HOW THE HYDRAULIC AND MECHANICAL PROPERTIES OF WOOD

INFLUENCE BRANCH FORM IN NORWAY MAPLE (*ACER PLATANOIDES* L.)

by

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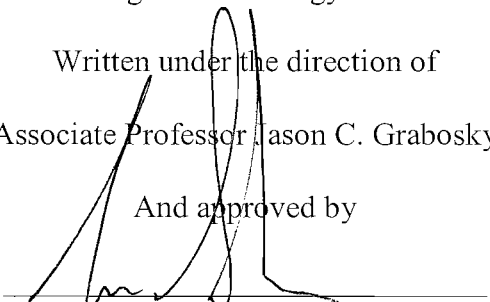
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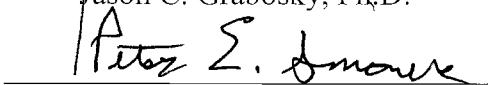For the degree of

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Written under the direction of

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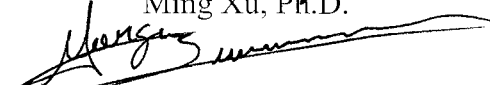
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ABSTRACT OF THE DISSERTATION

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An in-depth understanding of the functions of branches (hydraulics and mechanics) and how they influence canopy form is needed in order to assess the impacts of cultural practices such as pruning in the future. This dissertation is comprised of three studies that investigate how anatomical and material properties of wood vary along *Acer platanoides* L. (Aceraceae) branches and whether the variation influences branch form.

The hydraulic study found that vessel radii size decreased and density increased in the distal direction, consistent with the hydraulic flow found in previous studies. Vessel density was highest 5 cm proximal to the most recent terminal bud scale scar, suggesting that the increase in vessels may be due to hydraulic constrictions and partitioning through the branch attachment zones for the paired lateral branches.

The mechanics study observed that modulus of elasticity (E) was 75% lower at the branch tips than in the proximal (structural) locations. Density-specific stiffness (E/ρ) was not found to vary between the three structural locations, suggesting that the elastic

similarity modeled cannot be rejected due to variation in E/ρ. Variation in E was negatively correlated with the percent area of vessels and positively correlated with mean fiber cell wall size, suggesting a balance between hydraulics and mechanics.

The allometric study found branches transitioned from a log-log curvilinear relationship converging to a linear relationship after 3 m in length. The linear relationship was best modeled with the elastic similarity model. The shift in allometry corresponds to a shift from increasing slenderness ratio (length / radius) with increasing branch length to a decreasing ratio as flexible sun branches transition to stiffer structural branches. The number of subordinate branches was found to increase after the primary branch length passed 3 m, suggesting that branches transition to a structural role as size increases.

The differences in anatomical and material properties, the increase in the number of lateral branches and the shift in allometry are probably related to wood development type. Torsional balance of bending moments were found to be relatively evenly distributed along the left and right side of the branches.

ACKNOWLEDGEMENTS

DEDICATION

To Iwonaka

I came to New Jersey to pursue my doctorate degree.

As I finish, I realize than I gained much more - the gift of your love.

Thank you for everything.

Now and Forever . . .

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INTRODUCTION

Trees are capable of growing to great heights and overall dimensions, and as plants, they must balance several competing functions. Water transportation, storage of water and carbohydrates, mechanical support, and defense are considered to be principle functions for tree stems (Gartner *et al*. 2003, Tyree & Zimmermann 2002, Chiu and Ewers 1992, Niklas 1992). Niklas (1992) used a diamond to describe a balance between plant functions throughout their lives, anchored by; photosynthesis, hydraulic support, mechanical support and reproduction (Fig. 1). Sullivan (1896) suggested that in building design, as well as in nature, one can see that form follows function. As a tree canopy changes with time, the functions of branches and stems change from principally solar collectors and water transporter, to include the ever increasing need to support both static and dynamic loading. My governing hypothesis is that the shift in function corresponds to a change in form, as branches develop from small sun branches to larger structural branches.

Plant biologists are interested in understanding how trees have evolved to withstand external loading events (wind, snow, ice, and etc.) and survive often for hundreds or thousands of years. Arboriculture, a sub-discipline of applied plant biology, discusses the pruning of trees to develop and maintain canopy structure with the overall goal of maximizing canopy benefits, (aesthetic & property value, shade, carbon sequestering, etc.), while minimizing the risk of failure (Harris et al. 2004). It is hoped that the removal of tissue will direct growth in order to develop 'good' canopy structure. Good structure is hard to define and is often limited to qualitative or arbitrary goals for canopy stability with limited research data pertaining to stability or branch form. One such description is that of the distribution permanent branch arrangement along the trunk

with a radial distribution of 5 to 7 over 360 degrees spaced approximately 30 - 45 cm apart for trees greater than 12 m (Gilman 2002; Gilman and Lilly 2002). While describing branch arrangement is useful in terms of developing permanent branches, it does not aid in evaluating branch form or the distribution of subordinate branches. Most standards utilized by industry often describe a goal of developing a stable canopy by removing un-desirable structures and defects, such as co-dominate branching or branch unions with included bark (Gilman 2002; Gilman and Lilly 2002). Yet again we are not left with a reasonable description of the form of 'good' branch. Although it is unrealistic to suggest that trees can withstand all loading events, a stable canopy can be thought of as one that can withstand all but the most serious storm event without a significant stem or branch failure. Pruning and plant spacing can influence canopy form. Damaging wind, ice or cultural practices, such as topping, can deform a tree's canopy. Restoration pruning attempts to improve the structure and form of a damaged tree (American National Standards Institute 2001). The ultimate goal of restoration pruning is to return a damaged canopy to a condition that can provide similar benefits to that of the original canopy, with acceptable levels of risk of failure. Since the arborist has limited information on a formal definition of 'good' canopy structure, he/she must rely on personal experience and intuition when deciding how to use pruning to guide canopy development or restoration.

The underlying structure of a canopy rests on individual branch form; yet, little is known on how to predict, objectively and reliably, canopy stability and strength from branch form. The ability to define stable canopy structure from branch form could help the arborist direct growth and develop the goal of a stable canopy. This research was designed to: (1) describe anatomical differences as they occurred in the secondary xylem

tissues of the same growth year along the branch axis, (2) determine the impact of anatomical shifts on wood material properties as branches grew, and (3) investigate whether canopy development lead to predictable patterns of iterative growth. This project was designed to aid in establishing fundamental knowledge of how branches develop in a stable canopy and become the structural support for the ever growing canopy. It is hoped that in the future the knowledge gained through this research can be transferred into the development of guidelines for the restoration of damaged canopies.

Two of Niklas' functions are filled exclusively by primary growth (axial extension): photosynthesis and reproduction. The principle function of primary tissue is water and nutrient absorption in the fine roots and that of net primary production, typically carried out in the leaves (Kozlowski & Pallardy 1997). In order to maximize solar interception, primary growth increases stem/branch length, placing the leaves in the sun (Kozlowski & Pallardy 1997). Additionally, primary growth plays an important role in both hydraulic and mechanical functions. Gymnosperms utilize tracheids for both hydraulics and mechanical support of the leaves (Esau 1977). In angiosperms, water transportation is typically carried out by the vessels while mechanical support is left to the fibers and sometimes tracheids (Niklas 1992; Esau 1977).

The literature suggests that hydraulic continuity is one of the principle functions of secondary tissues (Sperry *et al.* 2006; Tyree and Zimmermann 2002). The ability to supply an adequate amount of water to drive the transpiration and the translocation stream necessary for photosynthesis is paramount for trees. Secondary xylem utilizes the same cell type for hydraulics as primary xylem, involving tracheids in gymnosperms while angiosperms conduct water through vessels and occasionally tracheids.

Mechanical support is also an important function for a stem or branch, particularly if hydraulic capacity is not limiting (Niklas 1992; Spatz and Brüechert 2000). Supporting a branch that is not providing adequate sugars to the tree would create a carbohydrate sink, and a tree often cuts off the water supply by reducing the amount of vascular tissue connected to a branch, effectively aborting the branch. This is termed self-pruning and is common in both gymnosperms and angiosperms. The importance of hydraulics should not diminish the significance of mechanical support. In order to survive decades or even hundreds of years, a tree must be capable of resisting the load placed on the woody tissues by the constant force of gravity (static or self-loading) and resist loads applied externally by elements such as wind, ice or snow (static and dynamic loading).

A tree must balance hydraulics and mechanics, yet the literature does not comprehensively address the tradeoffs between them (Gartner *et al.* 2003; Searson *et al.* 2004). Indeed our knowledge of wood anatomy far out weighs our knowledge of comparative wood function (Sperry *et al.* 2006). It has been suggested that researchers should concentrate on biomechanical and physiological studies (Sperry *et al.* 2006).

I proposed to investigate the balance between two of Niklas' four functions; hydraulics and mechanics, as manifested in branch form. While reproduction is of high importance in genetic transfer and the evolution of a species, it is not directly tied to the everyday trials of withstanding internal and external loading. Photosynthesis provides the assimilates needed for continual growth for added mechanics and is supplied by hydraulics; yet, over successive years is not directly related to the ability to withstand loading events. One way to measure this balance is a ratio of vessel elements to fibers. A large vessel:fiber (V:F) ratio in transverse section would suggest a large investment in

hydraulic capacity at the expense of mechanical support, while a small ratio would indicate an increased investment in mechanics. Three studies were conducted to shed light on this interrelationship between anatomy (function in terms of hydraulics) and mechanics (function in terms of physical support), and allometry (form).

This dissertation is assembled into 6 sections: this introduction, four primary chapters and a conclusion. The first chapter is a literature review, the second details the allometry study, the third describes the hydraulics study and the fourth chapter discusses the mechanics study. The conclusion summarizes the results and important findings.

The branch allometry study (chapter two) investigated whether canopy architecture could be modeled as a series of iterative cantilevered beams. First, second and third order branches were measured, and allometric relationship was developed to determine whether subordinate branches are scaled versions of larger parent branches and how they feed into larger branches. Emphasis was on power laws ($L \propto aR^b$) and slenderness ratios (L:R), where L is length and R is radius. These relationships were then compared to results from the hydraulics and mechanics studies, in the attempt to determine whether either hydraulics or mechanics is a governing factor in allometric form. Additionally natural branch shedding may disrupt the inherent phyllotaxic pattern. Research was conducted to determine if branch shedding developed in a manner that minimized torsion along the left and right side of a developing branch.

The hydraulic study (chapter three) was conducted to determine whether anatomical features vary in the same growth year along the branch axis. Staining and microscopy techniques were utilized to determine whether tissue and cell properties vary either axially along a branch, or from the top to the bottom of the branch. Additionally,

vessel taper and density were compared along branches to determine whether branches follow current views on hydraulic flow.

The mechanical study (chapter four) investigated whether material properties varied axially along a branch, as well as top versus bottom, with regard to reaction wood formation. This study concentrated on the potential influence of modulus of elasticity (E), density-dependent stiffness, presence of reaction wood, and tissue and cellular composition on branch form.

Acer platanoides L. (Aceraceae) (Norway maple) was selected to represent trees that are a common component in urban forests throughout the United States. Studies have shown that this exotic species has been heavily planted through the U.S., representing often as much as 40 - 50% of street tree populations (Valentine *et al*. 1978; Manion 1981; Nowak and Rowntree 1990). The opposite branching patterns and diffuse porous wood anatomy (Panshin and de Zeeuw 1980; Dirr 1998) made this species well suited for this study. We were interested in minimizing growth rate as a factor in the mechanical study, and Haygreen and Bowyer (1982) suggested that growth rate does not affect material properties in diffuse porous trees. The habit of opposite branching was desired to determine whether natural branch shedding influenced torsional load distribution in branches. Additionally, two plantations, one mixed (Horticultural Farm III, Fig. 2) and a monoculture (Rutgers Gardens, Fig. 3) were available for destructive sampling.

Chapter submission to journals (current in review and proposed submissions):

Chapter 1. Review of Pertinent Literature on the Allometric Relationships in Tree Stems and Branches. This manuscript was re-submitted in January 2009 to Arboriculture and Urban Forestry. The chapter included in this dissertation reflects the most recent submission.

Chapter 2. Allometric patterns in *Acer platanoides* (Aceraceae) branches. This manuscript was submitted in November 11, 2008 to Trees: Structure and Function. The chapter included in this dissertation reflects the current submission.

Chapter 3. Variation in anatomical features along *Acer platanoides* (Aceraceae) branches.

Chapter 4. Variation in Modulus of Elasticity (*E*) along *Acer platanoides* (Aceraceae) branches. This chapter will be submitted to Trees: Structure and Function.

Conclusion: This chapter will be submitted to the Arborist News for publication in this popular press magazine.

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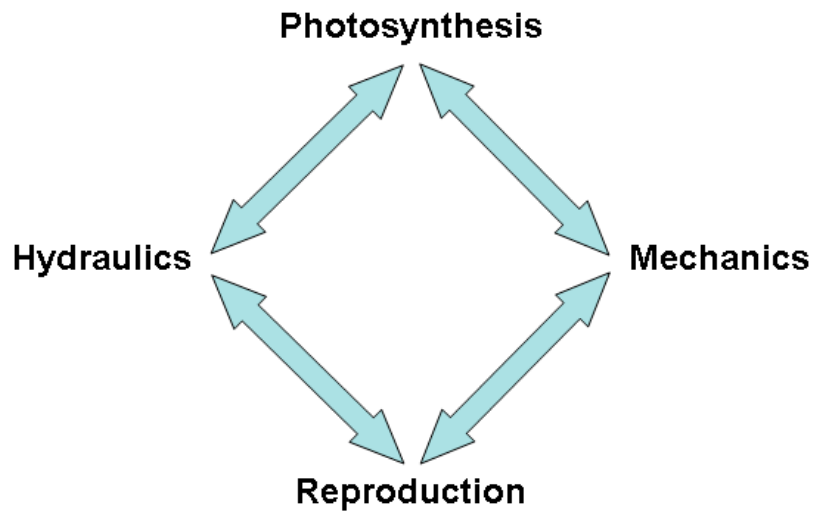
Figure 1. Trees need to balance the vegetative functions (photosynthesis, hydraulics and mechanics) and reproduction to maintain the species. Adapted from the book <u>Plant Biomechanics</u> by Karl Niklas (1992).

Figure 2. Mixed plantation growing at Rutgers Horticultural Farm III. Sampling for the allometric study (chapter 2) and the hydraulic study (chapter 3) occurred on exterior growing branches on *Acer platanoides* in this plantation.

Figure 3. Plantation of *Acer platanoides* growing at Rutgers Gardens. Sampling for the mechanical properties (chapter 4) occurred on exterior growing branches of these trees.

CHAPTER 1

Review of Pertinent Literature on the Allometric Relationships in Tree Stems and Branches

ABSTRACT

The goal of maintenance pruning is the development of a tree canopy that meets a
defined objective while minimizing the risk of failure. An in-depth understanding of the
primary functions of branches and how they influence canopy form is needed in order to
assess the impacts of cultural practices such as pruning or plant spacing on canopy
development. Allometric modeling describes the relationship between size and shape of
organisms. This review paper explores three allometric methods of modeling branch form
(pipe model theory, fractal dimensioning, and power laws), and it explores their
applicability to the arboriculture community, particularly in terms of potential use in
guiding pruning research. Additionally, the two principle functions of plants, hydraulics
and mechanics, are discussed in light of their impact of stem and branch form. A better
understanding of branch form and function should help the arborists improve pruning
standards.

Key Words: Allometry; biomechanics; elastic similarity; hydraulics; mechanics;
slenderness ratio

INTRODUCTION

Arborists prune trees to develop and maintain canopy structure with the overall
goal of maximizing canopy benefits (aesthetic & property value, shade, carbon
sequestering, etc.), while minimizing the risk of failure (Harris et al. 2004). It is hoped
that the removal of tissue will direct growth in order to develop 'good' canopy structure.
Good structure is often hard to define, and often the goal is to develop a stable canopy by

removing un-desirable structures and defects such as, co-dominate branching or branch unions with included bark (Gilman 2002; Gilman and Lilly 2002). Although it is unrealistic to suggest that trees can withstand all loading events, a stable canopy can be thought of as one that can withstand all but the most serious storm event without a major stem or branch failure. Pruning and plant spacing can influence canopy form; however, damaging wind, ice or cultural practices, such as topping, can deform a tree's canopy. Restoration pruning attempts to improve the structure and form of a damaged tree (American National Standards Institute 2001). The ultimate goal of restoration pruning is to return a damaged canopy to a condition where it can provide similar benefits to that of the original canopy, with acceptable levels of risk of failure. The arborist has limited information on a formal definition of stable canopy structure. Therefore he/she must rely on personal experience and intuition when deciding how to use pruning to guide canopy development or restoration. The underlying structure of a canopy rests on individual branch form, yet little is known how to objectively and reliably predict canopy stability and strength from branch form. A more thorough understanding of how a stable canopy is structured is needed in order to develop meaningful standards to guide the arborist during canopy restoration.

Sullivan (1896) suggested that in building design, as well as in nature, one can see that form follows function. Niklas (1992) suggested that plants balance four functions throughout their lives: photosynthesis, reproduction, hydraulics and mechanical support. While photosynthesis and reproduction are important, it is hydraulics and mechanics that are directly archived during growth. As a tree develops, the function of stems and branches changes from a heavy investment in water transport with moderate investment

in mechanics, to an increasing investment in mechanics in order to support both static and dynamic loading as lateral branches develop. In order to survive, a tree must be capable of resisting self-applied and external loads. As a branch increases in size and weight, mechanical support becomes an increasingly important function particularly if hydraulic supply is not limiting (Niklas 1992; Spatz and Brüchert 2000).

Pruning removes tissue in the attempt to direct growth for a desired benefit, and therefore, shifts canopy form. Knowledge of form placed in a biological context can help the arboricultural community understand how to guide this shift. Plant biologists use allometry to describe the relationship between size and shape of organisms, and various allometric relationships have been forwarded to describe growth patterns in trees. This review discusses three allometric methods of modeling branch form (pipe model theory, fractal dimensioning, and power laws) and explores their applicability to the arboriculture community particularly in terms of potential use in guiding pruning research.

PIPE MODEL THEORY

Pipe model theory predicts leaf biomass from stem basal area and is often used in carbon sequestration and canopy growth models (Berninger and Nikinmaa 1997; Chiba 1998; Mäkelä 2002). The stem is considered a 'unit pipe', a non-photosynthetic organ, which supports the leaves (Fig. 4). The summation of the cross-sectional area of the stems at any given point predicts leaf mass (equation 1) (Shinozaki et al. 1964).

Equation 1: $M = \sum \Pi R_s^2$

Where: M = leaf mass

R_s = radius of stem

The theory works well with smaller branches, but it is less applicable towards the base of the tree, since larger stems have a larger proportion of inactive wood (heartwood) (Berninger and Nikinmaa 1997; Suzuki and Hiura 2000; Taneda and Tateno 2004). The additive effect of increased tissue at branch attachments, due to hydraulic segmentation in the branch protection zone (Eisner et al. 2002) and circular vessels (Lev-Yadun and Aloni 1990), may have an impact on the robustness of the pipe model theory in larger branches and stems.

Initially static, the pipe model has been modified to account for heartwood formation and the subsequent removal of unused pipes (Mäkelä 2002). This is incorporated into computer growth models such as a dichotomous threshold for heartwood formation in the LIGNUM and MORPHO (Berezovskava et al. 1997; Perttunen et al. 1998) and a transitory manner in TREE and WHORL models (Mäkelä 2002). While models have been used to simulate growth in idealized conifer form in forest stands, it might be possible to incorporate such models to investigate how the removal of tissue during pruning influences growth in amenity trees and individual branches. Recent research has shown that trunk movement and bending moment vary with pruning dose and technique (Smiley and Kane 2006; Gilman et al. 2008 a & b; Pavlis et al. 2008). Arboricultural researchers may wish to investigate the applicability of these models in terms of growth responses to pruning and shifts in form and stability.

One adaptation of the pipe model was to estimate the amount of foliage removed during pruning from branch cross-sectional area. Grabosky et al. (2007) showed that, while branch area (πR_s^2, where R_s is stem or branch radius) can be used to estimate the amount of leaf area removed in small (< 5.5 cm, 2.2 inches) live oak (*Quercus*

virginiana) branches, the summation of r_s^4 was more reasonable at explaining model error than cross-sectional area along the trunk. Researchers have adapted the pipe model theory to include hydraulic modeling (Valentine 1985; Mäkelä 1986) and it is possible that the robustness of the pipe model might be increased with inclusion of R^4, especially in larger branches, as hydraulic flow capacity in confined tubes is typically modeled as an r^4 function (see equation 2) (Zimmermann 1978; Tyree and Ewers 1991).

Hydraulics Literature

Water is necessary for growth, photosynthesis and metabolic activity such as respiration and the exchange of gases during transpiration (Kozlowski and Pallardy 1997). Understanding how a tree builds the system to deliver water is important to understanding the investment in this important function. Trees need to be able to pull water up longer vascular networks to the distal leaves, thereby overcoming the force of gravity. This flow occurs in the tracheids in gymnosperms and principally in the vessel elements of angiosperms. Tracheid cells play a dual role, as the lumen serves as the location for water and nutrient transportation, while the thick cell walls provide mechanical support (Panshin de Zeeuw 1980; Sperry et al. 2006). Angiosperms typically separate these two functions between vessel members and fibers respectively (Esau 1977; Sperry et al. 2006). Vessel members have thin cell walls that prevent local buckling, but add little if any structural support at the organ level (Cochard and Tyree 1990; Davis et al. 1999; Hacke and Sperry 2001; Hacke et al. 2006). The movement of water through vessel lumen is similar to that of a pipe. It is slowest against the sidewalls, due to adhesion, and increases parabolically towards the center of the cylinder (Tyree and

Zimmermann 2002). This pattern is described by the Hagen-Poiseuille law of hydraulics (equation 2)

$$\text{Equation 2. } K_{capillary} = \frac{R_p{}^4 P \pi}{8 \eta L_c}$$

Where: $K_{capillary}$ = hydraulic conductivity
L_c = length of conduit
η = viscosity of liquid
P = hydraulic pressure head
R_p = radius of conduit

which shows that conductance will increase by the fourth power as the radius of the cylinder increases, if length is factored out. Since tracheids and vessels are not perfect pipes, the Hagen-Poiseuille equation overestimates conductance in trees. In order to pass from one conduit to the other, the water must pass through pit membranes (tracheids) and perforation plates (vessels), which reduce conductance. Researchers have compared conductance estimated by Hagen-Poiseuille to measured conductance and found that gymnosperms are only 26-43% efficient (Zimmermann and Brown 1971 citing Ewart 1905 and Münch 1943) and that angiosperms are 33-67% efficient (Tyree and Zimmerman 1971; Petty 1978 and 1981). Although neither tracheids nor vessels are considered to be perfect cylinders, researchers suggest that the Hagen-Poiseuille prediction is proportional to actual flow rates and that $R_p{}^4$ provides a reasonable fit for theoretical conductance of water in xylem conduit lumens (Zimmermann 1978; Tyree et al. 1994; Tyree and Ewers 1991).

The maximum diameter of vessels and tracheids tends to increase with cambial age (Fisher and Ewers 1995; Gartner et al. 1997; Domec and Gartner 2002; Sperry et al. 2006), although this was not true for holly oak (*Q. ilex*) (Dünisch et al. 2004). From

equation 2, one might expect that the diameter of vessels and tracheids to increase as stems and branches continually grow in order to maximize efficiency on the axial length. Maximum conduit size, however is, limited by embolisms (Tyree et al. 1994; Hacke and Sperry. 2001; Gartner et al. 2003). The primary cause of embolism is water stress which creates large negative pressures that disrupt the cohesive water column (Ewers 1985). Additionally, embolisms occur if air bubbles form when water is frozen and not reabsorbed during thawing. Since smaller diameter conduits are less prone to embolism, it is likely that a balance between efficiency and risk occurs in regions prone to drought stress or freezing events during the growing season (Tyree and Zimmerman 2002).

It appears that hydraulics can be modified in response to mechanical needs as gymnosperms and angiosperms have been found to reduce specific conductivity (a measurement of flow capacity) in favor of mechanical needs (Ewers 1985; Gartner et al. 1990; Spicer and Gartner 1998a, 1998b). Mean vessel element diameter was found to be larger in supported vines than in non-supported plants (Chiu and Ewers 1992; Gartner 1991a), and vessel diameter decreased in tension wood (Kaeiser and Boyce 1965; Jourez et al. 2001). A reduced investment in hydraulics and increased investment in mechanics appear to lead to increased radial growth. Branch allometry will probably change with branches becoming less slender as mechanical support becomes more vital. This change in slenderness may prove a useful tool in identifying whether a developing branch might be retained to serve as a scaffold or removed during pruning. Researchers may wish to explore how shifts in the balance between hydraulics and mechanics are manifested in changes in stem or branch allometry. Insights into shifts in branch form could then influence pruning location.

FRACTAL DIMENSIONING

Researchers have incorporated fractal dimensioning when investigating allometric patterns in trees. Fractal dimensioning measures the relationships in self similar geometric shapes (La Barbera and Rosso 1989). The fractal dimension (D) is a description of how much two (D=2) or three (D=3) dimensional space is filled by the object(s) being modeled (La Barbera and Rosso 1989) (equation 3).

Equation 3. $D = Log (R_b) / Log (R_L)$

Where: D = fractal dimension

R_b = bifurcation ratio

R_L = link length

Fractals have been incorporated in computer modeling of tree growth (Fig.5). Berezovskava et al. (1997) devised the MORPHO system, which used Lindenmayer systems (L-systems) (Lindenmayer 1968) modeling to show that branch thickness in Norway spruce (*Picea abies*) was dependent on the branch length. Similarly, the L-PEACH model utilizes source-sink relationships based on carbon and water to simulate growth based on water stress and fruit thinning (Allen et al. 2005). Although these models show it is possible to develop algorithms for computer modeling, L-systems and fractals have not been empirically tested (Casella and Sinoquet 2003; Pearcy et al. 2005).

