

The Pennsylvania State University
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College of Agricultural Sciences

**TREE SPECIES DISTRIBUTION IN RELATION TO STEM HYDRAULIC
TRAITS AND SOIL MOISTURE IN A MIXED HARDWOOD FOREST
IN CENTRAL PENNSYLVANIA**

A Thesis in
Horticulture
by
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ABSTRACT

The hydraulic architecture of a tree could contribute to its ability to tolerate drier soils by increasing resistance to xylem cavitation and improving the efficiency of water transport. This study examined six co-occurring tree species within three genera (3 congeneric contrasts; *Carya glabra* and *C. tomentosa*, *Pinus strobus* and *P. virginiana*, *Quercus alba* and *Q. prinus*) under naturally occurring soil moisture gradients. Within each genus, species differed significantly in distribution along gradients of soil moisture ($P < 0.003$), with one species preferentially occupying wetter sites and the other occupying drier sites. I hypothesized that hydraulic architecture might partially explain variation in the distribution of species. I measured a suite of hydraulic architecture parameters including maximum specific hydraulic conductivity ($k_{s \max}$), leaf specific hydraulic conductivity (LSC), and xylem vulnerability at three levels of percent loss of maximum hydraulic conductivity (P20, P50, and P70). The congeneric contrasts within oaks and within hickories showed no significant differences for any of the parameters. For pines, the species associated with drier sites, *P. virginiana*, was more resistant to cavitation, which was consistent with my hypothesis. In general, species that preferentially occurred on drier sites tended to have higher maximum specific conductivity ($P = 0.0039$), which was opposite the expected water-conserving strategy hypothesized for drought-adapted species. These results suggest that these measures of hydraulic architecture of stems in mature trees may play only a minor role in explaining species-level variation in distribution on the landscape. This research invites further investigation into other potential limiting factors that may be controlling tree species distribution in the hill and valley region of central Pennsylvania.

Keywords: hydraulic architecture, xylem vulnerability, conductivity

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CHAPTER ONE

INTRODUCTION

Climate models predict changes in precipitation that could alter water availability at landscape scales. However, it is necessary to better understand how species distributions are related to soil moisture conditions in order to predict species shifts under changing precipitation regimes. Past studies have shown a relationship between a tree's ability to tolerate drought and the structure and properties of its xylem hydraulic pathways (Guthrie 1989, Abrams 1990, Shumway et al., 1991, Borghetti et al., 1993, Cochard et al., 1996, Ewers et al., 2000, Addington et al., 2006). Individual tree species have been shown to be able to adjust to varying soil moisture conditions by modulating various hydraulic architecture traits to maintain the efficiency and integrity of water transport from roots to leaves (Shumway et al., 1991). Because the transpirational water loss of a tree depends at least partly upon its hydraulic transport capacity, hydraulic architecture can limit the leaf area supported, which in turn limits stomatal conductance, transpiration, and photosynthesis (Shumway et al., 1991). Studies have shown that within a species, adjustments may be made along a tree's hydraulic pathway, such as stomatal activity and root area to leaf area ratio, to offset soil moisture differences (Ewers et al., 2000, Addington et al., 2006). These studies have typically considered soil moisture effects on a large scale, often the entire geographic spread of a species (Abrams 1990, Borghetti et al., 1993, Abrams 1994). However, there is evidence that hydraulic characteristics such as xylem anatomy and maximum hydraulic conductance play a critical role in the dominance of a tree species along a moisture gradient on a finer scale (Guthrie 1989, Cavender-Bares et al., 2004). To date, studies linking hydraulic

architecture and natural soil moisture conditions have focused on genotypic and phenotypic plasticity within a species (Abrams 1990, Abrams and Kubiske 1990, Shumway et al., 1991, Addington et al., 2006). Additionally, research has typically been conducted on seedlings or in a greenhouse setting, conditions that may not accurately reflect the responses of mature individuals (Cavender-Bares and Bazzaz 2000). I am not aware of any studies that have investigated the linkage between fine-scale species distributions along a natural soil moisture gradient and hydraulic architecture.

The following is an attempt to approach hydraulic architecture from an ecological perspective, to begin with observed patterns in a natural growth forest and investigate whether the hydraulic architecture of a species is consistent with those patterns. This study was designed to ascertain whether the localized preferential distribution of co-occurring species within the same genus is correlated with soil moisture and the extent to which that relationship can be explained by hydraulic architecture. Specifically I tested the hypothesis that species preferentially occurring on drier sites have more conservative hydraulic architecture. Conservative classification was based on a tradeoff between efficiency and safety and defined as a species sacrificing the efficiency of water transport in order to maximize safety (Tyree et al., 1994, Hacke et al., 2006). To characterize the hydraulic architecture, I hypothesized that more conservative species would have narrower xylem conduits, leading to lower maximum hydraulic conductivity, lower leaf specific conductivity, and greater resistance to xylem embolism.

CHAPTER TWO

LITERATURE REVIEW

Observations about plant water relations date back to the Egyptians, who noted plant dependence on water and created irrigation systems for their crops. Circa 350 B.C. Aristotle hypothesized that plants drew water and nutrients from the soil in amounts controlled by a “vital principle” (Kramer and Boyer 1995). While little advancement was made in plant physiology between Aristotle and the 19th century, Renaissance man Leonardo da Vinci recorded his view of tree architecture in his notebooks from the late 15th and early 16th centuries. He wrote detailed descriptions of the structure and placement of tree branches and leaves as well as noting geotropic and heliographic tendencies of plants. Perhaps most notable is da Vinci’s observation that, “All the branches of trees at every stage of their height, united together, are equal to the thickness of their trunk. All the ramifications of the waters at every stage of their length being of equal movement are equal to the size of their parent stream”(da Vinci, 1989). Da Vinci’s description was the first observation of what was later scientifically defined as the unit pipe model (Kramer and Boyer 1995). However insightful his observations, da Vinci’s notes were limited in that they were simply qualitative, without basis in scientific experimentation.

The first attempt to quantify plant water relations is attributed to Stephen Hales in his 1727 work “Vegetable Staticks” wherein he describes the transport system of plants thus: “Tho’ vegetables (which are inanimate) have not an engine, which, by its alternate dilatations and contractions, does in animals forcibly drive the blood through the arteries and veins; yet has nature wonderfully contrived other means, most powerfully to raise

and keep in motion the sap” (Hales 1727). Hales also made some of the first measurements of gases released by plants. Despite Hales’ strides, plant physiology did not exist as a discrete subject until the 19th century, when Julius von Sachs created a professorship in the subject. Sachs is considered the father of plant physiology, contributing greatly to the understanding of seed germination, organ development, and nutrient and water transportation. Contemporaneous to the work of Sachs was Asa Gray, who explained the movement of sap in terms most concurrent with our modern understanding when he wrote that “in a leafy plant or tree the sap is not forced up from below, but is drawn up from above” (Kramer and Boyer 1995). In the 1895, Dixon and Joly formalized this concept explaining that transpiration at the leaf surface exerts a negative pressure or tension that pulls water from the soil through the plant (Dixon and Joly 1985).

After the work of these researchers, the field of plant physiology, specifically water relations, expanded quickly and significantly. Many of the models still used today came out of the productivity of the early 20th century. The idea of plant water balance was introduced in the 1920s by Montfort and Maximov. Both researchers found that plants tended to experience a water deficit at midday, which is to say that transpiration was greater than absorption. Maximov also studied mechanisms within plants related to control of whole plant water balance, such as the preferential transfer of water from older to younger leaves (Kramer and Boyer 1995). The concept of the soil-plant-atmosphere continuum (SPAC) also became popular during the 1920s, thanks to work of scientists such as Huber and Gradmann. The SPAC emphasizes the importance of each factor in the whole plant water status. Huber (1928) and Cowan (1965) built on the idea by applying

Ohm's Law, relating water flow along the SPAC to the flow of electricity (Tyree and Ewers 1991).

As scientific understanding of the general processes involved in water relations improved, the focus of research shifted from whole plant processes to plant physiology at the molecular level. Much of the work done in the 1990s concentrated on molecular genetics, the production of various enzymes and proteins, and their impact on water deficit related processes. Since the late 20th century, there has been a renewed interest in not only whole plant water use, but also plant water use in the context of ecosystems, specifically in scaling patterns to a whole system level (Abrams 1990).

