Reconstruction of Wetland Hydrology Dynamics Using Tree Rings

Allan P. Hascall III

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RECONSTRUCTION OF WETLAND HYDROLOGY DYNAMICS USING TREE RINGS

by

Allan P. Hascall III

A Dissertation
Submitted to the
Faculty of The Graduate College
in partial fulfillment of the
requirements for the
Degree of Doctor of Philosophy
Department of Geology

Western Michigan University
Kalamazoo, Michigan
April 1997
RECONSTRUCTION OF WETLAND HYDROLOGY DYNAMICS USING TREE RINGS

Allan P. Hascall III, Ph.D.
Western Michigan University, 1997

Increment core samples were collected and examined to test the hypothesis that the history of punctuated or intermediate-term changes in wetland soil-moisture conditions can be reconstructed from the annual growth-ring record of trees. The hypothesis is based on plant physiological principles that indicate a relationship between water surplus stress and impaired physiological activity that could lead to reduced growth.

Sampling sites were selected for their ostensible historic hydrologic variability and the availability of documentation of hydrologic disturbances. A conceptual model was developed by which trees were sampled along a hydrotopographic gradient for comparison of radial stem growth in uplands versus wetlands. In order to construct a protocol that could be practical for wetland scientists, cores were prepared for analysis using a simplified modification of existing techniques and growth rings were measured with common laboratory equipment. Processed tree ring data were compared to independent documentation of hydrologic influence at the sample sites, where appropriate, including historical aerial photographs, gauged streamflow and precipitation data. A variety of traditional dendrochronological data processing and analytical techniques and creative approaches were applied to the raw data to address the hypothesis.

The hydrologic signal was not strong in the observed wood samples and the hypothesis was therefore rejected. Pre-established analytical techniques were not
particularly useful for isolating the hydrologic variable from the data set. Some improved resolution was made possible through techniques developed in this study, e.g., deviation from the growth mean and ring-width index subchronologies. Weakness in the water surplus stress-growth signal may be attributed in part to the ability of some tree taxa to physiologically compensate for periodic inundation or soil saturation. Attempts to enhance the ring definition of diffuse-porous tree species were unsuccessful; therefore, the incorporation of ubiquitous midwestern region forested wetland species, such as *Acer saccharinum*, were excluded from the dendrohydrologic analyses. Lessons learned from the successes and failures of this study suggest that, with some refinement, the technique that was developed has the potential to recognize hydrologic changes through tree growth observations in selected settings.
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ACKNOWLEDGMENTS

I owe my deepest appreciation to Professor W. Thomas Straw for his contributions to this investigation, participation in the field over the past five years, extension to me of his vast knowledge of science, geology, wetlands, social behavior, and trivia, and unwavering concern for my welfare. Additional thanks are extended to Professors Alan Kehew and Alexander Enyedi for their participation on the dissertation committee and their feedback on the research.

If it were not for the life support and unconditional encouragement of my wife, Nancy, and my parents, Virginia and Perry Hascall, I would still be engaged in this study. My son Erik and daughter Jill volunteered their periodic assistance in computer editing and filing of papers.

Gratitude is also owed to colleagues who contributed to various parts of this study or allowed me the freedom to focus by covering some of my other responsibilities: Richie Laton, Bob Havira, Eliot Atekwana, Brian Haas. There are many unnamed landowners and people working in governmental agencies and academic institutions who provided me with information and made gathering the data set possible.

Two semesters of this study were graciously funded through the Dissertation Fellowship, awarded by The Graduate College at Western Michigan University. The Graduate College also provided additional moneys for research through the Graduate Student Research Fund.

Allan P. Hascall III
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CHAPTER I

INTRODUCTION

Complexities in Understanding Wetland Hydrology

Water is generally regarded by wetland scientists as the most fundamental defining characteristic of wetlands because it regulates their structure and function. The development of the wetland ecosystem over decades and centuries is closely tied to the hydrologic regime. Wetland hydrology is dynamic because it is climate-dependent and responsive to feedback from the other ecosystem components (e.g., the plant community).

The natural variability of the presence and distribution of water in wetlands through time is recognized as the hydroperiod. The hydroperiod in undisturbed temperate wetlands is sporadic on time scales of days and weeks; general trends may become apparent from the perspective of years and decades. The most obvious and regular hydroperiod pattern accompanies seasonal change. Since the variability of the wetland moisture regime is closely tied to climate, the timing and magnitude of the intra-seasonal highs and lows are largely unpredictable. Similarly, the magnitude of the net value of the annual wetland water budget is highly variable from year to year.

The physical hydrology of wetland systems is most commonly characterized by direct observations of the temporal and spatial fluctuations of groundwater and surface water. Groundwater fluctuations may be measured by the hydraulic head in wells and piezometers, whereas surface water fluctuations may be gauged and/or recorded by aerial imagery. These direct measurements are limited in practice by their distribution.
in time and space. The other components of the water budget, precipitation and evapotranspiration, are similarly complicated and are even more difficult to quantify.

In the past several decades, some wetland studies have begun to concentrate on gathering physical hydrologic data. However, few studies gather such data for more than several years (i.e., short-term data). Intermediate-term (several years to decades) hydrologic data cannot develop unless the responsibility for acquiring it at a particular wetland is maintained as a continuous legacy. In practice, therefore, the hydrologic data set based on direct measurement is small with respect to the longevity of wetland systems.

In order to obtain an improved understanding of the temporal and spatial variability in wetland hydrology, it is necessary to search beyond direct measurement. Fortuitously, the variation of moisture in a wetland ecosystem influences the character of the physical and biological components with which it comes into contact. Hydroperiod leaves a particularly strong signature on the chemistry of wetland soils and the composition of wetland plant communities. These components are capable of recording the history of hydrologic conditions at a site well beyond the practical period of direct measurement. For these reasons, regulatory procedures for determining the presence and boundaries of wetland conditions require the augmentation of direct and indirect observations (direct observations involve seeing the water, e.g., head in wells, staff gage; indirect observations involve seeing evidence of the water having been there, e.g., drift lines, water stains) of hydrology with readily recognizable field indicators of hydric soils and hydrophytic communities.

Wetland hydrology is necessarily a multidisciplinary science. The most complete understanding the hydrologic regime of a wetland system will be derived from integrated contributions of physical hydrology, hydrogeochemistry, geophysics, botany, invertebrate biology, climatology, remote sensing, soil science, and other
disciplines. It is an important challenge for wetland scientists to attempt to develop reliable alternative methods for reconstructing the intermediate-term hydrologic history of wetlands through interdisciplinary research. This need has guided the research of this dissertation.

The Research Problem

Dendrohydrology

Dendrohydrology is an applied science that relates the growth characteristics of woody plants to the availability of moisture. Water is one of many essential components of plant growth. When it is limited in supply or superabundant, less than optimal growth occurs (i.e., hydrologic "forcing"). The great challenge of dendrohydrology is to distinguish the hydrologic signal from the other variables that influence tree growth.

The most common use of dendrohydrology has been for the reconstruction of long-term (centuries to millennia) regional climatic fluctuations from tree-ring chronologies. This dissertation is one of relatively few dendrohydrologic studies that have attempted short- to intermediate-term, non-climatic historical hydrologic reconstructions on a site scale.

Potential for Using Trees in Reconstructing Historical Changes in Wetland Hydroperiod

Trees are present in many wetlands. Whether they dominate the plant community or are sparsely distributed, they have the potential to function as recorders of changes in hydroperiod. There are several potential advantages to considering the use of trees for wetland hydrologic analyses:
1. Trees are perennial plants, that is, they may live for many years (commonly decades to centuries).

2. Under natural conditions, tree position on the landscape remains fixed through time.

3. Temperate trees accrete an annual increment of wood as a datable growth-ring.

4. The sum of the growing conditions around a tree each year is preserved in the growth ring, which consequently varies in thickness and anatomy.

5. Water is an essential requirement for tree growth and survival.

6. As with other plants, tree physiology may be stressed by water deficits or surpluses.

Hypothesis and Objectives of Research

This study was based on a hypothesis: The history of punctuated or intermediate-term changes in wetland soil-moisture conditions can be reconstructed from the annual growth-ring record of trees.

The following objectives guided the research: (a) to collect wood samples from a broad taxonomic range of trees under a variety of wetland and marginal wetland settings; (b) to develop a practical laboratory procedure for the preparation and analysis of tree cores in wetland dendrohydrologic applications; (c) to collect and process tree-ring data for dendrohydrologic interpretation; (d) to compare growth-ring series data with historical records that may serve as potential indicators of dynamics in site hydrology (e.g., climate, streamflow, aerial photographs); (e) to develop a method for correlating growth ring sequences with site hydrologic history; and (f) to determine tree taxa that are reliable indicators of specific wetland moisture regimes in southwest Michigan and similar environmental settings.
Significance of the Research Problem

The practical significance of this research was to develop a methodology using growth rings of wetland and marginal wetland trees that will facilitate wetland delineations, contribute to the planning of engineered wetland projects, and to augment cumulative impact assessment methods.

Wetland Delineation

Wetland is defined in Section 30301 (d) of Michigan's Natural Resources Protection Act (State of Michigan, 1994) as "land characterized by the presence of water at a frequency and duration sufficient to support, and that under normal circumstances does support, wetland vegetation or aquatic life..." (Michigan Department of Environmental Quality, 1994). The Michigan Department of Natural Resources (1989) developed the point-determination method to establish the wetland-nonwetland boundary at a site.

Normal circumstances result from processes that are expected to exist in a wetland system. Abnormal circumstances are situations in which there have been recent and or severe disturbances to vegetation, soils or hydrology through which the wetlands have been dramatically changed. Therefore, the wetland determinations must consider the extent to which the abnormal circumstances have altered or changed the site characteristics (Michigan Department of Natural Resources, 1989, p. 4).

A site that presently does not fulfill the defining criteria of ‘wetland’ may be declared a wetland if abnormal circumstances are judged by historical data or ‘interpretations’ to have changed the hydrologic regime.

Meteorological records indicate that climate fluctuates naturally through time. Climatic variation is a normal circumstance because it is a process expected to influence the system, but it is nowhere mentioned in the point-determination method. The
definitions of 'recent' and 'severe' as conditions of abnormal circumstances are not clarified in the point determination method.

It appears that the point-determination method does not account for climatic variation through time because it is difficult to account for. The point-determination method is applied daily to many wetland delineations and must be conducted efficiently and confidently. It must stand up to challenges by landowners or the government in court. It must be conducive to use by Michigan Department of Environmental Quality (MDEQ) staff and private consultants who may have little training in wetland science, but are capable of following a straightforward, 'cookbook' approach. The current method is efficient; however, the MDEQ is backlogged on wetland use permit applications. A methodology that accounts for climatic variation or other historical changes in site hydrology and fulfills these criteria has not yet been developed. In the absence of intermediate-term observations at specific sites, such a method must be developed by indirect indicators of hydrology. Tree-ring analysis may satisfy this need.

**Engineered Wetland Projects**

Wetland creations and restorations are becoming increasingly practiced because of the recent enhanced awareness of wetland functions and values provided by the scientific community. Wetlands are valued for such functions as secondary wastewater treatment, protected areas for threatened and endangered species, habitat for game, flood attenuation or abatement, cultural activities, nutrient cycling, and production and harvest of renewable plant resources. Compensatory wetland mitigation has become a widely used practice of replacing wetlands that are lost to development. Replacement of functions and values, including those related to hydrology, is an important regulatory consideration in the wetland mitigation process.
Successful development of a tree-ring methodology may be used to evaluate the hydrologic history of wooded sites and therefore complement other methods used in site feasibility studies for these proposed engineering projects.

**Cumulative Impact Assessments**

Wetland ecosystems have been transformed or modified at an accelerating rate throughout this century. Less than twenty percent of the forested wetlands in the United States remain (Gosselink and Lee, 1989). Incremental forest loss has had deleterious effects on the wetland ecosystem, causing increased flooding, eutrophication of lakes and streams, and habitat loss. Cumulative impacts are the result of multiple human activities such as timber harvesting, agricultural drainage, stream impoundment for hydroelectric power production, levee construction for flood protection, and residential/commercial development. Individually, the impacts of these activities are often unnoticed because of lag time or scale perspectives, and demonstration of clear cause-and-effect relationships is difficult.

The importance of cumulative impact studies is to identify the relative and absolute significance of human activities on the wetland ecosystem. Recognition of these impacts will permit the formulation of intelligent wetland policy before the damage becomes irreversible or economically impractical to mitigate. The U.S. Army Corps of Engineers (COE) is conducting interdisciplinary scientific studies of cumulative impact assessment of wetlands, primarily in the extensive bottomland hardwood forests of the south-central and southeastern United States. They have recognized the potential for tree rings to provide information about intermediate-term hydrologic changes in forested wetlands, and may integrate a tree-ring methodology into their assessment strategy.
CHAPTER II

FOUNDATIONS OF TREE RING RESEARCH AND DENDROHYDROLOGY

Tree Ring Applications

Tree Rings as Dating Tools

In its broadest sense, tree-ring science has most commonly been referred to as dendrochronology because tree rings are particularly useful for dating events. Tree-ring sequences are time series. Backcounting annual rings from bark to center of live trees can be used to determine tree age. This is possible because the inner bark of temperate trees is the site of the current year’s radial growth. The putative event to be dated is associated with a particular growth ring and the date of occurrence is determined by backcounting rings from that of a positively dated ring. For a tree that died at an unknown date, positively dated rings are located by correlating the ring sequence of the tree with that of another tree that has a dated ring sequence. This cross-dating technique involves matching ring-width patterns.

In addition to being powerful dating tools, growth rings preserve a signature of the sum of the environmental conditions around the tree at the time of formation. Therefore, dendrochronology is comprised of a number of interrelated subdisciplines that exploit a variety of environmental information contained in the growth ring record. Dendroclimatology uses information in dated growth layers to study variability in present and past climates. Similarly, the field includes dendroecology, dendrochemistry, dendrohydrology, etc.
Origin and History of Dendrochronology

The science of dendrochronology began with the work of A. E. Douglass at the turn of the century (McGinnies, 1963). Douglass was an astronomer who sought to establish the relationship of climate to sunspot cycles, but lacked sufficient weather data. While on a trip through northern Arizona, he serendipitously observed that the tree rings on local pine logs had broad variations in ring width. He contrasted this observation with his recollections of wood samples in the northeast United States, which had more evenly distributed ring widths. He reasoned that the differences in growth conditions accounted for the differences in the growth signature in the trees and that the narrow rings reflected moisture deficiency stress. He began to examine ring sequences in stumps throughout the arid southwest United States and recognized patterns that could be correlated between trees and that could also be correlated with the precipitation record. With continued work, he developed the major principles of dendrochronology and was the founder of the Laboratory of Tree Ring Research at the University of Arizona (Tucson) in 1937, which remains the global center of dendrochronological research. Subsequent pioneers in the field of dendrochronology included E. Schulman and C. W. Stockton, and in recent years, much of the development at the Laboratory of Tree-Ring Research has occurred under the direction of H. C. Fritts.

Dendroclimatolgy and Unique Contributions of Tree Rings

The well-developed field of dendroclimatology has been used to reconstruct regional and global climate variations from trees on arid sites on a scale of decades to centuries. Climate variations have been reconstructed for a continuous period of thousands of years in some regions, based on correlation of overlapping tree-ring age
sequences from live and dead trees, for example, ancient timbers and buried forests (Figure 1).

Statistical techniques have been developed/adapted by dendroclimatologists to sort out these long-term climatic trends. The regional composite historical record based on a string of related tree growth sequences is called a tree-ring chronology.

Ring width is the most common characteristic used in dendroclimatologic analyses. In order for a tree to be a useful paleoclimatic indicator, it must occur on a site where climatic conditions have been limiting to growth. Otherwise, a climatic signature will not be present in the ring record. The fortuitous combination of old trees on climate-stressed (i.e., arid to semi-arid) sites has made it possible for a continuous climatic record to be reconstructed for several thousand years. Certain species of conifers are most commonly used in this analysis because individuals typically survive on these stressed sites for centuries or millennia. Many of these trees inhabit the mountains of western North America. The abundant, commonly used species that occupy arid sites include *Pseudotsuga menziesii*, *Pinus ponderosa*, *Pinus flexilis*, *Pinus longaeva*, *Pinus jeffreyi*, *Abies concolor*, and *Pinus edulis*.

A number of natural phenomena have been used as natural proxy records of past hydroclimatic behavior, such as fossil pollen profiles and encoded sediments in stream channels, lakes, wetlands, and ice layers (Loaiciga et al., 1993). However, tree-ring chronologies are often superior to these other records for reconstructions of the frequency, distribution, duration and magnitude of hydrologic phenomena because of their unusual length of record and annual resolution.

Variations in climate across the North American continent over the past 400 years were reconstructed by Fritts et al. (1979). Tree ring chronologies were correlated with temperature and precipitation data. *Pseudotsuga menziesii* and *Pinus ponderosa* have been used to establish a chronology for the western North America.
Figure 1. Crossdating Technique.
Source: Frits, 1976.
Inferences about fluctuations of moist and dry conditions based on this chronology have been mapped for each decade since 1500 A.D. (Fritts, 1971). The reconstructions have the potential for use in the development of climatic models and provide a broadened time perspective for comparing contemporary droughts.

Great Basin bristlecone pines are the oldest known organisms on earth and living specimens have been found to have more than 4900 growth rings (Harlow et al., 1979). They occupy the upper elevations (10,000-11,000 feet above mean sea level) of the White Mountains in the Sierra Nevada range of California (Ferguson, 1968). This environment is relatively arid (12-13 inches/year of precipitation) and the dolomitic soil is well drained. Using these living trees and scattered wood remnants of dead ones, a continuous tree-ring chronology spanning more than 8400 years has been established (Fritts, 1976).

The bristlecone pine chronology has been used to calibrate the C\textsuperscript{14} dating method (Schweingruber, 1988). For the past ~2000 years, the atmospheric production rate of carbon-14 has varied only slightly. However, prior to 2000 years BP, artificially more recent dates are consistently indicated by radiocarbon analysis. Dual dates (radiocarbon and dendrochronological) from 4000-3000 BC bristlecone pine specimens indicate a discrepancy of 800 years. Since dendrochronologically-determined ages are more accurate, the radiocarbon method has been calibrated by the bristlecone pine chronology. This relationship has made more accurate dating possible for wooden archaeological artifacts (e.g., ruins) worldwide (Ferguson, 1968).

Tree ring chronologies have also been used to extend global temperature reconstructions to the 17th century and have increased our understanding of the anthropogenic influence of greenhouse gas release against natural temperature change (D’Arrigo and Jacoby, 1993).
Tree Rings and Water Resource Planning

Water resource planning is a practical application of dendroclimatology. In response to concerns about long-term water supply to metropolitan Phoenix, Smith and Stockton (1981) used tree-ring data as a proxy to extend runoff records in the Salt River Valley region of central Arizona back to 1580 AD. Comparison of the extended tree-ring results with direct observations and gaged stream measurements since the late 1800's revealed several periods of sustained low annual discharge below any thus recorded. Prehistoric mean annual river flow was relatively low for periods of similar length to the gaged record. Therefore, the mean associated with the gaged record was determined to be an unreliable estimator of the dependable supply.

Tree Rings and Streamflow/Lake Level Reconstructions

Where ring-width measurements are available but no hydrologic records exist, streamflow records can be extended in time. Cleaveland and Stahle (1989) used nine regional tree-ring chronologies to reconstruct the 281-year annual runoff of the White River at Clarendon, Arkansas. The chronologies were calibrated using regression analysis with the gaged stream data for 1930-1980. Variance in runoff between the 20th and 19th centuries were attributed to anthropogenic factors and the information will be used to make probabilistic forecasts about future White River runoff. Similarly, Young (1994) extended the annual and spring streamflow record of the Verde and Salt Rivers of central Arizona back to 1589 using tree-ring chronologies, the monthly precipitation record, and records from three gauging stations. Fritts (1971) used similar techniques to extend the water level record for Lake Athabasca, Canada back to 1810 (Fritts, 1971).
Tree Rings and Isotopes

Stable isotopes of hydrogen and carbon in the cellulose of tree rings have been used to augment paleoclimatic inferences. The isotopic signature of non-exchangeable hydrogen in wood is related to the source water at the time of growth. That of carbon is derived from atmospheric carbon dioxide during photosynthesis. Krishnamurthy and Epstein (1985) correlated trends in the D/H ratio of non-exchangeable hydrogen in tree rings of *Juniperus procera* with recorded levels of Lake Victoria, Kenya. A peak and a valley in the D/H ratio also correlated well with meteorological data that indicated an extremely arid period in the 1920s and a record amount of rainfall in 1961, respectively. Trends in the $^{13}C/^{12}C$ ratio of tree-ring cellulose have also correlated well with low atmospheric CO$_2$ levels following the last glacial maximum, as determined from CO$_2$ concentrations preserved in ice cores and increased levels of anthropogenically-released CO$_2$ since 1750 (Krishnamurthy and Epstein, 1990). Comparison of $^{13}C/^{12}C$ from tree rings with independent $^{14}C$ concentration records over the past 400 years also show a parallel relationship (Krishnamurthy, 1996).

Tree Rings and Air, Groundwater, and Soil Chemistry

Since trees are highly toxitolerant, widely distributed, long-lived and easy to sample, they have the potential to be good historical monitors of contamination and its spatial distribution (Forget and Zayed, 1995). Uptake is possible through the roots, leaves or bark so that air, floodwater and soil/groundwater contamination may be recorded. Tree ring chemistry is controlled by physiological factors (e.g., cation capacity of the woody tissue, radial translocation, transformation of sapwood to heartwood, radial growth rates) and any environmental factors that influence tree growth (DeWalle et al., 1995). They appear to be good indicators of metal
contamination in soils and groundwater, for example, nickel (Yanoski and Vroblesky, 1995), manganese and strontium (DeWalle et al., 1995).

The elemental composition of trees rings has been determined in several studies. Vroblesky et al. (1992) found that the xylem of *Liriodendron tulipifera* trees growing on a hazardous waste landfill in Maryland had elevated concentrations of potassium (K) as compared to *Liriodendron tulipifera* trees located offsite. The wood K-concentrations correlated with that of the local shallow groundwater in each case, and the elevated K-concentrations corresponded with elevated concentrations of other elements (arsenic, cadmium, chloride, iron, manganese, zinc and organic solvents). In addition, the distribution of elevated K-concentrations in the ring sequences of trees on the landfill was comparable with the changes in groundwater chemistry through time. Vroblesky et al. (1992) concluded that tree-ring chemistry has the potential to serve as an indicator for the presence and historical movement groundwater contamination.

Iron peaks in wood samples from individual tree rings of *Liriodendron tulipifera* have been used to trace the pathway and migration rate of groundwater contaminated by a landfill (Vroblesky and Yanoski, 1990). Yanoski and Vroblesky (1995) found that minimum groundwater velocity calculations using chloride concentrations in tree rings from spatially separated trees compared well with calculations based well data using hydraulic gradient and permeability of aquifer materials. Yanoski and Vroblesky (1995) suggested that the dendrochemical data for estimating horizontal hydraulic conductivity may better represent broader areas of the aquifer than slug test data. Dendrochemical analyses have the potential to be used in lieu of aquifer performance tests ("pump tests") on contaminated sites because contaminated discharge waters are not involved and the dendrochemical technique is non-invasive.
Tree Ring Reconstructions of Mass Movement and Earthquake Events

In the mountains near Alma-Alta, Kazakhstan, trees (*Picea schrenkiana*) that survived the 1887 earthquake consistently showed a reduced rate of growth for 3-15 years following the event (Yadav and Kulieshius, 1992). Yadav and Kulieshius (1992) attributed the temporary growth rate reduction to a period of adjustment following tilting of the trees. Recognition of similar patterns of aberrant growth in other earthquake-prone zones may be of use in identifying and dating prehistoric earthquake events.

The time-precision tree-ring chronologies is particularly useful in refining dates provided by other methods. Outer rings from buried trees from three disjunct landslide lobes near Seattle, Washington, yielded radiocarbon dates of 1000 to 1300 years before present (ybp) (Jacoby et al., 1992). Comparison of the bark ring of these trees with regional tree-ring chronologies indicated that the trees all died during the same season of the same year. An identical date was determined for a tree in a probable tsunami deposit 14.3 miles to the northwest at Puget Sound. The tree-ring information thus made it possible to date a strong prehistoric earthquake in the Seattle area.

Annual growth rings of relict Sitka spruce *Picea sitchensis* have been used to date a rapid, seismic-induced subsidence event in California (Jacoby et al., 1995). This analysis was possible because the mortality of the marginal marine trees was attributed to a 2-5 foot sudden drop from the supratidal zone to the intertidal zone, where the roots became periodically submerged. The ~300 ybp event was interpreted to be rapid because herbaceous plants adjacent to the trees were preserved in their upright positions in the buried soil.
Tree Rings and Dating of Volcanic Events

Anomalous growth patterns in tree rings have been used to date volcanic eruptions. Yamaguchi (1983, 1985) dated two relatively recent eruptions of Mt. St. Helens from relict old-growth Douglas fir trees. He compared trees inside of the fallout zone with a control group of trees on sites known to be unaffected by tephra deposition. He identified conspicuous, positively dated rings shared by the two groups (marker rings) and compared the ring sequences to identify missing rings and to date abrupt changes in ring-width patterns. The commencement of a narrow ring pattern in trees within the fallout zone were used to confidently correct the date of the T eruption event (T tephra layer) from AD 1802 to AD 1800. The 1802 date was based on earlier tree-ring analysis, but did not account for a 2-year period of extremely fine or missing rings immediately following the event. The time interval length of the narrow ring sequences decreased with distance from the vent. Using the same cross-dating procedure, the We and Wn tephras were dated at AD 1480. They had been previously dated at approximately 1500 using the radiocarbon technique.

