

**LINKING TREE GROWTH to END-PRODUCT
PERFORMANCE:
LITERATURE REVIEW and
PROPOSED MODELLING STRATEGY**

J. C. Grace

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July 2003

Stand Growth Modelling Cooperative

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NOTE : Confidential to participants of the Stand Growth Modelling Cooperative.
: This is an unpublished report and must not be cited as a literature reference.

EXECUTIVE SUMMARY

The Stand Growth Modelling Cooperative first supported the development of stand level growth models, and then the development of modifiers for these models to account for genetic differences between seedlots. In recent years it has been supporting the development of individual tree stem growth models and branch growth models for growing mid-rotation inventory data forward in time. These models are linked together to form TreeBLOSSIM.

In recent years the quality of the timber, rather than the volume of the timber produced, has become an important focus for research. The Stand Growth Modelling Cooperative has acknowledged its importance by the incorporation of a new theme in its research strategy, namely, Internal Stem Modelling. This literature review and modelling strategy was the first project supported under this theme.

The ideal scenario would be to develop an integrated tree, crown and wood property growth model that provided sufficient detail on the within-stem variation in wood properties to link with models of end-product performance.

The papers reviewed indicate that:

- the growth and environmental conditions have a major impact on wood properties within the stem, but that there are still many questions that remain unanswered.
- the observed within-tree variation in wood properties appear to be of benefit to the tree and are probably a near-optimal solution for its survival, as a result of natural selection.
- models are being developed that can investigate the influence of within-stem wood property distributions on end-product performance.

Hence the development of an integrated tree, crown and wood property growth model is realistic, but such a model does not appear to have been developed before. To develop such a model for radiata pine will require intensive data collection across a range of sites, silvicultural regimes and genetic material. SGMC pilot studies being used to determine the feasibility of the approach and to develop appropriate sampling strategies.

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LINKING TREE GROWTH TO END-PRODUCT PERFORMANCE: LITERATURE REVIEW and PROPOSED MODELLING STRATEGY

INTRODUCTION

Traditionally tree growth research has been carried out in isolation to tree wood property (quality) research. Consequently there is a lot of descriptive knowledge for radiata pine on both stem diameter and height growth patterns, and on the variation in wood properties with position in the stem. However the fundamental knowledge to develop integrated models, that predict wood formation and wood properties as a function of tree growth, is lacking.

Integrated models of wood formation are needed because:

- Highly variable wood properties often lead to problems with end-use performance.
- The reasons for the variability in wood can be better understood by considering the developmental process of wood formation as an integral part of tree growth (Larson, 1969).
- External environment (climate and soil) and the genetic make-up of trees directly influence the functioning of the crown, which in turn influences the structure of wood cells (Larson, 1962).

Such models can be developed by:

- having a holistic view of tree development and,
- quantifying all aspects of tree growth and wood structure on carefully selected trees whose history is known.

This would be a long-term project and would require scientists working in many different specialised areas, collaborating and working towards a common goal

The objectives of this report are:

- To propose a modelling strategy (framework) that will allow the integration of the tree's growing environment with its growth (both stem and crown) and resultant wood properties.
- To review the literature to determine gaps in our current knowledge.
- To propose areas requiring further research.

MODELLING STRATEGY - PART 1: A BIO-CHEMO-MECHANICAL MODEL OF WOOD FORMATION

The ability to accurately predict tree growth and stem wood properties in response to differences in tree breed, site and silviculture is necessary for the effective management of a production forest. The use of computer simulation models for the prediction of tree growth goes back to the early 1960s and over the years many different models have been developed (see Grace 200x). Predicting the development of stem wood properties concurrently with tree growth is a new direction and recognises the fact that the wood properties as well as wood volume within a tree are important for the end-user.

A computer simulation model that links tree growth with end-product performance would be a tool for investigating how alternative silviculture regimes influence end-product performance. With such knowledge it would be feasible to design silvicultural regimes best-suited to particular end-products. Perstorper et al (1995a) consider that the modelling and optimisation of silviculture practice and log conversion should focus more directly on end-user related quality variables rather than a substitute parameter such as density.

The objective of the following literature review is to summarise current knowledge on how tree growth affects the development of the stem wood properties. From this knowledge we can then design an appropriate modelling strategy/ strategies that would allow the interactions between tree growth and timber end-use to be simulated. Regardless of the modelling approach used, relevant, good quality data are necessary pre-requisites for model development.

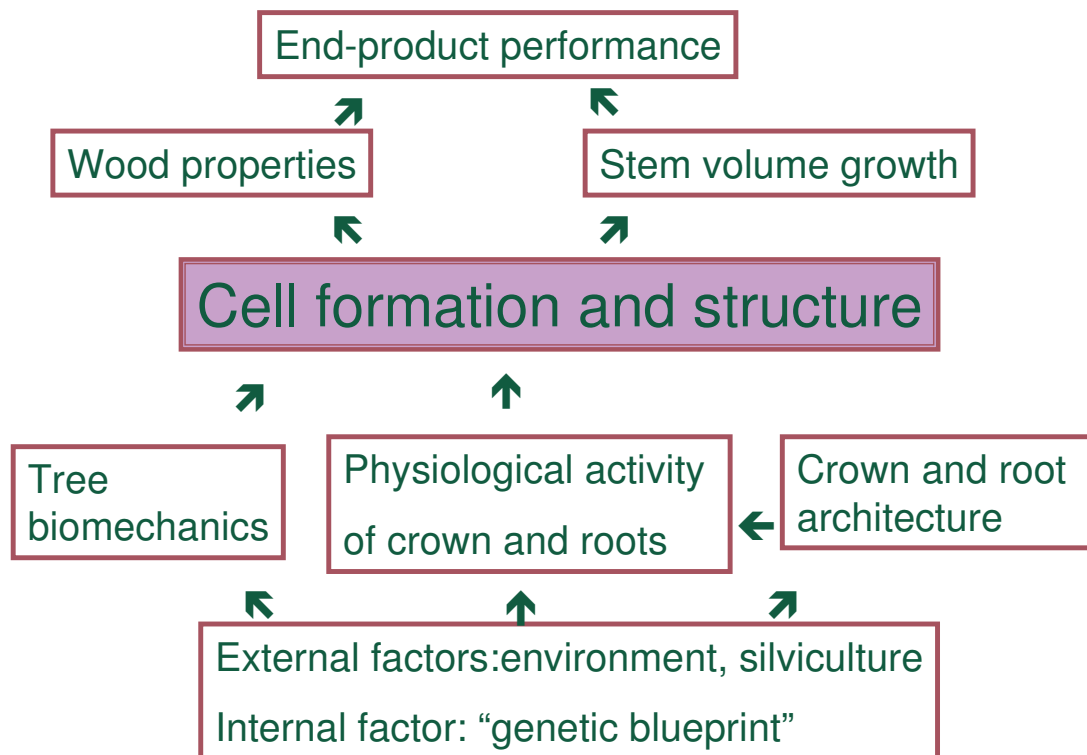
Figure 1, presents a high-level view of how genetics and environmental factors influence tree development and hence end-product performance (feed-back mechanisms have been ignored). It highlights the fact that:

- cell formation and structure is considered critical to understanding tree growth, wood properties and hence end-product performance.
- cell formation and structure is a consequence of both internal (“the genetic blueprint within the tree”) and external factors (the environmental conditions which in turn influence the structure and activity of the crown and the roots and the biomechanics of the tree).

Figure 1 was developed as a result of the literature review, but is presented first as it provides a framework for organising the literature review.

The name “bio-chemo-mechanical” arose from the fact that the proposed model will predict the formation of wood and the chemical structure of the wood cells from a mechanical perspective.

Such a modelling system is considered feasible. Research is currently underway in all areas – some in New Zealand and some overseas. Error propagation will need to be a major consideration in developing such a system. Each component model will need to be as accurate as possible, and the accuracy of each component will depend on having good quality data covering the range of genetics, environment and forest management practice.



Bio-chemo-mechanical model of wood formation

Figure 1. Proposed framework for linking tree growth with end-product performance

LITERATURE REVIEW

Outline

Many papers and books have been written on wood formation and wood properties and to review everything would have been an immense task. This review aims to present current knowledge on how tree growth influences wood formation, wood properties and hence end-use performance. Such knowledge is a pre-requisite to designing a modelling strategy.

The literature review covers the following topics:

1. End-use of New Zealand radiata pine resource
2. Structure and development of wood cells
3. Tree Biomechanics
4. Crown structure – implications for tree growth and wood properties
5. Wood Properties
6. The relative importance of the tree's local environment versus the tree's genetic make-up on tree growth and wood properties
7. Relationships between cell characteristics and performance characteristics
8. Characteristics affecting end-use
9. Current models
10. Climate Variability

End-Use of New Zealand Radiata Pine Resource.

In a production forest, trees are grown for the purpose of using the timber for some end-product. It is therefore important to understand how the environmental conditions, silvicultural regime and the genetic make-up of the tree influence the tree characteristics that determine the suitability of the timber for these end-uses.

In April 2001, radiata pine accounted for 89.4% of the estimated 1.8 million hectares of planted production forests in New Zealand. The silviculture regimes for the radiata pine resource can be split into 4 categories. To maximise clearwood production, 49% of the radiata pine plantations receive green crown pruning with early thinning to waste and no production thinning. James (1990) discussed the evolution of this regime. The three other alternatives are: green crown pruning with production thinning (18%); no pruning with production thinning (4%) and no silvicultural intervention (29%). The average (area-weighted) rotation age is 27 years (New Zealand Forest Owners Association, 2002).

For the year ending March 2001, 19.3 million m³ of timber (roundwood equivalent) was produced (99.5% from plantation forests). The end-use of this timber is shown in Table 1.

Table 1. End-use of timber produced from New Zealand forests.

| Industry | Volume (millions m ³ roundwood equivalent) | % of timber |
|-------------------------------------|--|-------------|
| Log Exports | 5.9 | 30.6% |
| Chip Exports | 0.3 | 1.6% |
| Pole Industry | 0.4 | 2.1% |
| Plywood | 0.2 | 1.0% |
| Lumber | 3.8 | 19.7% |
| Residues from plywood and lumber | 3.9 | 20.2% |
| Reconstituted panels | 1.2 + some residues | 6.2% |
| Pulp Industry | 3.6 + some residues | 18.6% |

Different criteria determine the suitability of the wood for a particular end-use. For example stiffness is important for structural timber whereas surface defects are important for appearance timber (see Table 2). There are many sets of timber grading rules (Standards Association of New Zealand, 1991). These are designed to ensure that timber is of appropriate “quality” for its intended end-use.

Table 2. Features influencing suitability of timber for a given end-use.

| End-Use | Characteristics influencing suitability |
|--|--|
| Structural Timber | Stiffness – low stiffness is undesirable. Knots – reduce stiffness of timber. Visual grading rules limit size of knots. Warp – Grading rules limit the amount of warp |
| Appearance Timber | Undesirable features include: warp, resin streaks, resin pockets, bark pockets, surface checks, and knots. Timber grading rules (e.g. Standards Association of New Zealand, 1991) limit number and size of defects. |
| Pulp and Paper | Desirable features for softwood pulps include: low to medium density softwoods, little within-ring variation in density, and long fibres with thin walls. Large knots are undesirable due to presence of denser compression wood. Such wood is often “undercooked” in chemical pulping; and knots are resistant to defibration in mechanical pulping (Walker, 1993) |
| Composites: plywood (including LVL- laminated veneer lumber), particleboard fibreboard (including MDF, triboard, hardboard and softboard) | Stiffness of timber is critical for LVL as it is used as a structural product. Wood properties have insignificant effects on particleboard and MDF (J. Warnes pers. comm.) Resin associated with loose knots caused problems in making plywood (comment made during a visit to a plywood manufacturer). |

Structure and development of wood cells

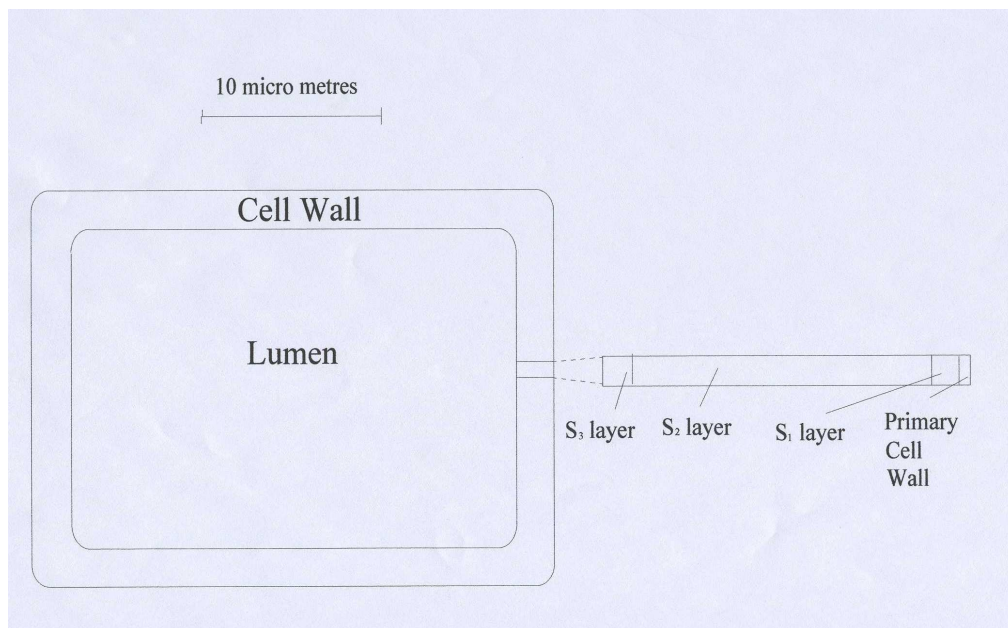
Cell Structure

There are several references describing the structure of cells in softwoods (for example, Kininmonth and Whitehouse (1991), Niklas (1992), Persson (2000), Harrington (2002)). The following is a synthesised description.

Approximately 95% of the cells in softwoods are “tracheids”, which are long in the axial direction and slender in the radial and tangential directions. Their dimensions are quite variable. The hollow lumen is used for the transport of water and dissolved mineral ions. The cell wall can be divided into three component layers (Figure 2):

- The primary cell wall (P), which is laid down at time of cell formation.
- The secondary cell wall, which forms inside the primary cell wall as the cell matures. It is divided into 3 layers (S₁, S₂, S₃). This division is based on the different orientation of the cellulose microfibrils each layer. However many distinct thin layers can be distinguished within the secondary wall using electron microscopy.
- The middle lamella is made up of an isotropic material that bonds adjoining cells together.

Figure 2. Structure and approximate dimensions of a radiata pine tracheid.



Softwood cells are composed of three main components, cellulose, hemicellulose and lignin. The proportion by volume varies for the different layers of the cell wall. Differences in cell structure will therefore result in different proportions of cellulose, hemicellulose and lignin.

Cellulose is a highly-ordered polymer, the outside of which can absorb water (Harrington, 2002). On average, cellulose accounts for 40-45% of cell wall volume. It is lowest in the middle lamella and primary cell wall and highest in the S₂ layer (Persson, 2000).

Hemicelluloses are a group of non-cellulosic polysaccharides, which have a low degree of polymerisation. This results in low stiffness and high moisture absorption capacity. On average, it accounts for about 30% of cell wall volume with little variation between layers (Persson, 2000).