The field of tree water relations has made great strides in expanding the volume of knowledge on this subject since the early 20th century. Since Zimmermann coined the term in the 1970s, hydraulic architecture has gained popularity as the preferred method for studying tree water relations because it helps to distill the vast amount of information about transport in trees into basic components (Zimmermann 1978). Cruiziat et al. (2002) identify these components as a driving force, pipes, reservoirs, and regulating systems (Table 1).

Components of any hydraulic system	Equivalent components of tree-like hydraulic system
Energy of transfer	Solar radiation on leaves
Pipes	Vascular system
Uptake system	Soil-Root interface
Reservoirs	"Elastic" tissues (living cells) and rigid tissues (dead cells)
Devices of regulation	Stomata

Table 1. Basic components of tree hydraulic system (adapted from Cruiziat et al., 2002)

Hydraulic architecture is particularly valuable to the study of water relations because it synthesizes several earlier theories and models to more fully explain water transport in plants, specifically the electrical analogy, the cohesion-tension theory, and quantitative parameters.

Electrical Analogy

An electrical analogy to explain long distance water transport in plants has been in use since the 1920s. Called the Ohm's law analogy, it equates water flux through the soil-plant-atmosphere continuum to the flow of an electrical current in a circuit. In this scenario, the inverse of hydraulic conductances, hydraulic resistances, are analogous to electrical resistances. The model can be generalized to account for water storage, or the capacitance, of individual elements. This inclusion creates a more realistic scenario in which the flux into and out of each portion of the continuum is not necessarily equal (Tyree and Ewers 1991). Despite this, the Ohm's law analogy is still too simplified a model to accurately characterize the movement of water through a tree.

Cohesion-Tension Theory

According to the cohesion-tension theory, water travels along a gradient of increasingly negative pressures along the soil-plant-atmosphere continuum. This is possible because of the strong hydrogen bonds between water molecules that allow water to remain liquid under tension. When the tension in the xylem elements surpasses a critical value, cavitation can occur. This means that liquid water is replaced by water vapor and through the diffusion of air into the conduit, the pressure inside becomes equal to atmospheric pressure (Tyree and Sperry 1988, Milburn 1991). Once the water vapor is

replaced by air, the vessel is considered embolized. When one conduit cavitates, all the remaining conduits are subjected to even more negative pressures, which can cause further embolism (Tyree and Sperry 1988, Sperry et al., 1998).

The number of xylem conduits and their various sizes impact the tension that draws water along the SPAC. To quantify the flow of a fluid through a pipe, the Hagen-Poiseuille equation is used. It is modified slightly to fit the context:

$$k_h = (\pi\rho/128\eta) \sum_{i=1}^n (d_i^4)$$

where k_h is hydraulic conductivity, ρ is the density of the fluid (kg m^{-3}), η is the dynamic viscosity of the fluid (MPa s^{-1}), d is diameter (m) of the i^{th} pipe, and n is the number of pipes (Tyree and Ewers 1991). The Hagen-Poiseuille Law demonstrates the importance of diameter in the transport of water through xylem conduits. Large vessels will conduct exponentially to the fourth power more water than the same number of smaller vessels. While the analogy of pipes is useful for conceptualizing the transport of water through the xylem of a tree, a tree's conductivity will not reach the theoretical value predicted by the Hagen-Poiseuille equation. This discrepancy is due to the restrictive membranes at the ends of vessels and tracheids that alter the hydraulic properties of the total conduit. The size and number of conduits or "pipes" influences the amount of leaf area that can be supported. However, the equation is useful for indentifying trends based on differences in xylem anatomy.

In the unit pipe model, a plant is seen as group of pipes, the cross-section of each of which is proportional to a given unit of leaf area that can be supplied with water

(Figure 1). While this general relationship has been well documented, it is not particularly useful in quantifying the hydraulics of a tree (Tyree and Ewers 1991, Cruiziat et al., 2002).

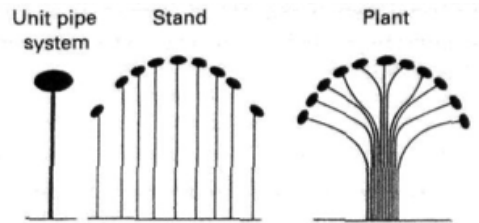


Figure 1. The unit pipe model. Plant transport systems are made up of a grouping of unit pipes, which each supply a given leaf area (Tyree and Ewers 1991).

This is because the unit pipe model is concerned with total xylem cross-section rather than the diameter of individual pipes, which, as the Hagen-Poiseuille equation shows, is a critical component in accurately

determining the conductivity. The diameter of the branch is not necessarily descriptive of the diameter of the vessels or tracheids, which is the hydraulically limiting factor. This discrepancy emphasizes the need to move beyond descriptive, qualitative measures to incorporate quantifiable hydraulic parameters.

Quantitative Parameters

The starting point for measuring a tree's ability to transport water is to quantify its hydraulic conductivity (k_h). Hydraulic conductivity is measured by calculating the ratio of water flux (kg s^{-1}) through a stem segment to the pressure gradient (MPa m^{-1}) driving flow. Hydraulic conductivity is a particularly useful measure because from it several other parameters can be derived.

Specific conductivity (k_s) measures the porosity of a stem segment. This parameter can be calculated by dividing k_h by the xylem conducting area (m^2) of the stem. Similarly, the leaf-specific conductivity (LSC) can be calculated by dividing the k_h by the leaf area (m^2) distal to the stem segment. The leaf-specific conductivity describes

the ability of a stem to supply the given leaf area with water. An analogous term is the Huber Value (HV), which estimates how much stem tissue is invested in supplying water to each unit of leaf area. The Huber Value is calculated by dividing the sapwood cross-section by the distal leaf area.

Also essential to the study of tree water relations is vulnerability of xylem to embolism. Water moves through the soil-plant-atmosphere continuum along a gradient of increasingly negative pressure. As the soil dries, ever more negative pressures are required to move water along the continuum. At a threshold, xylem cells are no longer able to withstand the tension and begin to cavitate. Eventually, the cavitating cells will fill with air or embolize. With each cell that embolizes, a stem's ability to conduct water decreases. By plotting the decrease in conductivity with decreasing water potential, a vulnerability curve can be drawn.

Notable Results

These quantitative parameters were first used by Zimmermann in the late 1970s. When Zimmermann and other scientists began investigating the hydraulic architecture of woody plants in the 1970s and 80s, one of the first observations made was that the primary source of resistance to water transport in a tree was at the branch-stem junction. Because of this, resistance to transport for most minor branches is approximately equal, regardless of its height above the ground (Zimmermann 1978, Tyree et al. 1983, Ewers and Zimmermann 1984a, Ewers and Zimmermann 1984b). This discovery led Zimmermann to propose the segmentation hypothesis, which states that the nodal

resistance helps confine cavitation and embolism events to minor branches (Zimmermann 1983).

In their seminal work from 1988, Tyree and Sperry proposed that woody plant species operate at the threshold of catastrophic xylem dysfunction. That is to say that trees regularly experience water potentials that could cause runaway embolism. For the species studied, it appears that trees sacrifice a substantial percentage of their conductivity on a daily basis. However, they are able to stop conductivity loss just short of the critical point that would lead to almost total loss of conductivity (Tyree and Sperry 1988). Cochard et al. (1996) found that runaway embolism was prevented by water loss regulation by stomatal closure at low water potentials. While it introduced an important topic, many aspects of Tyree and Sperry's paper have been revised as further research has been conducted. This paper (Tyree and Sperry 1988) was concerned with four species, three of which were conifers and one of which was diffuse porous. Since that time, scientists have worked to characterize the hydraulic architecture of many more species (Tyree and Ewers 1991, Tyree et al., 1999). Also, the Huber Value, which was commonly used in earlier work, has since been replaced by more physiologically informative parameters, such as leaf-specific hydraulic conductivity (Cruiziat et al., 2002).

