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# Wood Anatomy of Metasequoia - Separation from Glyptostrobus and Function/Structure Considerations

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# WOOD ANATOMY OF METASEQUOIA -- SEPARATION FROM GLYPTOSTROBUS AND FUNCTION/STRUCTURE CONSIDERATIONS

By

George E. Visscher

B.S. University of Maine, 2000

A THESIS

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Master of Science

(in Forestry)

The Graduate School

The University of Maine
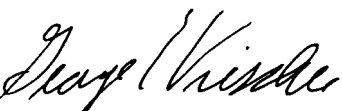
December, 2002

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# WOOD ANATOMY OF METASEQUIOA -- SEPARATION FROM GLYPTOSTROBUS AND FUNCTION/STRUCTURE CONSIDERATIONS

By George E. Visscher

Thesis Advisor: Dr. Richard Jagels

An Abstract of the Thesis Presented
in Partial Fulfillment of the Requirements for the
Degree of Master of Science
(in Forestry)
December, 2002

This thesis is part of a broader cooperative study aimed at understanding Paleo-forest dynamics -- namely those of the Eocene period in the Canadian High Arctic. Wood of the dominant tree species -- *Metasequoia* -- that grew on Axel Heiberg Island, Nunavut, Canada is the focus of this research. The text is divided into two chapters written as articles to be submitted to the International Association of Wood Anatomists Journal (IAWA).

The first chapter of this text is a direct result of classifying the fossil wood of Axel Heiberg. The wood of *Glyptostrobus* is similar to that of *Metasequoia*. Because both trees grew on the same sites, it was vital to be able to separate the wood of these species. We obtained extant wood samples of these relatively rare woods from herbaria around the world, tested previously published descriptions, and report observations that more consistently separate these species.

The second chapter of this text discusses the xylem strategies of *Metasequoia*. Because *Metasequoia* is a tall tree with a high water demand, its wood must be sufficiently strong, and provide the canopy with enough water to meet its needs. A microscopic analysis of tracheid parameters provides evidence for postulating strength and hydraulic conductance functions. The results indicate that *Metasequoia* possesses unique specific gravity and microfibril angle trends that may be adaptive strategies for this species at its unique high latitude sites. We have shown that as *Metasequoia* trees increase in diameter and height, they produce tracheids that concomitantly strengthen and potentially improve hydraulic efficiency. This finding provides a new perspective on the strength/hydraulic conductance compromise proposed by other researchers, and demonstrates a strategy of strength enhancement that does not involve significant latewood production.

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CHAPTER 1

# SEPARATION OF *METASEQUOIA* AND *GLYPTOSTROBUS* (CUPRESSACEAE) BASED ON WOOD ANATOMY

## SUMMARY

The wood anatomy of *Metasequoia* is similar to that of *Glyptostrobus*. Past descriptions of these woods often report unreliable or conflicting observations. With numerous samples we give updated descriptions of these woods. We also test previously published criteria and discuss those of real diagnostic value. We propose the use of a suite of characters to separate the woods, including: presence of ray cell separation, cells per square millimeter in transverse sections of the earlywood of mature wood, arrangement of cross-field pits, features of the horizontal end walls of longitudinal parenchyma, transition from earlywood to latewood, abundance/distribution of longitudinal parenchyma, and aroma.

***Keywords:*** *Metasequoia, Glyptostrobus,* ray cell separation, cells per area, fossil wood, wood identification.

## INTRODUCTION

Identification of tree species based on wood anatomy may be of interest to taxonomists studying extant flora, but it has even greater utility when studying fossil remains. Leaves or fruit may be present on fossil sites and can be used to create a taxonomic list of flora, but understanding paleo- forest dynamics requires accurate wood identification of stumps and logs. Correct identification of fossil wood to

family, genus, and/or species requires referencing to well described extant wood from vouchered sources.

The fossil record of *Metasequoia* and *Glyptostrobus* is extensive. They were often the dominant floristic components in many forests of North America, Europe, and Asia during the late Cretaceous into the middle Tertiary (Florin, 1952; Momohara, 1994; Kumagai et al., 1995; Stockey et al., 2001). Numerous fossil forests have been found in the arctic where no trees exist today (Creber & Chaloner, 1985; Momohara, 1994). Both species are known to inhabit similar sites -- past and present (Henry & McIntyre, 1926; Li, 1957; Bartholomew et al., 1983; Basinger, 1991; McIntyre, 1991). When fossil wood samples are preserved in a manner that enables anatomical observation it is important that reliable diagnostic features be used to classify the species.

*Metasequoia* and *Glyptostrobus* have shared a similar fate during and since their large paleo- populations. Both species are members of the former Taxodiaceae family, more recently incorporated into the Cupresseacae family -- *Metasequoia* in the sequoioid clade, *Glyptostrobus* in the taxodioid clade (Eckenwalder, 1976; Butala & Cridland, 1978, Judd, et al., 2002). They are currently monotypic. *Metasequoia* exists only as very small relict population on wet sites in south-central China and *Glyptostrobus* is known only as a planted tree, typically on wet sites as well (Henry & McIntyre, 1926; Florin, 1952; Liang et al., 1948; Momohara, 1994). *Metasequoia* and *Glyptostrobus* have been reported from the same paleo-arctic sites based on pollen, leaf, and reproductive structures (Basinger, 1991; McIntyre, 1991; Kumagai et al., 1995).

The wood of *Glyptostrobus* is very similar to that of *Metasequoia* (Basinger, 1980). Taxodiaceous woods generally lack true resin canals, lack indentures in horizontal walls of ray parenchyma, and have taxodioid type cross-field pitting (Greguss, 1955; Panshin & deZeeuw, 1980). Gromyko (1982) reported that specific identification of these species is difficult and may not be possible with conventional keys. Most studies exploring these woods are suspect because of their limited sample size that often results in observations that are not accurate in all situations (Henry & McIntyre, 1926; Li, 1948; Liang et al. 1948; Greguss, 1955; Hejnowicz, 1973; Basinger, 1981; Gromyko, 1982; Wu & Chern, 1995).

Wood properties vary within and amongst trees of the same species (Panshin & deZeeuw, 1980; Basinger, 1981; Larson, 1994). Ideally a study sampling from different environments and throughout a given tree is required to establish characters to definitively identify wood. Hejnowicz (1973) attempted to account for the variation of wood characters in *Metasequoia* at different heights and ring numbers; however, she only observed a single young stem. Gromyko (1982) observed intra-ring variation of several Taxodiaceous (now Cupressaceae) woods (including *Metasequoia* and *Glyptostrobus*), unfortunately, his sample size was small (3 *Metasequoia* and 2 *Glyptostrobus* trees). The purpose of this study was to determine whether *Metasequoia* and *Glyptostrobus* could be separated reliably on the basis of wood anatomy. We examined a larger pool of vouchered samples and a larger number of anatomical characteristics than previous studies.

MATERIALS AND METHODS

Extant samples of *Metasequoia* and *Glyptostrobus* were obtained from wood collections housed in the United States, United Kingdom, Japan, and The Netherlands. In total eleven *Metasequoia* and eight *Glyptostrobus* samples (Table 1.1) were obtained and prepared for microscopic observation. All samples used to establish criteria were assumed to be of mature stem wood because of the lack of compression wood and degree of curvature of rings across sample blocks.

Sections 18-22 µm thick were made with a sliding microtome (A.O. Spencer Model 860), stained overnight in 1% Bismark Brown, and mounted in a low viscosity medium (Cytoseal 60 – Richard-Allan Scientific) to make permanent slides. Observations were made using a light microscope (Axioskop: Zeiss) equipped with a digital camera (SPOT RT: Diagnostic Instruments, Inc.) connected to a PC (Toshiba equium 7350M). All measurements were made on the PC from digital images. Tracheid length and diameter measurements were made using the software provided with the camera. Cell count measurements were determined using Scion Image Beta 4.02 for Windows (Scion Corporation Inc., Fredrick, Maryland). Features observed in past studies were screened in our samples to determine their potential diagnostic value.

A technique to measure cells per area (CPA) quickly and repeatedly was established. Transverse images were magnified to 100x, beginning with the first formed cells of the annual ring, and included only earlywood cells. Images covered a default area of 1.02949 mm$^2$. Using the default settings of the Scion Image program, images were converted to threshold images. Images were then analyzed using the

Table 1.1: Wood samples used to determine cellular attributes of
*Metasequoia* and *Glyptostrobus*.

| Source | *Metasequoia* | *Glyptostrobus* |
|---|---|---|
| United States: U.S.D.A. F.S. Forest Products Laboratory | MAD-14913 MAD-13530 SJR-50317 SJR-45027 | SJR-850 SJR-29829 |
| Japan: Forestry and Forest Products Research Institute | TWTw-6420 TWTw-10942 TWTw-15613 TWTw-15986 | TWTw-10521 |
| The Netherlands: University of Utrecht | UN 450 | |
| The Netherlands: National Herbarium - University Leiden branch | vak XX 9897 Arboretum Wageningen | FRTGw 10 |
| United Kingdom: Royal Botanic Gardens, Kew | | KW 70264 KW 19014 KW 19015 |
| Japan: Kyoto University; Kamigamo Experimental Forest | | Cored tree* |

* Not a vouchered specimen

"Analyze Particles" command. This procedure automatically counted and measured objects by scanning across the image until it found the boundary of the object, and then outlined, measured, and redrew the object at a different gray level. Minimal particle size included in measurements was set at 100 pixels and cells that touched the image edge were included in the analysis. Values were adjusted to cells per square millimeter. Each section was measured from three different images and averaged to get the CPA value for that sample. The mean for all samples was calculated for determining a species CPA value.