Lignin is a complex compound having a 3-d molecular structure. On average, it accounts for about 30% of cell wall volume, but ranges from approximately 20% in the S₂ and S₃ layers to 62% in the middle lamella and primary cell wall (Persson, 2000).

Moisture and temperature significantly affect the properties of hemicellulose and lignin, but their influence on the properties of cellulose is at the most slight (Harrington pers comm.).

The remaining, approximately 5%, cells are ray cells which are aligned perpendicular to tracheids. They provide radial liquid transport and food storage in the trunk.

Cell Development

Tracheid development can be split into 4 separate phases (e.g. Deleuze and Houllier, 1998):

- process of cell formation
- process of cell expansion
- process of secondary wall thickening
- lignification.

For radiata pine in Victoria, Australia approximate time taken for the different phases are (Skene, 1969):

- cell division in the cambium and xylem mother cells: about 4 weeks
- cell expansion: between 1-3.5 weeks
- secondary wall thickening: about 3-4 weeks early in the season and 8-10 weeks later in the season

Cell division and expansion determine the annual ring width whereas secondary wall thickening determines the density of the wood (amount of cell wall per unit volume) (Antonova and Stasova, 1993). The two phases appear to be largely independent and controlled by different processes (e.g. Larson, 1969). Hence it is possible that the same annual ring width could be produced with widely varying climatic conditions, e.g. fertile site limited by water in summer versus less fertile site with adequate summer rainfall (Downes *et al* 1999). Such differences in development may be a possible reason for the confusing results on the relationship between wood density and ring width, and suggests that understanding the relationships between environment and cell development will help in prediction of wood properties for a given site.

Lignification

As each cell matures, the matrix material becomes permeated with lignin, which helps to stiffen the cell wall. This has several advantages:

- It prevents separation between wood cells and the layers within the cell walls (Uprichard, 1991).
- It can increase the compressive stresses that cell walls can sustain before they fracture (Niklas, 1992)

Several studies have examined the lignin concentration in the cell corner region of the middle lamella (CCML) in radiata pine (e.g. Donaldson 1993; Donaldson, 1985; Donaldson, 1986; Donaldson *et al*, 1997). These studies have shown that:

- Typically radiata pine trees have a lignin concentration of approximately 80% v/v in the cell corner region of the middle lamella. Trees with concentrations below 75% v/v are considered to be low lignin trees.
- The lignin concentration of the S₂ layer and CCML appeared to be independent of growth rate, stem eccentricity, site and silviculture. (Sample size: 10 trees spread across 3 sites and samples selected to avoid compression wood in eccentric trees).
- Between trees, there was a significant variation in the lignin concentration in the S₂ layer and in the CCML. Within a tree there was no significant variation with either age (samples 3 rings from bark versus samples 49 rings from bark) or between earlywood and latewood. (Sample size: 5 trees).
- There are significant variations between clones and trees within clones in the middle lamella lignin concentration. There were also interactions between trees and rings within a clone. (Sample size: 2 trees from each of 10 clones).
- Trees with the clone 850-55 as one of the parents had lower lignin concentration in the cell corner middle lamella. (Sample size: 3 groups of 5 trees).
- Cell wall fracturing was noted in trees with 850-55 as a parent suggesting that the wood was structurally weaker than unselected trees. (Sample size: 3 groups of 5 trees).

Lignification does not occur simultaneously in all layers of the cell. Lignification starts in the primary cell wall, followed by the middle lamella. Lignification of the secondary cell wall usually commences after lignification of the middle lamella is complete. However for one of the five trees examined, lignification of the middle lamella and secondary cell wall appeared to occur simultaneously and resulted in a “low lignin” tree (Donaldson, 1991).

Several studies have indicated that lignin deposition may be affected by environmental variables.

- Radiata pine trees growing under drought regimes contained bands of collapsed cells with little lignin. It was suggested that the bands of distorted cells contained tracheids that were in the enlarging phase at the time of periodic waterings used to maintain soil water at a sufficiently low-level to maintain drought conditions but prevent tree death (Barnett, 1976). (i.e. there was sufficient moisture for the cell to enlarge, but insufficient moisture to complete development.)
- Lignin content in the terminal latewood cells from 10 consecutive growth rings of Norway Spruce growing near the tree-line in Austria was found to be positively correlated with mean temperature for the period from beginning of September to 3rd week of October (Gindl *et al*, 2000).
- A severely deformed radiata pine tree growing on a copper-deficient site had lower lignin concentration in both compression wood and opposite wood compared to a straight tree growing on the same site (Downes *et al*, 1991)

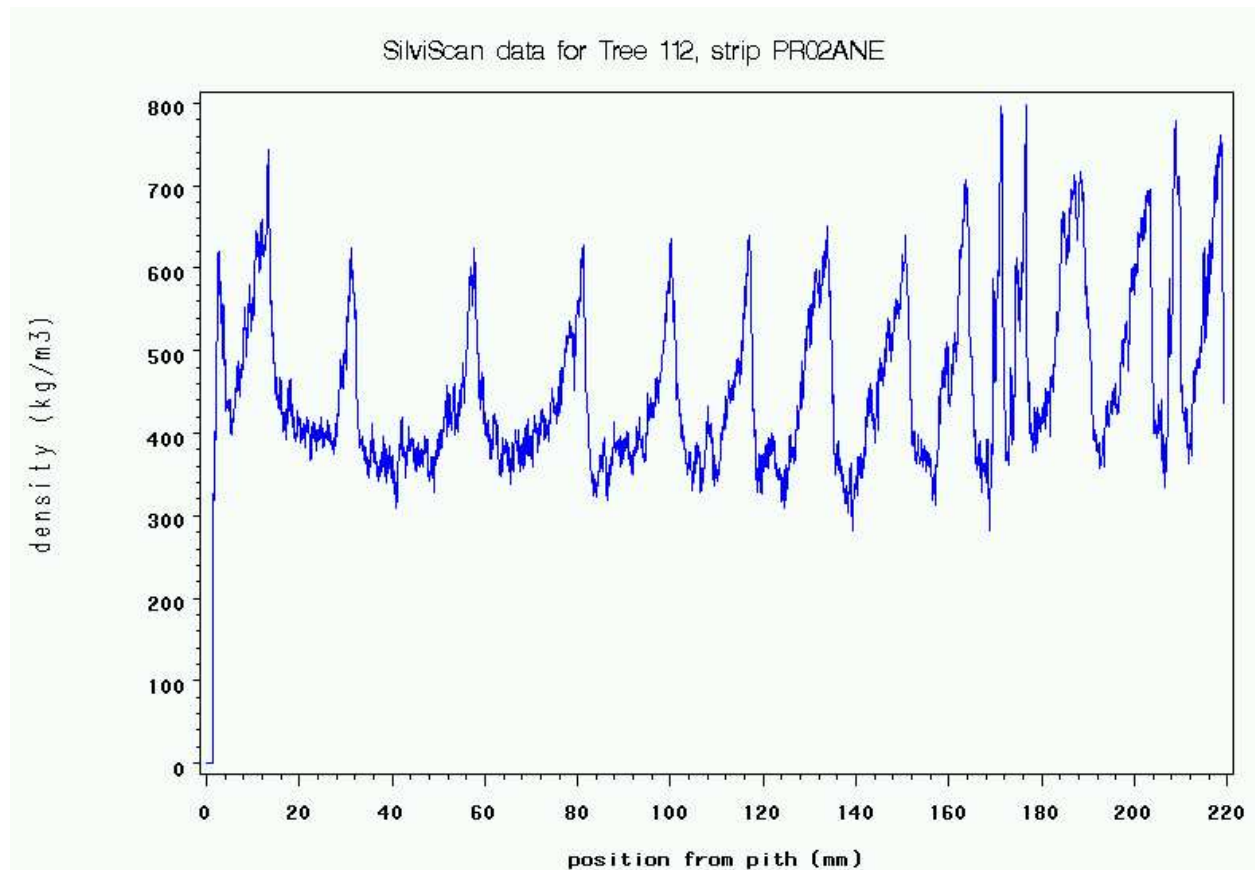
The above studies indicate that the lignin concentration varies between trees and can affect the strength of the wood. However, the sample sizes are very small. Recent evidence suggests that cell wall matrix may play an equally important role in dictating the mechanical behaviour of cell walls. The shear modulus of the cell wall matrix could conceivably be very important.

Earlywood and latewood

Cell structure, and hence wood properties vary continuously throughout a growth ring but it is often segregated into earlywood and latewood. Earlywood is the cells formed early in the growing season when fluid transport from root to needles is high. They have thin walls and large cavities (lumens) resulting in low density. Latewood is the cells formed towards the end of the growing season that have thicker cell walls resulting mainly from an increase in the thickness of

the S₂ layer (Persson, 2000). This results in higher density and, due to the different chemical composition of the different cell wall components, less lignin and more cellulose compared to earlywood. Figure 3 shows how density varies across a number of growth rings.

Figure 3. Density profile as measured by SilviScan for a strip of wood with 17 growth rings from the base of a tree growing in the Long Mile, Rotorua.



The definition of Mork (1928) is often used to define latewood. However in translating from German to English, two different definitions have been used (Denne, 1988). These are:

- A latewood tracheid is one where the double wall thickness $\times 2$ is greater than or equal to the lumen diameter.
- A latewood tracheid is one where the single wall thickness $\times 2$ is greater than or equal to the lumen diameter.

Another, practically equivalent, approach is to use a fixed density value to differentiate between earlywood and latewood. For example, Cown and Ball (2001) defined all wood with a density greater than 400 kg/m³ to be latewood. In contrast, Persson (2000) defined three zones within a ring, earlywood, transition wood and latewood zones.

The factors affecting cell wall thickness appear complex.

Larson (1969) considered that:

- earlywood formation was favoured by close proximity to the foliage organs.
- the seasonal onset of latewood formation (smaller cells and thicker walls) appeared to coincide with the cessation of height growth by the terminal shoot and new needle maturity.

Daylength may also be implicated in latewood formation as young red pine trees grown under a long day: short day: long day regime produced a false ring with narrow-diameter tracheids of latewood type in the growth ring corresponding to the short photoperiod (Larson, 1969).

Hormones have also been implicated in the regulation of cell diameter as experiments using synthetic hormones have been able to change the cell diameter (Larson, 1969).

Gindl *et al* (2000) suggest that a short cool growing season produces a narrow low-density ring whereas more favourable warmer conditions will lead to wider rings with higher latewood densities.

Data from Scots Pine (Antonova and Stasova, 1993) and Larch (Antonova and Stasava, 1997) indicated that both cell expansion and secondary wall thickening were influenced by temperature and rainfall but in different ways. In some instances high temperatures can lead to reduced secondary wall thickening, presumably due to reduced photosynthate availability. They conclude that it is not possible to simultaneously increase cell number, cell diameter, and cell wall thickness, i.e. compromises need to be made in tree selection and breeding programmes.

Sequences for examining wood properties

Duff and Nolan (1953) proposed 3 different sequences for examining wood properties:

- An oblique sequence that considers the wood laid down in 1 year. This sequence is the most useful to examine to develop links between tree growth and wood properties.
- A horizontal sequence that considers the wood laid down at one horizontal height. This is the most common way of measuring wood properties.
- A vertical sequence that considers the wood laid down at a given ring number from the pith.

Tree Biomechanics

Trees need to be mechanically reliable to grow and survive over a rotation. Trees adjust their mechanical properties through the addition of new cells and through the structure of these new cells (Wilson and Archer, 1979). Both tree flexure (when the stem moves in response to wind and returns to a vertical position), and lean correction (which occurs when a stem has been “permanently” displaced from the vertical) contribute to varying cell structures.

Several terms have been used to describe wood formed under different conditions. Wood formed in response tree flexure was termed “flexure wood” (Telewski, 1989) whereas the wood formed in non-flexed trees was termed “normal wood”. Wood formed to correct for stem lean is termed “reaction wood” in general, “compression wood” in conifers and “tension wood” in hardwoods. “Opposite wood” is used to describe wood formed on the opposite side of the stem to “reaction wood”. “Normal wood” is also used to describe wood formed in non-leaning trees.

Compressionwood

Compressionwood cells are formed in an attempt to correct any stem deviation from verticality. They differ in structure from “normal wood” cells (e.g. Harris, 1977) in that they may have some or all of the following features:

- The tracheids are more circular in cross-section so that intercellular spaces are formed.
- The tracheids are shorter and narrower.
- The tracheids contain less cellulose and more lignin.
- There is no S₃ cell wall layer.
- The microfibril angle in S₂ layer is larger.

These differences in cell structure affect the gross properties of compression wood compared with “normal wood”.

- The wood density is higher.
- The longitudinal modulus of elasticity is lower.
- It has greater longitudinal shrinkage but less transverse shrinkage.
- The relationship between microfibril angle and shrinkage is different.

Flexure Wood

Tracheids of flexure wood are similar to those of compression wood (Telewski, 1989) in that they:

- are shorter and narrower than normal wood
- have a microfibril orientation similar to the less extreme forms of compression wood
- have a higher density than normal wood

Tracheids of flexure wood differ from compressionwood (Telewski, 1989) in that they:

- are not rounded
- do not have intercellular spaces
- do not have a thicker S₂ layer

Uniform Stress Hypothesis

Mechanistic, hydraulic, nutritional and hormonal theories have been developed to explain stem form. The mechanistic theory was developed in the late 1800's and has been the subject of much research and controversy (Larson, 1963).

The essence of “the theory or axiom of uniform stress” is that trees grow in such a way to have uniform (bending) stress over their surface (see e.g. Morgan and Cannell, 1994; Mattheck, 1998, Dean *et al*, 2002).

Morgan and Cannell (1994) used the transfer matrix method to examine the axiom of uniform stress and concluded that:

- tree stems appear to grow to equalise the average stress at their outer surface
- for average wind-speeds in the range 2.5-10.0 m s⁻¹, differences in stem taper at different stockings may be related more to differences in crown dimensions than to differences in average wind speed.

Dean *et al* (2002) compared stem taper of several North American Conifers with the theoretical taper expected under the uniform stress hypothesis. Their data indicated that the axiom of uniform stress was reasonable for all but Douglas fir. In contrast, Niklas (2000) and Niklas and Spatz (2000) considered that the axiom of uniform stress did not apply to *Prunus serotina*, and that, as a safety mechanism, trees have areas where they will easily break more easily. Mattheck (2000) disputed this conclusion and considered their conclusion was a result of the assumptions they had made.

Regardless of which theory is correct, it is apparent that the structure of wood cells that are formed in any part of the tree at any time have been formed for a specific purpose and contribute to maintaining a good mechanical structure.

Growth Stress

Growth stress is associated with the development of wood cells and occurs in all tree species and there have been two major reviews (Archer, 1987 and Kubler, 1987).

The term “growth stress” is used to describe the mechanical stresses that develop in trees as they grow. Growth stress within a tree is the sum of two separate components:

- that due to the weight of the tree and
- that due to the maturation strains, which result from cell development.

Growth stresses are important factors in ensuring adequate strength and stability of trees. Differences in growth stress between one side of a tree stem and the other enables it to bend into more favourable positions. The magnitude of the difference determines the amount of reorientation. However, visible stem shape (lean and sweep) is a poor indicator of growth stress within the stem.

As each new layer of cells develops, “normal wood” cells tend to shrink in the longitudinal direction and increase in diameter, while “compression wood” cells tend to elongate in length and decrease in diameter. In both cases, the movement is constrained through being attached to the previous layer of cells. This results in new “normal wood” cells being in tension, and new “compression wood” cells being in compression. Mechanical equilibrium of stresses, means that an equal and opposite stress is distributed across the older cells.

