

proposal

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1 Introduction to wood structure and formation

As trees grow they produce wood in order to become taller and wider. Becoming taller and increasing canopy size is an effective way to out compete the other trees and plants for light. With increasing height and width comes increasing weight, wind drag and internal pressures (for water transport), which requires either enough redundant strength in the existing structure (such as young monocotyledons) or for the tree to strengthen its structure as it increases its size. In dicotyledons and gymnosperms this occurs in two ways, apical and cambial growth on branches, roots and the stem(s).

Softwoods have a simpler micro structure than hardwoods, consisting mainly of axially elongated pointed cells named tracheids which serve as both mechanical support structures and water conduits. Although varying with species, softwoods may also contain radially orientated tracheids, radially or axially orientated parenchyma cells and other cell types. Tracheids are the dominant form of cells within the stems and branches.

Hardwoods contain a more complex micro structure with a number of different cell types. Fibres provide structural support as their primary function, while similar to softwood tracheids they differ in some key aspects, being shorter in the longitudinal direction, more rounded in the transverse outline, tend to have smaller lumens and have little role in sap ascent. However the ends do taper to points as in softwood tracheids. Libriform fibres tend to be longer than fibre tracheids, have thicker walls and are solely for support. Fibre tracheids function in both conduction and support, as in softwoods, however their appearance in wood with vessels suggests that they function primarily for support, and perhaps are an intermediate evolutionary feature between the softwood tracheid and the libriform fibre. Septate fibres divide their cell lumens into chambers without crossing the primary cell wall. Septate fibres are produced in the late stages of division just prior to the death of the cytoplasm, and appear to resemble axial parenchyma cells, and have been hypothesised to store starches, oils and resins.

Vessels are the main conduits for sap ascent. Vessels are comprised of multiple vessel elements being joined at the ends to form long conduits, which can

extend short distances (often less than 200mm) or can be as long as the height of the tree. These elements are connected through pores or perforations in perforation plates at the end walls of the cells. The arrangement of vessels into groups is species dependent and usually described as ring porous (the vessels congregate in early wood) or diffuse porous (vessels are distributed throughout both early and late wood).

Rays are formed from radially orientated cells often tracheids or parenchyma. Hardwoods typically contain multiseriate parenchyma rays, but there are a number of species with uniseriate or a combination of ray sizes, comparatively softwoods rarely contain multiseriate rays. Parenchyma ray cells are living within sap wood, however during the transition to heartwood die and are used for storage of extractives. Rays also provide a mechanical advantage by diverting the axial force flow reducing buckling and shear stresses between fibres.

Further cell types also exist, such as vasicentric tracheids which have profuse side wall pitting exhibiting deformation from the expansion of the surrounding vessels. Axial parenchyma cells are generally abundant and tend to exist in vertical files and are expected to play a role in the development of heartwood. More detailed wood anatomy and has little bearing on this project and is discussed in a number of wood anatomy texts.

In order to reorient stems and branches of (most) trees produce reaction wood which provides a force in order to reorient the tissue. Typically this reorientation is toward the light or upwards as is defined by the negative gravitropism hypotheses. Other reasons for reorientation such as reducing wind drag have also been suggested. In softwoods this reorientation is caused by the production of compression wood. Compression wood forms on the outside of the stem or branch and (expands? so that it is under compression? causing a restoring force). Hardwoods on the other hand produce tension wood on the inside of the desired curve which (contracts?) resulting in a curve forming. Traditionally the G-layer (G-layer), a layer primarily consisting of low angle cellulose fibrils on the inside of the fibre tracheids, is credited with forming growth stresses within the tension wood. However some hardwoods produce tension wood without producing a G-layer such as Eucalyptus.