## RESULTS

Table 1.2 lists criteria that other researchers have used to describe the wood of *Metasequoia* and *Glyptostrobus*. Table 1.3 lists criteria that we have determined to be most diagnostic to separate our samples when used collectively. The format of the following species descriptions are modeled from Panshin and deZeeuw (1980).

**Chinese swamp cypress, water pine**
**(Cupressaceae)**

*Glyptostrobus pensilis* K.Koch.

**General Characteristics**

*Wood* with distinctive odor similar to that of *Thuja*; moderate to fine in texture; light (specific gravity 0.28 --1 sample estimate). *Growth rings* more or less distinct; transition from earlywood to latewood gradual. *Parenchyma* abundant, present in every growth ring, often arranged in tangential bands, visible with a hand lens. *Rays* fine. *Resin canals* wanting.

**Minute Anatomy**

*Tracheids* up to 45μm in tangential diameter; earlywood cells of mature stemwood averaging 1366 cells per mm$^2$; bordered pits in 1-3 (frequently 1-2) rows on radial walls; sparse tangential pitting in latewood; pits leading to ray parenchyma taxodioid to cupressoid type, 1-6 pits per cross-field, unorganized or arranged in 2 rows. *Longitudinal parenchyma* fairly abundant, often arranged in tangential bands; end walls nodular but occasionally smooth. *Rays* uniseriate to partly bi-seriate consisting entirely of ray parenchyma, the tallest up to 29 cells in height, often with a complete separation of the middle lamella of horizontal cell walls, ray tracheids wanting.

**Dawn Redwood**
**(Cupressaceae)**

*Metasequoia glyptostroboides* Hu et Cheng.

**General Characteristics**

*Wood* without distinctive odor; medium texture, light (specific gravity 0.26; Jagels et al., in prep), soft . *Sapwood* pale yellow to cream color, distinct from heartwood; *heartwood* orange/red to pinkish. *Growth rings* distinct, delineated by narrow latewood; often sinuous; discontinuous and false rings common; earlywood zone several times wider than latewood zone; transition from earlywood to latewood more or less abrupt. *Parenchyma* sparse and barely visibly with a hand lens. *Rays* fine. *Resin canals* wanting.

**Minute Characteristics**

*Tracheids* up to 69 μm in tangential diameter; earlywood cells of mature stem wood averaging 773 cells per mm$^2$; bordered pits 1-4 (frequently 1-2) rows on radial

walls; sparse tangential pitting in latewood; pits leading to ray parenchyma taxodioid to cupressoid type, fairly large, 1-5 (frequently 2-4) pits per cross-field, often not aligned in marginal cells, otherwise arranged in single horizontal row. *Longitudinal parenchyma* diffuse; end walls smooth to slightly nodular. *Rays* uniseriate to partly bi-seriate consisting entirely of ray parenchyma, the tallest up to 38 cells in height, ray tracheids wanting.

## DISCUSSION

Previous studies of the wood anatomy of *Metasequoia* and *Glyptostrobus* were based on small sample sizes and features were often contradicted between authors (Table 1.2). We addressed this issue by observing more samples than previous studies (Table 1.1), tested published observations, and noted any additional characters unique to either species. Although we found one feature that, if used quantitatively, consistently separated the two species (separation of ray cells), we are uncertain whether this character is reliable for trees growing in all environments. Thus, we suggest the use of the suite of characters in Table 1.3, ordered from top to bottom: strongest to weakest.

The character that we observed regularly in *Glyptostrobus* and only rarely in *Metasequoia* was the separation of ray cells (Fig. 1.2 A-D). We are unaware of any other studies that have reported ray cell separation as a taxonomic feature of wood. Several researchers have discussed the presence, formation, and purpose of intercellular spaces within the rays of conifers (Laming, 1974; Panshin & deZeeuw,

Table 1.2. Published observations on extant *Metasequoia* and *Glyptostrobus* wood.

| Cells | Feature | *Metasequoia glyptostroboides* | *Glyptostrobus pensilis* | Author |
|---|---|---|---|---|
| Longitudinal Parenchyma | Horizontal end walls | Nodular | | Liang et al. (1948) |
| | | Smooth | Tangential -- 1 node Radial -- 2-3 nodes | Gromyko (1982) |
| | | | Slightly swollen, 1-2 nodes | Henry & McIntyre (1926) |
| | | Smooth (occasional pitting) | 3-4 bead-like nodes | Greguss (1955) |
| | Occurrence | Not abundant | Present in every ring | Gromyco (1982) |
| | | Scattered | | Hejnowicz (1973) |
| | | | 1-3 irregular bands per ring | Henry & McIntyre (1926) |
| | | Not abundant | Fairly abundant | Greguss (1955) |
| | | Not abundant | | Liang et al. (1948) |
| | | Metatracheal | | Li (1948) |
| Rays | Cross-field Pitting | 1-3 cupressoid/taxodioid | | Hejnowicz (1973) |
| | | 3 orbicular | | Li (1948) |
| | | 2-4 (mostly 2) taxodioid | | Liang et al. (1948) |
| | | 1-4 cupressoid/taxodioid | 1-4 cupressoid | Gromyko (1982) |
| | | | 2-6 (mostly 3-4) | Henry & McIntyre (1926) |
| | | Single row, sometimes double rows at margin | Not one horizontal row | Liang et al. (1948) |
| | Height (cells) | 3 to 8 (20 max) | | Liang et al. (1948) |
| | | 5 to 11 (34 max) | | Hejnowicz (1973) |
| | | 7 to 11 (17 max) | | Li (1948) |
| | | | 2-14 | Henry & McIntyre (1926) |
| | | 1-23 | 1-30 | Gromyko (1982) |
| | | 8-10 (exceptionally 16-18) | 1-18 (30) | Greguss (1955) |
| Tracheids | Maximum tangential diameter (um) | 66 | | Li (1948) |
| | Transverse cells per mm² | 1300 | 2200 | Greguss (1955) |
| | Earlywood - Latewood transition | Distinct | | Hejnowicz (1973) |
| | | | Gradual (young tree) | Henry & McIntyre (1926) |
| | | Gradual | Gradual | Gromyko (1982) |
| | | Gradual | | Li (1948) |
| | | Distinct | | Gerry (1950) |
| | | Distinct - abrupt | | Liang et al. (1948) |

Table 1.3. Combined features useful in separation of *Metasequoia* and *Glyptostrobus*.

| Feature | *Metasequoia glyptostroboides* | *Glyptostrobus pensilis* |
|---|---|---|
| Separation of ray cells | Absent - rare | Visible in every sample |
| Average number of earlywood cells in mature stem (std. dev.) | 773 (186) | 1400 (154) |
| Arrangement of crossfield pits | Single horizontal rows; random in marginal cells | Random, not aligned. |
| Horizontal end wall of longitudinal parenchyma | Usually smooth; occasionally slightly nodular | Usually nodular; occasionally smooth |
| Transition from earlywood to latewood | Abrupt | Gradual |
| Relative abundance and distribution of longitudinal parenchyma | Sparse | Abundant – often banded |
| Aroma | Absent | Present – similar to *Thuja* |

1980; Larson, 1994). Both *Metasequoia* and *Glyptostrobus* have pronounced

intercellular spaces in their rays, as has been reported for other species of

pedominately wet areas (Larson, 1994). In all our *Glyptostrobus* samples, however,

in addition to typical ray intercellular spaces formed at the corner of a cell, a complete

separation of ray cells along the middle lamella of horizontal walls was observed.

The feature was best observed in radial view (Fig 1.2 C, D), but could also be seen in

tangential sections (Fig 1.2 A, B). Separation of ray cells was observed in

*Metasequoia* in only two samples only at the boundary of the annual ring, and never

extended for more than 45 μm, radially. Separation was common in all of our

*Glyptostrobus* samples, it occurred randomly throughout the growth ring, and was

observed to extend over 200 μm in radial view. The purpose or mode of formation of

Figure. 1.1. Wood of *Metasequoia glyptostroboides* and *Glyptostrobus pensilis*. –A: Transverse section of *G. pensilis* with gradual transition from earlywood to latewood. – B-G: *M. glyptostroboides*. –B: Transverse section showing abrupt transition from earlywood to latewood. –C: Radial longitudinal section showing taxodioid/cupressoid type cross-field pitting arranged in single horizontal row and narrow latewood region. –D-E: Tangential longitudinal sections. –D: Tangential pitting (white arrows) and ray height (black arrow = 38 cells in height). --E-G: Horizontal end walls of longitudinal parenchyma (arrows). –E: Smooth wall. –F: Single node. –G: Two nodes. –Scale bars: A&B = 1000µm. C= 150µm. D=75µm. E-G=50µm.