Other Applications of Tree Ring Studies

Backcounting rings in stump sprouts can be used to determine the time of lumbering and may correlate with otherwise unexplained increases in streamflow and sedimentation. Similarly, the history of such events as flooding, ice flows, snow avalanches or landslides can be reconstructed from the sprouts that emerge from fallen trees.

A scar is produced at the injury site where the cambium has been severed. Examples of such injuries are fire, impact of ice or rock, partial burial by volcanic lava or ash, or browsing by herbivores (Fritts, 1976). Continued growth of the
surrounding cambium produces subsequent growth rings on either side of the scar that eventually envelope it, and ultimately continuous radial growth resumes. Counting the number of rings back to the scar margin can be used to date the injury. Using the elevation of a scar as a reference, the dates of ice-bearing floods of various magnitudes can then be determined.

Tilting of trees can occur as a consequence of landslides, seismic activity, floods, windthrow and glacial ice pushing. If growth resumes in the leaning position, a gymnosperm tree will attempt to reorient its stem to a vertical position by differentially adding more wood to the downslope side (Phipps, 1970). The result is the commencement of an eccentric ring pattern enveloping a concentric one (Figure 2). For temperate angiosperm hardwood species, the wider component of the rings forms on the upper side of the inclined stem. The tilting event is marked by the eccentric-concentric ring interface and can be dated by backcounting rings in live trees, or through cross-dating procedures for ancient trees.

In 1992, a healthy *Quercus alba* growing in close proximity to the burial vault of Abraham Lincoln was removed because it was perceived as a physical threat to the structural integrity of the tomb (Sternberg, 1995). The stump was recovered and careful radial sectioning through its pith into 8 pie-shaped sections permitted detailed dissection of the wood. The epicotyl from the acorn was recovered from the stump core, indicating that the tree germinated in 1844. The continuous growth ring record permitted the dating of historical events related to the tomb since its establishment in 1865. Embedded scars in the wood record at ground level were linked to site clearing during the 1864-1865 dormant season when site clearing for construction of the tomb occurred. As evident from growth ring thicknesses, growth of the tree prior to 1865 was relatively slow, presumably due to competition with the dense savanna groundcover. Following 1865, growth was relatively rapid due to subsequent
Figure 2. Eccentric/Concentric Ring Patterns in Tilted Trees. Source: Fritts, 1976.

thinning of adjacent groundcover and saplings. X-ray analysis of a blue-stained area on one of the pie-shaped sections revealed embedded nails that penetrated and distorted annual rings from 1931 through the end of the 1936 growing season. Nail emplacement was dated at 1937 because wood growth during that season was circular around the nails, fibers were undamaged and the rust stain stopped at the 1936-1937 growth ring interface. This date was coincident with a major public event, the
dedication of the Servius Tullius Stone, and the nails were inferred to be vestiges of
crowd control barriers around the tomb.

Non-Climatic Dendrohydrologic Studies Incorporating Tree Ring Analyses

Most dendrohydrology studies to date have concentrated on regional
reconstructions of runoff from climatic inferences. Few studies have used tree-ring
analysis to examine site hydrology. Relatively few tree-ring studies have concentrated
on the effects of surface water and groundwater hydrology on tree growth. Therefore,
only a small foundation of similar studies exists in the scientific research literature that
can be used to compare to that of this study.

*Picea mariana* Forest Drainage Study

A *Picea mariana* forest drainage experiment in northern Ontario was begun in
1929 by the Abitibi Paper Company and the Ontario Department of Lands and Forests
(Payandeh, 1973). The primary objectives of the study were to determine the effects
of soil drainage on stand growth and yield, and to assess the economic feasibility of
peatland drainage for timber and pulpwood production. More than 8,500 linear feet of
ditches approximately 3 feet deep were hand-excavated in a network across the 66-acre
site. On average, the soil column was composed of about 1 to 2 feet of peat over a
thick clay layer. Sample plots were selected and the trees were inventoried for
diameter at breast height (DBH) and height. Although 10-year intervals were planned
for re-measurement, the first re-measurement did not occur until 1956 and one more
occurred in 1969. The 1969 re-measurement included many other site and stand
variables that were incorporated into statistical analyses of growth and discussed in
Payandeh (1973). Among the data were growth ring measurements from increment
cores and transverse sections of stumps.
The detailed statistical analyses of the data were inconclusive, but several important observations were made from the growth ring data in relation to the hydrodynamics of the site. First, there was a pronounced increase (up to threefold) in tree DBH growth following drainage. Second, the growth response of trees was greatest at some distance away from the ditches rather than closest to the ditches. The lesser growth response of trees proximal to the ditches was attributed to a combination of the effects of overdrainage, compaction of the soil banks and disturbance of the root systems.

Large-Scale Impoundment Study in the Upper Mississippi River Watershed

Green (1947) conducted a study in the upper Mississippi River watershed following the establishment of 13 dams by the COE for navigation improvement. Although a pre-impoundment massive forest clearing effort was initiated to facilitate navigation, it was incomplete and large tracts of live timber were flooded. Using increment cores, the changes in tree growth of surviving trees were compared within and adjacent to the impoundment.

Although no trees survived 4 years of flooding, little mortality occurred during the first year. By the second growing season, *Betula nigra* and *Acer saccharinum* suffered a virtually complete die-off. By the middle of the third growing season under continuous inundation, most stands of *Fraxinus pennsylvanica* and *Ulmus americana* were dead. Increment cores of trees within the impoundment revealed that after flooding, tree growth was generally equal to that before flooding until an abrupt, widespread mortality occurred. The period of time between inundation and mortality varied from species to species. Trees present along the margin of the impoundment within a 2 foot contour above the free water surface generally showed immediate increased growth increments following flooding. This increased vigor was sustained
for at least 2 years, and then dropped off to or below pre-flooding levels at some time thereafter, depending on species. The short-term growth stimulation was attributed to improvement in the availability of soil moisture to the trees. For any particular species, the survival period of inundated trees was remarkably uniform, regardless of water depth (from a few inches to 4 feet). The authors concluded that flood tolerance is more closely related to the response of the root system than the stem.

Flooding Frequency and Radial Growth in the Momence Forested Wetlands of Northeastern Illinois

Mitsch and Rust (1984) calibrated groundwater elevations and floodwater stages throughout the Momence bottomland hardwood forest in northeastern Illinois for part of 1 year to concurrent discharge data at a local U.S. Geological Survey (USGS) stream gaging station on the main channel of the Kankakee River. With this relationship they reconstructed the duration and extent of flood events into a wetland for the previous 63 years using USGS streamflow records. Tree ring widths from 3 species present on the floodplain (Ulmus americana, Quercus bicolor, and Fraxinus pennsylvanica) were measured from cross-sectional stump slabs of 18 recently harvested trees.

Inasmuch as no significant relationships between growth and flooding were recognized from the regression analyses, Mitsch and Rust (1984) concluded that tree growth on floodplains appears to be a complicated interplay of factors. However, two observations did stand out in the data. First, there was a 7-year period when tree growth was low or decreasing that corresponded with the highest frequency flooding during the period of record. Second, there was a 4-year period of relatively rapid growth that followed the year with the longest flood duration. Mitsch and Rust (1984) suggested that the first observation supported the idea that low growth may be related
to water surplus stress. The second observation of enhanced growth was speculated to have been a consequence of anaerobic mobilization of certain nutrients, especially phosphorous, in the soil following exceptional flooding events.

Principles of Tree Ring Research

Principle of Limiting Factors

The principle of limiting factors is the single most important research consideration in dendrochronological studies (Fritts, 1976). It states that the rate of a biological process, such as growth, cannot exceed that allowed by the most limiting factor. Limiting factors are environmental conditions that control physiology under the constraint of genetic predisposition. As a tree ages and/or the environmental conditions vary, limiting factors undergo replacement. Limiting factors may be individual or multiple. They may be directly or indirectly related to the biological response. The research objectives of a particular dendrochronological problem must address the appropriate limiting factor(s) and the expected signal(s) in the processed data.

Ecological Amplitude

Tree rings are biological response indicators because the sum of environmental conditions during the growth period is imprinted in the wood (Loaiciga et al., 1993). A species has the potential to grow and reproduce across a certain range of habitats under the constraint of hereditary factors (Fritts, 1976). This ecological amplitude varies considerably among species. Near the margin of its natural geographical range, a species tends to occupy a relatively small variety of sites because one or more environmental conditions (usually climate) becomes growth-limiting. A species with a
broad ecological amplitude (facultative species) has the advantage in tree-ring studies of having a large sample of individuals over a region. However, facultative species tend to adapt to a variety of conditions and therefore may contain a weak signal of stress in the growth record. These species are best sampled near the margin of their range. Species with a relatively narrow ecological amplitude are more desirable for tree-ring studies because they are more likely to preserve a stressed signal in the growth record.

The presence of growth-limiting factors per se does not necessarily produce growth patterns that are conducive to tree-ring analysis (Fritts, 1976). Such factors as photoperiod, shading, and soil nutrient availability, which may not vary significantly from year-to-year, may limit plant distribution and growth but will have little influence on the variability of ring width.

**Sensitivity**

Sensitivity refers to the magnitude of the growth ring response due to changes in the influence of a limiting factor (Ferguson, 1968). It is a function of the genetic predisposition of the species to respond to environmental conditions. Mean sensitivity (ms) can be calculated for a series of ring widths (i.e., a core or a ring-width chronology) as:

\[ m_{s_{i}} = \frac{1}{n-1} \sum_{i=1}^{n-1} \left| \frac{2(x_{i+1} - x_{i})}{x_{i+1} + x_{i}} \right| \]

where \( x \) = ring width or ring-width index for year \( i \), and \( n = \) total number of rings (Fritts, 1976). The component of the equation within the absolute value sign brackets is the sensitivity of one ring in relation to the next. It is the relative (mean percentage) change from each measured yearly ring-width value to the next. Values of mean sensitivity range from 0 (no difference) to 2 (zero
next to a nonzero value in the time sequence) (Fritts, 1976). Sensitivity reflects the year-to-year amplitude variability within a series (Schweingruber, 1988).

Sensitive rings and sets of rings are those that display narrow ring widths that represent intervals of stressed growth (Ferguson, 1968) (Figure 3). Conversely, a complacent record is one that exhibits little or no variation in ring width from year to year. Complacent records result from trees growing under favorable conditions; the limiting factor(s) is not significantly more limiting than other growth variables and other growth variables are capable of compensating for the limiting factor. As sensitivity increases, the probability that rings will be missing also increases. Complacent records do not correlate well with each other and do not show a close relationship with macroclimatic variation.

Sensitive ring series are required for dendroclimatological analyses. However, because of the missing rings associated with sensitive series, chronology building depends on complacent series or complacent intervals that overlap sensitive series among specimens. In addition, chronologies are more conveniently established from slabs or stem fragments than cores because missing rings in an increment core may

Figure 3. Sensitive Growth Ring Series, TLC 7 (Fraxinus americana).
only be discontinuous rings on a slab (Ferguson, 1968). Large wood specimens tend to have more surface area, providing more record and allowing more detailed study. Ideally, an entire cross-section of the stem is available to recognize discontinuous growth rings.

Mean sensitivity reflects short-term changes (high-frequency-variations) in the limiting factor because it measures the ring width changes among adjacent rings (Fritts, 1971). It is a relative measure of first differences and provides more of an indication of variation in narrow rings than wide rings. Fritts (1971) recommends that growth-ring sequences exhibiting a high mean sensitivity should be given preferential inclusion into the analyses because they indicate a high ring-width variability, a high signal-to-noise ratio, and are indicators of climatic responsiveness. These trees will yield the best correlation of ring widths with variations in the limiting factor(s). However, high mean sensitivity is not necessary for development of accurately dated ring-width chronologies. A low mean sensitivity value does not necessarily imply that a strong climate signal is absent. Cores with a low mean sensitivities may still be used for the development of accurately dated ring-width chronologies.

In order for a site to be suitable for a dendrochronological analysis, it must contain sample trees that are both dateable and sensitive (Fritts, 1965). "Dateability" relies on a sample of trees that have relatively complete sequences of less variable width (complacent series), allowing for cross-correlation and, therefore, time-control. "Sensitivity" analysis is possible only when the growth rings in a sequence are highly variable in width or missing. Dateable and sensitive trees can be found along a vegetation gradient. Fritts (1965) demonstrated that in the southwest United States, dateability begins with trees occupying the mesic forest interior, where macroclimatic effects are somewhat buffered by the forest community. Trees with sensitive ring sequences are more likely to occupy the semiarid forest border, where the effective
precipitation (that which influences plant processes) is lower due to higher evaporation. The complacent intervals of the sensitive series, created during non-stressful times, can be cross-correlated with the more continuous, dated series of the forest interior. Then the dates of the sensitive intervals can be bracketed. Tree-ring sequences at the extremes of complacency and sensitivity are undateable because ring-width variability is either insignificant or the ring series are excessively fragmented, respectively.

**Standardization and Chronology Development**

Ring-width measurements are nonstationary time series because mean ring width varies with tree age (Fritts, 1991). Standardization (or indexing) is a traditional dendrochronological procedure that estimates and removes the variation in ring width associated with increasing tree age and microsite differences. First, ring width vs. time is plotted for each tree core. A smoothing function, generally a regression line, is then fit to the growth curve. A standardized value, or ring-width index (or tree-ring index), is calculated for each year (growth ring) by dividing the observed ring width by the corresponding calculated (regression line value) width. The ring-width indices for each core are then plotted against time, as in the original plot. The annual ring-width indices for all sequences at a site are commonly averaged to produce a mean ring-width index for each growth ring-year. The mean ring-width indices are then plotted against time as a standardized ring-width chronology for the site.

Ring-width indices have an expectation value of 1.0 and a variance that is independent of tree age, position in the trunk and mean growth of the tree. The standard deviations of the ring-width indices are less than those for unprocessed ring widths, and sensitivity remains unchanged in the conversion (Fritts, 1976). Conversion to ring-width indices removes trends in growth associated with increasing
tree age and homogenizes the variance in width through time by removing low frequency variations (Ashby and Fritts, 1972; Duvick and Blasing, 1981). The procedure can be simplified by avoiding the young and fast-growing portion of trees and using only the oldest portions of the stems where the ring widths change the least with tree age and are most likely to have been most influenced by variations in climate (Fritts, 1971). Standardization maximizes the response of the limiting factor (typically climate) and minimizes other variations in the growth response (Hughes et al., 1982). Averaging the indices of series from samples across the site has the desired effect of decreasing the random error (E) associated with each series, resulting in a final chronology with a relatively high ratio of climatic signal to non-climatic noise.

Graybill (1982) summarizes the growth response in the equation:

\[ R(t) = C + B + D + E, \]

where:

- \( R(t) \) = measured ring width in year t
- \( C \) = macroclimatic signal common to trees at a site
- \( B \) = biological growth curve as a function of increasing tree age
- \( D \) = tree disturbance signal (noise)
  - \( D_1 \) = unique to a single specimen or tree and due to random events that affected its growth
  - \( D_2 \) = common to most or all specimens due to fire, insect damage, or other disturbance that affected an entire site
- \( E \) = the random growth signal unique to each specimen

In the case of a dendroclimatological study, the objective is to maximize \( C \) by recognizing and removing or controlling the other variables. The primary purpose of standardization is to remove \( B \) and \( D \).

The ontogenetic increase in ring width typically occurs for the first 10-30 years of the life of a tree (Fritts, 1976). The dendrochronologist has the option of
disregarding the youthful interval of growth or fitting a smoothing function that provides for the exclusion of this effect. Graybill (1982) recommends following a priority of curve-fitting options to obtain the best fit to the raw ring-width data (ranked from highest to lowest): (1) negative exponential (represents normal growth changes through the lifetime of a tree), (2) horizontal line through the mean (used when investigator has confidence that no discernible growth trend is present), (3) straight line of any slope, or (4) polynomial (sometimes appropriate when a variety of non-climatic factors influence growth that cannot be characterized by exponential or linear models). Curve fitting options (3) and (4) follow the equation \( Y(t) = a_0 + a_1x + a_2x^2 + \ldots + a_mx^n \), where \( x \) = ring width in year \( t \), \( a_1, \ldots, a_m \) = regression coefficients, and \( a_0 \) = constant.

**Cross-Dating**

Under ideal, consistent growing conditions, each growth ring of a living temperate tree is assumed to represent one year. Using this one-to-one correspondence, each growth ring can be dated by backcounting rings from bark to center of a stem cross-section and subtracting the number of years from present. Local climatic anomalies or other temporary stresses (e.g., insect infestation or fire) may cause aberrations in the growth of selected trees in a region, thus producing ring anomalies such as false rings or missing/discontinuous rings.

Cross-dating involves the recognition of synchronous patterns of ring-width variability between wood samples and permits the correct assignment of dates to specific rings. Cross-dating is possible when samples are compared from trees that overlap in age and their growth was sufficiently limited by the same factor(s). In the absence of a common limiting factor, there would be no pattern recognition between cores because the variability in ring width would be in response to independent
influences (Stokes and Smiley, 1968). Cross-dating of samples is possible only when the source trees are contemporaneously exposed to the same stress over a (semi-) continuous space (e.g. regional drought, floodplain inundation, insect epidemic). Cross-dating allows for the historical extension of a chronology through the overlap of generations of trees in a region (Figure 1). Wood specimens of unknown origin can be dated using chronologies. Chronologies developed for individual sites can be overlapped using the cross-dating technique to produce composite, regional chronologies.
CHAPTER III

WOOD ANATOMY, DEVELOPMENT AND GROWTH SIGNATURES OF TEMPERATE TREES

The tree species examined in this study were primarily angiosperm hardwoods. Therefore, the following discussion emphasizes angiosperm anatomy and development, but most of the principles are similar for gymnosperms.

Species Differences in Growth Rings

Tree species vary in their inherent utility in growth ring studies. Annual rings are not clearly defined or recognizable in some species. Some species have a propensity to accrete multiple rings or rings of circumferentially variable width. The physiological sensitivity of species to natural variations in environment is broad-ranged.

Wood Cell Origin

Growth in tree diameter is referred to as radial, or secondary growth. Following new shoot development, an increment of radial growth is normally added each year. Radial growth occurs as periclinal cell division in the vascular cambium, or lateral meristem (Figure 4). The cambium is located between the phloem (inner bark) and the xylem (wood). The cambial initials produce secondary xylem (wood) to the inside of the tree and secondary phloem to the outside. The cambium is displaced outward by the new xylem and new cambial initials are added to accommodate the tree's larger circumference. Most of the predominantly thin-walled secondary phloem
Figure 4. Bark-Wood Interface, Diffuse-Porous Wood.
cells are pushed outward and destroyed (Raven et al., 1992). New cork cells are formed by the cork cambium, which lies outside of the secondary phloem zone. All living and dead cells outside of the vascular cambium collectively comprise the bark.

Phloem development occurs rather uniformly throughout the growing season under most conditions (Panshin and deZeeuw, 1980). Xylem development is considerably more sensitive to environmental conditions. Under favorable conditions, the ratio of the formation of xylem cells to phloem cells is 4:1 to 6:1. This ratio decreases as environmental stresses increase.

Ideally, annual increments of xylem are added as vertically overlapping hollow cones beginning at the apical meristems and extending down the stems (Kozlowski, 1971a). If growing conditions are favorable for temperate zone deciduous hardwood trees, a single year of growth will produce an annual ring of secondary xylem when viewed in transverse (cross-) section (Raven et al., 1992). In general, the more favorable the growing conditions, the thicker the growth ring. Any change in growing conditions can cause an aberration in the thickness and continuity of the growth ring. Growth rings are permanent and do not change in thickness after they are formed for the remainder of the life of the tree.

The Growth Ring: Earlywood and Latewood

Early in the growing season, the xylem cells produced are relatively large, thin-walled and light colored, called earlywood, or springwood (Figure 5). As the growing season progresses, the (latewood or summerwood) xylem cells in some tree species become narrower, thicker-walled and darker, and the proportion of fibers increases (Spurr and Barnes, 1980). As a consequence, the wood becomes increasingly dense through the growing season. The earlywood-latewood transition may be abrupt, as in ring-porous tree species (Figure 6), or gradual, as in diffuse-porous tree species.
The difference in size between earlywood and latewood xylem cells in diffuse-porous hardwoods may be negligible. The dormant season is marked by the boundary between the previous year's latewood and following year's earlywood. The sharpness of this boundary varies from species to species. Because they have smaller, more uniformly-distributed vessels in the growth rings, many diffuse porous hardwoods have boundaries that are difficult to discern, even with high magnification microscopes and the use of ring enhancement techniques. Ring porous hardwood trees in temperate wetlands are desirable for dendrohydrological analyses because of the marked seasonal differentiation of cells.

The most conspicuous xylem cells are vessels, which are responsible for water conduction. In ring porous species, the diameters of earlywood vessels may be over a
Figure 6. Ring-Porous Hardwood, Transverse Section.
V = Vessel; 2 = Ring Boundaries; 3 = Ray, F = Fibers; Matrix Around Vessels = Parenchyma; EW = Earlywood; LW = Latewood.
Figure 7. Diffuse-Porous Hardwood, Transverse Section. V = Vessel; 2 = Ring Boundary; 3 = ray; Matrix Around Vessels = Parenchyma and Fibers. Adapted with permission from: Shigo, A. L. 1994. Tree Basics. Shigo and Trees, Associates, Durham, NH. p. 17.
hundred times that of latewood vessels (Kozlowski, 1971a). Latewood cells are more dense than earlywood cells because they have a thicker walls and, therefore, less interior pore space.

The vessels of ring-porous species originate during the previous growing season (Phipps, 1967). Ring-porous latewood appears to be structured similarly to the entire ring of diffuse-porous species. According to Phipps (1967), the differentiation and enlargement of the vessels in the earlywood of ring-porous species can occur in the early spring before the growth-regulating hormones work their way down the tree from the leaves. If this is the case, the earlywood of ring-porous species may correlate with early spring environmental conditions and ring-porous species may be recording the changing environmental conditions through the growing season. The entire ring width therefore represents the average growing conditions for that year. Comparison of earlywood thicknesses for various years (or, similarly for latewood) may be used to determine differences in spring time (or summer time) environmental conditions. Because diffuse-porous trees lack this early spring signature, they are less useful in an intra-ring dendrohydrologic analysis.

Radial Variation in Wood: Sapwood and Heartwood

Sapwood is the outermost portion of the xylem that serves as conducting tissue from the roots to the leaves. Only ~10% of sapwood is alive (Kozlowski, 1971a). Most water conduction occurs in the outermost ring and conductive efficiency decreases radially inward. The relatively large vessels of ring porous hardwoods conduct water about ten times faster than those of diffuse porous hardwoods. Heartwood is the central cylinder of darker, nonconducting, nonliving wood, functioning for support. It is composed of dead parenchyma cells that were formerly
sapwood. Substances such as oils, gums, resins and tannins are deposited in heartwood vessels.

**Cambial Activity**

The duration of cambial activity in the growing season is in part a function of environmental conditions (Panshin and deZeeuw, 1980). Younger portions of the stem generally have extended cambial activity. Favorable soil moisture, nutrient, and light conditions may also extend the cambial activity throughout the entire plant. The onset and duration of cambial activity and differentiation of growth increments is directly related to auxin concentrations, which is in turn controlled by environmental conditions.

The cambium of temperate-zone trees is dormant during the winter. The cambium generally reactivates when springtime mean daily temperatures rise above 40°F for longer than a week (Panshin and deZeeuw, 1980). Concurrently, the production of auxins in the expanding buds stimulates cambial activity near the shoot tips (Raven et al., 1992). Cambial reactivation then spreads along the branches and down the trunk (Phipps, 1970). As a tree grows in height, cambial reactivation at any position on the stem occurs at a later time each year and potentially under a different set of growing conditions. Therefore, in mature trees there may be no growth signature in the lower stem for the early part of the growing season. This wave of growth activity reaches the base of the stem most rapidly in ring porous species and may take up to several weeks in diffuse porous species. The rate of spread of cambial reactivation is also a function of tree age, vigor and exposure. The spread of cambial reactivation generally takes longer in more mature and less vigorous trees. The southwest side of a tree that is exposed to greater sun warmth may become active earlier than the other sides of the tree. If a frost occurs following the onset of cambial activity, the partially
differentiated xylem and phloem cells may be killed, thus disrupting the growth increment.

Variability, Aberrations, and Periodicity in Growth Ring Form

Under ideal growing conditions the crown, bole and root system of trees would be radially symmetrical. Ideal growing conditions for a tree refer primarily to favorable edaphic, climatic and competitive influences homogeneously distributed around the tree and with an absence of disease and disruption by other organisms. In this environment, wood should be accreted annually as circumferentially continuous, radially uniform concentric cylinders around the entire tree that would appear in cross-sections as rings of constant thickness. Trees rarely grow under such ideal conditions; usually one or more of these environmental factors is spatially variable around the tree. In addition, the timing and magnitude of environmental conditions may be unfavorable at times during some portion or portions of the growing season. Therefore, all or part of the tree may at times be subject to less than ideal and possibly stressful conditions. The growth of the tree may be affected and the net effect of the environmental conditions will be recorded in the growth ring record.

The most common variation in growth is reflected in ring thickness (width). Under the most variable or stressful conditions, additional growth signatures may form in the wood. Growth ring aberrations are commonly difficult for dendrochronologists to discriminate from “true” rings. Misinterpretation of them can result in inaccurate dating. These include missing rings and intra-annual response features, such as false (also called double or multiple) rings and discontinuous rings.

“Missing” rings represent years during which the tree was alive but no growth increment was added. The boundary between two successive rings actually represents a year of no growth. During a year of unfavorable growth, when the cambial stimulus
may not spread to the base of the tree, a growth ring may be missing from an increment sample selected at breast height.

