel and Buijtenen, 1989). Concerning compression wood classification, Burdon (1975) developed a useful practical method in his study on compression wood of 18 clones of 12-year-old radiata pine trees from different sites (Gilenbervie, Whaka,

Gwavas, and Berwick) in New Zealand. The compression wood was classified into 5 grades: (1) if latewood is patchily opaque when viewed in thin section, (2) if latewood is generally opaque, (3) if latewood is opaque and earlywood is partly opaque, (4) if latewood and earlywood are generally opaque, (5) if latewood and earlywood are highly opaque. He considered grades 1 and 2 as mild and grades 3-5 as severe compression wood.

2.12 Compression wood formation

Compression wood formation is caused by environmental stress (Timell, 1986; Cote *et al.*, 1968), such as wind action (Burdon and Low, 1992), a leaning stem (Burdon, 1975), heavy branches, fast growth (Cown, 1974; Reader and Kurmes, 1996), and tree species. It is more common in corewood (juvenile wood) than outerwood (mature wood) (Brown 1971; Harris, 1977), as young trees are lithe and easily bent, particularly in rapid growth materials (Timell, 1986; Zobel *et al.*, 1972). Burdon (1975) found it to comprise some 30-45% of the wood in 12-year old radiata pine.

Compression wood formation in radiata pine is caused mainly by wind. Burdon and Low (1992) reported on wood properties from 7 populations (5 native populations from California and 2 from New Zealand) in a *Pinus radiata* provenance-progeny trial in Kaingaroa Forest, New Zealand. Compression wood was most prevalent in the island populations, and least in those from mainland California.

Heavy branches and growth rate are other factors contributing to compression wood formation. Downes and Turvey (1992) found that heavy branching of radiata pine seedlings has been associated with stem deformation on ex-pasture sites. It was suggested that strong leaders may result in lighter branching. Cown (1974) indicated that compression wood formation was related to the rate of growth after thinning; it was not associated with increased eccentricity in the stem but was probably a response to the changed environment, eg, increased auxin production or increased wind sway in the opened-up stands.

2.13 Variation of compression wood

Amount of compression wood in the tree varies with tree age, stem position, species, and tree declination. Low (1964) studied the incidence of compression wood in 24- to 40-year-old Scots pine plantations. Compression wood varied from 5.4% to 57.1% of the merchantable volume. The prevailing wind appeared largely responsible for the initial development of stem inclination and consequent compression wood formation.

Haught (1957) studied on compression wood variation in loblolly pine, determined the amount of compression wood and found that the compression wood varied from 6% in reasonably straight trees, 9.1% in rather more crooked trees, and 67.1% in a very crooked tree. Further study by Haught (1958) indicated that in loblolly pine (*Pinus taeda*) the compression wood was 42% in corewood and only 7% in mature wood. Fewer than 10% of trees examined were found to be free from compression wood.

This work is matched by that of Bendtsen and Senft (1986) also working on loblolly pine. They recorded 35% compression wood in the early years, with a slight decrease in the percentage with ring number.

In summary, juvenile wood has more compression wood than mature wood, thus Timell (1986, Vol. 2, p. 77) states that compression wood is found more frequently in the first few growth rings at centre near the pith.

2.14 Compression wood properties

Compression wood properties are particularly important in short rotation plantation conifers. For understanding compression wood properties, the microfibril angle, tracheid length, density, and stiffness in compression wood will be reviewed in following sections. For example, Dutoit (1963) found the compression wood of radiata pine to be weaker than normal in all of its strength properties except hardness. He attributed these effects to its shorter tracheids, larger micrfibril angle, and higher density.

2.14.1 Microfibril angle and tracheid length of compression wood

Microfibril angle in compression wood is larger being about 45 degrees and tracheids are shorter than normal wood (Wardrop, 1951; Kocon, 1990; Robert, 1998).

Robert (1998) investigated the microfibril angle in a Norway spruce (*Picea abies*) wood sample containing normal and compression wood (by x-ray method). The result showed the microfibril angle was small in the normal wood zone, but increased dramatically in the compression wood zone, only to fall off gradually thereafter (Figure 2.17).

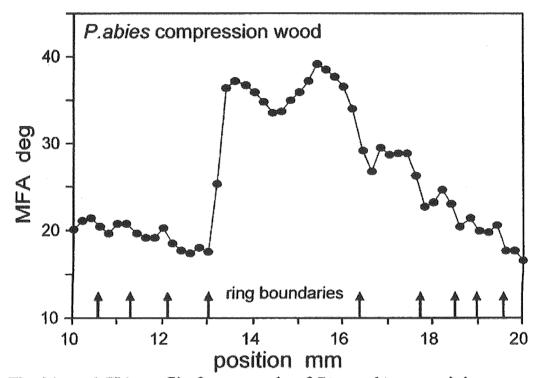


Fig. 21. MFA profile for a sample of *Picea abies* containing compression wood.

Figure 2.17 Microfibril angle in normal and compression wood areas of *Picea abies*.

From Figure 2.17, it is clear that between about 13-16 mm the tissue in a single growth ring is strongly compression wood, and that the severity of compression wood declines gradually thereafter for the next 4 growth rings (covering about 4 mm distance). The microfibril angle is small in normal wood zone, and then increases dramatically over a very short distance to the compression wood zone, to fall back gradually over the next four years.

Wardrop (1951) studied compression wood properties in first 12 growth rings of a leaning radiata pine tree, the normal wood and compression wood had different microfibril angles and tracheid lengths (Table 2.6).

Table 2.6 Properties of normal wood and compression wood (from Wardrop, 1951).

Growt ring		Compression	ı wood side o	fstem		Normal wood	d side of stem	
	Tracheid length (mm)	Microfibril angle	Latewood basic density (kg/m²)	Breaking load (g)	Tracheid length (mm)	Microfibril angle	Latewood basic density (kg/m³)	Breaking load (g)
1	1.59	43	483	261	1.44	46	436	278
2	1.77	•	489	400	1.75	+	462	356
3	2.08	45	491	414	2.02	41	391	386
4	2.18	42	531	340	2.30	37	452	336
5	2.49	42	522	445	2.67	40	505	669
6	2.48	***	568	552	3.02	•	545	961
7	2.61	38	568	585	3.07	33	515	881
8	2.90	No	617	780	3.32		545	1065
9	3.10	33	694	872	3.36	30	630	1387
10	3.24	φ.	633	1110	3.63	•	660	1615
11	3.41	35	606	1139	3.58	22	600	1238
12	3.32	34	712	1073	3.57	4	550	1075

From Table 2.6, it is noted that in the ring 1, there was no difference in microfibril angle between compression wood and normal wood, but after ring 3, the microfibril angle clearly became smaller in normal wood than in compression wood. The microfibril angle decreased steadily from pith to cambium in both wood types. Tracheid length was longer in normal wood than compression wood after ring 3. The density was significantly higher in compression wood than in normal wood in all growth rings.

Another study on tracheid length in normal and compression wood was reported by Ishengoma *et al.* in 1990. Twenty sample trees of 29-year-old *Pinus patula* from the Meru Project in Northern Tanzania were used to investigate tracheid length in normal and compression wood. The result showed that mean tracheid length of normal wood was 4.6 ± 0.3 mm while that of compression wood on the under side was 3.4 ± 0.2 mm; and tracheid length in compression wood was on average 35% shorter than in normal wood.

2.14.2 Density of compression wood

Compression wood has a significantly higher density than normal wood (Shelbourne and Ritchie, 1968). Ishengoma *et al.* (1990) studied wood basic density in normal and compression wood of 29-year-old *Pinus patula* from the Meru Project in Northern Tanzania. The results showed the basic density for normal wood to be 425 kg/m³, while the compression wood on the under side was 474 kg/m³. The compression wood basic density was significantly greater (by 12%) than that of normal wood.

The specific gravity of compression wood from conifer stems has been reviewed by Timell (1986, p.481). The density of compression wood in different species is different. The compression wood density is 40% heavier than normal wood in *Pinus ponderosa*, but in *Pinus taeda*, the difference is only 15%. Timell (1986, p. 479) reported that in *Pinus radiata* the air-dry specific gravity are higher in compression wood than in normal wood as reported by several researchers (Table 2.7).

Table 2.7 Comparison of specific gravity (air-dry) between compression and normal wood in radiata pine (after Timell, 1986, p.479).

Compression wood	Normal wood	Ratio	References
(kg/m^3)	(kg/m^3)		
470	401	1.17	Dutoit,1963
730	460	1.59	Kibblewhite, 1973
358	357	1.00	Harris, 1977
697	485	1.44	Nicholls, 1982

It is noted from Table 2.7 that the compression and normal wood had same density (from Harris, 1977). Similarly, and contrary to many reports, Shelbourne and Ritchie (1968) did not find any relationship between amount of compression wood and specific gravity in 11-year-old loblolly pine. The range in values reported in Table 2.7 may reflect the severity of the compression wood studied.

2.14.3 Stiffness and strength of compression wood

Lower stiffness in compression wood has been reported by several authors (Timell, 1986; Dhubhain *et al.*, 1988). Structurally sized boards of Sitka spruce (*Picea sitchensis*) from County Tipperary, Irish Republic, containing compression wood were

machine graded and tested for stiffness (MOE) and bending strength (MOR). The results indicated that the stiffness in static bending of boards decreased as the percentage of compression wood increased. Compression wood did not appear to influence strength (MOR) or machine grade output. More worryingly, 70% of boards containing more than 10% compression wood ruptured in a brash manner in a preliminary test of 27 specimens, which indicates that such timber can fail under impact without warning (Dhubhain *et al.* 1988).

Pechmann (1969) studied the formation of compression wood with examples (from Switzerland and south Germany) showing also the influence of provenance, sites, and forest association type. Data are reported on the variation in the modulus of elasticity for a *Pseudotsuga menziesii* stem (with a one-sided crown and paraboloidal cross-section) and for a normal stem, showing abnormally low stiffness (MOE) values (at a given wood density) in the compression wood.

The vibration method was used to estimate the dynamic modulus of elasticity (MOE) of compression wood of *Pinus densiflora* and the values were compared with those of static bending. Dynamic stiffness (and resonant frequency) of compression wood decreased, whereas that of normal wood increased, with an increase in specific gravity. There was a high correlation between dynamic and static stiffness values in both of compression wood and normal wood (Hong and Byeon, 1985).

Wordrop (1951) measured the breaking load for thin microtomed sections against density for normal wood and compression wood samples of radiata pine. The compression wood had a lower failure load than the normal wood under same density (Figure 2.18). Wardrop (1951) interpreted the lower values in compression wood in terms of the larger microfibril angle and shorter tracheids relative to those found in normal wood.

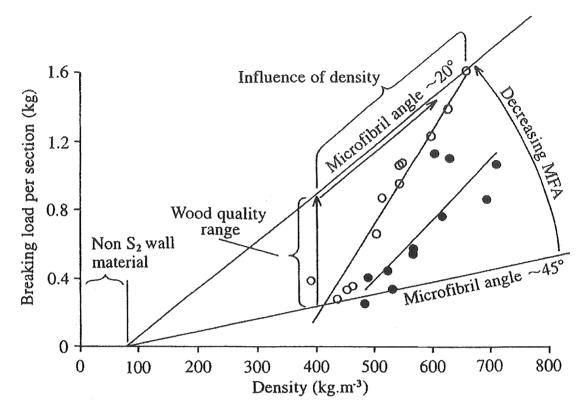


Figure 2.18 A reinterpretation of Wardrop's data (adapted from Wardrop, 1951). Wood quality confines the breaking load within an envelope bounded by the lower juvenile wood/compression wood line (short fibres and large microfibril angle) and the upper outerwood line (long fibres and small microfibril angle)(from Walker and Woollons, 1998).

2.15 Properties of wood type (compression and opposite wood)

There has been considerable discussion on the properties of wood formed on the opposite side of the stem to compression wood. Most people find that opposite wood is very similar to normal wood. For example, Timell (1973) reported that opposite wood has exactly the same lignin, cellulose, and hemicellulose content as the corresponding normal wood. However, Larson (1969) thought that opposite wood may not be normal because it sometimes has a higher cellulose and lower lignin content than normal wood. A different report by Nicholls (1982) suggested that opposite wood had slightly longer tracheids than normal wood.

Compression and opposite wood properties have been studied on radiata pine trees by Nicholls (1982). His results are shown in Figure 2.19.

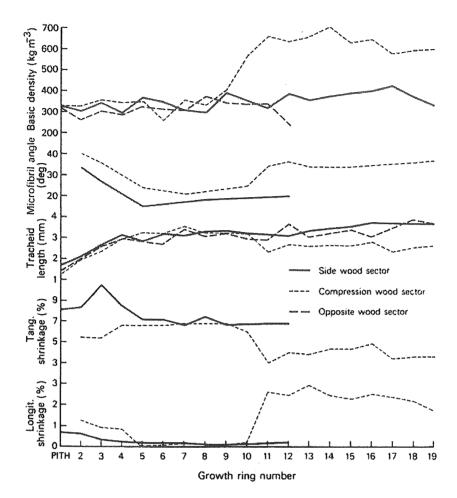


Fig. 11. The variation in longitudinal and tangential shrinkage, average tracheid length, microfibril angle and basic density of the early wood of successive growth rings from the pith in the side-wood, compression-wood and opposite-wood sectors of a disk from the butt of tree 52.

Figure 2.19 The variation in longtudinal and tangential shrinkage, average tracheid length, microfibrile angle and basic density of the sidewood, compression wood, and opposite wood sectors of a disk from the butt of tree 52 (from Nicholls, 1982).

From Figure 2.19, it is noted that all properties are very similar between wood types (compression- wood, opposite- wood, and side- wood) in ring 1 to ring 10, but beyond this point, there are obvious difference is between both normal and opposite wood compared to the compression wood. The compression wood had a higher density, larger microfibril angle, shorter tracheids, smaller transverse and larger longitudinal shrinkage than the other type woods.

Young et al. (1970) undertook an extensive study on the properties of single fibres from the opposite wood and compression wood of British-grown *Picea sitchensis*. Three

pulping processes were used, namely two-stage sulfite, neutral sulfite, and kraft. Various properties of single pulp fibres are shown in Table 2.8. The compression wood fibres were shorter throughout and had a smaller diameter but a much thicker cell wall than fibres from normal wood.

Table 2.8 Properties of single fibres from side and compression woods of *Picea sitchensis* (after Young *et al.* 1970).

	Julien (+ -	~ 1	
Pulp type	Wood	Fiber	Fiber	Fiber wall	tensile	Stretch	Failure
	type	length	diameter	thickness	strength		load
		(mm)	(µm)	(µm)	kg/mm ³	%	(g)
Two-stage	Side wood	3.14	37.6	3.6	28.8	6.5	14.1
sulfite	CW	2.46	34.1	5.2	8.2	6.0	4.9
Neutral	Side wood	3.11	39.7	4.1	32.7	9.4	19.1
sulfite	CW	2.49	31.3	5.2	19.3	10.9	11.3
Kraft	Side wood	3.21	35.1	3.3	46.7	7.2	19.6
	CW	2.42	32.4	5.0	12.2	7.8	6.7

Boyd and Foster (1974) studied on the properties of compression and opposite wood on radiata pine and obtained the following results (Table 2.9).

Table 2.9 A comparison of properties between compression and opposite wood (after Boyd and Foster, 1974).

Emiliar de la companya del la companya de la compan	Compression wood	Opposite wood
MFA (degrees)	27	12.3
Basic density (kg/m ³)	490	420
Klason lignin (%)	29.8	26.8

Contrary results on compression and opposite wood have got by some studies. The tracheid length of opposite and compression wood in loblolly pine branches was investigated by Taylor (1979). He measured relative density, growth rate, extractive content, and tracheid length from pith to bark and from insertion to the tip of loblolly pine branches. Variations within branches were noted and compared with variations in

the stem. The lower radius of branches contained a high proportion of compression wood. Hence, the wood samples from the lower radius had a higher density and wider growth rings than samples from the upper radius at all points along the branch. There were no significantly differences in tracheid length or extractive content between samples from the upper and lower radii of branches.

Microfibril angle of the opposite and compression wood in *Pinus radiata* studied by Harris (1977). He examined microfibril angle in 8 year-old radiata pine selected from Kaingaroa Forest, New Zealand, and found no significant difference between compression wood and opposite wood within the same growth ring.

A study by Wardrop and Dadswell (1950) using optical and X-ray methods examined microfibril angle and tracheid length in compression wood and relatively normal wood samples. The micrfibrils are inclined at a large angle to the longitudinal axis of the tracheid in compression wood. Such tracheids in *Pinus radiata* were shown to be appreciably shorter than would be the case if no compression wood were present. It was suggested that comparisons between compression wood and normal wood should be made on material of the same tracheid length and microfibril organization.

In this thesis, the wood properties will be examined in the seedlings from different seedlots and in clones under different treatments. These treatments include growing material on a lean to generate compression wood.

CHAPTER 3

THE ONTOGENY OF THE VASCULAR CAMBIUM AND WOOD FORMATION IN PINUS RADIATA CLONAL PLANTLETS

3.1 Introduction

The origin and development of the procambium, interfascicular cambium, and vascular cambium have been studied in a number of plantlets (Butterfield, 1976; Soh, 1972, 1974a, 1974b, 1991, 1992; Soh and Yang, 1987; Soh et al, 1989). Larson (1982) and Soh (1990) have also produced excellent reviews on the subject. The procambium has its origin in the actively dividing and enlarging shoot apex and is the source of the primary vascular tissues. The fascicular cambium has direct ontogenetic continuity with the residual meristem (Siebers, 1971a, 1971b, 1972; Soh et al., 1989; Soh, 1991, 1992). The interfascicular cambium does not have ontogenetic continuity with the residual meristem, but differentiates from interfascicular parenchyma (Esau, 1977; Cutter, 1978; Buvat, 1989; Fahn, 1990).

Structural differences between the procambium and cambium exist in many plantlets. Most of the end walls of the elongated procambial cells are essentially transverse, whereas the end walls of most fusiform cambial initials are tapered. The procambial cells elongate during the active internodal growth of the stem, whereas the lengths of the fusiform cambial initials remain relatively constant, increasing in length only with significant radial growth. Transverse divisions occur in the procambium but not in the cambium (Butterfield, 1975).

The transition from procambium to cambium has been studied in a number of different plantlets. It is usually impossible to separate the procambium and cambium in young growing shoot tips. Therefore, the procambium and the cambium are best regarded as two developmental stages of the same meristem (Esau, 1965). *Pinus radiata* is now a

major forest plantletation species in many countries. Our current research programme is aimed at improving the quality of radiata pine log by selecting seedlings with superior wood qualities. In order to do this we need to understand more about wood development in radiata pine and in particular the effects of compression wood formation on corewood properties.

Compression wood is a major problem in wood utilisation, both for pulp and lumber (Timell, 1986). Compression wood formation resulting from both internal and external stresses is well documented. These stresses include wind action (Burdon and Low, 1992; Nicholls, 1982; Low, 1964), inclined stems, branches (Downes and Turvey, 1992), differing growth rates (Cown, 1974), and all vary with tree species (Mitscherlich, 1942). Haught (1957) reported that compression wood is more common in juvenile than in mature wood. Haught reported 42% compression wood by volume in juvenile wood (laid down during the first 8 years of growth) as against 7% compression wood in mature trees. In Loblolly pine, fewer than 10% of the trees examined were found to be free from compression wood. The compression wood also varied from 6 % in reasonably straight trees to 9.1 % in more crooked trees and 67.1 % in a very crooked trees (Haught, 1958).

The incidence of compression wood in radiata pine in New Zealand is not well known. There are few published results on wood formation and wood structure of very young plantlets. To understand how the wood is formed and how the wood structure is effected by treatments, plantletes of two clones were grown under three treatments for study.

3.2 Materials and methods

Radiata pine plantlets of two clones (nominally referred to as clones 8 and 31) were supplied by Fletcher Challenge, Ltd. Note, the term *plantlet* is used here to describe the material studied rather then the term *seedling* on account of the tissue culture origin of the material. The 50 mm high plantlets were established in a glasshouse and grown for 8 months under 16 hours light at 25°C day and 18°C night temperatures. The plantlets were grown free (F), tied to vertical stakes (T), and tied to stakes at an angle of 45° (A). The heights, stem lengths and diameters of the plantlets were measured on the day of

harvest. 12 plantlets were selected for studying the tissue differentiation and wood properties. 6 of 12 plantlets (one plantlet for each clone and each treatment) were cut and fixed in formalin-acetic-alcohol, embedded and sectioned. Shoot tips were cut serially to examine the cambium ontogeny. Sections were also cut from lower internodes for wood anatomical study. Each plantlet was cut into stem lengths labelled base, stem 4, stem 3, stem 2, stem 1, tip 2, and tip 1. These lengths corresponded to the occurrence of the branch whorls. The percentage of pith, wood, compression wood, and cell wall area in normal and compression wood were recorded along with, and cell numbers per square mm in normal and compression on 10 µm thick transverse sections stained with Safranin and Fast Green. Observations were made under a microscope fitted with a high resolution video camera and digital images stored for later processing using MetaMorph (registered trade mark of Universal Imaging Corporation, USA).

Analysis of variance was used for identifying statistical differences in variables between clones, treatments, and stem positions. Prior to statistical analysis, percentage data were transformed to arcsine data for normality of distribution according to the following formula: P' = arcsin(SQRT(P)), P is original data and P' is transformed data (Zar, 1999, p 278). However, data in the tables and graphs of this paper have not been transformed.

3.3 Results

3.3.1 Plantlet growth

The mean height of the 12 plantlets on harvest was 774 mm and the mean diameter 9.6 mm (Table 3.1). The clone 31 plantlets were taller (825 mm) and thicker on average (11.7 mm) than the clone 8 plantlets (723 mm in height, and 9.1 mm in diameter). The most striking difference in response to the three treatments was reflected in the axial growth of the plantlets (Figure 3.1). With those tied to stakes growing the taller (899 mm) than those growing free (829 mm), while those tied to stakes and forced to grow at 45 degrees showed the least axial growth (593 mm). The angled tied plantlets were therefore the shortest with the thinnest stems, while the vertical tied plantlets were the tallest with the next thinnest stems.

Table 3.1	The	mean	height	and	diameter	of	the	12	plantlets.
-----------	-----	------	--------	-----	----------	----	-----	----	------------

	rituare constructor (See processes à mesoripopouveny en mesorificipare comparativament de situativament de s	Height (mm)	Stem diameter (mm)
Clone	8	723	9.1
	31	825	11.7
Treatment	Free	829	10.6
	Tied	593	9.5
	Angled	612.5	8.8
Mean		774	9.6

The heights and stem length of 12 plantlets from two clones 8 and 31 grown under three treatments (free, tied and angled) were shown in Figure 3.1, from which, the angled plantlets were much shorter and the tied plantlets taller than free grown ones. Note the difference in stem lengths is much clear at upper parts (from stem 2 to tip 1) than lower parts (base and stem 4). Clearly, the angled plantlets were shorter as their stem lengths were shorter than other treatment plantlets, especially in upper parts.

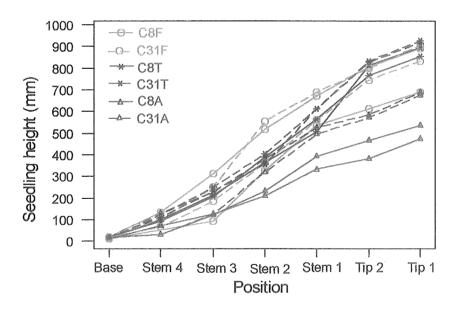


Figure 3.1 The height of the eight month-old *Pinus radiata* clonal plantlets.

3.3.2 Differentiation and development of the vascular tissues

Vascular tissues gradually differentiate as the growing shoot tip becomes further removed. Serial transverse sections behind the tip therefore reveal the processes of cambial ontogeny and vascular differentiation.

Apical meristem

The apical meristem is located at the tip of the stem and is covered by a number of enlarging leaves. Under the microscope, its cells varied in cell size, cell shape, pattern of division, and arrangement. No.1 of Plate 3.1 shows the pre-differentiation state of the vascular tissues in the apical meristem (M).

Differentiation of the pith and cortex

Increased cell vacuolation accompanies the differentiation of the cortex and pith, delimiting an approximately circular zone of section approximately 0.12 mm from the shoot top. The pith cells (P) are larger than those in the other areas (No.2 of Plate 3.2).

Bundle trace and development

As the pith differentiates, the procambial strands differentiate from the sub-meristem region approximately 0.5 mm from the shoot tip and separate the future pith and cortex. The strands are of different sizes and their cells generally smaller than those of the pith, cortex, and interprocambial sectors.

The origin of the procambial strands involves a number of subapical meristem parenchyma cells dividing both periclinally and anticlinally, the new cells forming groups of axially elongating cells. The procambial cells are derived from subapical meristem parenchyma cells which have in turn originated from the apical meristem cells. Interposed between the procambial strands are the interprocambial sectors (IS), often referred to as medullary or primary rays. The cells of the interprocambial sectors are larger than those in the procambial strands, and have a more homogeneous cell shape (No.3 of Plate 3.1).

Differentiation of protophloem and protoxylem

With increasing distance from the shoot tip, the procambial strands form a broken cylinder surrounding the pith interrupted by the interprocambial sectors. The protophloem cells (PP) are the first to differentiate within the procambial strands followed soon after by the protoxylem (PX). The procambial cells (PC) exhibit radial seriation by 1.7 mm from the tip (No.4 of Plate 3.1). Some procambial cells differentiate into protoxylem cells to the inside of the procambium and acquire secondary walls. Most of the procambial strands have at least one or two protoxylem cells by a very early stage. The cells of the interprocambial sectors expand radially and the cell shape changes from round to radially elongated in transverse view (Figs. 2c and 2d). These zones now form the primary medullary rays.

Procambial strands to fascicular bundles

During primary vascular differentiation, the procambial strands gradually transforms into fascicular bundles. Fascicular bundles are vascular strands containing primary xylem and phoem and some residual procambial meristematic cells. These meristematic cells divide and become transformed into the fascicular cambium (FC) as a result of repeated periclinal divisions. The interprocambial sectors become the interfascicular sectors as the bundles enlarge, and their cells continue to expand becoming radially elongated in transverse view. At approximately 2.5 mm from the shoot tip, the fascicular bundles contain three zones: the primary phloem (PP), fascicular cambium (FC), and primary xylem (PX) (No.1 of Plate 3.2). Some larger bundles contain more than 10 radial files of cells, whereas others are smaller and contain only one or a few files of cells.

With development, the fascicular bundles increase in radial width by repeated periclinal division, and expand in tangential width by anticlinal division within the fascicular cambium. The interfascicular sectors remain homogenous in appearance, though the cells continue to increase in size.

Initiation of the interfascicular cambium

Initiation of the interfascicular cambium begins in the interfascicular parenchyma cells. The parenchyma cells of the interfascicular sectors are derived from the subapical meristem parenchyma cells. Initially, the cells of the interfascicular sectors (IS) expand radially without division until activated to divide. These cells once activated, divide quickly by periclinal division and rapidly display cambial cell characteristics. With repeated periclinal and occasionally anticlinal division these cells become transformed into the interfascicular cambium. Transverse sections (No.2 of Plate 3.2) show that those cells adjoining the fascicular cambium (FC) show periclinal divisions first, whereas those not adjoining the fascicular cambium continue to expand without dividing. This results in some interfascicular periclinal divisions being delayed later than in the fascicular cambium. The new-formed interfascicular cambium connects with the fascicular cambium, resulting in the fascular cambium enlarging into the interfascicular zone. This process continues until the interfascicular sectors have been closed completely by the tangentially enlarging cambium. The developmental sequences suggest that the interfascicular cells do not divide periclinally until they are activated, possibly by their proximity to fascicular cambium.

Fascicular cambium to vascular cambium

The fascicular cambium gradually becomes transformed into a true vascular cambium through repeated periclinal and occasional anticlinal divisions. The developmental sequence shows that the fascicular cambium expands into the interfascicular zone merging with the newly forming interfascicular cambium. This occurs *et all* developmental stages from very early (in the procambium) to late stages (just before the cylinder of vascular cambium is completed). A few large cells of the interfascicular sector (IS) divide periclinally and the fascicular cambium connects together by approximately 11 mm from the shoot tip in the free and angled grown seedlings (No.1 and 2 of Plate 3.3), and approximately 16 mm in the tied plantlets. After several periclinal and some anticlinal divisions, a complete vascular cambium (VC) is established by 16 mm from the shoot tip in the free and angled plantlets and by approximately 25 mm in the tied plantlets (No.1 of Plate 3.4). The cells of the procambium and interfascicular cambium can be distinguished in transverse sections from the adjoining interfascicular sector parenchyma cells *et al*1 developmental stages.

Plate 3.5 shows a developmental sequence of the procambium which contained 1 to 2 cambial cells at early stage, and then 3 to 4, and 4-6 before the fascicular cambium was

formed. Plate 3.6 shows a developmental sequence of the interfascicular sector cells, which keep growing, and not dividing until they were switched on by the fascicular cambium.

Secondary growth

Secondary growth is defined here as commencing when periclinal divisions occur in the last remaining interfascicular sector parenchyma cells. Secondary growth starts some distance from the tip of the plantlets. In the free and angled plantlets, radial growth is well developed within the fascicular bundles by 11 mm from the tip, and the last interfascicular cells begin dividing periclinally. By 16 mm from the tip the last interfascicular cambial cells have divided periclinally to produce several radial files of cells (No.1 of Plate 3.4). This transition occurred over a 5 mm vertical zone in the free and angled plantlets and a 8-10 mm zone in the tied seedlings. The onset of secondary growth is a gradual process best considered as a process that is continuous transition from primary to secondary growth.

The results of observations on the initiation of secondary growth in the plantlets of clones 8 and 31 under the three treatments are summarised in Table 3.2. The onset of secondary growth was not influenced by clone in this study, but was strongly influenced by the treatment.

Table 3.2 The onset of the secondary growth (mm from the shoot tip) in free grown (F), tied vertically (T), and tied at 45 degrees (A) radiata clone 8 and 31 plantlets.

	C8F	C8T	C8A	C31F	C31T	C31A
First interfascicular cell		a)7 (1 + 1 - 1 - 1 - 1 - 1 - 1 - 1 - 1 - 1 -				araumati reteritime ilifono danna irramena
periclinal divisions	10.0	13.3	12.2	12.0	20.0	12.5
Complete cylinders of						
cambium established	15.0	21.3	17.6	16.5	30.5	17.5
Transition length	5.0	8.0	5.4	4.5	10.5	5.0

With secondary growth, secondary xylem and phloem cells are produced by the vascular cambium and form radial files of derivative cells. The secondary xylem establishes a well defined complete cylinder by about 30 mm from the shoot tip in the

free grown and angled plantlets, and by about 40 mm in the tied seedlings. By this stage the ray cells (R) are well developed and show marked radial elongation (No.2 of Plate 3.4).