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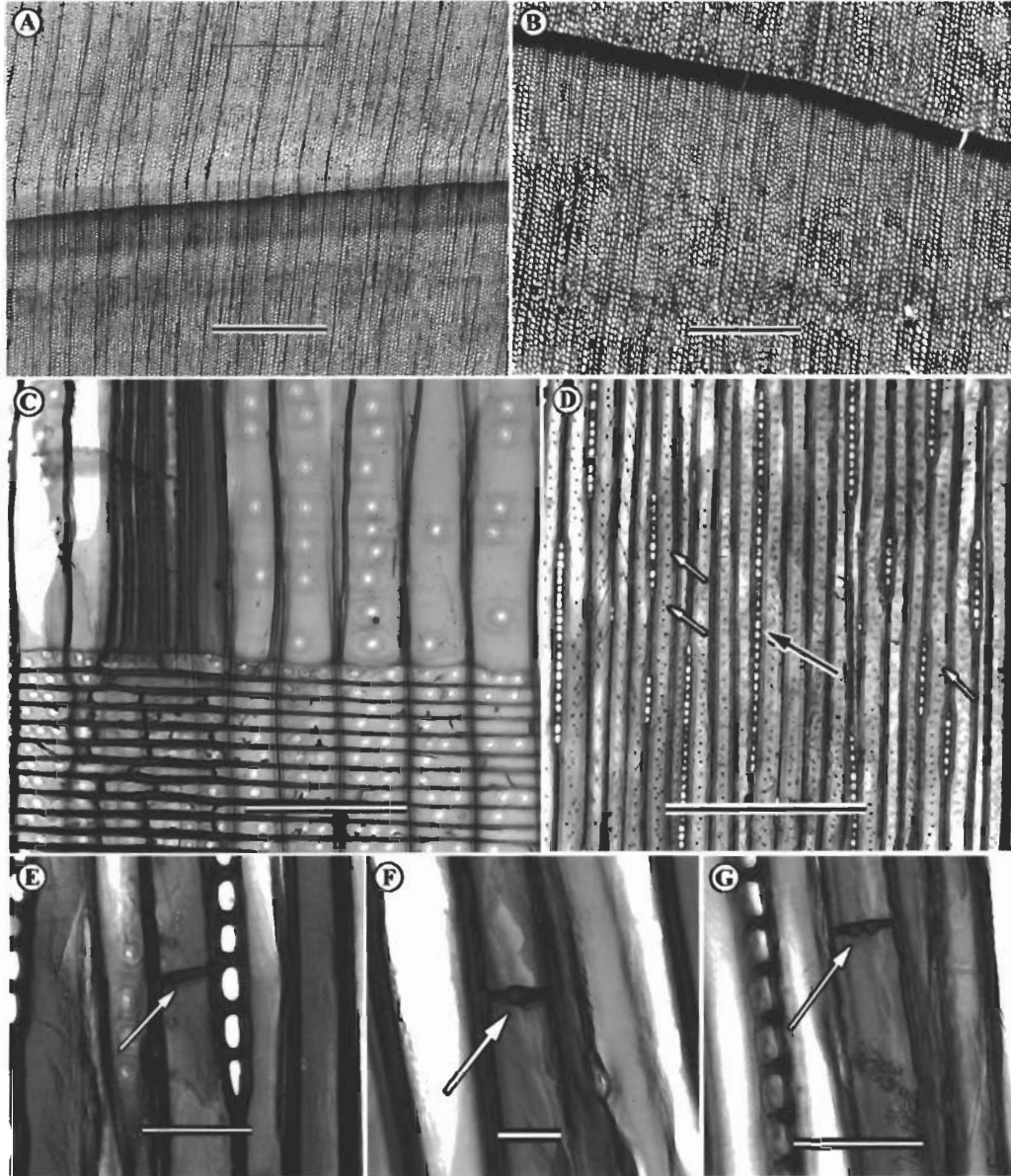
Figure 1.2. Wood of *Glyptostrobus pensilis*. –A&B: Tangential longitudinal sections, arrows indicating separation of ray cells. –C&D: Radial longitudinal sections, arrows indicating separation of ray cells. Note also, taxodioid/cupressoid type cross-field pitting with random pit arrangement. –E-G: Tangential longitudinal sections showing horizontal end walls of longitudinal parenchyma (arrows). –E: Smooth. –F: Single node. –G: Two nodes. – Scale bars: A&C=150µm. B, D-G=50µm.
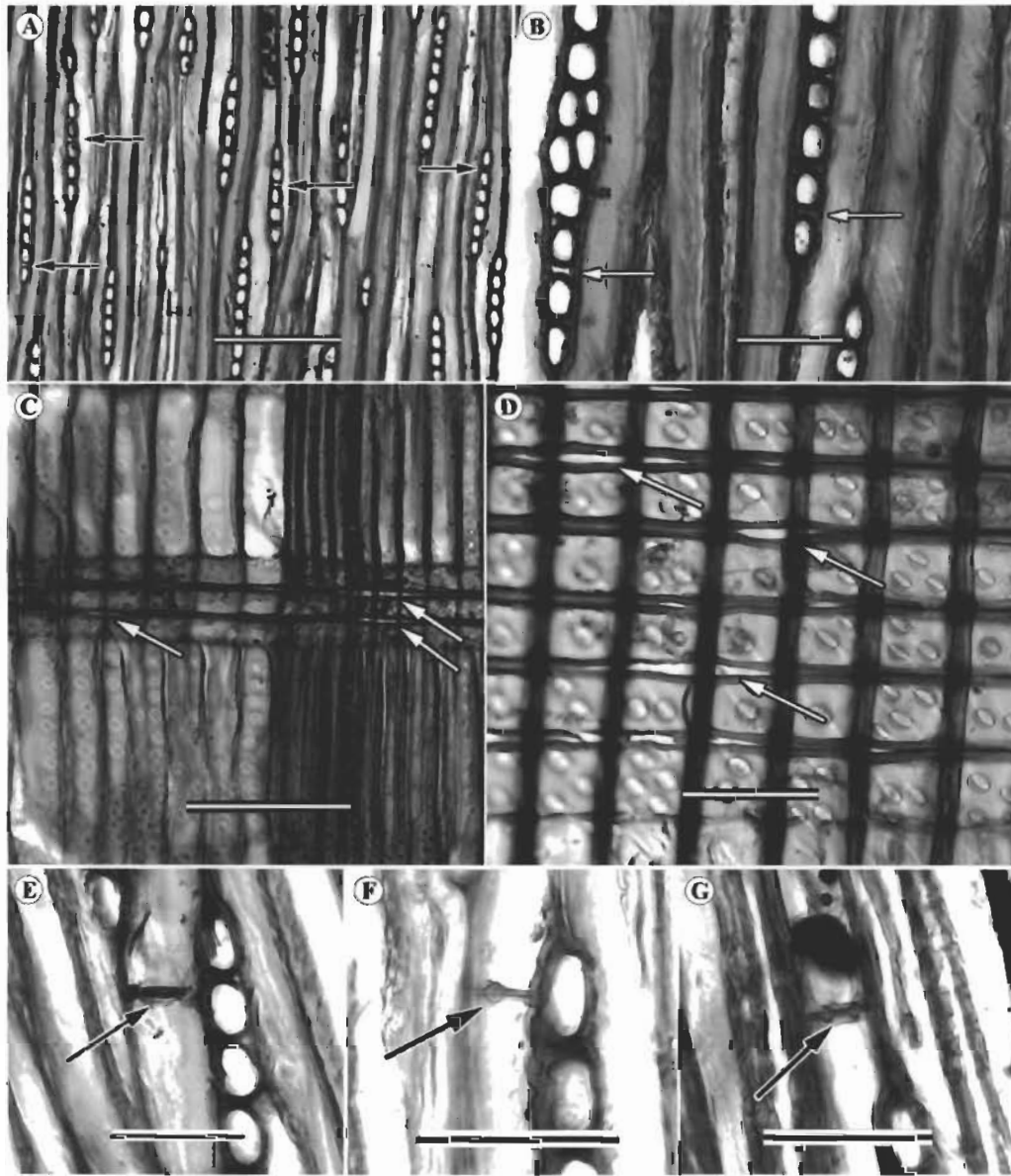
this feature is unknown. Because our samples may not be representative of all environments where *Glyptostrobus* may grow we suggest caution in using this feature as a sole indicator of the species.

Wood characters that we found in our samples did not always agree with those of previous studies (Table 1.2, 1.3). For example, we measured 772 and 1400 cells per mm$^2$ in the earlywood of *Metasequoia* and *Glyptostrobus*, respectively. Greguss (1955) reported values of 1300 and 2200 cells per mm$^2$. Possibly Greguss's observations were not of mature wood. In another study we obtained values up to 2427 cells per mm$^2$ at the pith of a 30-year-old *Metasequoia* (Visscher & Jagels, in prep). However, by the 14$^{th}$ ring, values were below those of *Glyptostrobus* and consistent with our vouchered samples by the 18$^{th}$ ring. Sample location is often unknown, especially in fossil wood, which adds to the complications of separating these woods. If average CPA values are less than 1400 cells/mm$^2$ for an unknown wood, it is unlikely to be *Glyptostrobus*. If higher CPA values are measured then it is possible that the wood may be juvenile *Metasequoia* or any age *Glyptostrobus*. In these cases, more emphasis should be placed on other features listed in Table 1.3. Based on our sampling ray cell separation and number of earlywood cells per mm$^2$ of mature stem wood, when combined, should consistently separate *Glyptostrobus* and *Metasequoia* in most cases.