Discontinuous rings pinch out circumferentially because of an interruption in the continuity of the wood tissue. If continuous tree core samples were taken around the stem or if a cross-section of the trunk were examined, the ring thickness for the particular year would be variable and missing from some sectors, that is, growth would be unevenly distributed around the stem and might not be present on some side(s). Discontinuous rings characteristically occur in overmature trees.

Trees that are defoliated, suppressed in the understory, or drought-stressed commonly have missing and/or discontinuous rings (Spurr and Barnes, 1980). Hormone deficiency or delayed arrival of hormones to the lower parts of the stem have been proposed as mechanisms to account for the sporadic or complete dormancy of the cambium of the lower part of the stem during a growing season (Panshin and deZeeuw, 1980). Because hormones and food supplies move down the stem during the growing season, a delay in cambial reactivation may cause the formation of only latewood. If insufficient hormones are available to accommodate the entire lower stem, some portions may not grow at all. In the absence of cross-dating, discontinuous or missing rings will lead to an underestimation of tree age.

If two or more bands of latewood occur in a single growing season, the increments are called false rings (or multiple rings or intra-annual growth bands) (Fritts, 1971). According to Panshin and deZeeuw (1980), false rings are recognized by the latter part of a latewood band grading into more porous (earlywood-like) tissue, followed by more latewood. The transition to the following earlywood is less abrupt than a true latewood-earlywood transition. False rings generally lead to an overestimation of tree age.
Intraseasonal pulses in the formation of auxins associated with defoliation have long been cited as causes of false rings (Panshin and deZeeuw, 1980). The defoliation results from late frosts, insect infestation, or strong climatic variation such as drought followed by heavy precipitation or a warm fall period. Multiple ring formation has also been attributed to wind damage, fire and heavy fruiting (Spurr and Barnes, 1980). Multiple rings are less prevalent in older trees than younger trees because older trees generally exhibit less vigorous growth.

A cause-and-effect relationship for the formation of multiple rings has been established experimentally (Young et al., 1993). False rings frequently occur in Taxodium distichum. Close examination of false rings reveals wide variance in cell size, cell wall distribution and distinctiveness of the terminal boundary. Saplings subjected to intermittent flooding developed false rings, whereas saplings under continuous flooding did not. The periodically flooded saplings had a significantly greater number of thicker-walled latewood cells and substantially less annual growth. It was concluded that continuous flooded conditions had a moderating effect on growth as an explanation for infrequent false ring formation. Young et al. (1993) suggested that cross-dating continuously flooded trees with proximal periodically flooded trees may be useful in the characterization of intraseasonal flooding events. The periods during which perturbations in growth occur may be short enough that false rings are restricted to the upper portions of the tree (Panshin and deZeeuw, 1980).
CHAPTER IV

TREE GROWTH ECOPHYSIOLOGY ON SATURATED SOILS

Hydrophytes and Non-hydrophytes

NWI Hydrologic Tree Classification

Tree and other plant species have been classified by scientists in a variety of ways to account for their propensity to occupy sites based on degree of wetness. The most commonly used plant species-wetness classification system is defined in the National List of Plant Species That Occur in Wetlands: 1988 (Reed, 1988) (hereafter referenced as the Wetland Plant List). It was devised by the U.S. Fish and Wildlife Service (FWS) for the National Wetlands Inventory (NWI). The system estimates the probable frequency of occurrence of a species in wetlands versus nonwetlands and assigns the species to 1 of 5 indicator categories (Figure 8). Michigan species are classified among those of the seven states that make up the North Central Region.

All taxa referred to in the text and figures of this document are identified in their latinized scientific name form. The taxa are listed in Appendix A with their common names, wetland indicator status, and reference codes used in the figures.

Definition of Hydrophyte

The concept of hydrophyte is variable across disciplines, regulatory agencies and individual scientists. According to Tiner (1991), a FACU species can be considered hydrophytic if it is a dominant plant in a wetland community. This is possible because FACU plants are within the 1%-33% frequency range. A dominant
Obligate Wetland (OBL): Occur almost always (estimated probability >99%) under natural conditions in wetlands.

Facultative Wetland (FACW): Usually occur in wetlands (estimated probability 67%-99%), but occasionally found in nonwetlands.

Facultative (FAC): Equally likely to occur in wetlands or nonwetlands (estimated probability 34%-66%).

Facultative Upland (FACU): Usually occur in nonwetlands (estimated probability 67%-99%), but occasionally found in wetlands (estimated probability 1%-33%).

Obligate Upland (UPL): Occur in wetlands in another region, but occur almost always (estimated probability >99%) under natural conditions in nonwetlands in the region specified.

* A positive sign following the indicator category abbreviation indicates a tendency towards the wetter end of the category. A negative sign following the indicator category abbreviation indicates a tendency towards the drier end of the category.

Figure 8. National Wetlands Inventory Indicator Categories for Plant Species That Occupy Wetlands (Reed, 1988).

A plant species is one that exerts a controlling influence on or defines the character of a community (Environmental Laboratory, 1987). Dominance is generally determined from stand basal area for trees and percent areal cover for herbs. The COE 1987 Wetlands Delineation Manual (Environmental Laboratory, 1987; hereafter referred to as the 1987 Manual) is the official guide used nationwide to determine the boundaries of regulated wetlands. Using the conventions set forth in the 1987 manual, a plant assemblage is considered to be wetland in character as long as more than 50% of the dominant species are listed as FAC or wetter on the Wetland Plant List.

The dominance of a FACU species in a wetland is an example of the individualistic adaptive plasticity of plants (Tiner, 1991). Therefore, the tabulated indicator statuses of plant species are merely a human attempt to establish classification boundaries on evolving organisms to facilitate the characterization of wetlands.

Tiner's definition of hydrophyte is individualistic and accounts for the broad ecological
amplitude of many plants: A hydrophyte is "an individual plant adapted for life in water and/or saturated soils (hydric soils) and growing in wetlands and deepwater habitats; may represent the entire population of a species or only a subset of individuals so adapted" (Tiner, 1991).

Despite its limitations, the NWI wetland plant classification system is a practical reference in discussions about plant-wetland relationships and is used in the remainder of this dissertation. Plant species that are classified as FACW or OBL will be considered typical occupants in wetlands and are considered to be hydrophytic, wetland or flood-tolerant types. Other species are considered facultative or upland or flood-intolerant types.

Chemistry of Saturated Soils

Oxygen Diffusion

Soil saturation (waterlogging) occurs in topographic lows as a result of a water table rise or flooding by lateral movement of surface waters or slow drainage. The oxygen diffusion rate (ODR) determines the rate that oxygen is restored to a formerly saturated soil from the atmosphere. The ODR is related to the partial pressure gradient for oxygen in the soil-atmosphere continuum, which is controlled by respiring roots and other soil flora and fauna that decrease the concentration of pore oxygen (Brady, 1974). ODR decreases rapidly with soil depth and water-filled pore space.

Gas movement in soils occurs primarily by diffusion in accordance with Fick’s first law (Armstrong, 1982). The gas moves along a gradient from higher to lower concentration. The rate of movement is controlled by diffusivity (diffusion coefficient), which is a function of the molecular size of the gas and characteristics of the medium, particularly porosity and composition. The diffusivity of oxygen is
approximately 10,000 times greater in air than in water (Ponnampemra, 1972). The ODR becomes increasingly limiting as water films enlarge around soil particles and soil pores fill with water. Therefore, when a soil becomes submerged or saturated, gas exchange between soil and air is immediately limited. The "effective diffusive resistance" is essentially infinite during the conditions of anaerobiosis (Armstrong, 1982). Mass transfer of oxygen from the atmosphere to the soil can be associated with diurnal changes in soil temperature and/or atmospheric pressure, circulation of surface waters and water table fluctuations (Stepniewski and Glinski, 1988).

**Oxygen Consumption**

Aerobic microorganisms consume most of the oxygen trapped in the soil pores within an hour and exhaust the oxygen supply within a day (Coutts and Armstrong, 1976; Black, 1968). Facultative and obligate anaerobes proliferate when the oxygen is used up by the aerobic organisms, and soil anaerobiosis begins. Respiration of organisms closer to the soil surface tends to intercept the slowly downward diffusing oxygen in saturated soils and thus deprives organisms at depth of oxygen (Armstrong, 1982). The rate of consumption of added oxygen always far exceeds that of oxygen replenishment to saturated soils.

Anaerobic organisms obtain their energy through anaerobic respiration and mediate the chemical reactions in waterlogged soils. The anaerobes benefit from the energy release in the reactions. During anaerobic respiration, the redox transformation sequence is followed, wherein NO$_3^-$, Mn$^{4+}$, Fe$^{3+}$, SO$_4^{2-}$, CO$_2$ and H$^+$ are reduced to N$_2$, Mn$^{2+}$, Fe$^{2+}$, H$_2$S, CH$_4$ and H$_2$(g), respectively (Good and Patrick, 1987). Redox potential (Eh) generally decreases w/depth and time under saturated conditions (Lugo, et al., 1990). The rate of organic matter decomposition is reduced because it is
governed primarily by the respiration of aerobic organisms and can result in the accumulation of peat or muck soils over time (Kozlowski et al., 1991).

The diffusivity of oxygen in a well-drained soil is normally sufficient to support the respiratory activity of soil fauna and flora, as well as the roots of plants growing on the surface. After anaerobiosis begins, however, the plants must respond physiologically to the absence of oxygen and the liberation of potentially toxic substances in the root environment.

**Tree Water Balance**

**Importance of Water**

Tree growth and productivity are a function of water availability. Water moves through the plant carrying substances such as carbohydrates (starches, sugars), amino acids and proteins, hormones, oxygen, and nutrients. Transpiration of water through leaf stomata and subsequent evaporation plays an important role in temperature regulation.

**Water Potential and Movement Through the Tree**

Movement of water through the tree is controlled by the water potential gradient (Taiz and Zeiger, 1991). Water is continuous from root to leaf and moves downgradient in the plant-soil-water potential system. Water potential values in the tree are primarily controlled by hydrostatic pressure and solute concentrations (osmotic potential). Dissolved solutes reduce the water potential of a solution. Hydrostatic pressure is positive in living cells (e.g., turgor pressure in leaves) and negative in dead cells (e.g., xylem). The plant water potential ($\Psi_{plant}$) is the quantitative difference between the hydrostatic pressure and osmotic pressure. $\Psi_{plant}$ varies throughout the
tree and is primarily dependent on the hydrostatic pressure. Water potential is zero for pure water and negative in the plant, soil and atmosphere. Soil water potential ($\Psi_{\text{soil}}$) is greater (less negative) than $\Psi_{\text{plant}}$, which is greater than the atmospheric water potential ($\Psi_{\text{atm}}$). Therefore, the soil is the ultimate source of water to the tree through the roots.

Young sapwood vessels offer little resistance to flow of water and conduct more than 99% of the water through the tree. The upward tension gradient in the sapwood is driven by the water potential difference between the leaves and the soil.

**Variability in Soil Water Potential and Effect on Plant Water Balance**

During water deficiency stress, wilting may occur when the turgor pressure approaches zero because the hydrostatic pressure gradient between roots and leaves is relatively low. If leaf function is impaired by insufficient water supply, so too is growth. Conversely, when there is a surplus of water in the soil, water availability *per se* is not stressful to the tree. The secondary effects related to anaerobiosis are the source of physiological stress to the tree.

**Tree Growth**

**Idealized Tree Growth Curve**

Under constant environmental conditions, the generalized growth of a tree through time may be illustrated as curvilinear (Figure 9). The ordinate axis (S) represents the increment in tree diameter, although it could equally represent increment in height. During establishment, growth of the seedling is relatively slow. Growth is most rapid during the sapling stage (youth) and is maximized near maturity, where it levels off. Growth eventually declines during senescence (Husch et al., 1972).
The growth rate is best illustrated by plotting the first derivative of the cumulative growth increment \((dS)\) vs. time \((t)\) (Figure 10). Under consistent, favorable conditions, the growth rate increases rapidly until just prior to maturity, reaches a maximum at early maturity, and decreases through senescence until death. For a number of trees of a given species living together under uniform environmental conditions, there will be some variation in the shape of the growth curves. Comparison of the curves of different species will be reflected by greater differences in shape.

Tree longevity and the length of the life stages are variable among species. For long-lived species, the mature interval, which represents a stable growth rate, may be much longer than that represented on the Figure 9 and Figure 10 curves. Under such
circumstances, the cumulative growth curve (Figure 9) would have an extended middle segment of constant slope and the growth rate curve (Figure 10) would be flat-topped. Any variability in the availability and timing of growing conditions can influence the rate of plant growth and the resultant shape of these ontogenetic growth curves.

**Tree Growth-Moisture Relationship**

If all environmental conditions are held constant, except availability of water, a simple model can be constructed for its influence on tree growth in the form of a Gaussian curve (Figure 11). The annual growth increment (ring width) is impaired directly by soil water deficiency (Figure 11, region A) and also by the secondary effects associated with soil waterlogging (Figure 11, region C). Region B of Figure 11
Figure 11. Generalized Tree Growth Under a Range of Soil Moisture Conditions.

represents favorable soil moisture conditions, the center of which corresponds to those that are optimal.

The “bell” shape (height, width and skewness) of the curve is highly variable in nature between tree species and ecotypes. The curve would be skewed to the right for hydrophytic plant species because they are better adapted for life on saturated soil conditions. The curve is further complicated by temporal irregularities in the soil moisture regime, that is the timing, frequency, and duration of various soil moisture conditions.

Plant Responses and Adaptations to Anaerobiosis

Importance of Oxygen

Despite the hostile soil conditions in the wetland environment, a large number of hydrophytic plant species are endemic to or tolerant of waterlogged soils. These species are capable of employing one or more adaptive strategies that allows them to
survive and compete in a wetland setting. Non-hydrophytic plants that are exposed to
waterlogged soil conditions face physiological challenges to anaerobiosis that may be
deleterious or lethal because they lack the environmental resilience necessary to cope
with such conditions.

The survival time for trees species with roots exposed to continuous saturation
ranges from 24 hours to 2 years (Coutts and Philipson, 1978). As a consequence,
very few trees can survive two consecutive growing seasons of inundation
(Armstrong, 1982). Because oxygen is essential for root growth, trees are not
typically capable of producing roots into permanently anaerobic soil. Dormant trees
may survive weeks of flooding in the winter without negative consequences, but the
same trees during the growing season can be damaged by flooding or soil saturation
within a day.

Continued aeration of the root is required for long-term survival of the plant so
that the resistance to water uptake is lessened and restoration of hormonal
communication between the root and shoot can occur (Meko et al., 1985). The
provision of an adequate root ventilating system is essential for the long-term survival
and successful growth of trees (Armstrong, 1982). Survival of a plant in anaerobic
conditions is largely related to the hereditary predispositions of the species combined
with the time, frequency, magnitude and duration of flooding (Kozlowski et al.,

**Anaerobic Respiration**

Aerobic respiration is a redox reaction wherein glucose (six carbon sugar) is
oxidized to \( \text{CO}_2 \) and oxygen is reduced to water (Drew, 1988). The energy released is
stored in ATP (adenosine triphosphate), where the energy is available for cell
metabolism (Taiz and Zeiger, 1991). Respiration is actually a multistep series of three
reactions [glycolysis, the TCA (tricarboxylic acid or Krebs) cycle, and the electron transport chain] that may be generalized by the single equation: $\text{C}_6\text{H}_{12}\text{O}_6 + 6\text{O}_2 + 6\text{H}_2\text{O} > 6\text{CO}_2 + 12\text{H}_2\text{O}$.

The Krebs cycle and the electron transport chain cannot function in the absence of oxygen (Taiz and Zeiger, 1991). If $\text{O}_2$ is not available to the root, root cell respiration will ultimately cease and the energy normally produced by respiration will not be available for root cell metabolism (Mendelssohn and Burdick, 1988). When aerobic respiration stops due to soil saturation, some plants can temporarily use anaerobic respiration as a substitute. Pyruvate can be metabolized (reduced) by anaerobic respiration in the form of lactate fermentation or alcoholic fermentation, with lactate and ethanol as end-products (Raven et al., 1992). Lactate accumulation is more deleterious as an end-product than ethanol because it promotes acidification of cytosol (Taiz and Zeiger, 1991).

The more common end-product in higher plants is ethanol. The fermentation energy yield is only large enough to temporarily sustain cell activity and is insufficient for growth. Most of the energy from the original glucose molecule (~93%) goes to the alcohol rather than ATP (Raven et al., 1992). Ethanol has been shown to accumulate and become toxic to young tomato plants and reduces growth (Black, 1968). Under anaerobic conditions, ethanol can accumulate to the point where toxic concentrations exist, particularly to species not adapted to life in saturated or flooded conditions. The anaerobic respiration end-products of non-wetland plants tend to be much less toxic than ethanol, and therefore they are capable of surviving longer in anaerobic soil conditions (Armstrong, 1982). Species that accumulate relatively high concentrations of metabolic end-products in roots such as malic and shikimic acids (malate and shikimate) as alternatives to ethanol tend to be better adapted for life in anaerobic soils (Coutts and Armstrong, 1976).
Drew (1968) hypothesized that nitrate may function as a terminal electron acceptor in place of oxygen to help meet the respirative demands of flood-tolerant plants during soil anoxia, but there is no conclusive evidence that it plays this role.

If flooding periodicity is relatively long and flood duration is relatively short, a plant may not be exposed to anaerobic soil conditions long enough to put out adventitious roots. Under these circumstances, root mortality may be prevented through enhanced anaerobic respiration capability, but an available source of oxygen is required for active growth (Armstrong, 1982).

**Phytotoxic Substances**

Following the onset of anaerobiosis, compounds toxic to plants may be produced by the roots themselves or released from the soil. Those produced by the plants include ethanol, acetaldehyde, ethylene and hydrogen cyanide. Those compounds mobilized in the waterlogged soils include sulfides, carbon dioxide, iron and manganese (Coutts and Armstrong, 1976). Therefore, flood tolerance requires the tree to manage the production of, resistance to and/or avoidance of internal toxins as well as detoxify the soil environment around the root (Coutts and Philipson, 1978). Trees that can survive in anaerobic soils for more than one growing season commonly die after a second or third growing season because they cannot regenerate the nutrient and water absorbing regions of the roots (Coutts and Philipson, 1978).

The roots of plants that are intolerant to waterlogging are often incapable of discriminating the uptake of undesirable substances or toxic quantities of essential elements (Meko et al., 1985). Hypertrophied lenticels in some species function to ventilate gaseous toxic compounds in addition to root aeration (Newsome, et al., 1982). Although excess plant tissue concentrations of ethanol are deleterious, ethanol is readily eliminated by plants in this way.
According to (Kozlowski et al., 1991) and Armstrong, (1982), the adverse effects of \( O_2 \) deficiency far outweigh the effects of phytotoxic compounds. Depending on temperature, the availability of substrates and the relative rates of production and utilization by microorganisms, the accumulation of potentially toxic substances to injurious concentrations may take days or weeks. Evidence suggests that oxygen deficiency itself is the primary trigger for early plant response. Within hours, total anoxia in the root environment can lead to root tip mortality in both wetland and non-wetland plants. Disturbed root function attributable to oxygen deficiency has been implicated in many of the symptoms of shoot damage in non-wetland plants following waterlogging, including reduced transpiration, early leaf senescence, epinasty, wilting, and a slowing of shoot and leaf extension and dry matter accumulation.

The limited occurrence or exclusion of many mesophytic species from the wetland niche may be more a consequence of the limited internal supplies of oxygen in the roots than the lack of soil oxygen (Armstrong, 1982). Even most non-wetland species have a limited capacity for internal oxygenation, which allows for some buffering against soil anoxia. An abundant internal supply of oxygen permits the continuation of aerobic root respiration and the immobilization of soluble iron and manganese in the vicinity of the root.

From a plant physiological perspective, the most important chemical change that takes place under anaerobiosis in saturated soils is the reduction of iron from \( Fe^{3+} \) to \( Fe^{2+} \) and the accompanying increase in its solubility (Ponnamperuma, 1972). The reduction of iron is a consequence of the anaerobic metabolism of bacteria accompanied by lowering of the pH. Reduced forms of iron are much more soluble than the fully oxidized form and can be more readily taken up by roots and high concentrations of ferrous iron may result in acute phytotoxic effects and reduced uptake of nutrients such as phosphorus. Armstrong (1982) suggested that iron toxicity
is caused by internal precipitation of iron hydroxides. Elevated hydrogen sulfide concentrations associated with highly reduced soils may permit uptake of excessive amounts of ferrous iron, causing 'bronzing' disease in rice and blackened root rot ('die-back' disease) *Spartina* spp. (Armstrong, 1982).

Processes in anoxic soils commonly cause organic soil particles to form complexes with metals that are toxic to vegetation at high concentrations. The toxicity of such metals can be neutralized through chelation processes or root immobilization, and plants are thereby isolated from potentially deleterious effects of these materials (Lugo et al., 1990; Dykeman and Sousa, 1966).

Oxygen depletion in waterlogged soils is accompanied by a commensurate increase in carbon dioxide. However, because the solubility of carbon dioxide in water is significantly higher than that of oxygen, it is relatively rapidly dispersed from the sites of production and rarely attain concentrations lethal to plant roots (Armstrong, 1982).

**Nutrient Relations**

Nutrient relations of the plants change under anaerobic soil conditions (Kozlowski and Pallardy, 1984). Denitrification in the soil results in less available nitrogen for absorption into the plant (Gambrell and Patrick, 1978). Experiments have demonstrated that uptake of nitrogen, phosphorous and potassium is inhibited when the root zone is anoxic. Calcium and magnesium uptake are less inhibited. Sodium uptake appears to increase and may reach toxic levels in sodium-sensitive species. Reduced forms of iron and manganese are more readily taken up by roots and high concentrations of ferrous iron may result in acute phytotoxic effects and reduced uptake of other nutrients, for example, phosphorus.
Flood-induced root injury decreases the uptake of macronutrients by flood-intolerant plants but has little effect on the mineral relations of hydrophytic plants. The injury may be due to decreased root permeability, inadequate energy supplied by anaerobic respiration to sustain normal macronutrient uptake, and suppression of mycorrhizae (Kozlowski et al., 1991).

**Metabolic Responses**

Plants adapt metabolically to anoxia in two ways. The first is control of metabolic rate (Crawford and McMannon, 1968). Flood-tolerant plant species inhibit glycolytic activity upon exposure to anaerobiosis. Flood-intolerant species do not appear to be capable of controlling their glycolytic rate, which remains high during periods of anoxia (Meko et al., 1985). Control of glycolysis appears to be most common in flood-tolerant plants that are otherwise incapable of disposing of ethanol from roots, tubers, rhizomes and germinating seeds. The second adaptive strategy is the diversification of glycolytic end-products. Flood-tolerant species tend to produce more intermediate substances, for example, glycerol, shikimate, and malate, as opposed to pyruvate. Intermediate substances can serve as acceptors of protons released in the oxidation of glucose during glycolysis, and as a consequence, less pyruvate is available to reduce to ethanol (Coutts and Philipson, 1978). Proton disposal in flood-tolerant species is also facilitated by an increase in nitrate reduction coupled with amino acid production (Coutts and Philipson, 1978). Alterations in the end-products of glycolysis in flood-tolerant species are suspected to be controlled by enzymatic changes in response to flooding.
**Hormonal Responses**

Hormones are substances or groups of substances that regulate plant growth and development. Hormone research in relation to soil anaerobiosis is limited and the effects are not well understood. Variations in hormonal distribution and concentration in response to environmental changes are difficult to quantify because they can be active in extremely small concentrations and often produce a response only in certain tissues or cells within a plant at any given time. Hormones can act very rapidly and often their effects are reversible upon withdrawal.

Experimental evidence has demonstrated that ethylene and abscisic acid (ABA) activity varies with soil oxygen content (Jackson, 1988). ABA concentrations can increase many fold within several hours of oxygen deprivation in the root zone (Armstrong, 1982). The triggering mechanism is not clear, but the release of ABA causes early stomatal closure, reduction in transpiration, and likely inhibits shoot growth and causes premature leaf senescence. Ethylene levels increase in response to flooding in virtually all plants (Newsome, et al., 1982). More ethylene is released below the water table than above because most of it is produced in the roots, and it moves slowly up the plant due to suppressed transpiration rates. Ethylene is important because it plays a role in leaf epinasty and abscission, production of adventitious roots and hypertrophy of lenticels.

In the absence of other controls, leaf dehydration can occur rapidly following root submergence because root permeability is reduced (Jackson, 1988). ABA concentrations in leaves increase following root submergence because less photosynthate is transported to the roots. Increased ABA levels are directly associated with rapid (1-2 days following submergence) stomatal closure. The adaptive
significance of ABA-mediated stomatal closure is water conservation in the leaf to delay wilting, particularly when evaporative demands are high.

Shoot contents of auxin, ethylene and abscisic acid initially increase and levels of gibberellins and cytokinins decline (Reid and Bradford, 1984; Whitlow and Harris, 1979). Poor root aeration restricts gibberellin synthesis in roots and its translocation into shoots, thereby suppressing the rates of stem extension (Armstrong, 1982).

Increased levels of the hormones auxin and ethylene in shoots have been observed to be associated with stem hypertrophy, leaf epinasty and the initiation of adventitious roots (Armstrong, 1982). Although ethylene does not commonly attain lethal concentrations, it can depress growth.

Experimental evidence for ethylene-promoted leaf epinasty is strong (Jackson, 1988). An epinastic leaf is one that rolls up (young leaves) or droops (older leaves) because growth occurs faster on the adaxial side of the petiole. The effect resembles wilting but there is no related loss of leaf turgor pressure; it may temporarily increase if accompanied by stomatal closure. When this response occurs in relation to soil waterlogging, the inferred but uncertain function is a decreased evaporative demand due to less shoot surface area for radiant energy to strike, thus delaying leaf dehydration and wilting. It may also reduce the photosynthetic rate, causing less anaerobic water high in undesirable dissolved substances to enter the root.