Fractals can be useful in modeling overall geometric shape or space filling, but do not fully address branch dimensioning (Farnsworth and Niklas 1995; Casella and

Sinoquet 2003). Researchers have suggested that fractals may be useful in describing the complexity of branching, but the functional significance of fractals has not been fully determined (Fitter and Stickland 1992). Fractal analysis is best used when growth patterns are simple and continually repeating (Fitter and Stickland 1992), yet the literature suggests that the allometric pattern of branches is plastic (McMahon and Kronauer 1976; Bertram 1989; Farnsworth and Niklas 1995). The incorporation of fractal analysis in computer growth simulations may provide arboricultural researchers a meaningful tool in exploring the nature of allometric plasticity and how a shift from small flexible leaf bearing branches to larger structural scaffold branches might influence canopy stability. Additionally, phyllotaxy (or vegetative bud arrangement) results in a predictable lateral branch patterning which is lost to a degree over time as young lateral branches can be considered disposable and senesce due to self shading and other environmental cues (Maillette 1982, Wilson 1989 ; Suzuki and Hiura 2000). Thus modelers may wish to incorporate adaptive fractals that can account for the departures from the original fractal pattern in urban canopy growth models.

POWER LAW SCALING

Allometric research has often utilized log-log relationships, or power laws ($Y \propto aX^b$), to investigate plant form (McMahon 1975; Niklas 1994a). One advantage power laws hold is the ability to investigate variation in the scalar (b), using standard regression analysis of the log-log transformed data. McMahon (1975) presents three models which utilize power laws to compare allometric patterns in trees using length (L) and radius (R): geometric similarity model ($L \propto R^1$), static stress similarity model

($L \propto R^{1/2}$) and elastic similarity model ($L \propto R^{2/3}$). The geometric similarity model suggests that shape will remain the same as a tree grows in size. The geometric stress similarity model was found to fit many gymnosperms (Niklas 1994a). Sposito and Santos (2001) found that the geometric stress rather than elastic or static stress models held for eight *Cecropia spp.* trees in Brazil.

McMahon (1975) reported that scale modelers realize perfectly scaled prototypes will often behave in a slightly different manner than the full scale structure. Typically the models will need to have at least one physical parameter adjusted in order for the prototype to function as the full scale structure. While the geometric similarity model does not account for such an adjustment, both the static stress and elastic similarity models do as their scalars are less than 1.

The static stress similarity model was found to hold in mature pine trees; Scots (*Pinus sylvestris*) and lodgepole (*P. contorta*), as well as lodgepole sapling (Dean and Long 1986; Mäkelä 2002), while mature lodgepole pines also fit the elastic similarity model. The static stress similarity model has been known by a variety of names over the past century: concept of adaptive growth (Schwendener 1874; Metzger 1893 both cited in Brüchert and Gardiner 2006), constant stress theory (Mattheck and Breloer 1994) and uniform stress theory (Morgan and Cannell 1994). These theories suggest that the shape of a tree stem is influenced by mechanical loading (Brüchert and Gardiner 2006). The uniform stress theory suggests that under average conditions, stress will be distributed uniformly on the outer fibers but non-uniformly during extreme conditions, which can include snow or wind loading. McMahon (1975) suggested that maximum stress is held constant between beams, but not average stress. Stress levels have been found to vary

along stems (Niklas and Spatz 2000; Ancelin et al 2004; Kane et al 2008) and Niklas and

Spatz (2000) counter that the elastic similarity model is better at explaining mechanical

stability along stems and branches.

McMahon and Kronauer (1976) suggest the elastic similarity model is preserved

in large trees and the authors present a graph derived from a big tree register which

appears to fit the elastic similarity model. Niklas (1995) points out that the graph

represents a hand drawn best fit line rather than regression analysis. Yet the graph

launched further research which reports that the elastic similarity model holds in

dicotyledonous trees (Rich et al. 1986; King 1986; Niklas 1994b; O'Brien et al. 1995)

and a good fit was reported for tropical trees above 6 meters (20.4 feet, King 1996).

The elastic similarity model is based on the critical buckling length of a column

(equation 4, Greenhill 1881) and suggests that the critical length for a stem scales to the

radius raised to the 2/3 power (Fig.6).

Equation 4. $L_{critical} = C\left(\dfrac{E}{\rho}\right)^{\frac{1}{3}} R_s^{\frac{2}{3}}$

Where: $L_{critical}$ = Critical length
C = Proportionality constant
E = Modulus of elasticity
ρ = Wood density
R_s = Column radius at base

This formula is derived from the Greenhill critical load to cause buckling of columns and

not cantilevered beams, although researchers have applied the critical length formula for

use in branch allometry studies (McMahon and Kronauer 1976; Bertram 1989; Spatz and

Brüchert 2000).

The proportionality constant (*C*) was reported to be either 1.26 for cylinders without taper or 1.96 when tapered to a cone (Greenhill 1881). Additionally *C* should be calculated for complex shapes, non-uniformed materials, or to factor in external loading (Spatz and Brüchert 2000). Density-specific stiffness (*E*/*ρ*) remained fairly constant in dried milled wood (Green et al. 1999; Panshin and de Zeeuw 1980), but was reported to vary in samples from live trees due to the transition from sapwood to heartwood (Niklas 1997a & 1997c), changes in anatomical properties such as microfibril angles in the S2 layer of secondary cell walls, the percentage of latewood (Mencuccini et al. 1997), and stem slenderness (length / radius) in four year old trees (Watt et al. 2006). The variation in density-specific stiffness in living wood has not been fully addressed with regards to the influence in the critical length formula and researchers may wish to investigate the impact on stem/branch form. Despite the potential variation in density-specific stiffness, many researchers and practitioners continue to utilize the critical buckling formula and suggest that radius is the predominant factor in this equation.

The application of this formula to trees is an example of how plant biomechanics incorporates engineering principles into the biological sciences. Niklas et al. (2006) provide an historical overview of this subject, suggesting that Schwendener's 1874 seminal monograph established the field of study. One of the primary goals for arborists is to minimize the risk of tree or branch failure, and research has turned towards biomechanics in an effort to better understand how trees withstand loads. The incorporation of multiple disciplines increases the set of tools available to arboriculture researchers and this is important, since no single model will fit all trees as they scale differently over time and space. The arboriculture discipline should include investigation

of all models in order to determine which best fits trees growing in the urbanized environment.

Wood as a Structure

Understanding how wood imparts flexibility and strength is important in biomechanical studies. Wood is an organized structure having different material and physical properties, depending on which plane in being loaded (Panshin and de Zeeuw 1980). Wood is stronger under tension than under compression (Panshin and de Zeeuw 1980; Reiterer et al. 1999). Unlike synthetic materials, wood maintains some mechanical strength beyond the elastic range, which may explain why trees can remain standing after being subjected to extreme loads (Koehler and Telewski 2006).

Material properties of wood vary, based on many factors, among them are anatomical properties and moisture content. In green wood, moisture content is typically above 25-30% and this is considered the point at which fibers are saturated (Panshin and de Zeeuw 1980; Green et al. 1999), so moisture content does not typically affect the material properties in live tissue. Woody plant cells are composed of a primary and secondary wall. The primary cell wall serves to confine and support the cells during development. Secondary cell wall is formed during cell maturation and adds important mechanical components that support the mature cell and stem/branch. The secondary cell wall has three layers (S1-S3) that are found interior to the primary wall. Microfibrils provide tensile strength and vary in orientation with each layer, influencing the directional strength of the cell and tissue (Burgert 2006). In the S1 layer, the microfibrils are oriented in the transverse direction and resist outward buckling; microfibrils are

oriented in the radial direction in the S3 layer to prevent inward buckling (Esau 1977; Niklas 1992). The S2 layer provides the major mechanical support for the cell and the microfibrils are roughly aligned in the axial direction. Toughness, (amount of strain before fracture) was found to increase with microfibril angle in the S2 layer (zero being perpendicular to the longitudinal axis) (Reiterer et al. 1999). Strain is the movement of a material in relationship to the original length (Hibbeler 2006). Cells in young plants were found to have low microfibril angles, which allow flexibility (Lindström et al. 1998) while cells in mature wood have high microfibril angles, which makes them stiffer (Lichtenegger et al. 1999), and subsequently able to act as structural support for the canopy.

The cellulose microfibrils are embedded in lignin (Esau 1977) and it is lignification that adds rigidity to plants and the ability to withstand compression (Koehler and Telewski 2006). Lignification indirectly increases tensile strength by impeding water, which in turn would reduce the strength of the cellulose microfibrils (Niklas 1992). While the microfibril angle is useful in explaining strength patterns, many researchers have turned to modulus of elasticity as a predictor of wood stiffness or resistance to bending. Elasticity was found to be positively correlated with stem age in both black locust (*Robinia pseudoacacia*) (Niklas 1997a, 1997b, 1997c) and loblolly pine (*P. taeda*) (Groom et al. 2002). In Norway spruce, E decreased as stem height increased (Reiterer et al. 1999; Brüchert et al. 2000) and varied by branch diameter as well as vertical position in trees (Spatz and Brüchert 2000). Sapwood E was 35% lower than in heartwood, suggesting that younger stems and branches composed of sapwood are more flexible than wood composed predominately of heartwood (Niklas 1997a, 1997b, 1997c; Spatz and

Brüchert 2000). Values for *E* in lumber quality green wood (>28% moisture content) and dried wood (12% moisture content) are available in the literature, for example the Forest Products Laboratory's Wood Handbook (Green et al. 1999). Additionally, mechanical tests can be run to empirically determine *E*, generally using a load press in a laboratory setting, following specification detailed by the American Society for Testing and Materials (2005) or cantilevered bend tests on small samples (Gartner 1991b; Wagner et al. 1998).

The coefficient of variation for *E* was reported to be 22% (Green et al. 1999) suggesting that an inherent variation exists around the mean values for material properties of wood. Arboricultural researchers, concerned with modeling how trees withstand loading events, need to better understand how material properties vary in standing trees, rather than in milled lumber. Forest products researchers have investigated methods of nondestructive evaluation (NDE) testing, such as longitudinal wave transmission (Ross et al. 1997) to determine the relationship between *E* in logs and that of lumber, as well as stress wave techniques in standing trees and logs (Wang et al. 2000; Wang et al. 2004). Furthermore, engineers are adopting NDE such as acoustic emissions, impulse excitation technique, radar, ultrasound and active thermography to determine the material properties of standing structures comprised of steel and concrete (Mirmiran and Philip 2000; Maierhofer 2006; Swarnakar et al. 2007) as these tools might hold promise in the evaluation of standing trees.

Reaction wood is found in both gymnosperms and angiosperms. In general, gymnosperms develop compression wood on the lower side of the leaning trunk or branch, while angiosperms develop tension wood on the upper side. It has been noted that

angiosperms may be capable of producing compression wood (Niklas 1992; Clair et al. 2006). Tracheids in compression wood have shorter cells with thicker cell walls (Panshin and de Zeeuw 1980). While both the S1 and S2 layers are thicker, the S2 layer contains less cellulose and more lignin (Côté et al. 1968; Parham and Côté 1971). Vessel elements in tension wood tend to be smaller and less numerous (Barefoot 1965), while fibers have thicker cell walls, smaller lumen diameters and are longer in length (Kaeiser and Boyce 1965). The widths of both S1 and S2 layers in fibers were smaller and a gelatinous layer was found interior to the secondary layers. This gelatinous layer is mainly composed of cellulose with limited lignin (Panshin and de Zeeuw 1980). Alméras et al. (2005) reportes that E was higher in tension wood and lower in compression wood. Wood density was found to increase in tension wood, due to the presence of gelatinous fibers with thicker cell walls (Gartner et al. 2003). Researchers should investigate how the production of reaction wood influences branch development and allometry.

The ability to provide structural support in trees lies in the composition and thickness of cell walls or indirectly by the presences of lumens in tracheids, vessel members or fibers. Sone et al. (2006) reported that E was positively correlated with percent fiber and fiber cell wall thickness in redvein maple (*Acer rufinerve*), while E was found to be negatively correlated with fiber lumen diameter near the tips of five *Acer* species branches (Woodrum et al. 2003). Research has shown that trees alter anatomy in response to mechanical needs (Kaeiser and Boyce 1965; Gartner 1991a; Chiu and Ewers 1992; Jourez et al. 2001), yet, it is not certain if this is a direct tradeoff between hydraulics and mechanics (Woodrum et al. 2003). More research is needed to determine how these important functions are balanced during normal branch development and if so,

how the balance is manifested in branch form. Pruning has a direct consequence on load

distribution along the branch. Not only does pruning immediately and directly alter

branch form, it may lead to changes in anatomical features such as cell wall width, lumen

size or the formation of reaction wood in the future. Researchers may wish to investigate

how management activities, such as pruning, affect subsequent development at the

cellular and tissue levels, which may then lead to changes in branch allometry and

canopy stability.

ALLOMETRY OF BRANCHES

Returning to the three similarity models, Niklas (1994a, 1995) notes that none of

the three similarity models (geometric, elastic nor static stress) hold for trees or branches

throughout their lives, due to ontogenetic changes. The primary reason is that the rate of

lateral elongation slows with age but radial growth is indeterminate and declines less over

time. This growth pattern leads to the curvilinear relationship between height and

diameter in small plants, when plotted on a log-log scale, and converges to linear as

overall size increases (McMahon and Kronauer 1976; Bertram 1989; Niklas 1995).

Figure 7 is derived from a sub-sample of 65 Norway maple (*A. platanoides*) branches

which fit the curvilinear to linear relationship. This pattern was repeated in branches

where the elastic model was found to be robust, when length was greater than 3 m in both

white oak (*Q. alba*) (McMahon and Kronauer 1976) and silver maple (*A. saccharinum*)

(Bertram 1989), but not below the 3 m threshold. Additionally many researchers have

shown that the scalar changes when a plant moves from a small or intermediate size

(curvilinear > 2/3) to large size (linear at 2/3) (McMahon and Kronauer 1976; Bertram

1989; Niklas 1995; Suzuki and Hiura 2000; Niklas and Spatz 2000; Niklas and Spatz 2004; Niklas 2007).

The transition in scalars is likely due to a change in flexibility, where smaller branches and trees tend to be more elastic and larger branches are stiffer (Niklas 1997a, 1997b & 1997c; Niklas and Spatz 2000). Smaller branches can reconfigure in heavy winds and a tree can afford to loose a number of smaller branches, while larger branches are less flexible. The loss of even one large branch can be problematic, either in terms of loss of photosynthetic capability or invasion points for decay organisms. Therefore, small branches are free to invest more in elongation and hydraulics in order to place the leaves in the sun, while larger branches likely shift towards an increase in radial growth that balances hydraulics and mechanics.

Slenderness ratios (length/radius, see Fig. 8) have been used to define potential instability in trees, and values above 200 are considered unstable in gymnosperms (Petty and Worrel 1981; Cremer et al. 1982; Petty and Swain 1985). Bertram (1989) reports that slenderness increased as silver maple branches grew in size to a maximum slenderness of 260 and then decreased. The change in slenderness corresponded to a shift to the elastic similarity model, and the transition from flexible branches designed for solar collection to stiffer structural support branches. Researchers may wish to investigate if this pattern holds for other species and run empirical tests to determine the relationship between slenderness and branch stability. At the stand level, slenderness often increases with competition and was found to be positively correlated with density-specific stiffness in Monterey pine (*P. radiata*) plantations (Watt et al. 2006). It was suggested that the increase in density-specific stiffness increased stability in the slender stems. It is possible

that resource competition is similar in an individual canopy, and research should investigate if slenderness alone or in combination with density-specific stiffness could be used as a predictor of branch stability. Additionally, in restoration pruning, the arborist must selectively remove some watersprouts while retaining others. It may be that the one target for removal would be those watersprouts with high slenderness ratios. Dahle et al. (2006) found that silver maple watersprouts were 49% weaker than normally growing lateral branches. This research only looked at watersprouts up to 21 cm (8.4 inches) in diameter and it is possible that material properties may increase in the watersprouts at some point. The arborist may choose to use techniques like subordination to maintain higher slenderness ratios in waterspouts until mechanical properties increase over time.

It seems as though Louis Sullivan was correct for trees, form does follow function. Whether one uses a scalar, as in the three similarity models put forth by McMahon, or slenderness ratios, it appears that tree stems and branches modify the relationship between lateral elongation and radial growth over time. Whether this shift is due to a tradeoff or a balance between hydraulics and mechanics has not been satisfactorily answered. Further research is needed to fully understand how form is influenced by hydraulic and mechanical functions. A better understanding between the form and function should help the arborist community improve maintenance pruning standards as well as devise guidelines for canopy restoration.

ACKNOWLEDGEMENTS

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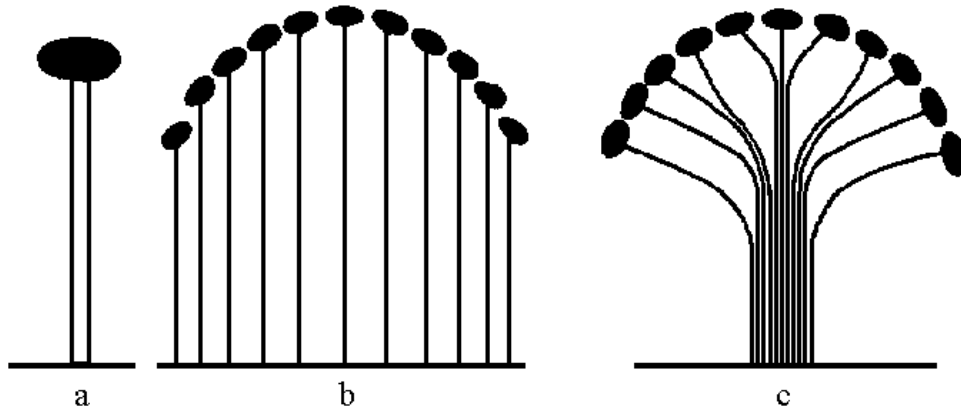
Figure 4. Depiction of pipe model theory showing (a) basic unit pipe, (b) stand level pipe model, and (c) tree form pipe model, adapted from Shinozaki et al. (1964).
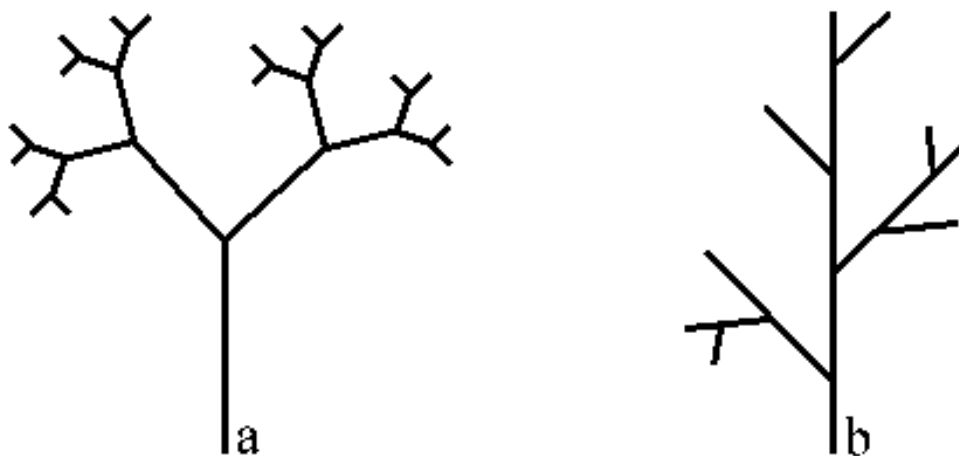
Figure 5. Depiction of fractal branching in (a) opposite (bifurcation) branching

pattern, and (b) alternate branching pattern.
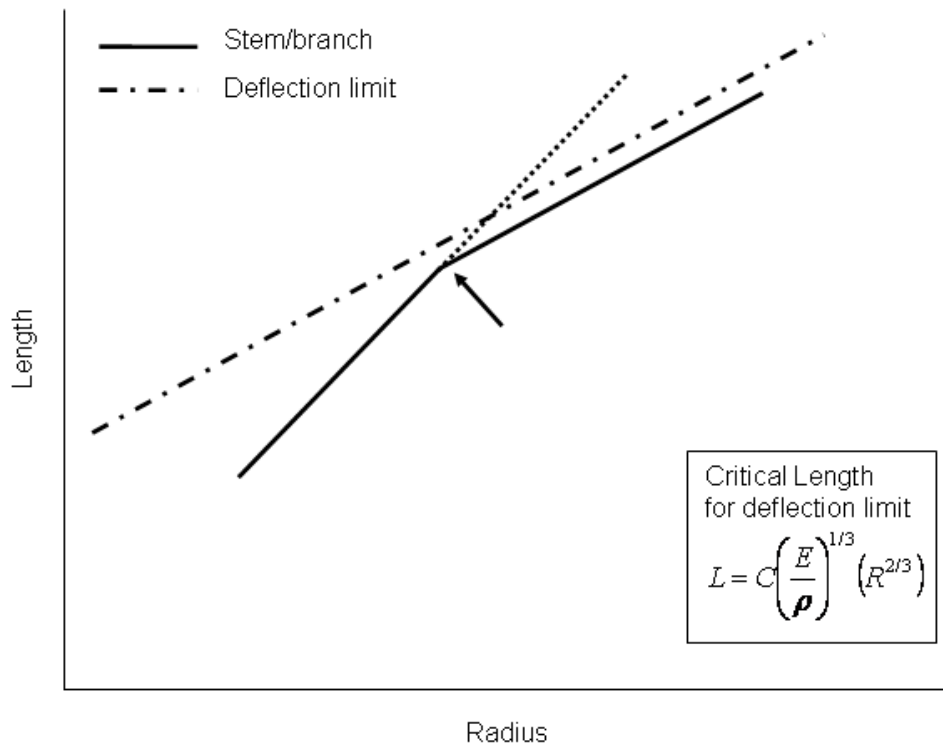
Figure 6. Diagram of stem / branch growth depicting that length scales to radius$^{2/3}$ before

the critical length is reached (arrow). Adapted from Bertram (1989).

Power Function
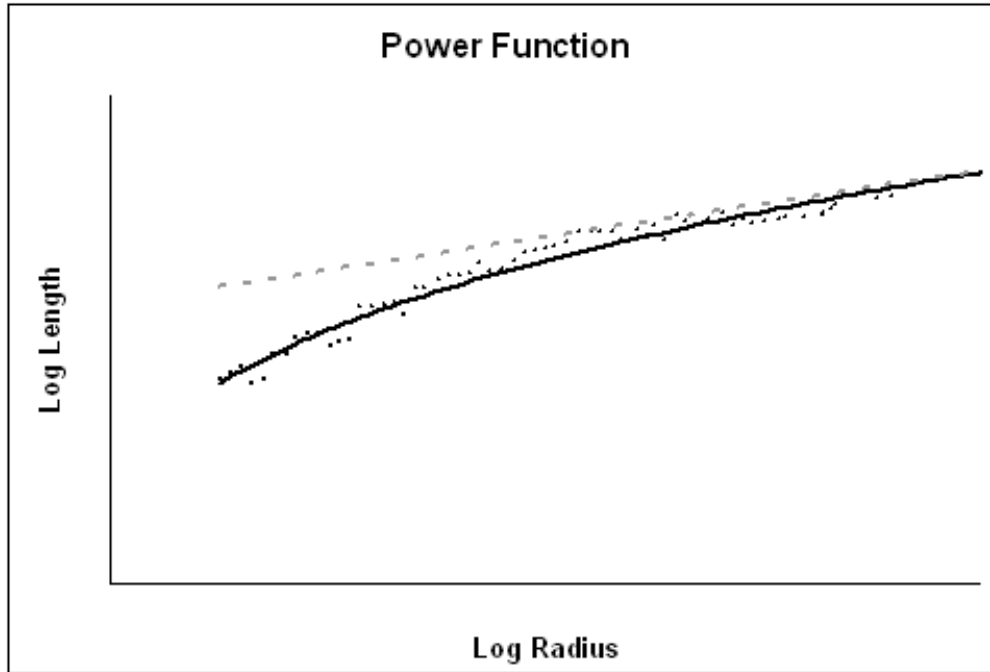
Figure 7. Log-log relationship between length and radius of a subset of 65 *Acer platanoides* branches depicting a generalized curvilinear relationship for small branches and a converging toward a linear relationship for larger branches. The dashed line depicts a length = radius$^{2/3}$ relationship as proposed by the elastic similarity model.
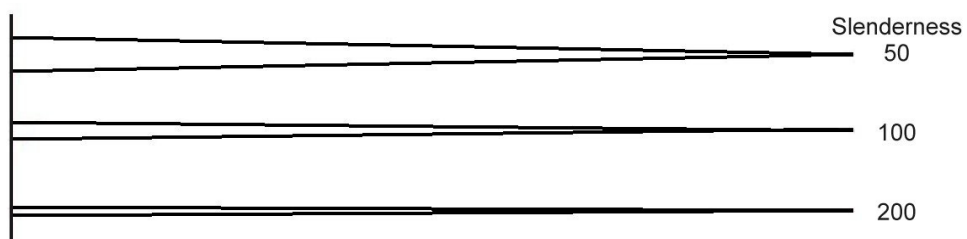
Figure 8. Depiction of three branches with slenderness ratio (length / radius) of 50, 100 and 200.

CHAPTER 2

Allometric patterns in *Acer platanoides* L. (Aceraceae) branches

ABSTRACT

Acer platanoides L. individuals were dissected to determine whether branch allometry changed as branches increased in length. Branches were found to transition from a log-log curvilinear relationship to a linear relationship after they reached 3 m in length. The log-log linear relationship was best modeled with the elastic similarity model. The shift in allometry appears to correspond to a shift from increasing slenderness ratio (length / radius) with increasing branch length to decreasing ratio, and is likely due to a transition from flexible sun branches to stiffer structural branches. The total number of subordinate lateral branches was found to increase rapidly after the primary branch length passed 3 m, further suggesting that branches are transitioning to a structural role as size increases.