Current Status

In the past 30 years, a substantial database of species-specific hydraulic architecture studies has been compiled. When the field of hydraulic architecture was first being investigated, just characterizing a species was a substantial contribution. While there are still many species-specific questions to be answered, such as what happens at

the tail end of vulnerability curves for ring porous species, the impact of adding one more species to the database has decreased. Researchers are now beginning to look beyond simply compiling information to looking for patterns and extrapolating to landscape levels in an environmental, ecological, and physiological context (Taneda and Sperry 2008). Schume et al. (2003) found that during a dry period, trees were the main cause of soil moisture variation and that the degree of variation was correlated with the water use characteristics of the species. Expanding on the relationship between soil moisture and species-specific trends, Tromp-van Meerveld and McDonnell (2006) took this idea to a larger scale when they found feedbacks between soil moisture, climate, and species distribution. Engelbrecht et al. (2007) found that drought sensitivity was correlated with species distribution in tropical climates.

A number of temperate tree species have been studied and it has been shown that a relationship exists between hydraulic architecture and drought resistance (Abrams 1990, Shumway et al., 1991, Abrams 1994, Tyree et al., 1999). However, studies have tended to focus on an individual species and the variation in moisture conditions across that species' entire distribution (Shumway et al., 1991, Abrams 1994). Also in temperate systems, other studies have found that many species within the same genus can co-occur at a fine scale by adapting to limiting environmental conditions to create a niche (Cavender-Bares and Holbrook 2001, Espeleta et al., 2009). However, the integration of these two results (the linkage of hydraulic architecture with drought resistance and fine-scale congeneric divergence along soil moisture gradients) has not been well studied. Further research is needed to understand species-level variation in drought tolerance as a function of hydraulic architecture at a finer geographic scale.

CHAPTER THREE

MATERIALS AND METHODS

Field Site

The Shale Hills Watershed (40.6631 N, -77.9066 W) is a 7.9 hectare (19.5 acre) area of forest in the Ridge and Valley region of central Pennsylvania. The basin is V-shaped with steeply sloping sides (25%-48%). The valley runs east to west, dividing true north-facing and south-facing slopes. Four landforms comprise the catchment: the north-facing slope with shallow soils and deciduous trees, the south-facing slope with deciduous trees and heavier underbrush, seven swales (all but two of which occur on the south-facing slope), and the valley floor, which is the floodplain for the stream. The stream is a first-order headwater of Shavers Creek, leading eventually to the Susquehanna River. The southern, north-facing slope has very shallow soils (< 0.3 m deep) while the northern, south-facing slope has shallow soils only on the ridge (< 0.3 m deep) and deeper soils in the swales that run perpendicular to the contours (> 1.0 m deep).

The woody vegetation at Shale Hills consists of 23 tree species within 14 genera. A managed forest maintained and harvested for timber, the trees were last harvested in the 1930s, making the current stand age 70-80 years old. The dominant genera are *Quercus*, *Carya*, and *Pinus*. *Quercus spp.* account for 63% of the total basal area in the watershed, *Carya spp.* for 13%, and *Pinus spp.* for 8% (Appendix A). Each of these genera has several species present, two of the most dominant of which were used for this study. Within each genus, the species are distributed along distinct soil-depth and soil-moisture gradients. *Quercus prinus* (Chestnut oak, abbreviated QUPR) is found along the

shallow soil, dry ridges, mostly on the north-facing slope. *Quercus alba* (White oak, abbreviated QUAL) appears in the valley, along the floodplain. *Quercus rubra* (Red oak) and *Quercus velutina* (Black oak) are also present, though with more limited distribution. There are four species of *Carya* in the watershed; however, two are very limited (*Carya ovata*, 26 individuals in the canopy and *Carya cordiformis*, 6 individuals). *Carya tomentosa* (Mockernut hickory, synonym *C. alba*, abbreviated CATO) is found on the south-facing slope with deeper soils while *Carya glabra* (Pignut hickory, abbreviated CAGL) is found primarily along the north-facing ridge. There are three *Pinus* species in the watershed, but *Pinus pungens* (Table mountain pine) has only two individuals in the canopy. *Pinus strobus* (Eastern white pine, abbreviated PIST) appears in the valley along the streambed. *Pinus virginiana* (Virginia pine, abbreviated PIVI) appears exclusively along the North-facing ridge.

Inventory and Survey

All trees reaching the canopy with a diameter at breast height (DBH) of 20 cm or greater were included in the inventory and survey. The included trees were identified with small, metal, numbered tags at the base of the tree. DBH was measured at 1.3 m above the ground using a tree diameter tape. The basal area (BA) of each tree was calculated using the following formula:

$$BA = \pi r^2$$

where π is the constant equaling 3.142, and r is the radius or DBH divided by two. The relative dominance (RDO) for each species was calculated as:

$$RDO = \left(\frac{TBA_{species}}{TBA_{total}} \right) 100$$

where $TBA_{species}$ is the total basal area of one species and TBA_{total} is the total basal area of all species (Schreuder et al., 1993). Density for each species was calculated with the equation:

$$D = \frac{trees}{hectare}$$

where D is density of all trees greater than 20 cm in diameter. Relative density (RDE) was also calculated for each species using the formula:

$$RDE = \left(\frac{D_{species}}{D_{total}} \right) 100$$

where $D_{species}$ is the density of one species and D_{total} is the density for all species. Finally, the overall importance value (IV) was calculated as:

$$IV = RDO + RDE$$

The location (latitude, longitude, and elevation) of each tagged tree was measured with a top gun (Model Set 5A series D2087) and recorded with an attached data logger (Trimble TSCe series 00042968). Data were then downloaded to a laptop computer and projected in Geographic Information Systems (GIS) using ArcGIS software. The survey data were used in conjunction with soil moisture and soil depth data provided by Dr. Henry Lin from Pennsylvania State University. The soil moisture data were collected six times from May to August of 2005 at depths of 0.1 m, 0.4 m, and 0.8 m at 77 sites across the watershed using Time Domain Reflectometry probes (TDR). Soil depth data were gathered during the same year.

Experimental Design

Two dominant species within each of the three dominant genera were selected for this study. Within each congeneric pair, one species was found primarily on drier soils

while the other appeared mostly on wetter soils. In all cases except one (*P. virginiana*), at least one individual of each species appeared on both wetter and drier soils. *Pinus virginiana* was located exclusively along the North-facing ridge. Based on the relationship between species distribution and soil moisture, four sites were selected throughout the watershed. Sites were selected to include several different soil moisture conditions and were restricted to areas where the six species co-occurred in close proximity (**Figure 2**). Two sites were chosen on the valley floor near the stream, the wettest area in the watershed. The other two sites were located along the southern ridge, the driest area in the watershed. All six species were present at each site, with the exception of *P. virginiana*, which was present at the ridge sites, but not the sites along the valley floor. This sampling design was chosen to minimize environmental variation among trees at the same site and to capture moisture variation across the watershed. The average soil moisture for the two ridge sites was statistically identical ($P = 0.999$) and significantly different from the two valley sites ($P < 0.0001$).