The role of ethylene in flooding-related plant growth is to promote shoot extension by increased cell length, rate of elongation, and, in some cases, cell number (Jackson, 1988). Plants occupying waterlogged soils have been observed to contain abnormally high concentrations of ethylene. This occurs from some combination of relatively high production rates and entrapment in submerged plant tissues due to restricted diffusive capacity. Successful colonization of diverse aquatic and semi-aquatic plant species in areas subject to water depth variation has been interpreted to be
facilitated by ethylene-controlled growth. The petioles or coleoptile stems of these plants elongates more rapidly in water than above it. This rapid growth minimizes the potential for physiological injury and disruption of the life cycle by shortening the duration of submergence, thus increasing chances for survival.

There is considerable evidence for the role of ethylene in the production of lysigenous aerenchyma tissues in roots, stems and leaf bases. The application of small amounts of ethylene to aerated roots can stimulate aerenchyma formation. The high ethylene concentration triggers an increase in cellulase activity which softens the cell walls in preparation for cell disintegration (Kawase, 1981; Kawase and Whitmoyer, 1980). Ethylene applied to stems induced aerenchyma development in non-wetland species (kidney bean, sunflower and tomato), which was abruptly terminated when AgNO₃, an ethylene antagonist, was applied. Ethylene also plays a role in leaf epinasty, hypertrophy of lenticels and cortical tissues, leaf senescence and leaf abscission (Newsome et al., 1982).

Increased ethylene production has been attributed to inducing morphological changes such as leaf epinasty, leaf senescence and abscission, aerenchyma formation and adventitious root formation (Tang and Kozlowski, 1984). High levels of ethylene may be produced in plants under a variety of other stressed environmental conditions (e.g., temperature extremes, insect attack, air pollution, disease) without inducing stem hypertrophy or adventitious root development. Therefore, other compounds may be required to accompany ethylene in flood-induced morphological adaptations. Other hormonal growth regulators such as auxins, cytokinins, abscisic acid and gibberellins increase ethylene production and probably influence the development of flood-induced morphologies (Tang and Kozlowski, 1984). The importance of these compounds and the identity of others in relation to flood-induced morphological responses has not been clearly established.
Modification of Root Aeration

The most common hydrophytic plant defense against assimilation of dissolved iron is oxidation in the area around the actively respiring roots. This is possible through diffusive radial oxygen loss from the roots, enzymatic oxidation within the root, and the oxidation reactions associated with soil microorganisms near the root (Armstrong, 1982; Coutts and Armstrong, 1976). The result is immobilization of soluble iron from sulfides around the roots in the form of red-brown iron oxyhydroxide plaques called an oxidized rhizosphere (Mendelssohn et al., 1995). The oxidized rhizosphere is also important in supplying mycorrhizal symbionts with oxygen (Meko et al., 1985). The extent of the oxidized rhizosphere is controlled by the root’s internal porosity and its respiratory demand for oxygen. Large internal air spaces develop in the cortex of the stems and roots and serve as pathways for gas exchange between the atmosphere and the roots (Black, 1968). Presence of oxidized iron in the soil around the roots is field evidence for oxygen being transported down through the plant and out the roots. Non-hydrophytic plants may also develop this adaptation. Because atmospheric oxygen diffusion directly into waterlogged soil is virtually absent, some plants can provide for an alternative pathway through the development of intercellular tissue in the root and stem via aerenchyma tissue formation. Aerenchyma tissue commonly develops in the cortex of adventitious roots that frequently replace the respiratory function lost by roots killed by flooding and are an effective aeration pathway linking the root interior with the atmosphere (Jackson, 1988; Coutts and Armstrong, 1976).

Although the physiological role of adventitious roots has been questioned, excision of flood-induced, submerged adventitious roots of Platanus occidentalis and Fraxinus pennsylvanica seedlings has been clearly shown to reduce stem growth
Newsome et al. (1982) have shown that both adventitious roots and hypertrophied lenticels begin to form within several days of flooding in *Ulmus americana*. In a study of a *Fraxinus pennsylvanica* dominated bottomland hardwood forest, Huffman and Forsythe (1981) demonstrated that the formation of adventitious roots often coincides with stomatal reopening and an increase in water uptake as an attempt to restore normal functions.

Aerenchyma tissue is a form of air space enlargement within the root that occurs by cell separation, cell disintegration and cell collapse (lysigenous breakdown) (Jackson, 1988). Oxygen is supplied to these tissues from leaf stomata in herbaceous plants and stem lenticels in woody plants (Armstrong, 1982). Stem lenticels within only one to two inches of the soil surface appear to function as the primary atmospheric oxygen intake areas of stems so adapted (Coutts and Philipson, 1978). Aerenchyma formation appears to be related to radial oxygen loss at the roots and oxidation of the rhizosphere (Armstrong, 1982). Armstrong (1968) experimentally demonstrated that if floodwater rises above these lenticels, radial oxygen loss at the roots declines sharply in *Salix* spp. The diffusion mechanism is effective for only short distances (Coutts and Philipson, 1978). Therefore, deep anchoring roots of flood-tolerant trees must employ other mechanisms to survive prolonged anaerobiosis. Aerenchyma tissue formation may be the most significant long-term adaptation of wetland species to soil waterlogging because it directly addresses the most critical problem: root oxygen supply.

Tree species adapted to flooding can rapidly produce adventitious roots from hypertrophied lenticels just below the floodwater surface or from the vascular cambium as occurs in *Nyssa sylvatica* (Hook et al., 1970). Flood-induced, conspicuous lenticels typically develop and/or enlarge within the lower 1-2 inches of the tree stem or on primary roots in the aerated zone (Coutts and Armstrong, 1976). Hypertrophied
lenticels of flood-tolerant *Salix* spp. have been shown to also permit upward diffusion and dissipation of toxic substances from the roots (Crawford, 1976; Tang and Kozlowski, 1984). This aeration mechanism appears to be most effective through adventitious roots because they contain more aerenchymatous tissue than "normal" roots. Adventitious roots also function as a secondary absorbing system and compensate for loss of root function due to decay of some of the original roots (Tang and Kozlowski, 1984).

Aerenchyma formation in xylem is rare and the cambium is a relatively impermeable barrier to gas movement. An exception develops in *Nyssa aquatica*, which has been shown to continue to oxidize the rhizosphere following girdling through the cambium. Oxygen movement may take place through longitudinal transport of gas through normally water-filled vessels in the secondary xylem (Hook and Brown, 1972). Stems of the hydrophytic species *Nyssa aquatica* and *Fraxinus pennsylvanica* have prominent intercellular spaces among the cambial ray initials that allow for gaseous exchange between the xylem and phloem (Hook and Brown, 1972). *Liquidambar styraciflua, Liriodendron tulipifera* and *Platanus occidentalis* have a relatively impermeable cambium; oxygen and carbon dioxide concentrations on the xylem side of the cambium are managed through the transpiration stream. Plants incapable of aerenchyma formation are generally intolerant of wet habitats and many mesophytes are capable of producing limited aerenchymatous tissue. Williams and Barber (1961) suggested that perhaps the most important role of aerenchyma formation is the reduction of root respiratory tissue and, therefore, oxygen demand. Compensation for loss of tissue occurs by the increased support of the honeycomb structure. Although this hypothesis has credence, the presence of an oxidized rhizosphere around aerenchymatous roots confirms the importance of the oxygen transport function.

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Bertness (1985) observed rhizosphere oxidation enhancement by roots growing in the vicinity of fiddler crab burrows, which increased the permeability of the sediment allowing for greater drainage and improved aeration. It has also been suggested that oxidized rhizospheres are more fully developed in plants that grow in association with other plants with oxidized rhizospheres.

**Shallow Root Systems**

Numerous herbaceous and woody species survive in wetlands by producing shallow root systems limited to the vadose zone (Coutts and Armstrong, 1976; Black, 1968). In some cases, adventitious roots can grow horizontally in the phreatic zone along a plane of tolerable redox conditions with ascending lateral roots into the vadose zone. A correlation may exist between the ability of flood-tolerant woody species, for example some *Salix* species, that are capable of producing adventitious roots to also readily propagate vegetatively. Some *Salix* species have also been reported to be capable of producing upwardly growing primary roots in response to a rise in water table.

Depth to water table is often correlated with rooting depth and trees with shallow, spreading root systems are prone to windthrow (Kozlowski et al., 1991). Lieffers and Rothwell (1987) compared observations of the depth of the root masses of *Picea mariana* and *Larix laricina* in north-central Alberta with head data from water table observation wells for one growing season. They found a strong correlation between root depth and water table elevation. Growth rates (measured as percent annual increase in basal area) were higher for trees on sites with greater depth to water table. The deeper the water table, the greater the mass of fine, non-woody roots.

Prolonged flooding commonly kills large parts of the existing root system as a result of increased activity of *Phytophthora* spp. fungi (Kozlowski, 1991). Fine, non-
woody roots are the most vulnerable. Prolonged rises in water table elevations causes higher mortality of the finer roots, and the root:shoot ratio decreases inversely with water table elevation.

Cambial Permeability

Hook and Brown (1972) have demonstrated that free gas exchange occurs through the intercellular spaces of the cambium in *Nyssa sylvatica* and *Fraxinus pennsylvanica*. These species have stems with prominent intercellular spaces among the cambial ray initials. Using *Liquidambar styraciflua* and *Liriodendron tulipifera* for comparison, Hook and Brown (1972) inferred that upland trees lack cambial permeability features for water conservation purposes and stem aeration is not necessary because oxygen is carried upward in xylem from aerated soil by relatively rapid transpiration.

Leaf Stomatal Aperture Regulation

Newsome et al. (1982) observed early stomatal closure in leaves of *Ulmus americana* seedlings that were fully expanded before flooding. Leaves that completed expansion after flooding did not respond in this way. Decreased photosynthetic capacity has been attributed in part to the stomatal closure, resulting in reduced leaf absorption of CO₂ (Kozlowski et al., 1991). In mesophytic species, it is also traceable to reduced leaf chlorophyll content, early senescence and abscission, and reduced leaf area as a result of fewer leaves produced (Pezeshki and Chambers, 1986).

Dionigi et al. (1985) demonstrated experimentally that the difference in flood tolerance of two closely-related willow species (*Salix exigua* and *S. nigra*) is attributed to stomatal size differences. Specimens of *Salix exigua*, the more flood-tolerant of the two species, had significantly higher leaf resistances to water vapor exchange because
it had significantly smaller stomata. Even though they were greater in number, the moisture loss control of smaller stomata collectively reduced the rate of root absorption of water containing phytotoxic compounds.

Several lines of evidence associate stomatal closure to the increased production of abscisic acid (ABA) in leaves (Kozlowski and Pallardy, 1984). ABA content in leaves increases significantly within hours following flooding. When ABA is applied to the leaves of non-flooded plants, the stomata close.

Several studies have shown that under oxygen-limiting conditions, the potassium content in leaves is reduced (Kozlowski and Pallardy, 1984). Stomatal closure appears to be associated with the migration of potassium ions from guard cells, resulting in loss of turgor due to osmotic changes. Increased production of abscisic acid and/or ethylene appears to play a role in this process.

Stomatal closure appears to be independent of leaf water potential (Kozlowski and Pallardy, 1984). In some species, e.g., *Liriodendron tulipifera*, the decreased water potential of leaves following flooding is a result of decreased permeability of the roots. Although stomatal closure occurs, continued leaf evaporation and decreased supply of water from the roots promotes leaf dehydration. In other species, e.g., *Quercus macrocarpa* and *Ulmus americana*, bulk leaf water potential increases significantly in response to flooding, perhaps as a result of stomatal closure. Apparently, reduction of root permeability in response to flooding varies interspecifically. In a controlled experiment exposing *Fraxinus pennsylvanica* seedlings to periods of soil saturation from one to six weeks, Kozlowski and Pallardy (1979) demonstrated that stomatal closure is directly related to flooding duration. The stomata of the *Fraxinus pennsylvanica* seedlings began to reopen following a critical period of flooding (several weeks) and stomatal recovery following restoration of soil aeration was rapid (1-2 days). The recovery of stomatal function was slower for
samples that were flooded for longer times, but it was nearly complete in all cases. There was evidence for some continued stomatal resistance for weeks after aerobic soil conditions were restored, suggesting permanent damage of some stomata even in this flood-tolerant species. *Ulmus americana* seedlings were exposed to the same treatments and exhibited more deleterious responses. It was concluded that *Fraxinus pennsylvanica* seedlings were better adapted to resume a balanced metabolic condition following release from soil saturation and are therefore considered more flood-tolerant than *Ulmus americana*. The ability for rapid recovery of stomatal function following drainage may be an important flood-tolerance characteristic (Pezeshki and Chambers, 1986).

Kozlowski and Pallardy (1979) measured changes in stomatal diffusion resistance of *Fraxinus pennsylvanica* leaves with a diffusion porometer under controlled flooding conditions. Widespread increase in resistance following flooding was attributed to stomatal closure. Full recovery of stomatal function occurred within 6-10 days after release from flooding.

Flooding-induced growth suppression is correlated with reduced photosynthetic and transpiration rates of many flood-tolerant and flood-intolerant tree species, and these functions are commonly related to the stomatal response (Kozlowski and Pallardy, 1979). Initially, these rate reductions are a consequence of stomatal closure. Long-term reduction of photosynthetic activity may be attributed to changes in carboxylation enzymes, reduced leaf chlorophyll content, premature leaf senescence and abscission, and reduced leaf area. Inhibition of carbohydrate translocation may be related to an accumulation of toxic products from anaerobic respiration, but the relationship is not well understood at this time.

To the contrary, preliminary research by Pezeshki and Chambers (1986) has shown that photosynthetic rates of flood-tolerant species, for example, *Fraxinus*
*pennsylvanica* and *Taxodium distichum*, do not necessarily decline significantly following flood-induced stomatal closure. Therefore, the cause-and-effect relationship of stomatal function and photosynthetic capacity may complicated by other physiological factors yet to be clearly identified. In addition, stomatal response to flooding appears to be independent of leaf water potential.

**Leaf Abscission**

The leaves of many flooded plants show evidence of chlorosis, followed by early senescence and abscission (Kramer, 1951; Kozlowski, 1984). There is considerable variation between species in the timing of premature leaf shedding. For example *Liriodendron tulipifera* loses all of its leaves within two weeks of flooding and *Ulmus americana* retains its leaves for up to eight weeks. Ethylene appears to be an important factor in this process (Hook and Scholtens, 1978; Kozlowski, 1984). When non-flooded plants are exposed to ethylene, leaf epinasty, senescence and ultimately abscission are induced.

**Transpiration Rate**

Plant transpiration rates decrease in response to flooding, although this transpirational decrease may sometimes be preceded by a temporary increase (Kramer, 1951; Parker, 1950).

Under laboratory conditions, transpiration of flood-tolerant trees typically increased temporarily before decreasing and returned to normal immediately following drainage. Transpiration of flood-intolerant trees, such as some species of *Ligustrum*, declined immediately upon flooding and recovered slowly after aerobic conditions were reestablished, but not to pre-flooding rates.
Morphological Adaptations

Typically, *Juncus* spp. and members of the family Ericaceae have stem and leaf morphologies in common with xerophytes. For xerophytes, the function of relatively small photosynthetic surface area and coriaceous leaves is water conservation. Hydrophytes with these same properties, however, use the reduced velocity of movement of water through the plant as a mechanism for increased time for oxidation of phytotoxins in the rhizosphere to occur (Armstrong, 1982).

The root systems of some herbaceous and woody species exposed to a fluctuating water table develop a ‘shaving brush’ pattern of distribution (Armstrong, 1982; Coutts and Armstrong, 1976). Mortality of the root apices in the lower soil zone where saturation occurs for longer periods is compensated for by replacement shoots off the surviving root base in the upper, more aerated soil position. The brush-like appearance is a consequence of repeated cycles of dieback and regrowth in coordination with the hydroperiod, resulting in relatively large diameter succulent primary roots with dense, fibrous lateral roots occupying the upper several inches of the soil (McIninch and Biggs, 1993).

Adaptations to Anaerobiosis-Summary

Hydrophytic plant species have adapted in one or more ways to anaerobic soil conditions. Three categories of adaptations are recognized by the COE in the current federal wetland delineation manual (Environmental Laboratory, 1987) and Tiner (1991): morphological adaptations, physiological adaptations, reproductive adaptations. Morphological adaptations are structural modifications the plant uses to increase buoyancy or support, or to facilitate the uptake of nutrients or oxygen gas. These adaptations include buttressed tree trunks, pneumatophores, adventitious roots,
succulent roots, heterophylly, lignification and suberization (thickening) of roots, aerenchymatous tissues in roots and stems, cavities in stems, shallow root systems, cambial permeability, inflated organs (e.g., leaves, stems or roots), polymorphic leaves, floating leaves and/or stems, hypertrophied lenticels, elongation of stem or petioles, and multiple trunks. Physiological adaptations typically involve alterations in the production or consumption of such chemical compounds as enzymes and metabolites, so that toxic conditions are prevented or delayed, or oxygen is used more efficiently. Examples of physiological adaptations are the accumulation of malate, increased levels of nitrate reductase, alteration of metabolic rates, increased ethylene production, rhizosphere oxidation, root growth in low oxygen tensions and the absence of alcohol dehydrogenase activity. Reproductive adaptations allow the species to become established on saturated soils. They include prolonged seed viability, viviparous seeds, seed germination under low oxygen tensions and flood-tolerant seedlings.

The adaptive strategies employed by hydrophytic species function to increase the efficiency of oxygen consumption by the plant and/or increase the supply of oxygen to the plant roots via importation from the atmosphere and/or reduce or delay certain physiological activities until the stress is relieved. Most hydrophytic plants employ two or more of these adaptive strategies in a complimentary way.

**Integrated Plant Responses to Anaerobiosis**

Two or more adaptations may complement each other in a single plant. For example, aerenchyma tissues in the stems and roots of some trees, notably species of *Salix*, function as pathways for the movement of oxygen to shallow roots where rhizosphere oxidation can take place through radial oxygen loss (Armstrong, 1982). McIninch and Biggs (1993) observed the formation of hypertrophied lenticels,
adventitious roots, shallow fibrous roots and the regeneration of succulent roots in potted *Fraxinus pennsylvanica* saplings exposed to fully saturated soils for a single growing season. Other woody plants that produced the same anatomical adaptations, for example, *Cephalanthus occidentalis* and *Acer rubrum*, had a much lower survival rate. McIninch and Biggs (1993) concluded that survival potential is greatest in plants that combine anatomical adaptations that transport oxygen to the roots, with metabolic adaptations that decrease root oxygen demand. Flood-tolerance of *Nyssa sylvatica* is attributed to the combined effects of accelerated anaerobic respiration, rhizosphere oxidation and high CO₂ tolerance in new roots (Hook et al., 1971).

Flooding sensitivity varies widely among even closely-related woody plants. For a given species, mature trees tolerate flooding better than overmature trees, juveniles or seedlings (Kozlowski et al., 1991). Interspecific differences are evident from the universal observation in wetlands that zonation of plant communities occurs parallel to hydrotopographic contours. Gill (1970) discusses the distribution of *Quercus palustris* as an example of intraspecific differences in flood tolerance. At some wetland sites, *Quercus palustris* has been observed to colonize lower positions than *Ulmus americana* and *Diospyros virginiana*, but at other wetland sites, *Quercus palustris* has been the first of the three species to die following flooding. Gill (1970) suggested that such anomalous examples indicate the development of genotypic or phenotypic differences in flood tolerance among distinct populations. This idea is in accordance with Tiner's (1991) individualistic definition of hydrophyte.

Temporary flooding can actually increase cambial growth in some species, for example, *Ulmus americana*, *Fraxinus pennsylvanica*, but if the flooding persists for more than one growing season, growth may sharply decline and the trees may die (Broadfoot and Williston, 1973).
Newsome et al. (1982) conducted greenhouse experiments exposing *Ulmus americana* seedlings to continuous soil saturation. In 1 to 2 weeks, all of the plants developed hypertrophied lenticels (intumescences), with adventitious roots emerging from them within two weeks. Although adventitious roots continued to develop with time, the root-to-leaf area ratio decreased. Rate of stem elongation of flooded plants was one-third to one-fifth that of unflooded plants. Height growth of the flooded plants ceased after two weeks while that of the unflooded plants continued. As compared to the unflooded plants, the flooded plants exhibited reduced leaf production, diminutive leaf growth, and chlorosis and senescence of the basal leaves. Flooded plants were one-half the dry weight of nonflooded plants. Ethylene production of flooded plants increased by 300% during the first week of flooding and 500% after 2 weeks. Despite the morphological adaptations that the seedlings developed under waterlogged conditions, the adverse impacts to existing tissues caused a net decrease in growth. The reduced root-to-leaf area ratio caused leaf water deficits following recession of the floodwaters, predisposing the seedlings to drought injury. For *Ulmus americana*, the morphological adaptations functioned more as temporary survival mechanisms than as proxies for favorable growing conditions.

**Anaerobiosis and Tree Ecology - Tree Distribution, Community Structure, and Growth**

In the spring of 1973, floodwaters overtopped levees in the Mississippi River Valley and inundated over 5 million acres of forest land, the longest lasting flood in that region in 2 centuries. Broadfoot and Williston (1973) observed the effects of flooding on the survival and growth of the trees in levee backwaters. Diameter growth of *Fraxinus pennsylvanica* increased 80% where floodwaters persisted through late summer. Observations over the previous sixteen years revealed improved diameter growth of many other hardwoods, attributed to the favorable residual moisture
conditions well into the growing season following dormant season flooding. It took up to 4 years of continuous inundation for many of the mature *Quercus lyrata*, *Q. nuttallii*, *Liquidambar styraciflua* and *Fraxinus pennsylvanica* trees to die. The high survival rate of these highly tolerant species is in part a consequence of their relatively late commencement of leaf production. Mature *Q. phellos* and *Q. nigra* trees died out within 3 to 4 growing seasons (tolerant species) and *Ulmus* spp. and *Platanus occidentalis* died during the second growing season (moderately tolerant species). Intolerant species were defined as those that died during the first continuously flooded growing season; among others, they included *Fraxinus americana*, *Prunus serotina*, *Liriodendron tulipifera*, *Acer saccharum*, *Quercus alba*, *Tilia americana* and *Fagus grandifolia*. Even seedlings of flood-tolerant hardwoods were damaged by deposits of alluvial sand and silt greater than 3 inches deep or in slow-draining depressions. Less damage was evident in the slackwater areas where clay deposition occurs because, unlike silt and sand, the desiccation cracks that form in clay-rich sediments during the dry season permit aeration of the soil and roots.

For most species, duration of flooding is a critical factor to tree physiology only during the growing season (Bedinger, 1978). Measurement of the tolerance of large trees is of little value for determining the relative establishment potential of species. The viability of seeds or the survival potential of seedlings following submergence is not necessarily directly correlated with the adaptive potential of the mature trees of the same species.

In a study of the terraced floodplain of the lower White River valley in Arkansas, Bedinger (1971) correlated the composition of forest communities with flood frequency and duration. In zones flooded 29-40 percent of the time, *Quercus lyrata* and *Carya aquatica* were dominant. A more diverse flora was present in the zone flooded 10-21 percent of the time, dominated by *Quercus phellos*, *Q. nuttallii*,
*Liquidambar styraciflua*, *Celtis laevigata* and *Ulmus americana*. Bedinger (1971) suggested that this empirical relationship can be used conversely; that is, that zonation of the forest species assemblages can be used as an indicator of flood frequency. If this relationship is consistent, compilation of additional assemblage-flooding observations over a broad geographic range could be of considerable use to the hydrologist as a proxy for unavailable stream gaging records.

**Community Structure Along an Environmental Gradient**

Riparian vegetation communities typically change in composition along a hydrologic gradient parallel to slope. Bell (1974) investigated the tree species distribution in a streamside forest along the Sangamon River and related it to the historical river stage record. A species diversity gradient paralleled the environmental gradient. Immediately proximal to the stream, within the first foot of elevation above flood stage, species richness was low; three species were present: *Acer saccharinum*, *Platanus occidentalis*, *Fraxinus pennsylvanica*. Progressive zones within each additional foot of elevation on the floodplain were occupied by greater numbers of species, with a maximum of twenty-nine. In the lower elevational half of the floodplain, *Acer saccharinum* was overwhelmingly dominant in number of individuals and relative basal area of the species as a whole. In more distal zones, increasingly more species became codominant in both numbers and relative basal area. First appearances of dominant/codominant species along the environmental gradient were as follows: *Fraxinus pennsylvanica*, *Ulmus americana*, *Celtis occidentalis*, *Quercus macrocarpa*, *Populus deltoides*, *Juglans nigra*, *Q. imbricaria*, *Q. rubra* and *Q. alba* dominated the adjacent upland.

Several important results emerged from this study. First, the composition of riparian plant communities varies along a hydrologic gradient. Second, forest species
diversity and productivity on the floodplain generally increases with increasing
distance from the channel. Third, a few tree species tend to dominate the community
in number and size, even when species diversity is high. Bell (1974) concluded that
the physical environment is a major determinant of species distribution, particularly in
the lower zones of the gradient.