The exact mechanism by which the cells change shape is not understood. Two theories have been proposed. Boyd (1972, 1985) suggested that growth stresses result from the lignification of the new cells. Bamber (1979, 1987) suggested that growth stresses result from the contraction of microfibrils in the new cells. However Yang and Waugh (2001) considered that neither theory is always applicable, and that a number of factors could be contributing to the stresses formed as a result of cell maturation.

While growth stresses are necessary in standing trees, they are undesirable when it comes to utilisation. Tree felling and cross-cutting of stems into logs will release longitudinal growth stresses near the cut. With large values of growth-stress, end-splitting can occur. When logs are sawn, growth stress release can cause lumber to warp and end-split.

Currently it is not possible to measure growth stresses directly; and they are usually derived from measurement of released strain.

Several studies, mentioned by Kubler (1987), indicate that stand structure and silviculture may influence growth stress. Trees in plantations, particularly heavily thinned or heavily pruned tend to develop strong growth stresses in order to achieve improved orientation, whereas trees that have little incentive to re-orientate (such as in multi-storied stands) have weak stresses.

Jacobs (1945) noted that in the first few years, conifers tend to develop longitudinal compressive stresses in the outer layers with complementary tensile stresses near the pith. This appears to contradict the previous summary and I wonder whether the sign of the growth stress depends on the relative dimensions of the new cells compared with the older cells.

Okuyama *et al* (1998) examined the relationship between growth stress and lignin content in a 11-year-old sugi tree (*Cryptomeria japonica* D.Don.) that had previously been tilted. They found a strong negative correlation between growth stress and lignin concentration in the secondary cell wall, in particular in the outer part of the latewood. In contrast there was no correlation between growth stress and lignin concentration in either the compound middle lamella or the cell corner region. Since both growth stress and lignin concentration vary between compression and non-compression wood, this could be a chance correlation due to the structure of compressionwood. However attempts to breed trees with low-growth stress resulted in trees where the lignin content increased as the growth-stress decreased (Yang and Waugh, 2001) suggesting that there is a “cause-effect” relationship between the two variables.

Yang *et al* (2002), examined the relationship between mean log growth strain, tree dbh, mean wood density at breast height and % of excessively distorted green boards cut from 10-year-old *Eucalyptus globulus*. The correlation between mean log growth strain and mean density at breast height was 0.63. This suggests, if density and growth stress are genetically correlated, breeding for lower growth stress could result in lower density. Path analysis indicated that mean log growth strain and tree dbh had direct causal effects on the % of excessively distorted boards.

Boyd and Foster (1974) measured growth strain on a 22-year-old *Pinus radiata* tree that had a substantial bend in the lower 2 m. Samples were taken at 10 circumferential positions 0.6 m above the ground. Growth strain values varied around the stem, from compressive growth strain in the direction of the most obvious compression wood (position 10) to tensile growth strain, with the highest tensile growth strains being measured at positions 4 and 8 which were at approximately 135° and 60° either side of position 10. The longitudinal modulus of elasticity, measured in both in both tension and compression, followed a similar pattern. Microfibril angle (measured using Preston's (1952) technique) was highest at position 10, but decreased with increasing angle from position 10.

Boyd (1977) examined 4 radiata pine trees (approximately 40 years-old) from plantations. Generally each tree had a lean such that the position of the stem near the base of the crown was 1.5 – 2m eccentric relative to the stem at the base. Two of the radiata pine trees had leans several times greater. Again growth strain varied with position around the stem. Longitudinal shrinkage was also measured (on samples approximately 100 mm long and 12 mm square). Longitudinal and volumetric shrinkage tended to increase as longitudinal growth strain increased. Microfibril angle pattern was similar to that of longitudinal shrinkage. However Boyd (1977) considered that variations in MFA alone do not provide a reliable guide to differences in shrinkage responses in tissues and that shrinkage was either not related directly or exclusively to strain values.

Boyd (1980) measured surface strains on eight logs cut from 5 radiata pine trees. The logs were divided into two groups, those from normal or slightly leaning trees and those from reorientating trees. The ratio of maximum to mean strain varied was higher for the reorientating trees.

However there was essentially no difference in the ratio of maximum to mean microfibril angle. (This does not imply that there was no circumferential variation in microfibril angle. In fact the range was 8.6° to 27° in normal trees and 9.2° to 34° in the reorientating trees).

The other interesting point emerging from this study was that there were both tensile and compressive strains around the circumference of all three normal /slightly leaning trees.

Negative Geotropism and Apical control

Negative geotropism ensures that the trunk grows upright against gravity. Apical control is a “mechanism” within the tree that prevents the branches competing with terminal shoot, i.e. the terminal shoot grows vertically and the branches grow at an angle from verticality. When the stem above a branch is broken or injured, a branch is released from apical control and bends upward due to the mechanical action of compression wood. The inhibition of branch growth by apical control has usually been attributed to the transport of auxins down the stem (Zimmermann and Brown, 1971).

Wilson and Gartner (2002) used stem phloem girdles to investigate apical control of branches in 6 conifer species. They found that if a girdle was placed 2 cm above a branch, then the branch responded by bending upwards. At the same time, compressionwood was formed in the lower portion of the branch and in the main stem below the branch. A stem girdle more than 20 cm below the branch did not release the branch from apical control. There were variable results (different results for different species) with a stem girdle 2cm below the branch.

Response to lean and stem deformation

Displacement of a plant's main stem from vertical inhibits the longitudinal and radial growth of both terminal shoot of the main stem and any lateral shoots on the underside of the tilted main stem. Growth in a lateral shoot on the upper side of the tilted main stem is not inhibited and may even be promoted. In extreme cases this can result in transfer of apical control (Wilson 2000) from the main stem to a branch on the upperside of the tilted stem (Little and Lavigne, 2002).

Downes *et al* (1994) examined how radiata pine seedlings responded to lean imposed by a weight attached 75mm below the tip of the tallest point. The experiment with seedlings from 4 families known to have different susceptibility to stem deformation, two levels of nitrogen supply and two different weights was carried out in a glass-house– thus removing the effect of wind.

There were significant differences between families with the more susceptible families exhibiting greater initial magnitudes of stem lean, greater rates of apical elongation following bending and resulted in more exaggerated stem bends. The differences could not be explained by whole stem modulus of elasticity. The differences in stem deformation were better explained by the slenderness of the stem with the more susceptible families having more slender stem form.

Burdon (1975) assessed compression wood in 18 radiata pine clones from each of 4 forest sites within New Zealand. He found that compression wood was more prevalent in the lower bole at all four sites. He concluded that clones differed in their propensity to form compression wood; moderately crooked stems may straighten with the formation of strongly developed compression wood, or remain crooked with only slight compression wood. This suggests that the variability in modulus of elasticity within/around the stem influences the ability of a tree to straighten.

Radiata pine growing on ex-pasture sites in South-east Australia tend to have poor stem form. This has been termed the “Toorour Syndrome” (Turvey *et al*, 1993). Trees deformed most markedly during a late-spring flush when the weather was warmer, wetter and windier than previously but it was not possible to define a single causative factor.

From an utilisation perspective the mild compression wood in a crooked stem may be better than a straight tree with severe compression wood and highly variable wood properties.

Wind

Wind can have a major impact on the productivity, wood properties and survival of forest stands. The term “thigmomorphogenesis” has been used to describe the physiological, biochemical and morphological responses of plants to wind. Responses quoted by Pruyn *et al* (2000) and Moore (2002) include:

- reduced drag and /or increased mechanical strength
- reduced height
- elliptical stem form and the formation of compression wood on the downside of the stem
- altered water-balance within a forest – For example the dry north-westerly wind of Canterbury can induce severe moisture stress. This causes a temporary reduction in growth – and cells tend towards a latewood rather than earlywood structure and as a result “false-rings” may be formed within an annual growth layer.
- defoliation of trees leading to reduced growth rates

A tree with a crown that is symmetric in a plane normal to the wind direction will be subject only to bending. If the crown is asymmetric in a plane normal to the wind direction, then tree is likely to be twisted by the wind as well. However few, if any, attempts have been made to measure the amount of twisting that occurs in forest trees (J. Moore, pers comm.). Skatter and Kucera (2000) investigated the possibility of tree failure due to either bending or twisting by assuming that trees had a 2-d rectangular but asymmetrical crown. Simulations indicated that when bending and twisting are modelled together, both bending and shear failure are approximately equally likely at the base of the crown. Having similar risks of failure from different sources is considered to be good from an engineering perspective.

Nicholls (1982) considered that pine plantations were sensitive to the effects of wind. In Australia, radiata pine plantations seemed to contain a fairly high proportion of trees that lean in the direction of the prevailing wind, and as a consequence, stems tend to be elliptical in cross-section with eccentric pith, and compression wood is formed on the lower side of the stem. Nicholls (1982) classified 770 trees, that formed part of a 23-year-old radiata pine plantation in Australia which located on sloping ground sloping to the north (slope not given) and sheltered from the west, as:

- straight and vertical (30.8%)
- straight and leaning (43.9%)
- curved (25.3%) (of these 195 trees, 105 had vertical stems above curved butts.)

43 of the straight but leaning trees, with lean $\leq 7^\circ$, were felled and a disc from approximately 2 m. Eccentricity was calculated as displacement of pith from the centre as percentage of the diameter. Ellipticity was calculated as the difference in diameter in the direction of the lean and at right angles, expressed as a percentage of the smaller diameter.

There was not a strong relationship between angle of lean and either eccentricity or ellipticity. Eccentricity was found to be a better index of the incidence of mild compression wood than angle of lean. This result is not surprising considering current stem shape is not considered to be a good indicator of what is inside.

Tree Flexure

Telewski (1989) uses the term “flexure wood” to describe wood formed by wind-induced flexure of the stem – when the stem returns to a vertical position. Since wind-induced movement always occurs in a natural environment, wood termed “normal wood” actually incorporates flexure wood. The amount of flexure varies with environmental conditions, and within a forest with stand density and position of tree in a stand.

The one-year-old leaders of 10 five-year-old *Abies fraseri* were flexed twenty times once a day for the duration of the shoot extension growth phase. Wood properties in discs cut from these trees were compared with the wood properties in discs from 10 non-flexed control trees. It was found that flexure wood had greater average ring density than normal wood. Microfibril angle increased in tracheids formed under influence of flexure. Values approached the less extreme values formed in compressionwood (Telewski, 1989).

A tree-flexing experiment using two poplar hybrids (one resistant and one susceptible to wind-toppling/ leaning) indicated that the two hybrids had different response strategies to flexing (i.e. wind). Flexure lead to a decrease in the modulus of elasticity (E) and an increase in the second moment of cross-sectional area (I) and flexure rigidity (EI). These changes were larger for the resistant hybrid, and it was concluded that the resistant hybrid responded by increasing the stem rigidity whereas the susceptible hybrid responded by reducing in stature (Pruyn *et al*, 2000).

An increased tendency to form compression wood as growth rate increases is a feature of many pines, Very vigorous trees may form mild compressionwood right round the stem. This is considered to be due to hormonal imbalances (Harris, 1977). A similar effect has been documented in thinning trials (e.g. Cown 1974). In this study the proportion of compression wood in a ring was positively correlated with growth rate at both butt and breast height (1.4 m). At 6m, there was a noticeable increase in compression wood following the late thinning. Since thinning is the best way to achieve increased growth rate, I wonder whether increased stem flexure has contributed to the observed increase in visible compression wood.

Stability

It is considered that trees will become mechanically unstable if they are too slender (i.e. have a high height to diameter ratio) compared to their weight (e.g. Holbrook and Putz, 1989; Spatz and Bruechert, 2000). Variables that can provide an estimate of stability include flexural stiffness, which is the product of the 2nd moment of area and modulus of elasticity; and whole-plant flexibility which is expressed as an angular deflection divided by applied force (Holbrook and Putz, 1989).

Holbrook and Putz (1989) compared 3 groups of sweet gum seedlings (control, guyed, and guyed and laterally shaded). After 2-years growth under these treatments, the main differences between the three groups were

- The height-diameter ratio. The guyed and laterally shaded trees were the most slender.
- The whole-tree flexibility. The guyed and laterally shaded trees were the most flexible.

There was no significant difference in density or modulus of elasticity.

Brüchert *et al* (2000) measured the wood properties of dominant and suppressed Norway spruce trees. Within a stand, flexural stiffness was higher in the lower part of the stem in dominant trees compared with suppressed trees. The difference in flexure stiffness between dominant and suppressed trees decreased with increasing height in the tree. In contrast, within a stand, structural modulus of elasticity was lower in the dominant trees compared with the suppressed trees. These data appear to indicate that the increased stem radial growth in dominant trees compensates for the lower modulus of elasticity.

Dunham and Cameron (2000) compared matched sets of snapped, overturned and undamaged Sitka spruce trees but found little difference in slenderness ratio (height/diameter). However the snapped trees tended to have slightly more compression wood and were consequently less stiff and of higher density. Surprisingly, crown silhouette area tended to be smaller in the damaged trees, but the authors admit that this may have been an artefact of the sampling procedure.

Hydraulic Design

As well as being mechanically well-designed to cope with fluctuating wind forces, and their own self-weight, a tree also needs to be hydraulically well-designed to cope with varying water availability.

Mencuccini *et al* (1997) examined the relationships between anatomical, hydraulic and mechanical properties for 30 Scots Pine (*Pinus sylvestris*) trees ranging from 7 to 59 years of age. Properties measured included:

- wood specific conductivity (permeability)
- tracheid lumen diameter in two directions at right angles from the outermost 4-5 rings (used to calculate a “hydraulic” diameter)
- tracheid length from outermost 4-5 rings
- modulus of elasticity
- basic wood density

They found that:

- hydraulic diameter increased asymptotically with tree age
- tracheid length increased more gradually with tree age
- measured specific conductivity increased asymptotically with tree age and was positively correlated with both hydraulic diameter and tracheid length
- Modulus of elasticity was positively correlated with hydraulic diameter, tracheid length, measured specific conductivity and density. The correlation was highest for measured specific conductivity (0.85) and lowest with density (0.45).

Increases in both specific conductivity and modulus of elasticity with tree age are seen as logical since increases in height influence both, the distance water must travel within the tree and the magnitude of the bending moment under dynamic wind loading.

Domec and Gartner (2002) measured and modelled hydraulic and mechanical properties in Douglas fir, and concluded that the large radial variation in wood anatomy was an adaptation to hydraulic rather than mechanical requirements. In particular, the structure of “juvenile wood” (wood formed in rings close to the pith) appeared to be able to better buffer water deficits than “mature wood” (wood formed in rings further from the pith). They suggest that breeding for trees with reduced “juvenile wood” may inadvertently create plants that are susceptible to drought.

Crown Structure – Implications for tree growth and wood properties

Crown structure is important for both tree growth and timber quality. Crown structure will influence wind movement. The arrangement of foliage within the crown, and consequently the arrangement of branches on the stem, influences the amount of light intercepted by the foliage (e.g. Whitehead *et al*, 1990). Photosynthesis (required for growth) is influenced by light availability and several studies have shown that the annual above-ground biomass increment of forest stands is linearly related to the annual light interception (e.g. Linder, 1985, Grace *et al*, 1987). However a major gap in our knowledge of tree development is the mechanism of carbon allocation (e.g. Ryan, 2002).