Keywords: Allometry, elastic similarity, slenderness, length, radius

INTRODUCTION

Plant biomechanics integrates principles of plant biology and engineering in order to better understand how organisms, such as trees, develop and withstand loading events over time. One of the important functions of secondary growth in trees is to provide the mechanical support for the trunk or branches against the constant force of gravity and periodic additional loading events, such as wind or ice storms. Most of the work in plant biomechanics concentrates on trees in the natural setting, where mechanical failure might lead to plant death with minor risk to plants or objects in the surrounding environment. In the case of open grown amenity trees, understanding how trees survive or fail during such

loading events is important as the risk of serious personal or property damage often increases in the urban setting.

Louis Sullivan (1896) suggested that building designers could turn to nature to learn how form follows function. He noted that if function holds steady, so should overall form. Researchers have utilized allometric relationships to describe and relate tree form and function, and a log-log relationship between length (L), or height, and radius (R) is often used in these models. McMahon (1975) forwarded three similarity models that describe growth patterns in trees as power law functions ($L \propto aR^b$). The geometric similarity model uses a scalar of b = 1.0, whereas the elastic similarity model uses b = 0.67, and the static stress similarity model scalar is 0.5. Previous workers have found different outcomes for allometry in different forest species, and it remains unclear which model is most applicable for trees in the natural or urban setting.

A large body of literature suggests that the elastic similarity model (2/3 power) is best suited when scaling tree height, relative to radius (McMahon 1973; McMahon 1975; McMahon and Kronauer 1976; King 1986; Rich et al. 1986; Niklas 1994b; Niklas 1995; O'Brien et al. 1995; King 1996; Niklas and Spatz 2004; Niklas 2007). Dean and Long (1986) found that the static stress similarity model (1/2 power) worked for both mature (> 13 m) and sapling (< 2.2 m) *Pinus contorta* Doug. Ex. Loud. trees, while mature trees also fit with the elastic similarity model. The geometric similarity model (1.0 power) was found to fit *Cecropia spp.* trees (Sposito and Santos 2001) and gymnosperms (Niklas 1994a). Finally, there is a suggestion that allometry might transition from the elastic to the stress similarity model at very large sizes, suggesting that function changes with size,

yet the authors do not list a specific size (Niklas 1997b; Niklas and Spatz 2000, Niklas 2007).

The allometry of branches has been found to be plastic with smaller branches following a curvilinear pattern in *Quercus alba* L. and *Acer saccharinum* L., until they reach approximately 3 m, after which they were best modeled with elastic similarity model (McMahon and Kronauer 1976; Bertram 1989). Suzuki and Hiura (2000) reported that the elastic similarity model fits first order branches (arising from the central trunk), but not current year shoots of broad leaved trees growing in forests. It has been suggested that branches probably move from a curvilinear log-log relationship to the elastic similarity relationship, as the function of branches transition from smaller, more flexible branches, to stiffer scaffold branches that provide the structural support to the smaller peripheral branches (Bertram 1989).

The elastic similarity model is based on the Euler-Greenhill formula for critical load buckling of cantilevered beam. An adaptation of this model can be used to derive the critical length for buckling [$L_{critical} = C*(E/\rho)^{1/3}*R^{2/3}$] where $L_{critical}$ is beam length, the proportionality constant (C) was reported to be either 1.26 for cylinders without taper or secondly, 1.96 when tapered to a cone (Greenhill 1881) or thirdly, calculated for complex shapes or non-uniformed materials, or fourthly, to factor in external loading (Spatz and Brüchert 2000). *E* is modulus of elasticity, ρ is wood density, *R* is beam radius (McMahon 1973, Niklas 1992). This model described buckling in terms of bending and does not address torsional loading. Individual lateral branches will impart a torsional load at the base of the primary branch, and it is not known whether overall torsional load is minimized during lateral branch development and senescence. The applicability of the

buckling models and, therefore, the elastic similarity model could be reduced with the inclusion of torsion due to self loading.

If branches shift from a curvilinear relationship to the elastic similarity relationship where the scalar is less than 1, slenderness (branch length / branch basal radius) will move from increasing to decreasing as branch size increases. Bertram (1989) plotted slenderness against branch radius and showed that slenderness increased in small peripheral branches (radius $\leq$ 10 mm), while decreasing in non-peripheral branches (radius $\geq$ 10 mm); however, he did not indicate whether a similar trend was seen between slenderness and branch length. Whether branch radius or length provides the better explanation of the apparent shift in slenderness remains untested.

This research was designed to determine whether branch allometric patterning shifts with size in open grown amenity trees. We hypothesized that form would change from a curvilinear nature to linear, fitting the elastic similarity model. Investigation will explore which variables best explain any allometric shift in branch form. Torsional loading must be minimized in order to use Euler-Greenhill formula in static bending and we hypothesize that lateral branch development will lead to torsional symmetry at the base of the primary branch. *Acer platanoides* L. (Aceraceae) (Norway maple) was chosen as a test species as it is common component in urban forests throughout the United States (Valentine *et al*. 1978, Manion 1981, Nowak and Rowntree 1990) and has a decurrent growth form that is frequently found in open grown trees.

MATERIALS AND METHODS

Sampling occurred at Rutgers University Horticultural Farm III, located in East Brunswick, Middlesex County, New Jersey. Four *A. platanoides* trees (31, 92, 96 & 97) growing on the perimeter of a mixed species plantation were randomly selected during the summers of 2005 and 2006 (Figs. 2 and 9). All sampling began after terminal bud set.

This study was designed to investigate the allometry of open grown urban *A. platanoides* canopies. Therefore, only branches growing on the exterior half of the trees were sampled. Branches were labeled as first order (arising from the central trunk), second order, or third order. A branch was subordinated to a lower order when the aspect ratio (branch basal radius / parent stem radius above the branch) was less then 0.8, following protocol set by Eisner et al. (2002). A condition rating was assigned using the following system: excellent (0 to 33% defoliated), fair (34 to 66% defoliated), poor (67 to 99% defoliated) and dead (dead or completely defoliated).

First order branches were removed from the tree and lowered to the ground using a rope to minimize breakage. Once on the ground, second and third order branches were subsequently removed and measured. Overall branch length was measured using a string to follow the contour of the given branch. Branch basal diameters were measured distal to any branch collar and converted to radius for analysis. The following measurements were also recorded: vertical height of the branch above the ground, diameter of trunk above and below the lateral branch, angle of departure from the trunk, horizontal angle (X, with zero being parallel to the ground) and azimuth (Z). Slenderness ratio was calculated as the branch length divided by branch radius. Due to time limitation in the field, any branch that was less than 100 mm in length and 1.5 mm in radius was considered a short shoot

(Harris et al. 2004; Gradziel et al. 2002) and not included during data collection. Only branches rated in excellent condition were used during allometric analysis.

Whole branch mass was measured using a Caston II crane scale, model 1THB to the nearest 453.6 g (1 lb) for all branches weighing more than 5000 g. Mass for smaller branches was collected using an Ohaus CD33 bench scale, and measured to the nearest gram. Mass was collected within 2 hours of branch harvest and taken with leaves in place. First order branches with a complete set of second order branch mass, including short shoots and all condition ratings, were analyzed for torsional mass balance, and secondary branches were designated as arising on either the left or right half of the first order branch. Second order branch mass was multiplied by the distance from the point of attachment of the first order branch to develop individual bending moments (BM), which were summed for each side (BM_{Left} and BM_{Right}). Torsional balance of the bending moments (T_{Bal}) (equation 5) and percent balance of moments (T_{Pct}) (equation 6) were calculated.

Equation 5: $T_{Bal} = \left| \sum BM_{Right} - \sum BM_{Left} \right|$

Eauation 6: $T_{Pct} = T_{Bal} / \left(\sum BM_{Right} + \sum BM_{Left} \right)$

A study was conducted to determine if a relationship between leaf mass and branch basal area could be identified. Branches were removed from the trees and lengths and diameters measured in the field. Leaves, and any seeds present, were stripped from a given branch weighed and oven dried at approximately 50°C for 3 to 5 days until a constant mass was reached. Mass measurements were collected to the nearest 0.1 g using a Mettler Toledo PB8001-S bench scale.

All data were analyzed using SAS 9.1 (SAS Institute). Mean and standard errors (SE) were run with Proc Means. Proc Univariate was used to verify normality of the data and residuals. ANOVAs were run with Proc GLM and means separations were analyzed using Tukey HSD, and Tukey adjusted mean separation LSD were calculated by hand to adjust when sample size were unequal.. All statistics used alpha = 0.05. Data were determined to be normally distributed and residuals were normally distributed, unless stated otherwise. Graphical output was produced in MINITAB® Release 14.20.

RESULTS

A total of 2,023 branches were collected from four trees between the two field seasons, with 1,735 (85.8%) in excellent condition, 71 (3.5%) fair, 31 (1.5%) poor and 186 (9.2%) dead. Mean tree height was 1,813.6 cm (± 73.1 SE), diameter at breast height (1.4 m above ground) was 33.6 cm (± 3.6 SE) and slenderness ratio (length / radius) was 111.4 (± 11.6 SE). Mean branch length (P = 0.7883, N = 1735) nor branch radius (P = 0.1174, N = 1735) were found to differ between trees.

Mean branch compass bearing was significantly lower for tree 31, than for tree 92, 96 and 97 (Table1, P <0.0001, N = 85). Significant regressions were not found between compass bearing and log branch length (P = 0.3762, N = 85) nor log branch radius (P = 0.3295, N = 85). The change in compass bearing from a western aspect (trees 92, 96 and 97) to a northern aspect (tree 31) did not influence branch form.

Branch angle did not appear to influence branch form, as mean branch angle (90° being perpendicular to the ground), did not vary between the trees (Table 1, P = 0.4227,

$N = 85$). Additionally, significant regressions were not found between branch angle and log branch length (P = 0.4528, $N = 85$) nor log branch radius (P = 0.1148, $N = 85$).

The angle of branch departure from the parent stem or branch was significantly lower in tree 96, than trees 31, 92 and 97 (Table 1, P <0.0001, $N = 85$). Significant regressions were not found between branch angle and log branch length (P = 0.4235, $N = 85$) nor log branch radius (P = 0.1851, $N = 85$). Despite the lower mean departure angle in tree 96, branch departure did not influence branch form.

A log-log plot of length (mm) versus radius (mm) for first, second and third order branches in excellent condition depicts a curvilinear relationship (Fig. 10) for branches less than 3000 mm. A significant linear log-log regression was found for all branches greater than 3000 mm in length, ($P < 0.001$, $N = 123$) (Fig. 11). The confidence interval about the slope (0.61 ± 0.03 SE) ranged from 0.55 to 0.67 and marginally fit the elastic similarity model (0.67), but neither the geometric (1.0) nor static stress (0.5) models. Log-log regression by individual trees found confidence intervals about the slopes (0.62 ± 0.04 SE, 0.69 ± 0.05 SE, 0.59 ± 0.08 SE, 0.70 ± 0.09 SE) that incorporated the elastic similarity model. While log length (Fig. 12) and log radius (Fig. 13) do not appear normally distributed with the full data set ($N = 1735$), both log length (Fig. 14) and log radius (Fig. 15) do appear approximately normally distributed when length is greater than 3000 mm ($N = 123$) and residuals from the regression presented in figure 11 were determined to be normally distributed.

The distribution of subordinate branches was investigated using thirteen first order branches identified as having a complete set of second order branches with known mass. Mean first order branch length for the thirteen branches was 4,381.9 (± 336.6 SE)

and radius 13.2 ($\pm$ 3.6 SE), both in mm. Mean T_{Bal} was 4,614.9 N m ($\pm$ 869.5 SE) and

regression analysis did not find a relationship between the log radius and T_{Bal} ($P =$

0.7602, $N = 13$) (Fig.16). Mean T_{Pct} was found to be 10.2% ($\pm$ 1.19 SE) and a relationship

was not found between log radius and T_{Pct} ($P = 0.2136$, $N = 13$) (Fig. 17). Thus

departures from zero were not linked to changes in branch radius. All of this suggests that

branches were balanced with minimal torsion due to self loading and therefore torsion

can be ignored in terms of utilizing the elastic similarity model. Therefore, it appears that

the elastic similarity model can not be ruled out in open grown *A. platanoides* in the

northeast US.

Log slenderness ratio for all first, second and third order branches, used in the

elastic similarity test, was plotted against the log of branch length (Fig. 18) and the log of

branch radius (Fig. 19). Slenderness increased in both plots until 3 m, when it peaked and

began reducing; indicating that branch form is altered as branch size increased. The plot

against branch length appears to have less scatter than that of branch radius, suggesting

that the shift in form is influenced more by a change in branch length extension than

branch radius.

The decrease in slenderness coincides with a sharp increase in the number of

second order branches growing upon first order branches around branch length of 2 - 3 m

(Fig. 20). As growth in primary branch length slowed, investment in elongation turnrd

towards the lateral branches and a significant quadratic regression was found between the

number of second order and the log of first order branch length ($P < 0.001$, $N = 69$) (Fig.

21). This regression showed that the number of laterals increased from 4 - 5 when 2 m

long, to 5 - 6 at 3 m length, and then 9 - 10 by 4 m length. Changes in branch form

(allometric scaling and slenderness) appeared correlated with a change in branch length extension, as branches increased investment in structural mechanics along the primary axis and redirect elongation into the lateral branches.

Fifty five branches were sampled in the leaf mass study and had a mean branch length of 761.9 mm ($\pm$ 104.5 SE), mean branch radius of 4.5 mm ($\pm$ 0.4 SE), mean slenderness of 136.2 ($\pm$ 9.3 SE) and percent leaf moisture of 65.3 ($\pm$ 0.4 SE). A significant linear regression was found between natural log of dry leaf mass (g) and natural log of branch area (mm^2) (P < 0.0001, N = 55) (Fig. 22).

DISCUSSION

Branches are of two types, with different roles: sun branches that place the leaves in position to intercept solar radiation to drive photosynthesis, and structural branches, upon which subordinated sun branches grow. The literature suggests that the allometric log-log relationship between branch length and radius is curvilinear for sun branches and linear for structural branches (McMahon and Kronauer 1976; Bertram 1989; Niklas 1992; Suzuki and Hiura 2000; Niklas and Spatz 2004). This study was designed to determine if the shift in growth form is applicable to open grown urban trees. Our data confirmed that a the log-log relationship between branch length and radius appeared to follow a curvilinear pattern (Fig. 10) until about 3 m in length, after which they converged toward a linear relationship with a 2/3 power (Fig. 11) labeled the elastic similarity model by McMahon (1975). It appeared that larger structural branches on open grown urban trees can be modeled as cantilevered beams using the elastic similarity model as our findings

are consistent with findings for *Q. alba* and *A. saccharinum* branches (McMahon and

Kronauer 1976; Bertram 1989).

The elastic similarity model was derived using the Euler-Greenhill formula for

cantilevered beams which suggests that as branches become more slender they approach

a point of instability known as the critical buckling length ($L_{critical}$). A change in

slenderness (branch length / branch basal radius) results from either a reduction in annual

length extension or an increase in annual radial growth. Bertram (1989) plotted

slenderness in relationship to branch radius and found that slenderness peak around 260

(a unit less number). Our *A. platanoides* branches peak near 300 (2.5 on a log scale) and

it appears that branch length (Fig.18) is more robust in explaining the shift in slenderness

than branch radius (Fig. 19). Modification of form, when branches approach potential

instability, makes sense if the branches are transitioning from a primary role of flexible

sun branch to that of a stiffer structural branch. Indeed, slenderness begins to decline at

lengths around 3 m. Although we did not test for mechanical stability in this study, Dahle

and Grabosky (unpublished, see chapter four) found that the modulus of elasticity

(descriptor of stiffness) increased from 2,157 MPa, just proximal to the terminal bud

scale scar, to 8,800 MPa, at the midpoint of *A. platanoides* branches that averaged 5.9 m

in length. Future research should investigate whether variation in modulus of elasticity

corresponds to a shift in branch allometry, especially as branches increase in length from

2 to 4 m. Additionally, slenderness values may provide a useful tool in predicting branch

instability. Arborists and managers of amenity trees may wish to explore this potential

important relationship across different species and genera.

If annual branch elongation is reducing as branches grow beyond 3 m, it is likely that a branch has assumed the role of permanent structural branch, while subordinate branches support the bulk of photosynthetic processes. Figure 20 shows that the number of second order branches begins to increase rapidly as branches approach 3 m in length, at least in relatively large shade trees displaying a more decurrent growth form. The quadratic regression in figure 21, shows that the number of second order branches arising axially along a first order branch in *A. platanoides* will increase from 4 - 5 (at 2 m length) to 5 - 6 (at 3 m length) and then jump to 9 - 10 (by 4 m in length). A corresponding decrease in slenderness with branch size suggests an increased investment in structural mechanics along the primary axis of growth, while the subordinate lateral branches fill the role of sun branches. Mäkelä (2002) used foliage growth as an input in branch modeling; the present study did not examine photosynthetic capacity of the branches and future work should explore the relationship between leaf area and branch slenderness ratios.

As lateral branches develop, natural death occurs due to resource competition, such as shading, hydraulic or carbon partitioning. If branches die at an unequal rate over time on one side of the vertical axis of growth (left side versus right), a disruption in the torsional balance of the branch may occur. If unbalanced, a branch could compensate by increasing investment in radial growth. No relationship was identified between branch radius and either T_{Bal} (Fig. 16) or T_{Pct} (Fig. 17), suggesting that torsion may not be influencing the shift in slenderness. Future research may wish to directly test the torsional effect.

This study suggests that the use of the elastic similarity model is appropriate for open grown urban trees with larger branches (>3 m). As branch length approaches 3 m, the function of branches transition from that of a flexible sun branch to a stiffer structural support branch and slenderness begins to decline. The variation in slenderness ratio in this study is more closely associated with branch length than with branch radius, and corresponds to an increase in the number of subordinate lateral branches along the principle axis of growth. It is these lateral branches that assume an increased role in placing the leaves in the sun until they approach the 3 m threshold. This knowledge can help managers of amenity trees understand how normal tree development leads to stability and help in identifying individual trees or branches with growth forms that are at higher risks of failure due to unstable growth forms.

ACKNOWLEDGEMENTS

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Table 1. Mean (± 1 SE) compass bearing, branch angle (zero being parallel with the ground) and angle of departure from the trunk for first order *Acer platanoides* branches. Means with the same letter are not significantly different using Tukey adjusted mean separation LSD calculated by hand to adjust when sample size were unequal, alpha = 0.05.

Tree #	N	Compass Bearing (degrees)	Branch Angle	Angle Departure
31	15	0.7 (± 16.3)b	36.1(± 4.4)a	51.6 (± 3.3)a
92	45	222.1 (± 13.8)a	32.7 (±3.7)a	58.8 (± 1.7)a
96	11	248.4 (± 15.1)a	45.2 (± 8.4)a	37.4 (± 3.7)b
97	14	215.6 (± 17.5)a	38.7 (± 5.2)a	50.3 (± 4.3)a
P-value		<.0001	0.4227	<.0001

Rutgers University Hort Farm III
Urban & Community Forestry Program Reserved Trees

Approx North
Not to Scale

98
97
96

92

90

78

77

51

32

50

31

16

1

15
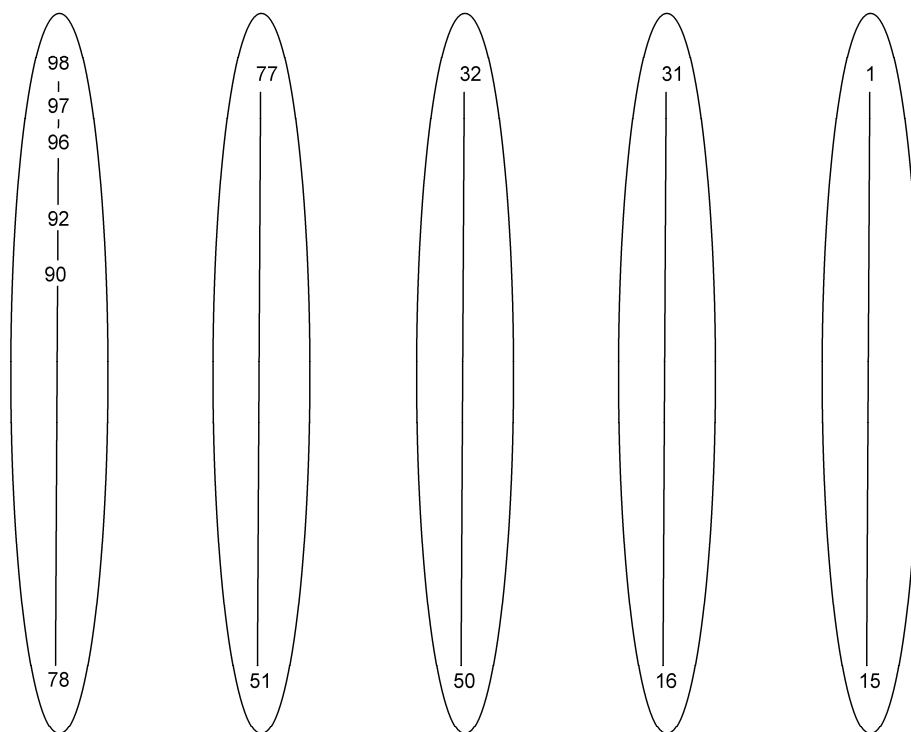
Figure 9. Mix species plantation growing at Rutgers Hort. Farm III located in East Brunswick, NJ. Sampling occurred on *Acer platanoides* trees 31, 92, 96 and 97.
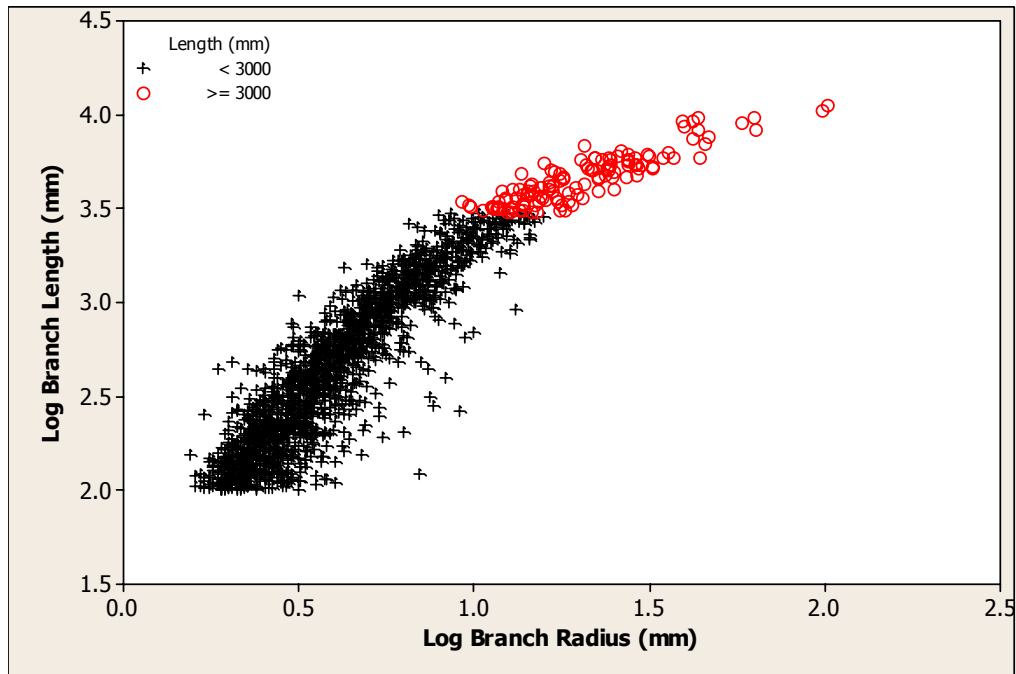
Figure 10. Log-log plot of length (mm) versus branch radius (mm) of *Acer platanoides*

first, second and third order branches. Branches are split into below and above 3000 mm

based on results of McMahon and Kronauer (1976) and Bertram (1989).
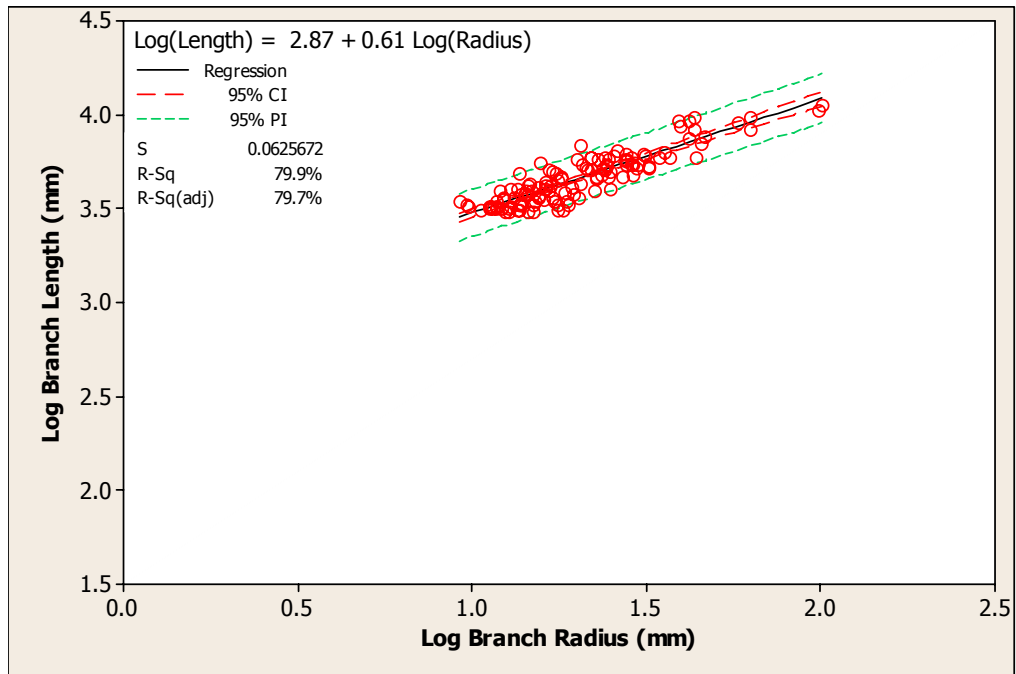
Figure 11. Log-log regression of length (mm) versus branch radius (mm) for *Acer*

