This is to certify that the
thesis entitled
HYDRAULIC, BIOMECHANICAL, AND ANATOMICAL STUDY OF XYLEM FROM FIVE TREE SPECIES OF ACER.
presented by
CARRIE LEIGH WOODRUM
has been accepted towards fulfillment of the requirements for
M.S: degree in Botany and Plant Pathology


Major professor
$\square$

## LIBRARY Michigan State University

PLACE IN RETURN BOX to remove this checkout from your record. TO AVOID FINES return on or before date due. MAY BE RECALLED with earlier due date if requested.

| DATE DUE | DATE DUE | DATE DUE |
| :---: | :---: | :---: |
|  |  |  |
|  |  |  |
|  |  |  |
|  |  |  |
|  |  |  |
|  |  |  |
|  |  |  |
|  |  |  |
|  |  |  |
|  |  |  |
|  |  |  |
|  |  |  |

6/01 c:/CIRC/DateDue.p65-p. 15

# HYDRAULIC, BIOMECHANICAL, AND ANATOMICAL STUDY OF XYLEM FROM FIVE TREE SPECIES OF $A C E R$ 

By<br>Carrie Leigh Woodrum

## A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

## MASTER OF SCIENCE

Department of Botany and Plant Pathology

# ABSTRACT <br> HYDRAULIC, BIOMECHANICAL, AND ANATOMICAL STUDY OF XYLEM FROM FIVE TREE SPECIES OF $A C E R$ 

## By

## Carrie Leigh Woodrum

Possible tradeoffs between hydraulic conductivity and mechanical properties of Acer negundo, A. saccharinum, A. rubrum, A. nigrum, and A. saccharum were assessed. It has been shown that tradeoffs between xylem specific conductivity ( $\mathrm{K}_{8}$ max ) and modulus of elasticity (MOE) and modulus of rupture (MOR) occur in cogeneric chaparral shrubs and vines versus trees and shrubs. The current study attempted to determine if this tradeoff is present in five cogeneric tree species in a similar habitat. Acer negundo, A. saccharinum, and $A$. rubrum are considered soft maples and are known to be fast growing and shade-intolerant. Conversely, A. nigrum and A. saccharum are classified as hard maples and are slow-growing and shade-tolerant. It was hypothesized that the soft maples would have lower MOE and MOR, but higher $\mathrm{K}_{8} \max$ than the hard maples. Minute anatomical and general morphological characteristics were measured in an attempt to correlate them to any water transport and/or mechanical strength differences between species. No difference was found between species in vessel diameter, water conductivity, or percent embolism. Similarly, no tradeoff was found between $\mathrm{K}_{\mathrm{s} \text { max }}$ and MOE or MOR across the genus. Fiber lumen diameter was inversely correlated to both MOE and MOR. Surprisingly, percent ray parenchyma was positively linearly related to MOE. This suggests that transport/mechanical tradeoffs are not universal across every genus within a similar environment.

## DEDICATION

To my parents; for their eternal love and support.

## ACKNOWLEDGEMENTS

I would like to thank Dr. Frank Ewers for serving as my advisor and mentor. His infinite knowledge and experience helped to make sense of a gaggle of data. Also, his encouragement furnished reassurance when I needed it most. Thank you to my other committee members, Dr. Frank Telewski and Dr. Pete Murphy for their advice and discussions on interpretation of results.

I would especially like to thank Dr. Bradley Marks, Agriculture Engineering, for teaching me the ins and outs of the Instron and its archaic software. Thank you to Dr. Alan Jones, Plant Research Lab, for use of his Leaf Area Meter and lab space.

Many thanks to Kris Kern, Nick Mirsky, and Dawn Langdon for the pre-dawn mornings and long days in the lab fighting with the Sperry Apparatus. I could not have finished this project without you!

## TABLE OF CONTENTS

GENERAL BACKGROUND ..... 1
Xylem Components. ..... 1
Hydraulic Conductivity ..... 2
Biomechanics ..... 4
Tradeoffs. ..... 7
MATERIALS AND METHODS ..... 11
Plant Material ..... 11
Site Description ..... 12
Vessel Lengths ..... 12
Hydraulic Conductivity: Variation among Species ..... 13
Biomechanics: Variation among Species ..... 15
Intra-tree Hydraulic Conductivity and Biomechanical Variation. ..... 17
Anatomical Study ..... 18
Maceration ..... 18
Cross Sections ..... 18
General Morphology ..... 19
Data Analysis ..... 19
RESULTS ..... 20
Vessel Lengths. ..... 20
Intra-tree Hydraulic Conductivity and Biomechanical Variation. ..... 20
Hydraulic Conductivity: Variation among Species. ..... 20
Biomechanics: Variation among Species ..... 20
Anatomical Study ..... 21
Macerations ..... 21
Cross Section. ..... 21
General Morphology ..... 22
Tradeoffs ..... 23
DISCUSSION ..... 39
LITERATURE CITED ..... 46

## LIST OF TABLES

Table 1: Mean Maximum Vessel Lengths. Each mean is followed by one standard error.
$\mathrm{n}=10$
Table 2: Intra-tree Hydraulic Conductivity Variation. Each mean is followed by one standard error. Values for $\mathrm{K}_{\mathrm{h} \text { initial }}\left(\mathrm{kg} \mathrm{m} \mathrm{MPa}^{-1} \mathrm{~s}^{-1}\right)$ are $10^{-5}$. Values for $\mathrm{K}_{\mathrm{h} \text { max }}$ ( $\mathrm{kg} \mathrm{m} \mathrm{MPa}{ }^{-1} \mathrm{~s}^{-1}$ ), $\mathrm{HV}\left(\mathrm{m}^{2} \mathrm{~m}^{-2}\right)$, and LSC $\left(\mathrm{kg} \mathrm{MPa}^{-1} \mathrm{~s}^{-1} \mathrm{~m}^{-1}\right)$ are $10^{-4}$. Units for $\mathrm{K}_{\mathrm{s} \text { max }}$ are $\left(\mathrm{kg} \mathrm{MPa}^{-1} \mathrm{~s}^{-1} \mathrm{~m}^{-1}\right) . \mathrm{n}=6$.

Table 3: Intra-tree Biomechanical Variation. Each mean is followed by one standard error. Values for $\mathrm{EI}\left(\mathrm{N} \mathrm{mm}^{2}\right)$ and MOE ( $\mathrm{N} \mathrm{mm}^{-2}$ ) are $10^{5}$. Values for MOR ${ }_{\sigma}$ $\left(\mathrm{N} \mathrm{mm}^{-2}\right)$ are $10^{3}$. Units for I are ( $\mathrm{N} \mathrm{mm}^{4}$ ). $\mathrm{n}=6$

Table 4: Hydraulic Conductivity. Each mean is followed by one standard error. Values for $\mathrm{K}_{\mathrm{h} \text { initial }}\left(\mathrm{kg} \mathrm{m} \mathrm{MPa}^{-1} \mathrm{~s}^{-1}\right)$ are $10^{-5}$. Values for $\mathrm{HV}\left(\mathrm{m}^{2} \mathrm{~m}^{-2}\right)$ are $10^{-4} \cdot \mathrm{n}=20$ for $\mathrm{K}_{\mathrm{h} \text { initial, }}$, and $\%$ Embolism. $\mathrm{n}=18$ for $\mathrm{K}_{\mathrm{max}}\left(\mathrm{kg} \mathrm{MPa}^{-1} \mathrm{~s}^{-1} \mathrm{~m}^{-1}\right)$, and $\mathrm{HV} \ldots \ldots \ldots . .26$

Table 5: Dry Modulus of Rupture (MOR ${ }_{D}$ ) ( $\mathrm{Nmm}^{-2}$ ). Each mean is followed by one standard error. $n=6$. .29

Table 6: Macerations: Each mean is followed by $\pm$ one standard error. $n=8$ for all variables except percent vessel lumen area and fiber lumen diameter ( $\mathrm{n}=18$ ). $\% \mathrm{~V}=$ percent vessels, $\% \mathrm{FT}=$ percent fibers, \%AP = percent axial parenchyma, $\mathrm{VL}_{\text {avg }}=$ average vessel lumen diameter, $\mathrm{VL}_{\max }=$ maximum vessel lumen diameter, $\mathrm{VL}_{\text {min }}=$ minimum vessel lumen diameter, $\mathrm{VW}=$ vessel wall thickness, $\mathrm{FL}=$ fiber lumen diameter, FW = fiber wall thickness, PL = parenchyma lumen diameter, PW = parenchyma wall thickness .30

Table 7: Cross Sections. Each mean is followed by $\pm$ one standard error. $n=18$. \% Vessels = percent vessel lumen area, \% Fibers = percent fiber area, \% Rays = percent ray parenchyma area, $\mathrm{VL}_{\text {avg }}=$ average vessel lumen diameter, $\mathrm{VL}_{\text {max }}=$ maximum vessel lumen diameter, $\mathrm{VL}_{\text {min }}=$ minimum vessel lumen diameter, $\mathrm{HD}=$ hydraulic diameter, Vessel Frequency $=10^{-4}$ vessels per $\mu \mathrm{m}^{2}$

Table 8: General Morphology. Means are followed by $\pm$ one standard error. $\mathrm{n}=20$ for Stem Diameter and Xylem Diameter. $\mathrm{n}=18$ for \% Conductive Growth Rings and Conductive Xylem Area. 35

## LIST OF FIGURES

Figure 1: Mean Maximum Hydraulic Conductivity $\left(\mathrm{K}_{\mathrm{h} \max }\right) \pm$ one standard error. $\mathrm{n}=20$.25
Figure 2: Mean Leaf Specific Conductivity (LSC) $\pm$ one standard error. $\mathrm{n}=18$ ..... 26
Figure 3: Mean Flexural Stiffness (EI) $\pm$ one standard error. $n=20$ ..... 27
Figure 4: Mean Second Moment of Cross Sectional Area (I) $\pm$ one standard error. $\mathrm{n}=20$. ..... 27
Figure 5: Mean Modulus of Elasticity (MOE) $\pm$ one standard error. $n=20$ ..... 28
Figure 6: Green Modulus of Rupture $\left(\mathrm{MOR}_{\mathrm{G}}\right) \pm$ one standard error. $\mathrm{n}=14$. ..... 28
Figure 7: Mean Fiber Lumen Diameter $\pm$ one standard error. $n=18$ ..... 29
Figure 8: Mean Pith Area $\pm$ one standard error. $\mathrm{n}=20$ ..... 32
Figure 9: Mean Number of Growth Rings $\pm$ one standard error. $\mathrm{n}=20$. ..... 32
Figure 10: Mean Bark Thickness $\pm$ one standard error. $\mathrm{n}=20$ ..... 33
Figure 11: Mean Green Wood Density (Densityg) $\pm$ one standard error. $\mathrm{n}=18$ ..... 33
Figure 12: Dry Density (Densityd) versus Green Density (Densityg). Vertical lines areone standard error of Density $\quad(n=6)$. Horizontal lines are one standard error ofDensity $_{\mathrm{g}}(\mathrm{n}=14) . \Delta=A$. negundo, $\star=A$. saccharinum, $\square=A$. rubrum,$\mathrm{X}=A$. nigrum, $\mathrm{x}=A$. saccharum .34
Figure 13: Mean Distal Leaf Area $\pm$ one standard error. $n=20$. ..... 34

Figure 14: Modulus of Elasticity (MOE) versus Maximum Specific Conductivity $\left(\mathrm{K}_{\mathrm{s} \max }\right)$. Vertical lines are one standard error of MOE $(\mathrm{n}=20)$. Horizontal lines are one standard error of $\mathrm{K}_{\mathrm{m} \max }(\mathrm{n}=18) . \Delta=A$. negundo, $*=A$. saccharinum, $■=$. rubrum, $\mathrm{X}=$ A. nigrum, $\mathrm{x}=$ A. saccharum.