Photosynthate produced by the crown is used in cell formation – initiation, expansion, and secondary wall thickening. In the 1980s detailed research was carried out in controlled environment conditions to understand cell development in radiata pine. Whitehead *et al*. (1983) found no significant differences in either tracheid double-wall thickness or lumen diameter when 2-year old *Pinus radiata* trees from 6 different clones in growth rooms under 3 markedly different (low medium and high) saturation deficits. Sheriff and Whitehead (1984) acclimatised trees from two different clones in growth rooms for 3 months, kept them well watered for a further 3 months then withheld water. Photosynthesis decreased sigmoidally with reductions in water potential. Initially, water deficits reduced lumen diameter of newly matured stem tracheids and increased wall thickness. After 1 month of water potentials of -2.4 MPa both lumen diameter and wall thickness were much reduced. Sheriff and Rook (1990) measured photosynthesis, respiration, growth, wood density and tracheid dimensions on 8 trees, two from each of 2 high and 2 low wood density clones. They concluded that there was no simple relationship between wood density and photosynthesis; and that more knowledge is needed of the mechanism by which carbon balance affects partitioning, and how allocation to tracheid wall thickness versus lumen size is regulated. One problem with the above studies was the small number of trees that could be sampled and the small number of tracheids that could be measured.

Two recently developed techniques have the potential to improve our understanding of how crown activity influences cell structure. Firstly measuring the ratio of Carbon-13 to Carbon-12 in wood provides a retrospective measure of the crown activity. Secondly the development of SilviScan allows the cell structure across wood strips to be measured. It is suggested that the use of these two techniques on the same or adjacent wood samples would be an excellent approach for determining the relationship between crown activity and the resultant cell structures.

During photosynthetic carbon uptake, the lighter ^{12}C isotope is favoured over the heavier ^{13}C isotope. Hence the ratio of ^{13}C to ^{12}C isotopes in wood provides an overall indication of both the physiological activity of the crown (Walcroft *et al*, 1997) and a measure of water use efficiency (Ponton *et al* 1999) at the time of wood formation. The isotope composition of the sample is expressed in delta units, $\delta^{13}\text{C}$, as the difference in $^{13}\text{C}/^{12}\text{C}$ ratios between the sample and a standard. The carbon isotope discrimination, the isotopic composition of the sample compared to that of air, which allows for changing atmospheric composition, is expressed as Δ .

Walcroft *et al* (1996) compared $\delta^{13}\text{C}$ for foliage from long and short (trimmed to make a hedge) radiata pine. The foliage at the end of long branches showed a marked drop in net photosynthetic rate as the saturation deficit increased whereas foliage at the end of short branches showed little change. They also compared $\delta^{13}\text{C}$ for foliage from a long internode seedlot and a multinodal planted at 4 different stockings. At each stocking, the long-internode seedlot had a longer branch

length and the foliage was less depleted in ^{13}C , again indicating a drop in net photosynthetic rate with the longer branch length.

Porté and Lousteau (2001) measured carbon isotope composition for seven 26-year-old maritime pine trees. Earlywood and latewood cellulose were analysed on an annual ring basis by combining samples from two discs (1 m and 2 m above ground) and four azimuth directions in each disc. Interannual variation in Δ followed a similar pattern in all trees. There was no obvious relationship with tree size with the two smallest trees having the most and least depleted tree in terms of Δ .

Ponton *et al* (1999) investigated whether carbon isotope discrimination varied between two important oak species in western Europe that occupy different ecological niches (*Quercus robur*, L. and *Quercus petraea* (Matt.) Liebl.). Under natural conditions *Q. robur* prefers to colonize wet bottom lands whereas *Q. petraea* prefers slopes and tops of hills. They sampled 8 cores from 20 trees (1 tree with a visually symmetrical crown from each species in each of 10 mixed-species plots). Species, tree within species, and time period all had a significant effect on Δ . There was a significant positive correlation between the mean annual Δ and average ring width for both species, but the regression equations differed between species. There was a strong positive correlation between average Δ per tree and average earlywood vessel surface area (EVSA). The regression equations did not differ with species. The results suggested that *Q. robur* appears to maximise water transport capacity in the xylem whereas *Q. petraea* seems to avoid drought-induced embolism.

SilviScan is a retrospective technique for measuring cell properties on small wood strips (Evans and Downes, 2001). It can provide estimates of cell dimensions, density, microfibril angle and modulus of elasticity.

SilviScan was used by Wimmer *et al* (2002) to examine microfibril angle in 6 *Eucalyptus nitens* trees, two from each of three treatments (adequate water, droughted, and irrigated/droughted). All showed high microfibril angles early in the growing season and lower angles during the latter part. The last group showed high variation in microfibril angle within the annual growth ring with high microfibril angles being formed as a response to release from soil-water stress.

SilviScan was used to investigate the difference between compression wood and opposite wood in radiata pine (Donaldson *et al* 200x). They found a higher microfibril angle in the compression wood compared to the opposite wood.

Branches also lead to knots, which constitute a defect for both appearance and mechanical reasons. There is reduced strength and stiffness in the vicinity of a knot. The reduced strength and stiffness is considered to be due to the complex arrangement of fibres in the vicinity of the knot (e.g. Phillips *et al*, 1981). There are alternate layers of fibres, one layer of fibres extends vertically through the stem and goes round the outside of a branch. The other layer of fibres extends from the bottom of the stem into the branch (Shigo, 1986). This results in disturbed grain angles in the vicinity of branches. Grain disturbance due to branches is considered to extend a distance almost equal to the diameter of the branch. Also, in one study, the wood up to 20 cm below the branch tended towards compression wood with higher density, and shorter tracheid lengths. In another study basic density varied throughout an internode. It was least at the mid-internode position and increased towards the branch clusters (Nicholls, 1986).

Wood Properties

Even though wood formation is an integral part of tree growth, wood properties have tended to be studied independently of tree growth and this point is considered to be the reason for confusing results in the wood quality literature (Larson, 1969).

Usually wood properties are studied in the clear timber away from branch clusters. Detailed information on the variation in wood characteristics within a given radiata pine tree is scarce and scattered. The within tree variation may exceed that between trees grown under the same conditions (Nicholls, 1986).

At a given level within a tree, the following variables have been found to increase with ring number from pith (Harris and Cown, 1991):

- tracheid length
- tracheid diameter
- tracheid wall thickness
- wood density
- tangential shrinkage
- radial shrinkage

In contrast, at a given level within a tree, the following variables generally decrease with ring number from pith (Harris and Cown, 1991):

- spiral grain – usually reaches maximum value by 2nd or 3rd ring and then decreases
- longitudinal shrinkage
- ring width – but will depend a lot on growing conditions

Much of the research on radiata pine has been on basic density (oven-dry weight of material divided by green volume) because it is easy to measure and is closely correlated with both major strength properties and the yield and quality of pulp.

A major survey of radiata pine wood properties in New Zealand was undertaken between 1977 and 1982 (Cown and McConchie, 1983). Breast height increment cores were collected from 7500 trees growing on 250 sites throughout New Zealand to determine the variations in basic density, tracheid length, and heartwood content. The exact details of the silvicultural history of each site were not recorded, however the trees selected had to be from planted stands at least 15 years old with a reasonable stocking level. Using data stored in the Permanent Sample Plot system, the likely average silvicultural regime was estimated and compared with that of more recent stands (Table 3). Apart from the change in silviculture, there has also been a change in planting stock, improved seedlots have become available. As a mathematical modeller, I would be extremely wary of using these data to develop models to predict wood properties for stands due to be felled within the next 10-20 years. A new comprehensive survey of radiata pine wood properties would be worthwhile.

Table 3. Silviculture for sample plots planted 1947-1967 and 1980-1990.

| | Sample plots planted between 1947 and 1967 (likely to be representative of stands surveyed) | Sample plots planted between 1980 and 1990 (likely to be felled within the next 10-20 years): |
|--|---|---|
| Number of Permanent Sample Plots considered | 2857 | 4056 |
| Average planting stocking | 2844 stem/ha | 1051 stems/ha |
| Average stocking after thinning (thinned plots only) | 371 stems/ha | 311 stem/ha |
| Average age at last thin | 13.6 years | 8.3 years |

Influence of environment on wood properties

Climate of the growing site has been shown to play an important part (second only to tree age) in the development of wood properties.

The wood property survey of radiata pine (Cown and McConchie, 1983) indicated that both corewood (rings 1-10 from pith) density and outerwood (rings 20-25 from pith) density were positively correlated with monthly, seasonal and annual mean temperature. The same tended to be true for rainfall, with winter rainfall having the highest correlation with density.

Tracheid length showed a regional distribution pattern similar to density but was less closely related to the environmental factors studied.

Influence of silviculture on wood properties

Larson (1969) considered that the manipulation of stand density was the best method available to silviculturalists for regulating both total wood yield and wood quality because stand density has a large influence on the quality of wood formed. Silvicultural treatments first lead to changes in the size and vigour of the crown, which in turn lead to altered wood properties in the developing cells (Megraw, 1985).

Given that a tree is considered to be a self-optimized structure (e.g. Mattheck, 1998), stem shape prior to silviculture is likely to be close to optimal for the initial conditions but will not be optimal for the new conditions. The tree needs to grow to adapt to these new conditions.

Silviculture treatment is likely to have a major impact tracheid (fibre) length since it is highly influenced by growth rate with reduced average tracheid length during periods of rapid growth. Earlywood tracheids should be shorter latewood tracheids when the tree is growing rapidly but not necessarily when the tree is growing more slowly (Megraw, 1985).

Silvicultural treatment is also likely to have a major impact on microfibril angle since many studies have shown that there is a strong negative correlation between microfibril angle and fibre length (see e.g. Preston, 1974; Megraw, 1985). Cell elongation has almost finished before the secondary cell wall starts to thicken. Hence Megraw (1985) assumed that the tracheid length influenced the microfibril angle but Preston (1974) is careful to point out that this may not be a causal relationship.

Silviculture treatment can influence wood density but the change is usually minor compared with the variability within and between trees, and the trends with age. Hence Harris and Cown (1991) stated that “rapid growth *per se* cannot be used as an indicator of low wood density”.

The effects of thinning are conflicting, but a slight decrease in density is often recorded. Pruning tends to increase density while fertilisation tends to decrease density. Sutton and Harris (1974) indicate that wood density does not respond to increased growth rates following thinning in the way that would be predicted from studies of unthinned stands and suggest that complex changes in the environment (including wind sway) induce growth responses not encountered in wood from unthinned stands.

While silviculture only causes small changes in some wood properties at a ring level, it does enable logs large enough for a particular end-use to be grown in a shorter time period (i.e. reduce felling age). As wood properties vary with age, silviculture can have a major impact on log properties as they will have a greater proportion of younger wood.

Thinning and pruning treatments were imposed on a radiata pine stand planted at 2314 stems/ha in 1961 in Kaingaroa Forest (Cown, 1973). There were 5 treatments:

1. moderate pruning – removed an average of 54% of crown length on 80 stems/ha in August 1968.
2. moderate pruning plus thinning – pruning as above (1), rest of trees poisoned thinned.
3. severe pruning - removed an average of 76% of crown length on 80 stems/ha in October 1967.
4. severe pruning plus thinning – pruning as above (3), rest of trees poisoned thinned.
5. control – unpruned dominants from treatments 1 and 3.

Wood properties were examined by taking one 10mm core from breast height and one 10mm core from 6.5 m (the base of the crown after pruning). For two years after treatment, the wood density in the 4 silvicultural treatments was larger than the control. The increase varied between about 5% and 7%. The largest increase (7%) being in the severely pruned stems. Tracheid length was noticeably affected by the radial growth of the trees. Tracheids produced at breast height during the 1970/71 growing season were on average 20% shorter in the thinned trees compared to the unthinned trees. At 6.5 m the differences were much smaller.

One disadvantage of this study is that poison thinning would lead to a gradual change in environmental conditions within the stand rather than an abrupt change as would occur with felling. Hence these results are likely to be less extreme than would be observed in a stand that was thinned to waste.

Cown (1974) examined density, tracheid length, and compression wood occurrence in Compartment 1099 Kaingaroa Forest, which was planted in 1947 at 3086 stems/ha. The area was pruned in 1956/57. Five hectares were thinned to 200 stems/ha in 1957/58 (tree age 10-11 years) while the remainder was initially thinned to 540 stems/ha, and then thinned to 200 stems/ha in 1966/67 (tree age 19-20 years). Discs were collected at 0.3m, 1.4m, 6.1m, 12.2m, 18.3m, 24.4m, and 30.5m for 10 trees from each treatment. Density was examined for 5 ring groups (1948-52, 1953-57, 1958-62, 1963-67, 1968-72) and averaged across trees within a treatment. The difference in density was only significantly lower in the heavier thinning for the 5 rings formed between 1963 and 1967 and then only at breast height and 6.1 m.

In an attempt to interpret these results with respect to tree growth, the Permanent Sample Plot System was searched for nearby plots controlled by *Forest Research*. The closest match was Experiment RO213 planted in 1947 in an adjacent compartment (Table 4). These values indicate that the discs at 30.5 m, 24.4 m, and 18.3 m would have been within the live crown for the 10 years when plots were at different stockings. The disc at 12.2 m was around the base of the live crown, and the lower discs were below the crown below the live crown. Hence the major changes in wood properties occurred in the section of stem below the live crown.

These two studies indicate that the differences in wood properties due to silviculture treatment are influenced by measurement position with respect to the live crown. The larger differences in wood properties with treatment occurred in a section of stem below the live crown.

Table 4. Plot characteristics from Experiment RO213 in Compartment 1068, Kaingaroa.

| Tree Age (years) | Mean Top Height (m) | Mean Crop Height (m) | Mean Crown Height (m) |
|------------------|---------------------|----------------------|-----------------------|
| 10.15 | 15.9 | 14.7 | - (not recorded) |
| 14.0 | 22.6 | 21.3 | 11.2 |
| 16.25 | 26.4 | 25.3 | 12.8 |
| 20.0 | 31.5 | 30.3 | 13.1 |

In a different study, Cown and Ball (2001) concluded that the predominant influence on average growth ring density was the latewood (wood $> 400 \text{ kg m}^{-3}$) percentage and that growth ring component densities (earlywood and latewood) varied very little. This suggests that the main influence of thinning on density has been to alter the proportion of earlywood to latewood below the live crown.

Influence of crown and tree size on wood properties

While Larson (1962, 1969) indicated that the crown would indirectly affect wood properties, there have been very few studies that have investigated the relationship between crown and wood properties. Amarasekara and Denne (2002) investigated the relationship between crown size and wood properties in Corsican pine. They sampled 9 straight, non-leaning, 23-24 year-old trees from a plantation on the island of Anglesey in Wales. Three dominant, three co-dominant and 3 suppressed trees were sampled. Leaf dry-weight was measured for each branch and summed to give a crown value. Eleven discs (from odd-numbered internodes) were collected. Two adjacent diametral strips were taken from each disc. One strip was used to measure ring width and latewood percentage (using Mork's 1928 definition). The other strip was used to measure specific gravity and tracheid length. In 8 of the even-numbered internodes, samples were cut for static bending and compression tests using green wood. Mean tree values were calculated for each wood property and compared with total dry leaf weight (see Table 5). These values indicate that crown has a significant influence on wood properties.