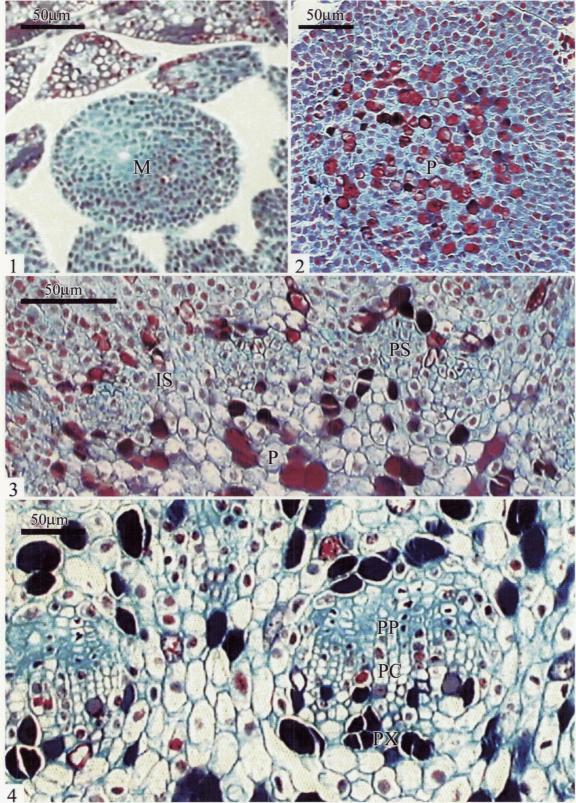


Plate 3.1. No. 1-4. The early development of the procambial strands - shoot tip down to 1.7 mm.

- No.1. The undifferentiated apical meristem (M) at the shoot tip.

- No.2. Pith cell (P) differentiating in the centre of the axially expanding axis.

 No. 3. Developing procambial strands (PS) separated by interprocambial sectors (IS).

 No. 4. Differentiation of the procambial strands into protoxylem (PX), procambium (PC) and protophloem (PP) tissues 1.7 mm from the shoot tip.

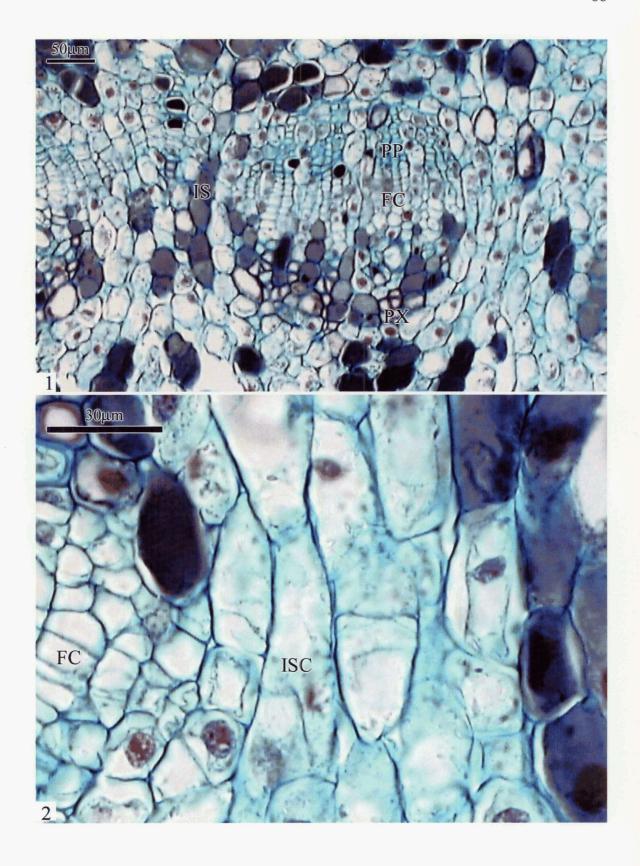
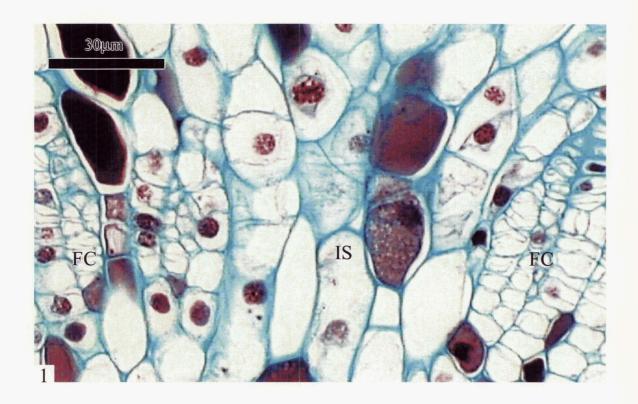


Plate 3.2. The closure of the interfascicular sectors 2.5 mm from the shoot tip.
No. 1. Enlarging vascular strands with well formed fascicular cambia (FC) showing radial seriation of recently divided cells.
No. 2. Radially stretched parenchyma cells of the interfacicular sectors (ISC).



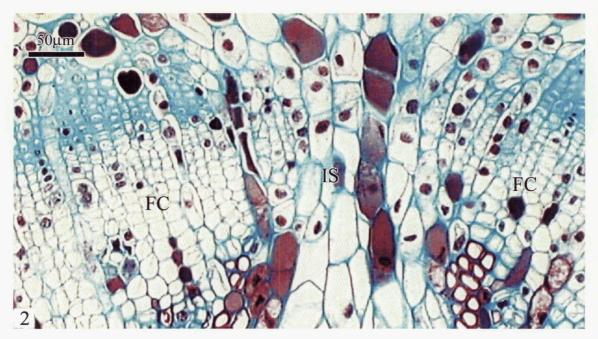


Plate 3.3. The onset of secondary growth - 11 mm from the shoot tip.
No. 1. Interfascicular parenchyma cells (IS) separating the young vascular bundles with well developed fascicular cambia (FC).
No. 2. Well developed bundles with active fascicular cambia (FC) separated by narrow interfascicular sectors (IS).

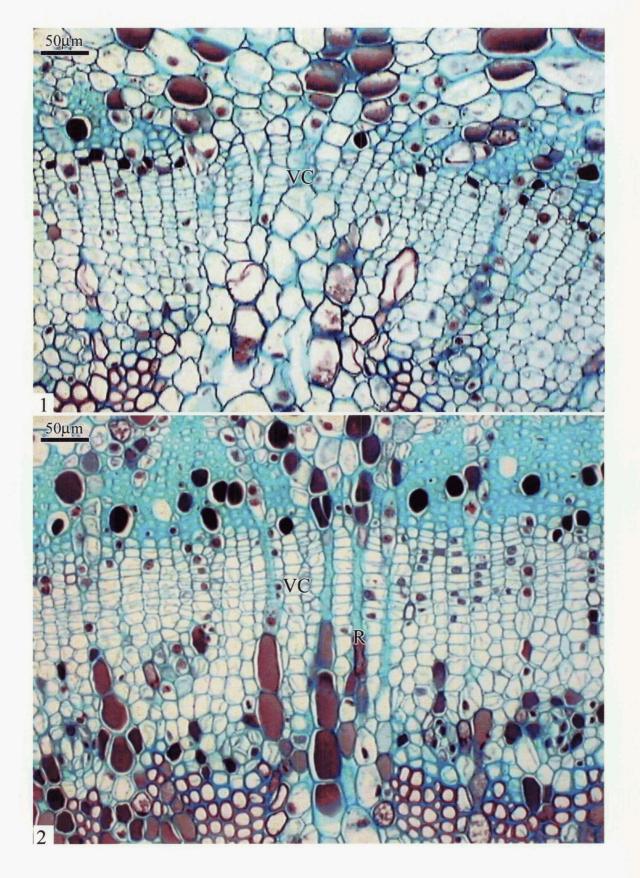
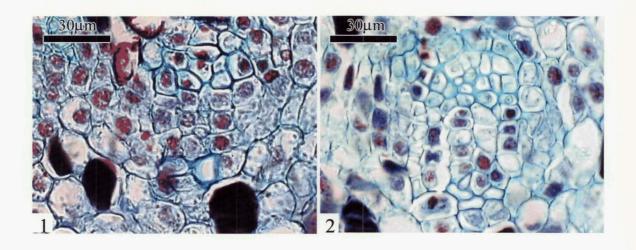


Plate 3.4. The radially expanding vascular cambium - 16-30 mm from the shoot tip. No. 1. The vascular cambium (VC) forms a complete cylinder about 16 mm from the shoot tip.

No. 2. The established vascular cambium (VC) 30 mm from the shoot tip is now a multiseriate zone of periclinally dividing meristematic cells. Secondary xylem and phloem cells have differentiated on either side of the cambium and include well developed uniseriate rays (R).



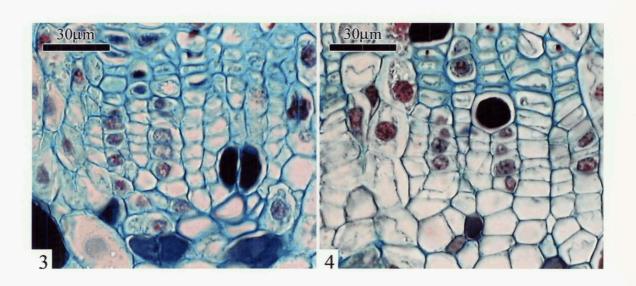
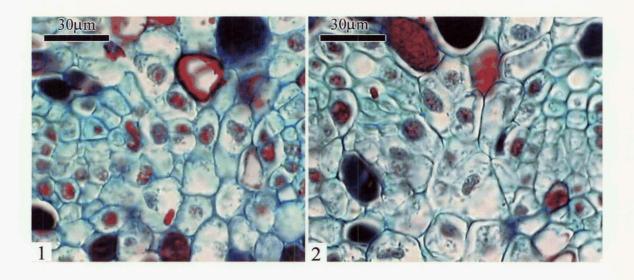


Plate 3.5. No. 1 - 4. An origin and developmental sequence of the procambium.



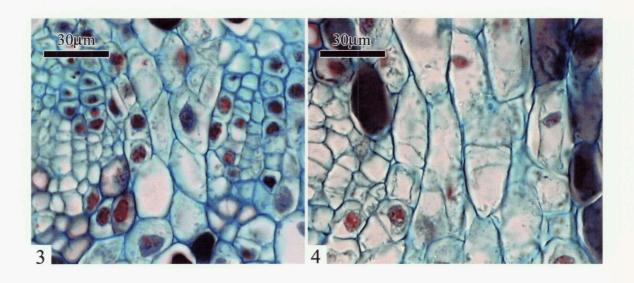


Plate 3.6. No. 1-4. A developmental sequence of the interfascicular cells.

3.3.3 Wood formation

Primary xylem and secondary xylem

With the development, the primary xylem and secondary xylem cells were produced fro primary and secondary meristem respectively. Two types of xylem cells can be found in the base of the tip parts of plantlets. The secondary xylem cells are younger and shorter (less than 1 mm), and the primary xylem cells are older (mature) and longer (reaching about 2-3 mm or more). By maceration, the cell structure of the primary xylem appears elastic, and the piece of primary wood look like a bundle of elastics. Plate 3.7 shows a primary xylem cell (No. 1) and its detail (No. 2). Plate 3.8 shows a double chain structure of the primary xylem cell. The function of the long primary xylem cells probably is to aid the stem tip stiffness.

Percent pith and wood

With growth, the percent pith area declined along the stems from 16% at tip 1 to 0.1% at the base. The decreasing patterns of percent pith are shown in Figure 3.2.

The percentage of wood per cross section increased down the stems from 9% at tip 1 to 61% by the base (Figure 3.3). The percentage of wood was similar in both clones (approximately 54%) (Table 3.2). However, the plantlets had significantly different percentages of wood depending on treatment (P = 0.051), with the angled (51.5%), free (55.4%) and tied (55.6%). As the pith diameters were similar with in all three treatments, these differences must be due to the angled plantlets having a thicker bark. The percent wood differed between stem positions (P = 0.000). Figure 3.3 shows each stem position had different amounts of wood with the base (59.7%), stem 4 (60.9%) and stem 3 (61.0%) having significantly more wood than stem 2 (52.5%) and stem 1 (37.6%) respectively. Averaged over all the plantlets, the stems contained 2.9% pith and 54.1% wood, in which, 23.5 is normal wood, and 30.6% is compression wood.

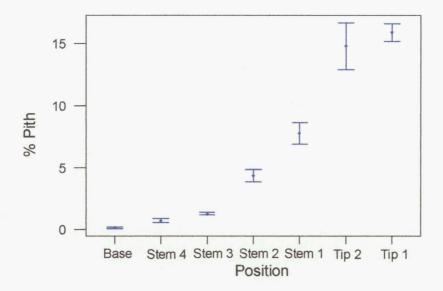


Figure 3.2 The pattern of percent pith from base to tip: Vertical bars represent the standard errors.

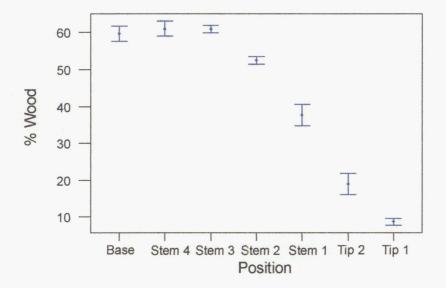


Figure 3.3 The percent wood from the base to tip: Vertical bars represent the standard errors.

From Figure 3.2 and 3.3, the pith decreasing and the wood increasing showed contrary pattern, both of them presented relatively stable at the base, stem 4 and 3, and showed large changes from stem 3 to tip 1. This implies that the wood cells were dropped quickly from younger cambium at upper parts than older cambium at lower parts of the plantlets.

Normal wood and compression wood

Normal wood and compression wood can be easily separated under the light microscope. Normal wood has rectangular cells with thinner walls. Compression wood, on the other hand, has rounded tracheids with thicker walls and intercellular spaces. Plate 3.9 shows normal (1) and compression wood structure (2).

Distribution of the compression wood

The distribution of compression wood differed between the free, tied, and angled plantlets (Plate 3.10). In the free grown plantlets, the compression wood formed regular arcs on different sides of the stem at differing heights. In the angled plantlets, the compression wood was formed a strong arc to the lower side. It was also noted that the compression wood in some area was severe and in some area was mild in both the free and angled plantlets.

Percent compression wood

The percent compression wood in clone 31 was slightly higher than in clone 8 (Figure 3.4). Significant differences in percent compression wood existed between treatments (P = 0.000). The angled plantlets had more compression wood (49.1%), and the tied plantlets had less compression wood (14.5%) than the free ones (27.9%). Clearly, compression wood formation was strongly effected by the growth stresses. Figure 3.5 shows the angled plantlets having higher percent compression wood than the free and tied plantlets *et al*l stem heights. The stem 4 of the angled clones had the highest percent compression wood being about 65%.

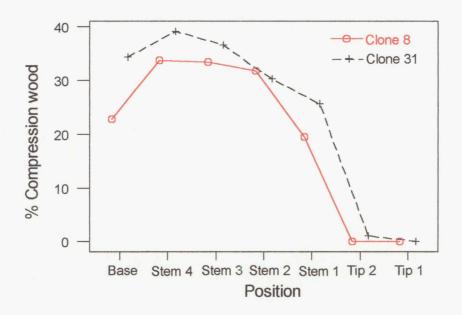


Figure 3.4 Percent compression wood in clones 8 and 31 with height.

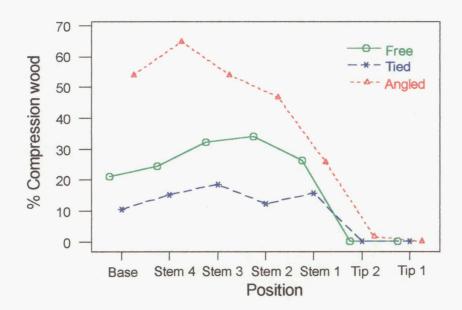


Figure 3.5 Percent compression wood in the free, tied and angled plantlets with height.

From Figure 3.5, it is clear that amount of compression wood in the angled treatment was higher than in the free and tied treatments, especially at lower levels in the plantlets.

Percent cell wall area in normal and compression wood

The percent cell wall area was examined in normal and compression wood respectively. Normal wood had 26.4% and compression wood had 40.3% cell wall areas by cross section area.

In normal wood area, the two clones had similar percent cell wall area being around 26% on average (Table 3.2). It is noted that the angled plantlets had a higher cell wall area (28.2%) than the free (25.1%) and tied ones (25.7%) in normal wood. This implies that the angled treatment not just influenced the cell walls in the compression wood and also in the normal (opposite) wood.

In the compression wood, the two clones had similar cell wall areas, being about 40%. There was a significantly difference in percent cell wall area between treatments (P = 0.000) in compression wood (Figure 3.7). The angled treatment had significantly higher (46.9%) and the tied plantlets had significantly lower percentage cell walls (34.3%) than the free ones (39.5%). These results clearly showed the angled plantlets having thicker cell wall in both normal and compression wood area than the free and tied plantlets. These results demonstrate that the percent cell wall area is strongly influenced by treatments.

A significantly difference in percent cell wall area existed between stem positions (P= 0.000) in normal wood. The base, stem 4, and stem 3 had significantly thicker cell walls (31.2%, 28.3%, and 25.9% respectively) than the stem 2 (23.8%) and stem 1 (22.9%). Figure 3.6 presents the percent cell wall area of normal wood *et al*1 stem positions of the three treatment plantlets. It is noted that the cell wall area decreased in thickness from base to tip. It is also clear the angled plantlets had thicker cell walls in all stems in the normal wood.

Cell numbers/mm² in normal and compression wood areas

The cell numbers/mm² differed in normal and compression wood. The normal wood had 2314.6 cells /mm², and the compression wood had 2145.3 cells /mm².

In the normal wood, the two clones had similar cell numbers being about 2314 cells/mm² (Table 3.2). There was a significant difference in the cell numbers/mm² between treatments (P = 0.001). The angled treatment had significantly more cells (2615 cells/mm²) than the free (2166 cells/mm²) and tied ones (2145 cells/mm²) (Figure 3.8).

In the compression wood, the two clones had cell numbers around 2145 cells/mm². The angled treatment had significantly more cells (2474 cells/mm^2) than the free (1932 cells/mm^2) and tied (2255 cells/mm^2) ones (P = 0.047). These results can be seen in Figure 3.9. It is clear in Figure 3.8 and 3.9 that the angled plantlets had more cells in all stems than free and tied ones in both normal wood and compression wood.

The cell numbers also different between stem positions (P = 0.046). The base had significantly more cells (2556 cells/mm²) than other stem positions. The cell numbers rapidly increased from the stem 1 to the tip in normal wood. It is suggests those cells in the tip have yet to reach their mature size. Fig. 3.9 also shows the compression wood tissue free in the tip parts of plantlets.

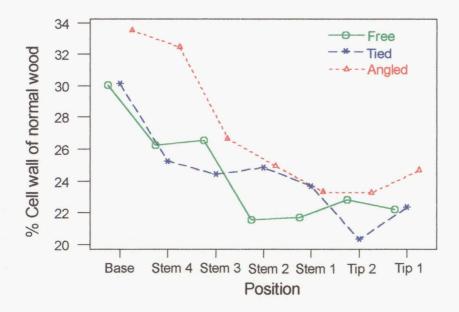


Figure 3.6 Percent cell wall area of the free, tied, and angled plantlets in the normal wood.

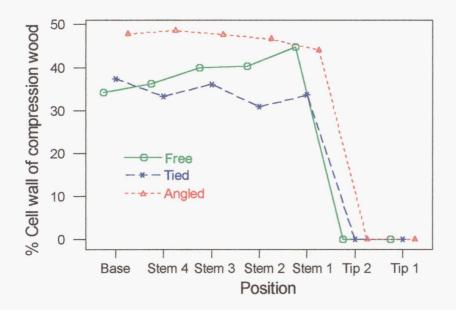


Figure 3.7 Percent cell wall area of the free, tied, and angled plantlets in the compression wood

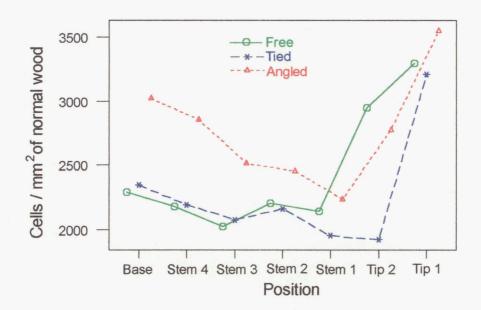


Figure 3.8 Cell numbers/mm² of the free, tied, and angled plantlets in the normal wood

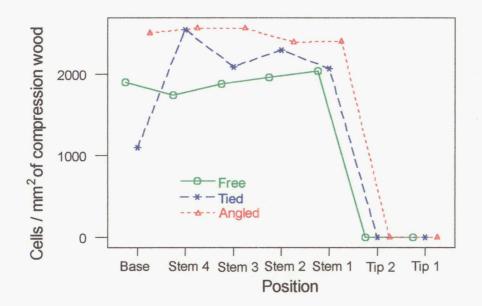


Figure 3.9 Cell numbers/mm² of the free, tied, and angled plantlets in the compression wood

The growing characteristics of the plantlets

The plantlets growth characteristics are summarised in Table 3.2 and 3.3 respectively.

Table 3.3 Comparison of variable means between clones, treatments, and stem positions. Different letters indicate means that are significantly different at 5% level.

	at 376 level.							
	Pith	Wood	CW	% Wall	% Wall	Cells/mm ²	Cells/mm ²	
	(%)	(%)	(%)	(NW)	(CW)	(NW)	(CW)	
Clone				***************************************				
8	2.8 (0.8)	53.0	27.8	26.9	39.2	2282.3	2182.7	
31	3.1 (0.9)	55.2	33.1	25.9	41.3	2344.7	2110.3	
Treatment								
free	3.5 (1.2)	55.4 a	27.9 b	25.1	39.5 b	2167.6 b	1923.4 b	
tied	2.3 (0.7)	55.6 a	14.5 с	25.7	34.3 с	2145.7 b	2015.2 b	
angled	3.1 (1.2)	51.5 b	49.1 a	28.2	46.9 a	2615.7 a	2475.0 a	
Position						N _e s	<i>#</i> ."	
Stem 1	7.8 (0.9) a	37.6 с	22.5	22.9 c	40.9	2110.3 b	2167.1	
Stem 2	4.4 (0.5) b	52.5 b	31.0	23.8 с	39.3	2273.7 ab	2211.3	
Stem 3	1.3 (0.1) c	61.0 a	34.9	25.9 bc	41.3	2204.3 b	2173.4	
Stem 4	0.7 (0.2) c	60.9 a	36.9	28.3 ab	40.1	2455.5 ab	2383.8	
base	(0.1) d	59.7 a	28.5	31.2 a	39.8	2552.6 a	1830.5	
Mean	2.9	54.1	30.6	26.4	40.3	2314.6	2145.3	

Table 3.4 The growth characteristics in the stems of the plantlets.

Stem	Pith	Wood	NW	CW	% Cell	% Cell wall		nm²
Position	%	%	%	%	NW	CW	NW	CW
Tip 1	15.9	8.8	8.8	0.0	23.1	_	3352	=
Tip 2	14.8	18.9	18.9	0.0	22.1	-	2250	200
Stem 1	7.8	37.6	15.1	22.5	22.9	40.9	2110	2167
Stem 2	4.4	52.5	21.5	31.0	23.8	39.3	2274	2211
Stem 3	1.3	61.0	26.0	34.9	25.9	41.3	2204	2173
Stem 4	0.7	60.9	31.1	36.9	28.3	40.1	2456	2384
Base	0.1	59.7	22.6	28.5	31.2	39.8	2552	18301

Overall, the angled plantlets were shorter and thinner forming less wood and more compression wood with thicker cell walls. The tied plantlets were taller and thinner and contained more normal wood with thinner cell walls. The free grown plantlets were taller than the angled plantlets but shorter than the tied plantlets, and had thicker stems containing variable amounts of compression wood.

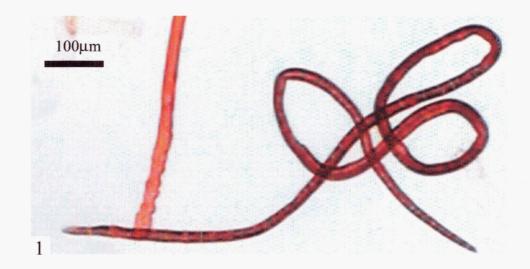




Plate 3.7 A primary xylem tracheid in low magnification (1) and in detail (2).

20μm



Plate 3.8 Primary xylem tracheids showing helical secondary thickening and intertracheid pit-pairs.

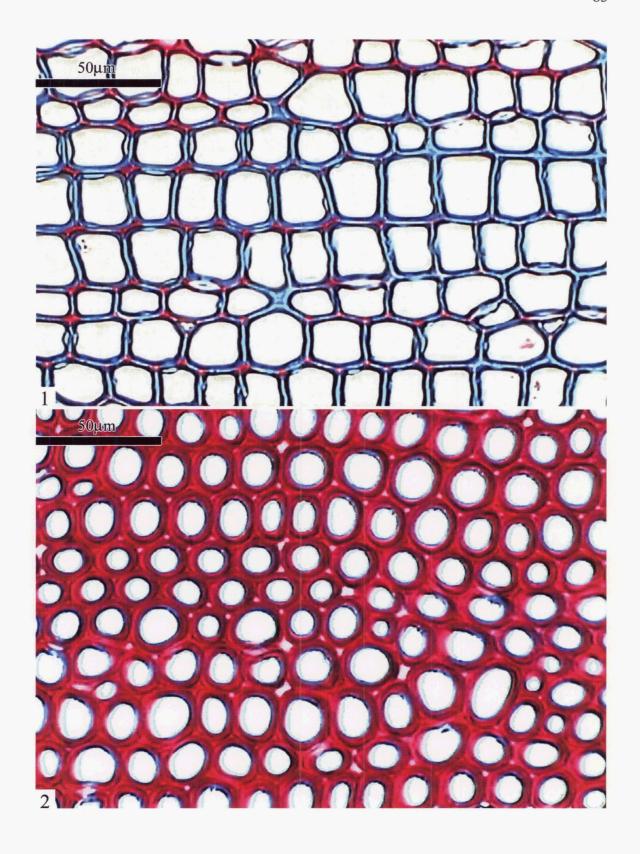


Plate 3.9. No. 1 - 2. Transverse sections from the base of angled plantlet. No. 1. Opposite wood. No. 2. Compression wood.

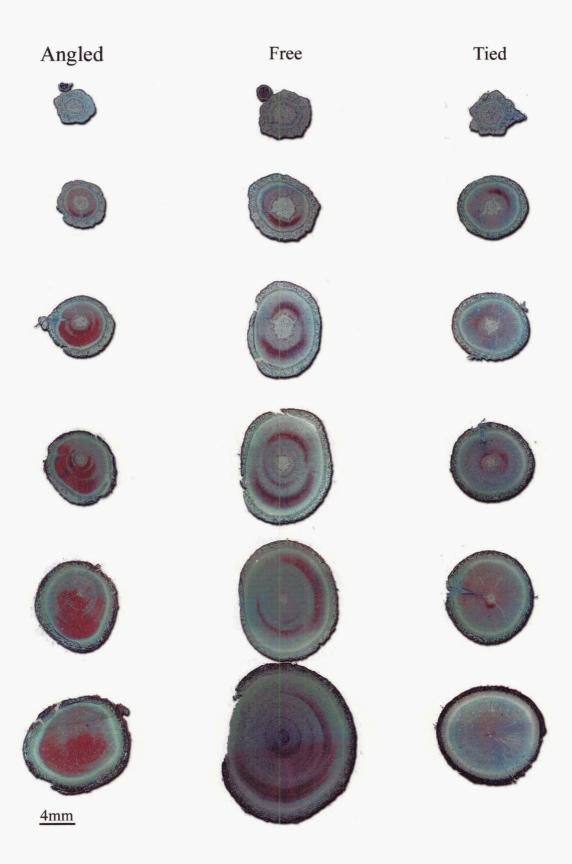


Plate 3.10. Cross sections through eight month-old *Pinus radiata* clonal plantlets. Showing the distribution of compression wood in the free, tied, and angled plantlets.

3.4 Discussion

This study on *Pinus radiata* demonstrates the relationship between the procambium, and the fascicular, interfascicular, and vascular cambial and details their origin and development in this species. Clonal material was selected for this study as it forms part of a larger programme on the selection of clonal plantlets possessing stiffer wood properties. Plantlets were grown free, tied, and tied at an angle in order to establish the amount and distribution of compression wood within young plantlets grown under these treatments. The ontogeny of the cambium was studied in plantlets subjected to all three treatments in order to record possible differences in response to these treatments.

The procambium in radiata clonal plantlets originates from the subapical meristem parenchyma cells, where periclinal division first produces procambial cells about 0.5 mm from the shoot tip. After repeated periclinal division a cylinder of procambial strands forms. The occurrence of repeated periclinal divisions in the procambium has already been reported for a number of plantlets (Esau, 1942, 1943; Sterling, 1946, 1947; Soh, 1972, 1974a, b; Fahn *et al.*, 1972). Repeated periclinal divisions are a characteristic of cambial cells.

The interfascicular cambium originates from interfascicular parenchyma cells which are derived from the subapical meristem. Interfascicular cambium formation is related to division in the fascicular cambium. Transverse sections showed that only those interfascicular cells adjacent to the fascicular cambium showed periclinal divisions, whereas those cells not adjoining the fascicular cambium continued radial expansion without division. Clearly, the periclinal division of the interfascicular cells is directly influenced by proximity to the fascicular cambium. These interfascicular cambial cells divide periclinally to form the interfascicular cambium. Many authors claim that the stimulus for the initiation of the interfascicular cambium arises in the fascicular cambium (Steeves and Sussex, 1972; Phillips, 1976). In addition, there is cytochemical evidence using the positive reaction to carboxylesterase that activity appears first in the cells adjacent to the vascular bundles and then spreads into the interfascicular tissue from both sides of the bundles (Rana and Gahan, 1983; Gahan, 1988). Furthermore, Gahan (1988) states that the signal for the initiation of the interfascicular cambium emanates from the adjacent fascicular cambium. In transverse sections of *Ricinus*

commnuis, periclinal cell division in the interfascicular region begins adjacent to the vascular bundles and advances across the interfascicular region (Soh, 1992). Such a division pattern has been commonly described in the older literature (Priestley, 1928; Esau, 1965; Fahn *et al*, 1972).

The observations in this study on *Pinus radiata* indicate that both the procambium and interfascicular cambium originate from subapical meristem parenchyma. Periclinal division, however, occurs earlier in the procambium than in the interfascicular cambium. The most likely reason being that the interfascicular cells are activated by the fascicular cambium before dividing periclinally. Hence, periclinal division in the interfascicular cambium always occurs later than in the fascicular cambium. The fascicular cambial cells initially divided repeatedly periclinally and occasionally anticlinally to form the fascicular cambium, whereas the interfascicular parenchyma cells enlarged radially until they were activated presumably by the fascicular cambium after which they divided periclinally to form the interfascicular cambium.

The procambium, fascicular cambium, interfascicular cambium are usually considered to be different developmental stages of the cambium that finally encircles the wood in trees. In radiata pine a clear relationship exists between the apical meristem, procambium, fascicular cambium, interfascicular cambium, and vascular cambium.

Some reports suggest that the interfascicular cambium does not have ontogenetic continuity from the residual meristem, but differentiates from interfascicular parenchyma (Salisbury and Parke, 1964; Esau, 1977; Cutter, 1978; Buvat, 1989; Fahn, 1990), whereas others claim that the interfascicular cambium shows ontogenetic continuity from the residual meristem (Siebers, 1971a, b; 1972; Soh, et al, 1989; Soh, 1991, 1992). The result of this study on *Pinus radiata* demonstrates that the interfascicular cambium originates from the interfascicular parenchyma which in turn is derived from the subapical meristem. This suggests that the vascular cambium may develop in a variety of ways in different species. This study on *Pinus radiata* further emphasizes the difficulty in separating the procambium and the cambium as distinct meristems.