Figure 15: Green Modulus of Rupture (MOR ${ }_{\mathbf{G}}$ ) versus Maximum Specific Conductivity $\left(K_{s} \max \right)$. Vertical lines are one standard error of MOR $_{G}(n=14)$. Horizontal lines are one standard error of $\mathrm{K}_{\mathrm{m} \max }(\mathrm{n}=18) . \Delta=$ A. negundo, $\uparrow=$. saccharinum, $■=$ A. rubrum, $\mathrm{X}=$ A. nigrum, $\mathrm{x}=A$. saccharum. 36

Figure 16: Modulus of Elasticity (MOE) versus Fiber Lumen Diameter. Vertical lines are one standard error of MOE $(\mathrm{n}=20)$. Horizontal lines are one standard error of fiber lumen diameter $(\mathrm{n}=18)$. $\Delta=A$. negundo, $\star=A$. saccharinum, $\square=$ A. rubrum, $\mathrm{X}=$ A. nigrum, $\mathbb{*}=A$. saccharum.

Figure 17: Green Modulus of Rupture $\left(\mathrm{MOR}_{\mathbf{G}}\right)$ versus Fiber cell wall thickness : Fiber lumen diameter. Vertical lines are one standard error of MOR $_{G}(n=14)$. Horizontal lines are one standard error of FW:FL ( $\mathrm{n}=8$ ).

Figure 18: Green Modulus of Rupture (MOR ${ }_{G}$ ) versus Fiber Lumen Diameter. Vertical lines are one standard error of $\mathrm{MOR}_{\mathrm{G}}(\mathrm{n}=14)$. Horizontal lines are one standard error of fiber lumen diameter $(\mathrm{n}=18)$. $\Delta=$ A. negundo, $\star=$ A. saccharinum, - = A. rubrum, $x=A$. nigrum, $\boldsymbol{x}=A$. saccharum

Figure 19: Modulus of Elasticity (MOE) versus Percent Ray Parenchyma. Vertical lines are one standard error of MOE $(\mathrm{n}=20)$. Horizontal lines are one standard error of percent ray parenchyma $(\mathrm{n}=18) . \Delta=A$. negundo, $\star=A$. saccharinum, $\square=$ A. rubrum, $\mathrm{x}=$ A. nigrum, $\aleph=A$. saccharum.

KEY TO ABBREVIATIONS

| Abbreviation |  |
| :---: | :---: |
| Densityg | Green density |
| Density ${ }_{\text {d }}$ | Dry density |
| EI | Flexural stiffness |
| FL | Fiber lumen diameter |
| FL:FW | Fiber cell wall thickness : lumen diameter |
| FW | Fiber cell wall thickness |
| HD | Hydraulic diameter |
| HV | Huber value |
| I | Second moment of area |
| $\mathrm{K}_{\text {h }}$ | Hydraulic conductivity |
| $\mathrm{K}_{\mathrm{hintial}}$ | Initial hydraulic conductivity |
| $\mathrm{K}_{\mathrm{h} \text { max }}$ | Maximum hydraulic conductivity |
| $\mathrm{K}_{\text {s }}$ | Specific conductivity |
| $\mathrm{K}_{\text {s max }}$ | Maximum specific conductivity |
| LSC | Leaf specific conductivity |
| MOE | Modulus of elasticity |
| $\mathrm{MOR}_{\text {D }}$ | Dry modulus of rupture |
| $\mathrm{MOR}_{\mathrm{G}}$ | Green modulus of rupture |
| \% AP | Percentage of cells in a maceration identified as axial parenchyma |
| \% F | Percentage of cells in a maceration identified as fibers. |
| \% Fibers | Percent of cross sectional area composed of fiber |
| \% Rays | Percent of cross sectional area composed of ray parenchyma |
| \% V | Percentage of cells in a maceration identified as vessels |
| \% Vessels | Percent of cross sectional area composed of vessel lumen area |
| PL | Axial parenchyma lumen diameter |
| PW | Axial parenchyma cell wall thickness |
| VLavg | Average vessel lumen diameter |
| $\mathrm{VL}_{\text {max }}$ | Maximum vessel lumen diameter |
| $\mathrm{VL}_{\text {min }}$ | Minimum vessel lumen diameter |
| VW | Vessel cell wall thickness |

## GENERAL BACKGROUND

## Xylem Components

The secondary xylem tissue (wood) of angiosperm trees is not a homogenous material. It is a complex tissue composed of parenchyma, vessel elements, and fibers. Each of these cell types serves an important role and will be addressed in turn.

Parenchyma is living tissue and serves several functions in wood. The pith of a stem or branch is comprised of parenchyma. The cells are filler-tissue and the surrounding wood takes on structural properties of a hollow cylinder (Niklas, 1992). Additionally, rays in secondary xylem are made of parenchyma. Here, the cells assist in storage of carbohydrates and minerals and in lateral water and mineral transport (Mauseth, 1988). There can also be axial parenchyma within the wood, however, this cell type is sparse in Acer and could be ignored for purposes of this study (Panshin and de Zeeuw, 1980).

Vessel elements fulfill a plant's need for water by acting as a transport conduit. They have large diameter lumens and thin cell walls relative to other xylem components. Since they lack end walls, vessel elements can stack end to end and form long, uninterrupted tubes conducive to water flow. A negative pressure in the xylem column occurs during transpiration when water is evaporated through stomata of leaves (Dixon, 1914). Combined with the cohesion properties of water, these factors allow xylem to act like a capillary tube, pulling water up through the trunk and branches (Zimmerman, 1983; Pockman et al., 1995; Sperry et al., 1996).

Fibers are the principal load bearing cells in dicot angiosperm wood. They serve as mechanical support and protect the other cell types from mechanical damage.

These cells are elongated in the direction of the stem or branch axis. Their lumens are narrow and they possess relatively thick cell walls (Niklas, 1992).

Theoretically, there is an infinite number of ways to construct wood. As long as basic requirements are fulfilled, only the available resources and evolutionary/gentic constrictions restrict the tree. On the contrary, ensuring the ability to effectively execute basic functions, such as water conduction and mechanical support, can be more complicated than one might think.

## Hydraulic Conductivity

In order to photosynthesize and grow, a plant must be supplied with adequate water. This immediately brings to mind rainfall or irrigation. Although having a sufficient source of water is of course crucial, the physics of how it is transported is just as important. Ideally, a plant needs to optimize water flow rates through the stem and branches in order to maximize growth rate.

According to Poiseuille's Law, theoretical hydraulic conductivity of a capillary tube is related to the radius to the fourth power (Zimmermann, 1983).

$$
L p=\pi r^{4} / 8 \mu
$$

Where, $r$ is the radius of the lumen and $\mu$ is the viscosity of the liquid. Since $r$ is raised to the fourth power, if radius is increased even slightly, hydraulic conductivity dramatically increases. Thus, the hydraulic conductivity of a branch or stem segment would be equal to the sum of the hydraulic conductivity for all vessels in a cross sectional area. Theoretically, a tree with a few wide vessels can have the same hydraulic conductivity as a tree with many, narrow vessels. However research suggests that species tend to increase vessel diameter rather than vessel frequency to
increase water transport (Arnold, 1999; Gartner, 1991a; Villar-Salvador et al., 1997). This is probably because the larger diameter vessels contribute disproportionately more to total conductivity than more narrow vessels. Furthermore, the production of cell wall material is an energetically expensive process.

It was once widely accepted that larger vessel diameters increased the susceptibility to embolism (Baas, 1983; Carlquist, 2001; Hargrave et al., 1994). Embolism reduces the ability of a plant to conduct water by blocking the water column with a bubble of air. If the extent of embolism is great enough metabolic processes are disrupted and growth is limited (Schultz \& Matthews, 1988). Zimmermann (1983) proposed the idea that drought-induced embolism occurs via airseeding. This occurs when air is pulled into a vessel from an adjacent embolized vessel. Sperry and Tyree (1988, 1990) and Sperry et al. (1991) supported his hypothesis. Sperry and Tyree (1988) developed an equation that could predict the pressure gradient at which air seeding would occur. Their equation was dependent, not on the conduit diameter, but the diameter of the pit pores on the pit membranes adjoining two cells. Further research has supported their hypothesis (Sperry and Tyree, 1988; Jarbeau et al., 1995; Alder et al., 1996).

The relationship of hydraulic conductivity to the architecture of the tree can be determined by calculating specific conductivity $\left(\mathrm{K}_{\mathrm{s}}\right)$. Specific conductivity is a measure of the porosity of a branch or stem segment. It is equal to maximum hydraulic conductivity divided by the cross-sectional area of the sapwood (Tyree and Ewers, 1991).

A common value used to quantify an individual tree's efficiency of xylem per leaf area is the Huber value (HV). This value is defined as the cross sectional area of the conductive tissue divided by the leaf area distal to that area (Zimmerman, 1983; Tyree and Ewers, 1991). A tree that is more adapted to support rather than conductivity will have a greater HV (Patino et al., 1995). Since water is less available, cell lumens must be narrow to prevent extensive embolism, the occlusion of a cell's lumen by an air pocket (Sperry and Sullivan, 1992). Therefore, the tree should be less efficient at conduction (i.e. more xylem area per leaf area, a greater HV) but have greater mechanical strength due to a large cell wall to lumen area ratio (i.e. greater wood density).

Trees with identical HV can have different amounts of water traversing that area of xylem. For a given area, the number and lumen diameter of conduits affects the quantity of available water. Therefore, another value, leaf specific conductivity (LSC) is also a useful tool for describing the water conducting sufficiency of a tree. This is equal to $K_{h}$ divided by the leaf area distal to the segment. This value is indicative of the relative amount of water available to the leaves. Leaf specific conductivity is also equal to HV multiplied by $\mathrm{K}_{\mathrm{s}}$ (Zimmerman, 1983; Tyree and Ewers, 1991).

## Biomechanics

The biomechanics of a tree are very important to consider because a tree's strength determines its ability to cope with both static and dynamic loading stress. If the mechanical strength of the xylem is not sufficient, loss of branches due to breakage will occur. This may be detrimental to the survival of the individual tree if
infection follows. Breakage of limbs also results in loss of photosynthetic areas and reproductive structures. Since xylem makes up the majority of the cross sectional area of a tree, it plays a crucial role in support. Self-loading due to gravity and forces from environmental factors such as wind, rain, snow, and ice are of utmost concern.

These environmental factors impose a stress, and may cause deformation in wood, called strain. The slope of a stress-strain curve is the ratio of external stress to the resultant displacement. This value is called the Young's modulus, or modulus of elasticity (MOE), and is a function of an elastic strain (Niklas, 1992). An elastic strain is reversible. The product of the elastic modulus and the second moment of area (I), the distribution of mass in the cross section, is flexural stiffness (EI). Flexural stiffness measures the ability of wood to resist bending. When the elastic strains are exceeded, changes in shape and structure occur which may become permanent, this is a plastic strain. Modulus of rupture (MOR) is a measure of the force at which breakage occurs, as can occur with plastic strains (Niklas, 1992).

Trees often form reaction wood in response to displacement with respect to the gravitational vector, a plastic strain (Telewski, 1995). For instance, reaction wood, specifically tension wood in angiosperms, is thought to be a mechanism for restoring branches and vertical axes to the desired orientation. Tension wood is characterized by an increase in gelatinous fibers with thicker cell walls than in normal wood (Telewski, 1995; Telewski et. al. 1995). The larger amount of cell wall material increases the density of the wood, and thus the mechanical strength.

The ratio of cell wall thickness to conduit lumen diameter and the number of cells per unit area impacts the density and mechanical strength of wood (Dinwoodie,
1981). The number of cells in a cross sectional area influences strength because neighboring cells act as buttresses which increases the stiffness of the tissue (Easterling et al., 1982; Gibson and Ashby, 1982).