Primarily, at different resolutions this work focuses on the fibre tracheids as they are the structural cells expected to be responsible for growth stresses in normal and reaction wood within hardwoods. The fibre tracheids consist of a number of cell wall layers depending on the species, the particular cell and its primary function. Normal wood fibres within Eucalyptus species (CHECK THIS) consist of a middle lamella (connecting the fibre to the surrounding cells) a primary cell wall and a secondary cell wall consisting of S1, S2 and S3 layers (produced in chronological order so the exact composition will change depending on the cell developmental stage). The S2 layer is the largest layer and consists of cellulose microfibrils wrapped helically around the cell longitudinal axis. This cellulose is contained within a matrix of hemicelluloses (examples) and lignin giving the cell wall properties of a fibre reinforced matrix. –how does this provide structure–

In order for the living cambial cells to produce wood, each cell must go

through division from its parent cell, growth and death. Because the cambium (and apical meristem) are continually dividing it allows for the tree to be a dynamic structure changing its form to become better adapted to its current environmental setting even though large portions (ie the wood) are dead. The transition from division through elongation and development to death is expected to play a role in the development of growth stresses within the stem.

1.1 Basic cell division

Dicotyledons and gymnosperms grow in two main ways, upward apical growth and outward cambial growth. Note monocotyledons (for example palms) do not produce secondary growth and instead diameter forms as part of primary growth.

As the cambium is forming, fusiform and ray initials are created. (how are the initials created) Fusiform initials are short radially and tangentially with tapered ends. From the cambial initials, cells to the inside create the vertical elements of xylem (tracheids, vessels, fibers, parenchyma, etc.), while cells outside become phloem. Ray initials produce horizontal elements (rays).

Cambial cells divide in two ways, periclinal and anticlinal. Periclinal cell division occurs to the inner and outer of the cambial layers. As the cell division to the inside occurs the volume of secondary xylem that is being formed increases the tangential stress on vascular cambium resulting in an extension of the cambial circumference. Although over time many plants show an increase in the longitudinal and tangential dimensions of the cambial initials it is likely that this expansion is mainly facilitated by anticlinal division followed by the expansion of the daughter cells next to the parent.

1.2 Cell formation, elongation and death

During primary wall formation rapid elongation occurs. When the cells divide from their parents they remain fixed to their neighbours via the middle lamella. The internal hydrostatic (turgor) pressure causes cell expansion. The osmotic flow of water from the outside the cell to the inside (due to a lower solute concentration outside the cell than in) which is constrained by the primary cell wall, the primary cell wall becomes under increasing tension as more water flows into the cell. Because the centre of the cell has restricted movement, in order for elongation (to dissipate the increasing tensile forces generated from the inflow of water) to occur the cell turns the biosynthesis of cell wall constituents to produce tip growth. Growth at the tips of the cells allows for the cells to remain a constant thickness, so no stretching is needed during the elongation phase, as has been suggested previously. The expansion of the cells is suspected to be controlled via modulation of the primary cell wall rather than via turgor pressure. – note that primary wall has randomly orientated MFs embedded in hemicellulose and pectic compounds and becomes lignified after S layer added, ML is non lignified, note often compound middle lamina is used to describe the ML and P at once as are hard to distinguish— Once the cell has reached its full

size biosynthesises of the S1 starts. Typically the S1 layer is thin and comprises of very high angle microfibrils, within the layer many laminates are found. Within each laminate the MFs are closely aligned, however between each laminate they can (but do not necessarily) differ greatly, or even reverse the direction of the helix the MFs form around the cell, although lower right to upper left orientation tends to be favored. Close to the S2 layer the MFA decreases rapidly. The S2 layer bound to the inside of S1 is typically much thicker and has more vertically orientated microfibrils compared to the primary, S1 and S3 layers, these MFs circle the cell axis from lower left to upper right. S2 contains the majority of the lignin within the cell. In some cases, most commonly in late wood a thin S3 layer is also produced with high MFA, reversing the direction of the MF helixes to lower right to upper left.

Finally if tension wood is being produced a Gelatus layer may be produced on the inside of the inner most wall (S2 or S3). The G-layer has near vertically orientated microfibrils and very little lignification. It is suspected that the G-layer plays an important role in the generation of reorientation stresses.