Secondary growth

A full cylinder of vascular cambium in radiata pine seedlings was established between 10 and 30 mm from the shoot tip. In this transition zone, the parenchyma cells of the last interfascicular sector began periclinal division and continued until the interfascicular cambium had closed off the interfascicular sector.

Treatment influenced the first appearance of a complete cambium in the plantlets. The free and angled plantlets developed a complete cambium earlier than the tied plantlets.

Compression wood formation

Compression wood was found in all the plantlets in this study. Significant differences in percent compression wood between different plantlets reflected the growth stresses. The relationship between compression wood formation and growth stresses has been reported for wind action (Mitscherlich, 1942; Burdon an Low, 1992), stem lean (Nicholls, 1982), heavy branches (Downes, 1992), growth rate (Cown, 1974), and tree species. The results of this study confirm the results reported elsewhere.

Wood structure

Plantlet growth stresses can modify wood structure, wood cell walls and cell shape (Butterfield and Meylan, 1980; Bamber and Burley, 1983). Normal wood has normal cells with thinner cell walls, and compression wood has rounder cells with thicker cell walls. These results demonstrate the compression stress acting on wood structure. The compression wood distribution to the under side of angled plantlets was clearly caused by the force from the compression due to the plantlets being tied at 45 degrees. The distribution in free grown plantlets was probably caused by the branches. And mild distribution of the compassion wood in the tied plantlets indicates that the tied plantlets were not subject to the same when tied to vertical stakes.

Percent cell wall area and cell numbers/mm²

In general the cell wall shows a decreasing thickening from the base to tip. This trend can be clearly seen in the normal wood, but is less obvious in compression wood. The angled plantlets had much more cells and thicker walls in both normal and compression wood areas than the free and tied plantlets. Clearly, the cell number and cell wall thickness can be modified by growth stress.

3.5 Conclusions

- 1 Cambial ontogeny in radiata pine is a continuous process behind the apical meristem, with the subapical, procambial, fascicular, and interfascicular meristems forming a complete vascular cambium.
- 2 The procambium originates from the subapical meristem parenchyma cells. And the interfascicular cambium originates from the interfascicular parenchyma cells. Interfascicular cambial development appears to be initiated by the fascicular cambium with the interfascicular cells nearest the bundles dividing first.
- The pith in decreased along the stems from 16% at the tip to 0.1% by the base. The wood increased from 9% at the tip to 61% at the base. Totally, in the stems, the pith occupied 2.9%, and wood is 54.3%, in which, 23.3% is normal wood, and 31.0% is compression wood. Angled plantlets had significantly less wood (51.5%) than the free (55.4%) and tied (55.6%) plantlets.
- 4 The formation of compression wood caused by the plantlet growth stress. The angled plantlets had significantly more compression wood (49.1%), and the tied plantlets had significantly less compression wood (14.5%) than the free grown ones (27.9%).
- 5 The compression wood had thicker cell walls (40.3%) than the normal wood (26.4%). The angled plantlets had more cells/mm² and significantly thicker cell walls (46.9%) than the free (39.5%) and tied ones (34.3%) in compression wood area.
- 6 The angled plantlets were shorter and thinner contained more compression wood with more cells/mm² and thicker cell walls, and the tied plantlets were taller and thinner having less compression wood and thinner cell walls than the free ones.

CHAPTER 4

PROPERTIES OF WOOD IN 8 MONTH-OLD CLONAL PLANTLETS

4.1 Introduction

As mentioned in Chapter 1 and discussed in the literature review in Chapter 2 and studied in Chapter 3, it is known that the low stiffness radiata pine corewood contains some undesirable characteristics, including a large proportion of compression wood. To improve radiata pine corewood quality, it is important to know more about the corewood and compression wood properties, especially in very young trees. Radiata pine trees grown on the Canterbury Plains of New Zealand are subject to prevalent high wind growing conditions. In this Chapter, the 8-month-old clonal plantlets grown in a glasshouse under three treatments have been selected to study very young wood properties and compression wood properties, including tracheid length, density, stiffness by tension, cell numbers/mm², and cell wall area. Different growing conditions are applied to see how these influence the wood structure and properties. A number of issues are explored in this Chapter:

- a) Differences in wood properties between clones. Clones 8 and 31 were selected and planted in the same glasshouse (providing the same growing environment). Therefore any differences between the properties of the two clones should be under genetic control.
- b) Differences in wood properties between the three treatments. One treatment is to tie some plantlets of clone 8 and 31 vertically to stakes called "tied" (T). The aim is to simulate growth without wind and to reduce the forces from the branches on the stemwood. The second treatment is to tie some plantlets of clones 8 and 31 to stakes at an angle of 45 degrees called "angled" (A). The aim is to imitate growth subject to strong wind and generate relatively pure compression wood on the lower side of the stem. This permits the comparison of wood properties between opposite and

compression wood zones. The third treatment is free growth - called "free" (F). This is as a contrast to the tied and angled treatments.

- c) Difference in wood properties up the stem. As is well known, samples from different positions within a tree present different results as wood at the different positions was laid down at different times. This is especially important for 8-month-old plantlets. The base of these plantlets is 8-month-old, whereas the most of top parts differentiated from cambium very recently. To measure wood properties in different developmental stages, each plantlet divided into 5 stem positions from the top to the bottom.
- d) Differences in wood properties between compression, opposite, normal, and mixed wood samples. Compression, normal and opposite wood samples are obtained from the angled plantlets only.

Regressions and correlations are used to search for relationships between wood properties.

4.2 Materials and methods

4.2.1 Materials

50 mm tall plantlets of clones 8 and 31 were established in a glasshouse and grown for 8 months with 16 hours daylight at 25°C and 18°C at night. Three treatments were used: free growth (F), tied to vertical stakes (T), and tied to stakes at an angle of 45° (A). The height, stem length and diameter of the plantlets were measured on the day of harvest. 12 plantlets (two plantlets for each clone and each treatment) were selected for the study wood of properties. 6 of the 12 plantlets (one plantlet for each clone and each treatment) were cut at each internode into two parts. Part A of stem (see Figure 4.1), the shorter lower piece, is used to measure cell numbers/mm² and cell wall area percentage. Part B of the stem from each plantlet together with the other six plantlets were stored dry in paper bags for later wood property testing.

4.2.2 Methods

Each plantlet was cut into 5 parts and numbered from the top to bottom as "stem position 1 (top), 2, 3, 4, and 5 (base)" respectively. Thus the 12 plantlets were cut to give 60 stem blocks. Each stem position was sub-divided into the part A and part B. Every part A was immediately fixed in F.A.A. (formalin + acetic acid + alcohol) and sectioned for examination of percent wood, pith, normal wood, and compression wood in the stem cross section areas (as studied in Chapter 3). When examining sections for percent cell wall area and cell numbers per unit area the presence of compression in the section was also noted. Therefore, the cell numbers/mm² and percent cell wall area were examined for compression and normal wood respectively for whole stem sections. Every part B was cut into 4 stick samples (quadrants) for wood property testing: Stiffness, density, and tracheid length was determined as shown in Figure 4.1. A total of 240 samples were split from all part B from the 60 stem blocks of the 12 plantlets.

4.2.2.1 Preparation of samples from the free, tied and angled plantlets

Part B stem sections from the free, tied, and angled plantlets were cut into about 60 mm long blocks and then split into 4 stick samples removing the bark and pith. These samples were for stiffness testing. These stick samples have different cross-sectional dimensions because the stems had different diameters. The 160 stick samples from the free and tied plantlets contained some compression wood, but its distribution was highly variable.

80 stick samples were split out from the angled plantlets. In order to compare wood properties between wood types, the compression, normal, mixed, and opposite wood samples were split from the angled plantlets which presented an eccentric stem pattern with the underside of these eccentric stems containing relatively pure compression wood. The compression wood samples were cut from underside of the stem. The opposite wood samples were from the upper side of the stems. Relatively pure normal wood samples came from the sidewood between compression and opposite wood, while mixed wood samples, also from sidewood quadrants, contained both normal and compression wood.

4.2.2.2 Equipment and testing procedure

Stiffness (MOE)

Stiffness was determined by tension testing using an Instron machine in an air-conditioned room (humidity 60%, and temperature 20°C). The tensile testing machine was set up with a 50 mm span length between two grips. The sample in the jaws was in series with a load cell that measured the applied load. Before testing, the samples were conditioned for more than 24 hours to let the stick samples reach 12 % moisture content. The elongation (mm) observed on each sample was measured by an extensometer over a 25 mm span and recorded on a computer. The test result were automatically displayed on a computer screen and the modulus of elasticity value was calculated from this graph as shown in Figure 2.8. The modulus of elasticity for each sample was calculated from the following formula:

 $MOE = stress / strain = (N / A) / (\partial L / L)$ (12 % M.C.)

Where:

N = load;

A = cross section area of stick sample;

 ∂L = change in length of stick sample;

L = testing span length of stick sample.

Once the stress-strain plot had been obtained, then the modulus of elasticity was obtained by measuring the cross-sectional area of each sample. The stem stiffness was calculated from the area-weighted modulus of elasticity for each quadrant in that stem section.

Density

The unextracted air-dry density (at 12% M.C) was determined for each sample after modulus of elasticity testing. First a 25 mm length (span length) was cut from each sample. The weight, length, and average cross-sectional area - four cross-sections were measured for each sample - were measured in an air-conditioned room, and the density value for each stick was calculated by the following formula.

Density = weight / L*A (12% M. C.)

Where:

L = length of stick sample,

A = average cross-sectional area of the stick sample.

Tracheid length

Macerations were prepared using a 1:1 mixture of hydrogen peroxide and glacial acetic acid.

Two small pieces of wood were taken from the locations 1 and 2 respectively (Figure 4.1) from each stem quadrant and placed in the solution at 90° C for about 2 hours, then washed in water several times. One slide was made for each location: 2 slides for each stick sample. 25 intact tracheids were measured on each slide, 50 for each stick sample, 200 for each stem section, and 1000 for each plantlet. In total, 12000 tracheids were measured using MetaMorph imaging system and software.

Cell numbers per square mm and percent cell wall area

Part A of the stems was fixed in F.A.A. (formalin + acetic acid + alcohol) immediately after harvesting for sectioning to determine cell numbers per unit area and percent cell wall area for whole stem cross-section. This examination was also carried out for compression wood and normal wood (including opposite wood) respectively. The dehydration of wood materials used T.B.A (tertiary butyl alcohol) and embedding in wax (paraffin) (Dickson, 1994). 10 µm thick sections were cut, mounted on slides, stained with Safranin and Fast Green, before examining under a microscope. The reason for using these stains is to distinguish between wood tissues. Safranin is specific for lignin, staining lignified secondary walls red. Differences in intensity of staining are due to differences in lignin content. Therefore, compression wood with higher lignin content was stained darker red. Fast green is specific for cellulose, but it was less successful as the red safranin dominates. The number of cells per square millimetre, and percent cell wall area were determined using standard image analysis techniques on a PC running MetaMorph imaging software. Ray cells and resin canals were eliminated from the cell counts by using size elimination filters.

The observation and calculation of cell numbers/mm² and percent cell wall area in each view was calculated as follows:

Cell numbers/mm² = Σ (cell numbers/view area)/n (0.47 mm² / view)

% Cell wall area = \sum (% cell wall area/view)/n (0.47 mm² / view)

Where:

n = number of views

4.2.2.3 Data analysis

This experiment is a three-factor experiment and split-plot design (Zar, 1999). Analysis of variance (ANOVA) was used to analyse differences in wood properties between clones, treatments, and positions up the stem, and between compression wood, opposite wood, mixed wood, and normal wood using the Minitab version 11 software. Correlation and regression analyses were also carried out to seek relationships between these young wood properties.

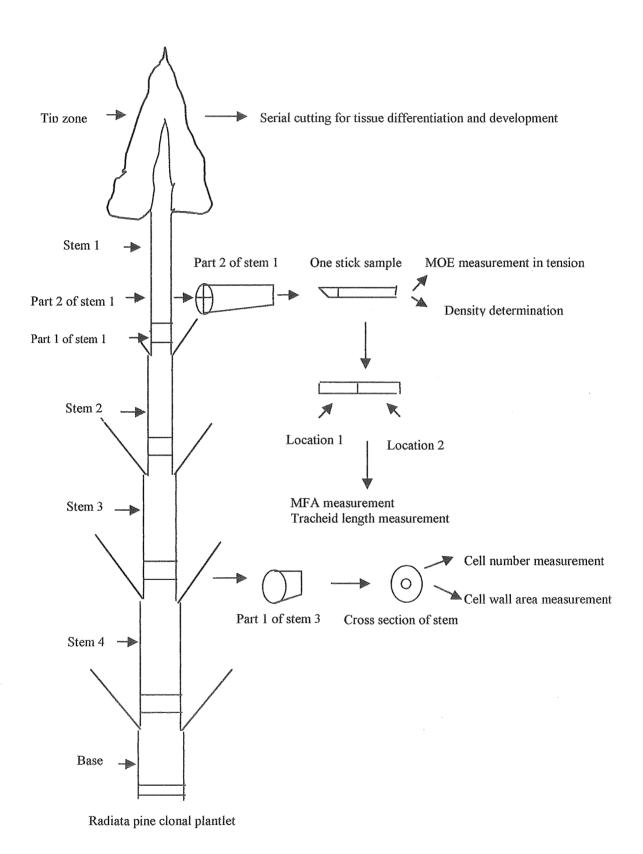


Figure 4.1 Sampling from 8 month-old radiata pine clonal plantlet.

4.3 Results for the angled plantlets

The results from the four angled plantlets are considered first, to establish differences (if any) in the wood properties of compression wood, opposite wood, normal and mixed wood. Subsequently the wood properties of clones, treatments and stem positions for all plantlets will be compared (Section 4.4).

As discussed earlier (Chapters 1 and 2), one of the objectives of this experiment was to identify and determine the anatomical, physical and mechanical properties of compression wood, opposite wood, mixed and normal wood respectively. This was possible by splitting the stemwood from the four angled plantlets into four quadrants according to wood types (Figure 4.2). Compression wood forms on the underside of the stem so compression wood samples were taken from this location. Opposite wood samples came from upper side of the stems. Whereas the side wood found in the quadrants separating the compression and opposite wood was classified into normal and mixed wood samples depending on whether it included some mild compression wood in addition to normal wood. As shown in Figure 4.2, the compression wood samples contained relatively pure compression wood, and the mixed wood samples had a variable amount of compression wood.

4.3.1 Test samples

The modulus of elasticity in tension (12% moisture content), density (12% moisture content) and tracheid length were obtained for all four quadrants. Cell numbers/mm² and percent cell wall area were only gathered for compression and opposite wood: these were calculated using Metamorph software after examination of the stem cross-section under the microscope.

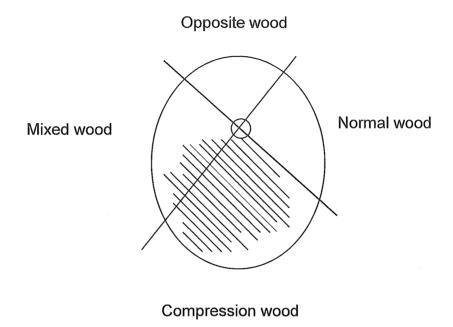


Figure 4.2 Splitting the angled stem made isolation of the wood types possible.

Where a side quadrant contained both normal and some compression wood, this material was classified as mixed wood.

4.3.2 Wood properties of the four wood types

The mean values for the modulus of elasticity, density, tracheid length for the four type wood samples and cell numbers/mm² and percent cell wall area for compression and opposite wood samples in each position are given in Table 4.1. The results of analysis of variance (P values) for wood properties of the four wood types are given in Table 4.2. Overall, the compression wood in each position is stiffer and denser with thicker cell walls than other type woods. The wood properties were weighted-average for each stem position according to each wood sample's stem cross-section area. The weighted-means of wood properties for each stem position are given in Table 4.2. The results of analysis of variance (P values) for wood properties of stems are also summarised in Table 4.2.

Table 4.1 The means of wood properties for compression wood, opposite wood, mixed wood, and normal wood by stem position.

	Stem 1	Stem 2	Stem 3	Stem 4	Base
MOE (GPa)					
CW	1.00	1.80	1.30	2.70	2.44
OpW	0.32	1.00	1.01		1.61
MW	0.66	0.81	1.18	2.08	2.25
NW	0.81	0.71	1.07		0.92
Density (kg/m ³)					
CW	485	568	631	613	614
OpW	465	458	441		447
MW	479	470	440	497	460
NW		403	461		469
Tracheid L. (mm)					
CW	0.92	0.98	0.87	0.83	0.93
OpW	0.91	0.97	1.00		0.96
MW	0.70	0.97	0.96	0.88	0.95
Nw	0.88	1.08	0.96		0.94
Cells/mm ²					
CW	2396	2388	2548	2552	2491
OpW	2237	2453	2513	2856	3020
Cell wall area (%)					
CW	44.2	46.7	47.7	48.6	47.9
OpW	23.3	25.0	26.7	32.5	33.6

Table 4.2 Means of modulus of elasticity, density, tracheid length, cell numbers/mm², and percent cell wall area by wood type and position in the angled plantlets. Standard errors are shown in parentheses.

4044494449479950950444444444444444444444	MOE	Density	Tracheid L.	Cells/	Cell wall
	(Gpa)	(kg/m^3)	(mm)	mm^2	area (%)
Type					
CW	1.85 (0.23)	590 (11.7)	0.91 (0.02)	2475 (49.6)	47.0 (1.82)
OpW	1.15 (0.15)	451 (14.7)	0.96 (0.03)	2616 (118)	28.2 (1.59)
MW	1.26 (0.19)	467 (16.4)	0.92 (0.06)		
NW	0.88 (0.09)	473 (23.0)	0.96 (0.03)		
P value	0.015	0.000	0.371	0.285	0.000
Position					
Stem 1	0.76 (0.2)	479 (22.1)	0.87 (0.04)	2316 (80.6)	33.7 (6.70)
Stem 2	1.16 (0.2)	491 (19.3)	0.98 (0.03)	2420 (34.1)	35.8 (6.51)
Stem 3	1.15 (0.1)	504 (28.0)	0.94 (0.02)	2531 (44.6)	37.2 (6.57)
Stem 4	2.39 (0.4)	555 (19.3)	0.85 (0.03)	2704 (182)	40.5 (5.53)
Base	1.85 (0.2)	513 (27.1)	0.94 (0.01)	2755 (206)	40.7 (4.20)
P value	0.006	0.243	0.216	0.364	0.213

Table 4.2 shows that the modulus of elasticity, density, and cell wall area percentage were significantly different between wood types (P = 0.015, 0.000, and 0.000 respectively); the modulus of elasticity significantly differs between stem positions (P = 0.015). These differences in wood properties are considered in the following sections.

4.3.2.1 Variations in stiffness between wood types

The values for the modulus of elasticity differ significantly between the four wood types (P = 0.015). The average values for compression wood, opposite wood, mixed wood, and normal wood were 1.84, 1.15, 1.26, and 0.88 GPa respectively. Figure 4.3 shows how stiffness for these four wood types varies with stem position.

From Figure 4.3, the compression wood had higher values of stiffness at all stem positions. The mean value of compression wood was 1.85 GPa, and for opposite wood was 1.15 GPa. The compression wood is 37% stiffer than the opposite wood. It is noted that the stiffness of compression wood had a big variation along the stems. This

big variation of stiffness in compression wood suggested that these compression wood samples contained large variable amounts of severe compression wood cells and mild compression wood cells in both of the same stem positions and between stem positions.

Vertical variations in stiffness

Table 4.2 shows that the modulus of elasticity is effected by stem position (P = 0.006). Stiffness decreases up the stem, with the highest value for the modulus of elasticity occurring at stem position 4 (2.39 GPa). This is probably because stem 4 had a higher percent cell wall (40.5%) and density (555 kg/m³) than the other stems positions as the stem 4 contained more severe compression wood.

4.3.2.2 Variations in density between wood types

Density significantly differs between wood types (P = 0.000). The compression wood had the highest density (590.3 kg/m³) and the opposite wood had the lowest density (450.6 kg/m³) with mixed wood (466.5 kg/m³) and normal wood (473.1 kg/m³) intermediate between the two. These results are presented in Figure 4.4. Opposite wood had similar densities for all stem positions, whereas the density of compression wood varies greatly between stem positions. The base, stem 4 and stem 3 had higher densities and stem 1 had a lower density than the others as it is difficult to tie the inclined stem close to the growing tip and it could be argued that wood from position 1 should be omitted from such analysis. As expected, the compression wood was denser than the other wood types, being 31% denser than opposite wood and 25% denser than normal wood.

The base and stem 4 and 3 positions had much higher density being around and over 600 kg/m³. All values are puzzling as one would expect values around 350 kg/m³ for most wood types and perhaps values of 400 kg/m³ or somewhat greater in compression wood of such young stems. This problem is discussed later.

4.3.2.3 Variations in tracheids length between wood types

Tracheid lengths in these angled plantlets were very short, most of them were less than 1 mm long. Tracheid length varied between wood types and stem positions. It is noted

that compression and mixed wood quadrants at position 4 had shorter tracheids than at other stem positions and suggests the stem 4 contained more severe compression wood.

No significant differences in tracheid length existed between wood types and stem positions (Table 4.2). However as one would expect, there is a suggestion that the opposite and normal wood had slightly longer tracheids (about 0.96 mm) than the compression wood (about 0.91 mm) and mixed wood (0.92 mm). Figure 4.5 shows the tracheid length of compression and opposite wood in all stem positions. It is noted that the compression wood had shorter tracheids than opposite wood samples at the bottom of the plantlets, at the base, stem 4, and stem 3, where compression wood might be expected to be expressed most strongly. Probably the compression wood in these locations was severe, and the compression wood in the top parts was milder. It is difficult to tie the inclined stem close to the growing tip and it could be argued that wood from position 1 should be omitted from such analysis.

4.3.2.4 Variation in cell numbers/mm²

Cell numbers/mm² varied in both compression and opposite wood. Cell numbers/mm² decreased with height up the stem in the opposite wood and this is matched by a reduced percent cell wall. The same trends are seen in compression wood although this effect is less regular.

No significant difference in cell numbers/mm² was observed between wood types and stem positions. However, Figure 4.6 shows that opposite wood had more cells/mm² than the compression wood at the base and stem 4. It is suggested that at the base and stem 4 the compression wood cells were more rounded resulting in less cell numbers in per millimetre square.

4.3.2.5 Variation in percent cell wall area between wood types

The percent cell wall area was significantly different between compression and opposite wood (P = 0.000) with compression wood having a higher percent cell wall area (47.0%) compared to that for opposite wood (28.2%). As expected, compression wood had much thicker cell walls than opposite wood (Table 4.2). This result can be seen in Figure 4.7, with the compression wood displaying a higher percent cell wall area than

opposite wood in all stem positions. Another characteristics is that the compression wood had almost equal percent cell wall area from stem 1 to base, whereas the percent cell wall area of opposite wood showed an increasing trend from stem 1 to base.

Overall, the compression wood is superior to other type woods in stiffness, density and percent cell wall area. Severe compression wood had fewer cells/mm² and shorter tracheids.

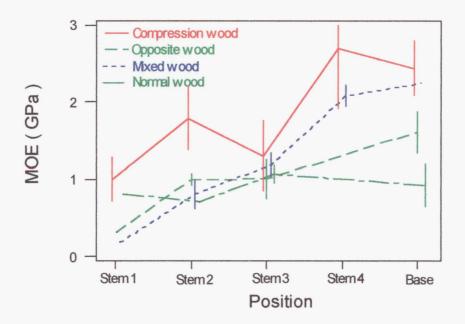


Figure 4.3 Modulus of elasticity for compression, opposite, normal, and mixed wood: the vertical lines represent standard errors.

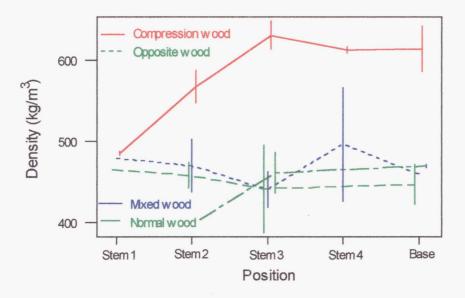


Figure 4.4 The density of compression, opposite, normal, and mixed wood: vertical lines represent standard errors.

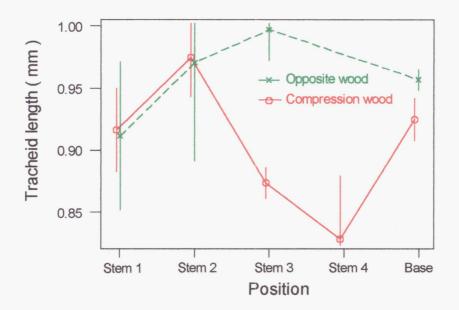


Figure 4.5 Tracheid length of compression and opposite wood: vertical lines represent standard errors.

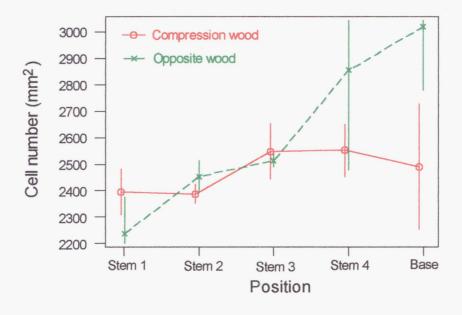


Figure 4.6 Cell numbers/mm² in compression and opposite wood: vertical lines represent standard errors.

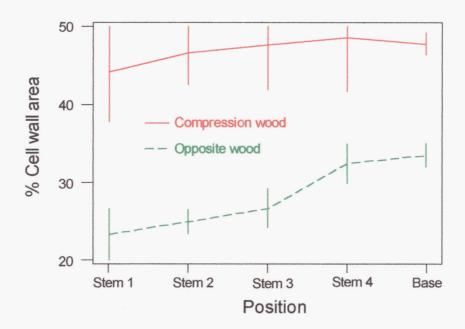


Figure 4.7 Percent cell wall area of compression wood and opposite wood: vertical lines represent standard errors.

4.3.3 Influence of angled clones on wood properties

Wood properties for the four wood types of the two angled clones are summarised in Table 4.3 and 4.4, respectively. There is a lot of noise in the data. In general, for the angled plantlets of clone 8 (Table 4.3) the modulus of elasticity, density, cell numbers/mm² and wall area decreased up the plantlets. Overall compression wood had higher stiffness values and densities in all stems compared with other wood types. With clone 31 (Table 4.4) similar results were obtained.

Table 4.3 Property means for compression wood, opposite wood, normal wood and mixed wood according to stem position in the angled clone 8.

	Wood type	Stem 1	Stem 2	Stem 3	Stem 4	Base
MOE	CW	1.28	1.57	1.95	3.48	2.83
(GPa)	OpW		1.05	0.83		2.04
	MW	0.66	0.93	1.13	2.22	
	NW			1.01		
Density	CW	488	589	645	609	596
(kg/m^3)	OpW		458	455		482
, - ,	MW	479	493	424	426	
	NW			487		
Tracheid	CW	0.88	1.00	0.89	0.88	0.90
length.	OpW	0.85	1.06	1.03		0.96
(mm)	МW		0.89	0.96	0.92	
	NW			0.99		
Cells/	CW	2482	2352	2652	2652	2727
mm^2	OpW	2099	2394	2537	3233	3261
Cell wall	ĊŴ	37.9	42.6	41.9	41.7	46.5
area (%)	OpW	19.9	23.4	24.2	35.1	35.1

Table 4.4 The property means for compression wood, opposite wood, normal wood and mixed wood according to stem position in the angled clone 31.

***************************************	000 000 000 000 000 000 000 000 000 00	Stem 1	Stem 2	Stem 3	Stem 4	Base
MOE	CW	0.72	2.02	0.65	1.93	2.05
(GPa)	OpW	0.32	0.94	1.10		1.19
	MW		0.69	1.30	1.94	2.25
	NW	0.81	0.71	1.09		0.92
Density	CW	482	546	617	617	632
(kg/m^3)	OpW	465	458	435		412
	\overline{MW}		446	474	567	460
	NW		403	448		469
Tracheid	CW	0.95	0.95	0.86	0.78	0.95
length.	OpW	0.97	0.88	0.98		0.95
(mm)	MW	0.70	0.88	0.95	0.83	0.95
	NW	0.88	1.08	0.94		0.94
Cells/	CW	2310	2423	2445	2453	2255
mm^2	OpW	2375	2513	2489	2479	2779
Cell wall	ĊW	50.5	50.7	53.4	55.5	49.2
area (%)	OpW	26.7	26.5	29.2	29.9	32.0

Variations in wood properties between angled clones

The mean values for the wood properties of two angled clones are summarised in Table 4.5. Only 2 angled plantlets were tested for each clone, so an analysis of variance was not performed to determine the potentially significant differences in wood properties.

Table 4.5 Wood properties, weighted average for cross section, at all heights up the stem for 4 angled plantlets. Standard errors are shown in parentheses.

Clone	MOE	Density	Tracheid L.	Cells	Cell wall
	(GPa)	(kg/m^3)	(mm)	(mm^2)	area (%)
8	1.63 (0.58)	581 (18.7)	0.86 (0.15)	2817 (118)	37.8 (3.9)
31	1.47 (0.18)	538 (5.1)	0.91 (0.03)	2464 (56)	42.9 (5.9)

From Table 4.5, the angled clone 8 was superior than angled clone 31 in modulus of elasticity, density and cell numbers/mm². There are inconsistencies in that clone 8 had a higher density but lower cell wall area than clone 31. However, clone 8 had more cells per square millimetre than clone 31.

4.3.4 Statistical relationships between wood properties of wood types

A correlation analysis performed between wood properties of the four wood types. The results are given in Table 4.6. Note, the relationships between cell numbers/mm² and percent cell wall area with other wood properties will be analysed later as they were just examined for compression and opposite wood.

Table 4.6 Correlation analyses for stiffness, density, and tracheid length in angled clonal plantlets.

	r values	P values
MOE - Density	0.528***	0.000
MOE - Tracheid length	- 0.096	0.53
Density - Tracheid length	- 0.22	0.144

^{***} at 0.1% significant level.

There was a significant correlation between stiffness and density in angled clones (r = 0.528***). The data for stiffness against density in each wood type samples were plotted in Figure 4.8. The regression equation is:

MOE = -1.06 + 0.00488 density

Figure 4.8 shows a modest relationship between stiffness and density; the greater the density, the higher the stiffness. The compression wood samples had a higher density and stiffness than the other wood types, but their stiffness values are extraordinarily variable.

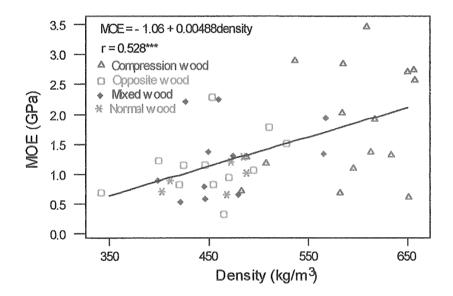


Figure 4.8 Relationship between MOE and density for various wood types.