Several authors have discussed end wall features of longitudinal parenchyma to aid in the identification of the two species (Greguss, 1955; Basinger 1981; Gromyko, 1982); characterizing *Metasequoia* with smooth end walls and *Glyptostrobus* with nodular end walls. We found that the features of the horizontal

end walls of longitudinal parenchyma are variable in both species. Although end wall features can be seen in both radial and tangential sections, they are more easily determined in the latter. While the majority of end walls in our *Metasequoia* samples are smooth, some are unquestionably nodular (Fig. 1.1 E-H). Those of *Glyptostrobus* are mostly nodular with 1, 2, or rarely 3 bead-like nodes (Fig. 1.2 F,G), although, we occasionally observed smooth end walls in this species (Fig. 1.2-E). Maácz (1955), Basinger (1981), and Gromyko (1982) also reported variability in this character. Maácz (1955) found that only 6% of horizontal end walls in a mature *Metasequoia* tree were smooth, 84% were swollen to slightly nodular, and 10% had a bead-like node.

The last three features listed in Table 1.3 are somewhat subjective with no quantitative value or present/absent indicator attributed to them. Transition from earlywood to latewood is often used in wood identification keys to describe how quickly earlywood tracheids change into thicker walled latewood tracheids. For example, it is used to separate hard from soft pines as well as a general feature to describe other species (Panshin & deZeeuw, 1980; Hoadley, 1990). We considered the transition from earlywood to latewood in mature *Metasequoia* to be abrupt (Fig. 1.1 B) and in *Glyptostrobus* to be gradual (Fig. 1.1 A). Other reports of this feature in *Metasequoia* are variable, while those for *Glyptostrobus* are consistent with our observations (Table 1.2).

Although the relative abundance and distribution of longitudinal parenchyma are parameters not easily quantified because of random variation within and among trees, these features have been used as diagnostic characters. For instance,

parenchyma is frequent and consistent in *Sequoia* and *Taxodium* and absent or

infrequent in *Pinus*, *Taxus*, *Torreya*, and *Larix* (Panshin & deZeeuw, 1980).

Transverse sections show diffuse longitudinal parenchyma in *Metasequoia*, while

parenchyma was consistently more abundant and somewhat banded in *Glyptostrobus*.

*Glyptostrobus* produces a strong and distinctive odor similar to that of *Thuja*

species. We did not find this character for *Glyptostrobus* wood reported in the

literature. We cannot confirm the "distinctive odor" in *Metasequoia* reported by

Gerry (1950) and Linnard (1966). Aroma is often used as a gross character

diagnostic to some species (Hoadley, 1990). Of course, regardless of its value for

relatively fresh wood, aroma would have no value for fossil samples.

As indicated by Panshin and deZeeuw (1980) maximum tangential tracheid

diameter may have diagnostic value, especially for species with unusually large (as in

*Sequoia*) or small (as in *Taxus*) diameters. We measured maximum tangential

diameters of 69 μm in *Metasequoia* and 45 μm in *Glyptostrobus*. T-tests on these

data do show distinct patterns, however, it is possible to have a *Metasequoia* sample

with maximum tangential diameters that fits within the upper limits of *Glyptostrobus*.

We measured maximum values in some *Metasequoia* samples below 45 μm. In most

conifers tracheid diameter increases with increasing distance from the pith (Panshin

& deZeeuw, 1980). Therefore, values may depend on sample location. By

measuring the number of tracheids per square millimeter in transverse sections (CPA)

a large number of tracheids are observed, increasing sample size and leading to

distinct, non-overlapping populations. This feature can be inferred qualitatively from

the somewhat finer texture of *Glyptostrobus* when compared directly to *Metasequoia* (Fig. 1.1 A, B).

Several authors observed the presence of traumatic resin canals or cysts in extant *Metasequoia* (Liang et al., 1948; Gerry, 1950; Greguss, 1955; Schönfeld, 1955). Basinger (1981) and Schönfeld (1955) reported the presence of traumatic resin canals in fossil wood identified as *Metasequoia*. We did not observe this feature in any of our extant samples. However, the absence of this feature from our samples is not significant because the feature depends on environmental perturbation and is, therefore, not of taxonomic value. The reason for mentioning the feature here is because it seems quite prevalent in *Metasequoia/Glyptostrobus* type fossil wood. We have observed what appear to be traumatic resin canals on several occasions in fossil *Metasequoia* wood.

To test the veracity of our anatomical separation of these species we examined a fossil wood sample that we had previously identified as *Metasequoia/Glyptostrobus* type. The sample was well preserved, but somewhat compressed in all directions. It had cross-field pitting similar to that of modern *Metasequoia*, longitudinal parenchyma end walls that were smooth, sparse occurrences of longitudinal parenchyma, and no separation of ray cells. CPA was intermediate between the two species. Compression of cells, especially in the earlywood region, however, likely inflates the measured CPA. Transition from earlywood to latewood could not be determined. These observations make a compelling case for placing the fossil in *Metasequoia*.

CHAPTER 2

# THE INFLUENCE OF CELL GEOMETRY ON WOOD STRENGTH

# IN *METASEQUOIA GLYPTOSTROBOIDES*

## SUMMARY

In this study we explore tracheid dimensions as they may reflect strength properties

of *Metasequoia* wood. Previous research of *Metasequoia* wood has shown that wood

strength increases from pith to bark, independent of specific gravity and microfibril

angle (Jagels et al., in prep). We have found that earlywood tracheid size (diameter

and length) as well as wall thickness increase from pith to bark. We hypothesize that

the increase in wood strength is due primarily to the increase in wall thickness

expressed mostly as an increase in the $S_2$ layer of the tracheid wall. We suggest that

this pattern enables wood with a small proportion of latewood (as in *Metasequoia*) to

increase in strength while creating hydraulically efficient cells (i.e. long, large

diameter and thick walled tracheids)

*Keywords:* *Metasequoia*, wood strength, hydraulic efficiency, $S_2$ layer, microfibril

angle, specific gravity, tracheid wall thickness

## INTRODUCTION

Conifers rely on one cell -- the tracheid -- for both support and water

transport. Any changes in tracheid dimensions will affect one or both functions of the

cell (Niklas, 1992; Domec & Gartner, 2002). The mechanical and hydraulic needs

and capabilities of tracheids change with age, species, and environmental conditions. However, most trees tend to follow the same general patterns of cell structure and resulting function. Being able to isolate the influences of an individual function is complicated by the intricate relationships between tracheid dimensions and function.

Traditional thought suggests that as strength increases hydraulic conductivity must decrease (Carlquist, 1975; Tyree et al., 1994; Domec & Gartner, 2002). This generality is based on the idea that as specific gravity (SG) increases the concomitant wall thickness increase will lead to smaller cell lumen diameter, reducing hydraulic efficiency. However, the mechanics of reaction wood clearly demonstrate that there is more to wood strength then the quantity of cell wall material per unit area. The quality of cell wall is variable between tracheids resulting in wood strength independent of SG. Most notably, the orientation of microfibrils in the $S_2$ layer of the tracheid wall has been shown to be important to wood strength (Cave & Walker, 1994; Nakada, et al., 1998; Walker & Woollons, 1998). Theoretically, a tree could increase tensile strength by altering its microfibril angle (MFA) yet still have the same hydraulic efficiency -- SG and tracheid diameter remaining constant.

Is it possible, however, for wood to increase in both strength and hydraulic efficiency without changing MFA or SG? The answer may lie in the distribution of cell wall material within and between tracheids in a growth ring. Conifers often produce earlywood tracheids that are mechanically weak but hydraulically efficient, and latewood tracheids that are mechanically strong but hydraulically inefficient. It is possible for trees to improve both functions with age by producing wider and longer earlywood tracheids along with thicker walled and more latewood tracheids (Domec

& Gartner, 2002). Some conifers, however, lack a well-defined latewood. The question we explore is how these species deal with strength and hydraulic efficiency within earlywood cells. We chose *Metasequoia* because it is hydraulically efficient and tall -- in need of sufficient mechanical strength (Jagels & Day, in prep; Jagels, et al. in prep).

Jagels, et al. (in prep) presented evidence that this species maximizes hydraulic conductance by producing relatively weak wood. Nevertheless, they found that two measures of wood strength -- modulus of elasticity (MOE), and modulus of rupture (MOR) -- increased from pith to bark. However, unlike most conifers, MFA and SG did not change much from pith to bark. These patterns motivate our study of tracheid form and function. In this study we investigate the influence of cell wall distribution as a function of tracheid diameter and cell wall thickness and relate these to changing strength values in *Metasequoia*.

## MATERIALS AND METHODS

Two *Metasequoia glyptostroboides* trees from closed canopy stands consisting mostly of *Metasequoia* were observed. One from New Jersey (PNJ – 28 annual rings at breast height) the other from the northern Jiangsu Province, China (JPC – 30 annual rings at breast height). The PNJ tree had previously been analyzed for MFA, tracheid length, SG, MOE, and MOR in a previous study (Jagels, et al., in prep).

Samples for anatomical work were taken at breast height and analyzed from pith to bark along opposing axes of a radial strip approximately 2cm by 2cm. Radial strips were selected to avoid compression wood, knots, and sinuses of the fluted stem.

Strips were progressively smoothed to a 600 grit sandpaper and scanned on a color flatbed scanner. Images were processed in WinDendro v. 6.3a (Régent Instruments Inc. – Québec, Qc, Canada) to obtain ring width data. Because of *Metasequoia*'s tendency to form false and incomplete growth rings every ring marked by the program was checked under a dissecting microscope to ensure that it was a true ring.