Mechanical strength properties of a particular wood will vary depending on what type of stress the sample is subjected to. There are tension, compression, and shear stresses. Wood has greater tensile and compressive strength in the longitudinal direction than in radial or tangential (Wainwright, 1976). In the present study, breakage of limbs due to self-loading due to gravity and weight from foliage, fruit, snow, ice, and other environmental factors are of concern. Loss of limbs, and their leaves and fruits, reduce the photosynthetic area and the contribution of offspring to the next generation. Therefore, the present study will focus on bending strength.

Theory concerning the biomechanics of dried wood is well established as a result of the use of wooden beams in construction (Gere and Timoshenko, 1984). However, the biomechanics of green wood is a relatively new field. In applying beam theory to trees we use several assumptions. For simplicity, branches are treated as solid, homogenous cylinders despite the fact that wood is a anisotropic material and its MOE depends on the amount and distribution of the various component layers (Niklas, 1992). Secondly, green wood lacks a precise MOR (Spatz and Bruechert, 2000). A branch can be strained past the elastic phase and still not break, but is plastically deformed. Although the tissue will be damaged, it is advantageous for the tree to retain the branch if it is still functional.

## Tradeoffs

It seems intuitive that as vessel lumen area increases, conductivity would also increase, but that the strength of the branch would be reduced due to less cell wall material. However, wood is an anisotropic material and other anatomical variables can confound the influence of the number and diameter of conduits. These include variables such as percent tension wood, pith diameter, ray width, percentage of fiber per unit area, and fiber cell wall thickness, to name a few. Since selective pressures differ between environments, "optimum" structures vary by habitat.

Due to the complexity of the interactions between anatomy, hydraulic conductivity and mechanical strength of wood, there have been few studies addressing all three variables. Early work focused on just two factors at a time.

Gartner (1991a,b) showed that in Toxicodendron diversilobum HV was smaller but that $\mathrm{K}_{\mathrm{s} \text { max }}$ was greater, for the vine (supported) growth habit than for the unsupported shrubs. This was due to the fact that the supported vines had similar vessel frequency but greater lumen area than shrubs. It was found that although vines had a smaller maximum fiber wall thickness than shrubs, the shrub was significantly more dense only at $\mathrm{p}<0.054$. As a result, it was concluded that structural stability was a function of the second moment of area rather than material stiffness.

Ewers and Fisher (1991) found that a vine in the genus Bauhinia had less xylem per distal leaf area than a tree or shrub of the same genus. Vines allocate fewer resources to xylem since they are not free standing and instead depend on other plants or structures for support. To compensate hydraulically for the reduced xylem area, vines have long and wide vessels. However, that study used specimens from a
botanical garden and not a natural habitat. In addition, the mechanical strength of the test specimens was not directly measured.

Similarly, Chiu and Ewers (1992) found that free-standing shrubs had a greater amount of xylem but a smaller percent conductive xylem than a vine of the same genus (Lonicera). In this case, the plant dedicates the greatest portion of its wood to mechanical support. Again, this study utilized specimens cultivated in pots rather than native habitat and mechanical strength was not tested.

Wagner et al. (1998) compared two pairs of chaparral shrubs in a similar habitat. Adenostoma sparsifolium had significantly greater mean and maximum vessel diameters, corresponding to a $34 \%$ greater vessel lumen area and a two-fold $\mathrm{K}_{\text {s }}$
 density, 37\% smaller MOE, and 30\% smaller MOR. Similar tradeoffs occurred between Ceanothus megacarpus and C. spinosus.

Although their study was innovative, there was one confounding factor. The hydraulic conductivity and mechanical strength tests of a given species were not performed on the same segments. In fact, the branches for each test came from different sites. This is a problem because changes in selective pressures between sites can affect the anatomical development and evolution of each population. In addition, an average of conductivity and strength of a species is not as accurate as a particular hydraulic conductivity value to a measured vessel lumen area and a strength value to percentage of fiber and fiber wall thickness in a given branch. For this reason, the following research will evaluate the conductivity, mechanical strength, and anatomical characteristics of each segment.

This research was conducted in an effort to determine if tradeoffs really do occur in terms of conductivity and mechanical strength, as a result of anatomical characteristics. In light of past research, this study will examine five species of the same genus and growth habit to determine if tradeoffs occur across multiple species. A site where all species are native to the same general habitat has been chosen as the test site. This will allow for moderate control over habitat-related physiological differences. All species will be examined to quantify any differences in anatomy. The results will be used as rationale for any significant variation between species in hydraulic conductivity and/or mechanical strength properties.

Wood density is inversely correlated with growth and positively related to longevity (Putz et al., 1983). Furthermore, Lawton (1982) showed that shade tolerance was positively related to wood density. Thus, trees that are shade tolerant are, in general, slow growing, long-lived and greater in wood density than shade intolerant species.

The United States Department of Agriculture conducted research on strength properties of commercially important woods including A. saccharum, A. nigrum, A. saccharinum, and $A$. rubrum (Handbook 72). Measurements were taken in the green condition (moisture content of $58-66 \%$ ). The specific gravity of $A$. saccharum and A. nigrum was 0.56 and 0.52 , respectively. The specific gravity of Acer saccharinum and $A$. rubrum was 0.44 and 0.49 , respectively. They found that the MOE and MOR for $A$. saccharum was the largest of all four species. Additionally, $A$. saccharinum had a significantly smaller MOE and MOR than the other species.

The microhabitat in which a tree typically grows may reflect the priorities that have evolved for that species. For instance, Acer negundo is often found in moist areas near streambeds and is a mechanically weak tree. On the other hand, Acer saccharum prefers well-drained soils and is a much stronger tree (Barnes 1981). Therefore, one might expect that $A$. negundo will have a greater $\mathrm{K}_{\mathrm{s} \max }$, and thus wider vessel lumens, than $A$. saccharum due to a more abundant water source. Perhaps $A$. negundo has evolved to conduct more water transport at the expense of mechanical strength and $A$. saccharum evolved to maximize mechanical strength over conduction.

Based on the above, the hypotheses were as follows: Acer nigrum and $A$. saccharum are expected to be statistically similar and to have the most narrow vessels and highest percentage of fiber content. Subsequently, they would have the lowest $\mathrm{K}_{\mathrm{s}}$ ${ }_{\text {max }}$ and highest MOE and MOR of the five species. Significantly larger diameter vessels and a smaller percentage of fiber are anticipated for $A$. saccharinum and $A$. rubrum. Their $\mathrm{K}_{\mathrm{s} \max }$ hypothesized to be comparable to one another, yet statistically greater than that of $A$. nigrum and A. saccharum. Lastly, A. negundo is expected to have the widest vessels and lowest percentage of fiber, resulting in the lowest MOE and MOR with the highest $\mathrm{K}_{\mathrm{s} \text { max }}$.

## MATERIALS AND METHODS

## Plant Material

The timber industry divides the relative strength of timber produced by various species into softwood (conifers) and hardwood (broad-leafed trees) according to the hardness of the wood. Furthermore, within each division there is a relative gradient of wood strength. Acer is a hardwood genus that has a diverse range of strengths by species.

Soft maples include $A$. saccharinum L . and $A$. rubrum L and $A$. negundo. These three species are included in Section Rubra Pax. Microscopically, these species are virtually indistinguishable from one another. The woods are diffuseporous with rays that are never wider than the broadest vessel. Uniseriate rays are common in $A$. rubrum but scarce in $A$. saccharinum which tends to have up to 5seriate rays (Panshin and de Zeeuw, 1980).

Acer nigrum and A. saccharum are included within hard maples. In fact, Gelderen (1994) places them both in Section Acer, Series Saccharodendron (Rafinesque) Murray, A. saccharum Marshall ssp. saccharum being the type species and the former, a subspecies, A. saccharum ssp. nigrum (Michaux f) Desmarais. They also have diffuse-porous wood, but have two types of rays (Panshin and de Zeeuw, 1980). The broader rays are mostly 5-7-seriate contrast with narrow rays, which are typically uniseriate. A. nigrum and A. saccharum hybridize readily and thus are often sold indiscriminately as hard maples (Panshin and de Zeeuw, 1980).

## Site Description

Several species of Acer are native to the southern Lower Peninsula of Michigan. Five of these: Acer saccharinum L., Acer nigrum Michx. f., Acer rubrum L., Acer saccharum Marsh., and Acer negundo L., occur at Lott Woodlot in Ingham County. Lott Woodlot is an undeveloped natural area under the management of Michigan State University. The 17.8 ha area is dominated by Acer saccharum, Fagus grandifolia, and Ulmus americana (Frye, 1976). The diversity of soil type, topography and seed bank led Darlene Frye (1976) to divide the woodlot into ten distinct microhabitats. These range from dry upland beech-maple forest in the north, to the poorly drained floodplain around Felton Drain on the east.

After bud break the canopy of Lott Woodlot becomes closed, creating a densely shaded understory. However, Felton Drain and several trails cut through the site creating gaps in the canopy. With a few exceptions, native maples are relatively tolerant of filtered light. Acer saccharum and A. nigrum in particular thrive in the shade (Barnes, 1981). In fact, the understory of Lott is dominated by A. saccharum saplings (Frye, 1976). Acer negundo, in contrast, occurs mostly in disturbed or open areas where sunlight is more abundant (Barnes, 1981).

## Vessel Lengths

On five days between late May and early July in 2000 entire horizontal, first order branches were collected from two individuals of each of the five species. Branches were cut off and placed in black plastic bags with wet paper towels to prevent dehydration. In the lab, within two hours of collection, the branch tip was cut off (at a diameter of approximately seven mm ) and the distal end of the remaining
branch was attached to a pressurized $\mathrm{N}_{2}$ tank. Maximum vessel lengths were determined via modified air method (Zimmermann and Jeje, 1981). A pressure not to exceed 172 kPa was applied as the proximal end of the branch was held under water. The proximal end was cut back with shears until bubbles appeared from the xylem. Care was taken to ensure bubbles had not originated from the bark or pith. The length of each segment was then measured with a ruler and added to one half the length of the last portion excised. The average axis diameter (with bark) of the distal and proximal ends was measured using a digital caliper.

## Hydraulic Conductivity: Variation among Species

On five days of late June and early July of 2000, and five days in July and early August of 2001, one branch from each of two individuals of all five species was collected. Branches were first order and from the lower crown. Efforts were made to pick portions that were relatively straight, about eight millimeters in diameter, unbranched, and without wounds.

The study of vessel length indicated that none of the species had average maximum vessel lengths longer than 36 cm . Consequently, the branch was cut from the tree at a length at least 36 cm proximal to the segment to be used for conductivity measurements. The branches were then placed in a black plastic bag to reduce evapotranspiration and subsequent introduction of embolism. In the lab, branches were recut under water, to prevent introduction of new embolism, to a final length of approximately 15 cm .

Leaves distal to the segment were collected and stored in a sealed plastic bag in a refrigerator until leaf areas were measured, usually within a week. Any leaves on
the segment itself were retained on the branch until the termination of the conductivity measurements and then stored like those aforementioned.

The bark was removed approximately three cm back from the cut ends of the segments. The segments were then fitted with rubber tubing and connected to a Sperry apparatus (Sperry et al., 1988). Degassed 10 mMol citric acid was filtered through a $0.2 \mu \mathrm{~m}$ mesh Gelman filter to discourage microbial growth and allowed to flow via gravity from a known height through the inlet pipe connected to the distal and of the branch segment. An outlet pipe collected citric acid in a beaker on a Sartorious ISO 9001 electronic balance. A timer was used to measure flow rate for each branch segment in order to calculate hydraulic conductivity in the native state ( $\mathrm{K}_{\mathrm{h} \text { initial }}$ ). Any emboli, native or mechanically induced during collection, were then removed via perfusion with citric acid at 172 kPa for fifteen minutes. Hydraulic conductivity measurements and perfusion were alternated until conductivity remained stable ( $\mathrm{K}_{\mathrm{h} \text { max }}$ ), within ten percent, between consecutive trials for a given branch, usually just two perfusions.