Seedling Survival and Flooding

The flood tolerance of a species often varies through stages of development. Usually, the seedling stage is more vulnerable to flood damage than the mature trees. The establishment and dominance of *Acer saccharinum* in the zone proximal to the stream, flooded up to 25% of the year, suggests relatively high flood tolerance of the seedling stage as compared to other tree species present on the floodplain. Conversely, other studies (e.g., Hosner, 1958) have shown that mature *Acer saccharinum* individuals are markedly intolerant of sustained inundation. These observations suggest that the wet extreme of the hydroperiod on this floodplain has been moderate during the history of the current forest community. Duration of flooding on floodplain sites in Mississippi studied by Bedinger (1981) ranged from 6 to 40%. This range can have considerable consequences for regeneration of floodplain forest stands because seed germination and seedling survival can be quite sensitive to flood duration. Hall and Smith (1955) observed that seedlings of all of 39 tree species were killed by flooding beyond half of a growing season at a reservoir margin. Seedlings of even highly flood-tolerant species are sensitive to floodwater magnitude; *Taxodium distichum* and *Cephalanthus occidentalis* seedlings are killed by complete inundation, ostensibly due to low light intensity and disruption of stomatal function (Gill, 1970).
Models of Effects of Anaerobic Stress on Tree Growth Physiology

The previous discussion identifies the integrated physiological responses to anaerobiosis that are directed at tree growth suppression. Two conceptual models were constructed to illustrate the common strategies employed by trees exposed to anaerobic stress. Anaerobic Stress Model 1 summarizes the network of physiological responses that can lead to growth suppression (Figure 12). Trees typically employ a combination of these strategies. Anaerobic Stress Model 2 illustrates the adaptive strategies employed by stress-tolerant trees to cope with life in an anaerobic soil environment (Figure 13). Some of the adaptive strategies in Figure 13 are repeated from Figure 12.

The functions of these strategies are a combination of two plant objectives. The first plant objective, a defensive one, is to suppress physiological activity until the stress is relieved. Suppression of activity, for example, transpiration, allows the plant to avoid assimilation of oxygen-deficient water and phytotoxins, and to minimize self-destructive processes such as the production of toxic glycolytic end-products. Growth suppression is generally a temporary solution because the plant is slowly dying. The plant may restore normal functions with little or no damage if the stress is ephemeral. The second plant objective is offensive and is directed at acquiring oxygen by alternative means to prevent tissue damage and sustain physiological function. These means include production of adventitious roots, generation of aerenchymatous tissues in roots, and ventilation through hypertrophied lenticels. The plant not only survives the stress, but can often maintain function for period of time, perhaps with minor growth suppression.

The hypothesis of this study is grounded on the principles outlined in the anaerobic stress models. Both models suggest that even trees that are well-adapted for

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Figure 12. Anaerobic Stress Model 1. Tree Growth Suppression During Soil Saturation.
Figure 13. Anaerobic Stress Model 2. Tree Defense Mechanisms Against Anaerobiosis.
life on saturated soils may experience reduced growth when the hydrologic stress is sufficiently long.

Environmental Variables That Influence Radial Growth in Trees

Tree and other plant species have genetic predispositions that define their ecological plasticity. The natural geographic distribution of plants is an expression of the interaction of genetic predisposition with environmental conditions. The growth of a tree can vary within limits, depending on the collection of environmental conditions imposed on it. The significance of any environmental condition to growth is usually influenced by one or more others in a complex interaction that is difficult to isolate. A change in one condition consequently leads to a change in others throughout the ecosystem. The soil aeration and saturation pattern associated with water table or surface water fluctuations is only one of many variables that influence the thickness of a growth ring.

Macroclimate is the aggregate of all meteorological phenomena that occur at the regional or site levels. The most important macroclimatic variables include precipitation, temperature, wind, sunshine, humidity, and barometric pressure. The macroclimatic variables are those widespread climatic variables that occur rather uniformly across a given site, independently of the ecological community. Microclimate, on the other hand, is the same set of factors that represent an overprinting of ecological influences on macroclimate. For example, the temperature within the forest may be stratified due to the retention of heat by the canopy. A gradient of humidity on a smaller scale is commonly present between a leaf surface and the open air around it. While considerable rainfall may be delivered to a site throughout the growing season as a function of macroclimate, interception by the canopy may prevent much of the rainfall from reaching the vegetation at the forest.
floor. Sunlight, the source of energy in photosynthesis, is preferentially distributed to the overstory trees, rather than the understory trees. For this reason, growth of understory trees is usually suppressed. Evapotranspiration at the canopy surface is influenced by direct sunlight and exposure to the regional winds. Understory trees in the same forest may be shielded from a large part of the sunlight and wind. As a consequence, strong differences in evapotranspiration can occur on a leaf of the same size on an understory tree as compared with an overstory tree of the same species. The competition among trees throughout a forest for sunshine and moisture is often strong and growth is similarly affected.

The texture of a soil influences its moisture retention capacity, drainage rate and cohesion for support of tree stems and roots. Soil composition, development of the soil column, and chemical parameters such as pH and redox state influence the availability of nutrients and growth inhibitors to the roots. Soil characteristics often vary considerably between the topographic highs and lows of a site, even if the parent materials were similar at the onset of soil genesis. The coordinated development of the biotic community and the soil column results in a mosaic of soil types across the landscape. The establishment and growth of trees across this landscape is similarly variable. Insect infestation, disease, logging, storm damage, pollution, browsing and fire are examples from the large list of additional variables that may influence tree growth.

This summary of growth variables is cursory. It serves to illustrate that growth is a complex process and that recognition of the influence of any particular variable requires identification and differentiation of the others. Different growth variables may be limiting to different trees in a forest at the same time and the status of a limiting factor may change momentarily.
CHAPTER V

METHODS AND ANALYTICAL FRAMEWORK

Research Design and Site/Sample Tree Selection Criteria

Units of Measurement

Data and information were provided for this study by a variety of sources in U.S. Standard Units (e.g., National Climatic Data Center, USGS, U.S.D.A. Natural Resources Conservation Service (NRCS; formerly the Soil Conservation Service, SCS)). Field and laboratory instruments used in the study (e.g., survey equipment, microscope scale) were also calibrated in U.S. Standard Units. Therefore, all measurement references, tabulated data, map scales and other numerical information in this paper are presented in U.S. Standard Units.

Definition of Wetland

This study focuses on the hydrology and related ecology of wetlands and the uplands and open waters that may border them. The definitions of wetlands and related terminology used in this study are varied in the lay, scientific, and regulatory literature.

Wetlands are federally regulated and the COE is the primary agency responsible for managing and protecting the resource. The definition of wetlands used by the COE is “…those areas that are inundated or saturated by surface or ground water at a frequency and duration sufficient to support, and that under normal circumstances do support, a prevalence of vegetation typically adapted for life in saturated soil
conditions. Wetlands generally include swamps, marshes, bogs, and similar areas (Federal Register, 1987).

The FWS is responsible for managing many of the federally-owned wetlands throughout the United States, particularly National Wildlife Refuges. The FWS defines wetlands as "...lands transitional between terrestrial and aquatic systems where the water table is usually at or near the surface or the land is covered by shallow water. ...[W]etlands must have one or more of the following three attributes: (1) at least periodically, the land supports predominantly hydrophytes; (2) the substrate is predominantly undrained hydric soil; and (3) the substrate is non-soil and is saturated with water or covered with shallow water at some time during the growing season of each year" (Cowardin et al., 1979).

The COE and FWS definitions are equally descriptive of the areas of study in this dissertation. The exact position of the regulated wetland boundary was not of concern in the field investigations. However, the sampling transects were oriented perpendicular to it and crossed it from well into the wetlands to the unequivocal uplands.

Hydrotopographic Gradient Model

A hydrotopographic gradient (HTG) model was constructed to guide the research problem. This term has been coined for convenience because this is the first known tree-ring study to examine the distribution of trees in the combined context of hydrology and topography. The HTG is oriented perpendicular to the land contours and ideally reflects an upward decrease in average soil moisture content from wetland to upland. Study trees are referenced according to their hydrotopographic position (HTP) on the gradient. Each HTP represents a unique combination of soil moisture
and vertical position on the landscape. Each position is coded so that a tree (or other feature) can be conveniently classified and relocated (Figure 14).

The HTG is applied to two unique hydrotopographic settings to classify the sample trees on the study sites: Depression Swamp HTG (Figure 15) and Floodplain Forest HTG (Figure 16). Each HTG type is named for the nature of wetland area that is included. It includes the adjacent water bodies (if present), the adjacent uplands, and the transitional areas joining them. Although wetlands are, by definition, transitional between aquatic and terrestrial habitats, the term 'transitional', as used here, refers to an undefined zone in which the wetland boundary is centered. Therefore, the wetlands, aquatic habitats, and uplands are considered distinct zones and the transitional areas include wetland and upland or, less commonly, wetland and aquatic habitat, since trees are less likely to be present in the aquatic habitat. These transitional areas are important because, under dynamic hydrologic conditions, they are occupied by tree species that have been exposed to historically-altered soil moisture conditions at some time since they became established. In other words, the individual tree species in the transition zone are better adapted to the wetland or the upland condition, but are present in both. Therefore, the transition zones are expected to be inhabited by strained trees. Tree core sampling continues into the adjacent uplands and wetlands for comparative analysis of the hydrologic extremes under which the same (or similar) species exist.

The hydrologic regime at each HTG is illustrated in the profiles. It is represented by the water table (WT) and surface water bodies, if present. Several hypothetical positions of the water table are shown to represent the typical range of fluctuations that may occur. Trees in wetlands are typically exposed to a fluctuating water table and experience both saturated and aerated soil conditions in a given water year.
These HTP codes accompany Hydrotopographic Gradient profile illustrations (Figures 15 and 16).

### Floodplain HTP
- **F1** = channel
  - F1x = channel proper, relatively high flow
  - F1z = shallow margin, embayment, oxbow, low flow
- **F2** = floodplain
  - F2x = proximal to stream (0 - 1/3 distance from channel margin to lower break in slope)
    (may be upland or wetland, shallow or abrupt slope)
  - F2y = interior (1/3-2/3 distance from channel margin to lower break in slope)
  - F2z = marginal (2/3+ distance from channel margin to lower break in slope)
- **F3** = floodplain/upland slope transition (floodplain break in slope)
  - F3x = near lower break
  - F3y = slope
  - F3z = near upper break, floodplain fringe
- **F4** = upland
  - F4x = sloped
  - F4z = horizontal

### Depression/Basin HTP
- **D1** = central depression
- **D2** = exposed "horizontal" basin bottom
  - D2x = proximal to central depression (0 - 1/3 distance from central depression margin to lower break in slope) (may be upland or wetland, shallow or abrupt slope)
  - D2y = interior (1/3-2/3 distance from central depression margin to lower break in slope)
  - D2z = marginal (distal) (2/3+ distance from central depression margin to lower break in slope)
- **D3** = basin/upland slope transition (basin break in slope) (may be upland or wetland, shallow or abrupt slope)
  - D3x = near lower break
  - D3y = slope
  - D3z = near upper break, basin fringe
- **D4** = upland
  - D4x = sloped
  - D4z = horizontal

### Topography Modifiers
- m = local mound or relatively high position
- s = local swale or relatively low position

### Hydrology Modifiers (record "T" if inferred from topographic position and soil types, or "E" if determined via excavation using a hand auger or shovel)
- dw = depth of surface water (if tree is in water, standing or flowing)
- dwx = depth of water table (if tree is on exposed soil, determined via auger hole or soil pit)
- a = submerged (F = flooded/P = ponded)
- ab = on soil saturated to surface (seepage face or ponding nearby indicating near/at surface water table) — root zone saturated
- ac = on soil with shallow water table (< 1 ft below surface) — root zone partly saturated, depending on depth of root mass
- ad = on soil with intermediate depth water table (1-3 ft below surface)
- ae = on soil with deep water table (> 3 ft below the surface) — root zone aerobic

**Hybrid HTP example:** A tree half in water on sloped basin margin = D1a-D3xc

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Figure 14. Hydrotopographic Position (HTP) Designations.
Figure 15. Depression Swamp Hydrotopographic Gradient Classification Model. (See explanation in Figure 14)
Figure 16. Floodplain Forest Hydrotopographic Gradient Classification Model. (See explanation in Figure 14)
Fluctuations in the surface water elevations are not shown. Rises and falls of surface water bodies are accompanied by lateral shoreline movement that intersects the land contour at the given water elevation. In the Floodplain Forest setting, part of the floodplain is typically flooded at least once annually. The 100-year flood would approximately rise to the position at WT3 (Figure 16). Flood frequencies and durations vary considerably among floodplain settings and temporally. Fluctuations in the water level of ponds and lakes could behave similarly, particularly if they are influenced by human intervention (e.g., reservoirs behind dams).

Each of the two HTGs is divided into two types of zones. The hydrotopographic zones are noted on the upper part of the illustrations. These zones divided the surface into unique regions of soil moisture conditions. They are internally divided into a gradient of possible positions that trees could occupy, designated by the code shown in the crown of the illustrated trees. As each tree was sampled, it was assigned an appropriate HTP code (Figure 14). Topographic and hydrologic modifiers were used place the sample trees precisely on the landscape-water regime. For the HTG description at each site, all or some of the individual HTPs could be present.

The second zonal division of the HTG, noted in the lower part of the illustrations, is used to estimate the sensitivity of the tree-ring sequence with respect to tree HTP. Trees located in areas where the residence time of soil saturation was relatively long were anticipated to have sensitive ring-width series according to the study hypothesis (Sensitive Zone). At the other extreme, upland trees were expected to have more complacent ring-width series (Complacent Zone). The region of uncertain, transitional soil-moisture status was designated as the Marginal Zone. This zonation was based solely on water as the limiting factor to growth.
Dendroclimatology vs. Dendrohydrology

Traditional dendroclimatological studies are typically guided by a common set of research conditions. The scale of the problem is regional, for example, the southwest United States. The time scale of climatic reconstructions is usually decades to millennia. The hydrologic setting of the sample trees is arid, the disturbance signature is drought, and relatively moist time intervals correspond with enhanced tree growth. Cores are compared from trees that experienced similar environmental influences.

This wetland dendrohydrology study is guided by a different set of conditions. The spatial scale of the problem is limited to a site that may be as small as an acre. As in dendroclimatology studies, water supply is also the limiting factor, but suppressed growth is expected only when it is present in excess. The climate of the study region is mesic and rarely moisture deficient; precipitation fluctuations are expected to impact growth only through their influence on the position of the water table or their impact on floodwaters. The ideal time scale of the stress signal is between 1 year and several decades. Cores are compared from trees occupying a variety of ecosystems and water surplus stress is expected to be the limiting factor to growth only in the wetlands.

The methods of this study were based in part on those developed throughout the history of dendrochronology and reported in scientific papers and books. However, given the unique nature of the research problem, a large component to this study was the development of suitable methods. Development of tree core sampling strategies, laboratory preparation and examination, data processing and interpretation procedures was a primary component of this study. Technique development occurred with the idea in mind that it might be useful to a broad range of wetland scientists.
Therefore, many of the methods require only a few tools specific to dendrochronology and most rely on readily available instruments and inexpensive woodworking tools.

**Site and Sample Tree Selection**

Site and tree selection in dendrochronological studies usually require directed, rather than random, sampling. In light of the desired information to be exploited, it is necessary for the field researcher to recognize the variables that influence tree growth and sample in such a way as to factor out extraneous ones. The dendrohydrologist requires samples that have been affected by water as a growth-limiting factor and therefore must deliberately stratify the sample set to maximize the signal and minimize the noise. In this study, for periods when water surplus was the limiting factor to tree growth, corresponding growth rings are expected to be narrow.

The search for favorable study sites was guided by a number of criteria. The best sites were expected to be those that historically had one or more distinct hydrologic disturbance “events”. “Event” is used here to describe a continuous condition or close connection of conditions that could be distinguished from “normal” conditions or preexistent conditions. Punctuated events and/or events with sudden beginnings and/or ends were most desirable. “Normal” conditions are those that occur on either side of an event and are more prevalent than the event. Examples of hydrologic disturbance events include: (a) installation or decommissioning of soil or surface water drainage features, for example, agricultural drain tiles or county drainage ditches; (b) a period of relatively frequent or long duration stream flooding, whether natural or artificially influenced; (c) development of a high capacity wellfield; or (d) a sudden permanent change in lake or stream level (e.g., beaver dam, hydroelectric dam). Hydrologic events involve shifts in episodes of soil saturation and soil aeration. Each period needed to be of sufficient duration to elicit a growth response, whether
stressed or released. Ideally, events had been monitored and documented records were available for comparison to the tree core data. Examples of useful records included: (a) drain tile records, (b) stream gauging station data, (c) precipitation data, (d) monitor well data, and (e) aerial photographs. Candidate sites were identified by: (a) review of hydrologic documentation (e.g., drainage ditch and tile files at the NRCS regional offices); (b) examination of USGS topographic maps, NWI wetland location/classification maps and plat sheets; (c) county soil survey soil sheets and hydric soil descriptions; (d) ASCS (Agricultural Stabilization and Conservation Service) Swampbuster maps (looking for Prior Converted farmland); (e) inspection of 9"X9" aerial photographs at the MDEQ and NRCS regional offices (looking for tile scars, historical difference in lake water surface area, abandoned meander channels, flooded forests, etc.); (f) recommendations of natural resource professionals and academic colleagues; and (g) serendipity (drive-bys).

If the disturbance and documentation criteria could be met, a visit to the site was necessary to determine if site conditions were suitable for study. The site had to be physically and legally accessible and permission was obtained for tree coring. As a general guideline, homogeneity of site conditions was preferred, with the exception of hydrotopographic gradient. There needed to be a sufficient sample size of trees with some combination of the following characteristics, which also guided their selection (listed from most to least important): (a) mature, even-aged and old specimens to provide the longest possible record and comparable sensitivities throughout their life histories; (b) uniform distribution of the species along the entire hydrotopographic gradient, for comparison of stressed and non-stressed growth responses; (c) presence of tree species with readable growth ring series, particularly ring-porous hardwoods; (d) a full, healthy bole and crown, so that aberrant growth associated with injury, disease, or imbalanced leaf distribution could be avoided; (e) stem rooted on level
ground with circular bole cross-section and vertical orientation to avoid eccentric
growth ring patterns and to preclude the need for replicate samples of the same tree; (f)
an open, sparse forest to minimize the effects of inter-tree competition for light,
nutrients and moisture; or, dominant or codominant position in a closed canopy; and
(g) a broad diversity of species for comparison of inter-specific growth response to
water surplus stress and recognition of useful water surplus stress indicator species.

Characteristics (d), (e) and (f) were particularly important in order to obtain a
sample of trees that were ostensibly grown under homogeneous conditions other than
moisture. In order for the water surplus stress signal to be recognized and
differentiated from the non-stress signal among the sample trees, it was necessary to
attempt to factor out the other growth-influencing factors through judicious sampling.

When present, trees were selected that had an upland or broad ecological
amplitude, that is, a UPL, FACU, FAC or FACW wetland indicator status. That way,
the same species could be compared in the uplands and the lowlands. UPL and FACU
forest communities that extended into the contiguous wetlands were expected to
contain the ideal sample trees because they are typically most sensitive to water surplus
as a limiting factor.

Dead trees were also candidates for sampling to determine the timing and
spatial distribution of hydrologic events, and to determine whether mortality was
abrupt or followed a growth decline. Understory trees were generally avoided, but
were not ruled out if they occupied an important position on the HTG that could
influence the dendrohydrologic reconstruction. The influence of root competition for
nutrients and moisture was minimized by selecting trees that had no nearby neighbors
and had a similar understory density to that around the other sample trees.

A county soil survey and soil auger borings were used to ascertain the degree
of uniformity in the distribution of soil types across the site. Where possible, sample
trees were selected from soils that had similar textural properties so that moisture retention and hydraulic conductivity were similar.

Information about site use-history was acquired to account for unanticipated disturbances to the ecology of the system and their effect on the growth of all or part of the forest.

Field Methods

Routine Field Characterization of Study Sites

Each study site was assigned a 2-letter code. Prior to and during sampling, field observations were collected at each site. The field observations included: (a) an estimate of extent of wetland area and position and shape of wetland boundary; (b) a forest community inventory, including taxonomic composition, tree dominance profile from basal area and relative stem frequencies, crown classes and species-height stratification, species age distribution, and canopy fullness; (c) the nature of the local topography and geomorphology; (d) evidence of hydrologic (or other) disturbances and field indicators of surface water hydrology, such as trees in standing water, ice impact scars, water stains or bleaching on objects, drift lines, sediment deposits, and logging scars; (e) the presence of tree morphological adaptations to a wet environment as discussed in Chapter IV; and (f) the location of tree sampling transects or zones and relationship to the generalized hydrotopographic gradient.

Tree Core Sampling Procedures

Sample size was based on the site conditions. As a rule of thumb, all or most of the best candidate trees at each site were to be sampled. Typically, a single core was taken from the north side of each tree at breast height (~4.5 ft.). These coring
conventions were necessarily altered on a case-by-case basis. If the sample tree was located on a slope, the core was taken parallel to the elevation contour. Trees with elliptical boles were cored between the long and short diameters of the stem. If it was physically impractical to core the north side, for example a *Toxicodendron radicans* vine-covered trunk, the core was taken from the nearest convenient point from the north side.

Most of the following observations were made and recorded for each sample tree: (a) date of collection; (b) mapped position and wrt landmarks; (c) species or other taxon; (d) canopy position/crown class; (e) diameter at breast height as DBH in inches using a diameter tape; (f) coring side of stem (cardinal direction); (g) competition (distance to neighboring trees or density of understory); (h) HTP during time of sampling; (i) coring difficulty ranking; (j) basal area around tree; (k) slope degrees at tree base position; (l) height in feet, approximate; (m) physical condition: stem shape (straight, forked, clumped, bowed), stem orientation (vertical, leaning (indicate direction), fallen) stem x-section (circular, oval, irregular), tree health (healthy, unhealthy (diseased or infested), injured, dead), presence/absence of leaves; (n) stem additional comments: peculiar morphology of tree (e.g., burl, outstanding size), taper at ground surface, buttressing, presence of water stains, ice scars, water line, sediment in bark, moss, etc.; (o) root system morphology: roots spreading, roots crawling, clawed or perched roots along ground surface away from tree (identify number, thickness and distance, height off ground); (p) length of core; and (q) soil characteristics.

Crown class assignments followed the conventions of Johnson and Bell (1976). Dominant trees were those receiving direct sunlight on the top and sides of the crown. Codominant trees were those receiving direct sunlight only from the top of the crown. Intermediate trees were small overstory trees with crowns that receive some

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direct sunlight on top. Suppressed trees were small, understory trees receiving little or no direct sunlight.

Core samples were taken using a 16-inch Swedish increment borer with a 1/4-inch core barrel. It is a forestry tool commonly used to monitor commercial forest stand health and development. Unless the tree was more than 32 inches DBH, the core was attempted to be taken from the bark through the center of the stem to obtain a complete radially-oriented growth-ring record. Removal of the cylindrical core typically does not harm tree because the bark grows over hole during next growing season or two. A field core carrier fabricated of slotted wood was used to transport and protect the cores until they could be returned to the laboratory for processing. Each core was given an identification code using the 2 letter site code followed by “C” and the number that the core was taken in sequence from the site (e.g., core number KSC 14).

Recovery of Ring-Width Data

Laboratory Processing of Tree Cores

The cores were carefully transferred to storage boards for drying in the laboratory. They were dried under pressure for a minimum of 3 weeks before mounting to prevent warping. Individual core mount blocks were cut from 5/8-inch particle board and a 1/8-inch deep routed groove was cut using a 1/4-inch veining bit. Each core was glued into the groove of a block and labeled. Cylindrical core samples were extracted along a radial orientation into the tree, from bark to center. Therefore, the ends of the core are tangential surfaces of the wood and the circumferential surface of the core cylinder varies from 2 transverse-sectional views to 2 radial-sectional views. The cores were permanently mounted so that the transverse section was visible.
because the growth rings are best distinguished by the contrast in pore sizes, represented as truncated vessel traces. Following 1 week of drying, the raised half of each core was bisected along its length using a power plane with a high-speed rotating drum and carbide cutting teeth. The result was a longitudinally-bisected transverse view of the growth rings cut flush with the surface of the core mounting block.

**Growth Ring Boundary Enhancement**

The growth ring definition of ring-porous hardwoods (e.g., *Fraxinus* spp., *Quercus* spp.) was generally adequate for examination without further treatment because the transition between pore diameters in earlywood and latewood is abrupt. In diffuse-porous hardwoods (e.g., *Acer* spp.), the ring boundary is undefined or less well defined by a difference in color or a faint dark line between latewood to earlywood. One objective of this study was to improve the techniques for growth-ring enhancement of diffuse-porous hardwoods. *Acer saccharinum* and *Acer rubrum* are common and often dominant inhabitants of floodplain forests and depression wetland marginal swamps throughout southern Michigan. Growth-ring definition of these species was very obscure, particularly in the sapwood, and counting of the cut and smoothed surfaces without further enhancement of anatomical features was not possible. Therefore, improvement of ring definition in these woods could provide an opportunity to investigate the dendrohydrology of *Acer* swamps.

Two techniques for growth-ring enhancement have been reported in the scientific literature that were tried in this study. Patterson (1959) describes the application of a phloroglucinol (2-hydrate C\(_6\)H\(_6\)O\(_3\)) stain to tree cores for this purpose. Phenylpropane, the basic structural unit of lignin, reacts with phloroglucinol to stain red. Phenylpropane is lacking in the cellulose chain. Relative proportions of
lignin and cellulose vary within the normal annual growth increment, with a smaller cellulose:lignin ratio in the earlywood than the latewood (Figure 17).

![Graph showing lignin and cellulose composition](image)

**Figure 17. Intra-Growth Ring Composition: Lignin and Cellulose.**
Adapted from: Panshin and de Zeeuw, 1980.

The cellulose:lignin ratio also increases from pith to bark, thus increasing the contrast in the staining response in the more mature portion of the wood record. The preferential staining effect of phloroglucinol in the relatively high proportion of lignin in the earlywood of a growth increment produces a color intensity contrast at the ring boundaries. Viewed under fluorescent light, phloroglucinol stains lignin red and does not discolor the cellulose fraction of the wood.