At some point during the formation of the secondary cell wall, or soon after the cell shrinks vertically and expands tangentially. Because of the connectivity between cells this results in growth stresses forming within the stem, this phenomenon is discussed in greater detail in —. After the secondary wall formation cell ‘death’ occurs as part of the transition from sap wood into heartwood. While the hollow, dead cells play an important role in water transport and mechanical support of the tree, over time any residual nutrient that can be used by living cells— heartwood stuff—

What is the deal with Rays—

1.3 Cells and wood in the context of a whole tree

Wood as a material within the tree has three major functions to achieve; water transport, nutrient transport and mechanical structure. Softwoods achieve water transport and mechanical structure within tracheids, while parenchyma cells are used for nutrient transport. Hardwoods have evolved a more complicated internal structure of vessels and fibre tracheids in order to separate out the functions of water transport and mechanical support respectively.

—advantages and disadvantages of this—

The growth stresses that form as part of cell formation are thought to provide a superior mechanical structure. Because of the continual formation of new cells providing growth stresses on the periphery of the stem the older wood which has completed its formation and cell death must be contracted further with each new layer of cells attempting to contract. The result of this is the older wood near the centre of the stem becomes compressed while the newer cells can not contract to the extent that would leave them in their lowest energy state remain in tension, until the bond between the old wood and new is separated releasing the forces restricting this contraction (and extension in the centre)

Reaction wood as described above provides the ability for the stem to reorientate in order to be best adapted to its environment at any given time.

These properties of wood allow for an adaptive organism to survive..

2 History of work on growth stresses

It is suspected that growth stresses develop within tracheids during the formation the secondary cell wall, although the exact timing and mechanism for developing growth stresses is still of much debate. The most current theory is a hybrid of the older cellulose contraction and lignin swelling hypothesis.

A brief discussion of work relating to growth stresses prior to 1965 is given below, Archer (growth stresses book intro) provides a full review of suggested theories up until 1965.

Wood workers have unintentionally known of growth stresses within trees for centuries. Usually referred to as 'a pull towards the sap' when cutting boards good craftsmen would section the log in such a way as to get a straight board once it is removed from the log (and the growth stresses released). Most work early on in the study of growth stresses surrounded investigating how/why boards changed shape when cut from an intact stem.

Martley (1928) was possibly the first to study growth stresses in a scientific manner. Initially he argued that the curvature of planks sawn from logs was due to the current growth not being able to support the dead weight of the tree until lignification was complete. As a result the centre is under compression while the periphery had zero stress. However calculations showed that the self weight was not sufficient to cause the observed longitudinal dimension changes of the timber.

After Martley's work a small number of authors investigated growth stresses through the 30's and 40's. Jacobs, although testing 34 hardwood species, focused mainly on Eucalyptus and in 1938 argued that (longitudinal) tension successively develops in the outer layers of the stem as it grows, and as a consequence of the tension, compression must form in the centre of the stem. Jacobs later used *E. gigantea* to describe a strain gradient developing during growth. Experimentally Jacobs made use of strip planking, measuring the deflection of the board after removal from the log, and the length change when the planks were forced back straight. He showed that wood tends to shrink in the longitudinal direction at the periphery while extend near the pith (indicating in the log the planks are under compression in the centre and tension at the extremities).

Further Jacobs put forward a number of hypothesis to explain how the growth stresses were forming. First arguing that it is very unlikely that dead cells (wood) could extend within the core in order to create the observed stress gradient. Instead suggesting the causes of; weight of the tree, surface tension and sap stream forces, cellulose and colloidal complexes, lignin intercellular substances and the primary or secondary cell wall. Although without any evidence did not claim any of these to be the major cause.