Samples for thin sections were taken beginning with the second ring and every forth ring thereafter; seven and eight rings in total for the PNJ and JPC trees respectively. Transverse sections (18-22 $\mu$m) were made using a sliding microtome (A.O. model 860) and stained overnight in 1% Bismark Brown before being mounted in a low viscosity medium (Cytoseal 60 – Richard-Allan Scientific) on microscope slides. Images were taken using a SPOT RT digital camera and software (Diagnostic Instruments) attached to a light microscope (Zeiss Axioskop) and PC (Toshiba Equium 7350M).

Measurements of the number of cells per square millimeter (CPA) were made using black and white images of transverse sections, at a magnification of 100x. Images were taken at the beginning of the first formed earlywood covering a default area of 1.02949 $mm^2$. Images were analyzed in Scion Image Beta 3b (Scion Corporation, Frederick, Maryland). They were first converted to threshold images using default settings and then processed using the "Analyze particles" command. This procedure automatically counts and measures objects by scanning across the image until it finds the boundary of the object, outlines, measures, and then redraws the object in a different gray level. Minimal particle size included in the count was set at 100 pixels and cells that touched the image edge were included in the analysis.

Values were adjusted to cells per square millimeter. Three images were taken from each section and averaged to obtain a value for the ring on one side of the pith. Values from each side of the pith were averaged to obtain a mean for the entire ring (six measurements per ring).

Percent cell wall measurements were made on the same images used for CPA observations. A small border was added around each image before it could be properly analyzed in WinSeedle v. 5.1A (Régent Instruments Inc. – Quebec, Qc, Canada). This was done using Photo-Paint (Corel). Images were converted to threshold images in the WinSeedle program. Because of slight variations in staining and section and image quality, threshold levels were adjusted for each image. Levels were manually set to maximize the amount of wall area converted into black pixels. Images were then analyzed both as dark objects on a pale background (to obtain percent wall area) and light objects on a dark background (to obtain percent lumen area). The combined values represent the total number of pixels in each image (1,920,000 pixels). A ratio of the number of pixels per millimeter was used to convert values to percent wall (or lumen) per square millimeter.

## RESULTS AND DISCUSSION

Figures 2.1 and 2.2 show the variation of ring width, CPA, percent wall material, MFA, and tracheid length for the PNJ and JPC trees respectively. MFA and tracheid length data were incorporated from Jagels et al. (in prep). Both trees followed similar patterns from pith to bark. However, tracheid dimensions in the JPC tree were consistently smaller than those of the slightly faster growing PNJ tree –
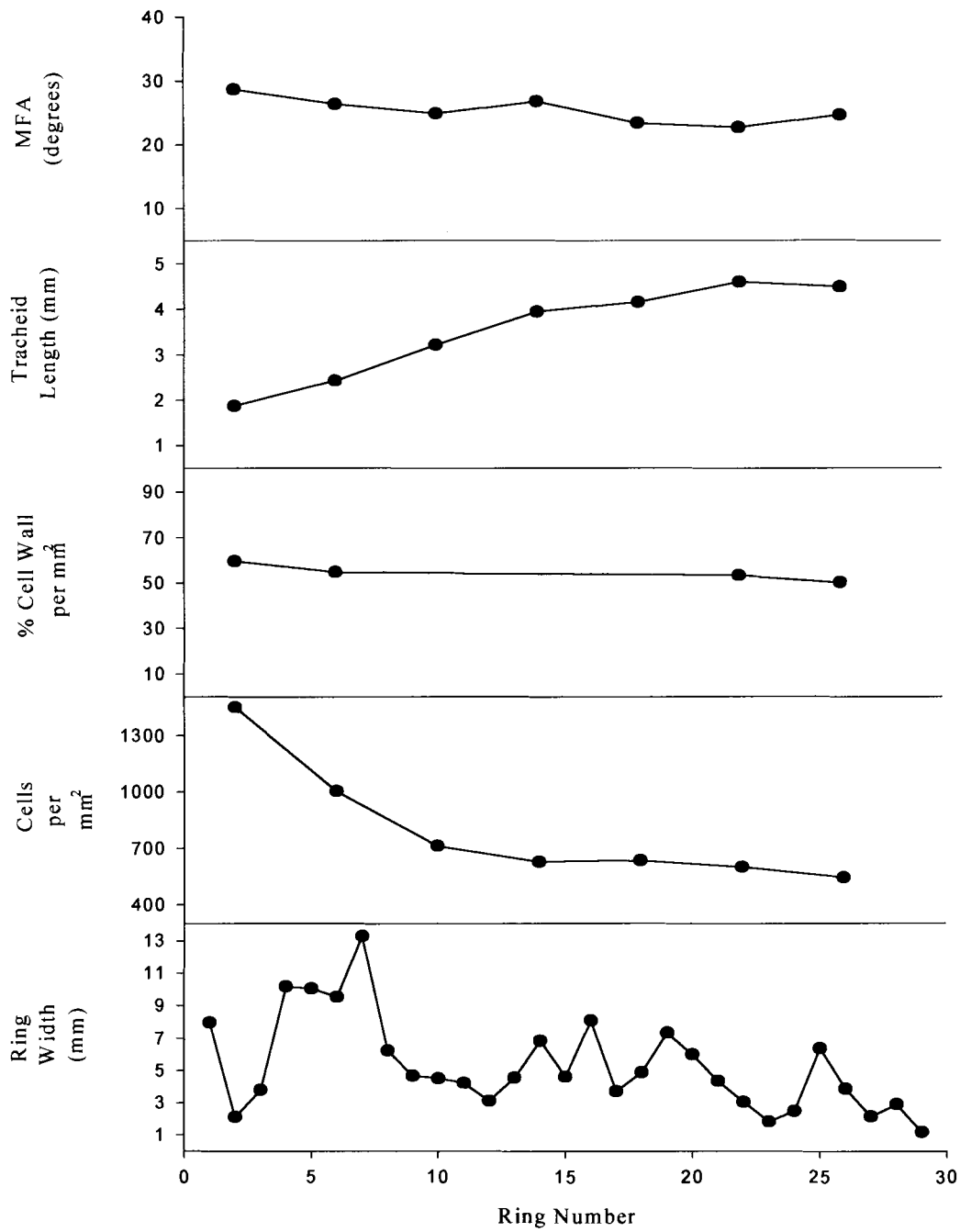
Figure 2.1 Tracheid dimensions of *Metasequoia glyptostroboides*
(PNJ tree) versus ring number from pith. (MFA and tracheid length
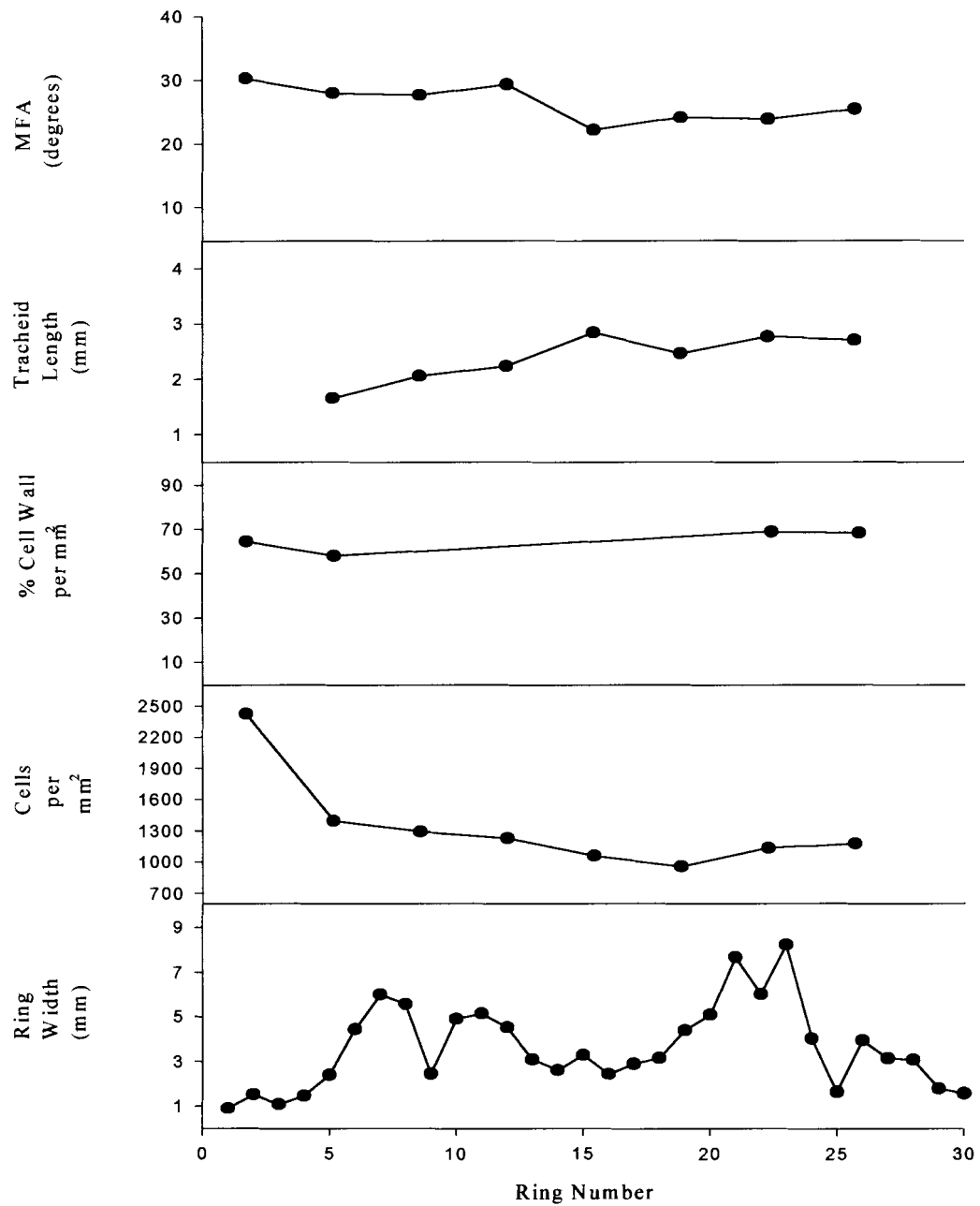adapted from Jagels et al., in prep)