Table 5. Correlation coefficient between total leaf dry weight and various wood properties

| Variable | Correlation coefficient |
|------------------------------|-------------------------|
| Ring width | 0.97 |
| Specific gravity | -0.38 |
| Latewood % | -0.83 |
| Tracheid length | 0.05 |
| Modulus of rupture | -0.84 |
| Modulus of elasticity | -0.36 |
| maximum compression strength | -0.80 |

In each crown class, mean latewood percentage is low for rings close to the pith but increases most rapidly with ring number from the pith for the suppressed trees, and least rapidly for the dominant trees. For dominant and co-dominant trees the latewood percentage is low for wood formed within the portion of the stem occupied by the crown.

In each crown class, mean tracheid length increases with ring number from the pith, but the differences between crown classes were not significant.

Persson (2000) measured wood properties on 11 Norway Spruce trees in Sweden, a dominant, a co-dominant and a suppressed tree from each of 4 sites (there was no suppressed tree from 1 site through lack of a suitable sample tree). At 3 different heights in each tree, a disc was cut for microstructure measurements and a section cut for mechanical testing.

Some interesting facts that emerged from the data analyses include:

- Width of latewood band was poorly correlated with growth ring width.
- Ring density decreased with increasing ring width. However, the relationship was very weak for the dominant trees.
- The relationship between ring density and growth ring number varied between crown classes.
- Longitudinal modulus of elasticity tended to increase with ring number from the pith. The rate of increase was slowest at the base of the tree. This has also been observed in radiata pine (Grace *et al*, 2000).
- Longitudinal shrinkage at 12% moisture content decreases with ring number from the pith.
- Radial shrinkage coefficient at 12% moisture content remains approximately constant.
- Tangential shrinkage coefficient at 12% moisture content tends to increase with ring number from the pith.

The relative importance of the tree's local environment versus the tree's genetic make-up on tree growth and wood properties.

The Stand Growth Modelling Cooperative manages approximately 50 trials that, at rotation age, can be used to determine the relative importance of the tree's local environment versus internal factors (the tree's genetic make-up) on tree growth and wood properties. Below is an initial attempt to answer this question using published data and unpublished data from studies.

Two studies that have examined growth rate are Carson *et al* (1999a) and Carson *et al* (1999b). Carson *et al* (1999a) examined the differences in height and basal area growth between 4 different seedlots planted in large blocks (1978-1980 genetic gain trials). One trial was managed using a "pulpwood regime" while the rest were managed on a "direct-sawlog regime". This study showed an increase in the rate of basal area growth with improved genetic material but no significant improvement in the rate of height growth. Carson *et al* (1999b) examined the interactive effects of site, silviculture, and genetics in 8-year-old radiata pine from the "1987 silviculture/breed trials". This study indicated that while there were significant differences among seedlots; the differences in tree growth were many times greater among sites and silvicultural treatments than among genetically different seedlots.

Density has been the most widely studied wood property. Cown and Ball (2001) examined the effect of site and genetic family on density at breast height in the 1975 diallel trials. Data from this paper is summarised in Table 6 - Table 8. The difference between earlywood and latewood density stands out as an important source of variation in density (Table 8). The variation in both

earlywood and latewood density as a result of either site or genetics is much smaller (Table 6 and Table 7). The latewood percentage within a ring is also an important source of variation in density (Table 9). The increased latewood percentage in rings 11+ from the pith compared with rings 1-10 from pith is likely to be due to distance from the crown. The height of pruning maybe contributing to the larger range in rings 11+ from the pith. The trees at Taringatura have a less severe pruning than those in Woodhill. There is also likely to be an environmental reason for differences since a South Island site has the minimum value and a North Island site has the maximum value. This indicates that the environmental factors that favour latewood formation versus earlywood formation need to be investigated.

Another source of wood property variation is a result of stem form. The data presented in Table 10 have been extracted from two studies (Grace, Booker, and Pont, unpublished data) that are attempting to understand the influence of tree and crown growth on wood properties. In each study a nominally straight and a leaning tree from a known clone have been examined. Density and other wood properties have been assessed on a ring-by ring basis at several heights in the tree and several directions around the stem. The maximum within-ring variation in density was calculated for each ring and each height and then the mean variation calculated for a tree. Comparing the numbers in Table 10 with those in Table 6 - Table 8 indicates stem form has a major impact on within-tree variation in density. It is probably more important than site or genetics. Consequently it is suggested that the influence of stem form on wood properties urgently requires more research.

Table 6. Variation in density with site, averaged across 10 families in 1975 “850” diallel trials. (Numbers from Cown and Ball (2001). Earlywood /latewood boundary set at 400 kg/m³).

| Variable | average density | maximum difference between sites | Sites with minimum and maximum average density |
|---|------------------------|----------------------------------|--|
| Earlywood density in rings 1-10 from pith | 336 kg m ⁻³ | 42 kg m ⁻³ | Minimum: Taringatura Maximum: Woodhill |
| Earlywood density in rings 11+ from pith | 361 kg m ⁻³ | 38 kg m ⁻³ | Minimum: Taringatura Maximum: Woodhill |
| Latewood density in rings 1-10 from pith | 558 kg m ⁻³ | 31 kg m ⁻³ | Minimum: Mawhera Maximum: Golden Downs |
| Latewood density in rings 11+ from pith | 573 kg m ⁻³ | 69 kg m ⁻³ | Minimum: Mawhera Maximum: Golden Downs |

Table 7. Variation in density with family, averaged across sites in 1975 “850” diallel trials. (Numbers from Cown and Ball (2001). Earlywood /latewood boundary set at 400 kg/m³).

| Variable | average density | Maximum Difference between families |
|---|------------------------|-------------------------------------|
| Earlywood density in rings 1-10 from pith | 335 kg m ⁻³ | 40 kg m ⁻³ |
| Earlywood density in rings 11+ from pith | 360 kg m ⁻³ | 33 kg m ⁻³ |
| Latewood density in rings 1-10 from pith | 558 kg m ⁻³ | 34 kg m ⁻³ |
| Latewood density in rings 11+ from pith | 573 kg m ⁻³ | 38 kg m ⁻³ |

Table 8. Difference between earlywood and latewood density with site, averaged across families in 1975 “850” diallel trials. (Numbers from Cown and Ball (2001). Earlywood /latewood boundary set at 400 kg/m³).

| Variable | average difference between earlywood and latewood density | range of variation in average difference | Sites with minimum and maximum difference between earlywood and latewood density |
|---|---|--|--|
| Difference between earlywood and latewood densities in rings 1-10 from pith | 222 kg m ⁻³ | 42 kg m ⁻³ | Minimum: Woodhill Maximum: Golden Downs |
| Difference between early and latewood densities in rings 11+ from pith | 212 kg m ⁻³ | 22 kg m ⁻³ | Minimum: Eyrewell Maximum: Awahohonu |

Table 9. Variation in latewood percentage with site, averaged across 10 families in 1975 “850” diallel trials. (Numbers from Cown and Ball (2001). Earlywood /latewood boundary set at 400 kg/m³).

| Variable | average percentage | maximum difference | Site with minimum and maximum Latewood percentage |
|---------------------------------------|--------------------|--------------------|---|
| % latewood in rings 1 to 10 from pith | 7% | 6% | Minimum: Mawhera Maximum: Woodhill |
| % latewood in rings 11 + from pith | 20% | 39% | Minimum: Taringatura Maximum: Woodhill |

Table 10. Variation in basic density with stem shape (Grace, Booker and Pont, unpublished data)

| Clone | Tree Form | Tree | Mean variation in density within a ring (kg m ⁻³) | Minimum variation in density within a ring (kg m ⁻³) | maximum variation in density within a ring (kg m ⁻³) |
|-------|--------------------|--------------------------------|---|--|--|
| 1 | Nominally Straight | Tree 102 | 22.6 | 0.8 | 73.7 |
| 1 | Bent | Tree 103, levels 1-4 below 2 m | 72.8 | 0.4 | 244.0 |
| 1 | Bent | Tree103 above 2 m | 40.4 | 0.02 | 214.6 |
| 2 | Nominally Straight | Tree 112 | 14.8 | 0.3 | 47.6 |
| 2 | Bent | Tree113 | 71.7 | 0.3 | 219.9 |

Note: samples recorded as being resinous have been excluded.

Relationships between Cell Characteristics and Performance Characteristics

Relationship between Longitudinal modulus of elasticity, density and microfibril angle

Modulus of elasticity depends on the microfibril angle in the S_2 layer of the cell wall and density. Persson (2000) assumed that a unique relationship exists between these three variables, then developed an approximate simplified relationship.

Evans and Ilic (2001) have utilised the relationship between these three variables to enable modulus of elasticity to be predicted within the SilviScan system. This relationship, is considered to be robust across a wide range of species (Downes, pers comm.).

Microfibril angle and modulus of elasticity

Mott *et al* (2002) have developed a method that allows the mechanical properties of individual fibres to be measured. Using this method, they have been able to map the within tree variation of microfibril angle and modulus of elasticity for earlywood and latewood fibres for one 48-year-old loblolly pine from a conventional plantation. These maps indicate that the wood properties examined vary in a complex manner with respect to height in the tree and growth ring from the pith. In particular, the zone of poorer wood properties nearest the pith is not cylindrical. I suspect that some of the pattern may be due to stand silviculture, but unfortunately these details were not presented in the paper.

Treacy *et al* (2000) measured microfibril angle, modulus of elasticity and modulus of rupture on 32 Sitka spruce trees in Ireland. Eight trees with dbh close to the plot average were selected from each of 4 plots containing separate provenances. They found that microfibril angle differed significantly between provenances, differed significantly between different growth rings and that there was a significant interaction between ring and provenance with respect to microfibril angle. They also found that the relationship between microfibril angle and modulus of elasticity did not vary with provenance, indicating that modulus of elasticity is controlled, to a large extent, by microfibril angle. This result is quite interesting in the light of the fact that Telewski (1989) suggests that tree flexure alters microfibril angle. One might have expected similar microfibril angles for all provenances. The other factor that has been mentioned as controlling microfibril angle is growth rate itself (Megraw, 1985). The provenance with the highest growth rate had the highest microfibril angle in each ring examined, but the slowest growing provenance did not have the lowest microfibril angle, so the link between growth and microfibril angle is not clearcut for these data.

Cave (1968) measured cell wall stiffness itself and found a good relationship with microfibril angle. At low microfibril angles (below about 20 degrees) the lignin-hemicellulose matrix has almost no influence on axial stiffness, with axial stiffness being determined by the cellulose microfibrils in the S_2 layer. When microfibril angle exceeds about 40 degrees matrix alone determines axial stiffness

The modulus of elasticity (measured in bending parallel to the grain) for stem sections from 2-year-old fast grown radiata pine was found to be positively correlated with both microfibril angle and lignin content. An equation including these two variables explained 81.1% of the variation in modulus of elasticity (Downes *et al*, 1993). The positive correlation between microfibril angle and modulus of elasticity is opposite to current theory. This may result from the fact that the measured microfibril angles varied from 35° to 52°, and are hence of a size where the axial stiffness of fibres is mainly influenced by the properties of the cell matrix.

Characteristics Affecting End-use

Internal checking

Internal checking, a common feature in eucalypts, is becoming more prevalent in radiata pine.

Booker (1994) considers that both internal checking and collapse are caused by water stress within the tree. Internal checking will occur when differential stresses are created within the tree. For example: when water filled fibres contract due to water stress and the adjacent fibres contract less due to being either stronger or air-filled. Hence internal checking is influenced by both the amount of stress and the structure of the cells. These theoretical conclusions are supported by evidence presented by Ilic (1999). He found few internal checks in *Eucalyptus regnans* boards cut from the outer heartwood with basic densities above 520 kg m^{-3} . Below 520 kg m^{-3} , the number of checks was highly variable and not correlated with density.

Checks are known to form in wood due to high levels of differential shrinkage in local regions, and it is highly likely that they will be initiated in stress concentration zones of poorly lignified vessel and ray cell wall contact (summarised by Ilic, 1999)

Resin Pockets

Resin pockets are important for appearance grades not structural grades. Two factors that may contribute to the formation of resin pockets are strong winds and water stress (Kininmoth and Whiteside 1991). Booker (pers comm) has suggested a possible mechanism. He suggests that swaying of the tree coupled with the decrease in stem radius due to water tension.

Warp

A major disadvantage of timber for the building industry is that the timber can warp (i.e. move once it has been cut to size). Warp (bow, crook, twist) is caused by differential shrinkage in the longitudinal, radial and tangential directions when water is removed from the wood cells. While drying methods can affect the amount of warp, it is not possible to eliminate it completely (Johansson and Kliger, 2002). Therefore it is important to understand the underlying mechanisms that lead to warp. There are 4 components to warp:

- bow – the curvature along the length of a board, measured between horizontal and face (wide surface) of board
- crook – the curvature along the length of a board, measured between horizontal and edge (narrow longitudinal surface) of board
- cup – the concave curvature across the face, widest distance between horizontal and face of the board
- twist – the spiral distortion along the length of a piece of timber.

Perstorper et al (1995b) measured warp on timber from fast- grown Norway spruce stands in Sweden. They found:

- More twist in timber cut from near the pith compared to timber cut further from the pith. This is in agreement with other studies.
- Larger crook near the base of trees and nearer to the pith. This is in agreement with other studies.
- No consistent radial trend in bow. A variety of trends have been observed in other studies.

- That only the correlation between twist and distance from the pith exceeded 0.50 (but was less than 0.60).
- That the correlations between twist, crook and bow and ring width, density, knot area ratio, grain angle and compression wood were all less than 0.40.

Johansson and Kliger (2002) measured warp and several possible explanatory variables on 190 Norway Spruce boards ($45 \times 95 \times 2500$ mm). They found that:

- Statistically grain angle and annual ring curvature explained 71% of variation in twist.
- It was not possible to derive robust statistical models to predict bow and crook.
- There was a relationship between compression wood distribution and bow and crook.

Johansson and Kliger (2002) suggest two causes of bow and crook are:

- residual stresses in the timber (due to growth stress)
- uneven longitudinal shrinkage (due to wood cells within the piece of timber having different properties).

Johansson and Kliger (2002) suggest that a non-destructive technique that would identify the 3-d distribution of compression wood would be really helpful.

Mishiro *et al* (2000) examined the effect of single knots in a radiata pine board on bow and crook. They projected the position and shape of the knot onto a plane perpendicular to the axis of the board. For some projected shapes, crook was influenced by the offset between the board centroid and knot centroid. While for other projected shapes, the offset had no impact. The same applied for bow.

Perstorper *et al* (2001) examined the wood properties of $13 \times 13 \times 200$ specimens from Norway Spruce. They found that longitudinal shrinkage was almost 100% larger in specimens with knots with a knot area ratio (percentage of a cross section that a projection of the knot covers) of over 33% compared to specimens with no knots. Longitudinal shrinkage was also higher in specimens with compression wood. In contrast in specimens with no knots, radial and tangential shrinkage decreased with increasing compression wood.

Current Models

A model can be thought of a series of mathematical equations that define the relationship between a set of inputs and a set of outputs.

Models can be used in two different ways:

- to explore the consequences of different initial conditions (a research question)
- to predict the output that will be obtained from a set of initial conditions (a management question)

Regardless of the use, models with empirical components should not be used outside the range of conditions used in developing the model. Hence models are likely to have a finite life-time and there is a need to be continually collecting good quality data relevant to current forestry practices.