From Figure 4.8, the plotted points of the compression wood samples showed a wide scatter in stiffness values for similar density. These compression wood samples may have varying amounts of compression wood tissue, therefore, each compression wood sample may have different characteristics, such as, different tracheid length and microfibril angle (Appendix 5). Pearson and Gilmore (1971) reported results on relationship between stiffness and density in juvenile wood of lobllolly pine. Their plot points for specimens from butt logs showed a very wide dispersion of stiffness for similar specific gravity, and suggested this due to the presence of variable amounts of compression wood.

4.3.5 Discussion

Compression wood having thick cell walls, high density, shorter tracheids, larger microfibril angle, and lower stiffness are well known in mature trees (Timell, 1986; Robert, 1998). In this study, similar results were obtained. The compression wood had thicker cell walls, higher density, and severe compression wood had less cell numbers and shorter tracheids when compared to other wood types.

There was a difference to be found that some compression wood had a higher stiffness than other type woods. This is a contrary result compared to the compression wood in the mature trees. The relationship between stiffness and density indicated that the higher stiffness accompanied with bigger density. Accordingly this suggests that the contribution of the density to stiffness was more important than the very short tracheids in these very young compression wood tissues. It is noted from Table 4.2 that compression wood, opposite wood, mixed wood and normal wood all had very short tracheids and with similar lengths (0.91, 0.96, 0.92, and 0.96 mm respectively), whereas the densities of these wood types were significantly different (590, 451, 467, and 473 kg/m³, respectively). It is suggested that compression wood had a higher stiffness as it had a higher density.

The behaviour of other type woods in this study was similar to those in mature trees. Timell (1986) states " in many respects normal conifer wood can be regarded as a transition form between opposite wood and compression wood". Harris (1977) observed that opposite wood generally exhibits normal characteristics other than a relatively slow rate of growth. In this study, side wood (mixed and normal wood) also presented intermediate values between compression and opposite wood for most of wood properties, but with values closer to that for opposite wood. On the other hand, several researchers (Timell, 1973, for referece) have observed slightly longer tracheids in opposite wood compared to normal wood and suggested that opposite wood has a slight tendency to the properties of tension wood. In this study, the opposite wood had a same tracheid length as normal wood.

The compression, opposite, mixed and normal wood had densities being 590 kg/m³, 451 kg/m³, 467 kg/m³, and 473 kg/m³ respectively. These values are much higher than the

results reported by Addis (1995) on 25-year-old radiata pine trees where the density of the compression wood was 452 kg/m³ and opposite was 434 kg/m³. He suggested the compression wood studied by him was mild. Maybe the greater density obtained from the young angled clonal plantlets is due their being grown tilted at 45 degrees resulting in severe compression wood. Austin (1988) examined specific gravity on 20-year-old slash pine in the USA, and found that the butt logs was 7% higher in specific gravity and 8% higher in modulus of elasticity.

The tracheid length of opposite wood is longer than in compression wood at the base, stem 4 and 3 positions. The stem sections near the base of the plantlets showed more compression wood and accordingly had a higher percentage of rounded cells. The compression wood cells in these parts were much shorter and with very thicker cell walls. Nicholls (1982) reported that the compression wood formation is more intense in the former than in the latter. The stem position 4 was subjected to more bending stresses than other parts of the stem. It is suggested that because the wood at stem 4 displays a higher stiffness, thicker cell walls, greater density, and shorter tracheids due to cells being formed under a severe stress for a longer time so forming Imore severe compression wood.

It is suggested that influence of auxin induced in the leaning stems is most noticeable away from the axial tip of the plantlet (which is more likely to be less restrained and closer to the vertical). Both this and the severity of the lean at the base of the stem accounts for more severe expression of compression wood formation.

The positive relationship between stiffness and density demonstrated that density is a good contributor to stiffness, or, is a useful predictor for stiffness in the angled clonal plantlets. Such a relationship would be expected and has been shown for mature loblolly pine by Pearson and Gilmore (1971).

This study sought to determine in some detail the variations in wood properties within very small plantlets by splitting the thin stems along the grain into four quadrants. The variations of some measurements look quite big. Some reasons might be as follows. Firstly, the angled plantlets had a green stem diameter of about 8.8 mm (including pith

and bark) being about 6 mm at stem 1 and 12 mm at the base. After air-drying, these plantlets were thinner and then split into four quadrants: compression, opposite, mixed, and normal wood. The compression wood samples contained variable amounts of severe and mild compression wood cells and some normal wood cells (Plate 3.10). As these samples were very thin small differences in severe compression wood cell content can result in clear differences in wood properties. These compression wood samples had different amounts of severe compression wood cells. Therefore resulting in large variations in wood properties (Figure 4.8). Also, the irregular dimensions of the split samples probably influenced the measurement accuracy for cross-section area and so also the estimate of the volume of the samples that is needed for the stiffness and density values. This is a major influence on experimental error. However, as would be anticipated most compression wood properties were different from opposite and side wood, reflecting its stiffness and density.

4.3.6 Conclusions

The main results of this study are summarised as follows:

- 1 Compression wood had significantly higher percent cell wall area, density, and stiffness than the opposite, mixed, and normal wood. Severe compression wood contained fewer cells/mm² and shorter tracheids.
- The wood at stem 4 position showed the highest stiffness, density, and the shortest tracheids compared to other stem positions in the angled plantlets.
- The stem position strongly effected stiffness. The stiffness decreased up the stem .
- Stiffness is related to density in the angled clones (P = 0.528**). The higher stiffness was effected by the bigger density.

4.4 Results of clonal wood properties

In this section, the effect of clone, treatment, and stem position on wood properties will be examined.

4.4.1 Test samples

The samples were obtained from the free, tied and angled clonal plantlets through splitting their stems into quadrants (test samples) for stiffness testing in tension (air-dry to 12% moisture content), density (air-dry at 12% moisture content) and tracheid length. The cell numbers/mm² and percent cell wall area were examined over the entire stem cross-section (green wood) using standard image analysis techniques on PC running MetaMorph imaging software. Ray cells and resin canals were eliminated from the cell counts by applying size elimination filters.

4.4.2 Comparison of wood properties between clones, treatments and stem positions

To know how the wood properties were effected by the genetic factors (clones), by plantlet growth conditions (treatments), and the plantlet development stages (stem positions), the means of wood properties were calculated and the analysis of variance were undertaken to compare wood properties between clones, treatments and stem positions. Where appropriate these values have been volume weighted to account for the greater stem diameter at the base of the plantlets and for the larger quadrant area of compression wood in the angled plantlets. These results were listed in Table 4.8.

Table 4.8 indicates that there were no significant differences in wood properties between the two clones. Density, tracheid length, cells/mm² and the percent cell wall area differed significantly between treatments. Stiffness, tracheid length and percent cell wall area significantly differed between stem positions. The results of analysis of variance indicate an interaction in density and in tracheid length between treatments and stem positions. These differences in wood properties are considered in following sections.

Table 4.7 Weighted-means of stiffness, density, tracheid length, cells/mm², and percent cell wall area for clones, treatments, and stem positions at all height up the stems for all treatment plantlets: standard errors are shown in parentheses

	MOE	Density	Tracheid L.	Cells/	Cell wall
	(GPa)	(kg/m^3)	(mm)	mm^2	area (%)
Clone			TO THE PERSON NAMED AND ADDRESS OF THE PERSON NAMED AND ADDRES	an m Amazen a car	
8	1.73 (0.17)	495 (32.2)	1.05 (0.06)	2337 (149)	33.0 (2.9)
31	1.77 (0.18)	464 (24.2)	1.06 (0.05)	2291 (121)	32.9 (5.0)
P value	0.901	0.101	0.700	0.851	0.981
Treatmen	t				
Free	2.02 (0.2)	461 (23)	1.13 (0.02)	2135 (66.8)	30.6 (2.0)
Tied	1.67 (0.04)	418 (6.1)	1.14 (0.03)	2166 (87.8)	27.9 (1.8)
Angled	1.55 (0.19)	559 (14.6)	0.87 (0.02)	2641 (96.9)	40.4 (2.3)
P value	0.393	0.001	0.001	0.004	0.000
Position					
Stem 1	1.07 (0.15)	478 (19.4)	0.99 (0.0472)	2112 (75.4)	27.3 (1.71)
Stem 2	1.43 (0.11)	473 (16.5)	1.04 (0.0266)	2239 (63.3)	29.5 (1.87)
Stem 3	1.59 (0.16)	477 (23.6)	1.07 (0.0359)	2187 (119)	32.0 (2.58)
Stem 4	2.44 (0.22)	446 (20.9)	1.11 (0.0507)	2352 (163)	33.2 (4.00)
Base	1.78 (0.16)	478 (20.7)	1.08 (0.0332)	2413 (150)	34.6 (2.36)
P value	0.000	0.678	0.000	0.194	0.005

4.4.2.1 Stiffness

Stiffness between clones

Table 4.8 indicated that the clones 8 and 31 had similar stiffness values, on average being around 1.7 GPa. The mean values for stiffness in clones 8 and 31 at various positions up the stem in each treatment are summarised in Table 4.9. The mean values of stiffness decreased with height. Wood at stem 4 position had higher values than other stem positions in every treatment. Overall, the angled plantlets had lower stiffness values at stem 1, 2 and 3 than the free and tied clones. It is clear from Table 4.9 that apart from stem 4 position, the tied clones had higher and the angled clones had lower stiffness than the free clones.

Table 4.8 The mean values of stiffness (GPa) of the stems of free (F), tied (T) and angled (A) clones 8 and 31.

All the side of th	Stem 1	Stem 2	Stem 3	Stem 4	Base
C8(F)	0.76	1.12	1.99	2.47	1.89
C31(F)	1.11	1.63	1.33	2.76	1.73
Mean	0.94	1.38	1.66	2.62	1.81
C8(T)	1.06	1.59	1.79	2.49	1.01
C31(T)	1.52	1.58	1.93	2.26	1.33
Mean	1.29	1.59	1.86	2.38	1.17
C8(A)	1.28	1.30	1.50	2.98	2.63
C31(A)	0.65	1.34	0.87	1.93	1.79
Mean	0.96	1.32	1.18	2.45	2.21

Stiffness between three treatments

Table 4.8 indicates that there was not significant difference in stiffness between clones 8 and 31. However, there is an evidence that the angled plantlets had weaker wood (1.55 GPa) than free ones (2.02 GPa) and tied ones (1.67 GPa). This implies that if tied the plantlets to 45 degrees their wood will become weaker. This probably was due to tracheid length becomes shorter under the angled treatment.

Stiffness variations along the stem

A significant difference in stiffness existed between stem positions (P = 0.000). The mean values of stiffness for each stem position from the base to stem 1 position are 1.92, 2.44, 1.59, 1.43 and 1.07 GPa respectively. Stem 4 had the largest stiffness values, and the stem 1 had the smallest stiffness. There was a general trend of decreasing stiffness values with increasing height up the plantlets. Stiffness increases gradually from stem 1 to stem 3 and then sharply increases to stem 4 before decreasing from stem 4 to base (Figure 4.9).

From Table 4.9, the stiffness declined from stem 4 to the base. The stem 4 having higher stiffness suggests the wood tissue in stem 4 being maturer than stem 3, 2, and 1. The less stiff wood in the base zone suggests that the behaviour of base log was like butt log in mature trees.

Overall, the stiffness largely varied between stem positions, increasing from the top to the bottom. It did not change much with treatments. However, there was evidence that the tied plants had stiffer wood, and the angled plants had less stiff wood compared with free grown ones.

4.4.2.2 Density

Density between clones

Table 4.8 shows that clone 8 had a slightly higher density (495 kg/m³) than clone 31 (464 kg/m³). Mean values for the density of two clones in the three treatments are given in Table 4.10. In the free (untied) treatment, clone 8 had a higher density than clone 31 at all stems positions. There are no systematic differences between stem positions in the two clones when staked vertically or at an angle. It is noted that the angled clones had higher density values and the tied clones had lower values than the free clones at all stem positions. It is clear from Table 4.10 that the density of two clones had a little change between stem positions, but had a large change between treatments.

Table 4.9 The mean values of density (kg/m³) of the stems of free (F), tied (T) and angled (A) clones 8 and 31.

philosophic and an experimental philosophic and a second philosophic an	Stem 1	Stem 2	Stem 3	Stem 4	Base
C8(F)	540	532	518	428	468
C31(F)	496	475	432	410	446
Mean	518	504	475	419	457
C8(T)	453	416	382	411	435
C31(T)	425	401	401	417	433
Mean	439	409	392	414	434
C8(A)	483	533	578	569	568
C31(A)	489	506	565	554	559
Mean	486	519	572	562	564

Effect of treatments on density

Density is very sensitive to the treatments. A significant difference in density between treatments is evident in Table 4.8 (P = 0.001). From Table 4.8, for the free, tied, and angled plantlets, the mean density values are 461, 418 and 559 kg/m³ respectively. The angled plantlets were denser than the free and the tied ones especially in the lower part of the stem (Figure 4.10). The angled treatment, with the formation of compression wood on the underside of the leaning plantlets, increased in density by 21% compared to the freely growing plantlets, and by 34% more than the tied plantlets.

Figure 4.10 shows the density of three treatments along the stems. An interaction in density was found between treatments and stem positions (P = 0.000), that is, the angled plantlets were much denser in the lower stem whereas the free ones were denser in the upper stem (Figure 4.10).

Clearly, the density was much variable with treatments, but did not change much between stem positions: 478, 473, 477, 446, and 478 kg/m³ (this may be because these plantlets were too young to change their density). Environmental stress resulted in different wood cell types and densities for plantlets. Angled plantlets produced more compression wood with bigger density. Tied plantlets were not subject to these eccentric gravitational forces, and so they produced more normal wood with light density. This result illustrates that plantlets in different growing situations will produce different wood cells with different density to adapt to their growing conditions.

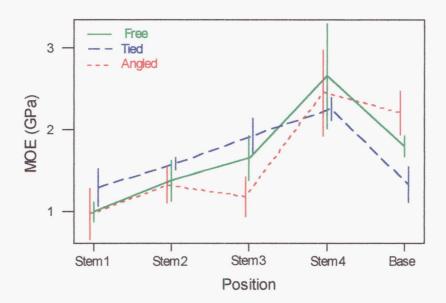


Figure 4.9 Stiffness of wood up the stem: vertical lines represent standard errors.

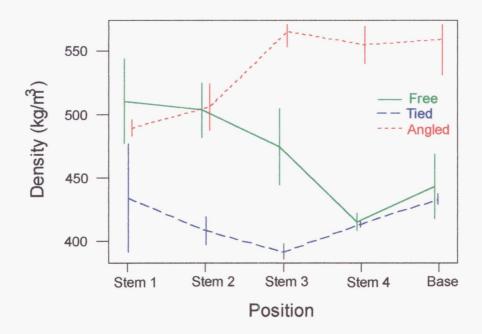


Figure 4.10. Density variations up the stem: vertical lines represent standard errors.

4.2.2.3 Tracheid length

25 tracheids were measured using image analysis from each macerated sample. With two replicates this means 50 tracheids for each quadrant, 200 for each stem and 1000 for each plantlet. The results for the tracheid length distributions in the clones, treatments, and stem positions are listed in Appendix 2, which include tracheid numbers, means, standard deviations, standard errors, and coefficients of variations.

Tracheid length in clones

The clones 8 and 31 had same tracheid length on average being about 1.06 mm. The tracheid lengths for the free, tied and angled plantlets are listed in Table 4.11. It is clear that the tracheid lengths decreased with stem height. The angled plantlets had shorter tracheids than the free and tied clones. It is noted that stem 4 position for the free and tied plantlets had longer tracheids while the angled plantlets had shorter tracheids than those in the other stem positions. It is suggested that cells at the stem 4 position were subject to more severe compression forces than at other stem positions.

Table 4.10 The mean values for tracheid length (mm) in the stems of free (F), tied (T) and angled (A) plantlets of clones 8 and 31.

30000000000000000000000000000000000000	Stem 1	Stem 2	Stem 3	Stem 4	Base
C8(F)	1.02	1.03	1.08	1.21	1.15
C31(F)	1.06	1.08	1.16	1.16	1.16
Mean	1.04	1.05	1.12	1.19	1.16
C8(T)	1.06	1.09	1.19	1.21	1.15
C31(T)	1.19	1.13	1.19	1.18	1.17
Mean	1.13	1.11	1.19	1.19	1.16
C8(A)	0.87	1.25	0.94	0.89	0.92
C31(A)	0.84	0.97	0.92	0.85	0.94
Mean	0.86	1.11	0.93	0.87	0.93

The effect of treatments on tracheid length

Tracheid length significantly differ between treatments (P = 0.001). The mean tracheid length in the free grown plantlets was 1.13 mm, for the tied stems was 1.14 mm, and for the angled stems was 0.87 mm. The angled clones had the shortest tracheids, especially at stem 4 position where the tracheid length was much shorter. The free and tied

plantlets had similarly tracheid lengths (about 1.13 mm) which is 31 % longer than the angled ones. Clearly, the angled treatment strongly influenced tracheid length.

Vertical variations in tracheid length

The tracheid length was also influenced by stem position (P = 0.000). There is a gradual decrease in tracheid length up the stem, being 1.08 (base), 1.11, 1.07, 1.04, and 0.99 mm (position 1) respectively. The tracheid increases 10% from stem 1 to base. It is conceivable that there are a few longer primary tracheids in stem 1 of the tied treatment but these should have been readily identified. They were not observed.

Overall, the results of these measurements demonstrated that the tracheids became progressively longer down the stem. Tracheid length also was strongly influenced by growth conditions, the tied treatment plantlets grow the longest tracheids, and the angled treatment results in the shortest tracheids. The variations in tracheid length along the stem in three treatments are shown in Figure 4.11.

There was an interaction in tracheid length between treatment and stem position (P = 0.001), that is in the angled treatment stem 4 had the shortest tracheids while in the free and tied plantlets stem 4 section had the longest tracheids.

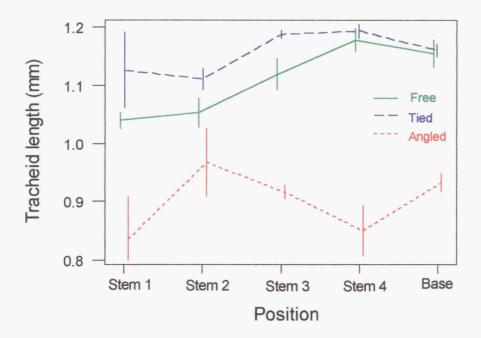


Figure 4.11 Tracheid length variations up the stem: vertical lines represent standard errors.

4.2.2.4 Cell numbers/mm²

Cell numbers/mm² of clones

The clones 8 and 31 had similar cell numbers. Cells/mm² for the free, tied and angled plantlets of clones 8 and 31 are listed in Table 4.12. It is noted that clones 8 and 31 had more cells/mm² in the angled treatment than in the free and tied treatments at all stem positions.

Table 4.11 The mean number of cells/mm² at various positions up the stem for the free (F), tied (T) and angled (A) plantlets of clones 8 and 31.

en marine en e	Stem 1	Stem 2	Stem 3	Stem 4	Base
C8(F)	2000	2055	2054		2374
C31(F)	2228	2207	1906	2072	2049
Mean	2114	2131	1980	2072	2212
C8(T)	1822	2160	1906	1984	2013
C31(T)	2118	2164	2193	2338	2574
Mean	1970	2162	2049	2161	2294
C8(A)	2291	2373	2594	2942	2994
C31(A)	2342	2468	2467	2466	2517
Mean	2317	2421	2531	2704	2756

The effect of treatment on cell numbers/mm²

Table 4.8 indicates that cell numbers/mm² were effected by treatments (P = 0.004). The stem for the angled treatment had more cells (2641 cells/mm²) than the free (2135 cells/mm²) and the tied ones (2166 cells/mm²). The difference in cell numbers/mm² between treatments is shown in Figure 4.12. The cell numbers/mm² for the angled treatment suggests a steady decline up the stem.

4.2.2.5 Percent cell wall area

Percent cell wall area in the clones

The clones 8 and 31 had similar percent cell wall area being around 33%.

The results of the percent cell wall area of the free, tied and angled clones 8 and 31 are given in Table 4.13. It is clear that the percent cell wall areas in the angled clones was higher than in the free and the tied clones at all stem positions. Also it is noted that the free-standing plantlets of clone 8 had higher percent cell wall areas at all positions up the stem than did clone 31, whereas the angled plantlets of clone 31 had higher percent cell wall areas than did clone 8 in all positions up the stem. These results reflect the fact that the two clones had different responses to the angled treatment: clone 8 was more tolerance than clone 31 as clone 8 had less thick cell walls than the clone 31 under angled treatment.

Table 4.12 Mean percent cell wall area up the stems of the free (F), tied (T) and angled (A) plantlets for clones 8 and 31.

Books as multiple communication and acceptance and acceptance and the state of the	Stem 1	Stem 2	Stem 3	Stem 4	Base
C8(F)	29.1	28.6	34.8	N/A	34.3
C31(F)	26.4	27.2	26.9	28.7	27.5
Mean	27.8	27.9	30.9	28.7	30.9
C8(T)	25.5	26.0	25.0	25.3	32.6
C31(T)	24.9	25.1	29.0	27.1	30.4
Mean	25.2	25.6	27.0	26.2	31.5
C8(A)	28.9	33.0	33.1	38.4	40.8
C31(A)	38.6	38.6	41.3	42.7	40.6
Mean	33.8	35.8	37.2	40.6	40.7

Effect of treatment and stem position on percent cell wall area

The percent cell wall area was significantly different between treatments (P = 0.000). The angled treatments had a greater percent cell wall area than the free and tied ones (Table 4.8), 40.4% cell area for the angled treatments, 30.6% and 27.9% for the free and tied ones respectively. Because the percent cell wall area was strongly influenced by the angled treatment, the percent cell wall area for the angled treatments is 32% more than the free ones, and 45% more than tied ones. It increases very quickly from tip to base in the angled plantlets, but increased only slightly from stem position to stem position in free and tied plantlets (Figure 4.13).

The percent cell wall area differed between stem positions (P = 0.005). From the base to stem 1, the percent cell wall areas are 34.6, 33.2, 31.9, 29.5, and 27.3% respectively. This increasing trend of percent cell wall area from stem 1 to base is shown in Figure 4.13.

Clearly, The angled plants had much more percent cell walls, and the tied seedlings had much less percent cell walls than the free grown ones.

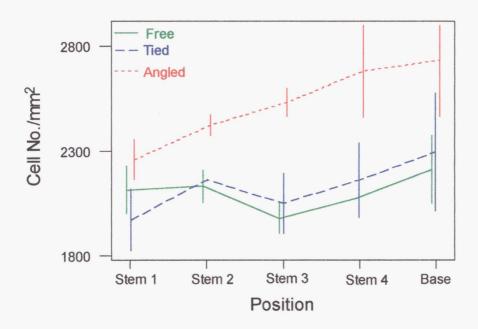


Figure 4.12 Variations in cell numbers/mm² up the stem: vertical lines represent standard errors.

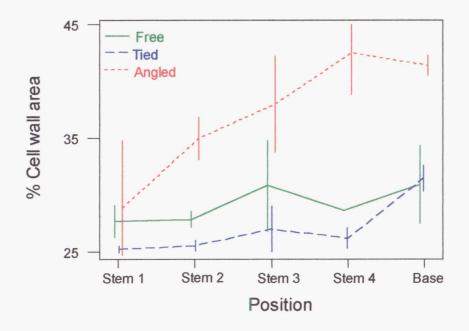


Figure 4.13 Percent cell wall area of treatments: vertical lines represent standard errors.

4.4.3 Discussion

In this study, the effecting of clone, treatment, and stem position on wood properties have been investigated. The results indicated that the two clones had similar behaviour in wood properties in each treatment. This suggests that the two clones studied here probably had close genotypes. However, the two clones had different responses when tied to 45 degrees, in clone 8 the cell wall area changed less than clone 31.

The treatments had a strong influence on wood properties, especially the angled treatment. Different treatments let the plantlets produce different responses in both cell types (compression wood etc) and distribution. These differences resulted in different wood property values. The problem of variability is clearly seen in the data (Appendix 5) where wood of similar tissue type, eg, compression wood and of similar density could show such huge differences in stiffness-by a factor of 3. This experimental variability is believed to be due to the small physical size of the material being studied.

The results in this study also demonstrated that the stem position systematically influenced wood properties. Most of wood properties showed declining patterns from stem 4 to stem 1. These probably related to wood maturity, that is the wood in stem 4 zone was maturer than stem zones 3, 2, and 1. Therefore, the stem 4 had stiffer wood and longer tracheids. The base always had lower values compared to stem 4. Probably, the behaviour of the wood at the base zone like the wood in butt log of mature trees where the wood had lower qualities being reported before (Ping Xu and John Walker, 2000). It is probably wise to treat this zone as transitional between root and stem wood.

4.4.4 Conclusions

Comparing the young wood properties between clones, treatments, and stem positions, one concludes that:

1 Clones 8 and 31 were similar in most of wood properties, but the clone 31 had thicker cell walls than clone 8 under the angled treatment.

- The angled treatment strongly influenced wood properties. Both clones 8 and 31 grown under the angled treatment had more cells, thicker cell walls, higher densities, shorter tracheids, and lower stiffness.
- 3 The tied treatment had lower density, fewer cell numbers/mm², lower percent cell wall area, longer tracheids, and higher stiffness.
- 4 The free grown plantlets had the values of wood properties that were intermediate between the angled and tied treatments.
- 5 On going down the stem, the tracheids became longer, the cell walls thicker, and the wood stiffer.

4.4.5 Results of the relationships between young wood properties

The statistical relationships between clonal wood properties have been investigated in this study.

Relationships between stiffness, density and tracheid length for the all plantlets Correlation analysis was used to determine the relationships between stiffness, density and tracheid length using 240 samples from the various quadrants and positions up the stem for 12 plantlets from the three treatments (taken together). The results are set out in Table 4.14. Stiffness was positively related to tracheid length, and the density negatively related to tracheid length. Their P values reached 0.1% significance level.

Table 4.13 The results of correlations between stiffness, density, and tracheid length of clonal plantlet wood.

Relationship	r value	P value	
MOE - Density	0.01	0.919	
MOE - Tracheid length	0.28***	0.000	
Density-Tracheid length	- 0.52***	0.000	

^{***} at 0.1% significant level.

Stiffness - Density

A relationship between stiffness and density was not found here when using all treatment samples. This is totally unexpected as all the literature emphasises a strong positive correlation between stiffness and density (Pearson and Gilmore, 1971; Addis, 1995; Mishiro and Eiji, 1997). This will discuss in section 4.4.4.3.

Stiffness - Tracheid length

There was a modest relationship between stiffness (GPa) and tracheids length (mm) (r = 0.28***). The higher stiffness accompanied longer tracheids. The data of stiffness against tracheid length was plotted for all samples from 12 plantlets in Figure 4.14. The regression equation is:

$$MOE = -0.321 + 1.77$$
 tracheid length (r = 0.28***)

Figure 4.14 showed that the tied treatments had longer tracheids and slightly higher stiffness whereas the angled plantlets had shorter tracheids and lower stiffness. There are two problems with this analysis. First the stiffness values are extraordinarily variable, and second the wood properties of the angled plantlets are likely to be different from those of the free and tied plantlets (for this reason there is a further section in this chapter which analyses these two populations separately).

Density - Tracheids length

A negative relationship existed between density and tracheid length (r = -0.52***). Stems with higher densities had shorter tracheids and vice visa. A plot of density against the mean tracheid length together with the fitted line are shown in Figure 4.15. The regression equation is:

Density =
$$841-353$$
 tracheid length (r = $-0.52***$)

The tied plantlets had longer tracheids and a lower density, whereas the angled plantlets had shorter tracheids and a higher density, which emphasises the view that the angled treatment should be analysed separately, as with compression wood one might expect the shorter tracheids to be denser. This plot is contrary to observations by many workers who have studied such relationships in trees from plantations and natural forests (Wardrop, 1951; Addis, 1998). In order to understand the relationships between stiffness, density and tracheids length within different treatments, or any influence of treatments on relationships between wood properties, individual analyses for the angled plantlets, and for the free and tied plantlets (taken together) need to be carried out separately.

From Figure 4.14 and 15, it is noted that the data points from the tied plantlets are less scattered and the angled ones show considerable scatter. These distribution patterns of the data points imply that the tied plantlets had relatively uniform wood structure, and the angled plantlets had highly variable wood structures.

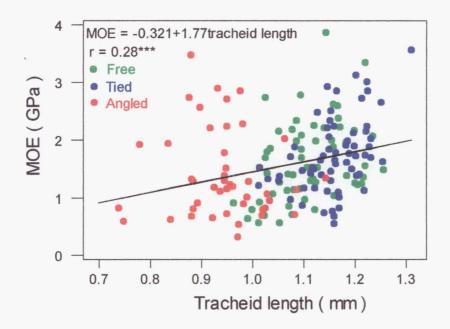


Figure 4.14 Relationship between stiffness and tracheid length in plantlets

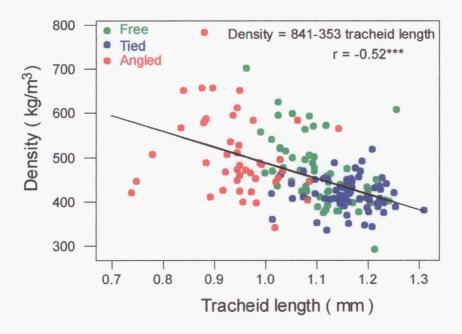


Figure 4.15 Relationship between density and tracheid length in plantlets

4.4.5.1 Relationships between wood properties of the angled plantlets

The results of correlation analysis for stiffness, density, and tracheid length in the angled treatments are given in Table 4.15. A correlation between stiffness and density for the angled plantlets is now apparent whereas it was lacking when all treatments were taken together in Table 4.14.

Table 4.14 Correlations between modulus of elasticity, density and tracheid length for the angled plantlets.

Relationship	r value	P value	
MOE - Density	0.528***	0.003	
MOE - Tracheid L.	-0.10	0.530	
Density - Tracheid L.	-0.22	0.144	

^{**} at 1% significant level.

Stiffness - density

For the angled plantlets of both clones 8 and 31, the stiffness increased with density (Figure 4.16). The regression equation was:

$$MOE = -1.06 + 0.00488 \text{ density} \quad (r = 0.528***)$$

Figure 4.16 is a replot of Figure 4.8 showing the behaviour of clones 8 and 31. It is noted that the scattered data points are compression wood samples from the angled plantlets (see Figure 4.8). The compression wood samples showed very large stiffness variations while the density at around 600 kg/m³ at most of stem positions, varied somewhat less. These different values in stiffness and less variable values in density resulted in the data distribution in Figure 4.16. It is possible that these compression wood samples had unequal amounts of compression wood cells; further some samples might have severe compression wood and some mild compression wood.