Figure 2.2 Tracheid dimensions of *Metasequoia glyptostroboides* (JPC tree) versus ring number from pith. (MFA and tracheid length adapted from Jagels et al. in prep)

average tracheid length 2.39 mm and 3.53 mm respectively (Jagels et al., in prep). Of

the measurements made for this study only CPA varied significantly from pith to

bark. Average ring width for PNJ was 4.79 mm (std. dev. 0.73) with its largest rings

towards the center of the tree. The JPC tree had larger rings toward the bark with an

average ring width of 3.50 mm (std. dev. 0.87). Tracheid length and MFA have been

associated with ring width (Bannan, 1965, 1967; Hiller & Brown, 1967; McMillin,

1973; Fujiwara & Yang, 2000), but we did not observe a correlation between any

tracheid dimension and ring width in *Metasequoia*.

As previously shown (Jagels et al., in prep) *Metasequoia* follows normal

trends of increasing wood strength from pith to bark (Cave & Walker, 1994; Domec

& Gartner, 2002). A significant increase in MOR (29,100; 32,200 kPa), and a nearly

significant (p 0.0674) increase in MOE (3,470; 4,920 MPa) was measured between

inner and outer rings by Jagels et al. (in prep). Many studies have shown that wood

strength is most strongly correlated with specific gravity (Panshin & deZeeuw, 1980;

Easterling, 1982; Niklas 1992). Thus more cell wall material per unit area should

yield greater strength. Walker and Woollons (1997) found this to be true in a broad

general sense and is demonstrated in our Table 2.1 between different SG "groups".

*Metasequoia* supports this generality by being a very low-density wood that is

correspondingly weak, however, when SG is similar between species or within a tree

variations in wood strength must be attributed to other causes. For example, SG did

not vary in the PNJ tree from pith (0.28) to bark (0.27), while strength did (Jagels, et

al., in prep).

Table 2.1. Comparison of average tracheid diameter and strength characteristics of conifers species. Values obtained from Alden (1997) and Panshin and deZeeuw (1980).

| Species | Specific gravity (green value) | Average tangential diameter (um) | Modulus of rupture (kPa) | Modulus of elasticity (MPa) |
|---|---|---|---|---|
| Western Red Cedar *Thuja plicata* | 0.31 | **30-40** | **35800** | **6480** |
| Atlantic White Cedar *Chamaecyparis thyoides* | 0.31 | 25-30 | 32000 | 5200 |
| Northern White Cedar *Thuja occidentalis* | 0.29 | 20-30 | 29000 | 4410 |
| Port-Orford -Cedar Chamaecyparis lawsonia | 0.39 | **35-40** | **45500** | **8960** |
| Alaskan Yellow Cedar *Chamaecyparis nootkatensis* | 0.42 | 25-35 | 44000 | 7900 |
| Black Spruce *Picea mariana* | 0.38 | 25-30 | **42100** | **9510** |
| Sitka Spruce *Picea sitchensis* | 0.37 | **35-45** | 39300 | 8480 |
| Red Spruce *Picea rubens* | 0.37 | 25-30 | 41400 | 9170 |

Excluding reaction wood, researchers have sometimes noted that woods with similar specific gravities exhibit different strength values (Mark, 1967). These discrepancies have been explained by noting differences in microscopic properties of tracheid cell walls. Most notably microfibril angle of the $S_2$ layer has been found to have a profound impact on the mechanical properties of wood (Cave & Walker, 1994; Donaldson, 1998). Larger angles are usually associated with weaker, less stable wood. Juvenile (core) wood produced near the center of the tree, has larger angles than mature (outer) wood of the same species (Butterfield & Pal, 1998; Donaldson, 1998; Matsumura & Butterfield, 2001). In *Metasequoia*, there was a statistical difference between slightly higher MFA's at the second ring (28.7°, 30.3°) compared to MFA's of the outermost measured rings (24.7°, 25.5°) of the PNJ and JPC trees respectively. However, the decreasing trend was relatively flat (slopes = -0.1866 for PNJ and –0.2137 for JPC) and MFA's remained higher than those for most commercial woods of similar age (Hiller & Brown, 1967; Cave & Walker, 1998). Similar trends (flat slope and high MFA) have been measured in plantation grown *Pinus taeda* (McMillin, 1973) and the latewood of *Cryptomeria japonica* (Nakada et al., 1998). In the latter study mechanical tests were done in which one tree experienced the traditional negative correlation between MFA and MOE while in another tree no relationship between MFA and MOE was observed. Since SG and MFA in *Metasequoia* remain nearly constant from pith to bark, we explored other explanations for changes in wood strength.

Tracheid length of *Metasequoia* follows a typical pattern of rapidly increasing from the pith and leveling off around 15 growth increments (Panshin & deZeeuw,

1980; Jagels et al., in prep). Some studies have associated increasing strength to increased tracheid length (Wellwood 1962; Carlquist, 1975; Rundel & Stecker, 1977). Carlquist (1975) stated that trends of increasing tracheid length might be associated with an increased need for support. However, a plausible physical explanation that might link an increase in strength to an increase in tracheid length was not provided. Because tracheid length is usually associated with a decrease in MFA, (Wardrop & Dadswell, 1950; Hiller & Brown, 1967; Walker & Woollons, 1998) tracheid length may be acting as a surrogate for MFA. In *Metasequoia*, however, no relationship between tracheid length and MFA was observed. A similar lack of relationship has been reported in root wood of *Pinus radiata* and *P. nigra* (Matsumara & Butterfield 2001).

By considering wood as a composite material with tracheids as short fibers in a matrix, one can model the effect of fiber length on strength in the same way as for other composite materials. In short-fiber composites, once a minimum fiber aspect ratio (length/diameter: l/d) exceeds about 50:1 then increasing fiber length has little further impact on the strength of the composite (Agarwal & Broutman, 1990). Bannan (1965) observed tracheid l/d ratios for approximately 24 conifer species. The minimum average value he measured was 72:1 in a juvenile stem of *Thuja occidentalis*. The largest for mature wood was 143:1 for *Sequoia sempervirens*. From our measurements in *Metasequoia* we found a minimum l/d ratio of 80:1 at the center of the tree and 120:1 near the bark of the PNJ tree. Failure of fibers in short-fiber composites with low fiber aspect ratios involves fiber pullout, in which the fiber does not break, but separates from the matrix in which it is embedded. Mark (1967)

stated that failure in wood generally initiates in the $S_1$ layer of the cell wall, not between tracheids (i.e. the fiber itself breaks). Groom et al. (2002) showed that failure could occur when tracheids separate from each other. However, they observed this type of failure only in latewood tracheids of *Pseudotseuga menzenzii*. In earlywood cells, they only witnessed failure of tracheids themselves. *Metasequoia* does not produce a large amount of latewood, therefore, separation between tracheids is not likely to be the point of failure. Furthermore, our study only focused on earlywood. These empirical data support the hypothesis that tracheid length in *Metasequoia* exceeds minimal fiber aspect ratio and, therefore, should have little or no effect on strength.

Because SG, MFA, and tracheid length do not appear to be contributing to the differences in strength properties from pith to bark, we looked at other features in tracheid dimensions that might be responsible. While determining taxonomic characters for *Metasequoia* we developed a rapid technique to measure the number of tracheids per $mm^2$, which we designated cells per unit area (CPA) (Visscher & Jagels, in prep). A significant trend was noticed when this measurement was applied along pith-to-bark transects. CPA values for the PNJ tree was highest at the pith (1451 cells/$mm^2$), quickly decreased, leveling off by ring 10 (594 cells/$mm^2$), and reached a value of 544 cells/$mm^2$ by ring 26. Values for the JPC tree follow a similar trend, but the cells were somewhat smaller than those in the PNJ tree with 1867 cells/$mm^2$ at the pith and 827 cells/$mm^2$ near the bark. We used CPA values instead of average tracheid diameters because CPA measurements provide dimensional information

about a large group of tracheids rather than the smaller number of individual tracheids usually measured to create an average transverse tracheid parameter.

We also measured percent wall area per square millimeter near the center and outer rings of both trees on the same images from which CPA values were obtained. Percent wall area is a surrogate density measurement, and follows a similar pattern to SG. There was no significant change in the percent of wall material per square millimeter from pith to bark in either tree. Values of the second and outermost ring measured were, respectively, approximately 60% (std. dev. 4.7%) and 50% (std. dev. 2.7%) for the PNJ tree and 65% (std. dev. 15.7%) and 69% (std. dev. 2.4%) for the JPC tree. By looking at the CPA and percent wall area measurements it can be assumed that tracheid diameter and wall thickness of are increasing from pith to bark. This is shown in Figure 2.3 A and B, images from the $2^{nd}$ and $26^{th}$ ring of the PNJ tree respectively.