Model of cambial activity

The model TreeRing (Version 3) (Fritts *et al*, 1999) predicts the development of wood cells on a daily time step. This model incorporates:

- tree water balance – water deficits can affect the enlargement of cells in the cambium and cell division can be reduced or stopped
- tree photosynthesis
- leaf growth
- root growth
- stem growth
- cell division
- cell enlargement – the exact mechanisms controlling cell enlargement and its variation over time are not known
- cell maturation (cell wall thickening)

The authors acknowledge that this model is still in the process of development. In particular the model does not consider branch and crown development and changes in photosynthetic capacity from one year to the next. Neither does it consider the deposition of lignin in cells.

Deleuze and Houllier (1998) also constructed a model of xylem development. In this model it was assumed that:

- cell division was a function of temperature
- cell enlargement was a function of water availability
- cell wall thickening was a function of photosynthate availability

Model of within-tree variation in wood density

Using previously collected data on wood density from 40 trees in two different stands of radiata pine, Tian *et al* (1995b) developed a mathematical equation to predict average within-tree density as a function of ring number from the pith and height within the tree. While this equation describes the pattern of within tree variation in density, it has several downsides. Firstly it is derived from a limited number of trees, and secondly it implies that wood density in a given ring from the pith will be independent of silvicultural treatment.

Model of within-tree variation in spiral grain

Tian *et al* (1995a) developed a mathematical equation to predict spiral grain in radiata pine as a function of ring number from the pith and height within the tree. Again this equation was derived from a limited number of trees from a few sites; and has the same downsides as the above model for wood density.

Modelling the influence of branches on performance

As stated previously, knots in wood lead to reduced strength and stiffness due to the arrangement of branch fibres.

Philips *et al* (1981) used equations that predict the laminar flow around an elliptical object, as a model of the grain deviation around a branch in the longitudinal-tangential plane. Zandsberg and Smith (1988) incorporated this approach in a 2-d finite element model that predicted the behaviour of a piece of wood containing a branch when placed under tension. The model was used to simulate the failure of an actual specimen.

Masuda and Honda (1994) used what appears to be a 2-d finite element model to investigate the influence of knots on the bending of lumber. Grain-flow analogy was used in generating the mesh. A 3-point and a 4-point bending test was simulated with lumber containing either an edge knot (1/2 the knot within the board) or a central knot whose diameter was 2, 3 or 4 cm in a piece of lumber 9 cm × 9 cm × 207 cm.

Knots reduced the MOE compared with a clear piece of timber. Edge knots reduced MOE more than central knots. Larger knots reduced MOE more than smaller knots. The reduction in MOE with the 3-point bending test was almost twice that with the 4-point bending test. The nearer the knot is to the central loading point, the greater the reduction in MOE.

General models of performance

Pellicane and Franco (1994) used a 3-d finite element model to investigate failure of wood poles. The flow-grain analogy was used to develop empirical relationships to represent the localised grain deviation surrounding a knot. This approach was considered reasonable as no methods had been developed to incorporate the flow-grain analogy into a 3-d model and the computer time would have been prohibitive. Model results were compared the results from testing 9 poles to failure. The failure load was predicted to better than 17% on an individual pole. The height of failure was well predicted for 6 of the 9 poles.

Zink et al (1995) used a stress transformation approach to predict the failure of wood when loaded in uniaxial tension at any angle with respect to the grain. It appears that Pellicane and Franco (1994) used this approach in modelling the effects of grain deviation due to knots.

Modelling finger-joints

A finite element model was used to investigate the stresses in finger-joints. The ratio of numerical to nominal stress increased from 1.0 to 1.83 as the ratio of longitudinal MOE for the two joined pieces increased from 1.0 to 3.0 (Pellicane, 1984). This illustrates the importance of knowing the properties of the pieces before glueing.

Modelling tree response to lean

Fourcaud and Lac (1996) developed a computer simulation model that predicts how a tree will grow and correct for stem lean. This research was perceived to be important for understanding how tree growth will affect the internal properties of the stem. The inputs for the model are tree architecture parameters and wood properties (longitudinal MOE and growth stresses).

In order to determine the suitability of this model to simulate the growth of radiata pine, data have been collected from 4 radiata pine trees, a “nominally straight” and a “severely bent” tree from each of two clones.

One test simulation (using the model of Fourcaud and Lac) compared the within-stem stresses from assuming a constant pith-bark longitudinal modulus of elasticity (MOE_L) test versus an increase in MOE_L from pith to bark. The second (more realistic assumption) resulted in less stress within the stem (Fourcaud, Pont and Grace, unpublished result). Another simulation indicated that growth stresses have a major role to play in the ability of a tree to respond to lean. This suggests that measurement of growth stresses for families within the breeding population will be important.

Modelling the influence of spiral grain

Skatter and Archer (200x) have simulated the effect of spiral grain on within-stem stresses. They compared two assumptions, constant spiral grain from pith to bark and a radially varying spiral grain (changing linearly from a negative value at the pith to a positive value at the bark). The second assumption resulted in lower shear stress in the longitudinal-tangential fibre direction and lower stress in the tangential fibre direction.

Material properties that affect end-product performance

Wood is usually considered as a linear elastic orthotropic material (i.e. having different properties in the longitudinal, radial and tangential directions) below limit of proportionality. When wood is subjected to loading above limit of proportionality, irreversible changes in the material take place and the force-displacement relation becomes non-linear.

Due to the orthotropic nature of wood, there are at least 19 material properties that influence the performance of wood, including:

- 3 moduli of elasticity (a measure of stiffness)
- 3 moduli of shear
- 3 poisson ratios which relate the stress in one direction to the strain in another direction
- 3 shrinkage coefficients
- 7 mechano-sorption

Stiffness is greatest in longitudinal direction. Radial stiffness is about 1.5 times higher than stiffness in tangential direction. It is considered that the ray cells contribute to the increased increased stiffness in radial direction.

Shrinkage is least in the longitudinal direction. Radial shrinkage is approximately 10 times longitudinal shrinkage and tangential shrinkage is approximately twice radial shrinkage (Gu *et al* 2001). One of the main factors determining shrinkage is considered to be the arrangement and orientation of the microfibrils within the cell wall. However the exact reasons for the differential shrinkage in the radial and tangential directions is unknown and several different hypotheses have been proposed (Gu *et al*, 2001). Gu *et al* (2001) showed that the microfibril angle varied between the radial wall and the tangential wall and considers this contributes to the differential shrinkage.

Fibre saturation point is defined as the point at which the cell wall ceases to absorb additional water as the moisture content increases, Below fibre saturation point wood will shrink or swell with changes in moisture content.

Model of wood performance at the cell level

Persson (2000) developed a finite-element model that allowed the effect of cell structure on performance to be assessed. A technique called “homogenisation” was used to generate a homogeneous material that had equivalent properties to a cell, which has a complex periodic microstructure.

The main points to emerge from these simulations are that mechanical properties are highly dependent on the microfibril angle in the S₂ layer and that some mechanical properties improve with increasing microfibril angle, whereas other mechanical properties improve with decreasing microfibril angle. In particular:

- Microfibril angle and cell wall thickness have a large influence on longitudinal MOE.
- Longitudinal MOE decreases approx. sigmoidally with increasing microfibril angle.
- Longitudinal MOE is higher in latewood compared to earlywood (i.e. is influenced by cell wall thickness).
- Microfibril angle and cell wall thickness have very little influence on either radial or tangential MOE.
- Microfibril angle has a large influence on only one of the 3 shear moduli - the longitudinal-tangential modulus.
- Longitudinal-tangential shear modulus increases approx. sigmoidally with increasing microfibril angle.
- The longitudinal-tangential shear modulus is lower in the latewood cells (i.e. is influenced by cell wall thickness).
- All 3 poisson ratios are influenced by microfibril angle. ν_{lt} and ν_{lr} increase with increasing microfibril angle whereas ν_{rt} decreases with increasing microfibril angle.
- The longitudinal and tangential shrinkage coefficients are affected by microfibril angle. Longitudinal shrinkage increases with increasing microfibril angle, whereas tangential shrinkage decreases with increasing microfibril angle.

Persson (2000) also developed a homogenised structure for clearwood. These simulations indicated that microfibril angle and density altered material properties in different ways:

- Longitudinal MOE decreased with increasing microfibril angle
- For a given microfibril angle, longitudinal MOE increased with increasing density. The changes were larger at low microfibril angles.
- Radial and tangential MOE increased with increasing microfibril angle.
- For a given microfibril angle, both radial and tangential MOE increased with increasing density.
- All 3 shear moduli increase with increasing microfibril angle.
- For a given microfibril angle, all 3 shear moduli increase with increasing density.
- Poisson ratio ν_{lr} increases with increasing microfibril angle BUT decreases with increasing density
- Poisson ratio ν_{lt} increases with increasing microfibril angle and increasing density
- Poisson ratio ν_{rt} decreases with increasing microfibril angle and increases with increasing density
- Longitudinal shrinkage coefficient is minimum at a microfibril angle of approx. 20 degrees regardless of density and properties of chemical constituents.
- Radial shrinkage coefficient decreases with increasing microfibril angle, BUT is higher for higher density.
- Tangential shrinkage coefficient decreases with increasing microfibril angle but varies little with changes in density.

Persson (2000) used a structural model consisting of irregular hexagonal cells to determine stiffness and shrinkage properties along a radius from pith to bark at 10 mm increments. Different values of longitudinal MOE and density were used for different growth rings, and microfibril angle was calculated from MOE and density. These simulations showed pith to bark variation in material properties.

The following properties increased with ring number from the pith:

- longitudinal MOE
- poisson ratio ν_{rt}
- radial shrinkage coefficient
- tangential shrinkage coefficient

The following properties decrease with ring number from the pith:

- longitudinal – radial shear modulus
- poisson ratio ν_{lr}
- poisson ratio ν_{lt}

The following variables had a minimum value before ring 20 from the pith:

- radial MOE
- tangential MOE
- longitudinal-tangential shear modulus
- radial-tangential shear modulus
- longitudinal shrinkage coefficient

Again these results point to a tree being an exceedingly complex structure and suggest that attempts to alter (“improve”) one property of a tree may lead to poorer performance of some other property.

Modelling moisture-related distortions in sawn timber

The shape of a piece of timber after drying results from an interaction between the sawing pattern and the variation in wood properties within the log. For example, a board with very different wood properties on opposite sides would move more than a board with similar properties throughout. Therefore a detailed understanding of the pattern of wood properties within a tree is required to understand the reasons why a piece of timber will warp.

Ormarsson (1999) developed a finite-element model to investigate moisture-related distortion in boards. Within a board properties were assumed uniform. Simulations using this model indicated that:

- Effective modulus of elasticity in tension, flatwise bending and edgewise bending:
 - decreased with increasing spiral grain
 - were, to a lesser extent, influenced by distance from pith
- Effective modulus of elasticity in tension and flatwise bending:
 - increased with increasing ratio between E_l and E_t - the increase was larger at low spiral grain angles and decreased with increasing spiral grain.
 - increased with increasing shear modulus G_{lt} .
- Effective shear modulus in torsion is only slightly affected by spiral grain and distance from pith.

Starting with a nominal set of material properties for a board with the pith in centre of one side of the board, each parameter was reduced in turn by 50%.

- The simulations indicated that of the stiffness parameters:
 - E_r , E_t , G_{lr} , and G_{lt} have the most influence on twist development. Twist increases with decrease in E_t and decreases with decrease in E_r
 - E_r , E_t , and G_{rt} have most significant influence on development of cup. Cup increases with decrease in E_t and decreases with decrease in E_r
 - E_r , E_t , and G_{lt} have most significant influence on development of bow. Bow decreases with decrease in E_t and increases with decrease in E_r

- Altering the shrinkage parameters in either the tangential and radial directions had more influence on the development of twist and cup than altering the shrinkage parameter in the longitudinal direction. All 3 shrinkage parameters will influence bow.
- Of the mechano-sorption parameters, altering m_t and m_r had the most influence on the development of twist bow and cup.

These simulations are an important indication that longitudinal modulus of elasticity has a minimal impact on distortion and concur with a pilot study with radiata pine (Gaunt, unpublished results). Radial and tangential properties of the cell appear to be more important.

Climate Variability

In Europe, scientists have observed increased growth rates of forest trees over time and suggest that this is the result of “climate change”. It is considered that it would be difficult to detect such a change for radiata pine in New Zealand because of the short rotation length and the fact that tree breed and silvicultural practice have changed concurrently. However it is conceivable that “climate change” is having an impact on radiata pine growth and wood properties as there have been long-term fluctuations in climate as indicated by the following description of climatic variability from the NIWA website (www.niwa.co.nz).

One of the most obvious causes of climatic variability within New Zealand is the “El Niño – Southern Oscillation (ESNO) phenomenon”. During El Niño events, New Zealand tends to experience stronger and more frequent winds from the west in the summer, leading to drought in east coast areas and more rain in the west. In spring and autumn, southwesterlies tend to be stronger or more frequent. In winter the wind tends to be more from the south bringing colder conditions. During La Niña events, New Zealand tends to experience more northeasterly winds which bring moist rainy conditions to northeast parts of the North Island. Although El Niño has an important influence, it accounts for less than 25% of the year to year variance in seasonal rainfall at most New Zealand measurement sites.

Within New Zealand distinct regional changes in precipitation have occurred. For the period 1930-1950, summer rainfall was higher in North Canterbury and lower in north and west of the South Island. Between 1951-1975, there was increased east, and north-east airflow over New Zealand which brought increased rainfall to the North of the North Island, and rainfall decreases to the south-east of the South Island especially in summer. The period between 1976 and 1994, has been dominated by several strong El Niño events with rainfall decreases in the north of the North Island and increases in much of the South Island except the east.

It is considered that there has been a long-lasting “shift” in New Zealand’s climate since around 1977 which is characterised by more persistent westerlies.

MODELLING STRATEGY - PART 2: FUTURE RESEARCH

Larson (1962) states “ a ... logical approach would be to relate wood quality to growth and development of the crown, for it can be shown that external factors of climate and environment exert their influence directly on the crown and only indirectly on the growth and quality of wood”. This statement still makes sense over 40 years later, but I am unaware of any integrated model predicting tree growth and wood formation that has been developed for forest management.

Since it is the properties of and the variation of properties within, rather than the volume of, the stem that influences its end-use, it makes sense to develop models to predict the within-stem distribution of wood properties as a function of tree development (in particular crown structure and stem form). Within-stem distributions of wood properties should be predicted in sufficient detail to be able link with processing models. This would be a logical extension of the current Stand Growth Modelling Cooperative Research Programme that predicts stem volume growth and crown development and should complement the research of the Wood Quality Initiative.

Developing such models for radiata pine would be a long-term project and will first require data on both crown development and wood properties from carefully selected trees whose history is known. Ultimately trees should be sampled to cover a matrix of site, silviculture and genetics.

It is considered that the following questions should be addressed first, and the answers will contribute to the development of an appropriate data collection strategy and model.