Fritz (1939) suggested that the contrast between earlywood and latewood could be heightened by high speed sanding of the core surface. Pressure is applied to create
enough frictional heat to burn the wood. Latewood burns to a darker tone than earlywood.

**Ring Width Examination and Measurement**

A precision aluminum scale was fabricated specifically for this study by Alteneder, Inc. The scale was calibrated to increments of 0.01 inches. At a magnification of 10x, it could be read to ±1/2 of the distance between graduations, so ring-width measurements could be recorded to the nearest 0.005 inches with an accuracy of ±0.0025 inches. The scale was screwed to each core block in fixed holes so that it could be remounted in the same position for precise remeasurement.

The vascular cambium marked the zero reference for ring counting. Depending on the time of year that the sample was taken, the first ring was complete or partial. It was complete if the sample was taken during the dormant season. If taken during the growing season, the ring was truncated within the earlywood or latewood. Increasing ring numbers corresponded to increasing ring ages, with the center being the oldest. For this study, all core samples were collected within approximately one year. Therefore, the zero reference corresponded to the year 1994 or 1995. Since the sampled trees varied unpredictably in age, the total number of rings counted varied highly for the sample set.

The cores were observed and the rings counted using a Bausch and Lomb Stereozoom binocular dissection microscope with a variable-adjust 1- to 7-power objective and 10-power oculars, resulting in an effective range of magnification from 10 to 70 times. For ring counting, 10-power was routinely used. Higher magnifications were used to observe questionable ring boundaries and intra-ring anatomy.
A 32-inch wide microscope stage was constructed to work with the microscope and accommodate the core blocks, which were up to 18 inches long. A plastic laminate sheet was applied to the surface of stage for ease of movement of the core blocks across field of view when making detailed measurements. A ~2.5-inch sharpened copper wire was fixed within the field of view to serve as a reference for keeping track of ring boundaries during measurement. Dual lamps were positioned on either side of the microscope to project light at opposing angles on the mounted cores. Fluorescent 75 watt bulbs provided the best quality light for tree-ring observation and measurement. A low ultraviolet bulb was used to observe the specimens treated with phloroglucinol.

Continuous, cumulative ring-width measurements were recorded along the fixed scale from the bark-wood interface, at the left end of scale, to the center of the cores at the right end of scale. The bark-wood interface was the zero reference for all measurements because it was a known time mark for the cores. Recording cumulative ring widths, rather than individual ring widths, reduced the error in measurement considerably because an error in the measurement of one ring would be corrected in the measurement of the following ring. Individual ring widths were readily calculated from cumulative ring width. Compensation for the artificial addition of ring width due to cracks in some cores was subtracted out in a computer spreadsheet.

Ring-Width Data Processing

Site-Specific HTG Working Models

Using the field notes describing the distribution of the sample trees on the landscape, the sample trees from each site were plotted as circles in their appropriate positions on the HTG conceptual model profiles (Figures 18, 19, 20, 21). The
Figure 18. Cache River Floodplain Generalized Hydrotopographic Profile With Relative Sample Tree Positions.
Figure 19. Kalamazoo River at Swan Creek Generalized Hydrotopographic Profile With Relative Sample Tree Positions.

Taxonomic Code:
COc = Celtis occidentalis
FPe = Fraxinus pennsylvanica
QBi = Quercus bicolor
QRu = Quercus rubra
UAm = Ulmus americana
Figure 20. Twin Lakes Generalized Hydrotopographic Profile With Relative Sample Tree Positions.
Figure 21. Sherriff's Marsh Generalized Hydrotopographic Profile With Relative Sample Tree Positions.
illustrations are best viewed in two parts. The upper part is a profile view with generalized HTPs given as the tree-like figures on the surface, the codes of which are defined in Figure 14. The distribution of the plotted sample trees (circles) in the lower part of the illustrations is best considered a plan view of the forest with HTP boundaries extending downward from the corresponding positions on the surface. A code for the species name (referenced in Appendix A) and the core number(s) of each tree were labeled in the sample tree circles. These working models for each study site were used in the selection of cores for the various data analyses.

The HTG profile on each illustration was divided into sensitivity zones. The boundaries between sensitivity zones were arbitrarily assigned, based on the expected relative exposure time of the sample trees to water-surplus stress. Some of the core analyses compared growth in the Complacent Zone versus the Sensitive Zone.

Initial Data Processing and Basic Graphs

The cumulative ring-width data were transferred to a computer spreadsheet for processing. The cumulative width measurements were corrected for gaps due to core fractures. Each ring on a core was assigned a Ring Number (RN) with a corresponding computed and tabulated Ring Width (RW) in inches.

A line graph was constructed for each core as RW vs. RN (Appendices B, C, D, E). A line graph of cumulative ring width (CW) vs. RN was also constructed for selected cores. Because each RN normally corresponded to a time unit of 1 year, the x-axis was RN on these graphs. The youngest rings were listed on the left side of the axis and RN 1 always represented the first complete or partial ring inside the bark. RW or CW increases upward on the y-axis. Scaling of the x-axis was normally forced to RN 75, regardless of total number of actual rings on a core, so that the curves could be conveniently compared on a one-to-one basis with respect to time. For practical
purposes, only the most recent 75 years of the growth-ring record was included in the analyses. Many trees had more or less than 75-year records.

**Sensitivity Analyses**

The equation for calculating mean sensitivity introduced in Chapter II was applied to the individual ring-width data for each core. The mean sensitivity was calculated for each core, and collectively for each site using all of the tree cores. A sensitivity analysis histogram summary was prepared for each site (Figures 22, 23, 24, 25).

**Standardization**

The ring-width series of each core was standardized using the procedure described in Chapter II. The mean ring-width index (RWI) was calculated for all of the cores at each site and displayed as composite and taxon-specific ring-width chronology (RWC) histograms (Figures 26, 27, 28, 29). In certain cases, RWIs were computed and graphically illustrated for trees located within the sensitive zone compared to the complacent zone for a site. Selected RWCs were also graphically compared with hydrologic data.

**Minimum Tree Age Plots**

Tree age was estimated from the cores during microscopic analysis. As the center of the tree was approached while rings were measured from bark to center, one of two situations was present. If the core was taken as a true radial section, it intersected the true center of the tree. In this case, the “age” was equal to the total number of rings counted. More commonly, cores did not intersect the true center of the tree, but were oriented obliquely to the radial section. While measuring oblique
Figure 22. Cache River Floodplain, Sample Tree Core Sensitivity Summary.
Figure 23. Kalamazoo River at Swan Creek, Sample Tree Core Sensitivity Summary.
Figure 24. Twin Lakes, Sample Tree Core Sensitivity Summary.
Figure 25. Sherriff's Marsh, Sample Tree Core Sensitivity Summary.
Figure 26. Cache River Floodplain (CF) Composite Ring-Width Chronology.
Figure 27. Kalamazoo River at Swan Creek (KS) Composite Ring-Width Chronology.
Figure 28. Twin Lakes (TL) Composite Ring-Width Chronology.
Figure 29. Sherriff's Marsh (SM) Composite Ring-Width Chronology.
rings from bark to center, the true width of the rings was less than that which appeared in the cores. This effect became stronger towards the center of the tree. Since the true center of the tree was rarely intersected, an inflection was present in the rings that represented the point of reversal in the ring sequence. The growth ring at the inflection point appeared horizontal. Trees with greater than 32 inches DBH were usually cored to the maximum capability of the increment borer, 16 inches. Some trees were cored only through the known mature interval of wood. Since an unknown number of growth rings was absent from the inflection points or termination points to the true tree center, the tree age as represented in the cores was underestimated. The growth-ring count was considered a Minimum Tree Age (MTA). MTA vs. Core Number (CN) was plotted as a histogram for the cores examined at each site to illustrate the age distribution of the sample trees (Figures 30, 31, 32, 33).

Deviation From the Mean

Deviation from the Mean (DM) ring width analyses were conducted for the mature interval of the older trees at each site. For each site, determination of a growth time interval and sample tree candidacy for the DM analyses were based on the following 4 factors: (1) the minimum age at which trees were considered mature (mature age, MA), (2) the tree age distribution in the stand, (3) the perceived timing of hydrologic disturbance events or trends, and then (4) the utility of the resultant sample size. These factors are explained further below:

1. To maximize the validity of the growth comparisons between trees and to isolate hydrology as a growth variable, the sampling strategy targeted trees that were mature. A Mature Tree Age (MA) was selected at 30 years because the Fraxinus spp. and Quercus spp. encountered in SW Michigan during this study were about 6-9
Figure 30. Cache River Floodplain Cores: Minimum Tree "Age".
Figure 31. Kalamazoo River at Swan Creek Cores: Minimum Tree "Age".
Figure 32. Twin Lakes Cores: Minimum Tree "Age".
Figure 33. Sherriff's Marsh Cores: Minimum Tree "Age".
inches DBH at 30 years of age. Their growth rate had decreased considerably by age 30, corresponding with the beginning of the mature region on the idealized ontogenetic growth curves (Figures 9 and 10). Only trees with growth increments above this 30-year MA interval were considered for use in the DM analysis.

2. The Minimum Tree “Age” of each of the trees for which a ring count had been tabulated was plotted on a collective histogram for the site as MTA vs. CN (Figures 30, 31, 32, 33). “Age” is given in parenthesis to acknowledge the assumption that observed rings represented a one-to-one correspondence with years, that is, missing rings and multiple rings were not present. The 30-year MA cutoff was plotted as a horizontal line that represented the zero reference for which only older trees were considered in the DM analyses. The trees with MTA bars that extended above this line were considered mature trees at the time of sampling. The youngest tree above this line was considered first. Its MTA minus the 30-year MA cutoff equaled AV, the maximum time interval before present that could be used in the DM analyses. All of the older mature trees were included in a sample that included the youngest mature tree.

3. If documented hydrologic events or trends (e.g., precipitation or streamflow data) were to be compared with the ring-width data, the time intervals from present to the event period were determined. These were compared with the AV lengths described in factor 2.

4. If the AV governed by the youngest tree was considered to be too short to be meaningful in the analyses of events, successively older mature trees were considered and their associated larger AVs were evaluated with regard for their utility in the analyses. The tradeoff was that longer AVs required that younger trees were disregarded and the sample size for the DM analysis decreased. The ideal AV determination was arrived at by balancing the greatest possible sample size against the minimum AV for which a correlation with hydrologic conditions could be made.
When an AV was determined, Mean Ring Width (MN) was calculated for each tree by averaging the ring width for the period ranging from the date of collection, or a uniform reference date for all of the included tree samples, back the AV number of years. The reference lines for which an AV was used were included on the MTA histograms. A Mean Ring Width histogram for the selected AV period was constructed for all of the candidate trees at each site (Figures 34, 35, 36, 37). The MNs for the AV period were then presentable for comparison among tree cores.

DM was calculated for each growth ring in a sample tree core as mean ring width minus measured ring width (sign retained). A DM histogram was then constructed for each tree core. Only the composite derivatives of the individual histograms are provided in this document (Chapter VII). The central axis was the zero reference and represented the MN value for the core. For all of the candidate trees on the site, the extremes of the range of DMs were determined and used as a fixed quantity on the horizontal axis of all of the histograms for that site. Therefore, the DM data for each candidate tree were plotted on a template with constant dimensions for an accurate comparison of DM magnitudes across a site. Each core had a different MN value and therefore the vertical MN line was positioned differently (to the right or left) on each histogram as a floating mean. On the vertical axis of the histogram, the RNs were spread from youngest at top to oldest at the bottom. The DM value for each ring was plotted as a horizontal bar extending to the left, if negative, or the right, if positive, of the vertical MN reference line.
Figure 34. Cache River Floodplain Cores: AV 18 Mean Ring Width.
Figure 35. Kalamazoo River at Swan Creek Cores: AV 43 Mean Ring Width.
Figure 36. Twin Lakes Cores: AV 22 Mean Ring Width.
Figure 37. Sherriff's Marsh Cores: AV 25 Mean Ring Width.
Streamflow Analysis Procedures - Kalamazoo River at Swan Creek

Unpublished digital gaging station data for the Kalamazoo River at Swan Creek (KS) locality were acquired from the USGS in Lansing, MI. Station information and tabulated daily maximum discharge data were provided on computer diskettes. Rating tables were also provided for the years that the station was active.

The gaging station was located on the Kalamazoo River at the highway M-89 bridge. Stage of the Kalamazoo River was measured continuously from Water Year (WY) 1952 (beginning October, 1951) through WY 1993 (ending September, 1993). USGS personnel converted the maximum daily stage measurements to tabulated discharge data based on rating tables that were recalibrated about every decade. For the purposes of this study, it was necessary to decode the discharge data back to stage data using the rating tables. A modified data set was created whereas the stage data were tallied for number of days per month that stage exceeded specified elevations. It was then possible to examine the data in the form of monthly, seasonal and annual summaries.

The data were regrouped and recalculated for correlation of streamflow “events” to the tree growth-ring record on the floodplain near the gaging station. The elevation of the natural berm between the floodplain forest (swamp) and the Kalamazoo River was determined by a field survey using a surveyor’s level and rod. This berm functions as a barrier to the entry of overbank flow into the swamp until a certain water level is reached at its lowest point. Following recession of the river floodwaters, the berm functions to trap floodwater in swamp basin, constituting a hydrologic event. The elevation of the low point of the berm was therefore considered the critical stage by which to evaluate the streamflow data. For each rating curve time
block, the discharge that correlated to “berm stage” was determined. “Overberm flow days” were then picked from the historical streamflow records, tabulated, and graphed for comparison to the tree-ring data.

**Historical Shoreline Image Analysis Procedures - Twin Lakes West**

Historical aerial photographs and maps were used to reconstruct the historical surface area of Twin Lakes West (TL) since 1916. The resources were acquired from a number of sources: (a) Kalamazoo NRCS regional office: 6/38, 8/50, 7/60, 9/67; (b) MDEQ Plainwell district headquarters: 9/78, 6/88; (c) topographic maps: Kalamazoo SW, Mich. 7.5’ 1973; Kalamazoo, Mich. 15’ 1916; (d) USDA-SCS Soil Survey of Kalamazoo County: Soil Sheet #14, 1974; and (e) personal field observations of shoreline, fall 1994.

Using these data, a total of 10 “snapshots” of the shoreline positions were acquired for a 79-year interval. The aerial photographs and topographic maps were scanned into a computer document as layers and re-scaled to a common scale. For each image, the shoreline was traced on a separate layer. The photographs were hidden and a composite illustration of the layered historical shorelines was generated (Figure 38). In order to differentiate and compare the historical shoreline positions from each other for the shoreline analysis, shoreline traces for arbitrary paired years were extracted from the composite and presented as individual illustrations (Figures 39, 40, 41, 42, 43). The historical shoreline traces were not symmetrical about each other because the shoreline migrates across an irregular and changing topographic surface. Occasional overlap of historical shoreline traces also occurred due to photographic parallax with respect to variability in camera position over the landscape among photographs. In addition, photographic quality was highly variable from flight.
Figure 38. Historical Shoreline Positions, Twin Lakes (TL), Composite.

Figure 39. Historical Shoreline Positions, Twin Lakes (TL), 1938, 1950.
Figure 40. Historical Shoreline Positions, Twin Lakes (TL), 1960, 1978.

Figure 41. Historical Shoreline Positions, Twin Lakes (TL), 1916, 1973.
Figure 42. Historical Shoreline Positions, Twin Lakes (TL), 1974, 1988.

Figure 43. Historical Shoreline Positions, Twin Lakes (TL), 1967, 1995.
to flight and spatially within a photograph (e.g., differential reflection quality). Therefore, tracing shoreline positions from the photographs required interpretation.

**Climatic Data Analysis Procedures - Sherriff’s Marsh**

Digital precipitation data for Michigan were obtained from the Michigan Department of Agriculture (MDA)/Michigan State University Climatology Program. Historical monthly total precipitation values in inches liquid equivalent were computed and tabulated for 2 stations on either side of the Sherriff’s Marsh (SM) site and for 1 station near the Twin Lakes (TL) site: (1) Battle Creek, MI (Airport), approximately 9 miles southeast of SM; (2) Hickory Corners, MI (Gull Lake Biological Station), approximately 2 miles west of SM; Kalamazoo, MI (State Hospital), approximately 3 miles southeast of TL.

The data were summarized as total annual precipitation and further differentiated into growing season and dormant season totals. Precipitation vs. Time line graphs were constructed for the different periods of record (Figures 44, 45, 46, 47, 48, 49, 50, 51). Five-year and 10-year moving averages, polynomial regressions, and the cumulative departure from the mean were computed and plotted on selected annual and seasonal precipitation graphs.
Figure 44. Annual and Seasonal Precipitation, Gull Lake Biological Station, MI, 1948-1994.  
Data Source: Climatological Data - Michigan, MDA.

Summary:
Annual  
mean = 35.9; range = 20.7 - 49.0
Growing Season  
mean = 18.0; range = 12.3 - 32.0
Dormant Season  
mean = 18.0; range = 18.2 - 29.3

Precipitation (inches, liquid equivalent)
Figure 45. Annual Precipitation, Gull Lake Biological Station, MI, 5-Year Moving Average, 1948-1994. Data Source: Climatological Data - Michigan, MDA.
Figure 46. Annual Precipitation, Gull Lake Biological Station, MI, 10-Year Moving Average, 1948-1994. Data Source: Climatological Data - Michigan, MDA.
Figure 47. Annual and Seasonal Precipitation, Gull Lake Biological Station, MI, 10-Year Moving Averages, 1948-1994. Data Source: Climatological Data - Michigan, MDA.
y = -0.001x^3 + 0.0745x^2 - 1.3869x + 38.532
R^2 = 0.3412

Summary:
mean = 35.9 in
median = 35.5 in
range = 20.7 - 49.0 in

Figure 48. Annual Precipitation With 3rd Order Polynomial Regression Trendline, Gull Lake Biological Station, MI, 1948-1994.
Data Source: Climatological Data - Michigan, MDA.
Figure 49. Annual Precipitation, Cumulative Departure From Mean, Gull Lake Biological Station, MI, 1948-1994. Data Source: Climatological Data - Michigan, MDA.
Figure 50. Monthly Precipitation, Composite, Gull Lake Biological Station, MI, 1948-1996. Data Source: Climatological Data - Michigan, MDA.
Figure 51. Annual Precipitation, 10-Year Moving Average, Battle Creek, MI, 1948-1994.
Data Source: Climatological Data - Michigan, MDA.
CHAPTER VI

SAMPLING SITES

Study Site Descriptions, Relevance to the Study, and Tree Core Sampling Programs

Field and laboratory work were conducted at 14 study sites. Four sites were selected for detailed examination of the hypothesis. Each of the 4 sites had a unique set of circumstances that was appropriate for examination of the research problem, such as hydrologic setting and suspected hydrologic impacts, documentation of hydrologic history, and the nature of the vegetation communities. Three of the sites were located in southwest Michigan and one in northeast Arkansas.

Cache River Floodplain (CF)

Location

Arrangements were made by Professor W. Thomas Straw with researchers at the Waterways Experiment Station (WES) of the COE to conduct a tree-ring investigation of a transect on the Cache River Floodplain in northeast Arkansas. The site was located approximately 2 miles southeast of Gregory, Arkansas, and was concentrated on the NW 1/4 of Section 22, T 6 N, R 3 W, Point Township, Woodruff County (Figure 52).

Precipitation and Growing Season

Average annual precipitation in the region is about 50 inches, 70% of which occurs from November through May (Smith, 1996). The growing season is about 210
days, with the first freeze occurring around October 25 and the last freeze around March 31. Average annual evapotranspiration is about 31 inches.

Geomorphology and Hydrogeology

The Cache River watershed is part of the Western Lowlands of the Mississippi River Alluvial Plain (Walton et al., 1996a). The Black Swamp floodplain is about 2.5 miles wide and the average Cache River channel slope is 0.3 feet/mile. Cache River water levels typically vary 10 feet in an annual cycle and discharge ranges from no flow to about 9900 cubic feet per second (Kleiss, 1996a). Change in elevation from
the main channel margin to the uplands is about 2.5-6.5 feet (Smith, 1996). The sources of water to the floodplain are precipitation and overbank flow from the Cache River.

The following soils are present in the study area (Smith, 1996): (a) Kobel Series (Vertic Haplaquepts), silty clay loam texture, Hydric; (b) Commerce Series (AERIC Fluvaquents), silty clay loam texture, Hydric; (c) Tuckerman Series (Typic Ochraqualfs), silty clay loam texture, Hydric; and (d) McCrory Series (Albic Glossic Natraqualfs), fine sandy loam texture, Non-Hydric. The Hydric modifier in the list indicates that the soil series is listed on the Hydric Soils List (U.S. Department of Agriculture, 1991).

Forest Plant Community

The dominant tree species in the Cache River floodplain forest were Quercus nigra, Q. phellos, Q. nuttallii, Q. lyrata, Liquidambar styraciflua, Taxodium distichum, Carya aquatica and Nyssa aquatica. Less frequent members of the mature floodplain forest trees included Fraxinus pennsylvanica, Celtis laevigata, and Ulmus americana. The primary constituents of the understory included Cornus foemina, Carpinus caroliniana, Fraxinus pennsylvanica, Cephalanthus occidentalis and Diospyros virginiana (Smith, 1996). The forest composition along the hydrotopographic gradient is zoned (Figure 53). The soil moisture regime and dominant tree species of each Forest Zone are listed in Table 1.

Site Relevance to This Study

Bottomland hardwood (BLH) wetlands of the southern United States, and the Lower Mississippi Valley region in particular, have become a subject of controversy in the past decade because of their rapid conversion to farmland in an absence of an
Figure 53. Cache River Floodplain Generalized Hydrotopographic Profile With Forest Zones and Hypothetical Growth-Moisture Curve.
<table>
<thead>
<tr>
<th>Floodplain Position Index (^1)</th>
<th>Soil-Moisture Regime (^\text{II})</th>
<th>Forest Type and Dominant Cache River Floodplain Tree Species (^\text{III})</th>
</tr>
</thead>
<tbody>
<tr>
<td>I. Intermittently Exposed</td>
<td>Soil inundation or saturation by surface water or groundwater typically exists on a nearly permanent basis throughout the growing season of the prevalent* vegetation, except during extreme drought periods.</td>
<td>River Swamp Forest Nyssa aquatica Taxodium distichum</td>
</tr>
<tr>
<td>II. Semipermanently Inundated or Saturated</td>
<td>Soil inundation or saturation by surface water or groundwater occurs periodically** for a major part of the growing season of the prevalent vegetation. Typically occurs during the spring and summer months with a frequency ranging from 51 to 100 years per 100 years. The total duration of time for the seasonal event(s) typically exceeds 25% of the growing season.</td>
<td>Lower Swamp Forest Quercus nuttallii Quercus lyrata Carya aquatica</td>
</tr>
<tr>
<td>III. Seasonally Inundated or Saturated</td>
<td>Soil inundation or saturation by surface water or groundwater typically occurs periodically for 1 to 2 months during the growing season of the prevalent vegetation. Typically occurs up to the beginning of the summer season with a frequency ranging from 51 to 100 years per 100 years. The total duration of time for the seasonal event(s) typically ranges from 12.5% to 25% of the growing season.</td>
<td>Backwater Forest 1 Quercus phellos Liquidambar styraciflua</td>
</tr>
<tr>
<td>IV. Temporarily Inundated or Saturated</td>
<td>Soil inundation or saturation by surface water or groundwater typically occurs periodically for short periods during the growing season but not totaling more than 1 month for the entire growing season of the prevalent vegetation. Typical frequency ranges from 11 to 50 years (1 to 10 years per 100 years). The total duration of time for the seasonal event(s) typically ranges from 2% to 12.5% of the growing season.</td>
<td>Backwater Forest 2 Quercus nigra Quercus phellos</td>
</tr>
<tr>
<td>V. Intermittently Inundated or Saturated</td>
<td>Soil inundation or saturation by surface water or groundwater rarely occurs periodically during the growing season of the prevalent vegetation, except during exceptionally high floods or extreme wet periods. Typical frequency ranges from 1 to 10 years per 100 years). The total duration of time for the seasonal event(s) is typically &lt;2% of the growing season.</td>
<td>Marginal Forest</td>
</tr>
</tbody>
</table>

\(^1\) Zones are illustrated in Figure 53 and are identified by Forest Type.

\(^\text{II}\) Adapted from Huffman and Forsythe (1981)

\(^\text{III}\) Adapted from Smith (1996)

* "Prevalent" refers to perennial plant species having an estimated areal coverage per hectare ≥30%

** "Periodically" refers to saturated soil conditions or inundation resulting from ponding from groundwater and/or rainwater, overland flow, or stream flooding that occur(s) on a detectable regular or irregular basis within hours, days, weeks, months or even years between events.
adequate understanding of their functions and values. Landsat image analysis has
shown that the BLH forest cover area of the Cache River Basin has declined from 65%
to 15% in the past 50 years (Kress et al., 1996).

The 85 km² Black Swamp portion of the Cache River Basin has been selected
by the U.S. Army Engineer Waterways Experiment Station (WES) as a study site for
wetland functions and values analysis in light of cumulative losses through time. This
BLH wetland region is suitable for long-term study because it contains large blocks of
public land, the natural hydrology of the system has not been significantly altered, and
much of the BLH forest is intact (Kleiss, 1996b). A multidisciplinary study of the
Black Swamp was launched in 1986 and the Cache River wetlands have been
designated as a RAMSAR wetland area of international importance.