platanoides branches. Regression includes first, second and third order branches greater

than 3000 mm.
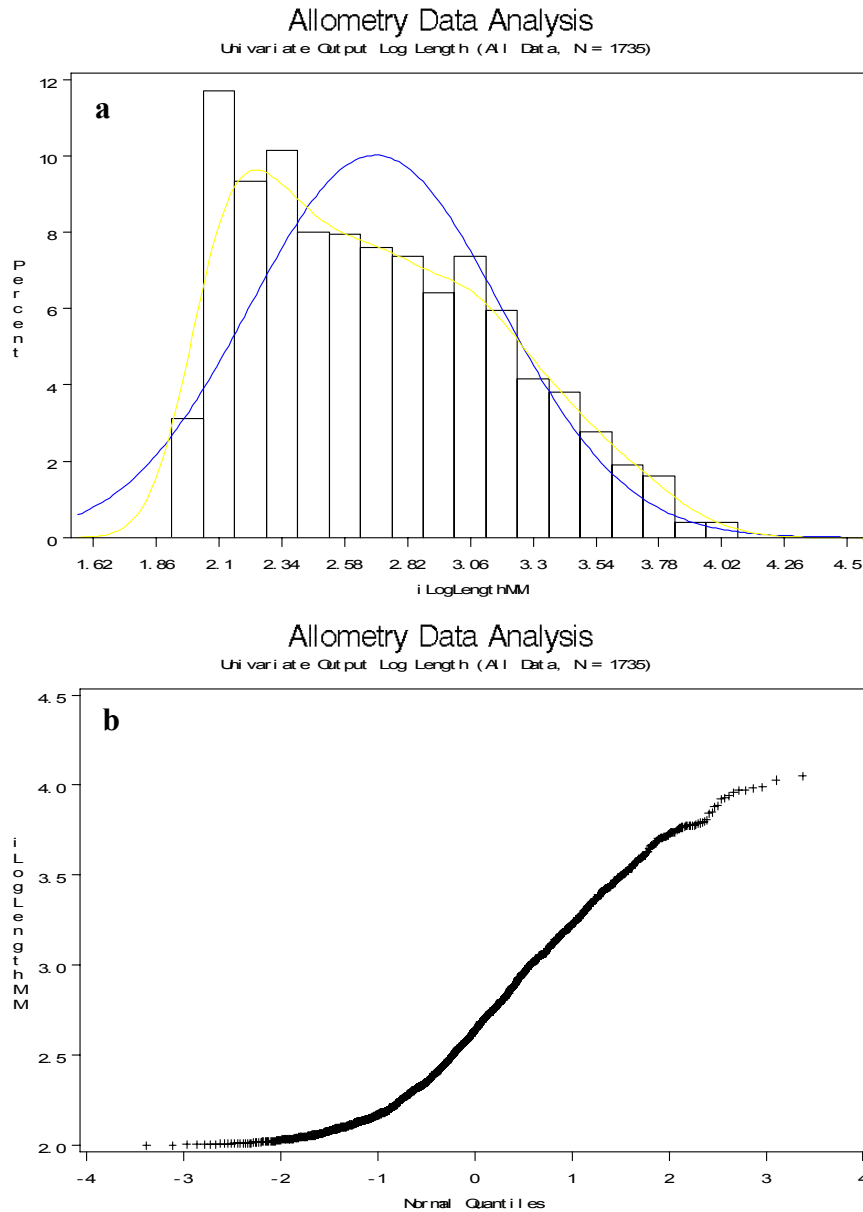
Figure 12. Frequency plot (a) and qqplot (b) for log branch length for all *Acer platanoides* branches (*N* = 1735) using Proc Univariate SAS. Data does not appear to follow a normal distribution.
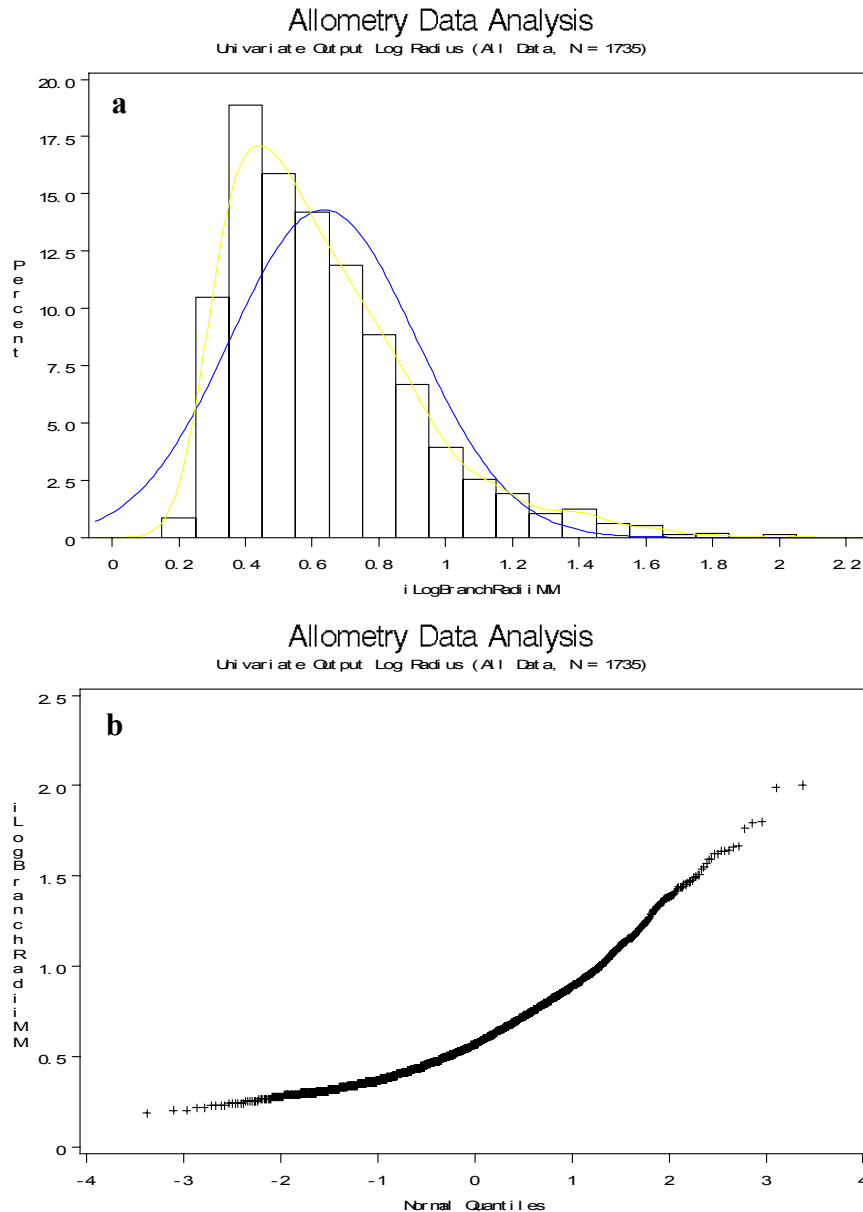
Figure 13. Frequency plot (a) and qqplot (b) for log branch radius for all *Acer platanoides* branches (*N* = 1735) using Proc Univariate SAS. Data does not appear to follow a normal distribution.
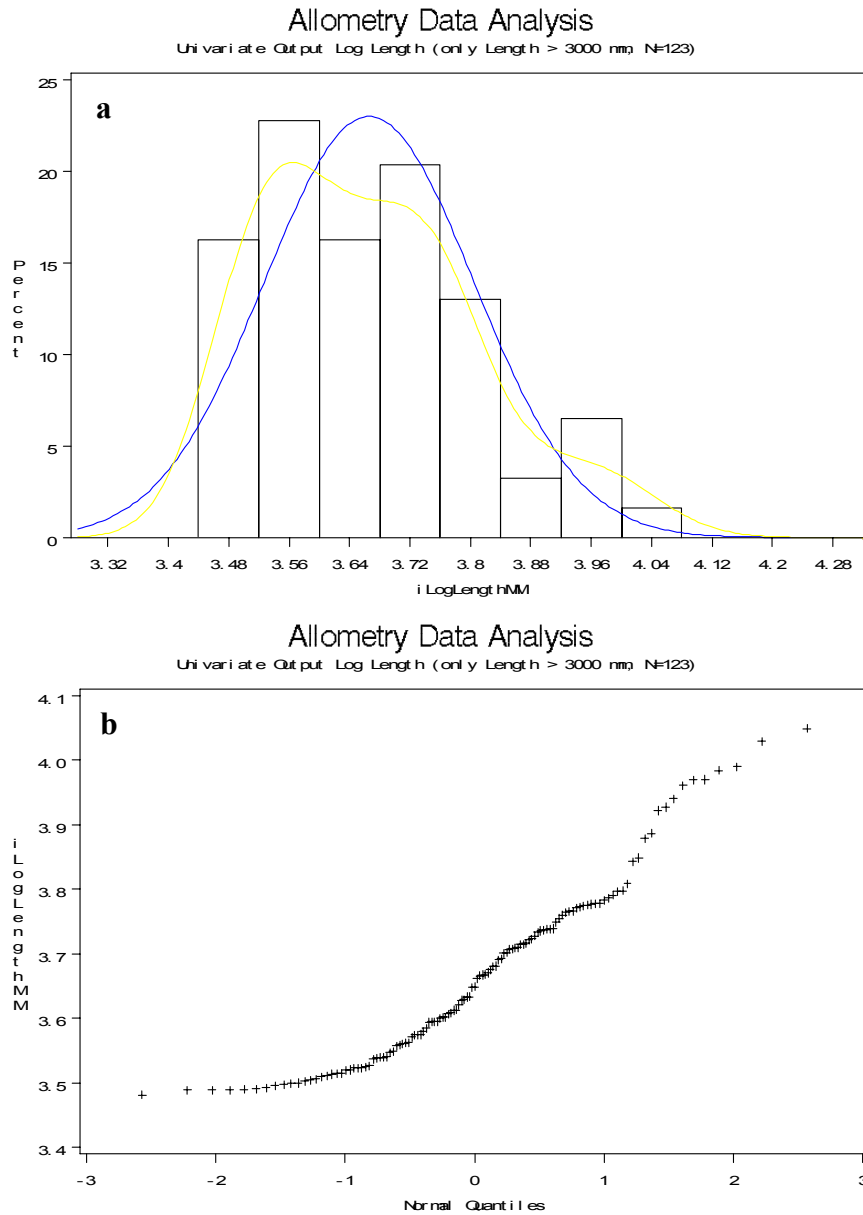
Figure 14. Frequency plot (a) and qqplot (b) for log branch length for *Acer platanoides* branches (*N* = 123) using Proc Univariate SAS. The data appears to approximate follow a normal distribution.
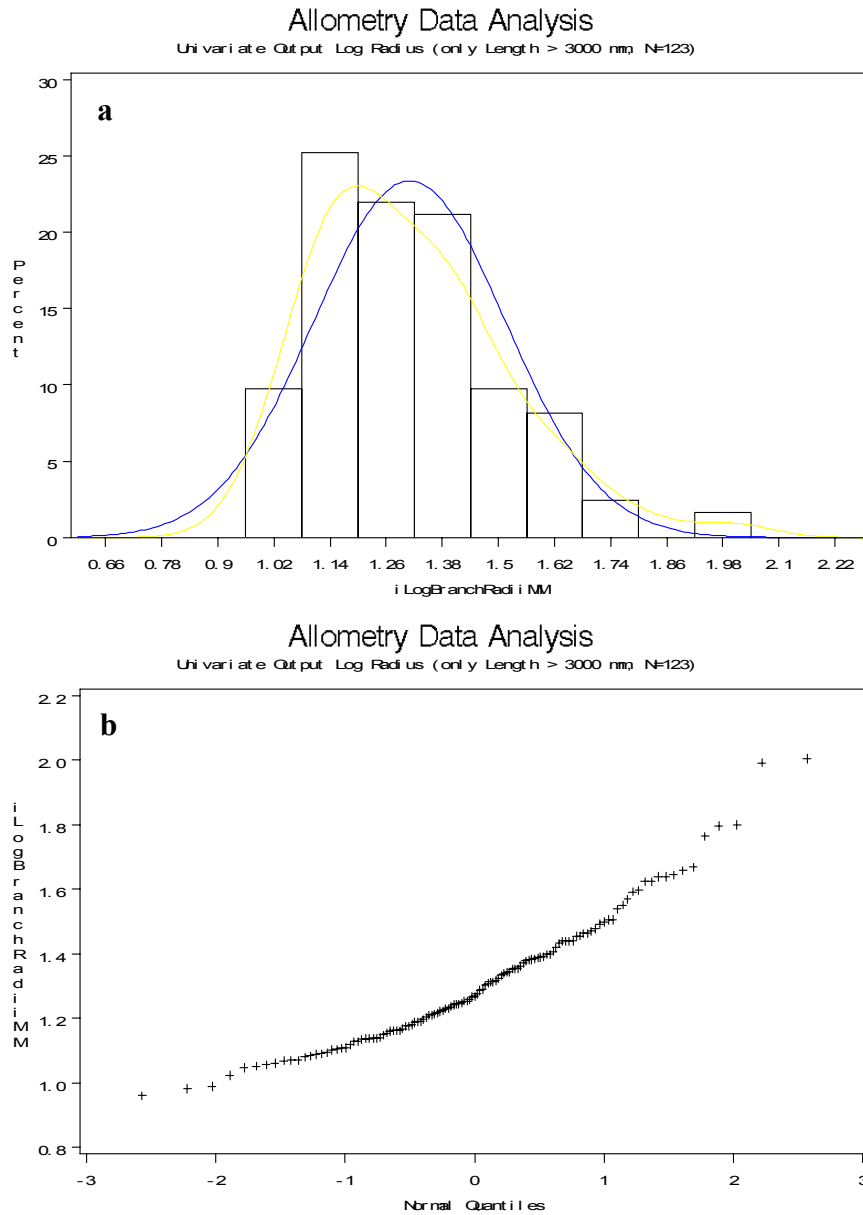
Figure 15. Frequency plot (a) and qqplot (b) for log branch radius for *Acer platanoides* branches (*N* = 123) using Proc Univariate in SAS. The data appears to approximate follow a normal distribution.
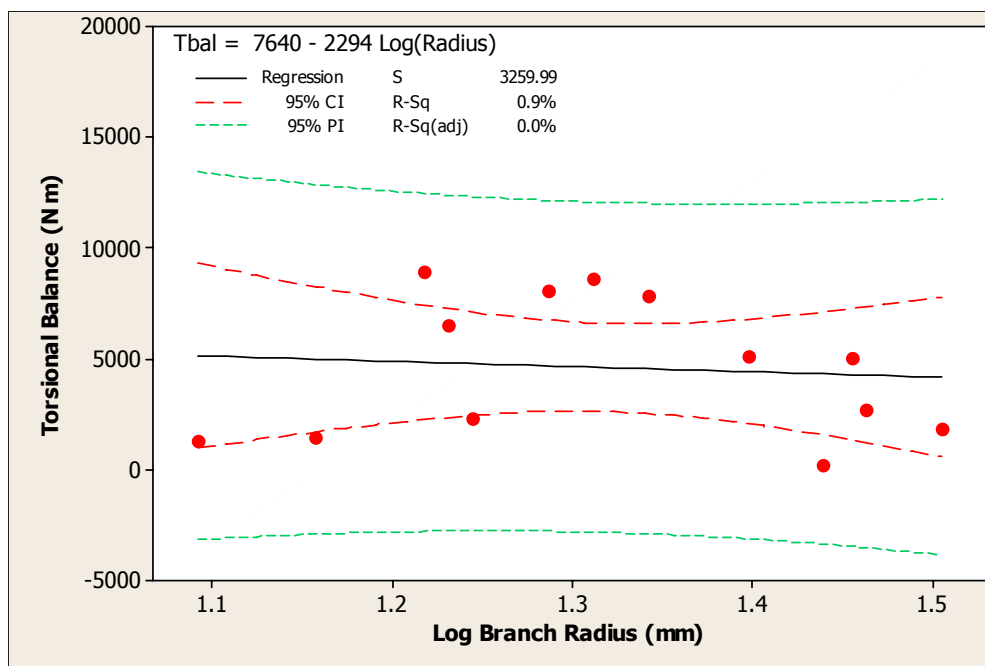
Figure 16. Regression of torsional balance of the bending moments (N m) versus log

branch radius for first order *Acer platanoides* branches.
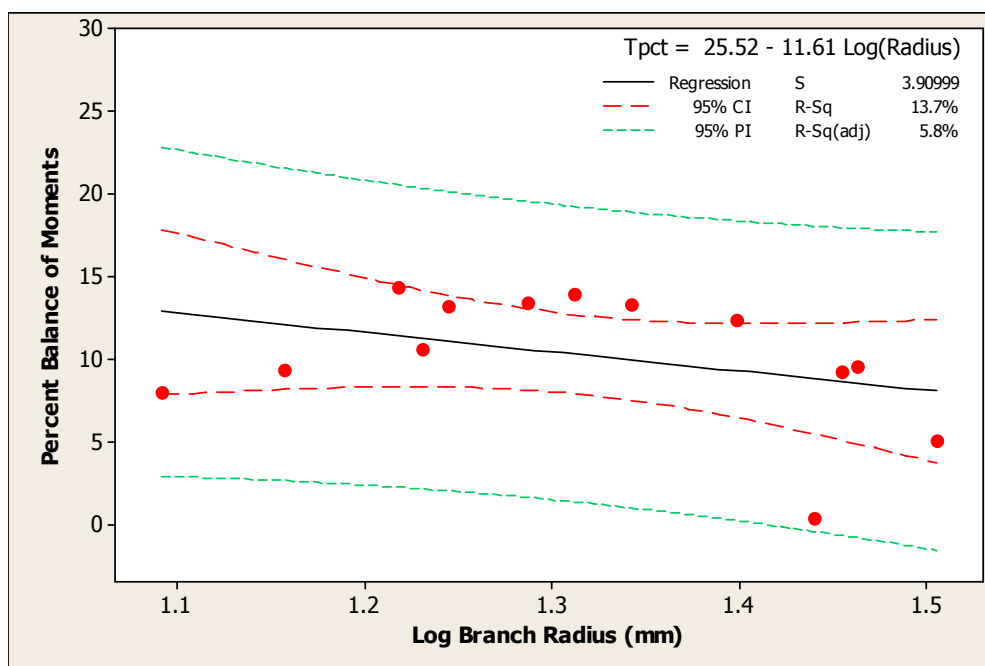
Figure 17. Percent balance of moments versus log branch radius (mm) for first order *Acer*

platanoides branches.
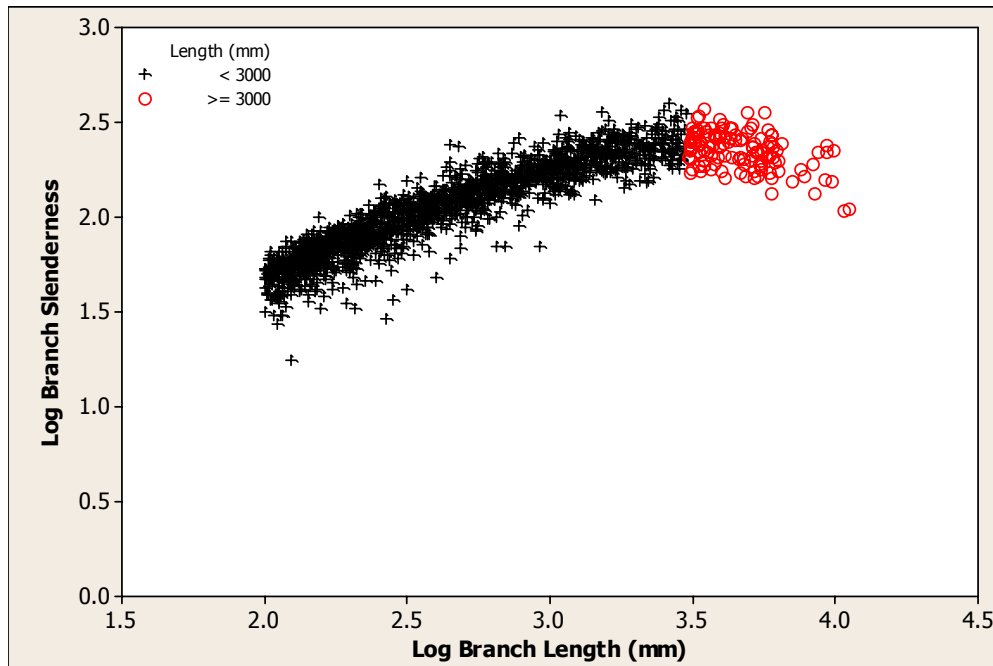
Figure 18. Log-log plot of slenderness (branch length / radius) versus branch length (mm)

for *Acer platanoides* first, second and third order branches.
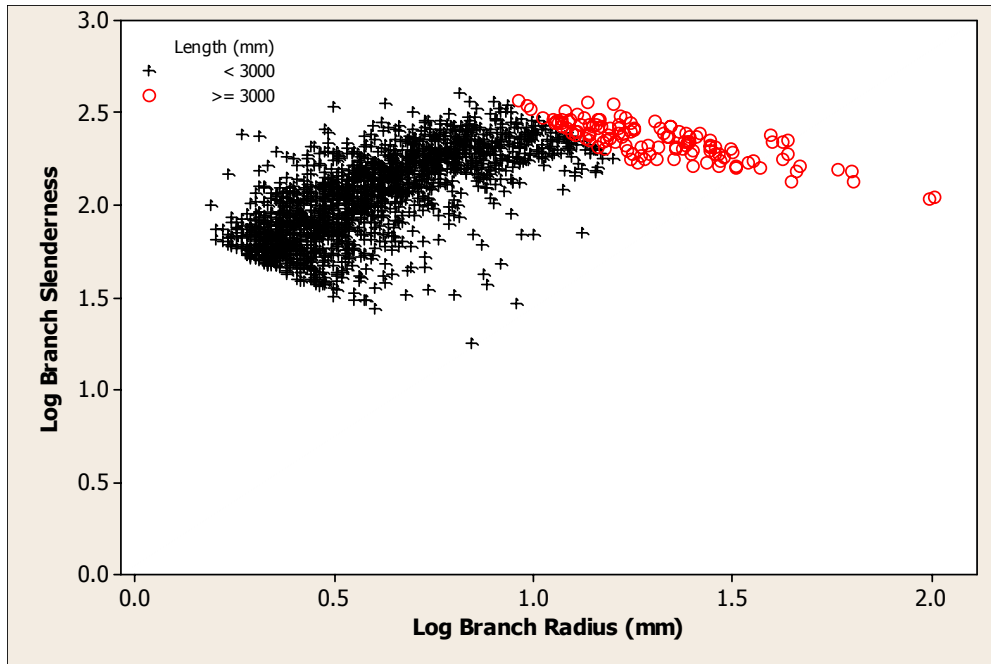
Figure 19. Log-log plot of slenderness (branch length / radius) versus branch radius (mm)

for *Acer platanoides* first, second and third order branches.
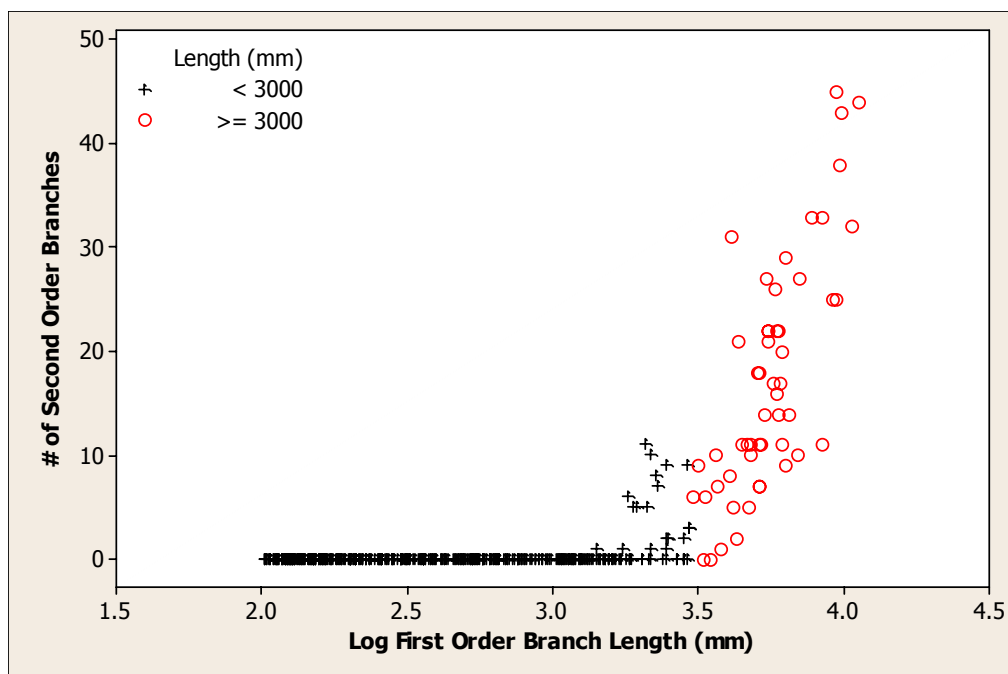
Figure 20. Plot of the number of second order *Acer platanoides* branches plotted against the log of first order branch length.
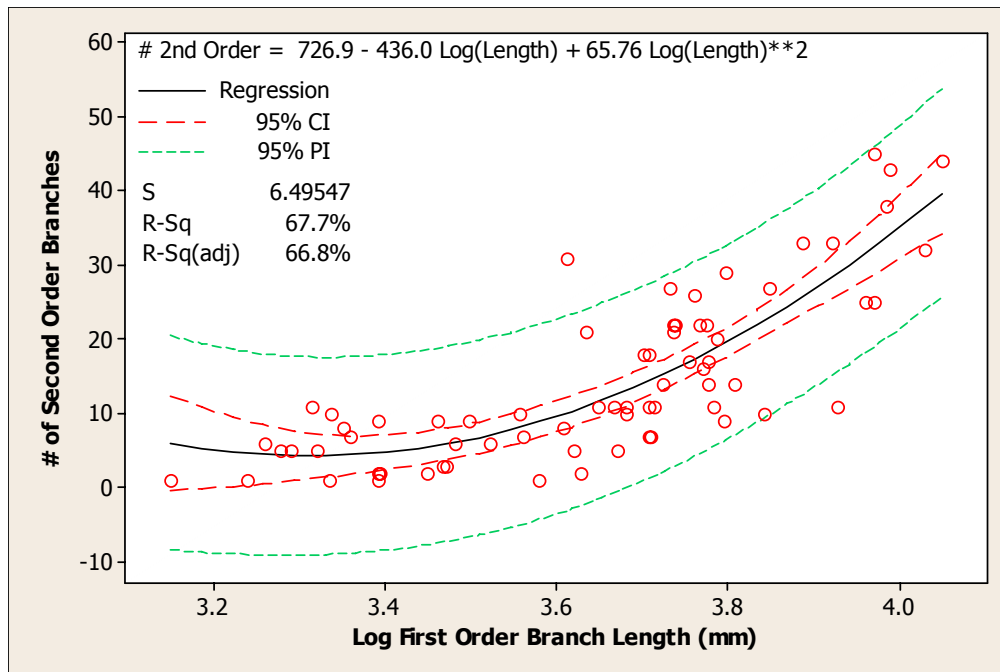
Figure 21. Quadratic regression of the number of second order *Acer platanoides* branches versus the log of first order branch length with one or more lateral branches.
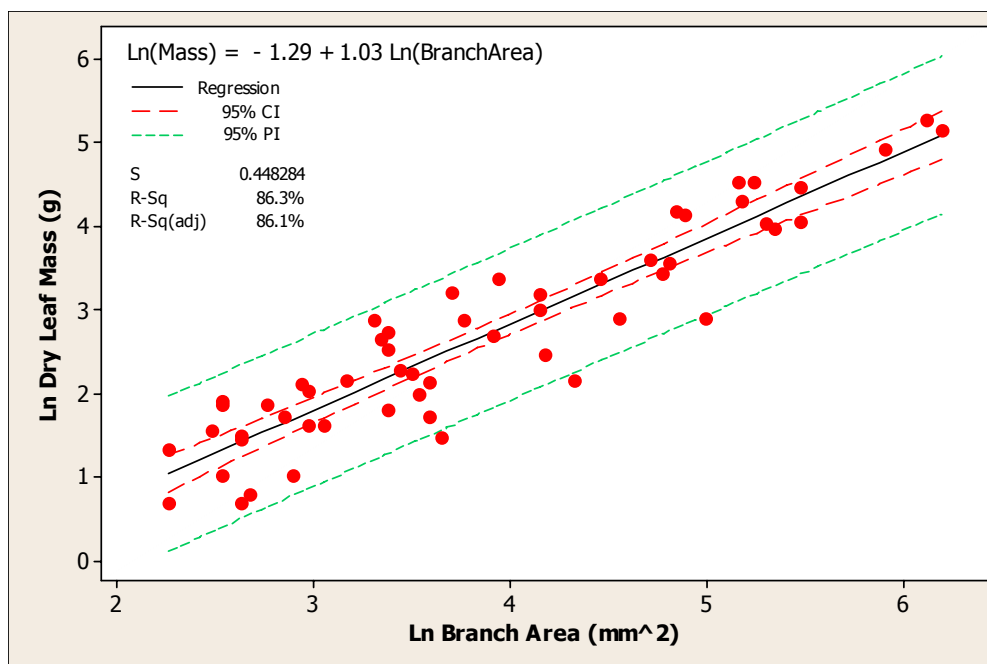
Figure 22. Ln-ln regression of dry leaf mass (g) versus branch area (mm^2) for first order

Acer platanoides branches.