- The effect of taking wood increment cores on the tree growth.
Dr. R. Booker has shown that fluid transport does not occur in the vicinity of an increment core, but the effect on growth is not known. As part of a FRST funded study, increment cores were collected from one seedlot (GF7) in the:
 - 1984 Genetic Gain Trial, Kaingaroa (RO1897)
 - 1987 Silviculture/Breed Trial, Kaingaroa (FR9)
 - 1987 Silviculture/Breed Trial, Glengarry (FR10)
 - 1990 Silviculture/Breed Trial, Tarawera (FR 121/6)We need to confirm that the growth of this seedlot was not unduly affected compared with other seedlots. This is particularly important as the SGMC trials are being used to develop growth models. If growth has been affected then increment cores should not be used in other trials.
- The possibility of using branch wood properties to predict stem wood properties.
If this were feasible it would be an improvement on increment cores as it would not leave a hole in the stem. It is proposed to address this question in the 2002-3 pilot study.
- The influence of branch size on the variability of wood properties within an internode.
Studies, quoted by Nicholls (1984), indicated that a branch can influence wood properties for a certain depth below the branch. I have observed patches of different coloured wood below a branch cluster in Golden Downs. The darker patches, which were below the branches, were probably “compression wood” This patchy distribution will contribute to variability of wood properties in the stem. It is proposed to address this question in the 2002-3 pilot study.

- The influence of crown structure on within-stem wood property distributions.
The pilot study proposed for 2002-3 proposes to address the question of whether between-tree variability in wood properties can be predicted from crown structure on nominally straight trees from various seedlots. One interesting concept is whether a multinodal tree will be expanding in height for a greater portion of the growing season and if so would this influence the ratio of earlywood to latewood.
- The influence of stem form on within-ring variation in wood properties.
Two previous unpublished studies by Grace *et al.* have investigated the variability in wood properties with stem form. These data will be used to examine the variability in wood properties with stem form to determine appropriate future sampling strategies.

It is proposed that following question be addressed in 2003-4.

- The relative importance of silviculture and genetics in influencing within-stem distribution in wood properties, and whether crown form can explain these differences.
While it is proposed to keep all SGMC trials to age 30 years, it is suggested that one of the 1987 trials is sacrificed to investigate this important question. The alternative would be to sample trees from one of the 1975 final crop stocking trials to investigate the influence of low stockings on wood properties, and one of the 1978 genetic gain trials to investigate the influence of genotype on wood properties. This second option is less satisfactory for two reasons. Firstly none of the 1975 and 1978 trials are very close together so site variability could affect the results. Secondly the sampling would be more costly due to the older age of the trees. Such a study would also help in determining appropriate data collection strategies.

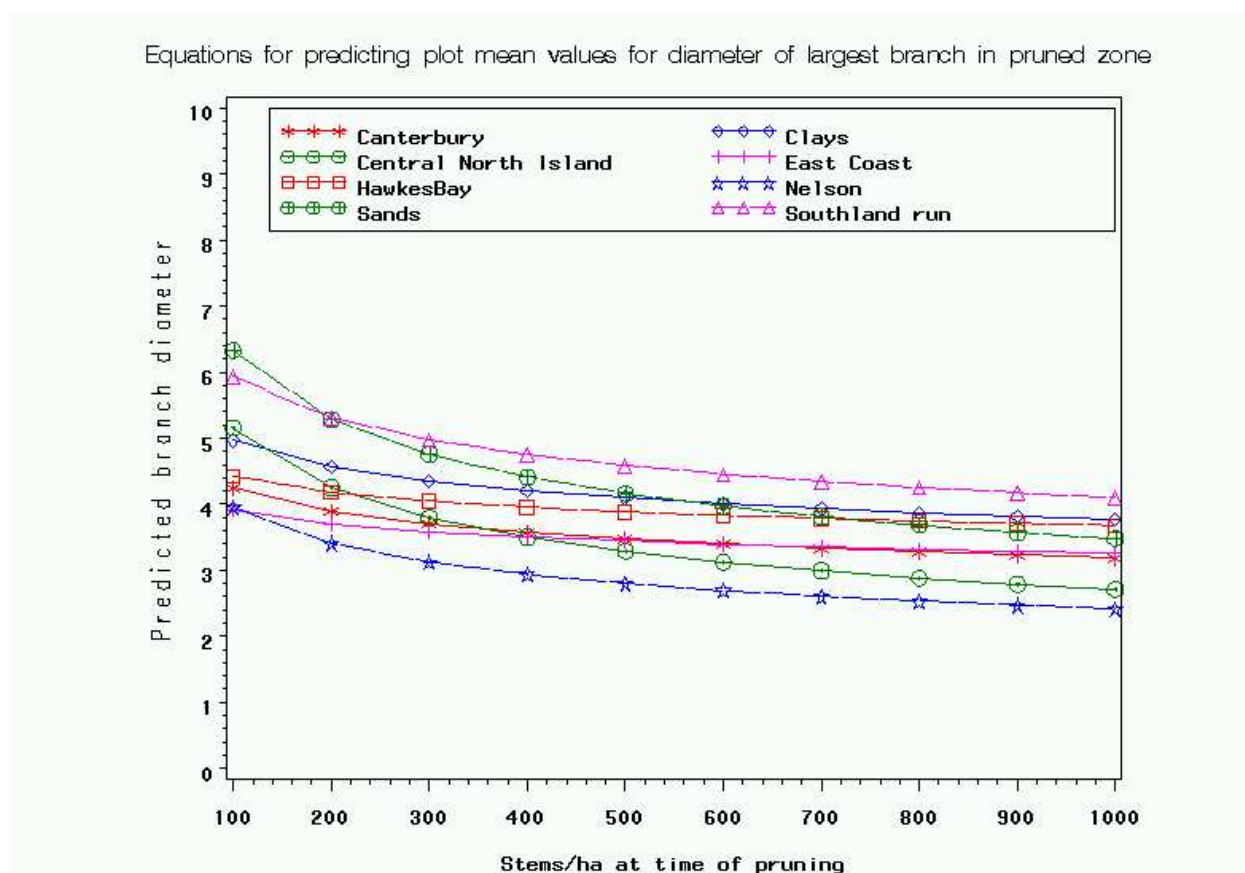
Of particular interest is influence of crown structure on wood properties at low stockings. The green crown length is likely to be longer, and hence a greater proportion of the stem is within the crown. Branch diameters are predicted to increase most rapidly with decreasing stocking when stocking is below approx. 300 stems/ha. Figure 4 shows how the diameter of the largest branch in the pruned zone is predicted to change with stocking. Some possible reasons for the increases are:

- the branch grows more in length to occupy the increased growing space
- the branch carries more foliage
- the branch carries more stem cones
- the branch needs to increase in diameter in response to more wind movement at lower stockings.

In reality it is probably a combination of all four. If increased foliage was the main cause, and as crown influences wood properties, it is conceivable that one might see more variation in wood properties with stocking when the stocking is approx. 300 stems/ha.

The above studies would allow us to develop a robust longer-term strategy to cover the range of sites, silviculture and genetics within New Zealand.

Figure 4. Equations predicting plot mean values for the diameter of the largest branch in the pruned zone.



Longer term we need to be able to link any models developed with inventory assessment of stem form. Hence it is considered that we need more information on how stem form changes through time and the percentages of non-straight trees with site.

- Monitoring change in stem form

Current stem form is not considered to be a good indicator of within-stem wood properties as stems grow to hide any lean. However it would be useful if inventory assessment of stem form could be used in predicting within-stem distributions of wood properties. By measuring tree DBH, we are assuming that the tree is circular in cross-section. This approach is less-suited for modelling wood properties since elliptical stem form implies variation in wood properties around the stem. Repeated measurement of stem form, either two diameters (at right angle to each other) or PhotoMARVL on selected trees would provide data for developing and testing models to predict changes in stem form with time.

The ultimate “vision” is:

- to be able assess stem form and branching characteristics, (subjectively or objectively using PhotoMARVL),
- to obtain a measure of stem wood properties,
- to then be able to generate a map of within-tree distribution of wood properties that has sufficient resolution to be able to determine the most appropriate way to utilise the tree.

REFERENCES

- Amarasekara, H.; Denne, M.P. 2002: Effects of crown size on wood characteristics of Corsican pine in relation to definitions of juvenile wood, crown formed wood and core wood. *Forestry*, 75: 51-61.
- Antonova, G.F.; Stasova, V.V. 1993: Effects of environmental factors on wood formation in Scots pine stems. *Trees, Structure and Function* 7(4): 214-219.
- Antonova, G.F.; Stasova, V.V. 1997: Effects of environmental factors on wood formation in larch (*Larix sibirica* LDb.) stems. *Trees, Structure and Function* 11(8) 462-468.
- Archer, R.R. 1987: Growth stresses and strains in trees. Springer-Verlag, Berlin, Germany. 240 pp.
- Bamber, R.K. 1979: The origin of growth stresses. *Forpride Digest* 8: 75-79, 96.
- Bamber, R.K. 1987: The origin of growth stresses: A rebuttal. *IAWA Bulletin* 8: 8-84.
- Barnett, J.R. 1976: Rings of collapsed cells in *Pinus radiata* stemwood from lysimeter-grown trees subjected to drought. *New Zealand Journal of Forestry Science*: 461-5.
- Booker, R.E. 1994: Internal checking and collapse – Which comes first? Proceedings of 4th IUFRO Wood Drying Conference, 9th-13th August 1994. New Zealand Forest Research Institute, Rotorua.
- Boyd, J.D. 1972: Tree Growth stresses – Part V: Evidence of an origin in differentiation and lignification. *Wood Science and Technology* 6:251-262.
- 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.
- Boyd, J.D. 1977: Relationship between fibre morphology and shrinkage of wood. *Wood science and Technology* 11: 3-22.
- Boyd, J.D. 1980: Relationships between fibre morphology, growth strains and physical properties of wood. *Australian Forest Research* 10: 337-360.
- Boyd, 1985. The key factor in growth stress generation in trees. Lignification or crystallisation? *IAWA Bulletin* 6: 139-150.
- Brüchert, F.; Becker, G.; Speck, T. 2000: The mechanics of Norway spruce (*Picea abies* (L.) Karst): mechanical properties of standing trees from different thinning regimes. *Forest Ecology and Management* 135: 45-62.
- Burdon, R.D. 1975: Compression wood in *Pinus radiata* clones on four different sites. *New Zealand Journal of Forestry Science* 5: 152-164.
- Carson, S.D.; Garcia, O.; Hayes, J.D. 1999a: Realized gain and prediction of yield with genetically improved *Pinus radiata* in New Zealand. *Forest Science* 45(2): 186-200

- Carson, S.D.; Kimberely, M.O.; Hayes, J.D.; Carson, M.J. 1999b: The effect of silviculture on genetic gain in growth of *Pinus radiata* at one-third rotation. Canadian Journal of Forest Research 29:1979-1984.
- Cave, I.D. 1968: The anisotropic elasticity of the plant cell wall. Wood Science and Technology 2(4): 268-278.
- Cown, D.J. 1973: Effects of severe thinning and pruning treatments on the intrinsic wood properties of young radiata pine. New Zealand Journal of Forest Science 3: 379-389.
- Cown, D.J. 1974: Comparison of the effects of two thinning regimes on some wood properties in radiata pine. New Zealand Journal of Forestry Science 4: 540-551.
- Cown, D.J.; Ball, R.D. 2001: Wood densitometry of 10 *Pinus radiata* families at seven contrasting sites: influence of tree age, site and genotype. New Zealand Journal of Forestry Science 31:88-100.
- Cown, D.J.; McConchie, D.L. 1983: Radiata pine wood properties survey (1977 – 1982). Forest Research Institute, New Zealand Forest Service, FRI Bulletin No. 50, 42 p.
- Dean, T.J.; Roberts, S.D.; Gilmore, D.W.; Maguire, D.A.; Long, J.N.; O'Hara, K.L.; Seymour, R.S. 2002: An evaluation of the uniform stress hypothesis based on stem geometry in selected North American conifers.
- Deleuze, C.; Houllier, F. 1998: A simple process-based xylem growth model for describing wood microdensitometric profiles. Journal of Theoretical Biology, 193: 99-113.
- Denne, M.P. 1988: Definition of latewood according to Mork (1928). IAWA Bulletin, 10: 59-62.
- Domec, J.C.; Gartner, B.L. 2002: Age- and position-related changes in hydraulic versus mechanical dysfunction of xylem: interranging the design criteria for Douglas-fir wood structure. Tree Physiology 22: 91-104.
- Donaldson, L.A. 1985: Within- and between-tree variation in lignin concentration in the tracheid cell wall of *Pinus radiata*. New Zealand Journal of Forestry Science 15: 361-369.
- Donaldson, L.A. 1986: Between-tree variation in lignin concentration in *Pinus radiata* tracheids with growth rate, stem eccentricity, site and silvicultural treatment. New Zealand Journal of Forestry Science 16: 118-123.
- Donaldson, L.A. 1991: Seasonal changes in lignin distribution during tracheid development in *Pinus radiata* D. Don. Wood Science and Technology 25: 15-24.
- Donaldson, L.A. 1993: Lignin distribution in wood from a progeny trial of genetically selected *Pinus radiata* D. Don. New Zealand Journal of Forestry Science 27: 391-395.
- Donaldson, L.A.; Croucher, M.; Uprichard, J.M. 1997: Clonal variation of wood chemistry variables in radiata pine (*Pinus radiata* D. Don) wood. Holzforschung 51: 537-542.
- Donaldson, L.A.; Grace, J.C.; Downes, G. 200x: Within tree variation in anatomical properties of compression wood in radiata pine (submitted for publication 2003).

Downes, G.; Beadle, C.; Worledge, D. 1999: Daily stem growth patterns in irrigated *Eucalyptus globulus* and *E. nitens* in relation to climate. *Trees* 14: 102-111.

Downes, G.M.; Beckers, E.P.J.; Turvey, N.D.; Porada, H. 1993: Strength and structure of stems from fast grown *Pinus radiata*. *Trees* 7: 131-136.

Downes, G.M.; Moore, G.A.; Turvey, N.D. 1994: Variations in response to induced stem bending in seedlings of *Pinus radiata*. *Trees* 8: 151-159.

Downes, G.M.; Ward, J.V.; Turvey, N.D. 1991: Lignin distribution across tracheid cell walls of poorly lignified wood from copper deficient *Pinus radiata* (D.Don). *Wood Science and Technology* 25: 7-14.

Duff, G.H.; Nolan, N.J. 1953: Growth and morphogenesis in Canadian forest species. I The controls of cambial and apical activity in *Pinus resinosa* Ait. *Canadian Journal of Botany* 31: 471-513.

Dunham, R.A.; Cameron, A.D. 2000: Crown, stem and wood properties of wind-damaged and undamaged Sitka spruce. *Forest Ecology and Management* 135: 73-81.

Evans, R. Downes, G. 2001: SilviScan – a tool for the rapid assessment of fibre properties in wood. Paper presented at 4th Wood Quality Workshop, Rotorua, New Zealand.

Evans, R.; Ilic, J.; 2001: Rapid prediction of wood stiffness from microfibril angle and density. *Forest Products Journal* 51(3): 53-57.

Fourcaud, T. and Lac, P. 1996: Mechanical analysis of the form and internal stresses of a growing tree by the finite element method. *Proc. Engineering design and analysis. ASME, Montpellier France, 1-4 July, 77 (5) 213-220.*

Fritts, H.C.; Shashkin, A.; Downes, G.M. 1999: A simulation model of conifer ring growth and cell structure. In: Wimmer, R.; Vetter, R.E. (ed). *Tree ring analysis: biological, methodological, and environmental aspects*. CABI Publishing, U.K. pp 3-32.

Gindl, W.; Grabner, M.; Wimmer, R. 2000: The influence of temperature on latewood lignin content in treeline Norway Spruce compared with maximum density and ring width. *Trees: Structure and Function*: 14(7): 409-414.