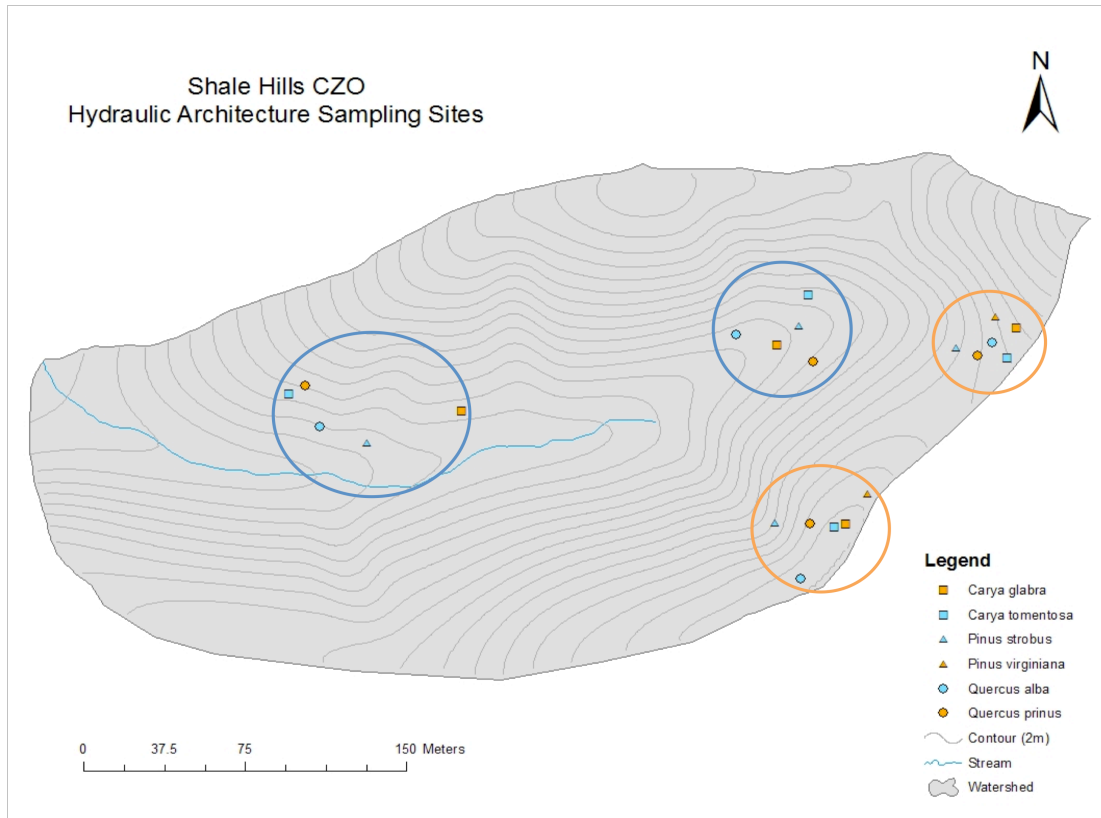


Figure 2. Four sites of different soil moistures were selected for sampling, two wet valley sites (blue circles) and two dry ridge sites (orange circles). Characterization of site moisture is based on statistical analysis of season-long (May-August 2005) soil moisture measurements weighted by depth to 80 cm. Blue symbols represent species preferentially occurring on wet sites and orange symbols represent species preferentially occurring on dry sites.

Sample Collection

Sampling occurred from July to September 2009. Samples were collected by climbing trees and using either hand loppers or a pole saw to obtain two branches approximately 0.5-1.5 cm in diameter from each tree. Branches were immediately placed in a black plastic bag. Two branches were collected from each tree. Typically one site, consisting of five to six trees and 10 to 12 samples, was sampled completely in one day. At the end of sampling, branches were transported back to the lab at the Penn State campus, approximately 20 minutes away.

Sample Processing

Upon returning to the lab, terminal segments ranging from 0.38 to 0.77 cm in diameter and 15 to 20 cm in length were cut from the branches. The leaves and needles distal to the selected segment were stripped from the segments and scanned to obtain leaf area (LiCor LI-3000A). The branch segments were marked with an arrow indicating direction of flow, stored in a desiccator filled with a 20 mM HCl solution and left under vacuum over night to reverse native embolism, fully hydrate stems, and prevent microbial infection (Sperry et al., 1988). The bark was removed from branch segments after vacuum infiltration. The terminal centimeter of each end of the segments was cut under water using hand clippers. The ends were then trimmed under water using a razor blade (Sperry et al., 1988). The length of the segment, as well as its diameter and the pressure head of the gravity-feed apparatus were recorded before each measurement.

Vulnerability curves were determined using the air injection method (Sperry and Saliendra 1994). To establish the curves, I measured hydraulic conductivity. The branch was attached to plastic tubing in a gravity-feed apparatus, oriented with the arrow indicating flow direction. A small piece of tubing was fitted to the opposite end of the branch and a 1mL graduated pipette was inserted into the tubing. The hydraulic head of the gravity-feed apparatus was adjusted according to species. Being ring porous, *Quercus* and *Carya spp.* required a lower pressure head than *Pinus spp.* because of the possibility of refilling long cavitated vessels that were open at both ends (Hacke et al. 2006). The HCl solution was used in measuring the conductivity of the segments. The flow rate of the solution through the segments was measured by timing the movement of the solution meniscus in the pipette over known intervals (either 0.01 mL or 0.05 mL). Maximum

specific conductivity ($k_{s \max}$, $\text{kg s}^{-1} \text{m}^{-1} \text{MPa}^{-1}$) was calculated using the following formula:

$$k_s = \frac{V * L}{t * A * \Delta p} \mu$$

where V is volume of the interval of measurement (m^3), L is the length of the stem (m), μ is the viscosity of water (MPa s), t is the average time between measurements (s), A is the conducting xylem area of the stem (m^2), and Δp is the pressure gradient (MPa m^{-1}).

The maximum specific conductivity having been measured, segments were pressurized to a predetermined value using a double-ended pressure chamber (PMS Instruments Model 1000 with cavitation chamber) and held there for two minutes (Sperry and Saliendra 1994). Segments were then allowed to depressurize for a period of approximately 10 minutes before remeasuring k_s . The process of measuring specific conductivity was repeated and percent loss of conductivity (PLC, %) was calculated using the following formula:

$$PLC = \frac{k_{s \max} - k_{sn}}{k_{s \max}} * 100$$

where $k_{s \max}$ is the maximum specific conductivity ($\text{kg s}^{-1} \text{m}^{-1} \text{MPa}^{-1}$) and k_{sn} is the specific conductivity of the stem at pressure n ($\text{kg s}^{-1} \text{m}^{-1} \text{MPa}^{-1}$). Stems were subjected to increasing pressures to mimic a pressure differential, until they reached 90% PLC. Samples were stored in water and edges were trimmed with a razor blade between each measurement. Because some species lost conductivity under very low tensions, in limited cases, only two data points could be measured and a curve could not be fitted. To

maintain equal sample sizes, vulnerability curves were fitted to the six data sets with the highest r^2 values for each species. A Weibull function was used to fit the curves and calculate the 20, 50, and 70 percent loss of hydraulic conductivity points (P20, P50, P70) (Neifeld et al., 1992). These six segments per species were used to generate a mean vulnerability curve.

CHAPTER FOUR

RESULTS

Soil Moisture and Species Distribution

Survey data showed that the species were not distributed randomly, but occupied specific regions of the watershed. Within each genus, species differentiation was apparent (Figures 3a-c). The pines showed the most distinct pattern. *Pinus strobus* appeared along the valley bottom and floodplain whereas *Pinus virginiana* was found exclusively along the southern ridge. In the hickory genus, *Carya glabra* was found primarily along the southern ridge while *Carya tomentosa* tended to occupy the midslope position on the northern side of the watershed. The pattern also was consistent for *Quercus* species. *Q. alba* occupied the valley floor and toe slope of the northern hill while *Q. prinus* appeared mostly on the mid and upper slope positions of both ridges.

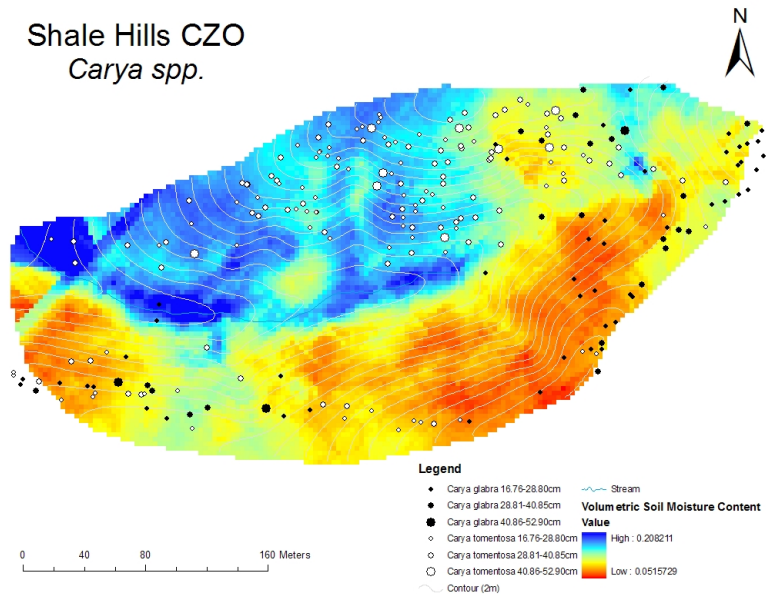


Figure 3a. Species distribution for *Carya* spp. at Shale Hills Critical Zone Observatory. *Carya tomentosa* (○) occupies mid-slope positions on the South-facing slope while *Carya glabra* (●) appears more on the North-facing slope and ridges. Volumetric soil moisture content data (m^3/m^3) were collected in August 2005 at 10cm depth.