CHAPTER 3

Variation in anatomical features along *Acer platanoides* L. (Aceraceae) branches

ABSTRACT

This paper investigates the balance between hydraulics and mechanics in trees by analyzing changes in the percentage of area composed of four cell types along *Acer platanoides* L. branches. Percent area composed of vessel members, fibers, ray parenchyma and axial parenchyma were compared at five locations along each branch from the stem towards the branch tips. Cell type percentages were not found to be correlated with the angle of branch attachment to the trunk, nor at the top versus bottom of each branch location. In general, vessel radial size decreased in the distal direction along each branch. Percent area comprised of vessels was highest in the middle of the branches and lowest at both ends. Percent area for fibers did not differ in the secondary (radial) growth and vessel to fiber ratios were found to vary in the same way as percent area vessel, suggesting that water movement is governing the balance between hydraulics and mechanics in these branches.

Keywords: anatomy; vessel; fiber; branches; hydraulics; mechanics

INTRODUCTION

Water transportation, storage of water and sugars, mechanical support, and defense are considered to be principle functions for xylem (Niklas 1992; Tyree and Zimmermann 2002; Gartner et al. 2003). Niklas (1992) suggests that a plant must balance four functions through its life: photosynthesis, hydraulic support, mechanical support and reproduction. Two of these functions are filled exclusively by primary tissues,

photosynthesis and reproduction. Primary tissues also play an important role in both hydraulic and mechanical functions.

One of the principal functions of secondary tissues is hydraulic support (Tyree and Zimmermann 2002; Sperry et al. 2006). The ability to supply an adequate amount of water to drive the transportation stream necessary for photosynthesis is paramount for trees. The importance of hydraulics should not diminish the significance of mechanical support, the other principal function of secondary tissue. In order to survive decades or even hundreds of years, a tree must be capable of resisting the load placed on the woody tissues by the constant force of gravity (self-loading) and resist loads applied externally by factors, such as wind, ice and snow.

Xylem in angiosperms is heavily comprised of vessel elements and fibers, and separates the principal functions of secondary wood between these two cells types (Esau 1977; Niklas 1992; Sperry et al. 2006). Vessels are the conduits for water and nutrients and they have large lumens and relatively thin cell walls. While the walls resist cavitation (Sperry et al. 2006), they provide little structural support to the stem or branch. Additionally, the open void of the vessel lumen is an inherently weak location in the wood. Fibers, on the other hand, have relatively small lumens and thick cell walls and provide the bulk of the mechanical support in angiosperm xylem (Niklas 1992; Woodrum et al. 2003; Sperry et al. 2006).

The tree must balance hydraulics and mechanics, yet the literature does not comprehensively address the potential tradeoff between them (Gartner et al. 2003; Woodrum et al. 2003). Indeed, our knowledge of wood anatomy far outweighs our knowledge of function, and it has been suggested that research should concentrate on

biomechanical and physiological studies (Sperry et al. 2006). One way to measure this trade-off would be a comparison of the percentage of area comprised of vessels to that of fibers. An increase in the percentage of area containing vessels may suggest an investment in hydraulic capacity, potentially at the expense of mechanical support, while an increase in the percentage of area with fibers may suggest added investment in mechanics or a change in the pattern of hydraulics.

The Hagen-Poiseuille equation (equation 2) shows that flow in pipes is governed by R^4; see Tyree and Zimmermann (2002) for detailed equation and discussion. Vessel size is constrained by cavitation pressure and minimally by structural support (Tyree and Zimmermann 2002; Sperry et al. 2006). Research has shown that conduit diameter (vessel & tracheids) is smaller in juvenile wood than adult wood and tends to taper in the distal direction in stems and branches (Bannan 1943; Gartner 1995; Domec and Gartner 2002; Anfodillo et al. 2005). The WBE model utilized conduit tapering (narrowing distally) to explain vertical hydraulic supply in xylem as a function of tree height (West et al. 1999). As vessels become larger, flow efficiency increases and fewer vessels are required, potentially making more room for fibers and mechanical support.

The literature suggests that hydraulics can be modified in response to mechanical needs. Conifers have been shown to reduce specific conductivity in favor of increased mechanical support in leaning stems (Spicer and Gartner 1998a, 1998b, 2002). Angiosperm vines and lianas were found to have higher specific conductivity than self-supporting angiosperms like trees and shrubs (Ewers 1985; Gartner et al. 1990). Vessel diameter and the percent area of vessels in *Toxicodendron diversilobum* (T&G) Green (Anacardiaceae) were found to be lower in self-supported than staked plants, leading to a

reduction in specific conductivity and more cross-sectional space for mechanics (Gartner 1991a). This loss in hydraulic capability was compensated by a decrease in leaf specific conductivity, so a similar pressure gradient was expected. Chiu and Ewers (1992) found that *Lonicera japonica* Thunb. (Caprifoliaceae), a twiner vine, had smaller stems and larger vessels than self supported stems in *L. maackii* (Rupr.) Maxim or scrambling *L. sempervirens* L. (initially a self-supported plant, then leaning against other plants or the ground). This suggests that mechanics, not hydraulics, is the governing factor in the differences between the self-supported and staked plants. Vessel diameters were found to decrease in tension wood which should lead to increased mechanical strength (Kaeiser and Boyce 1965; Jourez et al. 2001). Finally, Woodrum et al. (2003) found that wood strength was negatively related to fiber lumen diameter and reported that no trade-off was found between hydraulics and mechanics in five species of *Acer* (Aceraceae). A trade-off implies that an increase in investment in one function is a direct cost to the other, so it may be better to consider that hydraulics and mechanics are balanced in trees.

This study was designed to understand whether the composition of four principle cell types (vessel elements, fibers, ray files and axial parenchyma) vary along the top versus bottom or axially along branches in order to gain insight into the balance between hydraulics and mechanics in *Acer platanoides* L. (Aceraceae) (Norway maple). Investigation also examined whether vessel element tapering occurred, suggesting a shift in hydraulic capacity. *A. platanoides* was chosen as a test species as it is a common component in the urban forests of both the US and Europe (Valentine et al. 1978; Manion 1981; Nowak and Rowntree 1990; Sæbo et al. 2002).

MATERIALS AND METHODS

Twelve first order *A. platanoides* branches, four from each of three trees (32, 90, and 98), were harvested between March 19 and April 2, 2007 from Norway maple trees at Rutgers University Horticultural Farm III in East Brunswick, NJ (Figs. 2 and 23). The trees were located along the perimeter of a mixed plantation with bare ground and mixed grass beginning approximately half way between the trunk and canopy drip line. All sample branches were growing towards the exterior of the plot and considered dormant, as the terminal buds had not begun to swell. Branch diameter and branch angle, zero being parallel to the ground, were measured and the upper side of the branch was marked at the point of attachment to the central trunk. Each branch was removed and divided into 5 sections (P_1, S_1, S_2, S_3, S_4) with a top and bottom sample at each section (Fig. 24). P_1 was harvested approximately 5 cm distally to the most recent bud scale scar, representing primary elongating tissue. S_1 was obtained 5 cm proximal to the most recent bud scale scar and thus the outer growth ring consisted of secondary (radial) growth. S_2 was at the middle of the branch and S_3 was harvested from the midpoint between S_2 and S_4. Finally S_4 was collected from the base of the branch, 5 cm distal to any branch collar. The sections were placed in bags, containing wet paper towels and stored in a refrigerator for up to seven days until milling and slide preparation.

A band saw was used to cut sections S2 - S4 in half, through the pith, and the top and bottom sections were milled to approximately 1 cm wide and 2 - 3 cm long (Fig. 25). Sections P1 and S1 were cut to 2 - 3 cm long and split in half, using a razor knife to create the top and bottom sections. A Reichert sliding microtome was used to cut three transverse sections approximately 30 μm thick for sample S2 - S4 and 40 μm for P1 and

S1. Each sample was stained in a solution of 67% alcian blue and 33% safranin, rinsed twice in distilled water baths, dehydrated in a series of ethanol baths (50%, 70%, 95%, 100%) and finally bathed in Histoclear (National Diagnostics; Jansen et al. 1998). The tissues were submerged in all baths (stain, ethanol, Histoclear) for two minutes. The sections were permanently mounted on slides using Permount (Fisher Scientific).

Samples were photographed under a dissecting microscope (Nikon SMZ1500) using a digital camera (Nikon Coolpix 5000). Photographs were processed in Adobe Photoshop version 7.0 (Adobe Systems Inc.) and the center-most sector, bordered by contiguous ray parenchyma cells, and two adjoining sectors were located for each sample (Fig. 26). The photos were cropped to contain the three sectors and saved as grayscale TIFF files without compression to minimize distortion. All anatomical analyses were conducted on the outermost growth ring using WinCELL Pro version 2007a (Regent Instruments Inc.). Analysis excluded areas of primary xylem cells in section P1, so only secondary tissues were compare across each of the 5 branch locations.

A preliminary study was conducted to determine the minimum area needed for classification of vessels. Photographs were analyzed from thirty randomly selected slides, five each from top and bottom from positions P1, S2, and S3. Lumen areas for all vessels in three sections bordered by continuous rays were measured. The minimum vessel lumen area was found to be 153.3 μm^2, and a minimum threshold of 150 μm^2 was therefore used to classify cells as vessels in the image analytical part of this study.

Two image analyses were conducted for each slide photograph. The first analysis determined the total area measured, along with total number vessels, individual vessel area, and total area comprised of vessels. The second analysis determined the area of the

four ray parenchyma, two interior (sector 1, see Fig.26) and two exterior border ray (sectors 2 & 3). Data files were transferred into an Excel spreadsheet (Microsoft Corp.). Vessel radius ([measured lumen area/π]$^{-0.5}$), percent area of vessels, rays, and fiber [(total area - (area vessels + area ray files+ mean area axial parenchyma))/total area] were calculated. Vessel density (# vessels / mm^2) was derived, as were two unitless ratios; slenderness (length / radius) and vessel to fiber (V:F) (percent area vessel / percent area fiber). Theoretical % cumulative mean flow capacity was calculated using a weighted percentage equation 7:

$$\text{Equation 7: } Theoretical\%MeanFlowCapacity = \frac{R_{ij}^{\ 4} * n_{ij}}{\sum \left(R_{ij}^{\ 4} * n_{ij} \right)}$$

Where: $R_{ij}^{\ 4}$ = mean vessel radius^4

i = 5 μm vessel size class

j = branch location

n = vessel count.

Estimated mean area for axial parenchyma was determined in a follow up study of twenty randomly selected slides, four from each branch location. Slides were photographed under a microscope (Zeiss Axioskop 40) with a digital camera (Insight Spot Firewise 4, model 18.2). *Acer* is considered to have scanty paratracheal parenchyma with axial parenchyma cells, which are usually found only surrounding the vessels (Panshin and de Zeeuw 1980). One photograph, centered on a randomly select vessel element, was taken from each of the three sectors per slide. Axial parenchyma cells were identified, measured for area and percentage of area calculated for each branch location.

All data were analyzed using SAS 9.1 (SAS Institute). Mean and standard errors (SE) were run with Proc Means. Proc Univariate was used to verify normality of the residuals. ANOVAs were run with Proc GLM and means separations were analyzed using Tukey HSD. All statistics used alpha = 0.05. Data were determined to be normally distributed and residuals were normally distributed. Graphical output was produced in MINITAB® Release 14.20.

RESULTS

Mean branch length was 5,716.4 mm (± 269.523 SE), mean branch radius was 31.0 mm (± 1.1 SE) and mean slenderness ratio was 184.3 (± 5.2 SE). A significant difference was found between branch radius at the five sampling locations along the branches. Mean radius decreased distally in secondary (radial) growth along the branches (S4 to S1), and P1 was not significantly different than S1 (Table 2). Tree, branch angle, compass bearing, and angle of departure affects were tested against the following variables: vessel radius, % area vessel, % area fiber, % area ray parenchyma and V:F (Table 3). No significant tree affects were identified. Mean branch angle was 61.3° (± 3.1 SE). No significant branch angle affects were identified except percent area ray parenchyma (P = 0.0157). Mean compass bearing was 234.8° (± 30.6 SE). No significant compass bearing affects were identified except percent area fiber (P = 0.0394). Mean angle of departure was 42.4° (± 4.7 SE). No significant angle of departure affects were identified with any variable.

No significant differences were found between top and bottom samples at each branch location for mean vessel radius, vessel density, % area vessel, % area fiber, %

area ray and V:F (Table 4). One exception was mean vessel radius at branch location S3 (P = 0.0262), where the top had an average vessel radius of 18.01 μm and the bottom an average of 15.95 μm. Although mean vessel radius was significantly different at this single location, a difference was not identified at any of the other four locations, and it was deemed acceptable to group the top and bottom samples for all six variables in the subsequent analyses.

Mean vessel radius was larger in the proximal half (S2 - S4) of the branch than at the tip (S1 and P1; Table 5). Vessel density was highest at location S1, significantly lower at P1 and further reduced from S2 to S4. Locations S1 - S3 were found to have higher percentages of area comprised of vessels, than either end of the branches (P1 and S4). No significant differences were found in percent area fiber in locations with secondary growth (S1 - S4), yet S2 and S3 were found to be different from P1, while S1 and S4 were not. Vessel to fiber ratio was highest in the middle of the branches (S1 - S3) and significantly lower at the ends (S4 & P1). The percent areas for ray parenchyma and axial parenchyma were not found to differ along the branches. Figure 27 shows the theoretical percent cumulative mean flow capacity (R^4) along the branches and vessel radius range at each location was: S4 = 6.99 - 83.39 (N = 4130), S3 = 6.99 - 62.45 (N = 3833), S2 = 6.99 - 55.94 (N = 4433), S1 = 6.99 - 37.11 (N = 2555), and P1 = 6.99 - 26.37 (N = 2105).

DISCUSSION

One of the goals of this study was to determine whether branch angle had an effect on the basic anatomical features along branches. It was anticipated that a decrease

in branch angle would lead to a change in vessel size, or the proportion of vessels and fibers from the top versus bottom. The only location where the vessel radius differed was at S3 (Table 4) where the top was found to have larger vessel radii. This is contrary to findings of reduced radius in tension wood (Kaeiser and Boyce 1965; Aloni et al. 1997; Jourez et al. 2001). The percentages of area for the four cell types were not found to vary with angle, nor were there any differences between the top and bottom sections along the branches. This suggests that the amount of any given cell type laid down during growth in these branches, was not influenced by branch angle during the growth year that was examined.

It is likely that any compensation due to branch angle and/or radial location is at the microcellular level. Reaction wood in angiosperms is typically found on the upper side of a leaning stem or branch and labeled as tension wood. While tension wood was not measured in this study, gelatinous cell wall layers, a direct sign of tension wood formation, were identified during cursory high power microscopic examination of a few tissue samples from the top portion of the branches. Fibers in tension wood have thicker cell walls and smaller lumen diameters than normal fibers (Chow 1971; Kaeiser and Boyce 1965). Although Woodrum et al. (2003) found that fiber lumen diameter was inversely related to strength in five species of *Acer*, the authors did not report whether tension wood was present. While the percent area of fibers does not appear to vary from top to bottom in our branches, future studies should concentrate on fiber lumen diameter, presence of gelatinous layers and cell wall thickness.

Vessel size has been reported to decrease in the distal direction in both trunks and branches (Bannan 1943; Gartner 1995; Domec and Gartner 2002; Tyree and Zimmerman

2002; Anfodillo et al. 2005). Our branches showed similar patterns; larger vessels were found in the proximal half of the branches (S2 - S4), reduced at S1 and smallest at P1 (Table 5). Indeed the Hagen-Poiseuille equation and WBE model suggest this occurs to maintain a constant flow along a branch and the theoretical hydraulic flow in our branches fit this standard pattern (Fig. 27). Vessel density increased in the proximal direction, except at the tip where P1 was lower than S1 despite being only 10 cm apart. Tyree and Zimmerman (2002) suggested that it is common for vessels to end at nodes. Indeed S1 is 5 cm from the previous years' terminal bud, and vessels formed at this location during the current year, supply three points of growth; the continuation of the branch axis and two new lateral branches. Additionally, hydraulic constrictions have been found through the branch protection zone (Tyree and Ewers 1991; Aloni et al. 1997; Eisner et al. 2002), and future research is needed to address whether the increase in vessel density at S1 is associated with any potential hydraulic constriction.

The percent area of vessels should be a function of size and density, and therefore, it is not surprising to see a sharp drop between locations S1 and P1 (Table 5). Vessels at P1 are smaller and less dense as they most likely supply less leaf area. Moving toward the base S2 and S3 had the same percent area of vessels due to lower densities and high vessel size. Furthermore, percent area vessel was lower at the base of the branches which corresponds to larger flow capacity. The Hagen-Poiseuille equation suggests that flow capacity is proportional to the radius raised to the fourth power, assuming that all other factors are held constant. An estimate of flow capacity shows the influence of a few large vessels; a single 35 μm vessel is approximately as efficient as two 25 μm vessels. The estimated cumulative flow lines in our branches are similar for S2 - S4, until around 25 -

30 μm, where S4 is only at 64% of total theoretical capacity, S3 at 74%, and S2 at 90%, while S1 and P1 begin to peak around 15 - 20 μm, and by 20 - 25 μm are essentially at full capacity (95% and 100%, respectively).

As the percentage of vessel area decreased, one would expect to see a corresponding increase in the percent area with fibers. The pattern for variation in percent area of fiber was not as clear as with the vessels; all the secondary wood had the same percentages of area as fiber, but S2 and S4 did not differ from primary wood (P1). Woodrum et al. (2003) did not observe a difference in the percentage of area of fibers at the branch midpoint on five species of *Acer*, yet their values were slightly higher (81 - 82%) than this study (S2 = 71.1%). It appears that the percent area of fibers does not vary greatly in branches, again suggesting that variation to compensate for mechanics in fibers might be at the microcellular level.

Vessel to fiber ratios (V:F) were found to vary along the branches with the base (S4) and tip (P1) having a smaller mean V:F ratio (Table 5). A lower V:F ratio indicates either a reduction in the presence of vessels or an increase in fibers. Since the percentage of area composed of vessels varied with the same pattern as that of the reduction in V:F, it appears that vessels had the most influence on the ratio, and that hydraulics may be governing the balance at the cellular level. Research is underway to determine whether the variation in V:F is correlated with material properties of wood. Additionally, the percent of area composed of fibers along the branches did not vary greatly, and researchers should also concentrate on the influence of microcellular features, such as fiber cell wall thickness, lumen size or the presence of gelatinous layers on the potential changes in mechanical strength along branches.

It appears that trees balance the important functions of hydraulics and mechanics along branches. While no differences between four cell types were found between the top and bottom location, differences were found in vessels and fibers along the branches. Variation in the area composed of fibers was not different in the secondary growth, yet slightly higher in the primary wood compared to the middle portion of branches. Future research should investigate the influence of fiber cell wall and lumen size on mechanical properties along branches. It seems that hydraulics may be the principle function in branches, as a more distinct pattern was found in the percent area of vessels and the ratio of vessel to fiber, where the branch ends was lower than the middle locations. Research should determine whether V:F can be used to predict mechanical properties along branches. Additionally, vessel radius decreased in the distal direction while density generally increased, following patterns that maintain constant hydraulic flow. Vessel density decreased in the primary growth compared to the most recent secondary growth, and future researcher should investigate if the difference is due to hydraulic constriction in the internode and lateral branch attachment zone.

ACKNOWLEDGEMENTS

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Table 2. Mean branch radius (± SE) for each location along 12 first order *Acer*

platanoides branches. Values with the same letter were not found to be significantly

different using a Tukey HSD comparison (P < 0.0001).

Branch Location	Mean Branch Radius μm
S4	29.2 (± 1.1)a
S3	22.4 (± 0.9)b
S2	16.0 (± 0.7)c
S1	3.4 (± 0.3)d
P1	2.9 (± 0.3)d

Table 3. ANOVA P-values for affect of tree, branch angle (zero parallel to the ground), compass bearing, and angle of branch departure (from trunk) against tissue measurements in first order *Acer platanoides* branches. Sample size was 120 and significant P-values, alpha > 0.05, are noted with an asterisk.

Variable	P-value			
	Tree Affect	Branch Angle Affect	Compass Bearing Affect	Angle Departure Affect
Mean vessel radius (µm)	0.0712	0.3699	0.1073	0.4133
Vessel Density (#/mm^2)	0.2195	0.1754	0.0546	0.1197
% Area Vessel	0.3635	0.9440	0.8096	0.4484
% Area Fiber	0.0926	0.0799	0.0927	0.0394*
% Area Ray Parenchyma	0.2335	0.0157*	0.1095	0.1371
Vessel to Fiber ratio (V:F)	0.1347	0.9314	0.5947	0.1857

Table 4. ANOVA P-values for of top versus bottom sample at each location along first order *Acer platanoides* branches. Significant value, alpha = 0.05, is noted with an asterisk. Sample size was 24 at each location, 12 top and 12 bottom.

Variable	p-value for Branch Location				
	S4	S3	S2	S1	P1
Mean vessel radius (μm)	0.7830	0.0262*	0.6928	0.9870	0.5114
Vessel Density (#/mm^2)	0.2354	0.0967	0.1853	0.3803	0.7259
% Area Vessel	0.3028	0.5972	0.1949	0.2975	0.6894
% Area Fiber	0.6579	0.5605	0.0511	0.4336	0.7368
% Area Ray Parenchyma	0.8511	0.7169	0.1418	0.8792	0.8892
Vessel to Fiber ratio (V:F)	0.3376	0.5962	0.1161	0.2064	0.7263

Table 5. Mean values (± SE) at each location along first order *Acer platanoides* branches. Values with the same letter were not found to be significantly different using a Tukey HSD comparison (alpha = 0.05). Sample size was 120 for all samples, except % area axial parenchyma, where $N = 20$.