The spread of trees across a 1 mile floodplain gradient was expected to be a
favorable setting for comparison of growth trends to position on the floodplain. If tree
growth was sensitive to hydroperiod and the average residence time of floodwaters
decreased with distance from the channel, then a pattern of radial tree growth should be
apparent along the transect. If longer than average floodwater and residual soil
saturation residence times were directly related to increased plant physiological stress,
then, according to the study hypothesis, the rate of radial tree growth should have
increased towards the floodplain margins.

At a certain distance away from the channel, the floodwater residence time may
actually become favorable for growth rather than stressful. This hypothetical model is
illustrated as a Growth-Moisture Curve in the upper portion of Figure 53. The shape
and position of the curve are approximated. The premise of this argument is that a
certain frequency and duration of floodwaters is beneficial to tree growth. This would
occur in the Zone of Enhanced Growth (Figure 53) and is represented by the upward
rising limbs and inflection in the curve. Any greater flood frequency and/or duration,
as would be the case in the region closer to the channel, would be stressful to growth; hence, the Stress Zone. Nearer the floodplain margin, in the Zone of “Average” Growth, the reduced supply of floodwater would fall short of the moisture requirements for ideal growth and the curve would slope downward. The ordinary high water mark was expected to be the position on the floodplain that marks the change from enhanced growth to “average” growth. Its position on the diagram was estimated from field observations. In the upland where the moisture supply is entirely precipitation-dependent, tree growth would taper off.

The growth-moisture curve along the floodplain gradient is expected to vary among species due to their genetic predisposition to growth. Its shape is based solely on hydrology and assumes all other variables are held constant. Therefore, soil textural contrasts would allow for differential drainage along the profile. Soil composition contrasts would allow for variable nutrient availability to the roots. Competition among trees due to crown stratification would cause variable exposure to light for photosynthesis.

**Sampling Program**

Tree increment cores were taken from trees along an established transect (WES Transect B) in the Black Swamp (Figure 52). The ~1 mile long sampling transect was oriented NW (upland end) to SE (channel end), perpendicular to the Cache River. Cores were sampled from upland trees above the break in slope of the floodplain margin and periodically from floodplain trees down the subdued surface gradient to the Cache River channel. Thirty-four tree increment cores were taken from 8 species: *Quercus nigra*, *Q. phellos*, *Q. nuttallii*, *Q. lyrata*, *Liquidambar styraciflua*, *Celtis laevigata*, *Taxodium distichum*, and *Nyssa aquatica*. From the original sample, 20
were found to be suitable for the analysis. Their position on the Hydrotopographic Gradient was recorded at the time of sampling (Figure 18).

Kalamazoo River at Swan Creek (KS)

Location

The Kalamazoo River at Swan Creek site was located approximately 8 miles northwest of Allegan, Michigan, where highway M-89 crosses the Kalamazoo River (Figure 54). The study area straddled the center of the boundary between the top of Section 5 of Valley Township and the bottom of Section 32 of Heath Township in Allegan County. The study area was divided into northern and southern sections on the east side of the Kalamazoo River, separated by highway M-89.

Precipitation and Growing Season

Based on the first and last average frost dates, the growing season is generally May 15 to October 1, approximately 150 days long (U.S. Department of Agriculture, 1987). Average annual precipitation is 35.7 inches.

Geomorphology and Hydrogeology

The study area is centered on the Kalamazoo River floodplain, which varies in this region from about 1/4 mile to 1 mile across (Figure 54). The floodplain margin abruptly terminates at a steep slope into the upland on both sides of the river. The adjacent upland flats are an average of 50 to 60 feet above the floodplain. The sources of water to the floodplain are precipitation and periodic flooding. Overland flow from the steep slopes is probably limited to meltwater on frozen soils because the upland sandy soils otherwise have a high hydraulic conductivity.
Figure 54. Regional Topography - Kalamazoo River at Swan Creek (KS).

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Swan Creek Marsh was formerly used for crop production. Flooding was controlled by a private dike to retain Kalamazoo River floodwaters. The State of Michigan constructed the current dike in 1950, plus 3 dams on Swan Creek, that created a permanent flooding that is currently managed for waterfowl (esp. Canada geese) as part of the Allegan State Game Area (John Lerg, personal communication).

Soils on the floodplain in the study area are Sloan Series (Fluvaquentic Haplaquolls) with a silt loam texture (U.S. Department of Agriculture, 1987). They are included on the Hydric Soils List (U.S. Department of Agriculture, 1991). Soils in the uplands are Oakville Series (Typic Udipsamments) with a fine sand texture and are not included on the Hydric Soils List. Observations from soil borings indicated that depth to mottling begins at 6 inches near the channel margin to 18 inches at the base of the slope into the uplands. The coarser soils exhibited organic streaking, confirming the periodic presence of an aquic moisture regime.

A land survey was conducted to better understand the microtopography of the floodplain interior of the southern study area because the contour interval of the USGS topographic map was 10 feet (Figure 55). Water from overbank flow of the Kalamazoo River is inferred to become entrapped in a shallow depression at the center of the southern study area, bounded by a subdued berm parallel to the river to the south and west, the raised highway M-89 to the north, and the upland slope to the east (Figure 55). Loss of water from the wetland after flooding occurs by way of several mechanisms. During recession of the floodwaters, water drains back into the Kalamazoo River over the berm, across the parking lot at the public access, and across low drainage courses through the berm. Water retained in the depression, up to 2.5 feet deep, is drained through the soils and lost to the atmosphere through evapotranspiration. Given the full canopy of the forest, evapotranspiration could be a considerable hydrologic loss during the growing season.
Flooding of the southern section of the study area is expected to be more frequent than in the northern section because the M-89 bridge functions to constrict high flows and the dike on the south and west margins of the Kalamazoo River obstructs flow to the west that once flooded the Swan Creek Marsh (Figure 55). It is hypothesized here that the berm in the southern study area developed as a consequence of these human alterations to the local geomorphology. The suspended load of sand is deposited landward of the channel during flood stage due to the strong velocity contrast away from the channel. Using a hand auger, the berm was confirmed to have a sand core. Prior to the construction of M-89 and the bridge, the berm may not have been present.

Forest Plant Communities and Wetland Classification

The forest interior was an open-floored, dense, codominant canopy of mature *Fraxinus pennsylvanica* (60% of stems, basal area ~100 square feet/acre), *Acer saccharinum* (20% of stems, basal area ~45 square feet/acre), and *Quercus bicolor* (~5% of stems, basal area ~25 square feet/acre), with *Platanus occidentalis* (~5% of stems), and *Ulmus americana* (~2% of stems) concentrated at the margins. Most trees, particularly the *Fraxinus pennsylvanica*, had broad spreading root systems with buttresses. A shrub and sapling understory was absent. Ice scars were present as dents in tree stems up to 2 feet above the ground surface on all sides of the trees, distributed from the river margin to M-89. The vegetation on the raised berm had a more open canopy, composed of a relatively dry-adapted assemblage of *Ulmus americana*, *Juglans nigra*, *Platanus occidentalis*, and *Celtis occidentalis* with a dense shrubby understory of *Crataegus* sp.

The adjacent upland forest community was composed of *Quercus rubra* (~50% of stems, basal area ~80 ft²/ac), *Fagus grandifolia* (~15% of stems, basal area ~20
\(\text{ft}^2/\text{ac}\), \textit{Prunus serotina} (~20% of stems, basal area ~20 square feet/acre), with \textit{Quercus alba} and \textit{Pinus strobus} as minor constituents. The understory was almost entirely \textit{Acer saccharum} saplings.

The mature trees of the floodplain forest canopy were relatively even-aged and sized, averaging more than 80 years. A number of the \textit{Fraxinus pennsylvanica} and \textit{Quercus rubra} trees were more than 100 years old.

The wetlands of the study area are seasonally flooded lowland hardwood swamps (Eggers and Reed, 1987; Cowardin et al., 1979). They are part of the floodplain wetland system that parallels the Kalamazoo River on both sides along its course. It can therefore be classified as a hybrid of a surface-water slope and surface-water depression wetland, using Novitzki’s (1979) hydrogeomorphic classification system.

\textbf{Site Relevance to This Study}

The taxonomic character of the floodplain forest trees suggests moisture-tolerance. Historical changes in hydrology may have included climatically wet periods and punctuated or long-term long-duration streamflow residence times due to geomorphological changes caused by humans, such as the channel margin modifications and the M-89 bridge. Prolonged flooding during the growing season may have enhanced or retarded the growth of the trees. Correspondingly, relatively dry years with reduced flooding may have caused relatively retarded or enhanced growth. The study question at this site was: Can relatively long- or short-duration annual floodwater residence times be correlated with the growth ring record of the floodplain trees? The processed results of the streamflow record described in Chapter V were to be compared with the growth ring record of the floodplain trees in order to address this question.
Sampling Program

The study area included the environmental gradient beginning at the channel margin, and extended across the floodplain into the upland area above the break in slope at the floodplain margin. Increment core samples were taken from 31 trees of 8 species: *Fraxinus pennsylvanica*, *Acer saccharinum*, *Quercus rubra*, *Quercus bicolor*, *Platanus occidentalis*, *Ulmus americana*, *Juglans nigra*, and *Celtis occidentalis*. Twenty-five of the cores were used in the analysis. Distribution of the sample trees across the site was mapped in Figure 56 in plan view and plotted along the Hydrotopographic Gradient illustrated in Figure 19.

Twin Lakes (TL)

Location

The Twin Lakes study site was located approximately 2 miles north of the City of Kalamazoo, mostly in the W 1/2 of Section 36, T 1 S, R 12 W, Alamo Township, Kalamazoo County, Michigan (Figure 57).

The dendrohydrological analyses of this study were restricted to the west region of the lake system (hereafter referred to as Twin Lakes West). It was bounded on the west side by U.S. Highway 131 and the north side by Ravine Road, which also crossed the connection between the north and south basin segments.

Precipitation and Growing Season

Based on the first and last average frost dates, the growing season in Kalamazoo County is generally May 10 to October 1, approximately 160 days long (U.S. Department of Agriculture, 1979). Average annual precipitation is 34.4 inches.
Figure 56. Site Map With Sample Trees - Kalamazoo River at Swan Creek (KS).
Figure 57. Study Area Topography - Twin Lakes (TL).
Geomorphology and Hydrogeology

Twin Lakes lie at the center of an irregular closed depression in central Kalamazoo County, Michigan, located on the Galesburg-Vicksburg Outwash Plain deposits (Monaghan and Larson, 1982). There is no apparent surface drainage from the ~2 mi² basin. The west boundary of the depression was cut off by fill associated with the construction of highway U.S. 131. Equilibration of the water level across Ravine Road between the two lake segments has been maintained with culverts.

Local residents report a continuous, unprecedented rise in the level of the lake system since the late 1950s. This observation is supported by landowner photographs of widespread cultivated fields present in the mid-1950s that are now inundated. The “lake” at that time was limited to a few small disjunct ponds that were reported to dry up from time to time.

The cause of the water level rise is enigmatic. Local residents and scientists speculate about the obstruction of drainage of the system by highway U.S. 131. Seepage meter estimates conducted by the author in an independent study suggest a strong recharge gradient along the margin of the highway U.S. 131 fill at the lake margin, while discharge was present around the other lake margins. This preliminary hydrologic data is insufficient to characterize the recharge-discharge relationships of the system, but they are consistent with the general speculation about the influence of highway construction on the system hydrology.

The soils around the lakes in the study area are mapped as two types (U.S. Department of Agriculture, 1979; U.S. Department of Agriculture, 1991): (a) Spinks Series (Psammentic Hapludalfs), loamy sands, Non-Hydric; (b) Coloma Series (Alfic Udipsamments), loamy sands, Non-Hydric. Both of these soils are rapidly permeable.
and excessively drained. They extend across the shoreline into the lake at all sampling areas. Histosols were not observed at the lake margins.

**Forest Plant Community**

The forest around the lakes was a fairly uniform assemblage of *Acer rubrum*, *Fraxinus americana*, *Ostrya virginiana*, *Prunus serotina*, and *Quercus rubra*. The upland character of the forest continued across the lake margin into the lakes. Standing dead trees were common in the water around the entire lakes and their frequency decreases away from the shoreline. Nearer the margin, live trees were present in the water. Many of the submerged trees were apparently stressed or dying, as judged from the high frequency of leafless branches and mid-summer yellowing of many of the leaves. There was no forested wetland community around the lake. The lake clearly had the appearance of a recently flooded upland ecosystem.

Due to the relatively recent development of the current lake level, the wetland margins are biologically and edaphically youthful. Shoreline plants are limited to opportunistic emergent sedges, rushes and cattails, and the shrub zone is a monotypic community of *Cephalanthus occidentalis*.

**Site Relevance to This Study**

There has been an apparently continuous rise in lake water levels for the past 30 years. The shoreline has migrated well up into the adjacent uplands and has impacted the mixed mesophytic forest. These conditions allow for examination of the effect of anaerobic stress on upland trees. According to the hypothesis and the anaerobic stress models, upland trees are particularly vulnerable to strong physiological impairment when they are exposed to soil saturation. If the trees responded according to Anaerobic Stress Model 1 (Figure 12), a datable signature of
sensitive ring series should be useful in reconstructing the landward migration of the shoreline. Some control on the timing of lake area changes is available from 79 years of intermittent aerial photographs and maps.

**Sampling Program**

Tree increment cores were taken along the Hydrotopographic Gradient. Some dead and living submerged trees were included in the sample. Thirty-four tree cores were taken from 8 species and 24 of the cores from 3 species were used in the growth ring analyses (Figure 20).

**Sherriff's Marsh (SM)**

**Location**

Sherriff's Marsh is located at the extreme northeast corner of Kalamazoo County, in the W 1/2 of Section 11, T 1 S, R 9 W, Ross Township, Michigan. The study area was limited to an approximately 1/2 square mile region bounded by B Avenue to the north and 45th Street to the east (Figure 58).

**Precipitation and Growing Season**

Based on the first and last average frost dates, the growing season in Kalamazoo County is generally May 10 to October 1, approximately 160 days long (U.S. Department of Agriculture, 1979). Average annual precipitation is 34.4 inches.

**Geomorphology and Hydrogeology**

Sherriff's Marsh is located on the Augusta Creek Outwash deposits (Monaghan and Larson, 1982). It is part of a surface water flow-through wetland system that
Figure 58. Study Area Topography - Sherriff's Marsh (SM).
originates about 1 mile to the northeast of Hamilton Lake and feeds into Augusta Creek on its western border. The wetlands are mosaics of widespread palustrine shallow marshes with shrub-carr and hardwood swamp margins (Eggers and Reed, 1987; Cowardin et al., 1979).

Oshtemo Series (Typic Hapludalfs) soils were present in the uplands (U.S. Department of Agriculture, 1979). They are well-drained, moderately rapidly-permeable sandy loams and are not included on the Hydric Soils List (U.S. Department of Agriculture, 1991). In sharp contrast, the lowlands were characterized by Houghton Series (Typic Medisaprists) muck soils, which contain more than 51 inches of organic material at the surface and are typical hydric soils of a well-developed marsh ecosystem (U.S. Department of Agriculture, 1991).

Forest Plant Community

The wetland area studied was a marsh margin with the apparent encroachment of a wetland forest. The wetland trees were dominated by open-grown *Fraxinus* sp. with occasional *Quercus bicolor*. The wetland margin supported a distinct community of *Ulmus americana, Carpinus caroliniana* and clustered *Tilia americana*. The upland forest was characterized by *Fraxinus americana, Prunus serotina* and *Pinus strobus*. The specimens of upland *Fraxinus americana* were not morphologically differentiable from the *Fraxinus* sp. in the marsh.

Site Relevance to This Study

The close proximity of a weather station made this site especially suitable for comparison of upland and wetland tree growth with the 46-year precipitation record. Because mature trees were present well out into the marsh, it was hypothesized that during relatively dry sets of years, the wetland trees might be released from anaerobic
stress and the upland trees would experience water deficiency stress. Conversely, during wet periods, the wetland trees would experience reduced growth and the upland trees would have a signature of more favorable growth.

**Sampling Program**

Although three distinct sampling transects were used, they were treated as a composite site in the tree-ring analysis (Figure 58). The hydrologic and forest conditions were similar at the three transects. The transects were positioned along 2 peninsulas that extended into the wetland because there was a relatively large amount of wetland edge in these areas. Thirty-two cores were taken from 9 tree species and 24 of the cores from 7 species were used in the analysis. The composite distribution of the sample trees along the Hydrotopographic Gradient is illustrated in Figure 21.
CHAPTER VII

RESULTS AND DISCUSSION

Utility of the Tree Core Samples and Basic Data

One hundred eighty-six tree cores were collected from trees at 14 sites. They were all mounted and examined under the microscope. Ninety-seven of the cores were measured for growth ring widths over their entire length of record. The remaining cores were determined to be unsuitable for the quantitative analyses because they were taken from species that lacked sufficient ring boundary resolution to count the continuous time series, or they were judged to lack useful numerical information (e.g., complacent series or absence of comparative hydrologic data).

A table was prepared for the plant taxa discussed and analyzed in this study (Appendix A). It cross-references the authors of the scientific names, provides some of the common names, and lists the taxonomic abbreviations used in the figures, graphs and text. Using the NWI system listed in Figure 8, the indicator status of the taxon is also listed in Appendix A.

The unprocessed ring-width data for each core were initially plotted against ring number on RW vs. RN line graphs (Appendices B, C, D, E). These curves served as the baseline reference for differences in growth throughout the lifetime of the sample trees until they were sampled. Exponential or polynomial growth trendlines were fit to the RW vs. RN data as described in Chapter II. The coefficient of determination ($R^2$) of the trendlines was not expected to be high in the sensitive samples. Where there was a low $R^2$ associated with a trendline, it did not necessarily mean that the equation was not a good fit for the growth trend. Low $R^2$'s may have
been the result of a relatively strong deviation of the observed values from the expected values during periods when the influence of a certain limiting factor was prevalent. The exponential or second order polynomial smoothing functions provided the best fit in most cases.

A set of cores from the Sarett Nature Center site will be used to illustrate considerations used in ring-width interpretation. Three cores of *Fraxinus pennsylvanica* (SNC 1, 2, 7) were co-plotted on the same RW vs. RN graph (Figure 59). SNC 1 and SNC 2 were taken from the same tree at right angles to each other. They reveal closely coordinated growth patterns on different portions of the trunk. A simple linear regression analysis of the two sets of data plotted on a scattergram gave a coefficient of determination ($R^2$) of 0.90, indicating that 90% of the variation in ring width of one core could be explained by the corresponding ring widths in the other core (Figure 60). This correspondence was typical of other replicate samples from the same tree throughout this study. Therefore, single cores were routinely taken from most trees for analysis if the trees met the sample selection guidelines.

SNC 7 was taken from a tree of similar size about 50 feet away from SNC 1/SNC 2 on the submerged floodplain wetland mosaic. Two growth patterns were evident in the 2 trees. Of particular interest was the coordinated, temporary shift in growth reduction centered about 1931. The trees also showed a marked, relatively stable growth reduction at different times. For SNC 7 it began in the late 1940s. It was more pronounced in SNC 1/SNC 2, beginning in the late 1960s. In the absence of hydrologic data, the cause of these shifts is unknown. The data illustrate that cause-and-effect interpretations about tree growth should be based on strong coordinated shifts among 2 or more trees during short time intervals that represent punctuated events, or on the comparison of long-term trends in one or more trees that record slower changes in growing conditions.
Figure 59. Sarett Nature Center, Fraxinus pennsylvanica, Ring Width Distribution, SNC 1, 2, 7.
Figure 60. Scatter Plot of Two Cores From Same Tree (SNC 1,2), *Fraxinus pennsylvanica*.
Cumulative Growth Curves

Because ring width was always ≥0, it was possible to organize the data in a form that was cumulative with time. Cumulative ring width from the interior (CWR) vs. time graphs were constructed for most cores. Consecutive plotted points on the cumulative growth curves represent annual additions to the radial growth increment. The slope of the tangent or linear regression line for a selected time interval represents the average relative growth rate. The steeper the slope, the larger the growth rate for that period of time. The relative slopes of line segments corresponding to various intervals were used to compare the changes in growth rate throughout the life of a tree.

Three *Quercus bicolor* trees were sampled at Sherriff’s Marsh on the exposed basin fill (Figure 21). The cumulative growth curves of SMC 14, 16 and 17 have similar, but staggered morphologies (Figure 61). All three trees experienced a sudden, concomitant growth reduction in 1957 (Appendix E). Each tree also exhibited a break in slope on the cumulative growth curves that represented a growth surge in the 1960s (Figure 61). SMC 16 was the first to surge, beginning in 1963. The growth rate increase of SMC 17 began in 1965 and that of SMC 14 began in 1968. Following the surges, the growth of the trees fluctuated considerably. The growth suppression period of these trees matched quite well to the droughty interval of the late 1950s and early 1960s (Figures 44, 45, 46, 47, 48, 49, 51). These OBL/FACW+ trees all had root systems that were perched on histosols of the wetland interior, suggesting extremely shallow root development on saturated soil conditions. The tree roots were able to effectively exploit the thin aerobic surface layer of the saturated soils as long as the water table was high during the growing season. It is suggested here that during the subsequent dry years, the water table in the wetland dropped significantly and the exposure of the roots to a water deficient environment was stressful to some trees. It
Figure 61. Sherriff's Marsh, Cumulative Growth Curves, *Quercus bicolor*. 
was only after the "normal", near surface water table was restored that the trees were able to function as they had prior to the drought.

**Marginal Tree Growth Responses**

Three cores were taken from a *Fraxinus americana* tree rooted on a steep slope in 21 inches of water in a small embayment at Twin Lakes during the winter of 1995 (Figure 62). TLC 30 and TLC 32 were taken from the downslope side of the stem, approximately 2.5 inches apart at the same height. Parallel changes in slope of the 2 cumulative growth curves through time represent a close correspondence in growth as would be expected under normal circumstances. TLC 31 was taken from the upslope side of the stem. Its growth pattern was markedly different from that on the other side. It experienced more rapid growth in the early life of the tree and then paralleled the growth on the other side for most of the tree's life. There were recognizable breaks in slope in TLC 30 and TLC 32 at 1952, 1973, 1985 and 1989 that were not apparent in TLC 31. Because the tree was otherwise straight, vertical, healthy and had a symmetrical, codominant crown, the sudden change in environment on one side of the tree may have been the rise of the water table, and, ultimately, submergence. The increase in growth from 1985 to 1991 on the downslope side may have been the result of the favorable moisture conditions associated with slow rise of the water table into the root zone. With continued water table rise and submergence, anaerobiosis may have begun to set in, resulting in stressed growth physiology in this FACU species. It is anticipated that, with continued submergence, this tree will ultimately die as others already have further downslope and further out into the lake.

The upslope side of the tree did not respond similarly in recent years. This may be related to the orientation of the root system with respect to the direction of rise of the water level. On the downslope side of a tree, the first part of the roots to
Figure 62. TLC 30, 31, 32 Cumulative Growth Curves (*Fraxinus americana*).
experience the increased moisture conditions that would accompany a lake level rise are
the root tips. Roots on the upslope side of the tree would encounter increased moisture
conditions first at the trunk and finally at the tips. If the tips are the most
physiologically active portion of the root, then the response to anaerobiosis on the
upslope side of the stem should be less abrupt and later than that on the downslope
side. These inferences are based on the hypothesis that circumferential variability in
the root environment is accompanied by differential growth responses in the stem on
the corresponding side of a tree.

A forked *Fraxinus americana* tree was found on a steep slope at the Twin Lakes
site that was half rooted in water. One fork was leaning slightly upland and the other
leaned slightly over the water. A core (TLC 7) was taken from the upland side of the
upland fork and another (TLC 5) was taken on the lake side of the other fork. A RW
vs. RN plot of both cores showed that growth was generally coordinated throughout
most of the tree’s life history (Figure 63). Growth decreased steadily from 1941
through 1967. A coordinated, temporary growth reduction occurred during 1949 and
1950. A spike of accelerated growth occurred between 1968 and 1978, followed by a
sudden growth reduction that persisted until the time of coring in 1994. During the
1968 to 1978 period, growth rates in the two stems diverged. The upland stem grew
at a more rapid rate than the other stem. Both stems responded to a growth

Annual precipitation for Kalamazoo was plotted against time (Figure 64) and
was also co-plotted with TLC 7 RW against time (Figure 65). The rise and fall in
growth from 1968 to 1978 did not directly correspond to the fluctuations in annual
precipitation. However, the increase in growth did follow the trend of recovery from
the drought of the early 1960s. The subsequent abrupt drop in growth after 1975
occurred while the precipitation trend continued to increase. The similar growth
Figure 63. Twin Lakes (TL), Fraxinus americana, Ring Width Distribution, TLC 5, 7.
Figure 64. Annual Precipitation, Kalamazoo, MI, 1931-1987.
Data Source: Climatological Data - Michigan, MDA.
Figure 65. Kalamazoo Annual Precipitation and TLC 7 Ring Width vs. Time.
reduction that was experienced by the stem leaning toward the lake (TLC 5) can be explained by the same reasoning used in the interpretation of TLC 30 and TLC 32. That is, the increase in water availability initially enhanced growth, but growth physiology was eventually impaired by the continued rise in water levels and anaerobiosis. There was no field evidence to indicate that the upslope stem had ever been submerged, given that the core was taken at the historical maximum in lake water level (discussed later in this chapter). It is possible that the water table rose close enough to the surface to cause anaerobiosis in the root zone of the upland stem. If this were not the case, the water surplus stress in the lakeward stem may have influenced the physiology of the landward stem.