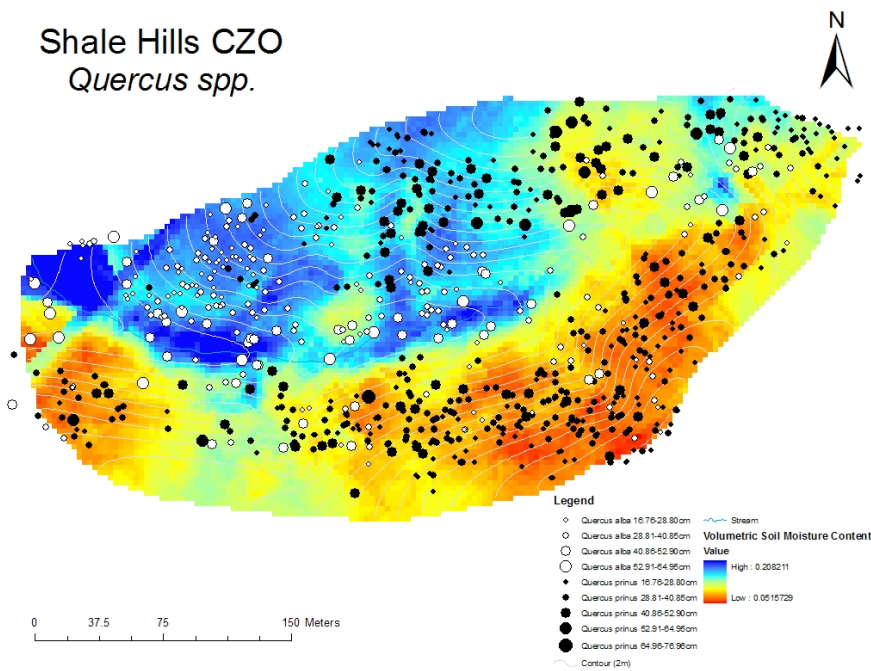


Figure 3b. Species distribution for *Quercus spp.* at Shale Hills Critical Zone Observatory. *Quercus alba* (○) appears on the floodplain and toe slope of the South-facing hillside. *Quercus prinus* (●) is found primarily on the mid to upper slope positions and North-facing ridge. Volumetric soil moisture content data (m^3/m^3) were collected in August 2005 at 10cm depth.

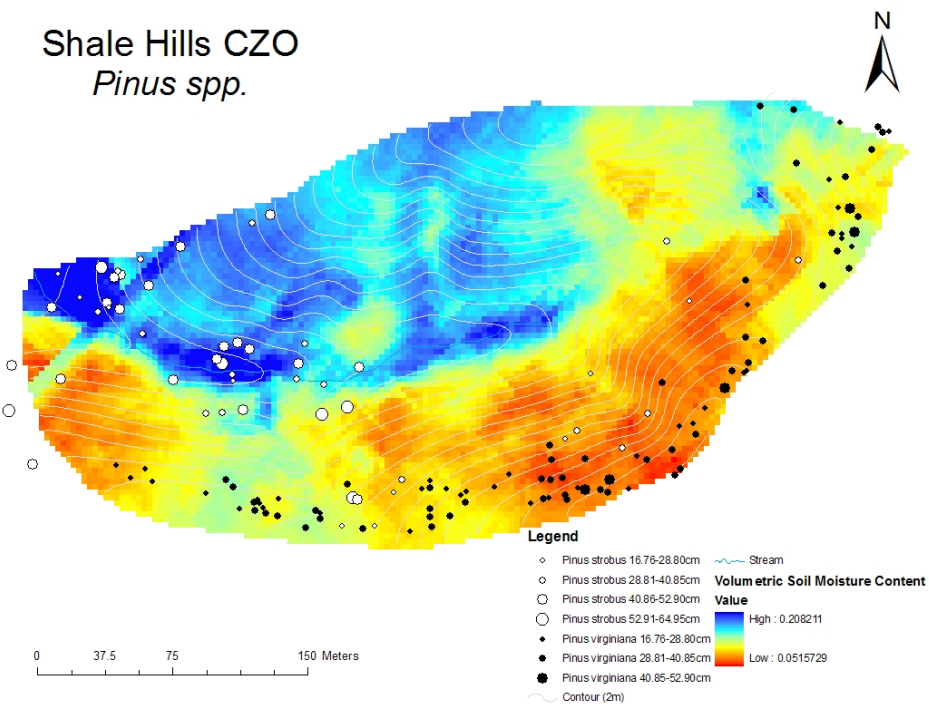
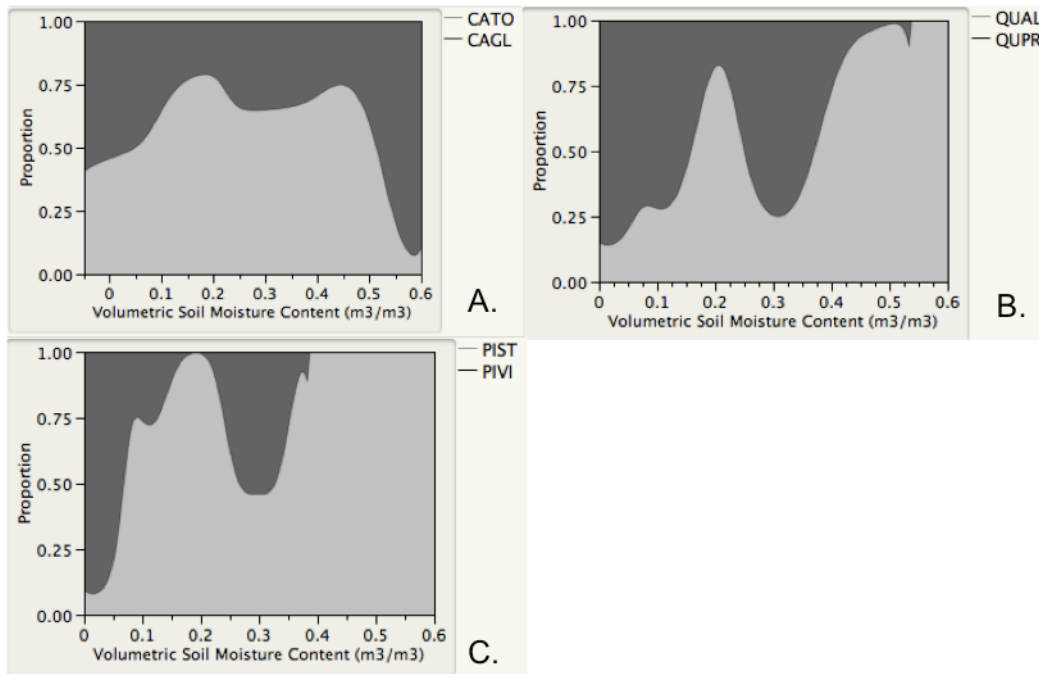


Figure 3c. Species distribution for *Pinus spp.* at Shale Hills Critical Zone Observatory. *Pinus strobus* (○) occupies the floodplain while *Pinus virginiana* (●) is found exclusively on the North-facing ridge. Volumetric soil moisture content data (m^3/m^3) were collected in August 2005 at 10cm depth.

There was a significant relationship between soil moisture and species distribution within each congeneric contrast, with species tending to occur on wetter or drier soils (Figures 4a-c). The pattern was less clear in the hickory genus because, in general, the genus occupied less extreme soil moisture than the oaks and pines. Within each pairing the seasonal average soil moisture content was higher for one species. For the oaks, *Quercus alba* had an average volumetric soil moisture content of 0.206 while *Quercus prinus* had an average of 0.092 for the season ($P < 0.0001$). The pines showed a similar relationship with soil moisture content being 0.170 for *Pinus strobus* and 0.035 for *Pinus virginiana* ($P < 0.0001$). The average soil moisture content for *Carya tomentosa* was 0.140 while it was 0.096 for *Carya glabra* ($P = 0.0026$) (Figure 5).