Following conductivity measurements, conductive vessels were stained using $0.5 \%$ Crystal Violet. Tubing was fitted to the distal end of each segment and filled with the dye. When Crystal Violet could be seen at the proximal end of the specimen, double distilled water was added to the tubing and allowed to flow through the stem to flush out any excess dye. Branch segments were then sealed in a plastic bag with a moist paper towel and refrigerated until mechanical testing, within ten days.

The average xylem cross-sectional area and heartwood areas were measured for each segment using digital calipers. Since heartwood does not contribute to
conductive tissue this area was subtracted from the total cross sectional area of the branch before conductivity calculations (Zimmermann, 1978). Hydraulic conductivity (initial and max) was calculated using the equation:

$$
\mathrm{K}_{\mathrm{h}}=\mathrm{F} /(\mathrm{dP} / \mathrm{dx})
$$

(Tyree and Ewers, 1991)
where F is the water flux $(\mathrm{kg} / \mathrm{s})$, and $\mathrm{dP} / \mathrm{dx}$ is the pressure difference causing the flow ( $\mathrm{MPa} / \mathrm{m}$ ). Maximum specific conductivity was calculated and is defined as:

$$
\mathrm{K}_{\mathrm{s}}=\mathrm{K}_{\mathrm{h} \max } / \mathrm{A}_{\mathrm{s}} \quad \text { (Tyree and Ewers, 1991) }
$$

where $A_{s}$ is the sapwood cross section area $\left(\mathrm{m}^{2}\right)$. The percent embolism was calculated via the equation:

$$
\% \text { embolism }=\left\{\left(\mathrm{K}_{\mathrm{h} \max }-\mathrm{K}_{\mathrm{h} \text { initial }}\right) / \mathrm{K}_{\mathrm{h} \max }\right\}^{*} 100 \%
$$

Leaf areas were measured using a LI-COR Portable Area Meter model LI3000 from Lambda Instruments Corporation. The leaf area of those leaves distal to the segment was added to one half the leaf area of those leaves on the segment. The total leaf area was used to calculate leaf specific conductivity via the equation:

$$
\mathrm{LSC}=\mathrm{K}_{\mathrm{h}} / \mathrm{A}_{\mathrm{l}}
$$

(Tyree and Ewers, 1991)
where $A_{l}$ is the total leaf area $\left(\mathrm{m}^{2}\right)$. The Huber value, defined as:

$$
H V=A_{s} / A_{\mathbf{l}}
$$

(Tyree and Ewers, 1991)
was also calculated.

## Biomechanics: Variation among Species

In the summer of 2000 branch segments were allowed to remain at room temperature for one to two hours before biomechanical testing. It has been shown that at $20^{\circ} \mathrm{C}$ the MOE of wood drops dramatically. This is approximately room temperature and thus, small fluctuations in room temperature can potentially have
significant effects on the measured strength values of the test specimens. Consequently, during the summer of 2001 branch segments were transported from refrigeration to the Instron in Styrofoam coolers. Branches were kept in the cooler at a temperature of approximately $18^{\circ} \mathrm{C}$ until just before mechanical testing.

Mechanical strength testing was conducted on an Instron Universal Machine, model 4202 , using a four-point test with a compression load cell of 100 lb . The span length (L), the distance between the two supported ends, was 13.5 cm . The load was applied at two points along the span length. The distance between one supported end and the nearest loading point (a) was 4.5 cm . The load cell was applied at a crosshead speed of $20 \mathrm{~mm} / \mathrm{min}$. Stress versus strain data was collected every 0.1 mm using Cy4200 software on a computer networked with the Instron. Branches were stressed until the load reached a maximum value (asymptote of the curve).

Due to the size, water content (assumed to be saturated) and juvenility of the wood, the branches did not rupture. The point at which the bending moment reaches a maximum is the critical strain and is the limit of the elastic range (Spatz and Bruechert, 2000). Therefore, modulus of rupture was estimated using the load value at the asymptote of the curve and the equation:

$$
\mathrm{MOR}=\mathrm{P}_{\max } * \mathrm{a}^{*} \mathrm{r}_{\text {major }} / \mathrm{I}
$$

Where $\mathrm{P}_{\max }$ is the load at failure, $\mathrm{r}_{\text {major }}$ is the major radius of the branch segment minus the pith, and I is the second moment of the cross sectional area for a hollow ellipse:

$$
\mathrm{I}=\pi\left(\mathrm{r}_{\text {major }}{ }^{*} \mathrm{r}_{\text {minor }}{ }^{3}\right) / 4
$$

as described in Gere and Timoshenko (1984). Flexural stiffness (EI) was calculated using the slope ( $\mathrm{P} / \mathrm{V}$ ) of the linear portion (elastic portion) of the curve and the equation:

$$
\mathrm{EI}=\mathrm{P} / \mathrm{V}\left(\mathrm{a}^{2} / 12\right)(3 \mathrm{~L}-4 \mathrm{a})
$$

(Gere and Timoshenko, 1984)
Flexural stiffness was divided by second moment of area to get the modulus of elasticity (MOE) of the wood.

In order to determine any correlation between estimated green MOR $\left(\mathrm{MOR}_{\mathbf{G}}\right)$ and actual dried MOR (MOR ${ }_{D}$ ) a subset of six branches from each species collected in 2000 was taken only through its elastic phase and then load was released, not compromising the property of the wood. These branches were then oven dried at $60^{\circ} \mathrm{C}$ in a Lipshaw Incubator oven (model \#249) until the weight of the segment was stable (to $100^{\text {th }}$ of a gram) from one day to the next. They were then fractured using a four-point test and MOR was calculated.

Branches collected in 2000 were placed in brown paper bags until sectioning (up to 16 months). Those from 2001 were restored in sealed plastic bags with a moist paper towel in a refrigerator until thin sections were made (within one week).

## Intra-tree Hydraulic Conductivity and Biomechanical Variation

Two first-order branches were collected from each of three trees of both $A$.
nigrum and $A$. negundo on three separate days during July 2001. Hydraulic conductivity (initial and maximum), $\mathrm{K}_{\mathrm{s} \max }, \%$ embolism, LSC, and HV were calculated. Conductive vessels were stained with $0.5 \%$ Crystal Violet. Specimens were tested on the Instron in the green state. Flexural stiffness, $\mathrm{I}, \mathrm{MOR}_{\mathrm{G}}, \mathrm{MOR}_{\mathrm{G}}$ were calculated.

## Anatomical Study

## Macerations

Macerations were made from eight control segments of each species collected in 2000 and all samples from 2001. Thick and thin shavings were placed in Jeffries solution (1:1 10\% Nitric acid: 10\% Chromic acid) in a 60 degree oven for four days. Shavings were then pelleted and washed three times with double distilled water and stored in Glycerine. Wood macerations were then stained with Safranin and semipermanently mounted on slides. They were then analyzed using a light microscope interfaced with a CCD video camera and multi-scan analog monitor (model VE 1000 CCD, Dage-MTI, Inc., Michigan City, Indiana, USA). NIH Image 1.5 analysis was used to measure cell wall thickness and lumen diameters of 25 vessels, 10 fibers, and 10 axial parenchyma cells from each segment. Fiber cell wall thickness to lumen diameter ratios were calculated a random cell count of 300 was used to determine the relative abundance of each cell type.

## Cross Sections

Eight branches from each species collected in 2000 and all branches collected in 2001 were used for further analysis of anatomical differences. Thin sections approximately $40 \mu \mathrm{~m}$ thick were made from the middle of each branch segment using a sliding microtome. Sections were taken through a dehydration series of ethanol and xylene (modified from Johansen, 1940) and mounted on slides using Permount.

Sections were analyzed using a light microscope interfaced with a CCD video camera and multi-scan analog monitor. Image analysis was performed on a pieshaped wedge, bordered by rays, of a lateral side of each branch cross section. NIH

Image 1.5 software was used to measure vessel lumen areas, fibers per unit area, and ray parenchyma per unit area in the wood. In addition, two samples from each species were sectioned and stained with phloroglucinol to qualitatively determine the presence or absence of lignin in ray parenchyma cell walls.

## General Morphology

Green wood density was determined for all branch segments. Mass was measured on a Mettler AJI00 electronic balance and water displacement was determined using a graduated cylinder. The dry wood density of the six branches from 2000 that were oven dried was also calculated in order to access any correlation between green and dried wood density.

Stem Diameter, xylem diameter, pith area, and cortex thicknesses were measured with a digital caliper. The number of growth rings and the percentage of rings that were conductive were determined with a Zeiss light microscope.

## Data Analysis

All data were analyzed using SAS version 8.1. ANOVAs were run to identify any differences between species for all variables tested. Means were graphed in Excel 97 and trendlines plotted to attain $R^{2}$ values.

## RESULTS

## Vessel Lengths

Differences in average maximum vessel lengths were not statistically significant between species $(p=0.2012)$. Lengths ranged from 26 cm for Acer nigrum to 36 cm for Acer saccharinum (Table 1).

## Intra-Tree Hydraulic Conductivity and Biomechanical Variation

Variance between $A$. negundo and $A$. nigrum for $\mathrm{K}_{\mathrm{h} \text { initial, }}, \mathrm{K}_{\mathrm{h} \text { max }}$, percent embolism, $\mathrm{K}_{\mathrm{s} \text { max }}, \mathrm{HV}$, and LSC were not statistically significant. Likewise, variances between trees of a species for all parameters were not significantly different (Table 2).

Variances between $A$. negundo and $A$. nigrum for MOE, MOR $_{G}$, MOR $_{\mathrm{D}}$, and I were not statistically significant. Flexural stiffness was significantly different between species $(p=0.0293)$. Variations between trees of a species for all parameters were not significantly different (Table 3).

## Hydraulic Conductivity: Variation among Species

Of the hydraulic parameters only $\mathrm{K}_{\mathrm{h} \max }(\mathrm{p}=0.0160)$ and $\mathrm{LSC}(\mathrm{p}=0.0180)$ were significantly different between species (Figure 1, 2). No significant differences were found for $\mathrm{K}_{\mathrm{h} \text { initial }}, \mathrm{K}_{\mathrm{s} \text { max }}$, percent embolism, HV , or LSC (Table 4).

## Biomechanics: Variation among Species

Flexural stiffness exhibited a trend relatively similar to that which was hypothesized (Figure 3). A. saccharum and A. nigrum had a much higher EI than that of A. rubrum and A. saccharinum ( $\mathrm{p}<0.0001$ ). In addition, A. negundo had an EI that was significantly smaller than that of the hard maples ( $p<0.0001$ ). However, it was statistically similar to the $A$. rubrum and $A$. saccharinum. Also, A. saccharum and $A$.
nigrum were significantly different in EI, the former maintaining a greater stiffness ( $\mathrm{p}=$ $0.0145)$ (Table 5).

Sampled stems of Acer negundo had a significantly smaller I than the other four species $(p=0.0360)$ (Figure 4). The hard maples had a significantly larger MOE $(p=$ $0.0337)$ and $\mathrm{MOR}_{\mathrm{G}}(\mathrm{p}=0.0362)$ than A. rubrum and A. saccharinum, as predicted (Figures 5, 6). Green modulus of rupture was smaller in $A$. negundo than in the $A$. saccharum and A. nigrum $(\mathrm{p}=0.0060)$ (Figure 6). However, no significant difference between species was found in $\mathrm{MOR}_{\mathrm{D}}$ (Table 5). Nor was there a statistically significant correlation between $\mathrm{MOR}_{\mathrm{G}}$ and $\mathrm{MOR}_{\mathrm{D}}$.