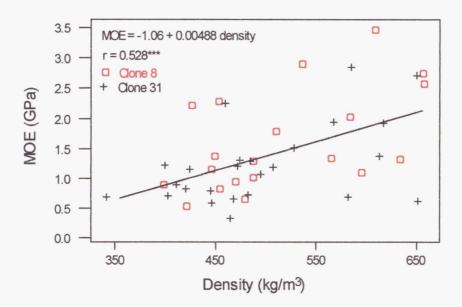


Figure 4.16 Relationship between stiffness and density for the angled plantlets

Overall, from Figure 4.14, 4.15, and 4.16, it was found that the scatter points were from the compression wood of the angled plantlets (see Figure 4.8). These data points suggested that each compression wood sample had unequal amounts of compression wood tissue both in extent and severity, that is some samples had more severe compression wood cells, some had more mild compression wood cells (Plate 3.10). Most of the adverse characteristics of compression wood are related to the more severe form (Zobel and Buijtenen, 1989). This un-unique wood tissue may lead to each compression wood samples having different characteristics, such as different density, tracheid length, and microfibril angle (these factors all are important for stiffness) (see Appendix 5). It is well known that the compression wood varies from mild to severe and varies greatly with growth conditions, tree species, and tree age. The similar problem was reported by Pearson and Gilmore (1971) in juvenile wood of loblolly pine that there was a very wide dispersion of modulus of elasticity among butt log specimens of similar specific gravity. And a hypothesis for explaining highly variable was due to the presence of variable amounts of compression wood in these butt log samples.

4.4.5.2 Relationships between wood properties of the free and tied plantlets

The results of correlation analyses between stiffness, density, and tracheid length in free and tied plantlets are shown in Table 4.16. The stiffness appears related to tracheid length in the free and tied plantlets, but is unrelated to density (again an unexpected observation, this will discuss in section 4.4.5.3). Density is negatively related to tracheid length.

Table 4.16 Correlations between modulus of elasticity, density, and tracheid length for the free and tied plantlets.

Relationship	r value	P value	
MOE - Density	-0.10	0.265	
MOE - Tracheid L.	0.40***	0.000	
Density - Tracheid L.	-0.47***	0.000	

^{***} at 0.1% significant level.

Stiffness - tracheid length

A plot of stiffness with tracheid length for the free and tied plantlets is shown in Figure 4.17. The regression equation is:

$$MOE = -2.74 + 3.89$$
 tracheid length $(r = 0.40***)$

From Figure 4.17, it is noted that the data points for these free and tied plantlets still show dispersion as the free and tied plantlets contained some compression wood randomly distributed within the four quadrants (Plate 3.10). Also other factors are related due to the influence on stiffness of characteristics such as microfibril angle (Appendix 5): that microfibril angle influences stiffness has been well document (Butterfield, 1998; Walker and Butterfield, 1996; Cave, 1969; Cave and Walker, 1994).

The juvenile wood of trees shows bigger variations in wood properties as well as high knot incidence and high spiral grain (Cown, 1992). However, our result demonstrates that the longer the tracheids the higher the stiffness. This result agrees with the results on mature trees by reported before, that the stiffness were related to tracheid length (Addis, 1998; Senft *et al.*, 1985; Wardrop, 1951).

Density - tracheid length

A negative relationship between density and tracheids length (r = -0.47***) was found in the free and tied plantlets (Figure 4.18). The regression equation is:

Density =
$$924 - 426$$
 tracheid length (r = $-0.47***$)

Figure 4.18 clearly shows a higher density with shorter tracheids and a lower density with longer tracheids. In forest trees, the density and tracheids length increase outwards from the centre of the tree (Cown and McConchie, 1980; Young *et al.*, 1992). This implies the tracheid length should positively relate to density. However, in this study the samples were from the first growth ring and from different treatments. The tracheids were influenced by the treatments, that is under the angled treatment tracheids became shorter and with thicker cell walls (higher density). For the vertically tied plantlets the tracheids became longer and with thinner cell walls (lower density). The negative relationship between density and tracheid length in this study clearly shows the tracheids changing behaviour in different treatments.

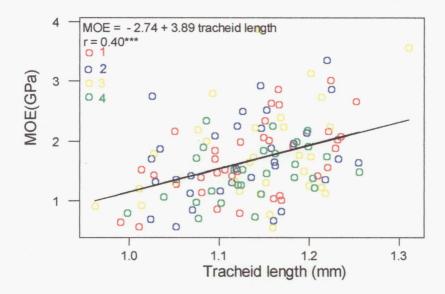


Figure 4.17 Relationship between modulus of elasticity and tracheid length of the free and tied clones only.

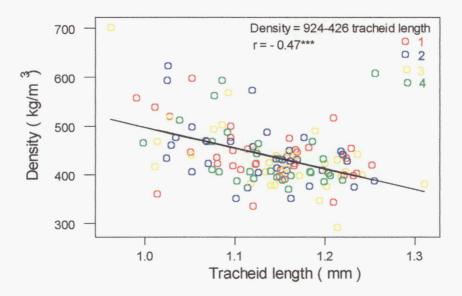


Figure 4.18 Relationship between density and tracheid length of the free and tied treatments

4.4.5.3 Altered relationships between wood properties

The results of relationships between stiffness, density, and tracheid length in free, tied and angled treatments demonstrated that the relationships between wood property can be altered under different treatments. The stiffness appears related to density in the angled treatment, whereas stiffness appears related to tracheid length in the free and tied treatments. Clearly, different growth conditions resulted in different relationships. It is also demonstrated that both density and tracheid length are major contributors to stiffness. In the case of angled treatment, the stiffness was clearly influenced by density as all wood types had different stiffnesses and densities but had similar tracheid lengths. Whereas in the case of free and tied treatments, the stiffness was clearly influenced by the tracheid length as all quadrant samples had different stiffnesses and tracheid lengths but had similar density.

Taylor (1979) reported a similar result about tracheid length in wood types of loblolly pine branches. His result showed that there was no significant difference in tracheid length between compression wood and opposite wood. The compression wood from lower side of branches had similar tracheid length and bigger density than samples from the upper side at all points along the branch. The angled plantlets in this study had similar behaviour.

Harris (1977) examined the variation of microfibril angle in relation to visual compression wood grade in radiata pine but found no significantly differences between compression wood and opposite wood within the same growth ring.

4.4.5.4 The relationships between wood properties of 6 plantlets

The work involved in measuring cell numbers/mm² and percent cell wall area was considerable, and so was restricted to only 6 plantlets (Table 4.17).

Table 4.16 Relationships between stiffness, density, tracheid length and cell numbers/mm², percent cell wall area of plantlets.

Relationship	r value	P value
Cell numbers/mm ² - MOE	0.32	0.101
Percent cell wall area - MOE	0.21	0.290
Cell numbers/mm ² - Density	0.54**	0.004
Percent cell wall area - Density	0.68***	0.000
Cell numbers/mm ² - Tracheid L.	-0.54**	0.004
Percent cell wall area - Tracheid L.	-0.61***	0.001
Cell numbers/mm ² - Percent cell wall area	0.69***	0.000

^{**} at 1% significant level.

No relationships were established between modulus of elasticity and cells/mm² and percent cell wall area.

Density - cells/mm²

A positive relationship exists between density and cells/mm² (r = 0.54**). Density increases with increasing cell numbers/mm², with the angled seedling having more cells/mm² and a higher density, and the tied plantlets having fewer cells/mm² and a lower density (Figure 4.19).

Density - percent cell wall area

A positive relationship between density and percent cell wall area was observed (r = 0.68***). The angled plantlets had more percent cell wall area and higher density, while the tied plantlets had less percent cell wall area and lower density (Figure 4.20).

It is noted from Figure 4.20 that the intercept on the y-axis is 243 kg/m³ when comparing density (air-dry) with percent cell wall area (green). There are several reasons to result in this big (non-zero) intercept: first, the density was air-dry density

^{***} at 0.1% significant level.

(12% moisture content) and the percent cell wall area was for green cell wall area and excluded the area of the ray cells, resin canal cells and pith. Also there should be a minor adjustment for when the fresh wood was fixed in F.A.A., a slightly swelling occurred to more than their fresh dimension.

Of particular interest was the fact that the ratio of the air-dry stem area (by summing the four quadrant areas of the stem) to the green stem area (fixation stem cross area) was unusually small being around 70 –80%. This amount cannot be explained by shrinkage alone. The young wood possibly contained some immature cells (close to cambium) and some primary wood cells (close to pith) which might collapse when air-dried as these immature cells had very thin walls and the primary cell walls were unligninfied.

It is possible that the young tissue (especially just 8-month-old plantlets grown in a glasshouse) had a larger shrinkage when air-dried than the mature wood. Nicholls (1982) reported that leaning radiata pine trees grown in a 23-yr-old plantation of Australia contained some compression wood. These compression wood zones (ring 5-20) had a large tangential shrinkage, being 3.3%, and the normal tissue, being 7.1%, which is much larger than old mature wood. It is suggested that the large shrinkage and immature cell collapse in the 8-month-old young wood resulted in a small ratio of the air-dry stem area to the fresh stem area. As a result, a large intercept was made.

Tracheids length - cells/mm²

Tracheids length was negatively related to cell numbers/mm² (r = -0.54**). This relationship is shown in Figure 4.21. The results indicate that tracheid length increases as cell numbers/mm² decrease. The angled plantlets had more cells/mm² and shorter tracheids. The tied plantlets had longer tracheids and fewer cells/mm².

Tracheid length - Percent cell wall area

The tracheids length versus percent cell wall area shows a negative relationship (r = -0.61***). Figure 22 shows a plot of tracheid length against percent cell wall area. The angled plantlets had a higher percent cell wall area and shorter tracheids than the tied plantlets which had less percent cell wall area and longer tracheids.

Cells/mm² - Percent cell wall area

Cells/mm² were closely related to percent cell wall area (r=0.69***). This result is shown in Figure 23. The angled plantlets had more cells/mm² and a higher percent cell wall. The tied plantlets had fewer cells/mm² and a lower percent cell wall area.

Overall, the relationships between the wood properties in 6 plantlets indirectly agree with the results at the 12 plantlets. These results demonstrate that cell numbers/mm² and percent cell wall area are major contributors to density.

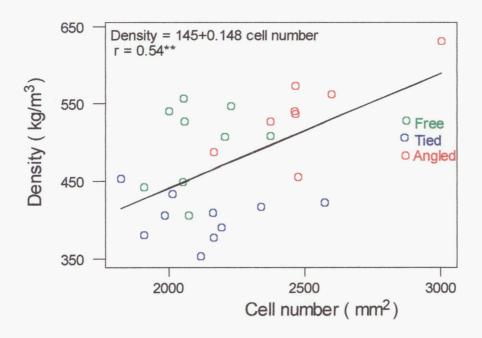


Figure 4.19 Relationship between density and cells/mm²

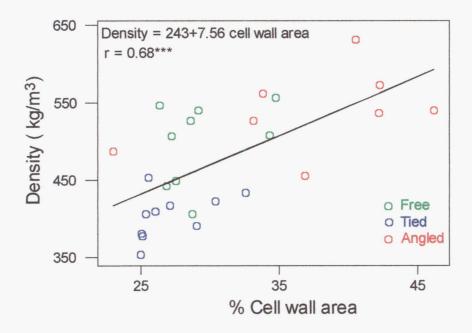


Figure 4.20 Relationship between air-dry density and percent cell wall area.

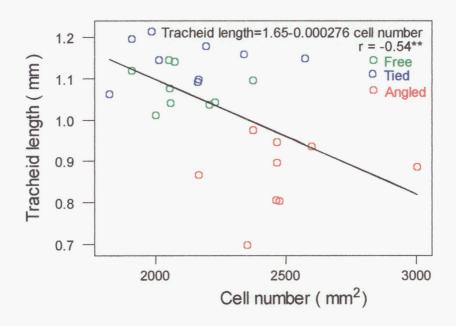


Figure 4.21 Relationship between tracheid length and cells/mm²

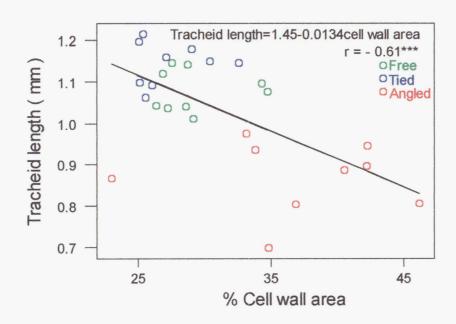


Figure 22 Relationship between tracheid length and percent cell wall area

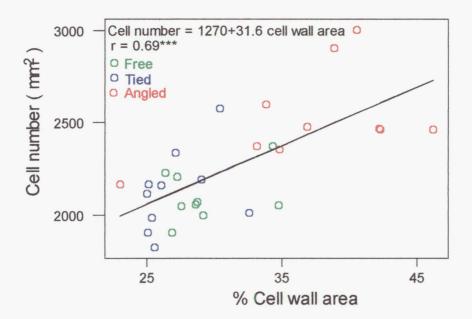


Figure 23. Relationship between cells /mm² and percent cell wall area

4.4.6 Conclusion

- 1 The relationships between wood properties can be altered in different treatments. Stiffness was related to tracheid length in the free and tied plants, and the stiffness was related to density in the angled plants.
- 2 Density was negatively related to tracheid length in the free and tied plants.
- 3 Density was related to cells/mm² and percent cell wall area.
- 4 Cell numbers/mm² and percent cell wall area are related to each other.

CHAPTER 5

PROPERTIES OF ONE AND TWO YEAR-OLD SEEDLING WOOD

5.1 Introduction

Wood properties of specific clones have been studied in Chapter 4. In this chapter, wood properties of genetically variable seedlings will be examined.

The aims of this chapter are to understand the variations of wood properties between seedlings and seedlots, and to investigate the effect of stem position and age on wood properties of seedlings. Stiffness (MOE) in compression, maximum crushing strength (MCS) in compression, air-dry density, and microfbril angle (MFA) will be determined using seedlings from different growth and form (GF) seedlots. The relationships between wood properties of seedlings will be also explored in this chapter.

5.2 Materials and methods

The seedlings were selected from the Port Levy clonal and seedlot trials established by the School of Forestry, Canterbury University, New Zealand. 32 seedlings were randomly selected from four seedlots: 1 year-old GF10, 1 year-old GF 28, 2 year-old GF10, and 2 year-old from GF28. The 8 seedlings were taken from each seedlot-age category.

The root and crown of the seedlings were removed the day following harvesting and the stems were then stored in refrigerator at -8°C until needed. Wood from the middle part of the stem was cut to give 1x1x4 mm³ samples (Figure 5.1). The samples from 1 year-old seedlings were cut from growth ring 1 (the samples probably contained variable amount of compression wood), and the samples from 2 year-old seedlings were cut from growth ring 2 (the samples were free of compression wood by checked). Only straight grain sticks were chosen for testing. Fourteen samples were prepared for each

seedling, providing a total of 448 samples from all the 32 seedlings. To compare wood properties between stem positions, the stems of each 2 year-old seedling were cut into 4 blocks numbered the 1, 2, 3 and 4. The blocks 1 and 2 named the upper two (the upper two position contained 7 samples), and the blocks 3 and 4 called the lower two (the lower two position contained 7 samples).

The length and width of the TLS and RLS faces of each sample were measured using a computer image measurement system (Metamorph). Each stick sample was weighed to the nearest 0.001 g to calculate stick density. The stiffness and failure strength of each sample was experimentally determined using a micro-compression tester interfaced to a computer. All measuring and testing was carried out at 60% relative humidity at a temperature of about 20°C.

The values for maximum crushing strength (MCS) were determined by compressing the sample to failure. The stiffness (MOE) was determined from the linear region of the force-deflection curve. Density is determined by the weight and volume of sample (12% moisture content). Microfibril angles were determined by the Cave-T method (X-ray diffraction) to obtain a mean microfbril angle for the sample.

Values of maximum crushing strength, stiffness, density and microfibril angle for each sample were calculated according to the following formulae:

MCS (MPa) = max. load (N) x
$$10^6$$
/cross-sectional area (mm²)

MOE (GPa) = (slope (N/mm) x specimen length (mm) x 10^6 /cross-sectional area (mm²))/1000

MFA (degrees) =
$$T = (xc2 - xc1 + 2w)/2$$

Density (kg/m^3) = (stick weight (mg)/stick length (mm) *RLS (mm) * TLS (mm))*1000

Analysis of variance was performance to determine significant differences in wood properties between seedlings, seedlots, stem position and age. Correlation and regression analyses were carried out to establish relationships between the wood properties of seedlings.

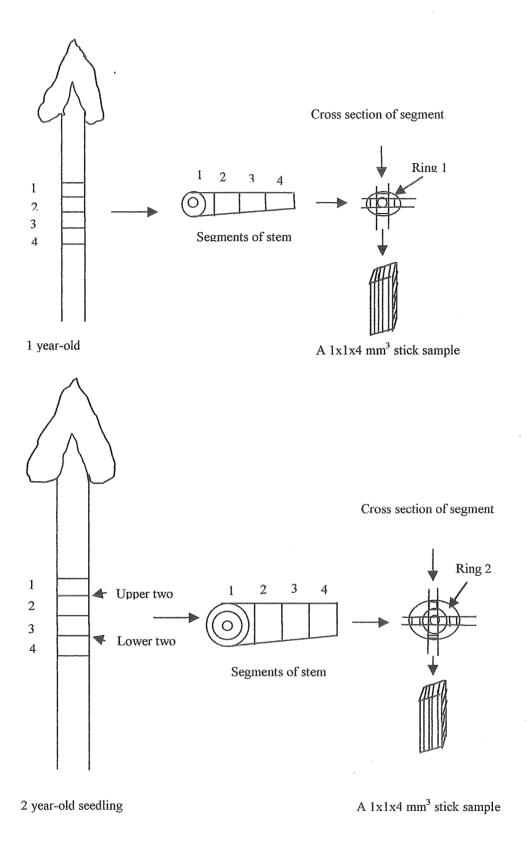


Figure 5.1 Sampling from one and two year-old seedlings.

5.3 Results of wood properties of seedlings

5.3.1 Variations in wood properties between seedlings

All samples were tested for stiffness (MOE), maximum crushing strength (MCS), airdry density, and microfibril angle. The means for the wood properties of these seedlings are given in Table 5.1. There is considerable variations in wood properties. Each property varied from seedling to seedling in both 1 and 2 year-old seedlots (GFs 10 and 28). These differences in wood properties between seedlings were significant (P = 0.000). This variation is to be expected as it reflects the enormous genetic diversity within any given seedlot.

Stiffness

Stiffness significantly varied between seedlings (P = 0.000). In 1 year-old seedlings, the values of stiffness ranged from 0.45 to 0.74 GPa in GF 28, and from 0.52 to 0.79 GPa in GF 10. The highest value is 53% greater than lowest one. In 2 year-old seedlings, the values of stiffness varied from 0.43 to 0.72 GPa in GF 10, and 0.55 to 0.68 GPa in GF28. It is noted that in 2 year-old seedling population the seedlings with the higher stiffness value were with smaller microfibril angle, and the seedlings with the lower stiffness value were with larger microfibril angle.

Maximum crushing strength

The maximum crushing strength significantly differed between seedlings (P = 0.000). In 1 year-old seedlings, the values of maximum crushing strength varied from 14.3 to 23.5 MPa in GF 10, and from 11.7 to 20.1 MPa in GF28. In 2 year-old seedlings, the values ranged from 12.3 to 17.0 MPa in GF 10 and from 11.2 to 16.7 MPa in GF 28.

Table 5.1 The means of maximum crushing strength, stiffness, microfibril angle, and density of 32 seedlings: standard errors are shown in parentheses.

					vii iii parentileses.
Name	Seedling	MCS	MOE	Cave-T	Density
	No.	(MPa)	(GPa)	MFA	(kg/m^3)
				(degrees)	
1-yr-old	1	21.3 (0.6)	0.65 (0.04)	63.2 (1.6)	391 (10)
seedlings	2	20.6 (1.3)	0.67 (0.05)	67.9 (1.9)	383 (10)
(GF10)	3	21.9 (0.8)	0.79 (0.05)	70.8 (1.2)	412 (10)
	4	20.6 (1.5)	0.78 (0.05)	63.9 (1.2)	394 (6)
	5	19.8 (0.8)	0.79 (0.05)	68.7 (1.5)	369 (20)
	6	23.5 (1.0)	0.72 (0.03)	64.3 (1.2)	441 (11)
	7	14.3 (0.7)	0.52 (0.04)	66.9 (1.3)	476 (13)
	8	15.9 (0.5)	0.65 (0.05)	68.5 (1.9)	430 (7)
	Mean	19.7	0.70	66.8	412
1-yr-old	1	20.1 (1.0)	0.74 (0.03)	69.1 (1.3)	388 (15)
seedlings	2	16.7 (0.8)	0.65 (0.05)	70.9 (1.5)	378 (15)
(GF28)	3	13.2 (0.6)	0.51 (0.04)	68.1 (1.8)	413 (11)
` ,	4	13.1 (05)	0.55(0.03)	57.5 (1.0)	384 (6)
	5	11.7 (0.6)	0.46(0.03)	62.6 (1.6)	444 (12)
	6	11.7 (0.6)	0.45(0.03)	60.5 (1.3)	397 (9)
	7	16.4 (1.6)	0.56(0.04)	67.9 (1.2)	544 (19)
, e	8	13.9 (0.6)	0.47(0.04)	69.9 (1.3)	443 (14)
	Mean	15.2	0.58	60.7	356.1
2-yr-old	1	13.7 (0.5)	0.56 (0.05)	58.4 (1.3)	355 (5)
seedlings	2	12.3 (0.3)	0.43 (0.02)	61.1 (1.0)	330 (6)
(GF10)	3	16.2 (0.6)	0.56(0.05)	62.1 (1.8)	381 (10)
,	4	16.5 (0.5)	0.57(0.03)	57.9 (1.0)	349 (6)
	5	15.6 (0.5)	0.59(0.05)	63.2 (1.6)	342 (3)
	6	14.8 (0.7)	0.53 (0.04)	70.7 (1.1)	383 (16)
	7	16.9 (0.6)	0.68 (0.05)	57.5 (0.8)	372 (9)
	8	15.8 (0.6)	0.72(0.05)	54.9 (0.7)	337 (8)
	Mean	14.3	0.55	65.8	424.0
2-yr-old	1	15.7 (0.7)	0.66 (0.04)	59.6 (1.6)	348 (7.4)
seedlings	2	11.2 (0.4)	0.55(0.03)	60.1 (1.3)	296 (7.2)
(GF28)	3	16.7 (0.6)	0.68(0.03)	62.6 (1.5)	361 (6.5)
` '	4	16.5 (0.6)	0.63 (0.04)	54.9 (1.2)	329 (5.4)
	5	12.2 (0.8)	0.58 (0.05)	66.2 (1.2)	301 (5.4)
	6	13.9 (0.8)	0.57 (0.03)	59.0 (1.3)	345 (10.7)
	7	15.1 (0.4)	0.63 (0.02)	60.2 (1.5)	346 (14.8)
	8	15.4 (0.7)	0.59 (0.04)	62.7 (1.2)	346 (7.9)
Total	Mean	14.6	0.61	60.7	334.1
mean		15.9	0.61	63.5	382

Density

The density widely varied between these seedlings (P = 0.000). In 1 year-old seedlings, the values of density were from 370 to 476 kg/m³ in GF10, and from 378 to 543 kg/m³ in GF 28. In 2 year-old seedlings, the values were from 330 to 383 kg/m³ in GF10 and

from 296 to 361 kg/m³ in GF28. It is noted that the densities decreased from growth ring 1 to ring 2. One immediate question is whether this is an intrinsic feature of very young radiata pine or whether this merely reflects the "contamination" of intrinsic wood quality values by large but variable amounts of compression wood.

Microfibril angle

Microfibril angle was significantly different between seedlings (P = 0.000). In 1 year-old seedlings, the microfibril angle values ranged from 63.1 to 70.8 degrees in GF10, and from 57.5 to 70.85 degrees in GF28. In 2 year-old seedlings, their values varied from 54.9 to 70.7 degrees in GF10, and 54.9 to 66.2 degrees in GF28.

Overall, the wood properties varied from seedling to seedling in every seedlot, Comparisons between the four seedlot-age populations are shown in Figures 5.2 to 5.5, in which, some seedlings were stiffer, some denser, some with smaller microfibril angle, some not. Some populations had more uniform wood property values, and some were very different.

Seedlots GF10 and GF28 are two different genetically improved populations with seeds obtained from parent trees by open pollination. Because the genes of both parent trees are recombined every seedling's genotype was different from others. Hence, each seedling had its own characteristics, or, different wood properties. As a result, these mixed wood property populations provide very useful indication of the genetic diversity available for selecting superior seedlings with stiffer wood and smaller microfibril angle. In GF10 seedlot, 5 of the 16 seedlings had stiffness values more than 0.70 GPa, whereas in GF28 there was only 1 out of 16. Hence, it might appear efficient to select the seedlot first, and then select seedlings from seedlot, but GF 10 trees are thought to have poorer growth and form, which is why the seedlot is rated GF10 rather than GF 28. The latter is believed to have superior growth and form.

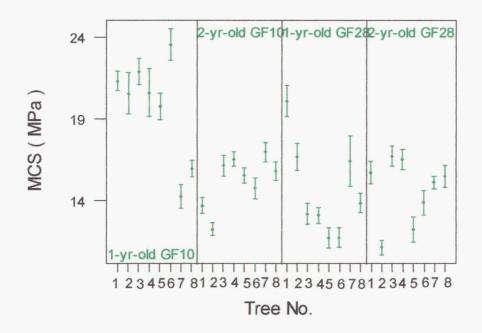


Figure 5.2 Maximum crushing strength of one and two year-old seedlings: vertical bars represent standard errors.

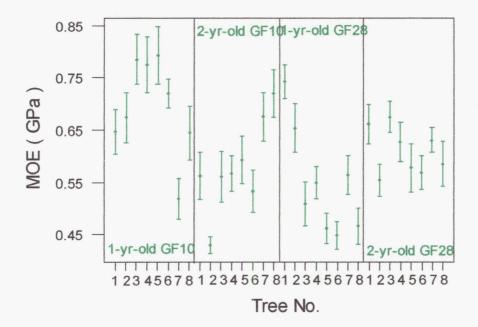


Figure 5.3 Stiffness of one and two year-old seedlings: vertical bars represent standard errors.

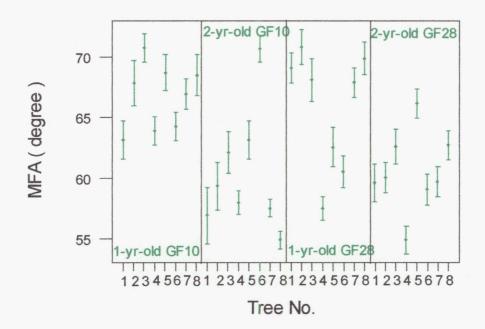


Figure 5.4 Microfibril angle of one and two year-old seedlings: vertical bars represent standard errors.

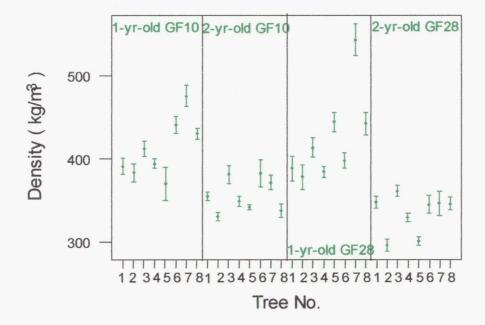


Figure 5.5 Density of one and two year-old seedlings: vertical bars represent standard errors.

5.3.2 Effect of stem position on the wood properties of seedlings

To understand the effect of stem position on wood properties of seedlings, the stems of the seedlings were cut into four segments numbered 1-4, 1 and 2 of them called the upper two, 3 and 4 the lower two (Figure 5.1). Seven samples were tested for the upper two and another seven samples for the lower two of seedling. The means of the wood properties and the results of analysis of variance for stem positions are listed in Table 5.2. There was a significant difference in microfibril angle between the upper two and the lower two segments (P = 0.000). And a difference in density (P = 0.062) existed between the stem positions. The difference in maximum crushing strength and stiffness between stem position did not reach to significant level.

Table 5.2 The means of wood properties in the upper two and lower two positions for 2 year-old seedlings: standard errors are shown in parentheses.

	V	<u> </u>		<u> </u>
Stem	MCS	MOE	Cave-T MFA	Density
position	(MPa)	(GPa)	(degree)	(kg/m^3)
Upper two	14.91 (0.25)	0.593 (0.01)	59.30 (0.50)	340.99 (4.04)
Lower two	14.92 (0.27)	0.598 (0.02)	62.08 (0.60)	349.12 (3.31)
P value	0.937	0.811	0.000	0.062

The stiffness values were similar between the upper two and lower two positions, being around 0.59 GPa, and the maximum crushing strength values were equal around 14.9 MPa. The lower two had a higher mean density (349.1 kg/m³) and a slightly larger microfibril angle (62.08 degrees) than the upper two (340.99 kg/m³, and 59.30 degrees for density and microfibril angle respectively). It maybe that the higher density is compensating for the large microfibril angle and *vice versa* so that the stiffness and maximum crushing stengths are equal. These results indicated that the microfbril angle and density were changing somewhat with stem position, that is, microfibril angle and density are sensitive to the stem development stage.

Figure 5.6 shows the variations of microfibril angle between the upper two and lower two positions for the 16 two year-old seedlings. Of the 16 pairs of points (1 pair of points per seedling), there are 13 pair of points that had higher values of microfibril angle at the lower two positions, two pair points had similar values, and only 1 pair

points had higher value at the upper two. It is clear that the microfibril angle reduced degrees from the lower two to the upper two positions.

Figure 5.7 shows the density of the upper two and lower two positions. In 16 pairs of points, 12 pairs had higher values of density at the lower two positions, 1 pair points had a similar value, and only 3 pairs had higher values at the upper two. This led to the density of the lower two positions being larger than the upper two (P = 0.062).

These results showed that the microfibril and density decreased from lower parts to upper parts in most of seedlings. This indicated that microfibril angle and density were significantly effected by stem positions.

Other researchers have described a decline in microfibril angle with height in several soft wood species. Pillow *et al.* (1953) measured microfibril angle in three trees of *Pinus teada* L. at breast height and 9 to 12 m where the microfibril angle values were significantly lower. Pedini (1992) also found a decline in microfibril angle within a ring with height in *Picea sitchensis*. The microfibril angle in this study revealed a similar pattern in 2 year-old seedlings.

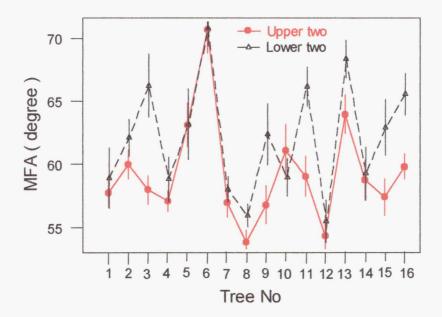


Figure 5.6 Microfibril angle at the upper two and lower two stem positions: vertical lines represent standard errors.

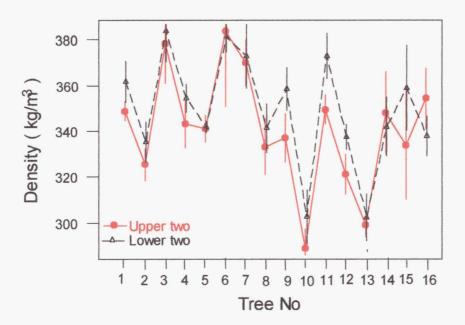


Figure 5.7 Density of stem at the upper two and lower two stem positions: vertical bars represent standard errors.

5.3.3 Variations in wood properties of seedlings between seedlots

The two seedlots at two ages had different wood properties. Table 5.3 gives the means of wood properties for 1year-old GF10, 1 year-old GF28, 2 year-old GF10 and 2year-old GF28. The four groups had significant differences in all wood properties. 1 and 2 year-old GF10 had higher maximum crushing strengths than GF28, 1 year-old GF10 had higher stiffness than the others. It is noted that the microfibril angle and density decreased from ring 1 to ring 2 in both GF10 and GF28.