Figures 4a-c. Proportional distribution of species within genera across soil moisture gradient. X-axis shows soil moisture and Y-axis shows the likelihood of the species with higher average soil moisture within a given genus occurring at a soil moisture value. Soil moisture values are weighted by depth to 80cm or depth of refusal. Soil moisture was considered 0.0 once depth of refusal was reached. *Carya* spp. (A.), *Quercus* spp. (B.) and *Pinus* spp. (C.). The dark shaded region represents species with lower average soil moisture (*C. glabra*, *Q. prinus*, *P. virginiana*) and the light shaded region represents species with higher average soil moisture (*C. tomentosa*, *Q. alba*, *P. strobus*).

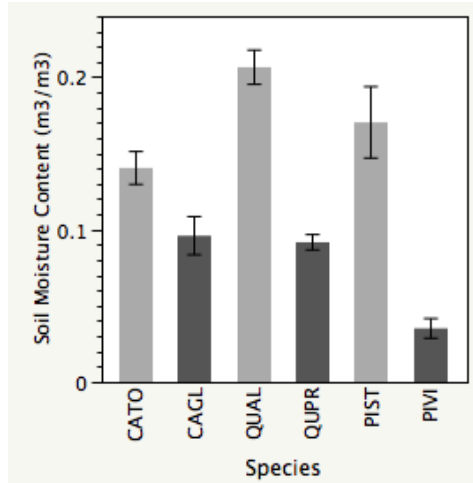
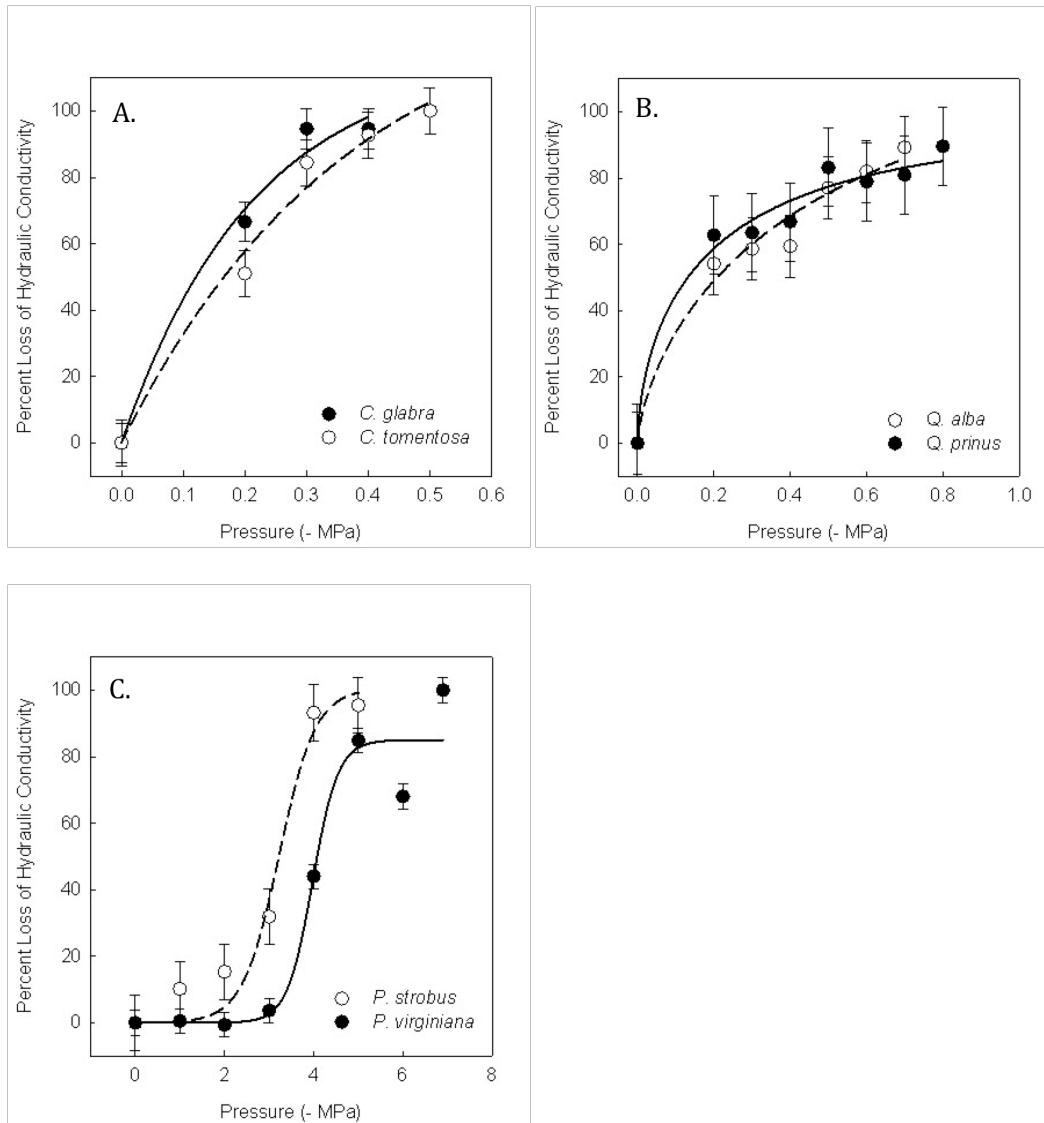


Figure 5. Average volumetric soil moisture content, weighted by depth to 80cm or depth of refusal. Soil moisture was considered 0.0 once depth of refusal was reached. Error bars are standard error. Lighter bars are species tending to occur on wetter soils; darker bars are species tending to occur on drier soils.

Hydraulic Architecture

I hypothesized that the xylem of species preferentially occurring on drier soils would be less vulnerable to cavitation. However, there was no discernable pattern for species that occurred on wet versus species that occurred on dry sites that was consistent across genera. At the genus level, species vulnerability curves showed that all *Quercus* and *Carya* species had a large loss of conductivity (60-80 PLC) at relatively small negative pressures (-0.3 to -0.6 MPa), beyond which the remaining conductivity tended to be lost less quickly. By comparison, both *Pinus* species showed little loss of conductivity at low tensions, followed by a steep increase beyond a threshold tension (**Figures 6a-c**).



Figures 6a-c. Vulnerability of xylem to cavitation in *Carya* spp. (A.), *Quercus* spp. (B.) and *Pinus* spp. (C.). Error bars are the average standard error for each species.

Paired vulnerability curves showed no significant differences at 20, 50, or 70 PLC for *Carya* species or *Quercus* species (all $P > 0.9$). However, *Pinus strobus* and *Pinus virginiana* did differ significantly at the P20 and P50 levels with the species from the drier site, *P. virginiana*, exhibiting greater resistance to cavitation ($P < 0.0001$ and $P = 0.0017$, respectively). There was no significant difference between the two pine species at 70 PLC ($P = 0.035$), but the pattern was consistent, with *P. virginiana* tending to reach 70 PLC at a more negative pressure.

For leaf-specific conductivity (LSC) the data showed no significant differences between species within genera (all $P > 0.9$) and no consistent trends across genera for species preferentially occurring on wet versus dry soils ($P = 0.1452$) (**Table 2** and **Figure 7**). For maximum hydraulic conductivity, I hypothesized that species on drier soils would have a lower maximum, reflecting a more conservative pattern of water use. There was a significant pattern across genera with the drier species having a higher maximum conductivity ($P = 0.0039$) (**Figure 8**). Statistical analyses for conductivity were performed on log-transformed data to correct for non-normal distribution and heterogeneity of variance. The Bonferroni Correction was used to account for the performance of multiple analyses on one data set, resulting in $\alpha = 0.01$.