## Anatomical Study

## Macerations

Fiber lumen diameter was significantly different between species ( $\mathrm{p}<0.0001$ ) (Figure 7). Hard maples produced fibers much more narrow in diameter than those of soft maples ( $\mathrm{p}<0.0001$ ). In addition, A. negundo fiber lumens were greater in diameter than those of $A$. saccharum and A. nigrum $(\mathrm{p}<0.0001)$ (Table 6).

No significant differences were found between species for: percent vessels, percent fibers, percent axial parenchyma, axial parenchyma lumen diameter and cell wall thickness, average, maximum, and minimum vessel lumen diameters and cell wall thickness, fiber cell wall thickness, and fiber cell wall thickness : lumen diameter ratio (Table 6).

## Cross Sections

Although there was not a statistically significant difference between species in percent cross sectional area composed of ray parenchyma, the p-value was only 0.0642 .

The means of $A$. saccharum and $A$. nigrum were greater than those of the other three species. Acer negundo seemed to have a similar amount of ray parenchyma to that of $A$. saccharinum and $A$. rubrum, but substantially smaller amounts than the hard maples. No significant differences between species were found for percent vessel lumen area, percent fiber area, average, maximum and minimum vessel lumen diameters, hydraulic diameter and vessel densities (Table 7).

Qualitative analysis of lignin in ray parenchyma cell walls revealed that all five species were similar in having lignified ray cells. Furthermore, the relative amount of staining was similar for ray parenchyma and vessels of the same branch segment.

## General Morphology

Pith area of $A$. negundo was significantly greater than that of the other four species $(p=0.0002)$. Additionally, A. saccharinum possessed a greater pith area than $A$. rubrum $(\mathrm{p}=0.0261)$ (Figure 8 ). Acer saccharum had, on average, more growth rings than that of $A$. nigrum $(\mathrm{p}=0.0105)$, meaning the stems were older and slower growing (Figure 9). Bark thickness was significantly greater in the three soft maples than for the two hard maples $(p=0.0003)$ (Figure 10).

As expected, the green wood density of hard and soft maples was significantly different, $A$. saccharum and $A$. nigrum with much more dense wood $(\mathrm{p}=0.0214)$. Furthermore, $A$. negundo wood was the least dense of all species $(p=0.001)$ (Figure 11). There was a statistically significant correlation between green and dry density ( $\mathrm{p}=$ 0.8233 ) (Figure 12).

Significant differences in distal leaf area were found ( $\mathrm{p}=0.0012$ ). Hard maples had a greater leaf area than that of soft maples $(\mathrm{p}=0.0017)$. Also, the leaf area of $A$. saccharum was drastically greater than that of $A$. nigrum ( $\mathrm{p}=0.0268$ ) (Figure 13).

No significant difference was found between species for area of conductive tissue, stem diameter, xylem diameter, and percent conductive rings (Table 8).

## Tradeoffs

Contrary to the hypothesis, there was no inverse relationship between MOE and $K_{s \text { max }}\left(R^{2}=0.0097\right)$ (Figure 14). Similarly, there was no relationship between MOR $_{G}$ and $K_{s \text { max }}\left(R^{2}=0.0876\right)$ (Figure 15). Percent ray parenchyma in the cross sectional area was highly correlated with $\operatorname{MOE}\left(\mathrm{R}^{2}=0.8006\right)$ (Figure 19).

Percent fiber area in a cross section was correlated with differences in MOE $\left(\mathrm{R}^{2}=\right.$ $0.461)$ and $\operatorname{MOR}_{G}\left(\mathrm{R}^{2}=0.4555\right)$. Although there was an inverse relationship between percent fiber area and $\mathrm{MOE}_{\mathrm{G}}$ and $\mathrm{MOR}_{\mathrm{G}}$, fiber lumen diameter is a better predictor of MOE $\left(\mathrm{R}^{2}=0.6806\right)$ (Figure 16). Fiber cell wall thickness : lumen diameter was highly correlated with and $\mathrm{MOR}_{\mathrm{G}}\left(\mathrm{R}^{2}=0.7233\right)$ but fiber lumen diameter alone accounted for more variation in $\mathrm{MOR}_{\mathrm{G}}\left(\mathrm{R}^{2}=0.8751\right)$ (Figure 17, 18).

Table 1. Mean Maximum Vessel Lengths. Each mean is followed by one standard error. $\mathrm{n}=10$.

|  | Vessel Lengths $(\mathrm{cm})$ |
| :--- | :--- |
| A. negundo | $27.09 \pm 3.363$ |
| A. saccharinum | $36.04 \pm 3.681$ |
| A. rubrum | $31.17 \pm 4.934$ |
| A. nigrum | $25.80 \pm 2.805$ |
| A. saccharum | $26.05 \pm 2.084$ |

Table 2. Intra-tree Hydraulic Conductivity Variation. Each mean is followed by one standard error. Units for $\mathrm{K}_{\mathrm{h} \text { initial }}\left(\mathrm{kg} \mathrm{m} \mathrm{MPa}^{-1} \mathrm{~s}^{-1}\right)$ are $10^{-5}$. Units for $\mathrm{K}_{\mathrm{h} \text { max }}$ $\left(\mathrm{kg} \mathrm{m} \mathrm{MPa}{ }^{-1} \mathrm{~s}^{-1}\right)$, $\mathrm{HV}\left(\mathrm{m}^{2} \mathrm{~m}^{-2}\right)$, and LSC $\left(\mathrm{kg} \mathrm{MPa}^{-1} \mathrm{~s}^{-1} \mathrm{~m}^{-1}\right)$ are $10^{-4}$. Units for $\mathrm{K}_{\mathrm{s}}$ $\max ^{\operatorname{are}}\left(\mathrm{kg} \mathrm{MPa} \mathrm{m}^{-1} \mathrm{~m}^{-1}\right) . \mathrm{n}=6$

|  | $\mathrm{K}_{\mathrm{h} \text { initial }}$ | $\mathrm{K}_{\mathrm{h} \max }$ | $\%$ <br> Embolism | $\mathrm{K}_{\mathrm{s} \max }$ | HV | LSC |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| A. negundo 1 | $6.37 \pm$ | $1.21 \pm$ | $43.6 \pm$ | $3.50 \pm$ | $1.42 \pm$ | $4.83 \pm$ |
|  | 1.49 | 0.265 | 11.6 | 0.617 | 0.130 | 0.696 |
| A. negundo 2 | $4.44 \pm$ | $1.55 \pm$ | $43.0 \pm$ | $5.15 \pm$ | $1.31 \pm$ | $6.94 \pm$ |
|  | 0.649 | 0.895 | 13.4 | 2.70 | 0.228 | 4.11 |
| A. negundo 3 | $7.23 \pm$ | $1.33 \pm$ | $44.5 \pm$ | $4.63 \pm$ | $1.41 \pm$ | $5.60 \pm$ |
|  | 1.41 | 0.199 | 6.60 | 0.847 | 0.283 | 0.639 |
| A. nigrum 1 | $7.78 \pm$ | $1.75 \pm$ | $47.9 \pm$ | $5.80 \pm$ | $1.00 \pm$ | $5.83 \pm$ |
|  | 1.58 | 0.445 | 10.5 | 1.49 | 0.129 | 1.70 |
| A. nigrum 2 | $7.63 \pm$ | $2.04 \pm$ | $49.4 \pm$ | $5.76 \pm$ | $0.561 \pm$ | $3.26 \pm$ |
|  | 1.27 | 0.676 | 12.0 | 1.70 | 0.0188 | 0.987 |
| A. nigrum 3 | $4.02 \pm$ | $0.792 \pm$ | $46.6 \pm$ | $2.69 \pm$ | $0.860 \pm$ | $2.77 \pm$ |
|  | 0.936 | 0.186 | 9.62 | 0.324 | 0.298 | 1.39 |

Table 3. Intra-tree Biomechanical Variation. Each mean is followed by one standard error. Units for $\mathrm{EI}\left(\mathrm{N} \mathrm{mm}^{2}\right)$ and MOE $\left(\mathrm{N} \mathrm{mm}^{-2}\right)$ are $10^{5}$. Units for $\mathrm{MOR}_{\mathrm{G}}$ $\left(\mathrm{N} \mathrm{mm}^{-2}\right)$ are $10^{3}$. Units for $I$ are $\left(\mathrm{N} \mathrm{mm}^{4}\right) . \mathrm{n}=6$.

|  | EI | I | MOE | $\mathrm{MOR}_{\mathrm{G}}$ |
| :--- | :--- | :--- | :--- | :--- |
| A. negundo 1 | $7.27 \pm 0.952$ | $15.2 \pm 3.13$ | $0.555 \pm 0.103$ | $0.708 \pm 0.111$ |
| A. negundo 2 | $7.51 \pm 1.01$ | $14.0 \pm 6.08$ | $3.01 \pm 2.40$ | $1.91 \pm 1.20$ |
| A. negundo 3 | $5.80 \pm 0.504$ | $11.2 \pm 3.97$ | $1.83 \pm 0.830$ | $1.37 \pm 0.521$ |
| A. nigrum 1 | $12.7 \pm 1.40$ | $13.2 \pm 2.42$ | $1.08 \pm 0.157$ | $1.24 \pm 0.152$ |
| A. nigrum 2 | $13.8 \pm 1.25$ | $15.0 \pm 3.30$ | $1.28 \pm 0.371$ | $1.38 \pm 0.255$ |
| A. nigrum 3 | $8.55 \pm 1.56$ | $10.7 \pm 4.04$ | $1.55 \pm 0.437$ | $1.51 \pm 0.252$ |



Figure 1. Mean maximum hydraulic conductivity $\left(\mathrm{K}_{\mathrm{h} \max }\right) \pm$ one standard error. $\mathrm{n}=20$


Figure 2. Mean Leaf Specific Conductivity (LSC) $\pm$ one standard error. $\mathrm{n}=18$

Table 4: Hydraulic Conductivity. Each mean is followed by one standard error. Units for $\mathrm{K}_{\mathrm{h} \text { initial }}\left(\mathrm{kg} \mathrm{m} \mathrm{MPa}^{-1} \mathrm{~s}^{-1}\right)$ are $10^{-5}$. Units for $\mathrm{HV}\left(\mathrm{m}^{2} \mathrm{~m}^{-2}\right)$ are $10^{-4} \cdot \mathrm{n}=20$ for $\mathrm{K}_{\mathrm{h} \text { initial, }}$, and $\%$ Embolism. $\mathrm{n}=18$ for $\mathrm{K}_{\mathrm{s} \text { max }}\left(\mathrm{kg} \mathrm{MPa}^{-1} \mathrm{~s}^{-1} \mathrm{~m}^{-1}\right)$, and HV.

|  | $\mathrm{K}_{\mathrm{h} \text { initial }}$ | \% <br> Embolism | $\mathrm{K}_{\mathrm{s} \text { max }}$ | HV |
| :--- | :--- | :--- | :--- | :--- |
| A. negundo | $4.66 \pm$ | $55.2 \pm$ | $8.56 \pm$ | $1.24 \pm$ |
|  | 0.793 | 7.58 | 1.61 | 0.158 |
| A. saccharinum | $4.21 \pm$ | $55.0 \pm$ | $4.69 \pm$ | $1.70 \pm$ |
|  | 0.751 | 6.97 | 0.476 | 0.402 |
| A. rubrum | $4.36 \pm$ | $54.7 \pm$ | $5.85 \pm$ | $1.21 \pm$ |
|  | 0.760 | 7.21 | 1.03 | 0.149 |
| A. nigrum | $4.76 \pm$ | $54.1 \pm$ | $4.53 \pm$ | $1.14 \pm$ |
|  | 0.766 | 6.46 | 0.467 | 0.166 |
| A. saccharum | $4.91 \pm$ | $61.1 \pm$ | $6.24 \pm$ | $1.13 \pm$ |
|  | 0.833 | 5.77 | 0.860 | 0.191 |



Figure 3. Mean Flexural Stiffness $(E I) \pm$ one standard error. $n=20$.