Variable	Branch Location					
	S4	S3	S2	S1	P1	P-value
Mean Vessel Radius (μm)	16.22 (± 0.22)a	16.98 (± 0.21)a	16.88 (± 0.21)a	13.18 (± 0.13)b	11.49 (± 0.14)c	<0.0001
Vessel Density (# / mm^2)	107.20 (± 3.24)d	148.51 (± 4.91)c,d	150.51 (± 4.31)c	240.32 (± 6.53)a	197.35 (± 4.27)b	<0.0001
% Area Vessel	10.1 (± 2.93)b	15.0 (± 3.86)a	14.7 (± 3.40)a	13.9 (± 3.00)a	8.9 (± 2.92)b	<0.0001
% Area Fiber	73.0 (± 4.92)a,b	70.3 (± 6.20)b	71.1 (± 5.32)b	71.5 (± 5.00)a,b	75.7 (± 6.00)a	0.0083
% Area Ray Parenchyma	16.1 (± 4.31)a	13.9 (± 4.31)a	13.7 (± 3.91)a	13.5 (± 5.33)a	14.0 (± 6.10)a	0.3654
% Area Axial Parenchyma	0.9 (± 0.43)a	0.7 (± 0.19)a	0.5 (± 0.15)a	1.2 (± 0.29)a	1.4 (± 0.78)a	0.0640
Vessel to fiber ratio	14.0 (± 4.64)b	21.9 (± 7.21)a	20.9 (± 6.09)a	19.5 (± 4.71)a	11.8 (± 4.07)b	<0.0001

Rutgers University Hort Farm III
Urban & Community Forestry Program Reserved Trees

Approx North
Not to Scale
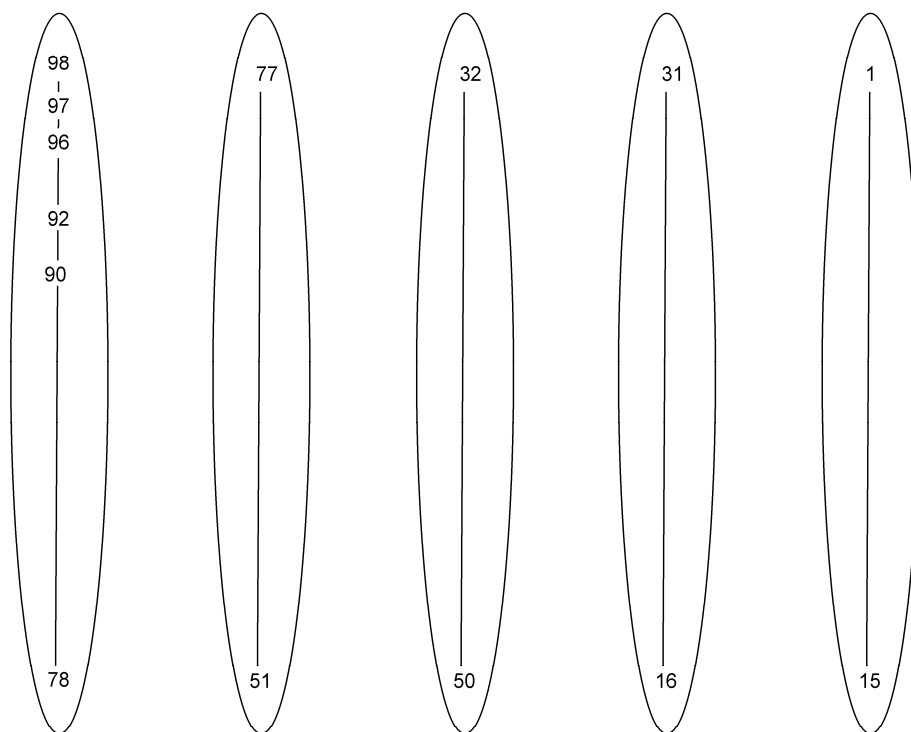
Figure 23. Mix species plantation growing at Rutgers Hort. Farm III located in East Brunswick, NJ. Sampling occurred on *Acer platanoides* trees 32, 90 and 98.
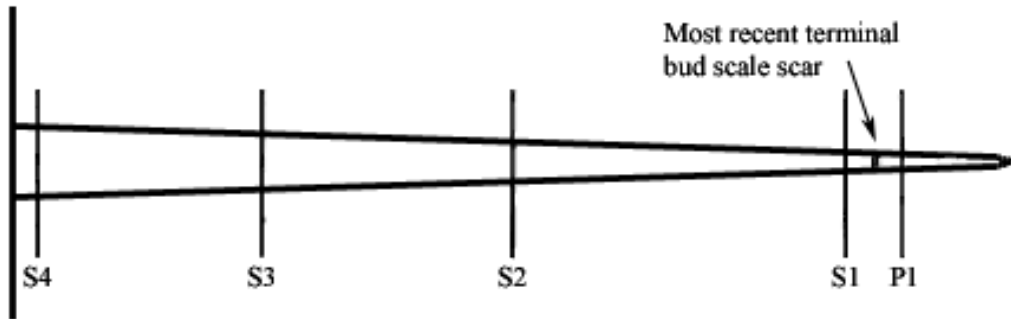
Figure 24. The five sampling locations along *Acer platanoides* branches. Sections S1 - S4 were taken from secondary (radial) growth, while P1 was obtained from primary elongation.
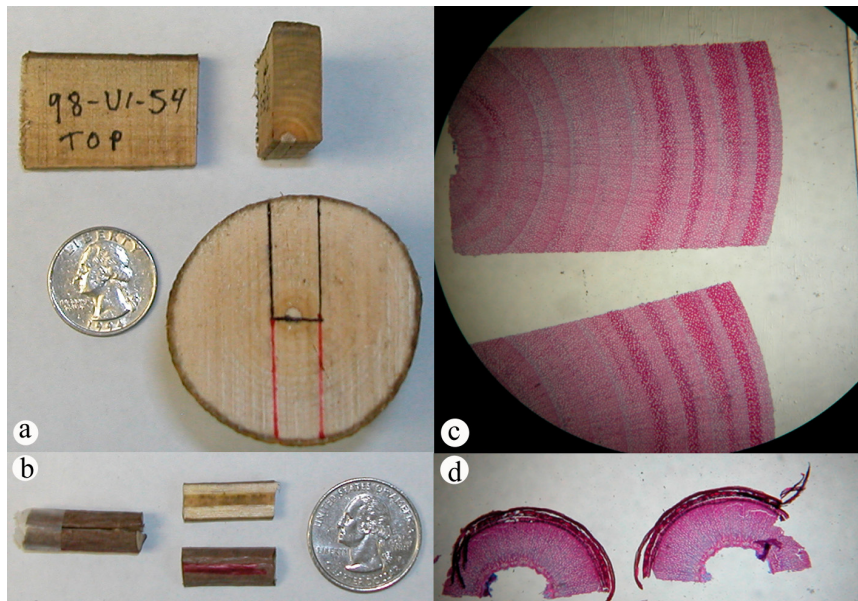
Figure 25. *Acer platanoides* milled sections (a) S4, and (b) P1. Prepared slide mounts of transverse sections for (c) S4, and (d) P1.
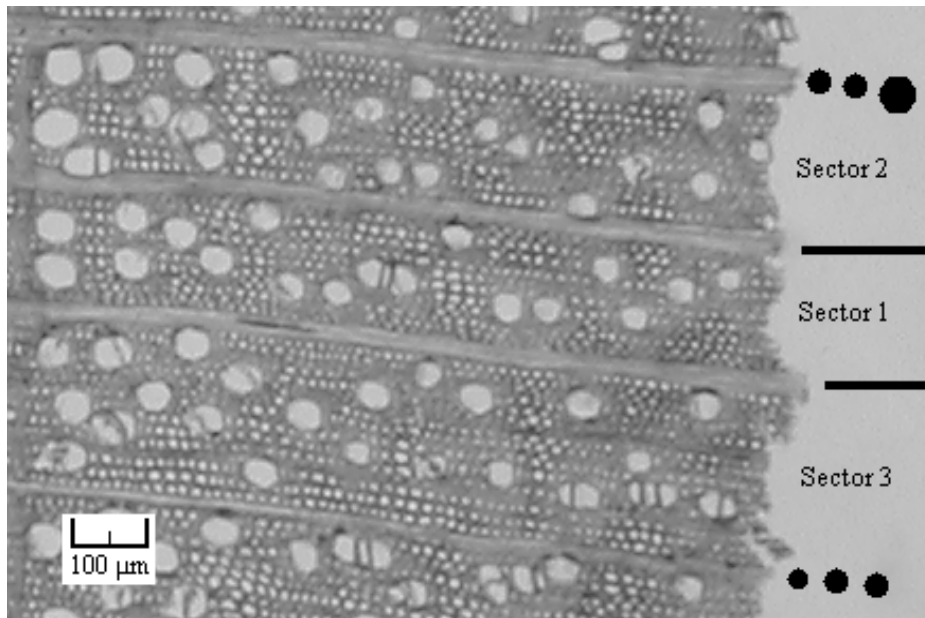
Figure 26. Prepared slide mounts of *Acer platanoides* tissue detailing the three sectors

utilized during cell measurements.
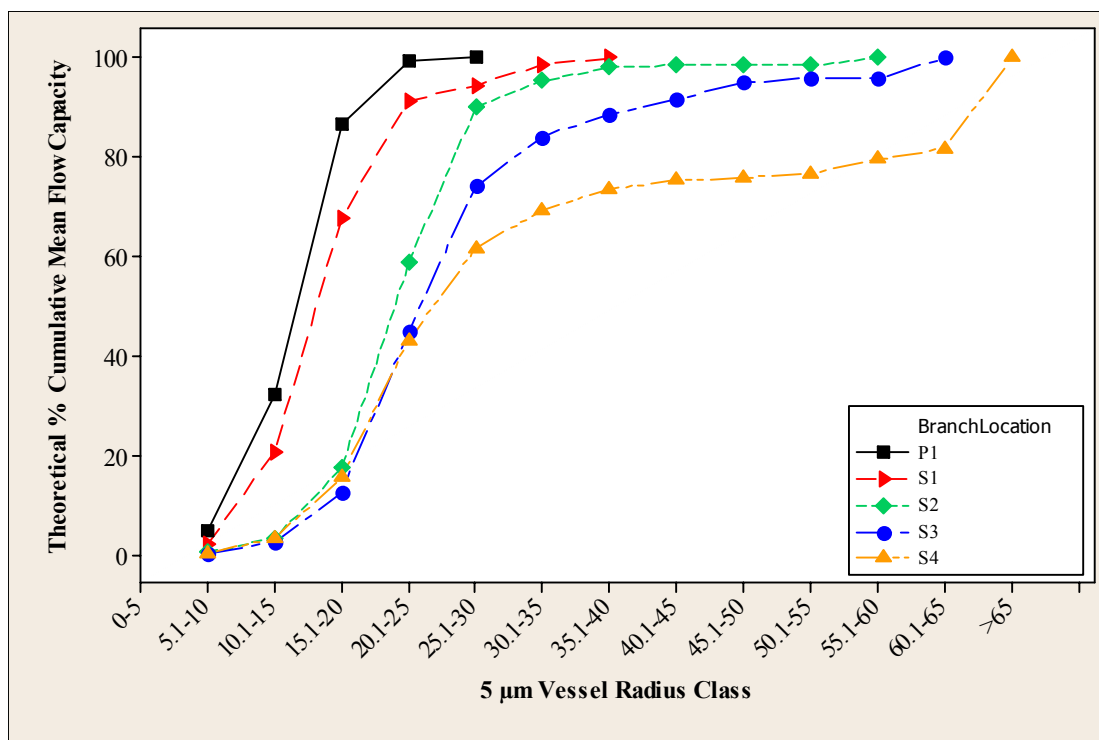
Figure 27. Theoretical % cumulative mean flow capacity (radius^4) per 5 µm radius size class for each location along first order *Acer platanoides* branches.

CHAPTER 4

Variation in Modulus of Elasticity (E) along *Acer platanoides* L.

(Aceraceae) branches

ABSTRACT

Knowledge of how material properties change along the branches would provide arborists and managers of amenity trees a base unit for understanding how tree canopies withstand loading events. Limited knowledge of Young's modulus of elasticity (E or stiffness) in branch wood is available in the literature and is typically measured at only one location on a branch. This study investigated variation of E and density-specific stiffness (E/ρ) at five locations along the axis of five branches. E and E/ρ were found to be 75% lower at the branch tips than in the proximal locations. Neither E nor E/ρ were found to vary between the three proximal (structural) branch locations, which suggests that the application of the elastic similarity modeled cannot be ruled out in branches due to variation in E/ρ. The variation in E was negatively correlated with the percentage of tissue area composed of vessels and positively correlated with mean fiber cell wall size, suggesting a balance between the two principle functions of hydraulics and mechanics. Reaction wood was observed in the form of gelatinous layers in fibers along the branch tops, but did not result in a difference in E between the top and bottoms at each branch location. It is proposed that differences in material properties are probably related to wood development type, as juvenile wood is considered to have lower stiffness than mature wood. Apical control is a likely factor in the shift from juvenile to mature wood and the observed increase in branch stiffness from the tip to the base.

Keywords: Density-specific stiffness, fiber cell wall, modulus of elasticity, reaction wood, vessel

INTRODUCTION

Arborists and managers of urban trees are concerned with risks associated with failures that can injure people or cause property damage (James *et al.* 2006). One of the primary goals for arborists is to minimize the risk of whole tree or large branch failure. Knowledge of how material properties change along the length of branches would provide a base unit for understanding how tree canopies withstand loading events. As the understanding of how a tree develops as a structural unit with annual growth, arborists can develop better pruning standards, aimed as minimizing the risk of failure.

An important material property is Young's modulus of elasticity (*E*), which describes stiffness or the resistance to displacement of material within the elastic range (Burgert 2006). Mechanical properties are known to vary in trees with respect to height, radial position and cambial age (Lindström et al. 1998; Lichtenegger et al. 1999; Reiterer et al. 1999; Brüchert et al. 2000; Spatz and Brüchert 2000). Much of the variation is accounted for by changes in tissue classification and *E* is typically lower in both juvenile and sapwood while higher in mature and heartwood (Panshin and de Zeeuw 1980; Niklas 1997a, 1997b, 1997c; Lindström et al. 1998; Plomion et al. 2001; Woodrum et al. 2003; Read and Stokes 2006).

Limited knowledge of *E* in branch wood is available in the literature. Most reports are either for lumber quality trunk wood (Green et al 1999a) or the central stem of living trees (Holbrook and Putz 1989; Niklas 1997a, 1997b, 1997c; Reiterer et al. 1999; Pruyn et al. 2000; Horáček and Praus 2001; Groom et al. 2002; Wagenführ 2003; Kern et al. 2005; Watt et al. 2006). Studies that report *E* in branch wood typically concentrate on single location along the branch (Spatz and Brüchert 2000; Woodrum et al. 2003; Sone et

al. 2006). Yet, it is likely that E will vary axially along a branch and this study was designed to investigate whether E, varies along the length of branches.

Additionally, understanding how E varies along branches is an important consideration when modeling branch allometry. Researchers have used the elastic similarity model (L $\propto$ R$^{2/3}$) to explain the relationship between branch length (L) and radius (R) in branches larger than 3000 mm (McMahon and Kronauer 1976; Bertram 1989; Dahle et al. 2009). The elastic similarity model was introduced by McMahon (1975) and based on the critical buckling length formula [$L_{critical}$=C(E/ρ)$^{1/3}$R$^{2/3}$] (Greenhill 1881). Since C only varies with the shape, this formula shows that critical length ($L_{critical}$) varies with radius as long as E/ρ (density-specific stiffness) is constant. While E/ρ is reported to be fairly constant in dried milled wood (Panshin and de Zeeuw 1980; Green et al. 1999), it has been shown to vary in samples from live tree stems due to the transition from juvenile to mature wood (Watt et al. 2006) or sapwood to heartwood (1997a & 1997c). If E/ρ remains constant in mature live branch wood, then the application of the elastic similarity model is valid. Additionally, it is not known whether E/ρ influences branch allometry, especially when branches grow beyond 2 - 4 meters in length (Dahle and Grabosky 2009).

Material properties and allometric patterns of branches can be affected by self-loading, which leads to the build up of tensile stress on the top of branches and compressive stress on the bottom, which can be modeled as a cantilevered beam (Niklas 1994a; Telewski 2006). Reaction wood in angiosperms is formed on the top portions of the branch or stem and is called tension wood. Alméras *et al.* (2005) report that E was

higher in tension wood, and this study was designed to determine how branch orientation influenced E in our branches.

Trees must balance mechanical support with the ability to supply water for the production and growth of new cells, respiration and gas exchange during photosynthesis. Fibers provide the structural support to wood in angiosperms and vessels serve as the conduit for water transport, via the hollow lumen. Trees alter anatomy in response to mechanical needs (Kaeiser and Boyce 1965; Ewers 1985; Gartner et al. 1990; Gartner 1991a; Spicer and Gartner 1998a, 1998b; Chiu and Ewers 1992; Jourez et al. 2001), yet, it is not certain if this is a direct tradeoff between hydraulics and mechanics (Woodrum et al. 2003). E has been shown to be positively correlated with fiber cell wall thickness and percent fiber (Sone et al 2006) and negatively correlated with fiber lumen diameter in branch tips (Woodrum et al 2003). This research was designed to investigate whether E is influenced by tissue composition and the makeup of fiber cells.

The research project was designed to determine whether mechanical properties vary between the top and bottom of branches, as well as along the principle branch axis. *Acer platanoides* L. (Aceraceae) was chosen as a test species, as it is a common component in the urban forests of both the US and Europe (Valentine et al. 1978; Manion 1981; Nowak and Rowntree 1990; Sæbo et al. 2002). We were interested in minimizing growth rate as a factor in the mechanical study, and Haygreen and Bowyer (1982) suggest that growth rate does not affect material properties in diffuse porous trees like *A. platanoides*. Additionally, influence of tissue cell type composition and presence of reaction wood on E will be investigated.

MATERIALS AND METHODS

Five first order branches were harvested from two *A. platanoides* trees (#17 and

18) located at Rutgers Gardens in New Brunswick NJ between August 25 and 28, 2008

(Figs. 3 and 28). Milling and mechanical testing occurred on the same day as harvesting

and all milled samples were kept wrapped in wet paper towels to avoid dehydration.

Tissue slide preparation occurred within eight days of branch harvest and all samples

were stored in plastic bags, then refrigerated until slide preparation.

Mechanics section

The branches were sectioned into five locations (P1, S1, S2, S3, & S4) (Fig. 24).

Branch location S4 was at the base of the branch, beginning approximately 5 cm distal to

the branch collar, while S3 was at the first quarter mark of the branch length and S2 at the

branch length midpoint. Location S1 was 5 cm proximally to the most recent bud scale

scar and P1 was 5 cm distal to the bud scale scar. Branch wood for S2 - S4 was milled

into wooden beams, measuring approximately 150 x 7 x 7 mm (L x W x H), from the top

and bottom location of the branch, as close to the bark as possible, but did not include

bark. The sections were free of lateral branches that did not appear to contain knots.

Locations S1 and P1 were cut into lengths of 150 mm and any paired, lateral branches or

leaves were removed at the base without cutting into the beam.

Apparent Young's modulus of elasticity (*E*) was determined using a cantilevered

beam test, modified from Gartner (1991b) and Wagner et al. (1998). The beams were

inserted into a clamping system which was then secured in a vise. The clamping system

for locations S2 - S4 consisted of two wooden blocks, each approximately 120 x 50 x 30

mm (L x W x D) and fastened by two bolts with washers and winged nuts. Beams for location S1 and P1 were secured in one of two sets of aluminum blocks measuring approximately 160 x 100 x 25 mm (L x W x D), with a series of pre-milled holes with radii between 1.0 - 3.5 mm and 4.0 - 5.5 mm and then with the radius increased in 0.5 mm increments. The samples were aligned horizontally and the initial height of the sample, prior to loading, was measured to the nearest (0.02 mm). All heights were measured using a height gauge (Mitutoyo) fitted with a dial test indicator Brown & Sharpe). A load was applied using a small cup with pre-measured weights, suspended with nylon fishing line, and then displaced height was measured (Fig. 29). Elasticity was derived using equation 8 (Hibbeler 2006, Soltis 1999):

Equation 8: $ApparentElasticity = \dfrac{PL^3}{3\delta I}$

Where: P = load applied (grams)

L = beam length (mm)

δ = vertical displacement (mm)

I = moment of inertia (mm^4)

Equation 8 is valid for minor displacements (1 - 5%), and in this study displacement did not exceed 3%. Moment of inertia (I) was calculated using either equation 9 for rectangular sections and equation 10 for circular sections Hibbeler 2005).

Equation 9: $I_{rectangle} = \dfrac{1}{12} XY^3$

Equation 10: $I_{circular} = \left(\dfrac{1}{4}\pi\left(R_{branch}\right)^4\right) - \left(\dfrac{1}{4}\pi\left(R_{pith}\right)^4\right)$

Where: X = width of the beam (mm)

Y = height (mm)

R_{branch} = branch section radius (mm) measured outside bark

R_{pith} = corresponding pith radius (mm) with all measurements were in

The moment of inertia for the area containing pith was subtracted, as the pith is not considered to provide any meaningful mechanical resistance (Woodrum et al. 2003; Wagner et al. 1998).

After the cantilevered tests two subsequent sections of approximately 30 mm were cut from each tested beam. One was used to determine moisture content and wood density (ρ) and the second for preparation of permanent tissue slides. Wood mass was measured using a Denver Instrument A-160 scale to the nearest 0.001 g. Moisture content was calculated as [100 * (green weight - dry weight) / green volume (L x W x H)], and ρ was calculated as green weight / green volume. Density-specific stiffness was derived as E/ρ.

Anatomy Section

Permanent transverse tissue slides were made from wood samples used during the mechanical testing, as it was assumed that the minor displacement did not exceed the elastic limit of the wood (Gartner 1991b). Tissue samples, approximately 30 μm thick for

sample S2 - S4 and 40 μm for P1 and S1, were cut with a Reichert sliding microtome. Each sample was stained in a solution of 67% alcian blue and 33% safranin, rinsed, dehydrated in a series of ethanol baths (50%, 70%, 95%, 100%), soaked in Histoclear (National Diagnostics) and mounted using Permount (Fisher Scientific, Jansen et al. 1998).

Four photographs from each prepared tissue slide were randomly selected and taken under a microscope (Zeiss Axioskop 40) with a digital camera (Insight Spot Firewise 4, model 18.2). Each photograph represented an area of 257,175 μm^2. Photos were saved as TIFF files without compression to minimize distortion, and converted to grayscale. Each photograph was analyzed with WinCELL Pro version 2007a (Regent Instruments Inc.) to identify area composed of vessel (A_v), ray parenchyma (A_{rp}), and axial parenchyma (A_{ap}) cells. Partial vessels falling along the perimeter of the photograph were excluded from the analysis and subsequently adjusted area (A_{adj}) measured was calculated as total area of photograph minus area of partial vessels excluded. Area of fiber was derived as $A_{adj} - (A_v + A_{rp} + A_{ap})$. Percentages for the four cell types were calculated as area measured / A_{adj}. One hundred fiber cells, twenty five from each photo per branch location, were randomly selected and measured for cell wall thickness and lumen radius.

All data were analyzed using SAS 9.1 (SAS Institute, Cary, NC, USA). Regression analysis was conducted using Proc Reg, and a stepwise procedure was run setting significance levels for variable selection at alpha = 0.15 to allow for variation as variables were added or removed, while alpha was set a 0.05 in the final model. Proc Univariate was used to verify normality of the residuals. Mean and standard errors (SE)

were run with Proc Means. *T*-test were run using Proc TTEST, ANOVA with Proc GLM and means separations were analyzed using Tukey HSD. All statistics used alpha = 0.05. Data were determined to be normally distributed and residuals were normally distributed. Graphical output was produced in MINITAB® Release 14.20.

RESULTS

Mean branch age was 12.4 years (± 0.7 SE), length 5,880 mm (± 474.4 SE), diameter 70mm (± 4.9 SE) and slenderness (length / radius) 170.5 (± 15.8 SE). Mean attachment angle for the branches was 49.2° (± 4.0° SE), with zero degrees being parallel to the ground, mean compass bearing was 131.0° (± 39.7° SE) and angle of departure 41.4° (± 6.4° SE). No significant tree affect was identified (Table 6). No significant branch angle affect was identified (Table 6). No significant differences compass bearing affects was identified (Table 6). No significant angle of departure affects was identified (Table 6).

T-tests found no differences between *E* on the top versus bottom at branch locations S2 (P = 0.8056, *N* = 10), S3 (P = 0.5829, *N* = 10), and S4 (P = 0.8696, *N* = 10). Further analysis concentrated on the top section for each branch location (S2 - S4) and the whole sample for S1 and P1. *E* was found to be higher in the proximal end (S2 - S4) of the branches than the distal end (S1, P1) (Table 7). Density (ρ) was found to vary along the branches, but did not appear to follow a set pattern (Table 7). Density-specific stiffness (*E*/ρ, Table 7) was found to follow the same pattern as *E*, suggesting that mechanical properties are lower in the tips, increase by the middle of the branch and

remain stable thereafter. All samples were maintained above fiber saturation point, as moisture content ranged from 35% - 47%.

Stiffness for locations S2 - S4 was pooled and called structural, while S1 and P1 were pooled and called tips. A *t*-test determined that mean *E* for structural wood, 9,305 MPa (± 670.3 SE), was significantly higher than that of the tip locations, 2,377 MPa (± 188.7 SE), (P < 0.0001, *N* = 25). Density-specific stiffness followed the same pattern with structural locations, 9,292 N mm kg^{-1} (± 693.1 SE), being larger than tip locations, 2,506 N mm kg^{-1} (± 220.6 SE). These results suggest that branches develop flexible tips (low density-specific stiffness), while the proximal end lays down wood with higher stiffness to provide structural support for the whole branch. A scatter plot of *E* by the distance from the branch terminal bud suggests that by 2000 - 3000 mm from the terminal bud, radial growth is producing wood with structural levels of *E* (Fig. 30).

The mean width of the fiber cell wall and lumen radius were found to vary along the branches. Mean fiber cell wall was found to be significantly thinner at branch locations P1 and S1, larger in S2 and highest in S3 and S4 (Table8) (P < 0.0001, *N* = 2,500). An increase in fiber cell wall should lead to an increase in branch stiffness. An inverse pattern was identified with fiber lumen radius where P1 and S1 were larger, S2 smaller and S3 and S4 the smallest (P < 0.0001, *N* = 2,500). A gelatinous layer, indicating formation of reaction wood, was not observed during visual examination of photographs for location P1 nor for the bottoms from locations S2 - S4. Gelatinous layers were observed in 60% of the tissue sample photographs from S1 and S2 top locations, as well as for 100% of the top locations S3 and S4. The presence of reaction wood was not found to influence values for *E* at the top or bottom locations along at branch location S1

(P = 0.8378, N = 5), S2 (P = 0.5724, N = 10), S3 (P = 0.5829, N = 10), S4 (P = 0.8696, N

= 10) suggesting that reaction wood may be utilized in maintaining orientation in these

branches.