Species	$k_{s \max}$ ($10^{-4} \text{ kg s}^{-1} \text{ m}^{-1} \text{ MPa}^{-1}$)	LSC ($10^{-4} \text{ kg s}^{-1} \text{ m}^{-1} \text{ MPa}^{-1}$)
<i>Carya tomentosa</i>	2.62 (ab)	0.45 (a)
<i>Carya glabra</i>	13.84 (abc)	1.86 (ab)
<i>Quercus alba</i>	16.56 (bc)	3.29 (b)
<i>Quercus prinus</i>	23.87 (c)	3.28 (b)
<i>Pinus strobus</i>	2.15 (a)	1.55 (ab)
<i>Pinus virginiana</i>	4.18 (abc)	1.82 (ab)

Table 2. Maximum specific conductivity and leaf specific conductivity by species (mean). Means within a column followed by the same letter are not significantly different at $P = 0.01$.

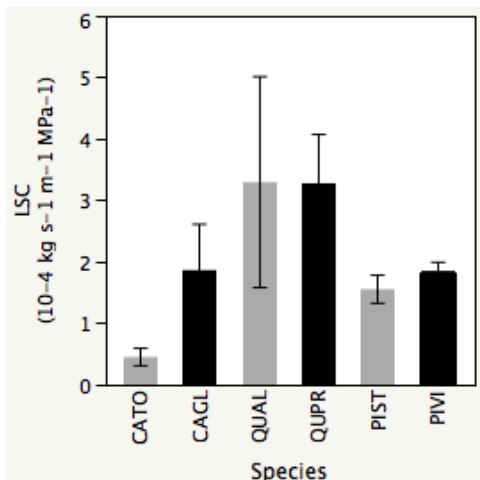


Figure 7. Mean leaf specific conductivity by species. Gray bars represent wet site species and black bars represent dry site species. Error bars are standard error. Species abbreviations are explained in Materials and Methods.

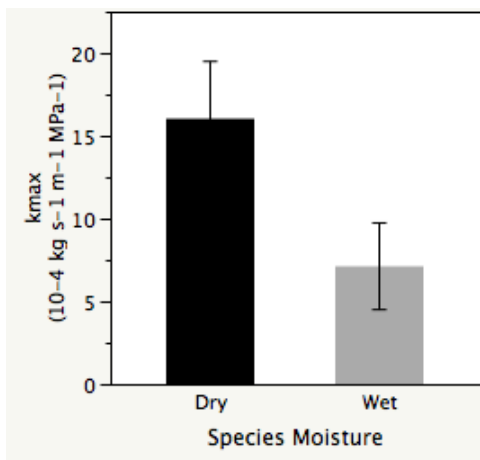


Figure 8. Mean maximum conductivity by species preferred soil moisture. The dry category includes *C. glabra*, *Q. prinus*, and *P. virginiana*. The wet category includes *C. tomentosa*, *Q. alba*, and *P. strobus*. Error bars are standard error.

CHAPTER FIVE

DISCUSSION

Species distributions in the Shale Hills watershed were consistent with typical distributions in the region for both slope position and soil moisture requirements (Burns and Honkala 1990). As such, the surveying data records a natural phenomenon, that is to say the non-random preferential distribution of species within the same genus along a soil moisture gradient. The high degree of significance in spatial patterns of species distributions with soil moisture provides evidence of species divergence for moisture within each of the three genera studied.

For the hickory and oak genera, vulnerability curves did not support the hypothesis that species occurring on drier sites would exhibit lower vulnerability to xylem cavitation. In these two genera, the species' curves were nearly identical. This result is not unprecedented (Cochard and Tyree 1990). However, I did find significant differences for the pine genus and in the hypothesized direction. This result is also supported by earlier research (Tognetti et al., 1998, Cavender-Bares and Holbrook 2001). The current understanding of the extent to which xylem vulnerability varies between species of the same genus along soil moisture gradients is limited. Studies to date have not been able to make a strong case for a sorting mechanism.

While species level differences in vulnerability are still unclear, I did observe clear differences based on xylem anatomy among genera. The *Carya* and *Quercus* species studied are all ring porous while the *Pinus* species have tracheids. The large drop in conductivity at pressures near zero exhibited by the hickories and oaks is typical of

ring porous xylem (Hacke et al., 2001, Cruiziat et al., 2002, Hacke et al., 2006, Taneda and Sperry 2008). The large vessels that develop during the early spring when water is plentiful are very vulnerable to cavitation whereas the other much smaller vessels that develop later in the growing season are more resistant to embolism and account for the gradual loss of conductivity after the initial rapid loss. In contrast, pines are composed of tracheids, which are comparatively uniform in size and much smaller in diameter. The pine species studied tend to be more resistant to cavitation in comparison to the ring porous species, but due to the uniform size of the elements, experience a large increase in conductivity lost once a critical tension is reached. These results give further support that ring porous trees exhibit a dramatic initial drop in conductivity at low xylem tensions (Hacke et al., 2001, Cruiziat et al., 2002, Hacke et al., 2006, Taneda and Sperry 2008).

The leaf-specific conductivity data were uninformative in explaining species distribution. When conductivity was divided by the leaf area supported, there were no statistical differences among any of the six species. This indicates that species employ different strategies to meet their needs. The oak species had leaf areas many times that of the pines, but all species showed the same ability to supply water per unit leaf area. Oak species need larger conduits in order to supply sufficient water to their large crown, especially during early spring leaf out, whereas the lower conductivity of pines is sufficient to support their smaller leaf area, the demands of which fluctuate less dramatically across seasons. It should be noted that the statistical analyses used were very conservative. While unlikely that other analyses would provide different results, the conservative nature of the parameters used may have dampened the significance of the observed trends.

I hypothesized that species that preferentially occupied drier sites would have more conservative hydraulic architecture, including narrower conduits, which would limit maximum conductivity. However, I found that drier species in general had higher maximum conductivity. This trend held true for each genus. This suggests that species on drier soils may not be experiencing substantial trade-offs between water conduction and tolerance of drought. It appears that while other studies have shown hydraulic architecture is related to drought tolerance and other water use mechanisms, the features I measured cannot explain the fine-scale variation in species correlation with soil moisture at our site in central Pennsylvania.

Despite the inability of these select features of hydraulic architecture to explain the species variation, the fact remains that the soils in the watershed are significantly drier on the slopes and ridges and there are distinct spatial patterns. If the measured traits are not compensating for limiting water conditions, there must be other mechanisms at work. It is possible that trees on the slopes and ridges are deeper rooted and have access to plentiful ground water, thereby avoiding drought conditions despite the shallow soil moisture conditions. I have gathered samples to test this theory using isotopic analysis of xylem water extracted from tree branches and am awaiting analysis. Currently a distillation line is being constructed to extract sap water from branch samples for analysis of hydrogen and oxygen isotopes. The results of this research are forthcoming.

Alternatively, it is possible that hydraulic architecture is an important factor, but that restrictions to water movement lie in other plant tissues. The majority of hydraulic architecture research to date centers on stem and branch measurements because branches have been considered the limiting element in the SPAC (Zimmermann 1983). Leaf

hydraulics are only recently being studied and results suggest that leaf traits may be more variable and play a more important role in hydraulic pathways than assumed (McCulloh and Sperry 2005, Sack et al., 2005, Woodruff et al., 2007). A more extensive look at whole tree hydraulic architecture may improve our understanding of the distribution and soil moisture correlation. Also, while hydraulic architecture may be important, research has shown that ontogeny can affect hydraulic architecture and drought tolerance, resulting in traits that vary with age and may play a more critical role at different life stages (Cavender-Bares and Bazzaz 2000). This suggests that distribution patterns found in mature forests may be due to traits that are limiting at the seedling stage and may not be apparent in mature trees.

Lastly, the mechanism driving species distribution may not be related to water at all. Light conditions vary between the north- and south-facing slopes and the ridges and valley. It is possible that light requirements rather than moisture requirements are causing the fine-scale differentiation within the watershed. This study calls attention to a naturally occurring phenomenon that requires further research to explain.