Because cell size clearly increases from pith to bark, we explored this as a possible influence on wood strength. While looking at parenchyma cells, Niklas (1992) discusses the effects of cell geometry and packing as influencing strength. He noted that when thin walled parenchyma cells that are closely packed their strength as a unit increases. This pattern is contrary to what we have found in the xylem of *Metasequoia*. However, Niklas's observation did not take changes of density into account. Easterling et al. (1982) discusses the strength of balsa wood with different densities. They analyze cellular strength using simple beam theory. In doing so they take into account both cell wall thickness and cell geometry. They analyzed changes in cell shape as wood is compressed in different directions. Its original and strongest

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Figure 2.3. Transverse sections of *Metasequoia glyptostroboides* (PNJ tree). – A: 2$^{nd}$ ring. –B: 26$^{th}$ ring. Note that the percent cell wall area in both images is statistically the similar. – Both images same at same magnification -- Scale bars = 400μm.
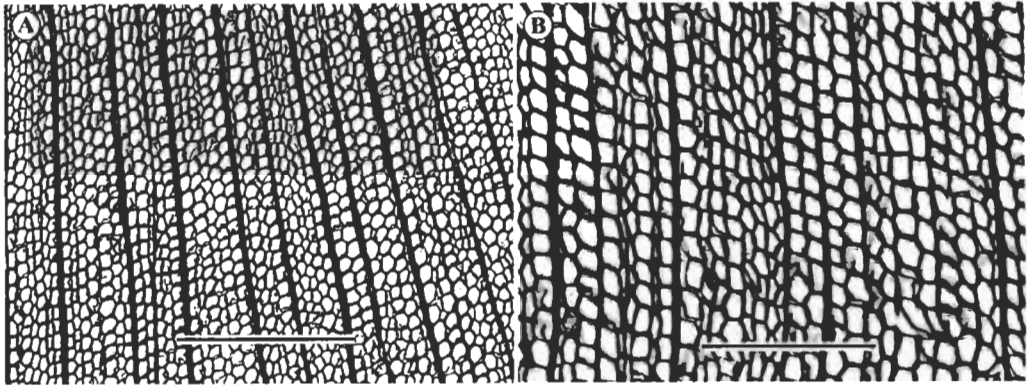
shape is a hexagonal prism. They concluded that this shape gives the cell axial stiffness but reduced transverse stiffness. The shape is similar to that of the cell used to make honeycomb composites. Marshall (1998) has shown that for honeycomb designs made from uniform homogeneous materials, such as aluminum, shear strength (similar to stresses that would be experienced by tracheids in bending) does not differ in honeycombs of the same density but with different cell size.

Unlike aluminum, wood is not a homogeneous material. The tracheid cell wall is multi-layered. The properties of each layer, as they affect strength, must be considered. Several authors have shown that the thickness of the primary (P) and $S_1$ layers is fixed and any increase in wall thickness is a consequence of additional production of the $S_2$ layer (Côté, 1965; Panshin & deZeeuw, 1980; Cave & Walker, 1994; Walker & Woollons, 1998). If this is the case, then the influence of the $S_2$ layer on wood properties will vary with wall thickness. Walker and Woollons (1998) noted that since 80% of the wall is the $S_2$ layer, its properties would most strongly influence the mechanical properties of wood. Other studies indicate the $S_2$ layer determines wood properties because it not only constitutes the majority of the cell wall, but also has a parallel microfibril arrangement (Kretschmann, et al., 1998). Huang et al. (1998) summarize this idea and discuss that strength and SG are highly correlated because SG and wall thickness are directly related -- thicker walls having more parallel microfibrils.

If the thickness of the P and $S_1$ layers are fixed in each tracheid, then the proportion per unit area of these layers is dependant on how many tracheids are present -- CPA. The total perimeter of CPA estimates the relative amount of P and $S_1$

material per unit area.  Figure 2.4 is a model of how total cell perimeter per area

changes with cell size.  In this model we have used smaller, but proportionally similar

values to those observed in the $2^{nd}$ and $26^{th}$ rings of the PNJ tree.  Assuming tracheids

as square in cross-section, by increasing cell size and decreasing CPA, *Metasequoia,*

has decreased its total perimeter per unit area, and thus has reduced the proportion of

P and $S_1$ layers per square millimeter.  Because cell wall area (or SG) does not change

significantly from pith to bark, outer rings contain a larger percentage of their cell

wall area in the stronger $S_2$ layer -- increasing strength despite the same SG and

MFA.

Comparing other Cuppressaceae woods with similar design strategies (woods

with little latewood) we see that there is support for a correlation between tracheid

diameter and strength when SG is held constant.  Table 2.1 is a compilation of

strength values at green conditions from Alden (1990) and tracheid dimensions from

Panshin and deZeeuw (1980).  Strength values are given green because these are

conditions closest to those in the living tree.  In each case for similar species with

matched SG, larger tracheids (i.e. larger diameters) are linked with stronger wood.  It

is possible that differences in MFA may be influencing these values, however,

assuming all the samples are mature wood, this should be minimized.  Also, because

cell wall thickness values were not available for these species, we assume that for

woods with the same SG those with larger tracheid diameters will also have thicker

cell walls.  Since these woods, like *Metasequoia,* lack significant latewood this is

likely a valid assumption.

Grid A                                    Grid B

Each grid = 1mm$^2$

|  | Cells per mm$^2$ | Total perimeter of all cells (mm) |
|---|---|---|
| Model (calculated) |  |  |
| Grid A | 36 | 24 |
| Grid B | 16 | 16 |
| Percent change (%) | 125 | 50 |
| PNJ Tree (estimated) |  |  |
| 2nd ring | 1467 | 152 |
| 26th ring | 633 | 100 |
| Percent change (%) | 132 | 52 |

Figure 2.4. Changes in total perimeter of all cells per mm$^2$ as a function of cell size in transverse sections -- theoretical model and estimated values from the PNJ tree.

In Table 2.1, the relationship between cell size and strength does not hold for *Picea* species -- trees with significant latewood. This is likely a consequence of the strength of latewood tracheids overwhelming the contribution of the earlywood tracheids, and, in fact probably represents a different design strategy for trees that produce a significant amount of latewood.

## CONCLUSIONS

*Metasequoia,* a low-density wood lacking a well-defined latewood, provides an opportunity to study the effects of cell wall thickness and cell shape on wood strength. Because tracheids are responsible for mechanical strength and hydraulic conductance, any variation in their structure will influence both functions. We previously suggested that *Metasequoia* produces wood that is specialized to maximize hydraulic conductance through enlarged tracheid diameters (Jagels et al., in prep). It appears that *Metasequoia* simultaneously improves both hydraulic function and mechanical strength with distance from the pith. While this trend is contrary to the traditional strength/conductance tradeoff view of xylem anatomy (Carlquist, 1975; Tyree, et al., 1994), we suggest that this adaptation may also occur in other species that lack well-defined latewood.

REFERENCES

Agarwal, B.D. & L.J. Broutman. 1990. Analysis and performance of fiber composites. John Wiley & Sons Inc., New York.

Alden H.A. 1997. Softwoods of North America. Forest Products Laboratory. General Technical Report. FPL-GTR-102.

Bannan, M.W. 1965. The length, tangential diameter, and length/width ratio of conifer tracheids. Can. J. Bot. 43: 967-984.

Bannan, M.W. 1967. Anticlinal divisions and cell length in conifer cambium. For. Prod. J. 17(6): 63-69.

Bartholomew, B., D.E. Boufford & S.A. Spongberg. 1983. Metasequioa Glyptostroboides - Its present status in Central China. J. Arnold Arbor. 64: 105-128.

Basinger, J.F. 1981. The vegetative body of Metasequoia milleri from the Middle Eocene of southern British Columbia. Can. J. Bot. 59: 2379-2410.

Basinger, J.F. 1984. Seed cones of Metasequoia milleri from the Middle Eocene of southern British Columbia. Can. J. Bot. 62: 281-289.

Basinger, J.F. 1991. The fossil forests of the Buchanan Lake Formation (early Tertiary), Axel Heiberg Island, Canadian high arctic: preliminary floristics And paleoclimate. In: R.L. Christie & N.J. McMillan (Eds.), The Fossil Forests of Tertiary Age in the Canadian Arctic Archipelago. Geol. Surv. Can. Bull. 403: 39-66.

Blanchette, R.A., K.R. Cease, A.R. Abad, T.A. Burnes & J.R. Obst. 1991. Ultrastructural characterization of wood from Tertiary fossil forest in the Canadian Arctic. Can. J. Bot. 69: 560-568.

Brazier, J.D. 1963. The timber of young plantation-grown Metasequoia. Quart. J. For. 57(2): 151-153.

Butala, J.R. & A.A. Cridland. 1978. Nomenclature of fossil Glyptostrobus in North America. Taxon. 27: 15-20.

Butterfield, B. & V. Pal. 1998. Relating microfibril angle to wood quality in clonal seedlings of radiata pine. In: B. Butterfield (Ed.), Microfibril angle in wood: 337-347. University of Canterbury, Christchurch.

Carlquist, S. 1975. Ecological strategies of xylem evolution. University of California Press, Berkley.

Cave, I.D. & J.C.F. Walker. 1994. Stiffness of wood in fast-grown plantation softwoods: the influence of microfibril angle. For. Prod. J. 44(5): 43-48.