Table 5.3 The means of wood properties for GF10 and GF28 at ages 1 and 2 years: standard errors are shown in parenthesis.

	MCS	MOE	Cave-T MFA	Density
	(MPa)	(GPa)	(degree)	(kg/m^3)
1-yr GF10	19.74 (1.10)	0.70 (0.03)	67.02 (0.88)	412.10 (12.40)
1-yr GF28	14.61 (1.03)	0.55 (0.04)	65.83 (1.74)	424.00 (19.30)
2-yr GF10	15.22 (0.56)	0.58 (0.03)	60.72 (1.72)	356.06 (7.13)
2-yr GF28	14.61 (0.71)	0.61 (0.020	60.62 (1.17)	334.05 (8.39)
P values	0.001	0.013	0.004	0.000

Table 5.4 lists the wood property means for GF10 and 28. The GF10 had a significantly higher value of stiffness (0.64 GPa), a higher value of maximum crushing strength (17.5 MPa), and a higher density (384 kg/m³) than GF28 (0.58 GPa for stiffness, 14.6 MPa for maximum crushing strength and 379 kg/m³ for density). Both of populations had similar values of microfibril angle being around 64 degrees. Clearly, the GF10 seedlings were stiffer than GF28.

Table 5.4 The means of wood properties for two GF groups: standard errors are shown in parenthesis.

Annanced transfer and control of the	MCS	MOE	Cave-T MFA	Density
	(MPa)	(GPa)	(degree)	(kg/m^3)
GF10	17.5 (0.83)	0.64 (0.03)	63.9 (1.2)	384 (10)
GF28	14.6 (0.60)	0.58 (0.02)	63.2 (1.2)	379 (15)
P	0.003	0.067	0.653	0.659

Effect of age on wood properties between one and two year-old seedlots

Table 5.5 gives the means of wood properties for I and 2 year-old seedlots of GF10 and 28, and the results of analysis of variance are also summarised in Table 5.5. Clearly, age significantly effected the maximum crushing strength (P = 0.016), density (P = 0.000) and microfibril angle (P = 0.000). The 1 year-old material had a higher maximum crushing strength, higher density, and larger microfibril angle than the 2 year-old material, whereas the stiffnesses were similar being around 0.6 GPa.

Table 5.5 The means of wood properties between 1-and 2 year-old seedlots: standard errors are shown in parenthesis.

Age of GF seedlings	MCS	MOE	Cave-T MFA	Density
seedlings	(MPa)	(GPa)	(degree)	(kg/m^3)
1-yr	17.17 (0.9)	0.62 (0.03)	66.42 (0.1)	418.1 (11)
2-yr	14.92 (0.4)	0.60 (0.02)	60.67 (1.0)	345.1 (6)
P	0.016	0.383	0.000	0.000

Density decreased 73 kg/m³, microfibril angle decreased about 6 degrees and maximum crushing strength decreased 2.3 MPa from growth ring 1 to ring 2. These results indicate that seedling age is an important factor influencing wood properties.

5.3.4 Relationships between wood properties of seedlings

To find relationships between wood properties, correlations and regression analysis were carried out for maximum crushing strength, stiffness, microfibril angle, and density in 1 and 2 year-old seedlings. The results of the correlations between wood properties are summarised in Table 5.6.

Table 5.6 The results of correlations between wood properties of seedlings (r values).

A STATE OF THE PROPERTY OF T	r value	age
MOE – Density	- 0.400	1
MOE - MFA	0.391	1
MOE - MCS	0.891***	1
Density – MFA	0.099	1
Density – MCS	-0.236	1
MCS - MFA	0.326	1
MOE – Density	0.134	2
MOE - MFA	-0.520*	2
MOE - MCS	0.624**	2
Density – MFA	0.171	2
Density – MCS	0.665**	2
MCS - MFA	-0.270	2

^{*} at 5% significant level,

5.3.4.1 The relationships between wood properties in one year-old seedlings

From Table 5.6, an excellent relationship between stiffness and maximum crushing strength was found in 1 year-old seedlings (r = 0.891***).

Stiffness and maximum crushing strength

A plot of mean value of stiffness of each seedling against maximum crushing strength for the 16 1 year-old seedlings is shown in Figure 5.8. The regression equation is:

$$MOE = 0.150 + 0.0275MCS$$

Figure 5.8 shows the stiffness increase accompanies the maximum crushing strength increase. The higher stiffness the higher maximum crushing strength. Clearly, most GF10 seedlings had higher stiffness and maximum crushing strength values than the GF28 ones.

^{**} at 1% significant level,

^{***} at 0.1% significant level.

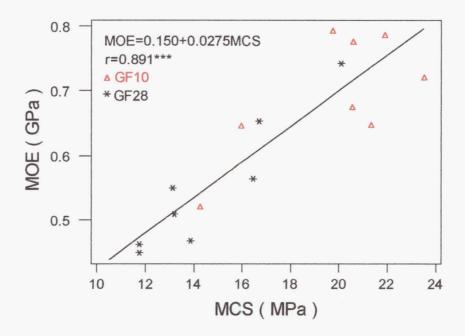


Figure 5.8 Relationship between stiffness and maximum crushing strength in 1 year-old seedlings.

5.3.4.2 Relationships of wood properties of two year-old seedlings

The results of regression and correlation between wood properties for the two year-old seedlings can be seen in Table 5.6. A negative relationship between stiffness and microfibril angle is clear, a positive relationship between maximum crushing strength and density, and another positive relationship between stiffness and maximum crushing strength existed in two year-old seedlings.

Stiffness and microfibril angle

A negative relationship between stiffness and microfibril angle existed in 2 year-old seedlings (P = -0.520*). Stiffness data of each seedling against microfibril angle were plotted for the 16 two year-old seedlings in Figure 5.9, in which, each plotted point is one seedling. The regression line for the 16 points has a negative slope. It is clear that the seedlings with the smaller microfibril angle had higher values of stiffness.

It is noted that in the 16 plot points of 2 year-old seedlings, one seedling (No. 2 of GF10) had an abnormally low stiffness value. This seedling had a larger microfibril angle (61.1 degrees) and lower density (330 kg/m 3) to form the lowest stiffness value (0.43 GPa). Therefore, in Figure 5.13 the r value (r = -0.520, P = 0.047), the fitted line and the regression equation did not consider this seedling. These results imply that stiffness is not just determined by microfibril angle but density is another major factor.

Maximum crushing strength and density

A plot of density against maximum crushing strength for the 16 2 year-old seedlings is shown in Figure 5.10. Clearly, a positive relationship of maximum crushing strength and density existed in 2 year-old seedlings (r = 0.665**). The seedlings with a higher density had a higher maximum crushing strength. Density may be the major factor in determining maximum crushing strength.

Stiffness and maximum crushing strength

Figure 5.11 shows a relationship between stiffness and maximum crushing strength (r = 0.624**). A seedling with a high stiffness also displayed a high maximum crushing strength and *vice versa*.

Overall, in 2 year-old seedlings, some relationships between wood properties are obvious. The results of correlation and regression analysis indicated that stiffness increases with microfibril angle decrease. The maximum crushing strength increases as density increase, while stiffness is positively related to the maximum crushing strength.

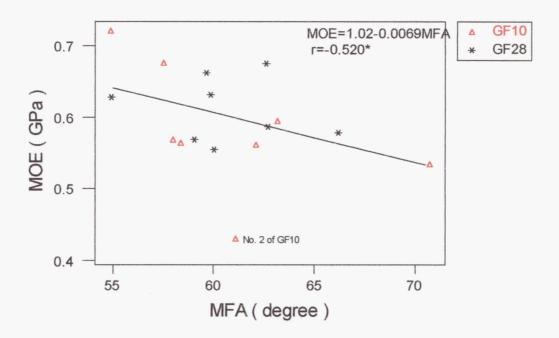


Figure 5.9 Relationship between stiffness and microfibril angle in 2 year-old seedlings.

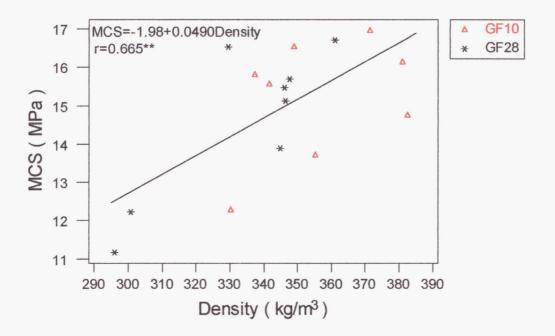


Figure 5.10 Relationship between maximum crushing strength and density in 2 year-old seedlings.

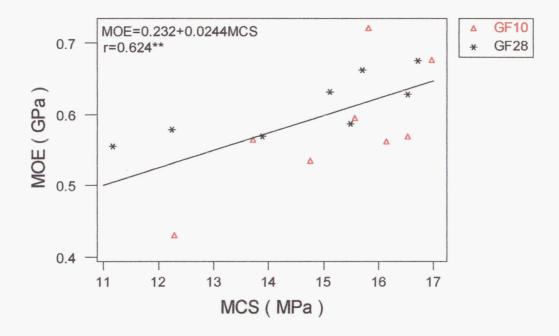


Figure 5.11 Relationship between stiffness and maximum crushing strength in 2 year-old seedlings.

5.3.4.3 Effect of age on relationships between wood properties

Comparison of relationships between stiffness and microfibril angle in one and two year-old seedlings

To compare relationship between stiffness and microfibril angle in 1 and 2 year-old seedlings, the data of stiffness against microfibril angle of each seedling were plotted for the 1 year-old and the 2 year-old seedlings in Figure 5.12.

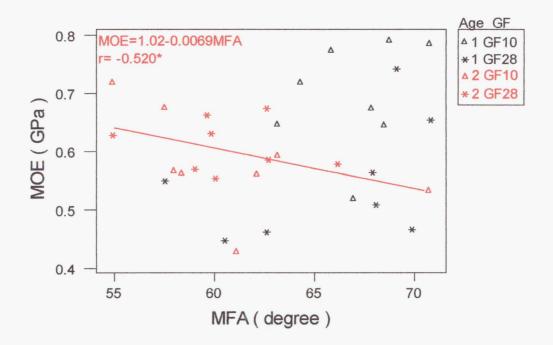


Figure 5.12 Comparison of relationships between stiffness and microfibril angle in 1 and 2 year-old seedlings.

In Figure 5.12, the 16 black plot points represent the 1 year-old seedlings. They had larger values for the Cave-T microfibril angle, and the distribution is more scattered (r = 0.391) with a positive slope. The 16 red plot points are the 2 year-old seedlings, they had somewhat smaller values of microfibril angle, and the distribution range a negative relation tendency, that is higher stiffness with smaller microfibril angle or vice versa. Clearly, the relationship between stiffness and microfibril angle is not as clear in 1 year-old seedling population: this may be due to the variable, but more abundant compression wood in the 1 year-old material.

Overall, the increase in stiffness values can be explained by the microfibril angle values decreasing 5.84 degrees on average from one year-old to two year-old. The MFA decrease resulted in stiffness increasing to form a negative relationship between stiffness and microfibril angle in two year-old seedlings. Stiffness increases about 0.04 GPa, and the microfibril angle decreases about 6 degrees from one year-old to two year-old on average, that is for an microfibril angle decrease at 1 degree, the stiffness will increase about 0.007 GPa at this young seedling stage.

Comparison of relationships between stiffness and maximum crushing strength in one and two year-old seedlings

The correlations and regression equations between stiffness and maximum crushing strength in one and two year-old seedlings have been plotted in Figure 5.13.

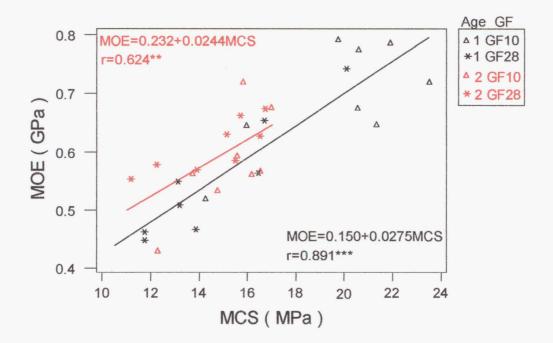


Figure 5.13 Relationships between stiffness and maximum crushing strength in 1 and 2 year-old seedlings.

The regression line for the two year-old seedlings lies above that for the one year-old seedlings, that is, at the same values of maximum crushing strength, the two year-old seedlings had higher values of stiffness than the one year-old ones. These results suggest that the values of stiffness in two year-old seedlings are higher than one year-old seedlings. However some one year-old seedlings had a higher mean values for both stiffness and maximum crushing strength than any two year-old seedlings. This might have been due to compression wood. Alternatively, it is possible that when random sampling in mixed populations some seedlings with extreme values can be selected, allowing the wood property means to become bigger or smaller. Hence, it is suggested that when sampling in mixed seedling populations, the sample size should be larger.

To further illustrate the stiffness increase from one to two year-old, a comparison of the ratios of stiffness to maximum crushing strength in one and two year-old seedlings is shown in Table 5.7.

Table 5.7 The ratio of MOE/MCS in one and two year-old seedlings.

	1-yr-old	2-yr-old	% increase
GF10	0.035	0.038	9
GF28	0.038	0.042	10

For the GF10 seedlings, the ratio of stiffness to maximum crushing strength increased 9% from growth ring 1 to ring 2, for GF28 seedlings, it increased 10%.

5.4 Discussion

The wood properties of 32 seedlings from two seedlots and two ages have been studied in this chapter. The results indicated that each seedling had different characteristics controlled by their different genotypes.

The analysis of relationships ought to demonstrate that two factors determine stiffness in these seedlings. One is density and the other is microfibril angle. As expected stiffness and microfibril angle are inversely related to each other $(r = -0.520^*)$ in clearwood samples (free of compression wood) of 2 year-old seedlings. As expected stiffness and density are positively but very weakly related to each other (r = 0.134) in clearwood samples (free of compression wood) of 2 year-old seedlings. On the other hand the correct relationships/ trends are not found in 1 year-old material.

While it has been well-reported that microfibril angle is a major factor to determine stiffness has been well-reported by researchers (Meylan, 1967, Cave, 1969; Cave and Walker, 1994, Walker and Butterfield, 1996; Butterfield, 1998), this is not the case for the 1 year-old seedlings of this study. A similar conclusion was obtained by Downes *et al.* (1993) on 2 year-old radiata pine seedlings. They suggested that the young tissue in leaders contained amount of compression wood having larger microfibril angles.

Mark Gillis (1973), using individual fibres, studied the relationship between stiffness and microfibril angle and reported that the axial stiffness of fibers with large angles more than 25 degrees is largely insensitive to the properties of the cellulose reinforcement and very dependent on the properties of the matrix. Conversely, the fibres with small angle less than 10 degrees is largely insensitive to matrix properties but extremely dependent upon the properties of cellulose.

The microfibril angle of the 1 year-old seedlings in the study reported here ranged from 58 to 71 degrees (Cave-T degrees) in a microfibril angle zone where stiffness has been shown by Cave (1969) and others to be relatively insensitive to the microfibril angle. This would imply that density (and even the presence of compression wood) is more influencial in effecting stiffness.

It is noted from this study that the microfibril angle was strongly effected by stem position and age. Expectedly the microfibril angle became smaller from stem position lower two (63 degrees) to upper two (59 degrees). And it was greater in one year-old (66 degrees) than in two year-old (60 degrees) seedlings.

In the young seedlings, especially in the first few growth rings, the microfibril angle decrease quite gradually before declining more steeply in right 5 to 10 (Figure 2.10) and stiffness can increase two or three-fold. Therefore, the role of microfibril angle to stiffness is much clear at that stage. But for 2- year-old seedlings, it is difficult to find so much different in stiffness between seedlings. The highest stiffness one was just 67% more than the lowest ones.

The major problem is that the samples from shorter and thinner 1 year-old seedling stems contained small amount of woody material. The stem diameter was only 6.4 mm on average. It was difficult to isolate samples that were free of compression wood. Hence, the study 1 year-old seedling wood was unsatisfactory and there is a need to develop other sampling and testing methods.

It appears possible to select superior 2-yr-old seedling as indicative of superior properties in the mature tree, that is, a stiffer seedling will become a stiffer mature tree.

According to Donalson (1991) of the five radiata pine trees studied, the result show that tree 1 had lower microfibril angle than other trees at an early stage (ring1 and 2), and still has a smaller microfibril angle in later stages. Further work by Donalson (1993) using three genetic groups of radiata pine, obtained a similar result. Using 3 yr-old clonal radiata pine seedlings (Butterfield and Pal, 1998) indicated that their clone 3 maintained smaller microfibril angles from ring 1 to ring 3 than did the other clones.

If the relationship between the stiffness and microfibril at an early stage is similar to that at later stages, it should be possible to select young seedlings at an early stage to get stiffer mature trees. The principal concern remains identifying and avoiding compression wood.

5.5 Conclusions

- 1 Seedlot GF10 is superior to GF28, having generally stiffer seedlings.
- 2 The microfibril angle and density decreased from stem position lower two to the upper two, and decreased from growth ring 1 to ring 2. The stiffness increased from growth ring 1 to ring 2.
- 3 Stiffness is negatively related to microfibril angle (r = -0.520*) in two year-old seedlings.
- 4 Maximum crushing strength is positively related to density in two year-old seedlings (r = 0.665**).
- 5 Stiffness and maximum crushing strength are related each other in both of one and two year-old seedlings (r = 0.650****, and 0.624*** respectively).

CHAPTER 6

GENERAL DISCUSSION

The material used in this study was 8 month-old clonal plantlets and 2 year-old GF (improved growth & form) seedlings of *Pinus radiata*. These were used to explore wood properties of very young material as the aim of this study is to improve corewood quality and preselection of superior trees at a early stage. This required an understanding of wood structure and properties in the first few growth rings. The first consideration was cambial development and wood formation. Subsequently the study considered how the young wood properties were effected by genetic factors and the environment in which the material was grown – by using both clones and seedlings – hopefully to establish the relationships between wood properties. The results and problems will be discussed in following sections.

6.1 The vascular cambium development and wood formation

The development of the vascular cambium in *Pinus radiata* was studied using 8 monthold clonal plantlets grown under three treatments (free growth, tied and angled). The results showed that a relationship existed between the apical meristem, procambium, fascicular cambium, interfascicular cambium, and vascular cambium. Observations of this study support the view that the procambium and cambium are best regarded as two developmental stages of the same meristem (Butterfield, 1976).

The initiation of secondary growth appeared be a developmental stage that extended over several millimetres in the tip parts of the plantlets. Like other characteristics, the development of the secondary growth was influenced by treatment. In the tied seedlings, the transition period to full secondary growth lasted about 8 mm, but in the free and angled seedlings this occurred over a distance of 5 mm in the tip parts. This is probably influenced by the tracheid length. Thus, the cambium was established earlier in the free and angled plantlets than in the tied plantlets. Accordingly, it is important to

provide a good growing condition so the cambium initials and tracheids can develop normally.

As is well known, wood cells are produced by the active cambium through the cambial initials' periclinal and anticlinal division, and this is accompanied by ray cell elongation. The cambial activity directly relates to the quantity of wood cells formed. Cambial activity is influenced by the apical region, age, season, temperature, climate as reported by a number of papers (Fraser, 1952; Wodzicki and Pede, 1963; Antonova and Stasova, 1993). The results in this study indicated that the cambial activity is influenced by treatments and stem positions. The angled plantlets had less amount of wood material than the free and tied plantlets. This means that the cambium in the angled plantlets was less activity except in compression wood side. The cambium on the compression wood side was more active than the opposite wood side being double the width. This demonstrated that cambial activity was influenced by hormonal activity. The more frequently the cells divide the shorter the tracheids. Wardrop (1948) suggested that the shorter tracheids of compression wood side arise as the result of an increased number of transverse divisions in the cambium.

Other studies have shown that the quality of the wood cells is influenced by the cambial initial quality. The shorter tracheids of dwarf trees was due to the cambium initials being shorter (Lim and Soh, 1997). Juvenile cambium produces shorter tracheids, and the mature cambium produces longer tracheids (David *et al.*, 1959). In this thesis, the angled treatment yielded shorter tracheids compared with the free and tied treatment. This result agrees with the results reported above as the cambial initials were divided more rapidly in the compression wood side. As a result, the angled treatment plantlets produced significantly more compression wood cells but fewer cells overall in the entire cross-section than plantlets grown in a normal environment. Accordingly it is suggested that to improve the wood cell quality needs to improve the cambial initial quality, ie grow the plantlets as straight as possible.

The cambium produced wood cells as a different rate in the various stem positions. The wood formation increased 15%, 20%, 15%, and 10% from the tip to stem 3 position respectively, and then remained constant. Clearly, the cambial activity can be

influenced by the plantlet's developmental stage. That is, the cambium is more active in the young stems than in the old stems.

Clearly, both the cambium activity and cambial initial quality can be influenced by growing conditions and development stages.

6.2 Compression wood

Compression wood formation is caused by the environmental stress (Burdon and Low, 1992; Downes and Turvey, 1992; Nicholls, 1982; Cown, 1974; Low, 1964; Mitscherlich, 1942). A similar result was obtained for compression wood formation in this study. From Plate 3.10 and Table 3.4, the compression wood can be found within every treatment for clones 8 and 31 plantlets. In the free growth treatment, the compression wood, by cross-sectional area, was found to be 27%, in the tied treatment was 14%, and in the angled treatment the compression wood was 47%. Clearly, the amount of compression wood formed is directly related to the environmental factors impacting on the growing plantlet.

A similar result was reported by Haught (1957) that the compression wood was 42% by volume in juvenile wood (laid down in first 8 years), 7% in mature wood, and fewer than 10% of trees examined were found to be free from obvious compression wood. That is, more compression wood occurs in young trees than in mature trees. A further study (Haught, 1958) on loblolly pine showed 6% compression wood in straight trees, 9.1% in crooked trees, and 67.1% in very crooked trees. These results indicated that compression wood formation related to environmental factors. Therefore, to reduce compression wood percentage and severity is necessary to minimise stem movement (tied) and stem inclination (leaning).

Compression wood is usually recorded as having shorter tracheids, larger microfibril angle and a lower stiffness (Madhu and Seth, 1992; Dhubhain *et al.*, 1988; Kocon, 1990; Wordrop, 1951).

But, a contrary result was reported by Addis Tsehaye (1995) on radiata pine trees (studied on the top parts of trees) that the compression wood had higher stiffness,

probably as a consequence of its bigger density, than normal and opposite wood. The same result was observed for the angled plantlets in this study. The stiffness of compression wood was significantly higher (1.85 GPa) than opposite wood (1.15 GPa), was significantly denser (590.9 kg/m³) and had a higher percent cell wall (47%) than the opposite wood (450.6kg/m³, and 28.2%, for density, and percent cell wall, respectively). There was no significant difference in tracheid length between the wood type samples. These results suggested that the compression wood had a high stiffness due to its great density rather than due to the influence of microfibril angle (whose effect is likely to be slight when this angle exceeds 45 degrees as it does in very young wood).

6.3 Compression wood samples and the angled plantlets

From this study, it is noted that the angled plantlets had a greater density and a lower stiffness than the free and tied plantlets, whereas the compression wood samples in angled plantlets had a great density and a higher stiffness than the opposite, normal, and mixed wood samples. These two results seem to be contrary. Further study results indicated that the compression wood samples had a higher stiffness due to its larger density (all samples had similar length of tracheids). Whereas the angled plantlets had a lower stiffness due to its significantly shorter tracheids, although its density was larger than the free and tied grown ones. These results imply that if the angled plantlets had a same tracheid length as the free and tied plantlets, the angled plantlets should have a higher stiffness than the free and tied plantlets. Wardrop and Dadwell (1950) suggested that when comparing compression and normal wood samples having similar tracheid length and microfibril angle should be used. In this thesis, in some cases, the contribution of density to stiffness is clear, in some cases, the contribution of tracheid length to stiffness is clear. It is concluded that the compression wood itself is stronger (higher MOE) due to its larger density, but the whole angled seedling is weaker (lower MOE) due to its shorter tracheids. It seems that tracheid length is more important to stiffness than density when tested under tensile load.

6.4 Stiffness (MOE) influenced by several factors

Stiffness is an index of wood quality, it varies by a factor of 3 to 5 during the first 30-years of growth (Cave and Walker, 1994). The results of this study indicated that the stiffness value was a combination of several factors, that is, it was directly influenced

by density, tracheid length and microfibril angle, and indirectly influenced by cell numbers/mm² and percentage cell wall area. At the same time, the genetic factor (such as clone and seedlot), developmental stage (stem position and age), and tree growing condition (treatments) also effect stiffness resulting in considerable variation.

The low stiffness of the angled plantlets was the result of its shorter tracheids, and the compression wood sample having stiffer wood was the result of its bigger density. Seedling No.8 of 2 year-old GF 10 had a higher stiffness value due to its bigger density and smaller microfibril angle, while seedling No. 2 of GF10 had the lowest stiffness due to its large microfibril angle and less density. Clearly, these results demonstrated that the stiffness is influenced by density, tracheid length and microfibril angle in this study. Therefore, the magnitude of density, the length of tracheids, and degree of microfibril angle all influence to stiffness. The results of this study also indicated that the stiffness can be indirectly influenced by cell numbers/mm² and percent cell wall area, as is the density.

That stiffness is related to density has been reported by a number of papers (Pearson and Gilmore, 1971; Pearson, 1988; Walker 1993; Mishiro, 1997). In the angled clones, the higher stiffness value accompanied the higher density. And in 2-yr old seedlings the stiffness is related to maximum crushing strength, with the maximum crushing strength being related to density: that is density can directly and indirectly contribute to stiffness. These results agree with other studies in mature wood.

That stiffness is effected by microfibril angle has been well documented (Cave, 1968; Butterfield, 1998; Walker and Woollons, 1998; Meylan and Propine, 1967; Donaldson, 1992). In this thesis, stiffness is shown to be related to microfibril angle in two year-old seedlings, the seedlings with smaller microfibril angle had higher stiffness.

Tracheid length is another factor influencing stiffness (Wardrop, 1951; Furukawa Ishii, 1998). In this study, the relationship between tracheid length and stiffness was clear in the free and tied seedlings, the longer the tracheids, the higher the stiffness.

Clearly, these results demonstrated that the stiffness was determined by several factors. Hence, to improve stiffness needs to improve individual property, such as microfibril angle, tracheid length, density (cell numbers/mm² and cell wall area percentage). Stiffness is also influenced by growing conditions. The free, tied and angled plantlets have different stiffness values means if the seedlings grown in different conditions, they will produce different stiff wood. Unfortunately, good growing conditions in some areas are not available, so to get high quality wood, superior seedlings that suit the local growing conditions should be selected.

6.5 Altered relationships of wood properties in different treatments

The relationships between a number of young wood properties have been investigated in this study, and the results demonstrate that the relationships between wood properties can be altered with treatments. In the angled treatment, stiffness is related to density. All the samples of the angled plantlets had similar tracheid lengths but different densities. The stiffness changed with density.

That stiffness is related to tracheid length was found in the free and tied plantlets. In the free and tied clonal plantlets of this study, all the wood samples had similar densities but different tracheid lengths - the longer the tracheids the higher the stiffness. These results demonstrated that if density remains the same, then stiffness is related to tracheid length, and if the tracheid length remains same, the stiffness is related to density.

6.6 Microfibril angle to stiffness in young wood

Small microfibril angle results in stiff wood has been reported in many of papers. Cave (1968) reported a fivefold increase in stiffness in the earlywood of *Pinus radiata*. Bendtsen and Senft also observed five fold increase in stiffness of whole growth rings for *Pinus taeda* (Figure 2.4). Cowdrey and Preston (1966) observed a sixfold increase in the stiffness in the early wood of *Picea sitchensis* as the microfibril angle decreased from 40 to 10 degrees.

In this thesis, there is a negative relationship between stiffness and microfibril angle in the two year-old seedlings. Seedlings with a small microfibril angle had a higher stiffness value, and seedling with larger microfibril angle had a lower stiffness value. But the results of this study show that the microfibril angle decrease is slight in these seedlings. Figure 2.5 indicates that the microfibril angle decrease is rapid from ring 5 to ring 15 (Figure 2.5). The regression line of the microfibril angle with age drops steeply from ring 5 to ring 15. But, in growth ring 1 and 5, the microfibril angle is quite large but decreases slowly.

In the one year-old seedlings of this study, the relationship between microfibril angle and stiffness is not clear. Downes and Turvey (1992) using two year-old radiata pine seedlings find a positive relationship between mirofibril angle and bending strength. With glasshouse-grown materials (Downes and Turvey, 1990) a similar weak correlation was evident. In a further study using glasshouse material (Downes and Turvey, 1992) bending strength was used in addition to stem lean, and no such relationship was found. Mark and Gillis (1973) measuring individual fibres state that curves demonstrate that the axial stiffness of fibres with large angles (>25°) is largely insensitive to the properties of the cellulose reinforcement, and very dependent on the properties of the matrix, conversely, the stiffness of small angle fibres (<10°) is largely insensitive to matrix properties, but extremely dependent upon the properties of cellulose. These results suggest that the microfibril angle is less important to stiffness at one year-old seedlings since it was too large to contribute to the stiffness in very young wood.

Although the relationship between microfibril angle and stiffness is not clear in one year-old seedlings, a seedling with small microfibril angle can be selected at an early stages for tree breeding. Butterfield and Pal (1998) and Donadlson (1993) report that where the microfibril angle in the growth ring 1 is small, it remains low in subsequent growth rings.

6.7 Variation of stiffness in young wood

Compared with mature wood, the young wood presented large variations in stiffness. The probable reasons are considered as follows. One is that the mature wood had a relatively uniform wood structure tissue, that is, the tracheids reach to their mature length with little change after growth ring 15 (Young, 1992). The microfibril angle remains relatively constant (Bendtsen and Senft (1986), as does the density after ring 10

to 15 (Cown, 1999). Also, the mature wood contains less compression wood tissue. Relatively uniform wood structure and relatively stability of wood properties in mature wood result in less stiffness variation. Further, the young wood contains more compression wood. Also, in the young wood, all wood properties are changing. Tracheids varies, the microfibril angle decreases, and the density is not stable, all of which results in the stiffness being highly variable. Another reason is the variable amount of compression wood. The compression wood is randomly distribution and of different severity in the young wood (Plate 3.10). This leads to each compression wood sample containing different degrees of microfibril angle, tracheid length and even density (Appendix 5). Different properties result in different stiffness. Therefore, the stiffness shows a hugh amount of scatter distribution when plotted with the density (Figure 4.8). Clearly, the presence of compression wood in small testing samples will have a large influence on wood properties. Therefore, it is suggested when studying young wood properties it is good to use samples free of compression wood tissue.

6.8 Effect of age and development stages on wood properties

Age is a major factor influencing wood properties (Addis Tsehaye *et al.*, 1991; Bendtsen and Senft, 1986; Koch, 1966; Walford, 1982; 1985). The stiffness, microfibril angle, and density of the GFs seedlings were all influenced by age. Seedling development stage is another factor influencing wood properties. In two year-old GFs seedlings, the microfibril angle decreased from stem position lower two to upper two (Figure 5.6 - 5.7). In the clonal plantlets, the stiffness increased 50%, tracheid length increased 10%, cell wall area increased 26% from stem 1 to the base.