APPENDIX A
INVENTORY AND SURVEY DATA

Species Code	Number of Trees	DBH (cm) Sum	DBH (cm) Average	Density (trees / ha)	Relative Density (%) (Density of each species / density of all species) * 100	Average Basal Area (m ²) (0.00007854(DBH) ²)	Total Basal Area (m ²)	Relative Dominance (%) (Basal area of each species / basal area of all trees)*100	Important Value (IV) Relative Abundance (%) (Relative density + Relative dominance)
Qupr	558	18369.79	32.92	70.63	27.13	0.085	47.503	24.84	51.97
Quru	287	11975.59	41.73	36.33	13.95	0.137	39.252	20.53	34.48
Qual	282	9803.13	34.76	35.70	13.71	0.095	26.769	14.00	27.71
Cato	181	5580.12	30.83	22.91	8.80	0.075	13.513	7.07	15.87
Tsca	164	5736.59	34.98	20.76	7.97	0.096	15.762	8.24	16.22
Accac	122	3611.88	29.61	15.44	5.93	0.069	8.399	4.39	10.32
Cagl	122	3469.39	28.44	15.44	5.93	0.064	7.750	4.05	9.98
Pivi	96	3004.57	31.30	12.15	4.67	0.077	7.386	3.86	8.53
Pist	59	2296.92	38.93	7.47	2.87	0.119	7.024	3.67	6.54
Quve	47	1965.71	41.82	5.95	2.28	0.137	6.458	3.38	5.66
Fram	36	1046.73	29.08	4.56	1.75	0.066	2.391	1.25	3.00
Caov	26	847.85	32.61	3.29	1.26	0.084	2.172	1.14	2.40
Acru	22	712.47	32.39	2.78	1.07	0.082	1.812	0.95	2.02
Litu	13	490.98	37.77	1.65	0.63	0.112	1.457	0.76	1.39
Bele	10	268.48	26.85	1.27	0.49	0.057	0.566	0.30	0.78
Faam	7	202.95	28.99	0.89	0.34	0.066	0.462	0.24	0.58
Caco	6	162.56	46.45	0.76	0.29	0.169	1.017	0.53	0.82
Nysy	5	162.81	32.56	0.63	0.24	0.083	0.416	0.22	0.46
Prse	5	135.38	27.08	0.63	0.24	0.058	0.288	0.15	0.39
Maac	3	113.79	37.93	0.38	0.15	0.113	0.339	0.18	0.32
Tiam	3	84.33	28.11	0.38	0.15	0.062	0.186	0.10	0.24
Pipu	2	72.64	36.32	0.25	0.10	0.104	0.207	0.11	0.21
Beal	2	46.99	23.50	0.25	0.10	0.043	0.087	0.05	0.14
SUM	2058	70161.66	764.93	260.51	100.05	2.053	191.216	100.00	200.05

APPENDIX B
HYDRAULIC ARCHITECTURE DATA

Tree ID	Species	Site	Branch	Latitude	Longitude	Soil Moisture	k_{max} ($10^{-4} \text{ kgs}^{-1} \text{ mPa}^{-1}$)	LSC ($10^{-4} \text{ kgs}^{-1} \text{ m}^{-1} \text{ MPa}^{-1}$)	P20 (MPa)	P50 (MPa)	P70 (MPa)
1788	CAGL	Dry 1	1	147800	587071	0.0171758	4.93	1.08	0.0703	0.1746	0.2437
1788	CAGL	Dry 1	2	147800	587071	0.0171758	41.30	5.69			
1905	CAGL	Dry 2	1	147897	587148	0.0209374	3.11	0.56	0.0422	0.1234	0.2031
1905	CAGL	Dry 2	2	147897	587148	0.0209374					
324	CAGL	Wet 1	1	147849	586891	0.1157758	1.30	0.23	0.0328	0.0961	0.1547
324	CAGL	Wet 1	2	147849	586891	0.1157758	2.74	0.72	0.0305	0.0891	0.1453
2023	CAGL	Wet 2	1	147886	587037	0.3163229	33.40	3.36	0.0859	0.2125	0.2969
2023	CAGL	Wet 2	2	147886	587037	0.3163229	10.10	1.40	0.0211	0.0656	0.1148
1787	CATO	Dry 1	1	147798	587066	0.0169149			0.2252	0.2583	0.2797
1787	CATO	Dry 1	2	147798	587066	0.0169149	2.32	0.11			
1890	CATO	Dry 2	1	147882	587144	0.0208957	4.49	0.54	0.1233	0.1531	0.1736
1890	CATO	Dry 2	2	147882	587144	0.0208957	2.11	0.51	0.0164	0.0595	0.1105
158	CATO	Wet 1	1	147855	586811	0.4098334	0.60	0.07	0.0925	0.1522	0.1915
158	CATO	Wet 1	2	147855	586811	0.4098334	2.15	0.61	0.1325	0.265	0.3242
777	CATO	Wet 2	1	147910	587050	0.3270412	1.37	0.17	0.1926	0.2153	0.2323
777	CATO	Wet 2	2	147910	587050	0.3270412	5.32	1.14			
1484	PIST	Dry 1	1	147799	587039	0.0164163					
1484	PIST	Dry 1	2	147799	587039	0.0164163	1.81	1.04	2.7969	3.506	3.768
1885	PIST	Dry 2	1	147887	587120	0.0180428	1.16	1.19	2.395	3.059	3.402
1885	PIST	Dry 2	2	147887	587120	0.0180428	2.72	1.83	2.505	3.4375	3.781
267	PIST	Wet 1	1	147832	586848	0.3903639	0.23	2.04			
267	PIST	Wet 1	2	147832	586848	0.3903639	1.30	0.89	3.0042	3.0607	3.0953
784	PIST	Wet 2	1	147895	587047	0.3029841	2.57	1.33	2.9381	2.9892	3.0206
784	PIST	Wet 2	2	147895	587047	0.3029841	5.29	2.55	3.121	3.5735	3.864
1689	PIVI	Dry 1	1	147815	587081	0.0161402	5.48	1.94	3.835	5.062	5.732
1689	PIVI	Dry 1	2	147815	587081	0.0161402	4.01	1.49	3.0285	3.0867	3.1235
1901	PIVI	Dry2	1	147902	587138	0.019703	3.51	2.24	3.9648	4.0185	4.0522
1901	PIVI	Dry2	2	147902	587138	0.019703	3.72	1.62	4.001	4.285	4.4531

Tree ID	Species	Site	Branch	Latitude	Longitude	Soil Moisture	k_{max} ($10^{-4} \text{ kgs}^{-1} \text{ m}^{-1} \text{ MPa}^{-1}$)	LSC ($10^{-4} \text{ kgs}^{-1} \text{ m}^{-1} \text{ MPa}^{-1}$)	P20 (MPa)	P50 (MPa)	P70 (MPa)
1772	QUAL	Dry 1	1	147773	587052	0.0144546	5.04	0.79	0.1	0.137	0.177
1772	QUAL	Dry 1	2	147773	587052	0.0144546	1.72	0.82			
1893	QUAL	Dry 2	1	147890	587137	0.0201111	22.60	2.23			
1893	QUAL	Dry 2	2	147890	587137	0.0201111	5.05	1.23	0.1352	0.2016	
197	QUAL	Wet 1	1	147839	586826	0.3990963	11.20	1.34	0.1339	0.273	0.376
197	QUAL	Wet 1	2	147839	586826	0.3990963			0.3325	0.4555	0.535
660	QUAL	Wet 2	1	147890	587018	0.3494161	53.40	13.40	0.0945	0.2788	0.4
660	QUAL	Wet 2	2	147890	587018	0.3494161	16.90	3.25	0.109	0.2745	0.3801
1755	QUPR	Dry 1	1	147799	587055	0.0161186	30.90	3.17	0.1206	0.1531	0.1781
1755	QUPR	Dry 1	2	147799	587055	0.0161186	7.92	0.91	0.1102	0.229	
1895	QUPR	Dry 2	1	147883	587130	0.0208877	10.90	1.25			
1895	QUPR	Dry 2	2	147883	587130	0.0208877	16.90	3.36			
203	QUPR	Wet 1	1	147859	586819	0.1277443	21.80	2.42	0.1855	0.1932	0.1994
203	QUPR	Wet 1	2	147859	586819	0.1277443	19.50	2.81	0.0975	0.2406	0.379
2008	QUPR	Wet 2	1	147878	587054	0.2643443	31.10	4.15	0.0762	0.245	0.3633
2008	QUPR	Wet 2	2	147878	587054	0.2643443	51.90	8.15	0.0625	0.202	0.294

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