Creber, G.T. & W.G. Chaloner. 1985. Tree growth in the Mesozoic and early Tertiary and the reconstruction of paleoclimates. PALAEO. 52: 35-60.

Côté, W.A. (Ed.) 1965. Cellular ultra structure of woody plants. Syracuse University Press, Syracuse.

Denne, M.P. 1973. Tracheid Dimensions in relation to shoot vigor in Picea. Forestry. 46(2): 117-124.

Domec, J.C. & B.L. Gartner. 2002. Age- and position-related changes in hydraulic versus mechanical dysfunction of xylem: inferring the design criteria for Douglas-fir wood structure. Tree Physiology. 22: 91-104.

Donaldson, L.A. 1998. Between-tracheid variability of microfibril angles in radiata pine. In: B. Butterfield (Ed.), Microfibril angle in wood: 206-224. University of Canterbury, Christchurch.

Easterling, K.E., R. Harrysson, L.J. Gibson & M.F. Ashby. 1982. On the mechanics of balsa and other woods. Proc. R. Soc. Lond. A. 383: 31-41.

Eckenwalder, J.E. 1976. Re-evaluation of Cuppressaceae and Taxodiaceae: A proposed merger. Madroño. 23(5): 237-300.

Florin, R. 1952. On Metasequoia, living and fossil. Botaniska Notiser. 105: 1-29.

Fujiwara, S. & K.C. Yang. 2000. The relationship between cell length and ring width and circumferential growth rate in five Canadian species. IAWA J. 21(3): 335-345.

Gerry, E. 1950. Information Leaflet -- Foreign Woods: "Dawn Redwood" – Metasequoia glyptostroboides. U.S.D.A. For. Prod. Lab. Wood.

Greguss, P. 1955. Identification of living gymnosperms on the basis of xylotomy. Academiai Liado, Budapest. (English translation by L. Joesik).

Gromyko, D.V. 1982. Comparative anatomical study of wood in the family Taxodiaceae. Botanicheskiaei zhurnal. 67(7): 898-906.

Groom, L., L. Mott & S. Shaler. 2002. Mechanical properties of individual Southern Pine fibers. Part I. Determination and variability of stress-strain curves with respect to tree height and juvenility. Wood and Fiber Sci. 34(1): 14-27.

Hejnowicz, A. 1973. Anatomical studies on the development of Metasequoia glyptostroboides Hu et Cheng wood. ACTA Societatis Botanicorum Poloniae. XLII(3): 473-491.

Henry, A. & M. McIntyre. 1926. The swamp cypresses, Glyptostrobus of China and Taxodium of America, with notes on allied genera. Proc. Royal Irish Acad. 37(13): 90-116.

Hiller, C.H. & R.S. Brown. 1967. Comparison of dimensions and fibril angles of loblolly pine tracheids formed in wet or dry growing seasons. Am. J. Bot. 54(4): 453-460.

Hirakawa, Y., K. Yamashita, Y. Fujisawa & Y. Kijidani. 1998. The effects of S2 microfibril angles and density on MOE in sugi logs. In: B. Butterfield (Ed.), Microfibril angle in wood: 312-322. University of Canterbury, Christchurch.

Hoadley, B.R. 1990. Identifying Wood: accurate results with simple tools. The Taunton Press, Newtown.

Huang, C-L., N.P. Kutcha, G.J. Leaf & R.A. Megraw. 1998. Comparison of microfibril measurements techniques. In: B. Butterfield (Ed.), Microfibril angle in wood: 177-205. University of Canterbury, Christchurch.

Jagles, R. & M.E. Day. In press. The adaptive physiology of Metasequoia to Eocene high-latitude environments.

Jagels, R., G.E. Visscher, J. Lucas & B. Gudell. In prep. Paleo-adaptive properties of the xylem of dawn redwood (Metasequoia glyptostroboides Hu et Cheng) – mechanical/hydraulic compromises.

Judd, W.S., C.S. Campbell, E.A. Kellogg, P.F. Stevens & M.J. Donoghue. 2002. Plant systematics: a phylogenetic approach, 2nd Ed. Sinauer Associates, Inc., Sunderland.

Kretschmann, D.E., H.A. Alden & S. Verrill. 1998. Variations of microfibril angle in loblolly pine: comparison of iodine crystallization and x-ray diffraction techniques. In: B. Butterfield (Ed.), Microfibril angle in wood: 157-176. University of Canterbury, Christchurch.

Kumagai, H., T. Sweda, K. Hayashi, S. Kojima, J.F. Basinger, M. Shibuya & Y. Fukaoa. 1995. Growth-ring analysis of Early Tertiary conifer woods from the Canadian High Arctic and its paleoclimatic interpretation. PALAEO. 116: 247-262.

Laming, P.B. 1974. On the intercellular spaces in the xylem ray parenchyma of Picea abies. Acta Bot. Neerl. 23(3): 217-223.

Larson, P.R. 1994. The vascular cambium: development and structure. Springer-Verlag, New York.

Li, H-L. 1957. The discovery and cultivation of Metasequoia. Morris Arb. Bull. 8(4): 49-53.

Li, J. Y-H. 1948. Anatomical study of the wood of "Shuisha" (Metasequoia glyptostroboides Hu Et Cheng). Tropical Woods. 94: 28-29.

Liang, H., K.Y. Chow & C.N. Au. 1948. Properties of a "living fossil" wood (Metasequoia glyptostroboides). Wood Technol. 1: 1-6.

Linnard, W. 1966. A note on the wood of Metasequoia. Wood. 31:46.

Maácz, Von G.J. 1955. Moacz; Holzanalytische untersuchungen bezüglich Metasequoia glyptostroboides Hu et Cheng. Acta biologica (Szeged, Hungary). 1: 36-40.

MacIntyre, D.J. 1991. Pollen and spore flora of an Eocene forest, Eastern Axel Heiberg Island, N.W.T. In: R.L. Christie and N.J. McMillan (Eds.), The fossil forests of Tertiary Age in the Canadian Arctic Archipelago. Geol. Surv. Can. Bull. 403: 83-98.

Mark, R.E. 1967. Cell wall mechanics of tracheids. Yale University Press, New Haven.

Marshall, A.C. 1998. Sandwich construction. In: S.T. Peters (Ed.), Handbook of composites: 254-290. Chapman & Hall, New York.

Matsumura, J. & B.G. Butterfield. 2001. Microfibril angle in the root wood of Pinus radiata and Pinus nigra. IAWA J. 22(1): 57-62.

McMillin, C.W. 1973. Fibril angle of loblolly pine wood as related to specific gravity, growth rate, and distance from pith. Wood Sci. Technol. 7: 251-255.

Matsumoto, M., T.A. Ohsawa, M. Nishida & H. Nishida. 1997. Glyptostrobus rubenosawaensis sp. nov., a new permineralized conifer species from the Middle Miocene, Central Hokkaido, Japan. Paleontological Res. 1(2): 81-99.

Momohara, A. 1994. Paleoecology and Paleobiogeography of Metasequoia. Fossils. 57: 24-30.

Nakada, R., Y. Fujisawa, K. Nishimura & Y. Hirakawa. 1998. Variation in $S_2$ microfibril angle of latewood among plus-tree clones and test stands in Cryptomeria japonica D. Don. In: B. Butterfield (Ed.), Microfibril angle in wood: 367-374. University of Canterbury, Christchurch.

Niklas, K.J. 1992. Plant biomechanics: An engineering approach to plant form and function. The University of Chicago Press, Chicago.

Panshin, A.J. & C. deZeeuw. 1980. Textbook of wood technology. 4th Ed. McGraw-Hill, Inc., New York.

Rundel, P.W. & R.E. Stecker. 1977. Morphological adaptations of tracheid structure to water stress gradients in the crown of Sequoiadendron giganteum. Oecologia, Berlin. 27(2): 135-139.

Schönfeld, E. 1955. Metasequoia in der Westdeutschen Braunkohle. Senckenbergiana lethaea. 36(5/6): 389-399.

Stockey, R.A., G.W. Rothwell & A.B. Falder. 2001. Diversity among taxodioid conifers: Metasequoia foxii sp. nov. from the Paleocene of central Alberta, Canada. Int. J. Plant Sci. 162(1): 221-234.

Tyree, M.T., S.D. Davis & H. Cochard. 1994. Biophysical prospectives of xylem evolution: Is there a tradeoff of hydraulic efficiency for vulnerability to dysfunction? IAWA J. 15(4): 335-360.

Visscher, G.E. & R. Jagles. In prep. Separation of Metasequoia from Glyptostrobus based on wood anatomy.

Walker, J.C.F. & R.C. Woollons. 1998. Cell wall organization and the properties of xylem – a speculative review. In: B. Butterfield (Ed.), Microfibril angle in wood: 13-26. University of Canterbury, Christchurch.

Wardrop, A.B. & H.E. Dadswell. 1950. The nature of reaction wood II. The cell Wall organization of compression wood tracheids. Aust. J. Sci. Res., B. 3: 1-12.

Wellwood, R.W. 1962. Tensile testing of small wood samples. Pulp Paper Mag. Can. 63(2): T61-T67.

Wu, S-C. & J-H. Chern. 1995. Group analysis as applied to wood anatomy of Taxodiaceae member. National Taiwan Univ. Ag. Col. research report. 35(3): 360-374.

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