Stresses relating to reaction wood received more attention through the 30s and 40s for both soft and hardwoods. Jacobs 1945 stated that the reorientation of stems is caused by a modification to the already existing stress gradient

throughout the stem. One option he presented was simply that the eccentric growth causes larger number of cell sheaves to be added to the upper side of the curve each providing the same amount of contraction force, this results in a angle correction even with identical cells. Sap tension is also considered, but more importantly Jacobs notes the possibility of tensions being formed within the cell walls of tension wood. Munch 1938 speculated that the addition of matter into the cell wall could cause compression wood. .. Jacobs 1945 also found that it was commonly the case that the amount of compression wood developed and the stem angle recovery had a poor relationship. He suggested maybe it was in fact the normal strain pattern in tension which correct the lean, the compression wood merely acted as a pivot, not contributing a tensile force on the lower side of the stem.

Boyd 1950 Developed a new experimental technique in order to investigate the stress profile further. By cutting a slit longitudinally in the centre of the log, attaching strain gauges onto the wood inside the slit and successively shortening the log from both ends he obtained direct extension measurements from inside the stem. —found that the crossover point is about $1/3$ rad of the log from the periphery—

Most commonly growth stresses were investigated from the longitudinal direction, however cells also change dimension in the transverse direction, this leads to a more complicated three dimensional stress field developing within even a straight stem. Koehler 1933 showed that a saw cut radially through a disk has a tendency to close near the periphery suggesting that the peripheral cells are under tangential compression with the inner cells under radial tension. He suggested this was the cause of shakes in standing timber. Jacobs 1945 removed inner circles from disks of a number of species and found when an inner portion is removed the disks circumference increases. Jacobs again argued that strain in the sap stream along with cells being wider tangentially than radially led to the observed lateral stresses. Although he also mentions the possibility of secondary thickening from the deposition of lignin as a possible contributing factor. Boyd 1950a developed an experiment whereby he removed a wedge from a disk and measured the radial expansion, showing the disks were in fact under radial tension. Further additional species were found to be in agreement with the results of Jacobs 1945 when the inner circles were removed from disks. Boyd also shows that the longitudinal stresses manifesting as transverse stresses via Poisson ratios are only approximately one tenth that of the measured stresses.

Boyd 1950c provides an in-depth rebuttal of the available theories at the time, arriving at the conclusion that the cell wall development must control the shape change which results in growth stresses. Further he postulates that cellulose is primarily responsible with lignin and carbohydrates also playing important roles when stresses are formed in normal, compression and tension wood.

The first major advancement in the understanding of the formation of growth stresses came from Wardrop (1965) where the cellulose contraction hypothesis was first theorised. — Bamber (1978) refined this hypothesis further.—

Wardrop 1965, Bamber 1978 A tensile stress generated in the cellulose microfibrils forces the TW and NW fiber with low microfibril angle to shrink.

Boyd (1972) presented the alternative hypothesis of lignin swelling compressive stress originating in the matrix pushes the CW tracheid with a high MFA to expand

Around the same time two other lesser known hypothesis were presented, strains due to changes in water content Hejnowicz 1967, argued that the stresses in compression wood are related to the inhibition of water by the cell walls, which results in swelling, because the expansion of compression wood is equal to the shrinkage due to drying. –paper disproving this–

brodzki 1972 hypothesised strains due to 1,3-linked glucan (laricinan) deposition within the helical checks of the S2 cell wall layer could be the most significant factor in longitudinal growth stress generation. Boyd 1978 refuted this idea arguing (along with other issues) that the laricinan would expand into the cell lumen not causing any stresses in the cell wall, unless a (non-observed) constraining median restricted the expansion.

Through the late 70's and 80's archer produced a number of studies investigating growth stress occurrence and formation. ... Cave paper somewhere around here? Gills 1973

More recently theories regarding the nature of hemicelluloses and their bonding have been used in an attempt to remove some of the issues associated with lignin swelling and cellulose contraction theories.