Clearly, wood properties are strongly dependent on the stem positions and age. Accordingly, when sampling from seedlings, the sample location is important for getting accurate results.

6.9 Effect of environmental factors on wood properties

Wood structure and properties are influenced by environmental factors (McAlister and Clark, 1991; Pellerin *et al.*, 1989). In this thesis, the treatments distinctly effect the wood structure and wood properties of clonal plantlets. The 8 month-old clones 8 and 31 were free-grown, tied, and angled. Each treatment resulted in different wood

structures and properties. The angled treatment plantlets produced more compression wood, which had round shaped cells with much thicker cell walls, giving high density tissue. The tied treatment plantlets produced mostly normal wood cells with rectangle cell shape and thin cell walls, resulting in wood of low density. In the angled treatment cell numbers/mm² increase 20%, percent cell wall area increase 28%, density increase 14%, tracheid length decrease 22%; the angled plantlets have denser and weaker wood. In the tied treatment the percent cell wall decrease 9%, density decrease 13%, tracheid length increase 5%; the tied plantlets have a lower density and stiffer wood.

These results demonstrate that seedling in different growing situations will produce different structure wood with different wood properties to suit its growing conditions.

6.10 Genetic factors and preselection

The results of this thesis indicate that both clones and seedlots can influence on wood properties. Under the angled treatment, clone 8 had a significantly higher stiffness (1.60 GPa) than clone 31 (1.20 GPa), and longer tracheids (0.96mm) than clone 31 (0.92 mm). GF10 had stiffer seedlings than GF28, both can be as a source for seedling selection. It is suggest that when selecting seedlings, selecting seedlot first is more efficient. The seedlings from GF10 and 28 had different genotypes and different characteristics, some seedlings were stiffer, some weaker, some similar, some very different. Clearly, the plantlets with different genotype had different wood properties.

6.11 Problems

The young wood properties at first and second growth ring have been studied in this thesis. The first problem was how to make small test samples. The 8 month-old clonal plantlets contained small amounts of woody tissue, especially in upper parts, such as stem 1. These stems were too small to prepare regular sample sizes. Splitting the stems into quadrants to give four test samples is a useful method. However, the irregular dimensions of the tiny samples probably effected the accuracy of cross-section area measurement which is needed for stiffness and density calculations. Consequently large standard errors of the means for wood properties were to be expected. It was possible to prepare enough 1x1x4 mm clearwood samples (after Butterfield, 1988) from ring 2 in two year-old seedling materials. But it was not possible to get clearwood samples free

of compression wood from one year-old seedlings. Therefore, for one year-old seedlings, it is not clear whether the larger density in one year-old wood was due to compression wood tissue, to crushing or to resin etc. Overall, it is obvious that the methods and equipment need to be improved to test such small young wood tissue.

Another problem is sampling from mixed seedling populations. The means of the wood properties may lose its meaning when comparing seedlots in some case. In this thesis, by sampling in the 1 and 2 year-old seedling populations of GF10 and GF28, and comparing wood properties the results showed that the mean of the stiffness value for the 1 year-old seedlings was nearly same as the 2 year-old seedlings. According to this comparison, it is considered that the 1 and 2 year- old seedlings had a similar stiffness. However, this study provides a basis for further investigation of young wood properties using small trees in *Pinus radiata*.

6.12 Further work

It is important for preselecting to understand that selecting a superior seedling at an early stage should result in a mature tree with superior characteristics at a later stage, in other words, a superior seedling with small microfibril angle, longer tracheids, and higher density should become a good mature tree still with these good characters. Hence, further works need to be done so that the wood properties are recorded and analysed at different clonal tree ages to explore the relationships of wood properties between young and mature trees.

The Ph.D. examiners recommend the award of the degree Ph.D. on the condition that the candidate adds a 1-2 pages Addendum into the final thesis before it is deposited in the Library.

The Addendum is to require to explain the large variability in stiffness, density, and cell wall area due to the experimental methods, and to comment on the difficulties that this caused in analyzing the data.

The greatest difficulty in this thesis has been working with very small pieces of wood (as small as 1x1x4 mm) of very young age (never more than two years old) and of considerable variability.

Characteristics (density, number of cell/mm²) and properties (stiffness) can vary by a factor of two or more. The following sets out the range of values found within individual treatment:

	Stiffness	Density	Cell wall	Cells/mm ²
	(GPa)	(kg/m^3)	area %	
Between clones	1.73 - 1.77	495 - 464	33.0 - 32.9	2337 - 2291
Within clones (samples)	0.76 - 2.98	382 - 568	24.9 - 42.7	1096 - 2994
Up the stem	0.94 - 2.45	392 - 572	25.2 - 40.7	1970 - 2756
With compression wood	1.28 - 3.48	482 - 645	37.9 - 55.5	2310 - 2727
Without compression wood	0.83 - 2.04	435 - 482	19.9 - 35.1	2099 - 3261

The causes of the variability are uncertain. Some arise from the methods employed. Thus in measuring small samples the derived densities can vary by 85%. When measuring cell wall area the derived % cell wall area can vary by 180%. Yet there is an unexplained error in these values which is reflected in Figure 4.19 and 4.20. Others have commented on the same discrepancy (between density and cell wall area measurements) in their own work, but the correlation is far poorer in this study because of experimental difficulties.

The other major difficulty lies in the relative high density values measured in the seedlings compared to the relatively low densities recorded in forest-based studies (where ring one may not be sampled). A partial explanation lies in the amount of compression wood measured in these seedlings/ clones compared to that quoted in the literature for forest trees. Another difficulty lies in the definition of compression wood (mild, moderate, severe) which are largely subjective terms.

However the overwhelming difficulty in drawing rigorous conclusions is due to the small sample sizes – despite the huge amount of material tested for the thesis. It might have been better to have sampled all material at a fixed height above ground level or a fixed number of branches from the top of the trees – but nothing was known about the

large variation in properties up the stem (Table 4.8, 4.9 and 4.10). It might have been better to have examined only one clone in detail. It might have been better to have looked at wood of a single age. It might have been better to have used only tilted material. But if such a limited strategy had been employed much that is still tentative would have been unknown. In the end this thesis is a scoping study which delineates the extent or variability in many matters without providing the desired quantitative rigour. However, that is the nature of a scoping study and is a weakness and a strength of the thesis depending on the view point adopted. This addendum is to emphasise that the thesis is open-ended and all conclusions must inevitably be tentative. Much remains to be done.

REFERENCES

- Addis Tsehaye, (1989) *Proof testing of juvenile wood*. M.For.Sc. Thesis, University of Canterbury, Christchurch.
- Addis Tsehaye, (1995) Within and between tree variations in the wood quality of radiata pine. Ph.D.For.Sc. Thesis, University of Canterbury, Christchurch.
- Addis Tsehaye, Buchanan, A. H.; Meder, R.; Newman, R. H. and Walker, J. F. C. (1998) Microfibril angle: determining wood stiffness in radiata pine. In: Butterfield, B. G. (ed) *Microfibril angle in wood*. University of Canterbury, Christchurch, pp.323-336.
- Addis Tsehaye, Buchanan, A. H.; Walker, J. C. F. (1991) Juvenile *Pinus radiata* for structural uses. *Journal of the Institute of Wood Science* 12: 211-216.
- Albert, S. and Shah, J. J. (1998) Early ontogeny of vascular meristem in the petiole of Gmelina arborea (Verbenaceae) and Tabebuia rosea (Bignoniaceae). Phytomorphology 48: 187-194.
- Antonova, G. F. and Stasova, V. V. (1993) Effects of environmental factors on wood formation in Scots pine stems. *Trees: structure and function* 7: 214-219.
- Austin, S. F. (1988) Quality yield of lumber and plywood produced from fast grown, short rotation Southern pine trees. School of Forostry, State Univ. Nacogdoches, Texas.
- Bailey, I. W. and Vestal, M. R. (1937) The orientation of cellulose in the secondary wall of tracheary cells. *J. Arnold arboretum* 18: 185-195.
- Bamber, R. K. and Burley, J. (1983) *The wood properties of radiata pine*. Commonwealth Agriculture Bureau, Slough.

- Bannister, M. H. (1973) The origins of radiata pine in cultivation. What's New in Forest Research No. 2, June, 1973.
- Bendtsen, B. A. (1985) Quality impacts of the changing timber resource on solid wood products. *Proc.* 47349, "Managing and marketing the changing timber resource", a conference sponsored by the For.Prod. Research Society. Fort Worth, TX. March 1986.
- Bendtsen, B. A.; Plantinga, P. L. and Snellgrove, T. A. (1988) The influence of juvenile wood on the mechanical properties of 2 x 4's cut from Douglas-fir plantations. *Proceedings*, 1988 International Conference on Timber Engineering, Washington State Univ., Pullman. WA, Vol. 1: 226-240.
- Bendtsen, B. A. and Senft, J. (1986) Mechanical and anatomical properties in individual growth rings of plantation -grown eastern cottonwood and loblolly pine. *Wood and Fiber Science* 18: 23-38.
- Boone, R. S. and Chudnoff, M. (1972) Compression wood formation and other characteristics of plantation growth Pinus caribaea. USDA. For. Serv., Res. Pap. ITF-13. Inst. Trop. Forestry. Puerto Rico.
- Boyd, J. D. and Foster, R. C. (1974) Tracheid anatomy changes as responses to changing structural requirements of the tree. *Wood Science and Technology* 8: 91-105.
- Brown, A. G. (1971) Improvement in log quality: a review: *Pinus radiata*. Proc. Pinus radiata symposium. Canberra Aug. 1970. *Aust. Nat. Univ., For. and timber Bur. and radiata pine Assoc. Bulletin* 1975: 13-14.
- Burdon, R. D. (1975) Compression wood in *P. radiata* clones on four different sites.

 New Zealand Journal of Forestry Science 5: 152-164.

- Burdon, R. D. and Low, C. B. (1992) Genetic survey of *Pinus radiata*. 6: wood properties: variation, heritabilities, and interrelationships with other traits. *New Zealand Journal of Forestry Science* 22: 228-245.
- Butterfield, B. G. (1973) Variation in the size of fusiform cambial initials and vessel members in *Hoheria angustifolia* Raoul. *New Zealand Journal of Botany* 2: 391.
- Butterfield, B. G. (1974) *Studies on the vascular cambium*. Ph.D. Thesis, University of Canterbury, Christchurch.
- Butterfield, B. G. (1975) Terminology used for describing the cambium. *IAWA*Bulletin 1975: 13-14.
- Butterfield, B. G. (1976) The ontogeny of the vascular cambium in *Hoheria* angustifolia Raoul. New Phytologist 77: 409-420.
- Butterfield, B. G. (1993) The structure of wood: an overview. In: Walker, J. C. F., *Primary wood processing: principle and practice*. Chapman and Hall, London, pp. 1-22.
- Butterfield, B. G. (1998) *Microfibril Angle in Wood*. University of Canterbury. Christchurch.
- Butterfield, B. G. and Hanna, R. B., 1994. The relationship between microfibril angle and wood properties in low density radiata grown in Canterbury, New Zealand.

 Proceedings of the Third Pacific Regional Wood Anatomy Conference, FIR Rotorua. Abstract in Journal of the International Association of Wood Anatomists 15: 200-201.
- Butterfield, B. G. and Meylan, B. A. (1980) *Three dimensional structure of wood: an ultrastructural approach*. 2nd ed., Chapman and Hall, London.

- Butterfield, B. G.; Meylan, B. A. and Eom, Y. G. (2000) *Three dimensional structure of wood*. Korean Wood Science Foundation, Seoul.
- Butterfield, B. G.; Meylan, B. A. and Peszlen, I. M. (1997) *Three dimensional structure of wood*. Faiperi Tudomanyos Alapitvany, Budapest.
- Butterfield, B. G. and Pal, V. (1998) Relating microfibril angle to wood quality in clonal seedlings of radiata pine. In: Butterfield, B. G. (ed.). *Microfibril angle in wood*. University of Canterbury, Canterbury. pp. 337-347.
- Buvat, R. (1989) *Ontogeny, Cell Differentiation and Structure of vascular Plants*. Springer-Verlag, Berlin. pp. 165-187.
- Cave, I. D. (1966) Theory of x-ray measurement of microfibril angle in wood. *Forest Products Journal* 16: 37 42.
- Cave, I. D. (1968) Anisotropic elasticity of the plant cell wall. Wood Science and Technology 2: 268-78.
- Cave, I. D. (1969) The longitudinal Young s modulus of *Pinus radiata*. Wood Science and Technology 3: 40-48.
- Cave, I. D. and Walker, J. C. F. (1994) Stiffness of wood in fast-grown plantation softwood: the influence of microfibril angle. *Forest products Journal* 44: 43-48.
- Chang, F. J. and Duh, M. H. (1988) Studies on chemical properties of some important local woods. (I) Comparison between normal wood and reaction wood. *Quarterly Journal of Chinese Forestry* 21: 77-85.
- Cote, W. A. Jr.; Kutscha, N. P. and Timell, T. E. (1968) Studies on compression wood. VIII. Formation of cavities in compression wood tracheids of *Abies balsamea* (L.) Mill. *Holzgorschung* 22: 138-144.

- Cowdrey, D. R. and Preston, R. D. (1966) Elasticity and microfibril angle in the wood of Sitka spruce. *Proc. of the Royal Soc.* B166(1004): 245-272.
- Cown, D. J. (1974) Comparison of the effects of two thinning regimes on some wood properties of radiata pine. *New Zealand Journal of Forestry Science* 4: 540-551.
- Cown, D. J. (1975) Variation in tracheid dimensions in the stem of a 26-yr-old radiata pine tree. *Appita* 28: 237-45.
- Cown, D. J. (1992) Corewood (juvenile wood) in *Pinus radiata* should we concerned? New Zealand Journal of Forestry Science 22: 87-95.
- Cown, D. J. (1999) Wood quality of New Zealand pine. Forest research bulletin 216. pp.5-24.
- Cown, D. J. and McConchie, D. L. (1980) Wood property variations in an old crop stand of radiata pine. *New Zealand Journal of Forestry Science* 10:508-520.
- Cown, D. J. and McConchie, D. L. (1983) Studies on the intrinsic properties of new-crop radiata pine. 1: wood characteristics of 10 trees from a 12-year-old stand grown incentralnNorth Island. FIR Bulletin No. 36. New Zealand Forestry Service, Forestry Research Institute, Rotorua.
- Cown, D. J.; McConchie, D. L. and Young, G. D. (1983) Wood properties of *Pinus caribaea var. hondurensis* grown in Fiji. *New Zealand Forest Service, FRI Bulletin* No. 17.
- Cown, D. J.; McConchie, D. L. and Young, G. D. (1991) Radiata pine wood properties survey. *New Zealand Ministry of Forestry, FRI Bulletin*. No 50.
- Cown, D. J. Young, G. D. and Kimberley, M. O. (1991) Spiral grain patterns in plantation grown *Pinus radiata*. New Zealand Journal of Forestry Science 21: 206-216.

- Cutter, E. G. (1978) *Plant anatomy*. Part I. 2nd ed. E. Arnold, London. pp. 81-116
- Dadswell, H. E.; Fielding, M. J.; Nichols, P. W. J. and Brown, G. A. (1961) Tree- to tree variations and the gross heritability of wood characteristics of *P. radiata*. *Tappi* 44: 174-179.
- Dadswell, H. E. and Wardrop, A. B. (1959) Growing trees with properties desirable for paper manufacture. *Appita* 12: 129-136.
- David, R.; Lapraz, G. and Bost, J. (1959) Influence of cambium age on tracheid length of *Pinus pinaster*. C.R.Soc.Biol., Paris 153: 1560-1562.
- Dhubhain, A. N.; Evertsen, J. A. and Gardiner, J. J. (1988) The influence of compression wood on the strength properties of Sitka spruce. *Forestry Products Journal* 38: 67-69.
- Dickson A, R. (1994) Aggregate rays in the xylem of the dicotyledons with emphasis on the species of Nothofagus indigenous to New Zealand. A Ph.D. thesis. University of Canterbury.
- Donaldson, L. A. (1991) The use of pit apertures as windows to measure microfibril angle in chemical pulp fibres. *Wood and Fibre Science* 23: 290-295.
- Donaldson, L. A. (1992) Within and between-tree variation in microfibril angle in *Pinus radiata*. New Zealand Journal of Forestry Science 22: 77-86.
- Donaldson, L. A. (1993) Variation in microfibril angle among three genetic groups of *Pinus radiata* trees. *New Zealand Journal of Forestry Science* 23: 90-100.
- Donaldson, L. A.; Singh, A. P.; Butterfield, B. G. and Whitehouse, L. J. (1995) *Recent Advances in Wood Anatomy*. NZ Forest Research Ltd, Rotorua.

- Downes, G. M.; Beckers, E. P. J.; Turvey, N. D. and Porada, H. (1993) Strength and structure of stems from fast grown *Pinus radiata*. *Trees: structure and function* 7: 131-136.
- Downes, G. M. and Turvey, N. D. (1990) The effect of nitrogen and copper on the characteristics of woody tissue in seedlings of *Pinus radiata* D. Don. *Canadian Journal Forest Research* 20: 1369-1377.
- Downes, G. M. and Turvey, N. D. (1992) Relationships between stem structure and bending strength in *Pinus radiata* seedlings. *Trees: structure and function* 7: 86-91.
- Dupont, G. and Mariaux, A. (1988) Determining the angle of microfibrils in wood by X-ray diffraction using wapa (Eperua). *Actes du 2e colloque. Sciences et industries du bois, Nancy, 22-24 avril, 1987.* Vol. 1: 301-307.
- Dutoit, A. J. (1963) A study of the influence of compression wood on the warping of Pinus radiata. *South African Forestry Journal* 44: 11-15.
- Esau, K. (1942) Vascular differentiation in the vegetative shoot of *Linum*. I. The procambium. *American Journal of Botany* 29: 738-747.
 - Esau, K. (1943) Ontogeny of the vascular bundle in *Zea Mays. Hilgardia* 15: 327-356.
- Esau, K. (1965) Vascular differentiation in plants. Holt, Rinehart & Winston, New York. pp. 37-60.
- Esau, K. (1977) Anatomy of Seed Plants. 2nd ed. John Wiley and Sons, New York.
- Fahn, A. (1990) Plant Anatomy. 4th ed. Pergamon Press, Oxford. pp.311-331.

- Fahn, A.; Ben-Sasson, R. and Sachs, T. (1972) The relation between the procambium and the cambium. In: Ghouse, A. K. M. and Yunus, M. (ed.). *Research trend in plant anatomy*. Tata McGrw-Hill, New Delhi. pp. 161-170.
- Farrar, J. L. and Fan, W. Y. (1969) Induction of tracheid development in decapitated Jack Pine seedlings (*Pinus banksiana* Lamb.) with indole-3-acetic acid and gibberellic acid. *Rep. Res. For. Bot. Glendon Hall Fac. For. Univ. Toronto* 1969/70, 1970 (8).
- Foslie, M. (1963) The strength properties of Scots Pine from Pasvik and from Ostland. Norsk Skogind. 17: 453-463.
- Fraser, D. A. (1952) Initiation of cambial activity in some forest trees in Ontario. *Ecology* 33: 259-273.
- Fujita, M.; Saiki, H.; Sakamoto, J.; Araki, N. and Harada, H. (1979) The secondary wall formation of compression wood tracheids. IV. Cell wall structure of transitional tracheids between normal wood and compression wood. *Bulletin, Kyoto University Forests.* 51: 247-256.
- Furukawa, I. and Ishtt, T. (1998) Variation-wood distribution within mechanically stress-graded post-timbers of small sugi logs. *Research Bulletin of the Tottori University Forests*. 25: 39-44.
- Gahan, P. B. (1988) Xylem and phloem differentiation in perspectives. In: Robert, L.
 W.; Gahan, P. B. and Aloni, A. Vascular differentiation and plant growth regulators. Springer-Verlag, Berlin. pp. 1-21.
- Gordon, J. E. (1973) The New Science of Strong Merials. Pelican Books, London.
- Hadi, P. (1992) *Proof-testing for radiata pine boxed-pith timber*. M. For. Sc. Univ. of Canterbury, Christchurch.

- Harris, J. M. (1965) A survey of the wood density, tracheid length, and latewood characteristics of radiata pine grown in New Zealand. *New Zealand Forest Service, FRI Technical Paper* No.47. 31pp.
- Harris, J. M. (1977) Shrinkage and density of radiata pine compression wood in relation to its anatomy and mode of formation. *New Zealand Journal of Forestry Science* 7: 91-106.
- Harris, J. M. (1981) Wood quality of radiata pine. Appita 35: 211-215.
- Harris, J. M. and Cown, D. J. (1991) Basic wood properties. In: Kininmonth, J. A and Whitehouse, L. J. (ed.). Properties and Uses of New Zealand Radiata Pine-Volume one-wood properties. Forest Research Institute, Ministry of Forestry, Rotorua, NZ.
- Haught, E. (1957) Distribution and extent of compression wood in Loblolly Pine. *1st Rep. For. Tree Impr. Progr. Sch. For. N.C. St. Coll.* 1957 (14).
- Haught, E. (1958) Further study on compression wood in Loblolly Pine. 2nd Rep. For. Tree Impr. Progr. Sch. For. N.C. St. Coll. 1958 (7).
- Higuchi, T. (1997) Biochemistry and molecular biology of wood. Springer Verlag, Berlin, Germany.
- Hong, B. W. and Byeon, H. S. (1985) Dynamic MOE and internal friction of compression woods in *Pinus densiflora*. Mogjae Gonghak Journal of the Korean Wood Science and Technology 23: 32-36.
- Huang, C. L.; Kutscha, N. P.; Leaf, G. J. and Megraw, R. A. (1998) Comparison of microfibril angle measurement techniques. In: Butterfield, B. G. (ed) *Microfibril* angle in wood. University of Canterbury, Christchurch, pp. 177-205.

- Huhrjanskaja, T. P. (1953) Effect of compression on the wood structure of Aspen and Pine. *Trud. Inst. Les.* 9: 444-447.
- Ishengoma, R. C.; Mrema, F. A. J. and Ringo, W. N. (1990) Basic density and tracheid length of normal and compression wood from plantation grown *Pinus patula*. Record Faculty of Forestry. Sokoine University of Agriculture. No. 44.
- Khattak, T. M. and Majeed, A. (1993) Seasonal activity of the cambium and radial growth of wood formation in chir pine (*Pinus roxburghii* Sarg.). *Sarhad Journal of Agriculture* 9: 205-208.
- Kibblewhite, (1973) Effects of beating and wood quality on radiata pine kraft paper properties. *New Zealand Journal of Forestry Science* 3: 220-39.
- Kininmonth, J. A; Whitehouse, L. J. (1992) *Properties and Uses of Radiata Pine*. New Zealand Ministry of Forestry. FRI, Rotorua.
- Kloot, N. H. (1957) Can the strength of radiata pine be improved? *For. Prod. Newsletter*. No. 232. Timber Mechanics Section, CSIRO, Melbourne.
- Koch, P. (1966) Straight studs from southern pine veneer cores. USDA. For. Serv., Res. Pap. So 25, 35pp. Southern Forest Exp. Sta., New Orleans.
- Kocon, J. (1990) Occurrence and structure of the reaction wood of the European larch (*Larix europaea* DC) and of Scots pine (*Pinus silvestris* L.) investigated with the X-ray diffraction and the electron scanning microscope. *Annals of Warsaw-Agricultural University SGGW AR, Forestry and Wood Technology*. 39: 71-78.
- Kretschmann, D. E. and Bendtsen, B. A. (1992) Ultimate tensile stress and modulus of elasticity of fast grown plantation loblolly pine lumber. *Wood and Fiber Science* 24: 189-203.

- Langlands, I. (1938) The mechanical properties of South Australia plantion grown P. radiata D. Don. Tech. Pap. No. 30, Division of Forestry Products, Commonwealth of Australia Council for Scientific and Industrial Research.
- Larson P. R. (1969) Incorporation of 14C in the developing walls of *Pinus resinosa* tracheids: compression wood and opposite wood. *Tappi* 52:2170-2177.
- Larson, P. R. (1976) Procambium vs. cambium and protoxylem vs. metaxylem in *Populus deltoides* seedlings. *American Journal of Botany* 63: 1332-1348.
- Larson, P. R. (1982) The concept of cambium. In, New Perspectives in Wood Anatomy, P. Baas (ed.), Martinus-Ni-jhoff Publ. The Hague. pp. 85-121.
- Larson, P. R. (1994) *The vascular cambium: development and structure*. Springerverlag Berlin Heidelberg, Germany.
- Lim, D. O. and Soh, W. Y. (1997) Cambial development and tracheid length of dwarf pines (*Pinus densiflora* and *P. thunbergii*). *IAWA Journal* 18: 301-310.
- Little, R. J. and Jones, C. E. (1980) *A Dictionary of Botany*. Nostrand Reinhold Co., New York.
- Low, A. J. (1964) A study of compression wood in Scots Pine (*Pinus sylvestris* L.). Forestry 37: 179-201.
- Madhu, B. and Seth, M. K. (1992) Intra-increment wood properties variation in compression wood rings of *Cedrus deodara* (Roxb.) Loud. *Indian Journal of Forestry* 15: 5-8.
- Mark R. E. and Gillis, P. P. (1973) The relationship between fibre modulus and S2 angle. *Tappi* 56: 164-167.

- Marts, R. O. (1955) Fluorescence microscopy for measuring fibril angles in pine tracheids. *Stain Tech.* 30: 243-248.
- McAlister, R. H. and Clark, A. (1991) Effect of geographic location and seed source on the bending properties of juvenile and mature loblolly pine. *Forest Products Journal* 41: 39-42.
- MeGraw, R. A.; Leaf, G. and Bremer, D. (1998) Longitudinal shrinkage and microfibril angle in Loblolly pine. In Butterfield, B. G. (ed.) *Microfibril angle in wood*. University of Canterbury, Christchurch, NZ.
- Meylan, B. A. (1967) Measurement of microfibril angle by x-ray diffraction. *Forest Products Journal* 17: 51-58.
- Meylan, B. A. and Butterfield, B. G. (1972) *Three-dimensional structure of wood: a scanning electron microscope study*. Reed Eduction, Wellington.
- Meylan, B. A. and Butterfield, B. G. (1978) *The Structure of New Zealand Woods*. NZ Dept. of Scientific and Industrial Research, Wellington.
- Meylan, B. A. and Probine, M. C. (1969) Microfibril angle as a parameter in timber quality assessment. *Forest Products Journal* 19:30-34.
- Mishiro, A. (1984) Wood quality of radiata pine. In: Sudo, S. (ed.). Proceedings, Pacific Regional Wood Anatomy Conference, October, 1-7, 1984, Tsukuba, Ibaraki, Japan. Pacific Regional Wood Anatomy Conference, Forestry and Forest Products Research Institute, Ibaraki, Japan, pp. 31-33.
- Mishiro, A. and Eiji, N. (1997) Wood properties of Japanese cedar, sugi (*Cryptomeria japonica* D. Don) grown in Niigata. *Research Bulletin of Niigata University Forests* 30: 43-62.

- Mitscherlich, G. (1942) The influence of sea wind on the growth of Pine, Spruce, Beech, Birch and Alder. *Thar. forstl. J.* 93: 345-373.
- Moor, N. J. (1999) *Tracheid length variation in Pinus radiata seedlings*. B. for Sc. thesis, University of Canterbury.
- Nicholls, J. W. P. (1982) Wind action, leaning trees and compression wood in *Pinus radiata* D. Don. *Australian Forest Research*. 12: 75-91.
- Patel, R. N. (1971) Anatomy of stem and root wood of *Pinus radiata D.Don. New Zealand Journal of Forestry Science* 1: 37-49.
- Pearson, R. G. (1988) Compressive properties of clear and knotty loblolly pine juvenile wood. *Forest Products Journal* 38: 15-22.
- Pearson, R. G. and Gilmore, R. C. (1971) Characterisation of the strength of juvenile wood of loblolly pine (*P.taeda* L.). Forest Products Journal 21: 23-50.
- Pechmann, H. (1969) The influence of heredity and environment on the formation of reaction wood. *Beiheft zu den Zeitschriften des Schweizerischen Forstvereins* 46: 159-169.
- Pedini, M. (1992) The variation in the microfibrillar angle within the juvenile wood of sitka spruce. *IAWA Bulletin n.s.* 13: 261.
- Pellerin, R. F.; Koch, P. anf Vogt, J. J. (1989) Mechanical properties of lodgepole pine: 6- and 9-inch diameter stems. *Forest Products Journal* 39: 13-20.
- Perem, E. (1960) The effect of compression wood on the mechanical properties of white spruce and red pine. F.P.L. tech.Note For.Prod.Lab., Can. No. 13 pp.22.
- Philipson, W. R.; Ward, J. M. and Butterfield, B. G. (1971) *The vascular cambium:* its development and activity. Chapman and Hall, London.

- Phillips, I. D. J. (1976) The cambium. In: Yeoman, M. M. (ed.). *Cell division in higher plants*. Academic Press, London. pp. 347-390.
- Pillow, M. Y.; Terrell, B. Z. and Hiller, C. H. (1959) Patterns of variation in fibril angles in Loblolly pine. Forest Prod. Lab., For. Serv., U.S. Dept. of Agriculture, Maidson, Wisconsin.
- Pleasants, S., Batchelor, W. and Parker, I. H. (1997) Measuring the fibril angle of bleached fibers using micro raman spectroscopy. 51st Appita annual general conference, Melbourne, Australia. 2: 545-549.
- Porandowski, J.; Rakowski, K. and Wodzicki, T. J. (1982) Apical control of xylem formation in the pine stem. II. Responses of differentiating tracheids. *Acta Societatis Botanicorum Poloniae* 51: 203-214.
- Preston, R. D. (1952) *The molecular architecture of plant cell walls*. Wiley, New York pp. 113-115.
- Preston, R. D. (1974) *Physical biology of plant cell walls*. Chapman and Hall, Lopndon.
- Priestley, J. H. (1928) The meristematic tissues of the plant. *Biological Reviews* 3:1-20.
- Rana, M. A. and Gahan, P. B. (1983) Determination of fascicular, interfascicular and cork cambial in dicotyledonous plants. *Saussurea* 14: 51-60.
- Reader, T. G. and Kurmes, E. A. (1996) The influence of thinning to different stocking levels on compression wood development in ponderosa pine. *Forest Products Journal* 46: 92-100.

- Robert, E. (1998) Rapid scanning of microfibril angle in increment cores by x-ray diffractometry. In Butterfield, B. G. (ed.) *Microfibril angle in wood*. University of Canterbury, Christchurch, NZ.
- Salisbury, F. B. and Parke, R. V. (1964) *Vascular Plants: Form and Function*. Wadsworth Publishing, Belmont pp. 40-46.
- Saranpaa, P. (1985) Length, diameter and cell wall thickness of tracheids in mature lodgepole pine bolewood. *Silva Fennica* 19: 21-32.
- Schneider, M. H; Sebastian, L. P. and Seepersad, J. (1991) Bending strength and stiffness of Caribbean pine from Trinidad and Tobago. *Wood and Fiber Science* 23: 468-471.
- Senft, J. F.; Bendtsen, B. A. and Galligan, W. L. (1985) Weak wood, fast grown trees make problem lumber. *Journal of Forestry* 83: 477-484.
- Shelbourne C. J. A. and Ritchie K. S. (1968) Relationships between degree of compression wood development and specific gravity and tracheid characteristics in loblolly pine (*Pinus taeda L*). *Holzforschung* 22: 185-190.
- Siebers, A. M. (1971a) Initiation of radial polarity in the interfascicular cambium of *Ricinus communis* L. *Acta Botanica Neerlandica* 20: 211-220.
- Siebers, A. M. (1971b) Differentiation of isolated interfascicular tissue of *Ricinus communis* L. *Acta Botanica Neerlandica* 20: 343-355.
- Siebers, A. M. (1972) Vascular bundle differentiation and cambium development in cultured tissue blocks excised from the embryo of *Ricinus communis* L. *Acta Botanica Neerlandica* 21: 327-342.