The percent area composed for three of the cell types (fiber P = 0.4128, ray

parenchyma P = 0.4819 and axial parenchyma P = 0.7717, N = 25 for each) did not vary

along the length of the branches, while percent area vessels did vary (P = 0.0027, N = 25)

(Table 7). Mean percent area composed of vessels was highest at location S1 and lowest

in the proximal half (S2 - S4), and intermediate in the first year wood of P1. This pattern

was observed in a sub-set of a previous study of the same species which found mean

vessel size tapered in the distal direction (chapter 3).

Individual regression analysis found significant relationships between Log(E) and

% area vessel (P < 0.0001, N = 25) (Fig. 31), mean fiber cell wall thickness (P = 0.0002,

N = 25) (Fig. 32), the ratio of vessel to fiber (P < 0.0001, N = 25) (Fig. 33) and % area

ray parenchyma (P = 0.0378, N = 25) (Fig. 34). A regression between Log(E) and mean

fiber lumen radius (P < 0.0001, N = 25) (Fig. 35)was identified, but residuals were not

found to be normally distributed. Significant regressions were not found between Log(E)

and % area fiber (P = 0.1214, N = 25) nor % area axial parenchyma (P = 0.3090, N = 25).

Stepwise regression found only one significant multiple regression model, that being

between Log(E), and % area vessel (x_1) and mean fiber cell wall width (x_2) [Log(E) =

3.61 - 0.05x_1 + 0.42x_2, P < 0.0001, R^2 = 0.7094, N = 25]. Overall model error (Root

MSE) = 0.179, $SE_{intercept}$ = 0.350, and SE_{x1} = 0.012 SE_{x2}=0.113. That both % vessel and

fiber cell wall thickness produced significant models and are included in the final model,

suggest that mechanical support is not solely a function of fibers and may be influenced by presence of vessels.

DISCUSSION

Mechanical properties are known to vary in trees with respect to wood development type. Juvenile wood is reported to have lower stiffness (E) and subsequently higher flexibility than mature wood (Panshin and de Zeeuw 1980; Plomion et al. 2001; Woodrum et al. 2003; Read and Stokes 2006). E for the tips (S1 & P1) in this study was approximately 75% lower than in the structural locations (S2 - S4). Holbrook and Putz (1989) found similar results in four year old sweetgums (*Liquidambar styraciflua* L.) saplings, where E was 85% lower than for larger plantation trees. Our results are consistent with expectations, given that the branch tip is composed of juvenile wood (Woodrum et al. 2003), and the new radial growth in the structural location is likely mature wood even though the developmental ages at each location were similar.

This strategy allows the branch tips to bend, due to low stiffness, while the proximal end is stiffer and provides structural support. This has been observed in stem wood (Niklas 1997a, 1997b, 1997c) in addition to our branch wood. Our results for the branch tip wood (2,377 MPa) appear within the range of other maples (*Acer spp.*) and clonal poplars (*Populus trichocarpa* Torr. & A. Gray x *P. deltoides*) (Pruyn et al. 2000; Woodrum et al. 2003; Kern et al. 2005). E for the proximal end (9,305 MPa) is slightly lower than published reports for *A. platanoides* lumber quality stem wood (12,100 - 12,500 MPa) (Horáček and Praus 2001; Wagenführ 2003). The lower E in this study is reasonable, as it similar to previous measures of trunk wood in the range of 40 cm which

would likely be different in behavior than our 6 - 9 cm branch wood. E was not found to vary in locations S2 - S4, suggesting that stiffness is relatively constant in branches of this size.

When plotting E by distance from branch terminal bud (Fig. 30), it appears that by 2000 - 3000 mm from the terminal bud, E has shifted to a level consistent with structural support. Wood transitions from juvenile to mature with increasing distance from the apical meristem in the terminal bud (Panshin and de Zeeuw 1980). Material stiffness in our branches changed as a function of length, and may also correspond to branch form as the number of lateral branches feed into the main branch axis and was reported to increase after the main branch length reached 3000 mm (Dahle et al. 2009). A similar shift in behavior, corresponding to form, has been reported for *Robinia pseudoacacia* L. stem wood (Niklas 1997b). Researches have shown that the log-log relationship between branch length and radius is curvilinear until around 3000 mm and then becomes linear, fitting the elastic similarity model (length $\propto$ radius$^{2/3}$) in *Quercus alba* L. (McMahon and Kronauer 1976), *A. saccharinum* L. (Bertram 1989) and in *A. platanoides* (Dahle et al. 2009) (Fig. 11), growing within 1.5 km of the trees sampled in this study. Since E/ρ was constant in the structural locations of the branches (table7), the application of elastic similarity model can be considered valid with regard to variation in material properties of branch wood. Niklas (1997b) suggested that the development of heartwood may influence the shift in allometry to the elastic similarity model in developing stems. Mechanical testing in this study was conducted on wood samples milled from near the bark and therefore unlikely to contain heartwood, especially since *A. platanoides* is reported to have delayed heartwood formation (Wagenführ 2003). In our branches it is

more likely the development of mature wood, as the nearly four fold increase E suggests, influences the shift in allometry, although additional research is needed to confirm this postulate. Additionally, the shift in allometry has been shown to lead to a decrease in slenderness (length / radius) (Bertram 1989; Dahle et al. 2009). Branches that are more robust (less slender) would be less prone to failure during loading events. Managers of amenity trees may wish to investigate the consequences of removing apical influence of the branch terminal bud, which could release subordinate branches, help develop more tapered branches and possibly accelerate the development of mature wood with higher density-specific stiffness.

Trees must balance two important functions (hydraulics and mechanics) in order to grow and survive. Consideration of this balance and the structure of the canopy could be an important management consideration, especially in the urban environment where failure of a large branch or whole tree can cause serious personal injury or property damage (James et al. 2006). The percentage of area composed of vessels was found to increase in the distal direction (table7) which is coupled with a decrease in mean vessel diameter in the same direction. Previous work with *A. platanoides* branches growing within 1.5 km found conduit tapering (table5). Although the percentage area composed of fibers did not vary in the current study (table7) mean fiber cell wall decreased and fiber lumen radius increased in the distal direction (table8), suggesting that mechanics is modified at the cellular level, not the tissue level. E was found to be positively correlated with fiber cell wall thickness ($r^2 = 0.45$; Fig. 32) and negatively correlated with percent area composed of vessel ($r^2 = 0.53$; Fig. 31) and the ratio of vessels to fiber (V:F, $r^2 = 0.50$; Fig. 33). While V:F can be used to predict E, it appears the best power for

explaining the balance between hydraulics and mechanics was the inclusion of percentage of vessels and fiber cell wall thickness, as together they explained over 70% of the variation in E.

The branches in this study were growing at an upward angle (mean 49°) which likely led to the formation of reaction wood along all the branches. A gelatinous layer was identified in the tissue sample obtained from the top sections of S1-S4. While the occurrence of reaction wood likely aids in maintaining branch orientation, it did not appear to add stiffness to the branches as E on the top and bottom sections were not found to differ at each of the locations. Alméras *et al.* (2005) report that E was higher in tension wood in stems, and future research should investigate how material properties vary with respect to the presence of reaction wood in branches.

The modulus of elasticity and density-specific stiffness were found to increase from the branch tips to the structural locations of the branch. While this pattern has been observed in stem wood, it has been attributed to the formation of heartwood. The study suggests that the increase in material properties is likely due to the transition from juvenile to mature wood. Since apical control can shift slenderness by releasing lateral branches, it may be in-part responsible for the observed allometric shift in branches. If so, managers of amenity trees concerned with branch failure may wish to investigate methods of pruning that will decrease apical influence in order to develop branches with lower slenderness ratios.

ACKNOWLEDGEMENTS

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Table 6. ANOVA P-values for affect of tree, branch angle (zero parallel to the ground), compass bearing, and angle of branch departure (from trunk) against percent of area for vessel, fiber, ray parenchyma, axial parenchyma cell types, fiber cell wall thickness, fiber lumen radius, log modulus of elasticity (E), wood density (p), and density-specific stiffness (E/ρ) in first order *Acer platanoides*. branches. Sample size was 25 and significant P-values and alpha =0.05.

Variable	P-value			
	Tree Affect	Branch Angle Affect	Compass Bearing Affect	Angle Departure Affect
% Area Vessel	0.4855	0.1249	0.1303	0.1303
% Area Fiber	0.9672	0.0905	0.1764	0.1764
% Area Ray Parenchyma	0.4305	0.1476	0.1449	0.1449
% Area Axial Parenchyma	0.5613	0.1616	0.2817	0.2817
Vessel to Fiber ratio (V:F)	0.5353	0.1053	0.1335	0.1335
Fiber cell wall thickness (μm)	0.4720	0.4368	0.6119	0.6119
Fiber lumen radius (μm)	0.7495	0.7026	0.8145	0.8145
Log E	0.7223	0.7645	0.8677	0.8677
E/ρ	0.6094	0.6777	0.7506	0.7506

Table 7. Mean (± 1 SE) percent of area for vessel, fiber, ray parenchyma, axial parenchyma cell types, modulus of elasticity (E), wood density (ρ), and density-specific stiffness (E/ρ) along five *Acer platanoides* branches. Means with the same letter, reading across a row, are not significantly different with a Tukey HSD comparison at alpha = 0.05, $N = 25$.

Variable	Branch Location					P-value
	S4	S3	S2	S1	P1	
% Vessel Area	12.4 (± 1.47)b	12.7 (± 0.66)b	14.0 (± 0.80)b	18.7 (± 0.98)a	15.8 (± 1.24)a,b	0.0027
% Fiber Area	73.2 (± 2.12)a	74.3 (± 1.36)a	72.3 (± 1.38)a	70.0 (± 1.40)a	72.5 (± 1.28)a	0.4128
% Ray Parenchyma Area	14.2 (± 1.26)a	12.9 (± 1.10)a	13.6 (± 1.55)a	11.0 (± 1.06)a	11.4 (± 2.02)a	0.4819
% Axial Parenchyma Area	0.17 (± 0.08)a	0.19 (± 0.06)a	0.15 (± 0.03)a	0.23 (± 0.03)a	0.15 (± 0.03)a	0.7717
E (MPa)	9635 (± 1152.7)a	9478 (± 919.1)a	8800 (± 1564.1)a	2157 (± 332.1)b	2598 (± 160.1)b	<0.0001
Wood Density (ρ)	1.056 (± 0.021)a	1.023 (± 0.023)a,b	0.934 (± 0.013)b	0.982 (± 0.018)a,b	0.933 (± 0.031)b	0.0021
E/ρ (N mm kg^{-1})	9181 (± 1216.7)a	9321 (± 1036.0)a	9373 (± 1576.4)a	2210 (± 356.8)b	2802 (± 218.6)b	<0.0001

Table 8. Mean (± 1 SE) fiber cell wall thickness (µm) and mean lumen radius (µm) along five *Acer platanoides* branches. Means with the same letter are not significantly different using a Tukey HSD comparison at alpha = 0.05, N = 2500.

Branch Location	Fiber Cell Wall Thickness(µm)	Fiber Lumen Radius (µm)
P1	1.89 (± 0.020)a	4.06 (± 0.044)c
S1	1.87 (± 0.019)a	3.95 (± 0.050)c
S2	2.22 (± 0.030)b	3.48 (± 0.057)b
S3	2.50 (± 0.024)c	2.86 (± 0.039)a
S4	2.41 (± 0.026)c	3.04 (± 0.045)a
P-value	<0.0001	<0.0001
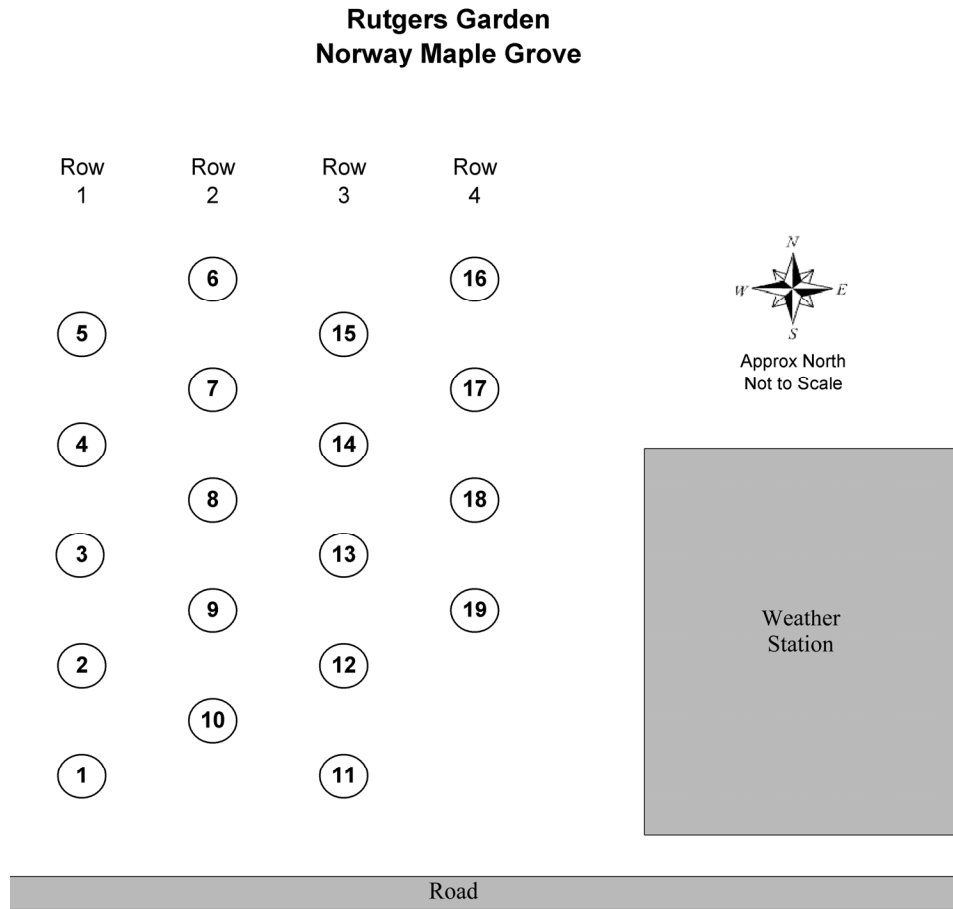
Figure 28. *Acer platanoides* plantation growing at Rutger's Gardens located in New Brunswick, NJ. Sampling occurred on *Acer platanoides* trees 17 and 18.
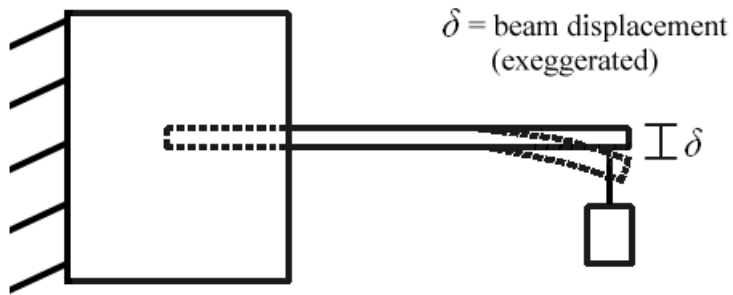
Figure 29. Depiction of cantilever beam testing with small cup suspended from a milled or intact branch segment. Displacement (δ) did not exceed 5% and is exaggerated in this drawing for demonstration purposes.
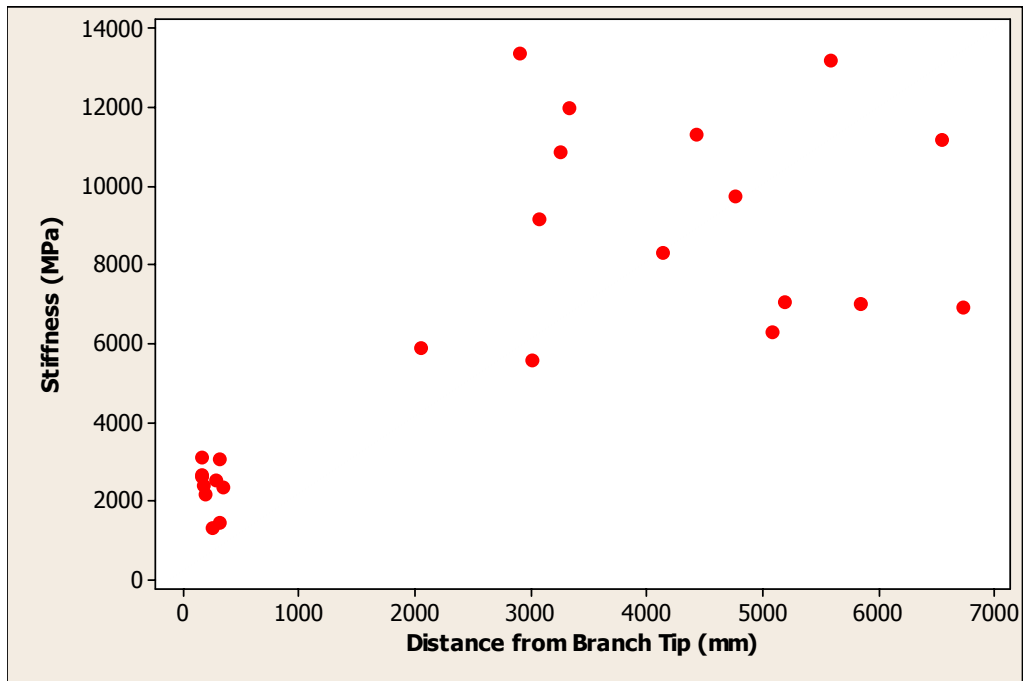
Figure 30. A scatter plot of modulus of elasticity (MPa) by the distance (mm) from the branch terminal bud for *Acer platanoides* branches.
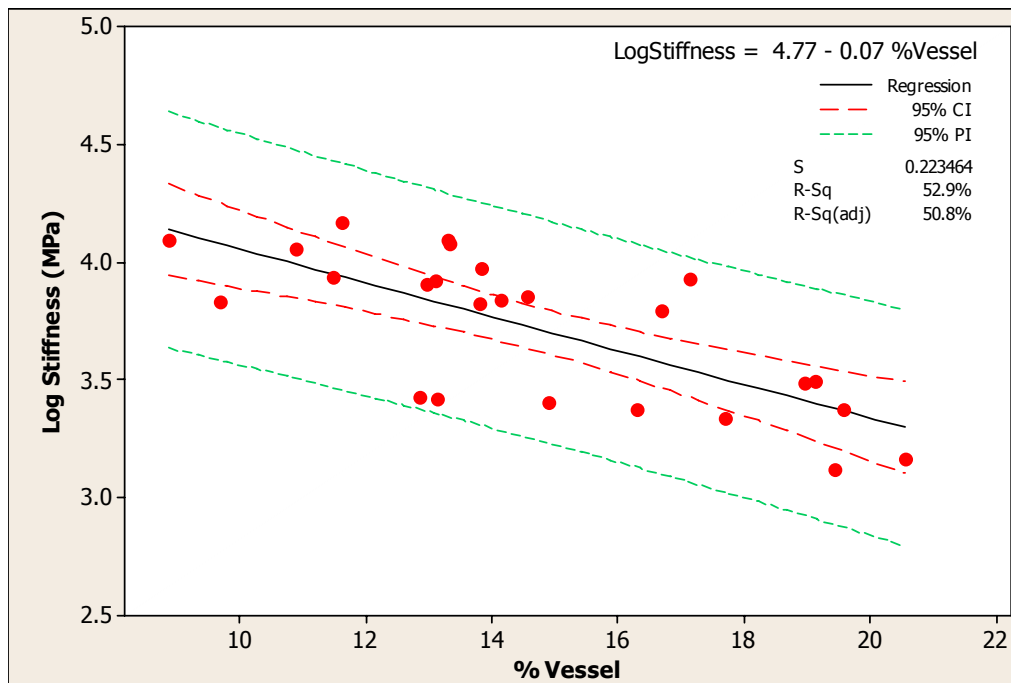
Figure 31. Regression of log stiffness (*E*, in MPa) versus % area vessel for *Acer platanoides* branches.
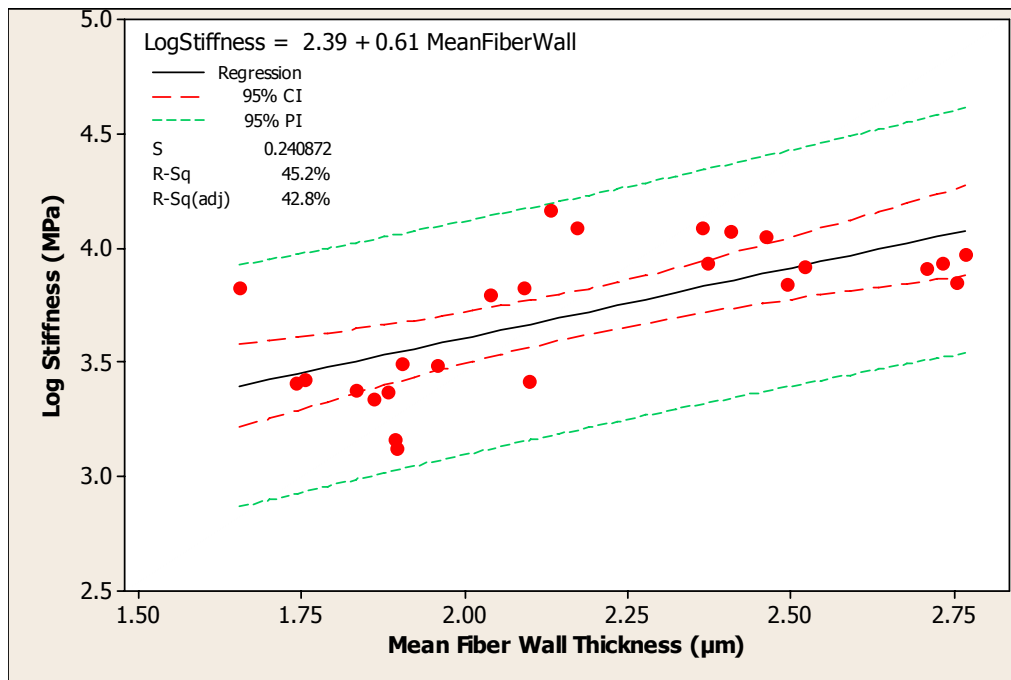
Figure 32. Regression of log stiffness (*E*, in MPa) versus mean fiber cell wall thickness (μm) for *Acer platanoides* branches.
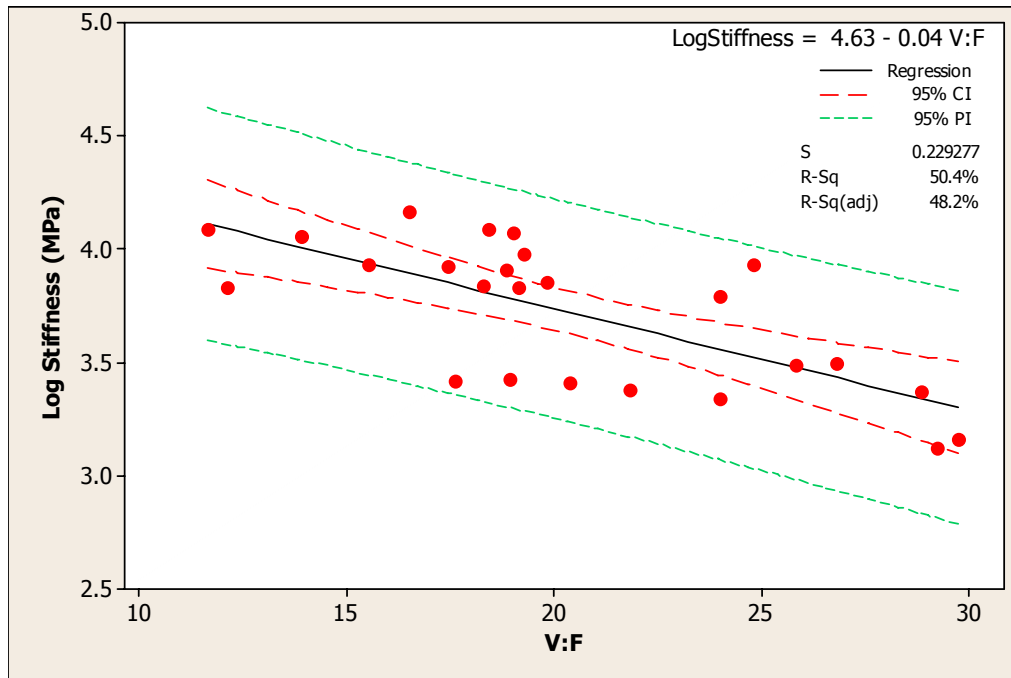
Figure 33. Regression of log stiffness (*E*, in MPa) versus vessel to fiber ratio (V:F) for *Acer platanoides* branches.
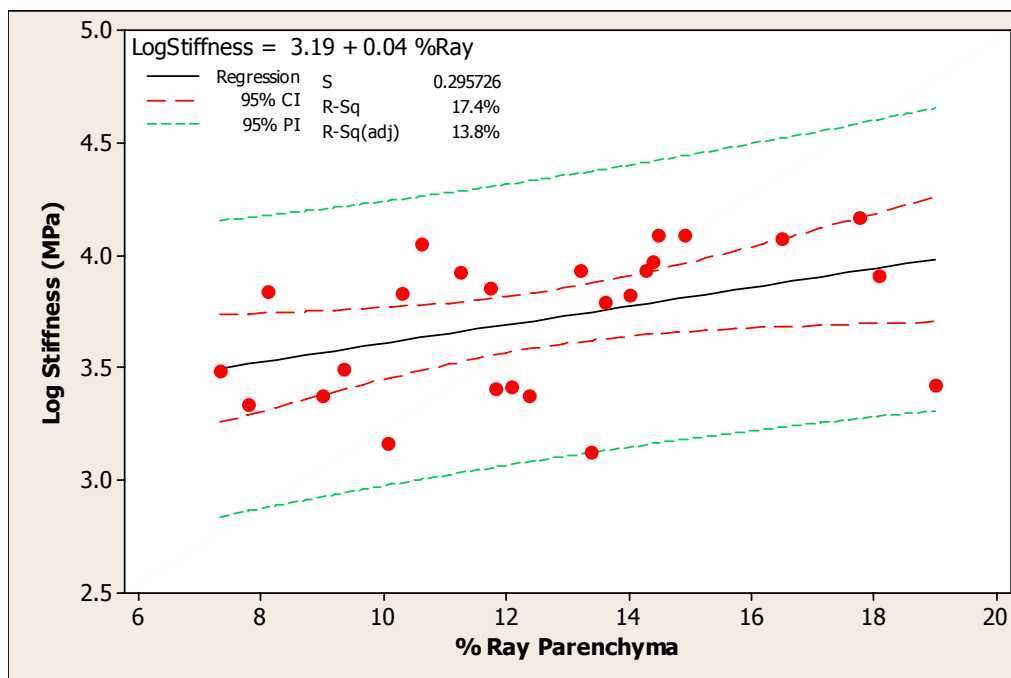
Figure 34. Regression of log stiffness (*E*, in MPa) versus percent area ray parenchyma for