The most recent attempts made to describe the formation of growth stresses have been made by Yamamoto and his team. They argue a combination of both lignin swelling and cellulose contraction is needed, called the unified hypothesis. By unifying the hypotheses they follow the current thinking of a number of authors in other areas of wood science that both tension and compression wood are not distinctly different types of wood and are instead extreme versions of normal wood.

issues with current understanding: When and how do the stresses get generated is still of much debate, over the last couple of decades it has become fairly widely accepted that the generation of the stresses occurs during or immediately after the deposition of the secondary cell wall. Most commonly either the G-Layer or the S2 layer are considered responsible. why do they vary so much between individuals and species? One of the more debated topics around growth stress generation is whether the generation mechanisms for stress in reactionwood are extreme versions of the same mechanisms in normal wood. The G-layer is not found in normal wood, however on rare occasions lignin swelling could potentially fit this criteria for normal and compression wood, however modification of Boyd's theory would be needed due to the dependence of a MFA as some wood with lower than about 40 degree MFA still produces compressive forces. Boyd's theory combined with excessive mild compression wood formation in corewood still allows for the same tensile generation mechanisms to be used by older cambiums, as long as the MFA is suited to the task. how can we quantify the mechanical advantage with so much variability what about the other unusual forms of reaction wood, hebe etc

2.1 Why growth stresses exist

Hardwoods typically have much larger growth stress magnitudes than softwoods. –why– is this true ‘xylem cell development’?— some have claimed conifers have compression throughout the stem when young, not until old that they follow the same trend as hardwoods

Perhapse the leading argument for the reason of growth stresses existence is the mechanical hypothesis. The mechanical hypothesis argues that a number of wood properties, including the development of growth stresses evolved in order to provide increase mechanical stability to trees in order to increase their survival. The mechanical hypothesis as applied to growth stresses argues that because wood is stronger in tension than compression by preloading the outer edge of the stem in tension it increasing the non-destructive bending radius on the inside of the curve when a force is applied causing the stem to bend. –doesn’t explain why hardwoods have larger GS than softwoods, or why young softwoods exhibit compression.– This hypothesis struggles to explain the differences between hard and softwoods, particularly at young ages. If mechanical stability is in fact the driver for growth stress generation at young ages, why do young angiosperms and gymnosperms produce essentially opposite solutions?.

If the reason conifers have compressive forces when young is excessive compression wood to enable reorientation, maybe this indicates that normal wood is more closely related to tension wood than compression wood. What forms of mild tension wood are known of?

speculation from various authors Typically when attempting to determine the reasons for why wood properties exist one of four hypotheses are used; mechanical, hydrolic, time dependent and a combination of the previous three. Initial speculation as to the reason for growth stresses existence came from Martley (1928) who briefly entertained the mechanical hypothesis based on self weight. Jacobs (1945) suggested they were a byproduct of sap tension, which he later retracted Jacobs (196?) when sap pressures were recalculated at a much lower value than the generally believed values at the time. .. Growth stresses undoubtedly have an effect on the mechanical stability of trees, although it is conceivable that the effect may be byproduct of another driver.

2.2 Intro to the issues growth stresses cause

for harvesting dangerous for feller splitting of log at felling internal checking
boyd 1950

within mills bending/bowing/warping during cutting jamming up saws, large proportion of waste, multiple cuts required to get boards to desired dims

lost revenue, final yield less than 30

3 Theoretical and experimental understanding of growth stresses

3.1 Background of breeding

Because growth stresses cause a number of issues for harvesting and milling timber tree breeding programs can be used in order to select for genetics which reduce these effects. –previous breeding for GS– There is no reason to expect breeding for growth stresses differs significantly from (conventional) breeding trees for any other trait, which is process which has been developed over centuries. Over the last few decades many advances have been made in experimental and statistical techniques which rapidly improve the time and accuracy of conventional breeding.

field techniques Typically breeding trials, like any scientific experiments are designed in order to minimise noise from uncontrolled variables,

laboratory techniques

stat techniques

mention tradeoff with durability etc

3.1.1 Breeding work in this thesis

What we actually have:

Harewood trial: dec 2014 has Bosistoana and argophloia copied from old planting that mon has GS data from. –from data can show (kind of as could argue same environmental effects caused it) genetic relationship. New Harewood trial, 2016 harvest, will have a number of species potential to copy bos again if needed.