- Smith and Briggs, (1986) Juvenile wood: Has it come of age? Proc. of a Cooperative Technical Workshop, Proc 47309. For. Prod. Research Society, Maidson, Wl. p. 5 9.
- Soh, W. Y. (1972) Early ontogeny of vascular cambium I. *Ginkgo biloba*. *Botanical Magazine Japan* 85: 111-124.
- Soh, W. Y. (1974a) Early ontogeny of vascular cambium II. Aucuba japonica and Weigela coraeensis. Botanical Magazine Japan 87: 17-32.
- Soh, W. Y. (1974b) Early ontogeny of vascular cambium III. *Robinia pseudo-acacia* and *Syringa oblata. Botanical Magazine Japan* 87: 99-112.
- Soh, W.Y. (1990) Origin and development of cambial cells. In: Iqbal, M. (ed.). *The vascular cambium*. John Wiley and Sons, New York, pp.37-62.
- Soh, W. Y. (1991) Ontogeny of the interfascicular cambium in the stem of Ginkgo biloba L. Res. Rep. KOSEF.
- Soh, W. Y. (1992) Origin and development of the interfascicular cambium from residual meristem in seed plants. *Korean Journal of Botany* 35: 273-281.
- Soh, W. Y.; Kang, K. D. and Yang, W. Y. (1989) Ontogeny of the interfascicular cambium in the hypocotyl of *Ricinus communis* L. *Proceedings, Second Pacific Regional Wood Anatoy Conference, College, Laguna, Philippines*. pp. 349-358.
- Soh, W. Y. and Yang, W. Y. (1987) The ontogeny of the interfascicular cambium in Ricinus communis hypocotyl. Proceedings of the Annual Meeting of the Korean Assocation for Biology p45.
- Soh, W. Y. and Young, W. (1992) Origin and development of the interfascicular cambium from residual meristem in seed plants. *Korean Journal of Botany* 35: 273-281.

- Sterling, C. (1946) Growth and vascular development in the shoot apex of *Sequoia sempervirens* (Lamb.) Endl. III. Cytological aspects of vascularization. *American Journal of Botany* 34: 35-45.
- Sterling, C. (1947) Organisation of the shoot of *Pseudotsuga taxifolia* (Lamb.) Britt. II. Vascularization. *American Journal of Botany* 51: 7-19.
- Stteves, T. A. and Susses, I. M. (1972) *Patterns in plant development*. Prentice-Hall, Englewood Califfs, New Jersey. pp. 241-261.
- Taylor, F. W. (1979) Variation of specific gravity and fibre length in loblolly pine branches. *Journal of the Institute of Wood Science* 8: 171-175.
- Timell, T. E. (1973) Studies on opposite wood in conifers. 1: Chemical composition. *Wood Sci. Technol* 7:1-5.
- Timell, T. E. (1978) Helical thickenings and helical cavities in normal and compression woods of Taxus baccata. *Wood Science and Technology* 12: 1-15.
- Timell, T. E. (1986) Compression wood in Gymnosperms. Springer-Verlag, Berlin. Vol. 1-3.
- Verbelen, J. P. and Stickens, D. (1995) In vivo determination of fibril orientation in plant cell walls with polarization CSLM. *J. Microscopy*. 177: 1-6.
- Walford, G. B. (1982) Current knowledge of the In-Grade bending strength of New Zealand Radiata pine. FRI Bull. 15. Rotorua, New Zealand.
- Walford, G. B. (1985) The mechanical properties of New Zealand-grown radiata pine for export to Australia. *FRI Bulletin, Forest Research Institute, New Zealand* No. 93.

- Walker, J. C. F. (1993) *Primary wood processing: principle and practice*. Chapman and Hall, London.
- Walker, J. C. F. and Butterfield, B. G. (1996) The importance of microfibril angle to the processing industries. *New Zealand Forestry* 40: 34-40.
- Walker, J. C. F. and Nakada, R. (1999) Understanding corewood in some softwoods: a selective review on stiffness and acoustics. *The International Forestry Review*. 1: 251-259.
- Walker, J. C. F. and Woollons, R. C. (1998) Cell wall organisation and the properties of xylem a speculative review. In: Butterfield, B. G. (ed.). *Microfibril Angle in Wood*. The University of Canterbury. pp. 13-26.
- Wardrop, A. B. (1948) The influence of pressure on the cell wall organisation of conifer tracheids. *Proceedings, Leeds Philosophical and Literary Society* (Scientific Section) pp.128-35.
- Wardrop, A. B. (1951) Cell wall organisation and the properties of the xylem I. Cell wall and the variation of breaking load in tension of the xylem in conifer stems.

 Australian J of Scientific Research 4B: 391-414.
- Wardrop, A. B. and Dadwell, H. E. (1950) The nature of reaction wood. II. The cell wall organisation of compression wood tracheids. *Australian J of Scientific Research* 3B: 1-13.
- Wardrop, A. B. and Davies, G. W. (1964) The nature of reaction wood. VIII. The structure and differentiation of compression wood. *Aust. J. Bot.* 12: 24-38.
- Webster, N. and Mckechnie, J. 1. (1980) Websters New Twentieth Century Dictionary of the English language unabridged. *William Collins*, 2129pp.

- Welch, M. B. (1927) Some mechanical properties of Australian grown *Pinus insignis* (*P. radiata*). *Journal and Proceedings of the Royal Society N.S.W.* 61, 354-370.
- Wilson, B. F. (1966) Mitotic activity in the cambial zone of *Pinus strobus*. *Am J Bot* 53: 364-372.
- Wodzicki, T. and Peda, T. (1963) Investigation on the annual ring of wood formation in European Silver Fir (*Abies pectinata* D.C.). *Acta Societatis Botanicorum Poloniae* 32: 609-618.
- Xu, P. and Walker, J. C. F. (2000) Wood quality gradients in trees. Workshop, 2000. Wood technology research centre, University of Canterbury.
- Xu, Y. M.; Chen, S. Y. and Fang, W. B. (1999) Variation of tracheid length and microfibril angle of slash pine in different sites and their correlation. *Journal of Huazhong Agricultural University* 18: 83-87.
- Young, G. D. (1992) Utilisation of 25-year- old *Pinus radiata*, part 1: wood properties. New Zealand Journal of Forestry Science 21: 217-227.
- Young, W. D.; Laidlaw, R. A. and Packman, D. F. (1970) Pulping of British-grown softwoods. VI. The pulping properties of Sitka spruce compression wood. *Holzforschung* 24:86-98.
 - Zar, J. H. (1999) Biostatistical analysis. Prentice-Hall, Inc.USA.
- Zobel, B. J. (1975) Using the wood quality concept in the southern pine. *South Pulp Paper Mfr.* 38:14-16.
- Zobel, B. J. and Buijtenen, J. P. van (1989) Wood variation: its cause and control. Sprnger-Verlag, Berlin.

- Zobel, B. J.; Kellison, R. C.; Mathias, M. F. and Hatcher, A. V. (1972) *Wood density of the southern pines*. Tech. Bull. No. 208. North Carolina Agri. Exp. Sta. Raleigh, North Carolina, 56pp.
- Zobel, B. J. and Talbert, J. (1984) *Applied Forest Tree Improvement*. Jown Wiley and Sons, New York.

APPENDICES

Appendix 1 The heights and the stem lengths of the 8 month-old plantlets of clone 8 and 31.

Table A.1.1 The height of the clones 8 and 31 (mm).

Seedling No.	Base	Stem 4	Stem 3	Stem 2	Stem 1	Tip
C8F (bag 1)	74	99 <u>9999</u> 999999	301	512	611	689
C8F (bag 15)	118	293	494	651	701	891
C8T (bag 13)	80	184	375	583	594	855
C8T (bag 19)	80	194	344	484	561	895
C8A (bag 11)	47	107	185	311	382	472
C8A (bag 17)	20	106	211	376	426	536
C31F (bag 12)	87	232	583	674	799	904
C31F (bag 14)	45	167	339	533	622	833
C31T (bag 20)	95	215	337	592	662	928
C31T (bag 12)	97	229	378	581	662	917
C31A (bag 24)	15	110	305	480	571	676
C31A (bag 2	115	210	365	510	584	689

Table A.1.2 The stem length of the clones 8 and 31 (mm).

Seedling No.	Base	Stem 4	Stem 3	Stem 2	Stem 1	Tip	Total
C8F (bag 1)	74		227	211	99	78	689
C8F (bag 15)	118	175	201	157	50	190	891
C8T (bag 13)	80	104	191	163	56	261	855
C8T (bag 19)	80	114	150	140	77	334	895
C8A (bag 11)	47	60	78	126	71	90	472
C8A (bag 17)	20	86	105	165	50	110	536
C31F (bag 20)	87	145	306	136	125	105	904
C31F (bag 14)	45	122	172	194	89	211	833
C31T (bag 20)	95	120	122	255	70	266	928
C31T (bag 12)	97	132	149	203	81	255	917
C31A (bag 24)	15	95	195	175	91	105	676
C31A (bag 22)	115	95	155	145	74	105	689

Appendix 2 Variability in tracheid length between clones 8 and 31, three treatments and stem positions.

A) Distributions of tracheid length of plantlets, clones, treatments, and stem positions.

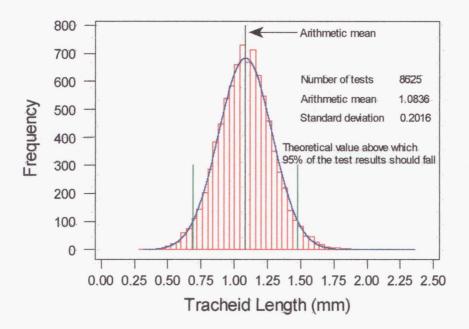


Figure A.2.1 Distribution of tracheid length of 8 month-old radiata pine plantlets.

Figure A 2.1 shows a distribution of the tracheid length of all plantlets. Totally 8625 tracheids were measured, 95% tracheid length are between 0.68 to 1.47 mm. Arithmetic mean is 1.0836 mm, and the standard deviation is 0.20 mm.

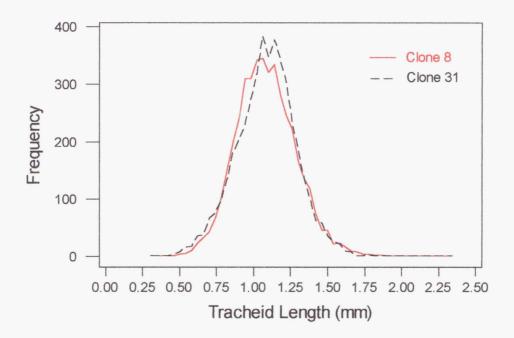


Figure A.2.2 Variation of the tracheid length between clones 8 and clone 31

It is not significantly different between two clones.

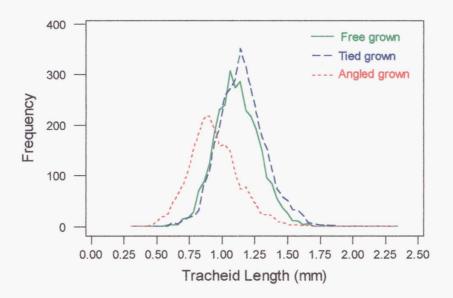


Figure A.2.3 Variations of the tracheid length between free, tied and angled treatments.

The angled plantlets had significant shorter tracheids than the free and tied ones.

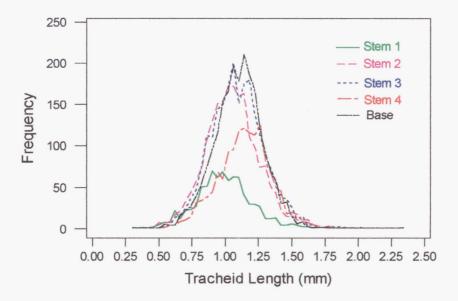


Figure A.2.4 The distribution of tracheid length between the stem positions. Figure A.2.4 shows the variation in tracheid length between stem positions.

B) Data Display

	-					
Row No.	Tree	Means	Stdv	Semean	Tracheid	CV%
	Stem				number	
	Stick No.					
1	111	1.030	0.232	0.046	25	4.5
2	121	0.990	0.186	0.026	50	2.6
3	122	1.052	0.165	0.023	50	2.2
4	123	0.962	0.209	0.029	50	3.1
5	124	0.997	0.135	0.019	50	1.9
6	131	1.095	0.144	0.020	50	1.8
7	132	1.068	0.189	0.026	50	2.5
8	133	1.076	0.169	0.023	50	2.2
9	134	1.121	0.182	0.025	50	2.3
10	141	1.235	0.163	0.023	50	1.9
11	142	1.219	0.140	0.019	50	1.6
12	143	1.167	0.153	0.021	50	1.8
13	144	1.198	0.146	0.020	50	1.7
14	151	1.157	0.147	0.020	50	1.7
15	152	1.212	0.185	0.026	50	2.1
16	153	1.213	0.164	0.023	50	1.9
17	154	1.255	0.139	0.019	50	1.6
18	211	1.011	0.267	0.037	50	3.4
19	221	1.079	0.184	0.026	50	2.4
20	222	1.024	0.181	0.025	50	2.5
21	223	1.027	0.207	0.029	50	2.8
22	224	1.038	0.153	0.021	50	2.1
23	231	1.094	0.187	0.026	50	2.4
24	232	1.025	0.159	0.022	50	2.2
25	233	1.093	0.159	0.022	50	2.1
26	234	1.092	0.158	0.022	50	2.1
27	251	1.123	0.161	0.023	50	2.0
28	252	1.095	0.125	0.018	50	1.6
29	253	1.085	0.143	0.020	50	1.9
30	254	1.086	0.134	0.018	50	1.7
31	311	1.052	0.106	0.021	25	2.0
32	312	1.024	0.118	0.023	25	2.2
33	321	1.027	0.111	0.022	25	2.1

34	322	1.034	0.082	0.011	50	1.1
35	323	1.013	0.065	0.013	25	1.2
36	324	1.077	0.137	0.019	50	1.8
37	331	1.160	0.094	0.019	25	1.6
38	332	1.070	0.098	0.020	25	1.8
39	333	1.145	0.132	0.019	50	1.6
40	334	1.124	0.132	0.019	50	1.7
41	341	1.155	0.112	0.016	50	1.4
42	342	1.182	0.121	0.017	50	1.4
43	343	1.117	0.141	0.020	50	1.8
44	344	1.126	0.138	0.019	50	1.7
45	351	1.122	0.134	0.018	50	1.7
46	352	1.118	0.102	0.014	50	1.3
47	353	1.144	0.122	0.017	50	1.5
48	354	1.205	0.122	0.017	50	1.4
49	411	1.080	0.181	0.026	50	2.4
50	412	1.068	0.180	0.025	50	2.4
51	421	1.050	0.175	0.025	50	2.3
52	422	1.120	0.157	0.022	50	1.9
53	423	1.199	0.194	0.027	50	2.2
54	431	1.220	0.168	0.024	50	1.9
55	432	1.217	0.159	0.022	50	1.8
56	433	1.171	0.216	0.031	50	2.6
57	434	1.182	0.133	0.019	50	1.6
58	441	1.166	0.150	0.021	50	1.8
59	442	1.158	0.198	0.028	50	2.4
60	443	1.241	0.199	0.039	25	3.2
61	451	1.106	0.122	0.017	50	1.6
62	452	1.113	0.166	0.023	50	2.2
63	453	1.139	0.149	0.021	50	1.8
64	454	1.101	0.131	0.018	50	1.7
65	511	1.097	0.218	0.031	50	2.8
66	512	1.029	0.128	0.018	50	1.7
67	513	1.010	0.140	0.020	50	1.9
68	514	1.074	0.160	0.022	50	2.1
69	521	1.097	0.160	0.022	50	2.0
70	522	1.052	0.215	0.030	50	2.9
71	523	1.134	0.201	0.028	50	2.5

72	524	1.082	0.141	0.020	50	1.8
73	531	1.149	0.135	0.019	50	1.7
74	532	1.255	0.170	0.024	50	1.9
75	533	1.194	0.175	0.024	50	2.1
76	534	1.199	0.148	0.021	50	1.7
77	541	1.252	0.161	0.023	50	1.8
78	542	1.196	0.161	0.023	50	1.9
79	543	1.201	0.140	0.020	50	1.7
80	544	1.219	0.183	0.026	50	2.1
81	551	1.114	0.118	0.017	50	1.4
82	552	1.169	0.129	0.018	50	1.6
83	553	1.156	0.154	0.022	50	1.9
84	554	1.149	0.159	0.023	50	2.0
85	611	0.884	0.192	0.027	50	3.1
86	612	0.814	0.154	0.031	25	3.8
87	621	1.013	0.137	0.002	50	0.2
88	622	1.135	0.237	0.033	50	2.9
89	623	1.189	0.263	0.037	50	3.1
90	631	1.232	0.217	0.031	50	2.5
91	632	1.162	0.170	0.024	50	2.1
92	633	1.201	0.253	0.036	50	3.0
93	634	1.074	0.157	0.022	50	2.1
94	641	1.224	0.164	0.023	50	1.9
95	642	1.152	0.145	0.021	50	1.8
96	643	1.310	0.223	0.032	50	2.4
97	644	1.204	0.180	0.025	50	2.1
98	651	1.169	0.152	0.022	50	1.8
99	652	1.160	0.146	0.021	50	1.8
100	653	1.159	0.154	0.022	50	1.9
101	654	1.139	0.152	0.021.	50	1.9
102	721	1.120	0.136	0.019	50	1.7
103	722	1.100	0.183	0.025	50	2.3
104	723	1.051	0.124	0.017	50	1.6
105	724	1.116	0.148	0.021	50	1.9
106	731	1.210	0.131	0.019	50	1.5
107	732	1.232	0.180	0.025	50	2.0
108	733	1.137	0.133	0.018	50	1.6
109	734	1.152	0.182	0.025	50	2.2

110	741	1.165	0.131	0.018	50	1.5
111	742	1.161	0.115	0.016	50	1.4
112	743	1.151	0.153	0.021	50	1.9
113	751	1.150	0.142	0.021	50	1.8
114	752	1.146	0.124	0.017	50	1.5
115	753	1.122	0.158	0.022	50	2.0
116	754	1.184	0.132	0.018	50	1.5
117	811	1.209	0.216	0.043	50	3.5
118	812	1.176	0.213	0.042	50	3.6
119	821	1.167	0.211	0.029	50	2.6
120	822	1.146	0.156	0.022	50	1.9
121	823	1.217	0.167	0.023	50	1.9
122	824	1.146	0.227	0.032	50	2.8
123	831	1.221	0.192	0.027	50	2.2
124	832	1.224	0.139	0.019	50	1.6
125	833	1.213	0.161	0.022	50	1.9
126	834	1.159	0.155	0.022	50	1.9
127	841	1.182	0.184	0.026	50	2.2
128	843	1.223	0.152	0.021	50	1.8
129	844	1.162	0.187	0.026	50	2.9
130	851	1.228	0.186	0.026	50	2.1
131	852	1.125	0.125	0.017	50	1.6
132	853	1.236	0.156	0.022	50	1.8
133	854	1.186	0.168	0.023	50	2.0
134	921	1.062	0.201	0.028	50	2.7
135	922	1.086	0.177	0.025	50	2.3
136	923	1.142	0.256	0.051	50	4.5
137	931	0.879	0.133	0.015	50	1.7
138	933	0.982	0.131	0.018	50	1.9
139	934	0.988	0.183	0.025	50	2.6
140	941	0.878	0.100	0.014	50	1.6
141	943	0.916	0.113	0.015	50	1.7
142	951	0.930	0.111	0.015	50	1.6
143	952	0.981	0.112	0.015	50	1.6
144	1011	0.883	0.169	0.023	50	2.7
145	1012	0.852	0.159	0.022	50	2.6
146	1021	0.936	0.181	0.025	50	2.7
147	1022	1.033	0.243	0.034	50	3.3

148	1023	0.971	0.300	0.060	25	6.1
149	1031	0.897	0.135	0.019	50	2.1
150	1032	1.025	0.174	0.024	50	2.4
151	1033	0.943	0.135	0.019	50	2.0
152	1051	0.875	0.140	0.019	50	2.2
153	1052	0.943	0.162	0.023	50	2.4
154	1113	0.697	0.240	0.048	25	6.8
155	1121	0.924	0.186	0.026	50	2.8
156	1122	0.736	0.138	0.019	50	2.6
157	1123	0.746	0.177	0.035	25	4.7
158	1131	0.879	0.138	0.019	50	2.2
159	1132	0.947	0.152	0.021	50	2.2
160	1134	0.892	0.183	0.025	50	2.9
161	1141	0.777	0.100	0.014	50	1.8
162	1143	0.833	0.132	0.018	50	2.2
163	1151	0.949	0.145	0.020	50	2.1
164	1152	0.948	0.192	0.027	50	2.8
165	1154	0.920	0.168	0.024	50	2.6
166	1211	0.949	0.168	0.023	50	2.5
167	1212	0.970	0.211	0.029	50	3.0
168	1214	0.882	0.216	0.043	50	4.9
169	1221	0.975	0.236	0.033	50	3.4
170	1222	1.028	0.235	0.033	50	3.2
171	1223	1.019	0.206	0.029	50	2.8
172	1224	1.083	0.197	0.028	50	2.5
173	1231	0.837	0.157	0.022	50	2.6
174	1232	1.018	0.169	0.023	50	2.3
175	1233	0.944	0.157	0.022	50	2.4
176	1234	0.990	0.197	0.028	50	2.8
177	1251	0.944	0.165	0.023	50	2.5
178	1252	0.955	0.200	0.028	50	2.9
179	1253	0.948	0.204	0.029	50	3.0
180	1254	0.959	0.189	0.027	50	2.8

Appendix 3 The relationships between wood properties of clonal plantlets

Table A.3.1 The r values, P values, and regression equations of the relationships between clonal wood properties

Relationship	Treatment	r values	P values	Regression equation
MOE - tracheid length	F, T, A	0.28	0.000	Y = -0.321 + 1.77x
MOE - tracheid length	F, T	0.40	0.000	Y = -2.47 + 3.89x
MOE - density	A	0.528	0.003	Y = -0.503 + 0.00371x
Density - tracheid length	F, T, A	-0.52	0.000	Y = 841 - 353x
Density - tracheid length	F, T	-0.47	0.000	Y = 924 - 426x
Density - cell numbers/mm ²	F,T,A	0.54	0.004	Y = 145 + 0.148x
Density - cell wall area %	F,T,A	0.68	0.000	Y = 243 + 7.56x
Tracheid length - cell numbers/mm ²	F,T,A	-0.54	0.004	Y = 1.65 - 0.000276x
Tracheid - cell wall area %	F,T,A	-0.61	0.001	Y = 1.45 - 0.0134x
Cell wall area % - cell numbers/mm ²	F,T,A	0.69	0.000	Y = 1270 + 31.6x

F, T, A are the treatments of the free, tied, and angled grown.

Appendix 4 The wood property weighted-means according to four quadrants area percentage on stem cross area.

Table A.4.1 Properties of the two angled clones compared: standard errors are shown in parentheses. (related to Table 4.5).

	Д			,	
Clone	MOE	Density	Tracheid L.	Cells	Cell wall
	(GPa)	(kg/m³)	(mm)	(mm²)	area (%)
8	1.62 (0.19)	516 (18.4)	0.96 (0.02)	2639 (119)	34.8 (2.93)
31	1.20 (0.13)	499 (16.4)	0.92 (0.02)	2452 (44.6)	40.3 (3.96)

Table A.4.2 Properties of the two clones, three treatments and stem positions compared: standard errors are shown in parentheses. (related to Table 4.8).

Commonwealth Commo	MOE	Density	Tracheid L.	Cells	Cell wall A.
	(GPa)	(kg/m³)	(mm)	/mm²	(%)
Clone			NAME OF THE OWNER OWNER OF THE OWNER OWNE		AUGUSTA ACCOUNTS OF THE PARTY O
8	1.72 (0.14)	482 (13)	1.06 (0.020)	2244 (97)	30.8 (1.4)
31	1.62 (0.12)	464 (11)	1.07 (0.027)	2271 (50)	31.7 (1.8)
P value	0.513	0.123	0.916	0.863	0.793
Treat					
Free	1.68 (0.17)	470 (13)	1.11 (0.015)	2105 (46)	29.3 (1.0)
Tied	1.72 (0.11)	415 (7)	1.16 (0.019)	2127 (68)	27.1 (0.8)
Angled	1.61 (0.17)	535 (10)	0.91 (0.021)	2526 (79)	37.2 (2.0)
P value	0.873	0.000	0.000	0.004	0.000
Position			T 100 11 100 100 100 100 100 100 100 100	a dan manananananananananananananananananan	
Stem 1	1.07 (0.15)	478 (19)	0.99 (0.047)	2112 (75)	27.3 (1.7)
Stem 2	1.43 (0.11)	473 (16)	1.04 (0.026)	2239 (63)	29.5 (1.8)
Stem 3	1.59 (0.16)	477 (23)	1.07 (0.035)	2187 (119)	32.0 (2.5)
Stem 4	2.44 (0.22)	446 (20)	1.11 (0.050)	2352 (163)	33.2 (4.0)
Base	1.78 (0.16)	478 (20)	1.08 (0.033)	2413 (150)	34.6 (2.3)
P value	0.000	0.678	0.000	0.194	0.005

Appendix 5 The influence of compression wood, clone, treatments, stem positions, and other factors (tracheid length and microfibril angle) on young-wood stiffness.

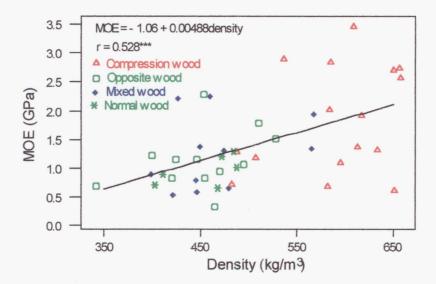


Figure A.5.1. The plot points were four wood types from the angled plantlets.

The compression wood had a large influence on stiffness for similar density. Probably the other factors influenced on stiffness as scatter distribution of plot points especially the compression wood.

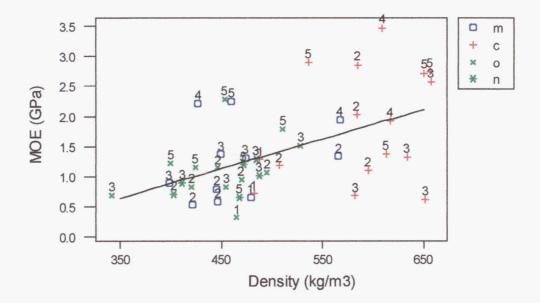


Figure A.5.2 A same plot of Figure A.5.1 are with stem position labelled (I to 5 are stem 1 to the base).

The one top and two low points are compression wood samples from stem 4 and 3 therefore suggest that the severe compression wood tissue had a large variation in these zones to form wider variation.

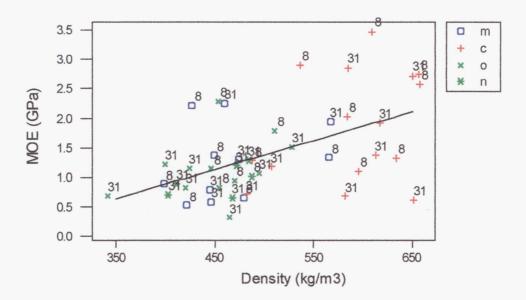


Figure A.5.3 A same plot of Figure A.5.1 is labelled with clones 8 and 31.

The top point is stem 4 from clone 8, and the two low points are stem 3 from clone 31. The stiffness of compression wood in clone 8 higher than clone 31, therefore together to form wider variation.

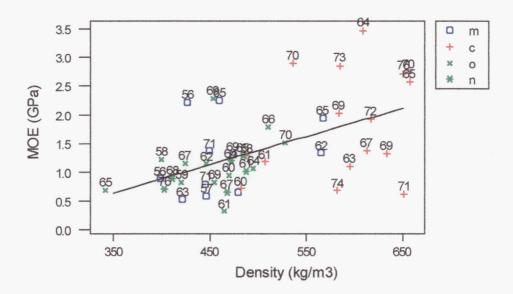


Figure A.5.4 same plot of Figure A.5.1 is labelled with microfibril angle.

The top point had small fibril angle (64 degrees), and the two low points had larger microfibril angle (74 and 71 degrees respectively). Clearly, the microfibril angle influenced on stiffness. Compression wood had similar density but had different microfibril angle resulted in wider variation. This graph shows that the density also is important to stiffness as in similar microfibril angle the density was bigger the stiffness is higher.

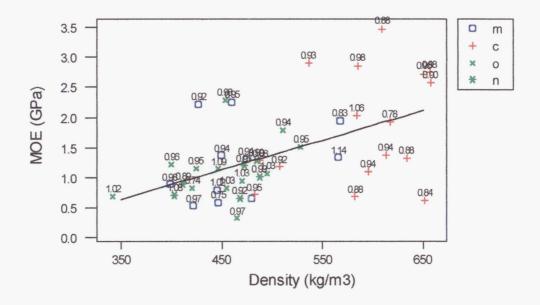


Figure A.5.5 A same plot of Figure A.5.1 is with tracheid length.

It is clear that the tracheid length was influenced on stiffness. Anyway, if the sample with longer tracheids but with lower density the stiffness still lower. The density look like more important than tracheids in so young angled plantlets as the tracheids too short to play a major role in this stage.

Appendix 6 The results of correlation analysis between stiffness and tracheid length for clones 8 and 31 (with 95% Confidence).

Quadrants data (all sample data):

The regression equation is

y (MOE) = - 0.321 + 1.77 x(tracheid length)

$$R-Sq = 7.9\%$$
 $R-Sq(adj) = 7.4\%$

Analysis of Variance for correlations.

Source	DF	, SS	MS	F	P
Regression	1	6.6156	6.6156	14.48	0.000
Error	168	76.7629	0.4569		
Total	169	83.3785			

Stem data

The regression equation is

$$y = -0.189 + 1.67 x$$

 $R-Sq = 11.8\%$ $R-Sq(adj) = 10.0\%$

Analysis of Variance

Source	DF	SS	MS	F	P
Regression	1	1.8281	1.8281	6.53	0.014
Error	49	13.7251	0.2801		
Total	50	15.5532			

Tree data

The regression equation is

y = 0.109 + 1.38 x

R-Sq = 43.2% R-Sq(adj) = 37.5%

Analysis of Variance

Source	DF	SS	MS	F	P
Regression	1	0.24658	0.24658	7.61	0.020
Error	10	0.32410	0.03241		
Total	11	0.57068			

Clone data

The regression equation is

y = -0.023 + 1.50 x

R-Sq = 66.5% R-Sq(adj) = 58.2%

Analysis of Variance

Source	DF	SS	MS	F	P
Regression	1	0.13067	0.13067	7.96	0.048
Error	4	0.06568	0.01642		
Total	5	0.19635			