Grace, J. C. 200x: Links between science and forest management: As illustrated by a model of branch development. Submitted for publication 2001.

Grace, J.C.; Booker, R.E.; Pont, D. 2000: The variation in modulus of elasticity and specific modulus for one radiata pine clone. *Forest Research Output No. 31602 (Unpublished)*.

Grace, J.C.; Jarvis, P.G.; Norman, J.M. 1987: Modelling the interception of solar radiant energy in intensively managed stands. *New Zealand Journal of Forestry Science* 17(2/3): 193-209.

Gu, H.; Zink-Sharp, A.; Sell, J. 2001: Hypothesis on the role of the cell wall structure in differential transverse shrinkage of wood. *Holz als Roh- und Werkstoff* 59: 436-442.

Harrington, J.J. 2002: Hierarchical modelling of softwood hygro-elastic properties. Ph.D. Thesis, University of Canterbury, New Zealand.

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(1): 91-106.

Harris, J.M. 1991b: Formation of Wood and Bark. Chapter 3 In Kininmonth, J.A.; Whitehouse, L.J. (ed) *Properties and uses of New Zealand radiata pine Vol. 1 – Wood properties*. Ministry of Forestry, Forest Research Institute, New Zealand.

Harris, J.M.; Cown, D.J. 1991: Basic wood properties. Chapter 6 In Kininmonth, J.A.; Whitehouse, L.J. (ed) *Properties and uses of New Zealand radiata pine Vol. 1 – Wood properties*. Ministry of Forestry, Forest Research Institute.

Holbrook, N.F.; Putz, F.E. 1989: Influence of neighbours on stem form: Effects of lateral shade and prevention of sway on the allometry of *Liquidambar styraciflua* (Sweet gum). *American Journal of Botany* 76(12): 1740-1749.

Ilic, J. 1999: Shrinkage-related degrade and its association with some physical properties in *Eucalyptus regnans* F. Muell. *Wood Science and Technology* 33: 425-437.

Jacobs, M.R. 1945: The growth stresses of woody stems. *Bulletin Forestry Bureau of Australia*. No. 28. 67 pp.

James, R.N. (1990) Evolution of silvicultural practice towards wide spacing and heavy thinning in New Zealand. In: James, R.N. and Tarlton, G.L. (ed.) *New approaches to spacing and thinning in plantation forestry*. FRI Bulletin 151 pp. 13-20.

Johansson, M.; Kliger, R. 2002: Influence of material characteristics on warp in Norway Spruce studs. *Wood and Fiber Science* 34(2): 325-336.

Kininmonth, J.A.; Whiteside, I.D. 1991: Log Quality. Chapter 5 In Kininmonth, J.A.; Whitehouse, L.J. (ed) *Properties and uses of New Zealand radiata pine Vol. 1 – Wood properties*. Ministry of Forestry, Forest Research Institute.

Kubler, H. 1987: Growth stresses in trees and related wood properties. *Forestry Abstracts* 48(3): 131-189.

Larson, P.R. 1962: A biological approach to wood quality. *Tappi* 45 (6): 443-8.

Larson, P.R. 1963: Stem form development of forest trees. *Forest Science Monograph*

Larson, P.R. 1969: Wood formation and the concept of wood quality. *Yale University, School of Forestry, Bulletin No. 74*, 54p.

Linder, S. 1985: Potential and actual production in Australian forest stands. In Landsberg, J.J.; Parsons, W. (eds) *Research for forest management*. CSIRO, Australia. pp 11-35.

Little, C.H.A.; Lavigne, M.B. 2002: Gravimorphism in current-year shoots of *Abies balsamea*: involvement of compensatory growth, indole-3-acetic acid transport and compression wood formation. *Tree Physiology* 22:311-320.

MacDonald, E.; Hubert, J. 2002: A review of the effects of silviculture on timber quality of Sitka Spruce. *Forestry* 75: 107-138.

Mäkinen, H; Saranpää, P.; Linder, S. 2001: Effect of nutrient optimization on branch characteristics in *Picea abies* (L.) Karst. *Scandinavian Journal of Forest Research* 16: 354-362.

Masuda, M.; Honda, R. 1994: Theoretical analysis on the bending of lumber containing knots by using finite element method. *Mokuzai Gakkaishi* Vol 40 (2) 127- 133.

Mattheck, C. 1998: *Design in nature : learning from trees*. Springer-Verlag, Germany. 276p

Mattheck, C. 2000: Comments on “Wind-induced stresses in cherry trees: evidence against the hypothesis of constant stress levels” by K.J.Niklas, H.-C. Spatz, *Trees* (2000)14:230-237. *Trees* 15:63.

Mencuccini, M.; Grace, J.; Fioravanti, M. 1997: Biomechanical and hydraulic determinants of tree structure in Scots pine: anatomical characteristics. *Tree Physiology* 17:105-113.

Megraw, R.A. 1985: *Wood quality factors in loblolly pine*. Tappi Press, Atlanta. 88pp.

Mishiro, A.; Booker, R.E.; Ward, N. 2000: Effect of knots on the development of bow and crook in radiata pine boards during drying. In Kim, Y.S. (ed) *New horizons in wood anatomy*. Chonnam Nation University Press, Kwangju. pp 319-324.

Moore, J.R. 2002: *Mechanical behaviour of coniferous trees subjected to wind loading*. Ph.D. Thesis, University of Oregon.

Mork, E. 1928: Die Qualität des Fichtenholzes unter besonderer Rücksichtnham auf Schleif- und Papierholz. *Der Papier Fabrikant* 26: 741-747.

Morgan, J.; Cannell, M.G.R. 1994: Shape of tree stems - a re-examination of the uniform stress hypothesis. *Tree Physiology* 14: 49-62.

Mott, L.; Groom, L.; Shaler, S. 2002. Mechanical properties of individual southern pine fibers. Part II. Comparison of earlywood and latewood fibers with respect to tree height and juvenility. *Wood and Fiber Science* 34(2): 221-237.

New Zealand Forest Owners Association 2002: *New Zealand Forest Industry, Facts and Figures, 2002/2003*. New Zealand Forest Owners Association, Wellington.

Nicholls, J.W.P. 1982: Wind action, leaning trees and compression wood. *Australian Forest Research* 12: 75-91.

Nicholls, J.W.P 1986: Within-tree variation in wood characteristics of *Pinus radiata* D. Don. *Australian Forest Research* 16: 313-35.

Niklas, K.J. 1992: *Plant Biomechanics. An engineering approach to plant form and function*. University of Chicago Press, Chicago. 607 pp.

- Niklas, K.J. 2000: Computing factors of safety against wind-induced tree stem damage. *Journal of Experimental Botany* 51 (No. 345): 797-806.
- Niklas, K.J.; Spatz, H-C. 2000: Wind-induced stressed in cherry trees: evidence against the hypothesis of constant stress levels. *Trees* 14:230-237.
- Okuyama, T.; Takeda, H.; Yamamoto, H.; Yoshida, M. 1998: Relationship between growth stress and lignin concentration in the cell wall: Ultraviolet microscopic spectral analysis. *Journal of Wood Science* 44:83-89.
- Ormarsson, S. 1999: Numerical analysis of moisture-related distortions in sawn timber. Department of Structural Mechanics, Chalmers University of Technology, Göteborg, Sweden, Publication 99:7.
- Pellicane, P.J. 1984: Finite element analysis of finger-joints in lumber with dissimilar laminate stiffnesses. *Forest Products Journal* 44 (3) 17-22.
- Pellicane, P.J.; Franco, N. 1994: Modeling wood pole failure. Part 2. Material and geometric considerations. *Wood Science and Technology* 28 (4) 261-274.
- Persson, K. 2000: Micromechanical modelling of wood and fibre properties. Doctoral Thesis, Department of Mechanics and Materials, Lund University, Lund, Sweden.
- Perstorper, M.; Pellicane, P.J.; Kliger, I.R.; Johansson, G. 1995a: Quality of timber products from Norway spruce. Part 1. Optimization, key variables and experimental study. *Wood Science and Technology* 29 (3) 157-170.
- Perstorper, M.; Pellicane, P.J.; Kliger, I.R.; Johansson, G. 1995b: Quality of timber products from Norway spruce. Part 2. Influence of spatial position and growth characteristics on warp. *Wood Science and Technology* 29 (5) 339-352.
- Perstorper, M.; Johansson, M.; Kliger, R.; Johansson, G. 2001: Distortion of Norway Spruce timber. Part 1. Variation in relevant wood properties. *Holz als Roh- und Werkstoff*. 59 (1-2) 94-103.
- Philips, G.E.; Bodig, J.; Goodman, J.R. 1981: Flow-Grain Analogy. *Wood Science* 14 (2) 55-64.
- Ponton, S.; Dupouey, J.-L.; Bréda, N.; Feuillat, F.; Bodénès, C.; Dreyer, E. 2001: Carbon isotope discrimination and wood anatomy variations in mixed stands of *Quercus robur* and *quercus petraea*. *Plant, Cell and Environment* 24: 861-868.
- Porté, A.; Lousteau, D. 2001: Seasonal and interannual variations in carbon isotope discrimination in a maritime pine (*Pinus pinaster*) stand assessed from the isotopic composition of cellulose in annual rings. *Tree Physiology* 21: 861-868.
- Preston, R.D. 1952: The molecular architecture of plant cell walls. Chapman and Hall, London. 211pp.
- Preston, R.D. 1974: The physical biology of plant cell walls. Chapman and Hall, London. 491pp.

- Pruyn, M.L.; Ewers III, B.J.; Telewski, F.W. 2000: Thigmomorphogenesis: changes in morphology and mechanical properties of two *Poppulus* hybrids in response to mechanical perturbation. *Tree Physiology* 20: 535-540.
- Ryan, M.G. 2002: Canopy processes research. *Tree Physiology* 22: 1035-1043
- Sheriff, D.W.; Whitehead, D. 1984: Photosynthesis and wood structure in *Pinus radiata* D. Don. during dehydration and immediately after rewatering. *Plant, Cell and Environment*, 7: 53-62.
- Sheriff, D.W.; Rook, D.A. 1990: Wood density and above-ground growth in high and low wood density clones of *Pinus radiata* D. Don. *Australian Journal of Plant Physiology* 17: 615-28.
- Shigo, A. 1986: The new tree biology. Shigo and Trees Associates, Durham, U.S.A.
- Skatter, S.; Archer, R.R. (200x): Within-stem growth stress distribution in the case of spiral grain.
- Skatter, S.; Kucera, B. 2000: Tree breakage from torsional wind loading due to crown asymmetry. *Forest Ecology and Management* 135: 97-103.
- Skene, D.S. 1969: The period of time taken by cambial derivatives to grow and differentiate into tracheids in *Pinus radiata* D. Don. *Ann. Bot.* 33: 254-62.
- Spatz, H-C.; Bruechert, F. 2000: Basic biomechanics of self-supporting plants: wind loads and gravitational loads on a Norway spruce tree. *Forest Ecology and Management* 135: 33-44.
- Standards Association of New Zealand 1991: New Zealand timber grading rules. Standards Association of New Zealand, Wellington. 112p.
- Sutton, W.R.J.; Harris, J.M. 1974: Effect of heavy thinning on wood density in radiata pine. *New Zealand Journal of Forestry Science* 4; 112-115.
- Tian, X.; Cown, D.J.; Lausberg, M.J.F. 1995a: Modelling *Pinus radiata* wood properties. Part 1: spiral grain. *New Zealand Journal of Forestry Science*. 25(2): 200-13.
- Tian, X.; Cown, D.J.; McConchie, D.L. 1995b: Modelling of *Pinus radiata* wood properties. Part 2: Basic density. *New Zealand Journal of Forestry Science*. 25(2): 214-30.
- Telewski, F.W. 1989: Structure and function of flexure wood in *Abies fraseri*. *Tree Physiology* 5:113-121.
- Telewski, F.W.; Pruyn, M.L. 1998: Thigmomorphogenesis: a dose response to flexing in *Umlus americana* seedlings. *Tree Physiology* 18:65-68.
- Treacy, M.; Dhubháin, A.N.; Evertsen, J. 2000: The influence of microfibril angle on modulus of elasticity and modulus of rupture in four provenances of Irish growth sitka spruce (*Picea sitchensis* (Bong.) Carr). *Journal of the Institute of Wood Science* 15: 211-220.
- Turvey, N.D.; Downes, G.M.; Hopmans, P.; Stark, N.; Tomkins, B.; Rogers, H. 1993: Stem deformation in fast grown *Pinus radiata*: an investigation of causes. *Forest Ecology and Management*. 62: 189-209.

Uprichard, J.M. 1991: Chemistry of wood and bark. Chapter 4 In Kininmonth, J.A.; Whitehouse, L.J. (ed) Properties and uses of New Zealand radiata pine Vol. 1 – Wood properties. Ministry of Forestry, Forest Research Institute, New Zealand.

Walcroft, A.S.; Silvester, W.B.; Grace, J.C.; Carson, S.D. and Waring, R.H. (1996) Effect of branch length on carbon isotope discrimination in *Pinus radiata*. *Tree Physiology* 16, 281-286.

Walcroft, A.S.; Silvester, W.B.; Whitehead, D. and Kelliher, F.M. (1997) Seasonal changes in stable carbon isotope ratios within annual rings of *Pinus radiata* reflect environmental regulation of growth processes. *Australian Journal of Plant Physiology* 24, 57-68.

Walker, J.C.F. 1993: Primary wood processing: Principles and practice. Chapman and Hall, London. 595pp.

Whitehead, D.; Grace, J.C.; Godfrey, M.J.S. 1990: Architectural distribution of foliage in individual *Pinus radiata* crown crowns and the effects of clumping on radiation interception. *Tree Physiology* 7:135-155.

Whitehead, D.; Sheriff, D.W.; Greer, D.H. 1983: The relationship between stomatal conductance, transpiration rate and tracheid structure in *Pinus radiata* clones grown at different water vapour saturation deficits. *Plant, Cell and Environment* 6: 703-710.

Wilson, B.F. 2000: Apical control of branch growth and angle in woody plants. *American Journal of Botany* 87(5): 601-7.

Wilson, B.F.; Archer, R.R. 1979: Tree Design: Some biological solutions to mechanical problems. *BioScience* 29: 293-298.

Wilson, B.F.; Gartner, B.L. 2002: Effects of phloem girdling in conifers on apical control of branches, growth allocation and air in wood. *Tree Physiology* 22: 347-353.

Wimmer, R.; Downes, G.M.; Evans, R. 2002: Temporal variation of microfibril angle in *Eucalyptus nitens* under different irrigation regimes. *Tree Physiology* 22:449-457.

Yang, J-L.; Waugh, G. 2001: Growth stress, its measurement and effects. *Australian Forestry* 62(2): 127-135.

Yang, J-L.; Fife, D.; Waugh, G.; Downes, G.; Blackwell, P. 2002: The effect of growth strain and other defects on sawn timber quality of 10-year-old *Eucalyptus globulus* Labill. *Australian Forestry*. 65(1) 31-37.

Zandbergs, J.G.; Smith, F.W. 1988: Finite element fracture predictions for wood with knots and cross grain. *Wood and Fibre Science* 20(1): 97-106.

Zimmermann, M.H.; Brown, C.L. 1971: Trees: structure and function. Springer-Verlag, New York. 336 pp.

Zink, A.G.; Pellicane, P.J.; Anthony, R.W. 1995: A stress transformation approach to predicting failure mode of wood. *Wood Science and technology* 30 (1) 21-30.