Figure 4. Mean Second Moment of Cross Sectional Area (I) $\pm$ one standard error. $\mathrm{n}=20$


Figure 5. Mean Modulus of Elasticity (MOE) $\pm$ one standard error. $n=20$.


Figure 6. Green Modulus of Rupture $\left(\mathrm{MOR}_{\mathrm{G}}\right) \pm$ one standard error. $\mathrm{n}=14$.

Table 5: Dry Modulus of Rupture $\left(\mathrm{MOR}_{\mathrm{D}}\right)\left(\mathrm{N} \mathrm{mm}^{-2}\right)$. Each mean is followed by one standard error. $\mathrm{n}=6$.

| Species | $\mathrm{MOR}_{\mathrm{D}}$ |
| :--- | :--- |
| A. negundo | $650+56.6$ |
| A. saccharinum | $541+36.6$ |
| A. rubrum | $539+76.3$ |
| A. nigrum | $832+140$ |
| A. saccharum | $807+256$ |



Figure 7. Mean Fiber Lumen Diameter $\pm$ one standard error. $n=18$.
Table 6. Macerations: Each mean is followed by $\pm$ one standard error. $\mathrm{n}=8$ for all variables except percent vessel and fiber lumen diameter ( $\mathrm{n}=18$ ). \%V = percent vessels, $\% \mathrm{FT}=$ percent fibers, $\% \mathrm{AP}=$ percent axial parenchyma, $\mathrm{VL}_{\text {vig }}=$ average vessel lumen diameter, $\mathrm{VL}_{\max }=$ maximum vessel lumen diameler, $\mathrm{V}_{\min }=$ minimum vessel lumen diameter, $\mathrm{VW}=$ vessel wall thickness liame PW , ,

|  | \%V | \%FT | \%AP | $\mathbf{V L}_{\text {ovg }}$ <br> $(\mu \mathrm{m})$ | $\mathbf{V L}_{\text {max }}$ <br> $(\mu \mathrm{m})$ | $\mathbf{V L}_{\text {min }}$ <br> $(\mu \mathrm{m})$ | VW <br> $(\mu \mathrm{m})$ | FL <br> $(\mu \mathrm{m})$ | FW <br> $(\mu \mathrm{m})$ | FW:FL | PL <br> $(\mu \mathrm{m})$ | PW <br> $(\mu \mathrm{m})$ |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| A. negundo | $6.37 \pm$ | $83.7 \pm$ | $10.1 \pm$ | $32.9 \pm$ | $59.7 \pm$ | $12.7 \pm$ | $0.84 \pm$ | $10.2 \pm$ | $1.00 \pm$ | $0.094 \pm$ | $9.21 \pm$ | $1.08 \pm$ |
|  | 0.418 | 2.17 | 2.37 | 1.76 | 2.77 | 1.76 | 0.023 | 0.354 | 0.051 | 0.009 | 0.614 | 0.150 |
| A. saccharinum | $7.11 \pm$ | $81.4 \pm$ | $11.0 \pm$ | $33.8 \pm$ | $58.2 \pm$ | $12.5 \pm$ | $0.87 \pm$ | $10.7 \pm$ | $1.17 \pm$ | $0.116 \pm$ | $8.93 \pm$ | $1.35 \pm$ |
|  | 0.523 | 2.07 | 22.0 | 2.46 | 4.00 | 0.782 | 0.039 | 0.330 | 0.155 | 0.016 | 0.725 | 0.139 |
| A. rubrum | $8.81 \pm$ | $80.2 \pm$ | $11.8 \pm$ | $32.7 \pm$ | $56.1 \pm$ | $11.7 \pm$ | $0.86 \pm$ | $9.74 \pm$ | $1.36 \pm$ | $0.136 \pm$ | $9.87 \pm$ | $1.62 \pm$ |
|  | 0.625 | 1.91 | 2.09 | 2.07 | 3.70 | 1.26 | 0.033 | 0.269 | 0.127 | 0.013 | 0.969 | 0.189 |
| A. nigrum | $5.89 \pm$ | $87.4 \pm$ | $6.62 \pm$ | $32.4 \pm$ | $55.6 \pm$ | $10.5 \pm$ | $0.89 \pm$ | $7.80 \pm$ | $1.22 \pm$ | $0.147 \pm$ | $7.96 \pm$ | $1.38 \pm$ |
|  | 0.655 | 1.87 | 1.58 | 2.00 | 3.09 | 1.75 | 0.035 | 0.312 | 0.113 | 0.020 | 0.792 | 0.157 |
| A. saccharum | $5.50 \pm$ | $85.7 \pm$ | $8.13 \pm$ | $35.2 \pm$ | $61.7 \pm$ | $10.8 \pm$ | $0.86 \pm$ | $8.42 \pm$ | $1.33 \pm$ | $0.158 \pm$ | $7.94 \pm$ | $1.46 \pm$ |
|  | 0.375 | 2.06 | 1.76 | 1.93 | 4.78 | 1.23 | 0.031 | 0.351 | 0.180 | 0.036 | 0.634 | 0.303 |

Table 7. Cross Sections. Each mean is followed by $\pm$ one standard error. $\mathrm{n}=18$. $\%$ Vessels = percent vessel lumen area, \% Fibers = percent fiber area, \% Rays = percent ray parenchyma area, $\mathrm{VL}_{\text {avg }}=$ average vessel lumen diameter, $\mathrm{VL}_{\max }=$ maximum vessel lumen diameter, $\mathrm{VL}_{\min }=$ minimum vessel lumen diameter, $\mathrm{HD}=$ hydraulic diameter, Vessel Frequency $=10^{-10}$ vessels per $\mathrm{mm}^{2}$.

|  | $\%$ <br> Vessels | \% <br> Fibers | $\%^{2}$ <br> Rays | $\mathrm{VL}_{\text {avg }}$ <br> $(\mu \mathrm{m})$ | $\mathrm{VL}_{\max }$ <br> $(\mu \mathrm{m})$ | $\mathrm{VL}_{\min }$ <br> $(\mu \mathrm{m})$ | HD <br> $(\mu \mathrm{m})$ | Vessel <br> Frequency |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| A. negundo | $13.0 \pm$ | $81.7 \pm$ | $5.28 \pm$ | $26.4 \pm$ | $47.6 \pm$ | $11.5 \pm$ | $30.9 \pm$ | $2.11 \pm$ |
|  | 1.02 | 1.53 | 0.826 | 0.646 | 3.76 | 0.907 | 0.958 | 0.119 |
| A. saccharinum | $12.5 \pm$ | $82.1 \pm$ | $5.40 \pm$ | $25.9 \pm$ | $49.8 \pm$ | $11.4 \pm$ | $30.7 \pm$ | $2.15 \pm$ |
|  | 0.758 | 1.46 | 0.849 | 0.564 | 8.31 | 0.770 | 1.85 | 0.113 |
| A. rubrum | $12.2 \pm$ | $81.4 \pm$ | $6.46 \pm$ | $24.5 \pm$ | $39.0 \pm$ | $9.20 \pm$ | $27.2 \pm$ | $2.50 \pm$ |
|  | 0.558 | 1.42 | 1.11 | 0.530 | 0.843 | 0.742 | 0.562 | 0.122 |
| A. nigrum | $11.1 \pm$ | $81.8 \pm$ | $7.16 \pm$ | $23.6 \pm$ | $48.1 \pm$ | $9.55 \pm$ | $29.0 \pm$ | $2.24 \pm$ |
|  | 0.907 | 1.52 | 1.36 | 0.487 | 9.32 | 0.688 | 2.74 | 0.118 |
| A. saccharum | $10.7 \pm$ | $81.3 \pm$ | $8.01 \pm$ | $24.4 \pm$ | $40.5 \pm$ | $9.59 \pm$ | $27.7 \pm$ | $2.09 \pm$ |
|  | 0.525 | 1.82 | 1.52 | 0.636 | 1.21 | 0.638 | 0.692 | 0.094 |



Figure 8. Mean Pith Area $\pm$ one standard error. $\mathrm{n}=20$.


Figure 9. Mean Number of Growth Rings $\pm$ one standard error. $n=20$.


Figure 10. Mean Bark Thickness $\pm$ one standard error. $\mathrm{n}=20$.


Figure 11. Mean Green Density $\left(\right.$ Density $\left._{\mathrm{G}}\right) \pm$ one standard error. $\mathrm{n}=18$.


Figure 12. Dry Density (Density ${ }_{D}$ ) versus Green Density (Density ${ }_{G}$ ). Vertical lines are one standard error of Density $_{D}(n=6)$. Horizontal lines are one standard error of Density $_{G}(\mathrm{n}=14)$.
$\mathbf{\Delta}=$ A. negundo,$\uparrow=$ A. saccharinum, $■=A$. rubrum, $\mathbf{X}=$ A. nigrum, * $=$ A. saccharum.


Figure 13. Mean Distal Leaf Area $\pm$ one standard error. $n=20$.

Table 8. General Morphology. Means are followed by $\pm$ one standard error. $\mathrm{n}=20$ for Stem Diameter and Xylem Diameter. $\mathrm{n}=18$ for $\%$ Conductive Growth Rings and Conductive Xylem Area.

| Species | Stem <br> Diameter <br> $(\mathrm{mm})$ | Xylem <br> Diameter <br> $(\mathrm{mm})$ | \% Cond. <br> Growth <br> Rings | Cond. <br> Xylem Area <br> $\left(\mathrm{mm}^{2}\right)$ |
| :--- | :--- | :--- | :--- | :--- |
| A. negundo | $7.55 \pm 0.139$ | $5.60 \pm 0.322$ | $3.83 \pm 0.326$ | $24.2 \pm 2.13$ |
| A. saccharinum | $7.40 \pm 0.117$ | $5.56 \pm 0.238$ | $4.89 \pm 0.332$ | $22.3 \pm 1.74$ |
| A. rubrum | $7.49 \pm 0.168$ | $5.54 \pm 0.251$ | $5.89 \pm 0.582$ | $24.0 \pm 1.61$ |
| A. nigrum | $7.38 \pm 0.136$ | $5.58 \pm 0.275$ | $5.61 \pm 0.710$ | $25.5 \pm 1.90$ |
| A. saccharum | $7.49 \pm 0.138$ | $5.69 \pm 0.296$ | $5.11 \pm 0.387$ | $27.5 \pm 1.65$ |



Figure 14. Modulus of Elasticity (MOE) versus Maximum Specific Conductivity ( $\mathrm{K}_{\mathrm{s} \text { max }}$ ). Vertical lines are one standard error of MOE $(\mathrm{n}=20)$. Horizontal lines are one standard error of $K_{s \text { max }}(n=18)$.
$\Delta=A$. negundo, $\uparrow=A$. saccharinum, $■=A$. rubrum, $\mathrm{x}=A$. nigrum, * $=$ A. saccharum.


Figure 15. Green Modulus of Rupture ( $\mathrm{MOR}_{\mathrm{G}}$ ) versus Maximum Specific Conductivity $\left(K_{s ~ m a x}\right)$. Vertical lines are one standard error of $\mathrm{MOR}_{\mathrm{G}}(\mathrm{n}=14)$. Horizontal lines are one standard error of $\mathrm{K}_{\mathrm{s} \text { max }}(\mathrm{n}=18)$.
$\mathbf{\Delta}=$ A. negundo,$=$ A. saccharinum, $■=A$. rubrum, $\mathbf{x}=$ A. nigrum, * $=$ A. saccharum.