Woodville, 2016/2017 harvest will have Bosistoana, argophloia and possibly globoidea. May or may not be the same families as the various drylands trials.

NOTE family means same mother, not same father. If collected at different times even from the same tree variability exists due to possibly of different set of fathers. Also some self propagate, but we don't know which ones or what proportion, so ignore this.

Progeny trials are alpha latitudes, harewood is a standard randomised individual trial.

Contact Ruth McConnachie: rgcmccnochie@xtra.co.nz for DFI details.

split tests Pairing Test and Longitudinal Growth Strain: Establishing the Association 2008 is the earliest paper I can find on the split/pairing test. note kens papers from mon

surface tests

Potentially use NIR <http://www.afs-journal.org/articles/forest/pdf/2002/05/05.pdf>

Has some useful info on wave lengths associated with bonds in cellulose

Non-destructive evaluation of surface longitudinal growth strain on Sugi (Cryptomeria japonica) green logs using near-infrared spectroscopy

statistics

Progeny trials are alpha latauses, harewood is a standard randomised individual trial.

- PLSR etc for NIR work
- normal breeding stats?

3.2 Background of chemistry work

lignin swelling

- cellulose contraction

- what has been done in the past? that xray syncotron experiment etc

3.2.1 Chemistry work in this thesis

Do all of the DFI species have a G-layer? Maybe include some Nitens tests if they don't. check MFA and SD for S_2 in tension, normal and compression/opposite wood Get cellulose lignin and hemicellulose(s) contents for tension normal and compression/opposite wood Split hemicelluloses where possible, eg xyloglucan etc. Torsion tests on individual cells, again for tension, normal and compression. Maybe remove G-Layer in tension wood and compare to normal and compression wood of similar MFA and compounds etc.

Could we somehow measure growth stress release on a single cell? Ideally, grow disordered cells invitro, and separate them from the parent cell as soon as possible, then record when in their formation they undergo what dimension changes. Is there some non-destructive test to check what is going on in the cell? or if we have multiple cells in the same conditions maybe we can destructively test some during the growth phase, under the assumption they are all growing at the same time. OR remove the cambial layer leaving top and bottom of cell attached to the stem on a large sample, then somehow remove the connection to the cells behind it, then release the top and measure the contraction.

3.3 Background of modeling

yamamoto's most recent attempt

- possible different methods i. FEM, DEM, molecular dynamics, geometry of stem and cells

3.3.1 Modeling in this thesis

cells as particles in relaxed state

- apply body force, ie the growth stress field

- get original/non cut stick back

- take groups of repressive cells and use composite theory and position dependent body force (growth strain field) from the sub domain above

- introduce time dependence to see how the stress field develops during maturation, composite scale still – each cell can have its own clock so that it has a maturation rate to change its field variables.

take individual cells at macromolecular level and try to produce stress field above during a time dependent maturation function

Molecular dynamics simulations to work out the molecular mechanisms developing the growth stresses

Using the MD sims parameterize a cell model

Using the cell model develop a time dependent field function

from the field function create representative cell blocks

put the cell blocks together into a stick

cut the stick ; do we get out what we put it?

4 Intentions

to improve breeding stock for NZ dryland forestry with respect to eucs being used for structural timber

to increase understanding of growth stress formation particularly in eucalyptus by chemical analysis and computer modeling

5 Objectives

to create a mathematical model and computer simulation of a piece of cambium forming growth

stresses at the macromolecular level

to investigate the chemical causes of GSs by chemical analysis ; how?

to improve breeding stock for eucs wrt growth stresses from field and lab testing to select appropriate families.

6 Costs

7 Timeline