

proposal

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January 19, 2015

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 E. Nitens.

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 cells developmental stage). The S2 layer is the largest layer and consists of cellulose microfibrils wrapped helically around the cells 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.

Wardrop 1965 commented that a tensile stress generated in the cellulose transitioning into a crystalline state could be the explanation for cells contracting during the formation of the secondary wall. Cellulose contraction aligned well with the observation of the G-layer (which has a very low MFA) being common in a number of tension wood producing species, and also gave the ability for low

MFA normal wood to contract. Bamber 1978 further argued cellulose contraction claiming turgor pressure in normal wood cells remained high enough that the cells did not contract before the lignin was deposited, once/during lignin deposition the cellulose became crystalline and shrunk, causing the cell to become shorter, the mechanism for tension wood is essentially the same. Compression wood on the other hand was explained by the cellulose being laid down and then the turgor pressure decreasing, causing the cell to contract before lignin was deposited. In turn the cellulose was under compression, resulting in the tendency for the compression wood cells to expand.

Boyd (1972) presented (or rather popularised) the alternative hypothesis of lignin swelling (first conceived by Munch 1938). Tensile stress is gained in cells of low MFA by lignin deposition into the cell wall, pushing the cellulose fibrils apart, which in turn shrinks the longitudinal length of the cell and increases the tangential width. When MFA is high, the opposite occurs, lengthening the cell and reducing its tangential width. This shape change is not readily apparent in compression wood (characterised as short fat tracheids) until the release of the stress acting on the CW, where by the cells become longer and skinnier.

Around the same time two other lesser known hypotheses 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 —refs— mainly concerning the mathematical treatment of the stress fields within trees. —Archer —

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 the cellulose contraction theory. One major issue of cellulose contraction is that in its initial form it was argued that the crystallisation process of cellulose shortens its length. —ref— showed that when cellulose crystallised it became longer as the chains increased order. Two theories have been advanced to combat the issue of lengthening during crystallisation in order to retain an updated version of the cellulose contraction hypothesis.

— argues that at the edge of the cellulose fibrils the cellulose becomes disordered and is consequently able to bond with hemicelluloses, which have a slightly shorter repeat length than the cellulose crystal. These hemicelluloses bond to the outside of the fibril cause the fibril to be compressed in the crystalline centre, while under tension on the surface. An interesting consequence is the contraction of the cellulose due to the hemicellulose bonding should be

dependent on the area/volume to circumference/surface area ratio. A potential way to test this hypothesis is discussed in section —

The second theory put forward in an attempt to correct the issues surrounding cellulose lengthening during crystallisation is from — who argues that hemicelluloses form within the fibrils and push them apart causing the cellulose fibrils to contract. Interestingly mechanically this is very similar to the lignin swelling hypothesis. By in causing the MFs to no longer run straight, instead they have to use some of their length to deviate passed a cluster of hemicelluloses consequently shortening the overall distance the fibril can cover. One side effect of having these deviations is fibrils should not have a consistent cross sectional area over their whole length, where the hemicelluloses have been deposited should result in an increased cross section. potential way to test this?—

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. It should be noted that — and others suggested that both theories were likely to contribute to growth stress generation. 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. — lots more in here —

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 Boyds 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. Boyds 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

Note Muller et al 2006 found low hemicellulose content in G-layer timell 1969 higher conc of lignin in S2 layer when G-fibres present

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 explains the low/negative GS sometimes reported

in young conifers.

Perhaps 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 increases 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, hydraulic, 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

At harvesting, if the stems are under large growth stresses, which particularly occurs when severe reaction wood is present due to a leaning tree increases the danger for the feller from effects such as 'barber chairing'. When the stem is felled, growth stresses are released around the saw cuts causing shortening at the periphery and extension in the centre. The dimension change is maximum at the saw cut, reducing as distance from the cut increases. When the contraction/extension force exceeds the yield limit of the stem splitting occurs during (or very shortly after) felling. The cracks tend to propagate in the radial direction by cell wall peeling, although the cracks tend to only be a few inches deep they significantly reduce the value recovery for both structural and peeler logs.

Prolonged compression at the centre of the stem during growth can exceed the elastic limit of the wood, resulting in internal checking.

felling internal checking

boyd 1950

Growth stresses in hardwood timber report

Within mills during processing growth stresses cause a number of issues leading to reductions in value recovery and efficiency. Because growth stresses are released when the stem is sectioned via quarter sawing or — the resulting shape change can cause the saws to jam. The main value loss at this stage of processing come from the need to saw boards multiple times in order to release the stresses while still allowing for the final board dimensions to be retrieved. Increasing the number of times the boards are sawn to get their end dimensions gives not only poor saw use efficiency but the major economic loss comes from the final yield being 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 (conventionally) 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 copice bos again if needed.

Woodvile, 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: rgcmccconnochie@xtra.co.nz for DFI details.
 slit tests Pairing Test and Longitudinal Growth Strain: Establishing the Association 2008 is the earliest paper I can find on the split/paring 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 ic 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 experement etc

3.2.1 Chemistry work in this thesis

The primary goal of the set of experments which will be presented within this chapter is to atempt to identify which cell wall constituents are controlling stress generation and how they are controlling stress generation under different conditions. In order to evaluate stress generation mechanisms a number of experimental techneques have been identified.