Acer platanoides branches.
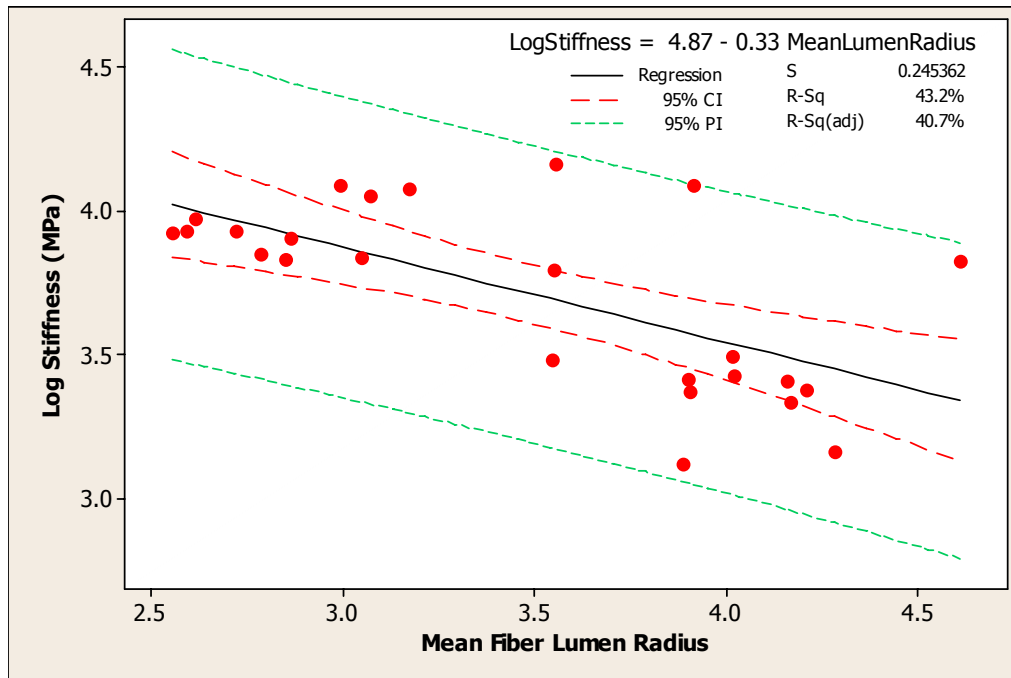
Figure 35. Regression of log stiffness (*E*, in MPa) versus mean fiber lumen radius for

Acer platanoides branches. Residuals were not found to be normally distributed.

CONCLUSION

Arborists and managers of amenity trees have an interest in maximizing the benefits gained from an urban canopy while minimizing the risk of failure (Harris et al. 2004). Arborists utilize plant selection, design and selective pruning to develop a canopy that can withstand loading events such as wind or ice storms. Pruning removes tissue in order to direct growth and develop 'good' canopy structure. As 'good' structure is difficult to define, typical pruning goals target vertical and radial permanent branch spacing, or the removal of un-desirable structure and defects such as dead, dying or diseased branches, co-dominate branches, or branch unions with included bark (Gilman 2002; Gilman and Lilly 2002). Missing is a reasonable discussion on branch form as the primary function changes over time. Additionally, if a canopy is damaged during storm events or due to improper cultural practice such as topping, the arborist must evaluate whether a canopy can be restored. Restoration pruning attempts to return a damage canopy to a condition where it can provide similar benefits to that of a 'natural' canopy, with acceptable levels of risk of failure (American National Standards Institute 2001). Yet again, we are left without a formal description of what a 'natural' canopy looks like.

The ability to define good canopy structure from branch form could help the arborist direct growth and develop the goal of a stable canopy. The underlining premise of this research was that form follows function (Sullivan 1896), and the governing hypothesis was that the shift in function corresponds to a change in form as branches transition from small sun branches into larger structural branches. This research was designed to: (1) describe anatomic differences, as they occur in the secondary xylem tissues of the same growth year along the branch axis, (2) determine the impact of anatomical shifts on wood strength properties, as branches grow and (3) investigate

whether canopy development leads to predictable patterns of iterative growth. I believe that the three studies in this dissertation suggest that the shift in the form of *Acer platanoides* L. (Aceraceae) (Norway maple) branches is related to an increased need for mechanical support.

While the initial results of the hydraulic study suggest that both the percentage of area composed of vessels and fibers changed along the primary axis of a branch (Table5), the mechanical study found that only percent area of vessels changed (Table 7). A subsequent re-examination of the tissue slides from the hydraulic study, utilizing the protocol from the mechanics study, found a similar pattern as in the mechanics study (Table 9), that only percent area of vessels changed along the branches. I believe these differences were due to modification of the sampling protocol. The initial hydraulic study predefined the sampling region (Fig. 36a), and both the mechanics and hydraulic follow up study randomly selected areas photographed at higher resolution (Fig. 36b). Selecting a pre-defined region potentially biased towards ray parenchyma cells, as the inclusion of four ray files was forced in the initial study. The randomized sampling of the same regions of 15 slides found a reduction in the area of ray parenchyma of 2 - 6% and a moderating effect in percent area of vessel. A follow up study is needed to determine whether the vessel taper and density are constant, but it is reasonable hypothesis to test. The selection of a pre-defined region is a compounding difference in the mechanics study, as the region was not confined to a single growth year. The tissue mounts from the mechanical study include the whole transverse section of the beam. Subsequently, multiple growth rings were included on the slides. The randomized sampling took place without regard to a given growth ring, as the applied load was subject to the whole beam.

I believe that the results from the mechanical study provide the most insight into the influence of anatomical variation on material properties, as it was more representative of the cross-sectional area upon which loading occurred.

Findings from the mechanics study could prove of great interest to the arboricultural community. Young's modulus of elasticity (E) and density-dependent stiffness (E/ρ) were found to increase from the branch tips to the structural locations of the branch base (Table7). This shift corresponded to a decrease in the percentage of vessel and an increase in the size of the fiber cell wall. While similar patterns have been observed in stem wood (Niklas 1997a, 1997b, 1997c), it has been attributed there to the formation of heartwood. The increase in stiffness in our *A. platanoides* is likely due to the transition from juvenile to mature wood, which in turn is under hormonal influence, rather than aging as in heartwood (Panshin and de Zeeuw 1980). If managers are interested in the accelerating the development of structural branches, it may be possible to utilize reduction and subordination pruning to modify hormonal influence. This may result in the development of wood in the proximal regions with larger fiber cell walls and therefore increased mechanical properties. While it is beyond the scope of the research conducted for this dissertation; the distribution and concentration gradient of plant hormones, especially auxin, play an important role in branch development (Leyser 2003; Vieten et al. 2007). Researchers may wish to concentrate on the influence of hormones or synthetic growth regulators on fiber cell wall development.

Branch development does appear to lead to a predictable pattern of growth, at least in large trees. Studies have shown that the log-log relationship between length and radius is curvilinear, transitioning around 3000 mm to a linear pattern suggested by the

elastic similarity model. This pattern has now been reported in branches of three species; *Quercus alba* L., *Acer saccharinum* L.and *A. platanoides* (Fig. 11) growing in the Northeast (Massachusetts, New Jersey and Vermont) and the Midwest (Michigan) (McMahon and Kronauer 1976; Bertram 1989; Dahle et al. 2009). Additionally, a comparison between log-log scatter plots of length versus radius for all branches (first, second and third order) (Fig. 37) and those of only first order (Fig. 38) and second order (Fig. 39) show that the transition in form occurred regardless of branch ordination or vertical location in the canopy. While the elastic similarity model provides researchers with the tool to validate this shift in form, a practitioner would find this a difficult tool to utilize in the field. Slenderness ratios on the other hand, are easier to derive and the shift in *A. platanoides* branch form corresponded to a shift in slenderness between ratios of 250 - 300 (2.40 - 2.48 on a log scale) (Figs. 18 and 19). This could prove to be an important threshold for managers of large amenity trees concerned with reducing the risk of branch failure. It is likely that branches with a slenderness ratio beyond 250 are at an increased risk of failure, although research is needed to address directly the stability of branches with regard to slenderness in various species and possible geographical regions. The determination of a critical slenderness threshold for a given species would aid in describing a 'good' or stable canopy. The application of a critical slenderness threshold would aid the arborist in better identifying branches at higher risk of failure. Corrective action could then be prescribed, which may include branch reduction, subordination, removal or the inclusion of additional support via the installation of a cabling and/or bracing systems.

The shift in branch allometry is correlated with an increase in both the number of lateral branches as well as the mechanical properties of wood in *A. platanoides*. The shift in branch form occurred around 3000 mm (Fig. 11), which also coincided with the rapid increase in the number lateral branches (Figs 20 and 21) as well as branch stiffness (Fig. 30). It is not surprising that the increase in material properties of the parent branch corresponded with an increase in the number of lateral branches. As the lateral branches begin taking over the role of solar collectors, the primary axis of growth transitions to a structural role. A branch would need to increase stiffness to support the addition load (static and dynamic) from these added lateral branches. It is likely that the increase in mechanical stiffness is associated with apical influence from both the terminal bud and lateral branches. Selection criteria for branch retention or removal could include the number of laterals. Future research should determine if a logical management target, such as 6 - 7 second order laterals in some torsional balance, could be used as an appropriate threshold for different species and geographical regions.

Understanding how a 'natural' canopy is put together could aid researchers interested in restoration pruning. In order to restore a damaged canopy, an arborist selectively removes some of the newly arisen watersprouts while retaining others. Over time, additional watersprouts are removed, leaving just a few to develop into the structural branches upon with the new canopy grows. Deciding which watersprout to retain is left to experience and intuition.

Investigators may wish to compare the development of a damaged canopy to determine whether patterns differ from that of a normally arising canopy. In order to regain lost photosynthetic capacity, trees typically respond to severe canopy damage with

a flush of rapidly growing watersprouts. The watersprouts often show rapid length extension for a number of years, which gradually slows over time. It is likely that development initially leads to canopy comprised of watersprouts with high slenderness, which may over time become more robust. Additionally, it has been shown that *A. saccharinum* watersprouts are approximately 50% weaker than naturally occurring lateral branches (Dahle et al. 2006). The authors evaluated overall branch strength in terms of modulus of rupture (applied force per unit area to cause failure), but did not determine what led to the reduction in strength. It is possible that the shift in stiffness found in the *A. platanoides* in this dissertation explains the weakness of watersprouts. If the initial function of watersprouts is to place leaves in the sun, only limited investment would be placed in mechanics. Researchers should concentrate on anatomical properties in watersprouts, especially fiber cell wall thickness in various species. It may be that apical influence drives the production of fibers that are similar to smaller sun branches or tip wood. If so, managers may wish to investigate methods to accelerate the production of mature rather than juvenile wood. Understanding how watersprouts develop at the tissue and cellular level, coupled with knowledge of how material properties vary with wood type in individual species, may provide insight into how to minimize the apparent canopy weakness that occurs during canopy restoration.

Over the past decade, arboricultural researchers have begun to model how tree response to moderate and extreme wind loading events is altered, depending on pruning regimes (Smiley and Kane 2006; Gilman et al. 2008a, 2008b; Pavlis et al. 2008). It is hoped that the information in this dissertation, pertaining to branch form and function, could be integrated with knowledge gained from such wind loading experiments in order

to better understand how canopies are built to withstand the elements. The time is near when arboricultural researchers should consider utilizing the knowledge gained on branch form and mechanical structure to build a computer model of a representative amenity tree. This simulated tree could be integrated with data gained from on-going wind studies and then subjected to simulated loading events such as hurricane force winds. The simulated events could prove useful in developing predictions of canopy locations with inherent weakness. Researchers could then investigate how pruning techniques could be employed to increase canopy stability, both immediately and over time, as growth is added.

In closing, the two principle functions (hydraulics and mechanics) investigated during this research appear to change in predictable manners leading to a shift in branch form. Young branches are developed for solar interception via the leaves which in turn leads to interception of the wind. As such, investment in these smaller branches is predominately weighted towards hydraulics with limited mechanical stability. As branches grow in size, investment in mechanics is increased in order to protect against failure, which would lead to loss of photosynthetic capacity and serve as a potential entry point for decay pathogens. This shift occurred around 3000 mm and corresponds to an increase in fiber cell wall thickness which leads to an increase in branch stiffness (E) in *A. platanoides*. At this point the log-log relationship between length and radius moved from curvilinear to linear, suggesting an increase investment in mechanics (radial growth) and shifting investment in branch extension from the primary axis to lateral branches. Slenderness ratios were found to follow a similar pattern, peaking around 250 - 300 (2.40 - 2.48 on a log scale) when branch length reached 3000 mm. It is possible that

slenderness may be included as a criterion in evaluating branch stability, and arboricultural researchers should investigate the applicability of setting slenderness thresholds for a given species. It appears that in *Acer platanoides*, branch form does follow function and I believe that the research detailed in this dissertation can provide insight to researchers and practitioners interested in managing trees in the urban forest.

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Table 9. Mean (± 1 SE) percent of area for vessel, fiber, ray parenchyma, axial parenchyma cell types along five *Acer platanoides* branches. Means with the same letter, reading across a row, are not significantly different using a Tukey HSD comparison at alpha = 0.05, *N* = 15.

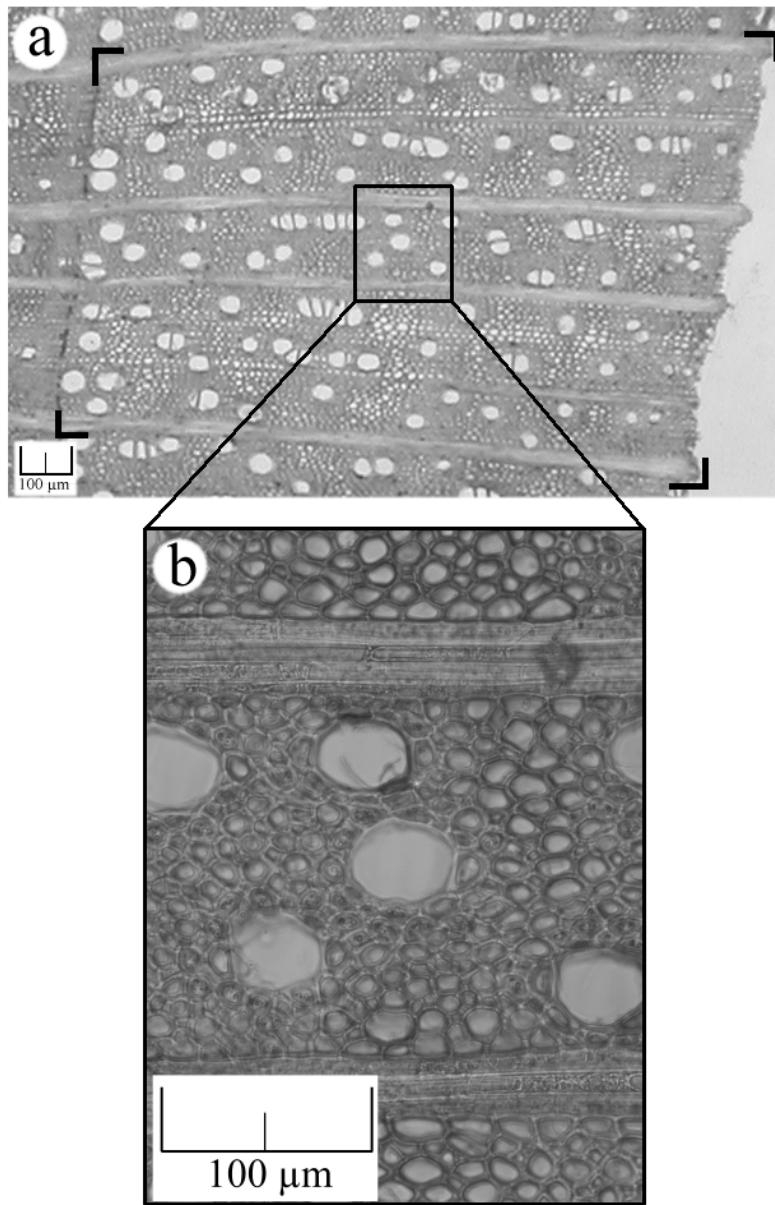| Variable	Branch Location					
	S4	S3	S2	S1	P1	P-value
% Vessel Area	11.1 (± 1.6)b	12.5 (± 1.4)b	12.3 (± 1.4)b	20.6 (± 0.7)a	13.6 (± 1.6)b	0.0049
% Fiber Area	75.3 (± 1.0)a	77.3 (± 2.2)a	75.6 (± 0.7)a	71.2 (± 0.9)a	76.4 (± 3.2)a	0.2484
% Ray Parenchyma Area	13.4 (± 0.6)a	10.0 (± 2.3)a	11.8 (± 1.0)a	7.9 (± 0.4)a	9.6 (± 2.0)a	0.1518
% Axial Parenchyma Area	0.2 (± 0.1)a	0.2 (± 0.1)a	0.3 (± 0.1)a	0.4 (± 0.1)a	0.4 (± 0.1)a	0.2088

Figure 36. Photos of a slide showing areas utilized during tissue analysis of *Acer platanoides* branches. The four brackets in the photo (a) show the entire region sampled following the protocol in the hydraulics study (chapter 3) which included three adjacent sectors bordered by ray parenchyma files. The inset region (b) was photographed at higher magnification for re-examination of the slide following protocol from the mechanics study (chapter 4).
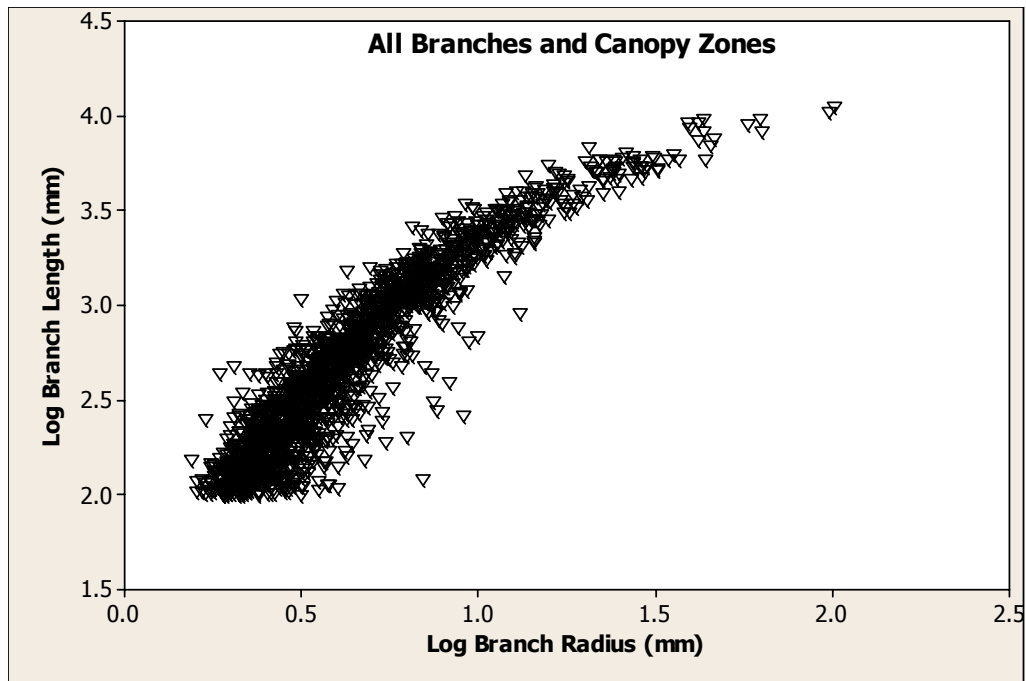
Figure 37. Log-log plot of length (mm) versus branch radius (mm) of all first, second and third order *Acer platanoides* branches.

Figure 38. Log-log plot of length (mm) versus branch radius (mm) of first order *Acer*

platanoides branches by canopy zone (top, middle, or lower third).

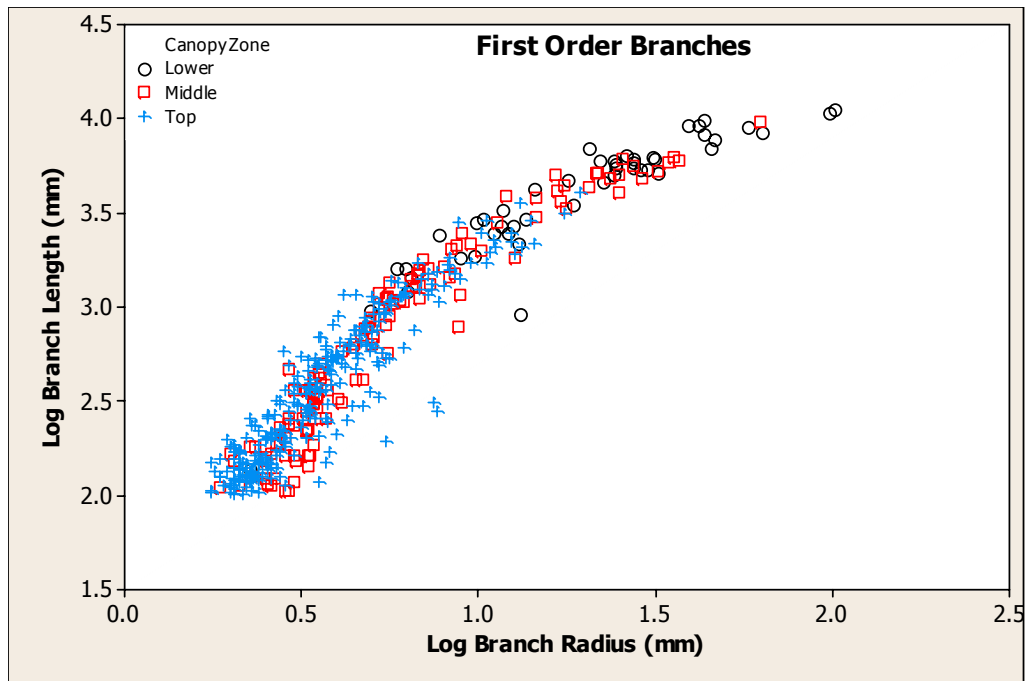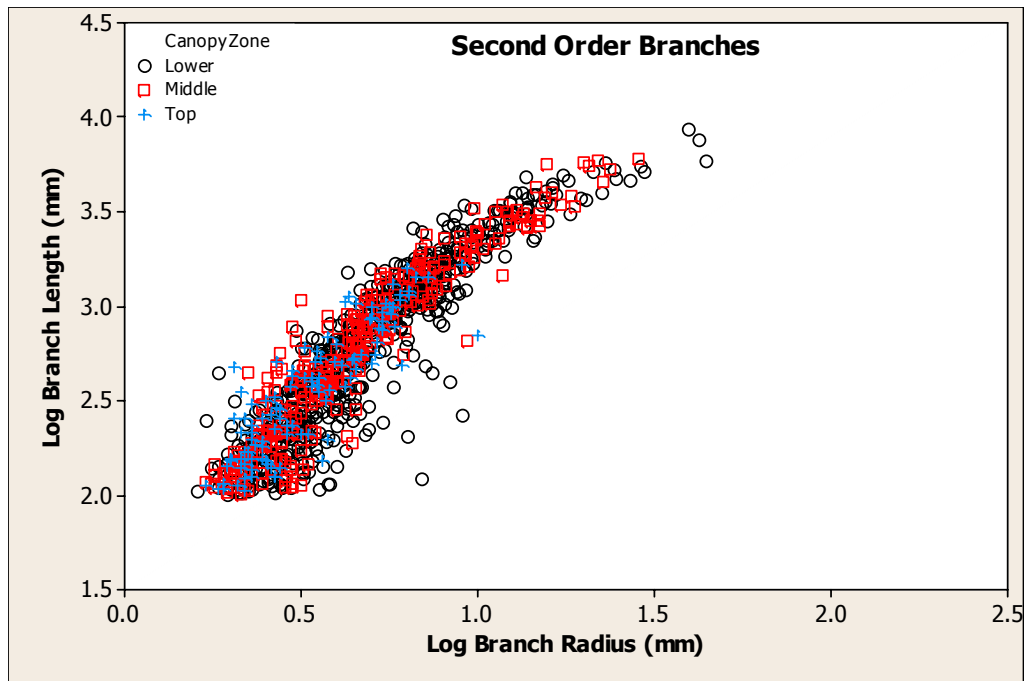Figure 39. Log-log plot of length (mm) versus branch radius (mm) of second order *Acer*

platanoides branches by canopy zone (top, middle, or lower third).

CURRICULUM VITA

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Education

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2005   Wind, Air & Trees - How trees effect air & noise pollution. Rutgers
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