Figure 16. Modulus of Elasticity (MOE) versus Fiber Lumen Diameter. Vertical lines are one standard error of MOE $(\mathrm{n}=20)$. Horizontal lines are one standard error of fiber lumen diameter $(\mathrm{n}=18)$.
$\mathbf{\Delta}=$ A. negundo, $\star=$ A. saccharinum, $\boldsymbol{\square}=$ A. rubrum, $\mathbf{x}=$ A. nigrum, * $=$ A. saccharum.


Figure 17. Green Modulus of Rupture $\left(\mathrm{MOR}_{G}\right)$ versus Fiber cell wall thickness : Fiber lumen diameter. Vertical lines are one standard error of MOR $_{G}(\mathrm{n}=14)$.
Horizontal lines are one standard error of FW:FL ( $n=8$ ).


Figure 18. Green Modulus of Rupture $\left(\mathrm{MOR}_{\mathrm{G}}\right)$ versus Fiber Lumen Diameter. Vertical lines are one standard error of $\mathrm{MOR}_{\mathrm{G}}(\mathrm{n}=14)$. Horizontal lines are one standard error of fiber lumen diameter ( $\mathrm{n}=18$ ).
$\mathbf{\Delta}=$ A. negundo,$\quad=$ A. saccharinum, $\quad=$ A. rubrum, $\mathrm{x}=$ A. nigrum, * $=$ A. saccharum.


Figure 19. Modulus of Elasticity (MOE) versus Percent Ray Parenchyma. Vertical lines are one standard error of MOE $(\mathrm{n}=20)$. Horizontal lines are one standard error of percent ray parenchyma $(\mathrm{n}=18)$.
$\mathbf{\Delta}=$ A. negundo, $\star$ A. saccharinum, $\square=A$. rubrum, $\mathrm{x}=$ A. nigrum, ж = A. saccharum.

## DISCUSSION

The present results show a case where differences in mechanical properties can be related to fiber anatomy. This differs from studies where mechanical differences were related to vessel diameter (Wagner et al., 1998; Chiu and Ewers, 1992; Ewers and Fisher, 1991; Gartner 1991a,b). Since the five Acer species were not significantly different in $\mathrm{K}_{\mathrm{s} \text { max }}$, the lack of a negative linear relationship between $\mathrm{K}_{\mathrm{s} \text { max }}$ and $\mathrm{MOE}_{\mathrm{G}}$ is not surprising. It is important to realize though that all but one of those studies compared contrasting growth habits within a genus. At best, Wagner et al. examined two pairs of chaparral shrubs but conductivity measurements were taken on segments collected at one site while mechanical strength properties were assessed on different segments from an additional two sites.

The explanation for a lack of correlation between $K_{s} \max$ and $\mathrm{MOE}_{G}$ or $\mathrm{MOR}_{G}$ in the current study is two-fold. First, $\mathrm{K}_{\mathrm{h} \max }$ was independent of conductive xylem area $\left(R^{2}=0.0013\right)$. Second, the method for calculating $\mathrm{MOE}_{G}$ and $\mathrm{MOR}_{\mathrm{G}}$ was biased. Pith and cortex areas were removed.

When the means of all five species were included in regression between conductive xylem area and $K_{h \text { max }}, R^{2}$ was only 0.0013 . Yet, the variance of $\mathrm{K}_{\mathrm{h} \text { max }}$ was so large for $A$. negundo that when the species is ignored and the remaining four are regressed $\mathrm{R}^{2}$ increases to 0.6709 .

There are two possible reasons for a large variance in $\mathrm{K}_{\mathrm{h} \max }$ of $A$. negundo. First, this species prefers disturbed habitat. Specifically, amounts of water and light can fluctuate dramatically temporally and spatially. To the extent that the anatomy is impacted by microenvironment, conductivity will vary accordingly. Large variance
in $\mathrm{K}_{\mathrm{h} \text { max }}$ may also be due to branch order. Abortion of terminal branch buds is frequent in A. negundo (personal observation) and lateral branches take over as the dominant leader. These were then considered to be the first order branch. Zimmermann (1978) found that in diffuse-porous tress there is a hydraulic constriction at the base of each branch. Furthermore, Ewers and Zimmermann (1984a, b) showed that HV was greater and LSC smaller in second order branches than in first order Abies balsamea and Tsuga canadensis. It is possible that second order branches have fewer and/or smaller diameter vessels than first order, subsequently reducing $\mathrm{K}_{\mathrm{s} \text { max }}$ and LSC and increasing the HV. I am unaware of any literature on this topic to date.

The second reason for lack of a tradeoff between $K_{s \text { max }}$ and $\mathrm{MOE}_{G}$ is based in the calculation of I. Flexural stiffness is determined, in part, by the relative contributions to the second moment of area by the pith, xylem, and cortex. The contribution of the cortex is low, except near the tips of stems and branches where it can make up $10-20 \%$ of the second moment of cross sectional area (Bruchert et al., 2000). This results in a decrease in EI. Although I was controlled for in the field by collecting branches approximately eight mm in diameter, only the xylem area was used in calculating branch second moment of area in this study, based on findings by Wagner et at. (1998). This could easily explain differences in EI between soft and hard maples found here since the soft maples had significantly thicker cortex. It might also explain why MOE for $A$. negundo was greater than expected. Second moment of area for $A$. negundo was smaller than the other species. Since MOE was
derived by EI divided by I, an underestimation of I by eliminating cortex would overestimate MOE.

There was one additional problem in the calculation of mechanical properties. There was no consistency in the orientation of the branch segments in the Instron. Whether the branch rested on its major or minor axis was not controlled in either year. In 2001 the orientation was recorded but no trend was found. The difficulty arises with the fact that the compression and tension sides of the branch have different mechanical strengths. Fredericksen et al. (1994) found that the compression side of a bent loblolly pine stem had significantly smaller MOE and MOR than control stems. Ideally, the branches would have been tested on the major axis with tension on the upper side as they occur in the field. However, since orientation seemed to be random, strength properties of some branches were inevitably overestimated.

Significant differences in LSC can be attributed to leaf area since $K_{s \text { max }}$ was not statistically significant between species. Greater leaf areas were found in the shade tolerant hard maples lowering LSC values dramatically. Although Schultz and Matthews (1993) found that leaf area did not change significantly between shaded and sun plants of grapevine, they did find a difference in leaf area ratio ( $\mathrm{cm}^{2}$ leaf area/g plant dry weight). It is possible that the genus Acer has adapted to shade environments but increasing leaf area ratios instead of, or in combination with, greater plant dry weight. Additionally, shaded environments require less water use by leaves and so the relationship between leaf area and xylem area may be altered.

The relative trends in biomechanical data for green branch tips from this experiment were supported by dried lumber data published by the USDA (Handbook
72). Acer saccharum had the highest EI, MOE, and MOR followed by $A$. nigrum, $A$. rubrum, and $A$. saccharinum, respectively. However, since a statistically significant linear relationship between $\mathrm{MOR}_{\mathrm{G}}$ and $\mathrm{MOR}_{\mathrm{D}}$ was not found in the current research, it is not recommended that strength values in the green state be used as predictors for strength of dried wood.

Specific gravity is equal to the density of wood over the density of water. Density is the mass per unit volume of the wood. The two measurements are related in that specific gravity is a unit-less number denoting relative wood density (Panshin and De Zeeuw, 1980). Increases of percent fiber associated with decreasing percent axial parenchyma have been shown to be the best predictor of increases in specific gravity. Increases in fiber wall thickness and decreases in fiber lumen diameter also significantly related to greater specific gravity but to a lesser extent (McDonald et al., 1995).

There was no difference in percent area composed of fibers but the number of cells within that area was not determined. Although cell wall thickness was not significantly different between species fiber lumen diameter was significantly smaller in hard maples. It might be expected then, that hard maples have a greater density of fibers.

Jeronimidis (1980) supports a correlation between decreased fiber lumen diameter and increased strength as found here for Acer species. Failure under compression is a function of the modulus of elasticity and cell wall thickness divided by the lumen diameter. Subsequently, a decrease in lumen diameter could support a greater load before buckling.

The S2 layer makes up nearly $80 \%$ of the cell wall area and is where mechanical strength of the wood is ultimately determined (Jeronimidis, 1980). More specifically, the angle of the microfibrils in the S2 layer is one factor that affects the relative stiffness of the wood. In wood formed in response to flexing, the microfibril angle in the cell wall is increased, resulting in a more bendable tissue (Telewski, 1989). It would be useful then to determine if low microfibril angle is correlated with high $\mathrm{MOE}_{\mathrm{G}}$ in these cogeneric species.

Latewood has a high percentage of cell wall material per volume which translates into a high wood density and specific gravity (Koslowski, 1971). As a result, as the amount of latewood in the annual rings increases so does the strength of the wood (Dinwoodie, 1981). The relative amount of latewood versus earlywood was not quantified. Based on the differences in $\mathrm{MOE}_{\mathrm{G}}$ and $\mathrm{MOR}_{\mathrm{G}}$ it would be expected that a greater portion of a given ring would be composed of latewood in hard maples than in soft maples.

This is the first time that a high correlation between percent ray parenchyma and compressive MOE has been shown. In contrast, a positive correlation between volume fraction of rays and transverse or radial tensile strength is well established (Beery et al., 1983; Schniewind, 1959; Burgert et al, 2000). However, these relationships may just be coincidental. Hard maples are slow growing, long-lived trees. This life history may require a greater volume of ray parenchyma in order to store adequate amounts of starch for reserve in lieu of prolonged environmental stresses. The narrower fiber lumens may more that compensate for the potential loss in structural support from high amounts of parenchyma.

Although a qualitative study was conducted on the presence of lignin in the ray parenchyma, a quantitative study would be more useful. Chafe (1974) and Murakami et al. (1999) differentiated between two types of ray parenchyma cells, those that are adjacent to vessels, contact cells, and those that are not in contact with vessels. Both studies showed that complete lignification of the contact cells was delayed until heartwood formation. Conversely, ray parenchyma not associated with vessels differentiated during the same year as their formation. Thus, the trend of increasing ray parenchyma area and mechanical strength from soft to hard maples may be explained by a greater amount of non-vessel associated ray parenchyma cells in hard maples.

One important factor to consider in this study is microhabitat. All the specimens were from the same 44-acre woodlot where general climate and photoperiod are similar. However, there exist many microhabitats in the area as categorized by Frye (1976). Wood density is correlated to a tree's ability to tolerate shade and its demographic habitat (Lawton 1984). Shade tolerant species have more dense wood than shade intolerant species. This correlation was supported by the distribution of the five species within the woodlot. Acer saccharinum and A. negundo were found in greater light microenvironments than A. saccharum and A. nigrum. Thus, environmental factors such as soil moisture, light intensity, and extent of disturbance may have differed appropriately for each species. In order to reduce possible effects from microhabitat differences, samples collected in summer 2001 were all sun branches.

Further experimentation in a controlled greenhouse would be ideal. There, access to light and atmosphere conditions would be identical. Several plants of each of the five species could be grown in individual pots to control population density. Soil water content and nutrient availability could be manipulated so as to determine potential phenotypic plasticity in each of the species. The five species may be not only similar in MOE and MOR, but also in $\mathrm{K}_{\mathrm{s} \text { max }}$. In combination with several treatments of differing light intensity this could determine if differences in MOE and EI in the present study were due to genetics, environment, or a combination of the two.

Additionally, it would be interesting to compare species with similar life histories but differing wood anatomy. That is, compare diffuse porous species to ring porous species; both of which were either slow growing and long lived or fast growing and short lived. However, this comparison would be complicated by genetic lineage.