Basic cell wall anatomy and geometry needs to be investigated for the NZDFI species involved in this project. The cell wall anatomy under different wood types (tension, normal and opsrite) needs to be investigated for the verious species (pinciply E.B.). The anatomy study will consist of investigating which species produce a G-layer and what cell wall structure is associated with its production. The cellulose, lignin and hemicellulose contents will be determined for tension, normal and opsrite wood along with the MFA and the MFA standard deviation for a number of samples in all three wood types. Fibre width, length and luman size will also be obtained. Within tension wood the removal of the G-layer (in G-layer producing species) will be needed in order to determain the seconday cell wall properties of tension wood.

The cell wall constituent study results will be used to make comparisons between the growth stresses produced by the stems and the different properties within the cell walls. With the anatomy results collected from tension, normal and opsrite wood comparisons can be made not only between these within trees but also between trees. By comparing tesnion wood with the G-layer removed with normal wood with similar properties some insight into the role of the G-

layer should be gained. Note that growth stresses for a large number of samples will be collected during the breeding work.

The other set of experiments proposed is to investigate the extent of an effect the G-layer has on tension generation within tension wood, and how the G-layer generates these tensions.

Proposed experiment one: Taking samples with G-layers and applying a vacuum pump to suck callase into the fibres and vessels to degrade the G-layer releasing the strain which the G-layer is applying to the samples will cause a shape change. By comparing the initial and final shape change the strain the G-layer was imposing on the samples can be obtained. Further the rest of the Growth stresses can be released using more traditional techniques such as split tests or planking, by releasing the remaining strain the proportion of stress associated with the G-layer and other cell wall components (assumed to be the S2 layer) can be determined.

Proposed experiment two: Release the stress with a split or planking test, then remove the G layer using the same method as above. When the tension caused by the G-layer is released relaxation back towards the initial state should be observed. The proportion of G-layer induced strain and S2 induced strain will then be evident.

Proposed experiment three: During growth induce tension wood production by forcing curvature into the living stem. By introducing callase to the plant while it is still transpiring should degrade the G-layer and reverse any straightening that was caused by the G-layer.

Any of the three proposed experiments, if they work will provide will provide the proportions of the strain in tension wood which can be attributed to the G-layer.

Any experiments where by we could show the mechanism of the G-layer?

Paper claiming *camaldulensis* has G-layer, note that it is a S1-G cell Chemical and anatomical characterization of the tension wood of *Eucalyptus camaldulensis* L. Mokuzai Gakkaishi

3.3 Background of modeling

yamamotos most recent attempt

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

3.3.1 Modeling in this thesis

Proposed model for cell: Modelling of a generic single cell with verifiable cell wall properties to investigate the required geometry and constituents to create maximum longitudinal and tangential extension and contraction via the lignin swelling hypothesis. The single cell model should have the capacity to put limits on what stress generation the lignin swelling hypothesis is theoretically capable of.

Because the proposed experiments induce servear tension wood in species both with and without G-layers and experimental upper limit of the lignin swelling hypothesis should be reached and compeared to the theoretical one derived above. The inclusion of the G-layer as descibed below can be added to the single cell model time permitting. By including the G-layer (assuming the experemental work shows the G-layer is a contributing factor to the production of growth stresses in tension wood) within the model, and comparing the required chemical make up and cell geometries with the servear compression wood experementally investigated light should be shed on the liklyhood of the lignin swelling hypothesis being extenable to include G-layer type tension wood.

If the G-layer is under tension due to bowing of the S2 layer (S2 under lignin swelling) contraction of the cell is more effcantly than the S2 layer due to the very low MFA in the G-layer. Within litriture it has been shown that often the MFA of the S2 layer is higher than in normal wood or tension wood without a G-layer present. Under the lignin swelling hypothesis a higher MFA leads to more tangential swelling, and because the outer of the cell is constrained by the primary and S1 walls the majority of the swelling should occur toward the luman, which is lined with the G-layer in tesion wood.

Time permitting if experements find that the lignin swelling models dont account for the strains present a previsor for cellulose contraction could be included. Between the experemental results and the cellular models, calculations as to how much contraction is needed should be posable, giving an inital starting point to look more indepth into cellulose contraction meachanisums.

Proposed model of stem: Because of the nature of the experemental work it is required to be undertaken at a macroscopic scale while the proposed theoretical model is at a cellular (nano to micro meter scale). The scale difference between the two methods causes an issue in that they are not directly comparable (as a sample of wood is not homogenious). In order to overcome the scalar dependency it is proposed a second theoretical model be produed which will operate at a macroscopic scale with the perpous of simulating the experements undertaken. By paramertarising with the single cell model (which has been parameterised with the expermentally derived cell anatomy and geometry) aproximations to the acutual sample being tested should be able to be made and compeared to the experemental outcomes. This proofing is required to make sure that the results of the single cell model is providing are realistic.

4 Intentions

5 Objectives

6 Costs

7 Timeline