This study shows that there is not a direct tradeoff between conductivity and mechanical strength, at least in the genus Acer. This could happen if water transport is not limiting, and subsequently there is no selection for wider vessel lumen diameters and thus, greater $\mathrm{K}_{\mathrm{s} \text { max }}$. It is also possible that the division of functional roles into separate cell types facilitates the decoupling of the water transport and mechanical roles. Or, maybe inverse relationships shown to date have been a consequence of environmental differences. Regardless, this suggests that other cogeneric species of similar growth habit should be investigated as well as the extent of their phenotypic plasticity as a result of contrasting habitats.

## Literature Cited

Alder, N. N., J. S. Sperry, and W. T. Pockman. 1996. Root and stem xylem embolism, stomatal conductance, and leaf turgor in Acer grandidentatum populations along a soil moisture gradient. Oecologia. 105: 293-301.

Arnold, David H., and James D. Mauseth. 1999. Effects of environmental factors on development of wood. American Journal of Botany. 86 (3): 367-371.

Baas, P. 1983. Ecological patterns in xylem anatomy. In: TJ Givnish, ed, On the Economy of Plant Form and Function. Cambridge University Press, Cambridge, UK, pp 321-352.

Barnes, Burton V. and Warren H. Wagner, Jr. 1981. Michigan Trees. University of Michigan Press: Ann Arbor.

Beery W. H., G. Ifju, and E. McLain. 1983. Quantitative wood anatomy - relating anatomy to transverse tensile strength. Wood Fiber Science. 15: 83-86.

Burgert, I., D. Eckstein, and A. Bernasconi. 2000. The strength and volume fraction of rays in trees subjected to radial tensile stresses. In: Plant Biomechanics 2000. Proceedings of the $3^{\text {rd }}$ Plant Biomechanics Conference. Freiburg-Badenweiler.

Bruchert, Franks, Gero Becker, and Thomas Speck. 2000. The mechanics of Norway spruce [ Picea abies (L.) Karst]: mechanical poperties of standing trees from different thinning regimes. Forest Ecology and Management. 135: 45-62.

Carlquist, Sherwin. 2001. Comparative wood anatomy: systematic, ecological, and evolutionary aspects of dicotyledon wood. Springer-Verlag: Berlin.

Chafe, S. C. 1974. Cell wall formation and "protective layer" development in the xylem parenchyma of trembling aspen. Protoplasma. 80: 335-354.

Chiu, Shau-Ting and Frank W. Ewers. 1992. Xylem structure and water transport in a twiner, a scrambler, and a shrub of Lonicera (Caprifoliaceae). Trees-Structure and Function. 6: 216-224.

Dinwoodie, J. M. 1981. Timber. Timber Press: Forest Grove, OR.
Dixon, H.H. 1914. Transpiration and the Ascent of Sap in Plants. Macmillan: London.

Easterling et al. 1982. Proceedings of the Royal Society of London. A383: 31-41.
Ewers, Frank W. and Jack B. Fisher. 1991. Why vines have narrow stems:
Histological trends in Bauhinia (Fabaceae). Oecologia. 88: 233-237.

Ewers, Frank W. and Martin H. Zimmermann. 1984a. The hydraulic architecture of eastern hemlock (Tsuga canadensis). Canadian Journal of Botany. 62: 940-946.

Ewers, F. W. and M. H. Zimmermann. 1984b. The hydraulic architecture of balsam fir (Abies balsamea). Physiologia Plantarum. 60: 453-458.

Fredericksen, T.S., R. L. Hedden, and S.A. Williams. 1994. Effect of stem bending on hydraulic conductivity and wood strength of loblolly pine. Canadian Journal of Forest Research 24: 442-446.

Frye, Darlene M. 1976. A botanical inventory of sandhill woodlot, Ingham county, Michigan I: The vegetation. The Michigan Botanist. 15: 131-140.

Gartner, Barbara L. 1991a. Stem hydraulic properties of vines vs. shrubs of western poison oak, Toxicodendron diversilobum. Oecologia. 87: 180-189.

Gartner, Barbara L. 1991b. Structural stability and architecture of vines vs. shrubs of poison oak, Toxicodendron diversilobum. Ecology. 72 (6): 2005-2015.

Gelderen, D. M., P.C. de Jong, and H. J. Oterdoom. 1994. Maples of the World. Timber Press: Portland, OR.

Gere, James M. and Stephen P. Timoshenko. 1984. Mechanics of materials. $2^{\text {nd }}$ ed. Pridle, Weber \& Schmidt Publishers: Belmont, CA.

Gibson, and Ashby. 1982. Proceedings of the Royal Society of London. A382: 4359.

Hargrave, K. R., K. J. Kolb, F. W. Ewers, and S. D. Davis. 1994. Conduit diameter and drought-induced embolism in Salvia mellifera Greene (Labiatae). New Phytologist 126: 695-705.

Jarbeau, J. A., F. W. Ewers, and S. D. Davis. 1995. The mechanism of water-stressinduced embolism in two species of chaparral shrubs. Plant, Cell and Environment. 18: 189-196.

Jeronimidis, G. 1980. Wood, one of nature's challenging composites. In: The Mechanical Properties of Biological Materials, XXXIVth Symposium of the Society for Experimental Biology. J. F. V. Vincent and J. D. Currey, Eds. Cambridge University Press. 169-182.

Johanse, Donald Alexander. 1940. Plant Microtechnique. McGraw-Hill Book Co.: New York.

Koslowski, T. T. 1971. Growth and development of trees. Vol II. Academic press: New York.

Lawton, Robert O. 1984. Ecological constraints on wood density in a tropical montane rain forest. American Journal of Botany. 71 (2): 261-267.

Mauseth, James D. 1988. Plant Anatomy. The Benjamin/Cummings Publishing Company, Inc.: Menlo Park, CA.

McDonald, Suzanne, G. Bruce Williamson, and Michael C. Wiemann. 1995. Wood specific gravity and anatomy in Heliocarpus appendiculatus (Tiliaceae). American Journal of Botany. 82 (7): 855-861.

Murakami, Y., R. Funada, Y. Sano, and J. Ohtani. 1999. The differentiation of contact cells in the xylem ray parenchyma of Populus maximowczii. Annals of Botany. 84: 429-435.

Niklas, Karl. 1992. Plant Biomechanics: An Engineering Approach to Plant Form and Function. University of Chicago Press: Chicago.

Panshin, A. J. and Carl de Zeeuw. 1980. Textbook of Wood Technology. McGrawHill, Inc.: New York.

Patino, Tyree, and Herre. 1995. Comparison of hydraulic architecture of woody plants of differing phylogeny and growth form with special reference to freestanding and hemi-epiphytic Ficus species from panama. New Phytologist. 129 (1): $125-$ 134.

Pockman, W. T., J S. Sperry, and J.W. O'Leary. 1995. Sustained and significant negative water pressure in xylem. Nature. 378: 715-716.

Putz, Francis E, Phyllis D. Coley, Karen Lu, Arlee Montalvo, and Annette Aiello. 1983. Uprooting and snapping of trees: structural determinants and ecological consequences. Canadian Journal of Forest Research 13: 1011-1020.

Schniewind, A. P., 1959. Transverse anisotropy of wood: a function of gross anatomic structure. Forest Products Journal. 9: 350-359.

Schultz, Hans R. and Mark A. Matthews. 1988. Resistance to water transport in shoots of Vitis vinifera L.: relation to growth at low water potential. Plant Physiology. 88: 718-724.

Schultz, Hans R. and Mark A. Matthews. 1993. Xylem development and hydrualic conductance in sun and shade shoots of grapevine (Vitis vinifera L.): evidence that low light uncouples water transport capacity from leaf area. Planta. 190: 393-406.

Shumway Durland L., Kim C. Steiner, \& Thomas E. Kolb. 1993. Variation in seedling hydraulic architecture as a function of species and environment. Tree Physiology. 12: 41-54.

Spatz, Hanns-Christof and Franka Bruechert. 2000. Basic biomechanics of selfsupporting plants: wind loads and gravitational loads on a Norway spruce tree. Forest Ecology and Management. 135: 33-44.

Sperry, John S. and Melvin T. Tyree. 1988. Mechanism of water stress-induced xylem embolism. Plant Physiology. 88: 581-587.

Sperry, J. S. and M. T. Tyree. 1990. Water-stress-induced xylem embolism in three species of conifers. Plant, Cell and Environment. 13: 427-436.

Sperry, J. S., J. R. Donnelly, and M. T. Tyree. 1988. A method for measuring hydraulic conductivity and embolism in xylem. Plant, Cell and Environment. 11:3540.

Sperry, J. S., A. H. Perry, and J. E. M. Sullivan. 1991. Pit membrane degradation and air-embolism formation in ageing xylem vessels of Populus tremuloides Michx. Journal of Experimental Botany. 42 (244): 1399-1406.

Sperry, J.S., N. Z. Saliendra, W. T. Pockman, H. Cochard, P. Cruiziat, S. D. Davis, F. W. Ewers, and M. T. Tyree. 1996. New evidence for large negative xylem pressures and their measurement by the pressure chamber method. Plant, Cell and Environment. 19: 427-436.

Sperry, John S. and June E. M. Sullivan. 1992. Xylem embolism in Response to Freeze-Thaw Cycles and Water Stress in Ring-Porous, Diffuse-Porous, and conifer Species. Plant Physiology. 100: 605-613.

Telewski, F. W. 1989. Structure and function of flexure wood in Abies fraseri. Tree Physiology. 5: 113-121.

Telewski, F. W. 1995. Wind-induced physiological and developmental responses in trees. In: Coutts, M. and J. Grace. Wind and Trees. Cambridge University Press. 237-262.

Tyree, Melvin T. and Frank W. Ewers. 1991. The hydraulic architecture of trees and other woody plants. New Phytologist. 119: 345-360.

Telewski, F. W. and M. J. Jaffe. 1986. Anatomical, morphological, and mechanical analysis of genetically different sibs of Pinus taeda in response to mechanical perturbation. Physiologia Plantarum. 66 (2): 219-226.
U. S. Department of Agriculture. Wood Handbook 72.

Ugural, A. C. 1991. Mechanics of materials. McGaw-Hill, New York.
Vander Willigen, Clare and N. W. Pammenter. 1998. Relationship between growth and xylem hydraulic characteristics of clones of Eucalyptus spp. at contrasting sites. Tree Physiology. 18: 595-600.

Vander Willigen, C., H. W. Sherwin and N. W. Pammenter. 2000. Xylem hydraulic characteristics of subtropical trees from contrasting habitats grown under identical environmental conditions. New Phytologist. 145: 51-59.

Villar-Salvador, Pedro, Pilar Castro-Diez, Carmen Perez-Rontome, and Gabriel Montserrat-Marti. 1997. Stem Xylem Features in three Quercus species along a climatic gradient in NE Spain. Trees - Structure and Function. 12 (2): 90-96.

Wagner, Kristofer R., Frank W. Ewers, and Stephen D. Davis. 1998. Tradeoffs between hydraulic efficiency and mechanical strength in the stems of four cooccurring speices of chaparral shrubs. Oecologia 117: 53-62.

Wainwright, S. A., W. D. Biggs, J. D. Currey, and J. M. Gosline. 1976. Mechanical Design in Organsims. Princeton University press: Princeton, New Jersey.

Zimmermann, Martin H. 1978. Hydraulic architecture of some diffuse-porous trees. Canadian Journal of Botany. 56: 2286-2295.

Zimmermann, M.H. 1983. Xylem structure and the ascent of sap. Springer-Verlag: Berlin.

Zimmermann, M. H. and A. A. Jeje. 1981. Vessel length distribution in stems of some American woody plants. Canadian Journal of Botany. 59: 1882-1892.