Dead Trees

Five dead trees in standing water were cored at Twin Lakes (Figure 20). TLC 22 was a *Fraxinus americana*, 34 feet offshore and under 32 inches of water. TLC 23 was a *Fraxinus americana*, 23 feet offshore and under 25 inches of water. TLC 24 was a *Fraxinus americana*, 15 feet offshore and standing in 19 inches of water. TLC 17 was a *Fraxinus americana* 18 feet offshore. TLC 12 was a *Quercus rubra*, 3 feet offshore and in 4 inches of water. Their cumulative growth curves are illustrated in Figure 66. Because the absolute time of death of the trees could not be established from regional chronologies, the cumulative growth curves are likely asynchronous and the x-axis yearly designations are approximations. The *Fraxinus americana* trees all experienced a period of reduced growth before mortality. The timing of the stress was pronounced in TLC 22 around year “1983” and the tree apparently functioned under stress for approximately 10 years before dying (Appendix D). It was located farthest from shore of the 5 trees and had the longest period of stressed growth. TLC 17, 23 and 24 all showed a marked reduction in growth about 5 years before death, followed
Figure 66. Twin Lakes, Cumulative Growth Curves, Dead Trees.
by a temporary recovery and sudden death (Appendix D). TLC 12 died abruptly, although the temporary growth decrease 5 years prior to death was possibly the initial response to soil saturation. Judging from these cores of dead trees and the survival of other submerged trees close to the lake margin, it appears that these two FACU species are adapted to cope with saturated soil conditions for about 5-10 years before mortality occurs.

**Tree-Ring Sensitivity Analyses**

Sensitivity analyses were performed on each core using the Mean Sensitivity formula presented in Chapter II (Figures 22, 23, 24, 25). The average mean sensitivity and mean sensitivity range for all of the cores at each site were also calculated. The average mean sensitivity ranged from 0.22 at TL to 0.28 at SM. The average mean sensitivity range across all 4 sites was 0.15 to 0.6, although only 2 cores from CF exceeded 0.4. These relatively homogeneous ranges that fall well below the maximum possible sensitivity of 2.0 suggest that the ring-to-ring variability in ring-width was low on average and that the signal-to-noise ratio was relatively weak. However, unremarkable mean sensitivity values do not preclude the presence of stressed growth ring intervals in individual cores.

**Standardization and Composite Ring-Width Chronologies**

Ring-width chronologies (RWCs) are typically prepared for a site in traditional dendrochronological studies. Composite RWCs were prepared for each of the 4 sites examined in this study (Figures 26, 27, 28, 29). These figures were based on all of the cores from all of the species at each site, as labeled on the site-specific generalized hydrotopographic profiles. Ring-width indices (RWIs) for each core were computed
using the curve fitting functions given in Appendices B, C, D, E. RWIs for replicate samples from the same trees were averaged before their inclusion into the summaries.

**Cache River Floodplain (CF) RWCs**

At the Cache River Floodplain site, the mean RWI ranged from 0.04 in 1927 to 1.55 in 1958 (Figure 26). The 1925-1931 interval was a pronounced low in the growth data and was the lowest set of RWI values among all of the 4 study sites. Intermittent lows occurred in 1934, 1937, 1954, 1963 and 1988. Intermittent highs occurred in 1946 and 1958.

In the absence of hydrologic data, it is not possible to attribute the 1925-1931 low in the mean RWI to a particular stress. The strong deviation of this interval from the remainder of the record suggests that there was a widespread stress to tree growth across the site in the late 1920s. Concurrent relatively dry or wet climatic conditions may have contributed to this widespread tree growth suppression.

**Kalamazoo River at Swan Creek (KS) RWCs**

The Kalamazoo River at Swan Creek site had the most uniform RWC (Figure 27). The maximum mean RWI value (1.58) occurred in 1937 and the second highest occurred in 1993. The minimum mean RWI value (0.79) occurred in 1932. The indices were otherwise distributed as apparently random fluctuations.

There were no obvious or suspect growth-stressed intervals in the composite RWC. Alternative analyses described later in this chapter were used to determine if a hidden stress response was present.
Twin Lakes (TL) RWCs

Several stressed intervals were apparent from the Twin Lakes RWC (Figure 28). The most pronounced interval was centered on the minimum mean RWI (0.67) for the site in 1966. The low was preceded by a decline over the previous 6 years, and was followed by a steady increase in mean RWI until 1974, the highest peak in more than 25 years. Other low periods included 1935 through 1938 and 1990 through 1992. The maximum RWI (1.64) occurred in 1919. A notable RWI high in 1983 was followed by a general decline until 1991. These results are compared to historical shoreline reconstructions and precipitation history later in this chapter.

Sherriff's Marsh (SM) RWCs

A marked low in the mean RWI occurred in 1959 at Sherriff's Marsh (Figure 29). The low was somewhat evenly spread over the period from 1956 through 1962. The inflection was preceded by a 13-year steady decline and followed by a rapid 8-year increase. Two precipitous peaks in mean RWI stood out from the remainder of the data in 1928 and 1979. These results are compared to local precipitation history later in this chapter.

Utility of the Composite Ring-Width Chronologies

In traditional dendroclimatological studies composite RWC is a good first indicator of widespread, significant physiological stresses to trees across a site or region (e.g., Fritts, 1976). However, the lack of an observed stress signature does not necessarily mean that significant growth-limiting conditions were not present. The limitations of composite RWCs in this dendrohydrological study are twofold. First, species differ in their genetic predisposition to physiologically respond to various
environmental stresses. The effect of mixing species in the composite chronology would be a diminution of the amplitude of the growth responses of the species. Stress-tolerant species would have the effect of decreasing the signal contributed by stress-sensitive species. Second, this study targeted sites where the trees were distributed along a hydrotopographic gradient. Hydrology was expected to be variably limiting to growth in trees positioned along this gradient. Therefore, the effects of stress differences along the gradient would be diluted in the composite chronology. Traditional dendroclimatological studies do not encounter this problem because the limiting factor, climate, is generally assumed to be uniformly distributed across a sampling site.

The traditional dendrochronological approach to constructing composite RWCs is not practical for dendrohydrological applications. However, compartmentalization of a site into zones where the hydrologic limiting factor is expected to be uniform allows for the construction of a set of internally-homogeneous chronologies that can be used to compare stressed and unstressed growth regions along the hydrotopographic gradient.

Taxon-Specific Ring-Width Chronologies

Taxon-specific RWCs have more potential than composite RWCs for illustrating conditions limiting to tree growth. In order for taxon-specific RWCs to express growth-limiting conditions, taxon selection is critical. The taxon must be physiologically sensitive to variability in exposure to the growth-limiting factor. Anaerobic stress sensitivity information in the botanical and dendrochronological literature is limited. Therefore, taxon selection in this study was somewhat arbitrary and guided primarily by the availability of samples. Only those species for which a sample of 12 or more specimens were available were used in the taxon-specific RWC
constructions. Information from taxa with a smaller sample size was judged to be less reliable because growth eccentricities in individual trees could have significantly altered the general trends. Larger samples allowed for the recognition and exclusion of trees or sequences that exhibited aberrant growth patterns.

The collective species of the genus *Quercus* were used in the taxon-specific RWC analysis for the CF site (Figure 67). A 1933 low and 1957 and 1974 highs in the mean RWI were outstanding from the other data. The mean RWI otherwise varied randomly in magnitude from year to year, as it did in the composite RWC.

Useable samples from the 3 southwest Michigan sites were all overwhelmingly dominated by *Fraxinus* spp. Although *Fraxinus* spp. were commonly among the dominants of both the upland and wetland forest assemblages, their dominance in the useable samples was also a consequence of their consistently readable sequences. There were other species (e.g., *Acer saccharinum*, *Acer rubrum*) that may have been present in higher relative frequencies, but their poor growth-ring readability precluded their use in the analysis. The *Fraxinus pennsylvanica* RWCs at the KS, TL and SM sites were all very similar to the corresponding composite RWCs, most likely because *Fraxinus pennsylvanica* dominated the composite RWCs (Figures 68, 69, 70).

**Taxon-Specific Ring-Width Subchronologies**

The taxon-specific RWGs were further differentiated with respect to tree position on the hydrotopographic gradient. The boundaries of the sensitive and complacent zones on the site-specific hydrotopographic profiles (Figures 18, 19, 20, 21) were used to group and average the RWIs for the same samples used in the taxon-specific RWGs. Core data from trees in the marginal zone were distributed among the sensitive zone or the complacent zone data sets, or were excluded from the analysis if their hydrologic status was uncertain.
Figure 67. Cache River Floodplain (CF), Quercus spp. Ring-Width Chronology.
2.5

Mean RWI = 1.08
Max RWI = 1.74
Min RWI = 0.72

Figure 68. Kalamazoo River at Swan Creek (KS), *Fraxinus pennsylvanica* Ring-Width Chronology.
Figure 69. Twin Lakes (TL), *Fraxinus americana* Ring-Width Chronology.
Figure 70. Sherriff’s Marsh (SM), *Fraxinus* spp. Ring-Width Chronology.
Using the same taxa as in the taxon-specific RWCs, two types of illustrations were constructed to characterize their distribution. First, the mean RWI for the taxon was plotted against time for each of the zones on the same set of axes (Figures 71, 72, 73, 74). These taxon-specific ring-width subchronologies (RWSs) permitted a qualitative assessment of the convergence and divergence of the mean RWI in the two zones through time. At all 4 sites, there was a mixture of close correspondence and considerable deviation in zoned RWSs through time.

A second plot was constructed of a single line that represented a year-by-year computation of the mean RWI difference (RWID) between the Sensitive Zone minus the Complacent Zone trees. At all 4 sites, there was a mixture of close correspondence and considerable deviation in zoned RWSs through time (Figures 75, 76, 77, 78). The sign was retained in the plot. When the two curves in the mean RWSs converged, the difference in the mean RWI approached zero. For a given year, when the mean RWI of the Sensitive Zone trees was larger than that of the Complacent Zone trees, the difference was positive and plotted above the horizontal axis. During periods when the mean RWI difference line was above the horizontal axis, average growth in the Sensitive Zone was greater than that in the Complacent Zone, and vice-versa. The positive or negative amplitude of the line reflected the magnitude of the growth difference between trees in the two zones.

For the CF site, the Quercus spp. mean RWID amplitude was strongest between 1955 and 1960, as trees in the Sensitive Zone grew faster than those in the Complacent Zone (Figure 75). Sensitive Zone growth was also favored in the periods 1965 through 1971 and 1984 through 1987. The longest period of favored Complacent Zone Growth was from 1972 through 1983.

Growth at the KS site was largely divided into two periods (Figure 76). From 1954 through 1972, Sensitive Zone growth was favored overall, but the RWID
Figure 71. Cache River Floodplain, Quercus spp., Ring-Width Subchronology.
Figure 72. Kalamazoo River at Swan Creek, *Fraxinus pennsylvanica* Ring-Width Subchronology.
Figure 73. Twin Lakes, *Fraxinus americana* Ring-Width Subchronology.
Figure 74. Sherriff's Marsh, *Fraxinus* spp. Ring-Width Subchronology.
Figure 75. Cache River Floodplain, Mean RWID, *Quercus* spp.
Figure 76. Kalamazoo River at Swan Creek, Mean RWI, *Fraxinus pennsylvanica*

*Fraxinus pennsylvanica* Mean RWI: Sensitive Zone - Complacent Zone
Figure 77. Twin Lakes, Mean RWID, *Fraxinus americana*.
Figure 78. Sherriff’s Marsh, Mean RWID, *Fraxinus* spp.

The TL site RWID signature was highly fluctuating through the period represented by the core samples (Figure 77). There were notable peaks of favored Sensitive Zone growth in 1925, 1931, and 1988-1989, and one of favored Complacent Zone growth in 1975-1976. The strongest signal was during the 1988-1989 period.

Considering the RWID magnitudes as compared to those of the other sites, the SM site growth fluctuations were relatively low in magnitude (Figure 78). The signal was also relatively erratic. The most notable observation was the consistent 1963-1969 period of favorable Sensitive Zone growth.

Minimum Tree Age Analysis and AV Interval Selection

The Minimum Tree Age (MTA) histograms were used to characterize the general age of the mature forests (Figures 30, 31, 32, 33). The cores with younger age bars were not necessarily younger trees; the increment cores may have only partially penetrated the trees. Therefore, the minimum and average MTA for all of the samples across a site would not be meaningful. The approximate average MTA of the older trees were used to estimate the maturity of the stand. At CF, the mature stand was more than 45 years old and the oldest tree was at least 74. The oldest stand was present at the KS site, where at least 16 of the 23 sample trees were more than 75 years old and several were more than 100. Thirteen of 19 trees at TL were more than 50 years old and several were more than 80. At SM, 13 of 24 sample trees were more than 50 years old and several were more than 75. The MTAs of the sample trees at the
sites were large enough to conduct further analyses of the mature intervals of most tree cores.

Using the 30-year MA cutoff, AV intervals were selected for the DM analysis using the procedure described in Chapter V, and the reference lines were plotted on Figures 30, 31, 32, and 33. At CF, AV=18 years of mature age allowed for the inclusion of 14 of the sample trees in the DM analysis (Figure 30). Fifteen trees at KS had a mature interval of 43 years to interpret (Figure 31). At TL, the AV=22 year interval contributed 12 trees to the DM analysis (Figure 32). Using an AV=25 year interval at SM, 13 trees were used in the DM analysis (Figure 33).

Mean Ring Width (MN) was computed for the AV interval of each of the sample trees and plotted on histograms (Figures 34, 35, 36, 37). Because these means were calculated only from the mature interval of the tree cores, they were considered more comparable than those calculated for the entire growth ring record of the trees. MN varied considerably among the trees across each site. Examples include QNu and TDi at CF, FPe and QRu at KS, FAm and QRu at TL, and Fsp at SM. Intraspecific variation in MN at a site was considered to be good evidence to suggest that growing conditions were spatially variable.

Deviation From the Mean Ring Width Analyses

The Deviation From the Mean (DM) ring width histograms permitted a year-by-year comparison of growth and were used to identify trends and coordinated or staggered shifts in growth rate. Short-term changes in magnitude of the histogram bars were ignored because they could have been the result of noise in the growth record. The noise may have been a consequence of the inherent instrumental error in ring measurement and/or a result of variance in non-hydrologic growth factors across the sampling site (e.g., differential shading, soil textural differences). The advantage
of the method is that enhanced and suppressed growth trends could be easily recognized.

Average DM histograms were constructed for all of the trees at each site (Figures 79, 80, 81, 82). It was possible to combine taxa in the analysis because the means were homogenized to a common zero reference by which all growth comparisons were relative. The primary limitation of this method was that taxa with relatively high average growth rates would weigh more on the composite calculation for each year and could obscure the contributions of slower growing taxa.

The CFC DM plot suggested two unique periods of growth (Figure 79). During the late 1970s, overall growth in the stand was above average. Beginning in the early 1980s and continuing into the early 1990s, overall growth in the stand was below average. An almost continuous trend of growth reduction occurred from 1975 through 1988. The DM histograms for the composite forests at KS and SM were characterized by frequent reversals across the mean (Figures 80, 82). No growth deviations of significant magnitude or duration were apparent. At TL, the early-to-mid 1980s appeared to be a transition period from above average growth in the mid-to-late 1970s to below average growth in the late 80's and early 1990s (Figure 81).

Average DM histograms were constructed for specific taxa across the HTG at each site as in the Taxon-Specific RWSs (Figures 83, 84, 85, 86). Complacent Zone growth was dominant for *Quercus* spp. at CF from the mid 1970's until the early 1980s, followed by dominant Sensitive Zone growth until the early 1990s (Figure 83). Complacent Zone growth was dominant for *Fraxinus pennsylvanica* at KS from the mid 1960's until the mid 1970s, followed by dominant Sensitive Zone growth from the early 1980s until the early 1990s (Figure 84). In 1989, a temporary, high magnitude Complacent Zone departure from the otherwise dominant Sensitive Zone growth interval was suspect. If this spike was not anomalous, it suggests that a
Figure 79. Cache River Floodplain, Deviation From the Mean Ring Width.
Figure 80. Kalamazoo River at Swan Creek, Deviation From the Mean Ring Width.
Figure 8.1. Twin Lakes, Deviation From the Mean Ring Width.
Figure 82. Sherriff's Marsh, Deviation From the Mean Ring Width.
Figure 83. Cache River Floodplain, *Quercus* spp., Deviation From the Mean, Sensitive Zone Minus Complacent Zone, AV 18.
Figure 84. Kalamazoo River at Swan Creek, *Fraxinus pennsylvanica*, Deviation From the Mean, Sensitive Zone Minus Marginal/Complacent Zone, AV 43.
Figure 85. Twin Lakes, *Fraxinus americana*, Deviation From the Mean, Sensitive Zone Minus Complacent Zone, AV 22.
Figure 86. Sherriff's Marsh, *Fraxinus* spp., Deviation From the Mean, Sensitive Zone Minus Complacent Zone, AV 25.
widespread environmental event occurred that favored the growth of Complacent Zone trees for 1 year. A strong Sensitive Zone growth signal for *Fraxinus americana* was apparent from 1987 through 1990 in the TL DM histograms (Figure 85). Complacent Zone growth was favored most of the time between 1974 and 1981. At SM, the period 1972 through 1978 was dominated by Complacent Zone growth, followed by variably dominant Sensitive Zone growth into the early 1990s (Figure 86).

**Cache River Floodplain Growth-Moisture Curve Analysis**

The growth of sample *Quercus* spp. trees on the Cache River Floodplain were compared to the conceptual growth model in Figure 53. The taxon-specific Sensitive Zone-Complacent Zone DM and RWID histograms both indicated that growth dominance along the floodplain has varied through time (Figures 83, 75). The shape of the conceptual growth rate curve in Figure 53 was not confirmed by the tree-ring data.

**Kalamazoo River at Swan Creek Streamflow-Growth Analysis**

Days of overberm flow per year are the basic hydrologic data used to compare to tree growth analyses. Following the recession of the Kalamazoo River floodwaters, the period of soil saturation exceeds that of inundation for several reasons. The evapotranspiration rate of the floodplain forest ranges from negligible during the winter to considerable during the summer. The proximity of the water table to the surface would influence the position of the capillary fringe, which may prolong saturated conditions in the visual absence of ponding, particularly in the fine-textured soils. The hydraulic conductivity of the flow-limiting layer of the soils would control the drainage rate of the trapped ponded waters and subsequent pore dewatering. In addition, rainfall or snowmelt prior to flooding can exceed the infiltration capacity of the soils or
raise the water table to create saturated conditions. Therefore, the length of the period of anaerobiosis can well exceed the period of flooding and disjunct flood events may be connected by a period of continuous soil saturation. It was not possible to estimate the extended time period of soil saturation on the KS floodplain in the absence of direct observations, but it is understood that it may be considerable with profound effects on tree growth physiology.

Overberm flow on the Kalamazoo River at Swan Creek site varied considerably through the USGS stream gaging period (Figure 87). During 7 of the 43 years of record, no overberm flow occurred. A single year of exceptional overberm flow (72 days) occurred in 1974, almost double that of the second highest year (1952, 40 days). Most overberm flow occurred during the dormant season in all but 3 years, when relatively high growing season streamflow was coupled with relatively low dormant season streamflow. During 21 (47%) of the years of record, all overberm flow was limited to the dormant season and overberm flow occurred during the growing season in only 15 years (35%) of the record. Overberm flow occurred only during the growing season in 1980, but only for 2 days. The year with the most growing season overberm flow days (23 days) was 1956. Less than 10 days of overberm flow occurred during 25 years (58%) of the record and more than 20 days of overberm flow occurred during 8 years (19%) of the record.

Intra-annual flow was further broken down into 4 categories and plotted as a histogram (Figure 88). October through February is the early dormant season, when overberm flow causes a recovery of the water table elevation in the absence of significant evapotranspiration. March through April, the late dormant season, was set apart as the period by which soil moisture conditions antecedent to the growing season were established. May through June is the typical interval of earlywood formation of temperate hardwood trees that generally accounts for the largest portion of growth ring
Figure 87. Kalamazoo River at Fennville: Overberm Flow, Annual Summary (Growing Season and Dormant Season). Data Source: U.S. Geological Survey.
Figure 88. Kalamazoo River at Swan Creek, Annual Summary ("Quarterly"), Overbem Flow.
Data Source: U.S. Geological Survey.
thickness. July through September is normally the season of highest evapotranspiration, water table decline and the formation of latewood. 1974 and 1976 were the years of the most flooding immediately prior to the growing season, with 43 and 31 days of overberm flow, respectively, spread over 2 months. 1956 was the year of greatest overberm flow (22 days during the early growing season).

Total annual precipitation was graphed with overberm flow against time (Figure 89). There was no apparent relationship between precipitation and flooding at KS (Figure 90).

The distribution of the overberm flow events through the years appears to have been random. The years of lowest and highest flow were evenly distributed through the time of record. The best opportunities for correlating streamflow events with tree growth were: (a) 1974, the year of an exceptional number of overberm flow days and the wettest antecedent conditions to the growing season; (b) 1956, the year of the greatest number of early growing season overberm flow days; (c) 1986, the year of second wettest antecedent conditions; and (d) 1953, 1957, 1961, 1964, 1984, 1988 and 1994, the years of no overberm flow.

Mean ring-width index difference between Sensitive Zone and Complacent Zone _Fraxinus pennsylvanica_ trees was co-plotted with overberm flow against time (Figure 91). In 1974, the highest spike in overberm flow corresponded with a major depression of mean RWID. However, 3 years later (1977), the lowest mean RWID corresponded with a major decrease of overberm flow. Only 6.5% (R² = 0.065) of the variability in RWID could be accounted for by overberm flow in a simple linear regression model. Relationships were not recognized between mean RWID and hydrologic conditions for the years listed in opportunities (a) through (d) listed above. There was no apparent relationship between mean RWID and overberm flow days.
Figure 89. Kalamazoo River at Swan Creek (KS), Days of Overbem Flow and Annual Precipitation, 1952-1991.
Figure 90. Kalamazoo River at Swan Creek (KS), Annual Precipitation vs. Days Overberm Flow, 1952-1991.

\[ y = 0.0032x + 36.941 \]

\[ R^2 = 5E-05 \]
Figure 91. Kalamazoo River at Swan Creek (KS), Annual Flooding and Growth Sensitivity, *Fraxinus pennsylvanica*.
Comparison of the DM histogram for FPe (Figure 84) with the overberm flow record (Figure 87) also showed no apparent growth-flow relationship.

The onset of growth suppression in the floodplain trees, if it occurs at all, appears to lag behind the development of soil anaerobiosis. This may result in uninterrupted or unrecognizable short-term suppression of growth. It should probably be no surprise that the mature forests that developed on the KS floodplains are well adapted to periodic soil saturation. It is somewhat surprising that during years having relatively long-duration growing season flooding events, tree growth was apparently unaffected.

Twin Lakes Historical Shoreline-Growth Analysis

The spatial resolution of the TL aerial photographs was insufficient to locate the positions of the individual sample trees with respect to the shoreline through time. However, reconstruction of the relative position of the shoreline through time was possible using the aerial photographs, and the variable shoreline positions could be related to the sample tree mosaic.

The shoreline traces and areas were quite accurate for those based on aerial photographs because the resolution was adequate. The traces related to topographic maps were assumed to be less accurate because the methods used for arriving at the lake configuration were unknown. For example, more credence should be given to the 1974 aerial photograph (lake area 118.6 acres) than the 1973 topographic map (lake area 32.7 acres). From the 1967 photo, however, the lake area was 31.3 acres. It is likely that the lake representation on the 1973 topographic map was valid for some time between 1967 and 1974, but it is unlikely that the major rise in water level from 1967 to 1974 all occurred in the last year of that period. The 1995 shoreline reconstruction was based on direct observation from a boat and from the shore during the 1994-1995
field visits; the lake outline was estimated by comparison with the topographic map contours and landmarks and is less accurate than that of an aerial photograph. The 1916 area determined by topographic map is suspect because it declined by a factor of 3 in the following 22 years. The addition of aerial photographs between 1900 and 1930 would have provided a useful perspective by which to compare the lake area changes between 1960 and 1995.

Acreage of surface water at Twin Lakes West over the past 79 years was calculated from the traces in Figures 39, 40, 41, 42 and 43 using an English area dot grid (Table 2). A Lake Area vs. Time graph was prepared to compare the water levels

<table>
<thead>
<tr>
<th>Year</th>
<th>Area (acres)</th>
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<tr>
<td>1916 (M)</td>
<td>117.5</td>
</tr>
<tr>
<td>1938 (P)</td>
<td>38.5</td>
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<tr>
<td>1950 (P)</td>
<td>92.0</td>
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<tr>
<td>1960 (P)</td>
<td>60.0</td>
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<td>1967 (P)</td>
<td>31.3</td>
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<td>1973 (M)</td>
<td>32.7</td>
</tr>
<tr>
<td>1974 (P)</td>
<td>118.6</td>
</tr>
<tr>
<td>1978 (P)</td>
<td>146.6</td>
</tr>
<tr>
<td>1988 (P)</td>
<td>146.3</td>
</tr>
<tr>
<td>1995 (O)</td>
<td>182.3</td>
</tr>
</tbody>
</table>

Sources of Information: M = Topographic Map, P = Aerial Photograph, O = Observation.
for the 10 “snapshots” (Figure 92).

The historical lake area plot was useful for identifying general variations in lake size and shape through time, but was interpreted with caution. For the time between plotted points (4-12 years between photographs), the lake area certainly fluctuated, perhaps significantly. The direction and magnitude of these variations could not be inferred from the plotted points and may have exceeded the plotted values at one or more times. In addition, the time of year that the photographs were taken was variable, spanning from June to September. Little seasonal migration of the shoreline was observed during 1994. During periods when the maximum annual area was much smaller, the annual variability was likely much more pronounced. Even with these major limitations in mind, the aerial photograph record remains the best source of information for lake area variability through time.

The lake area has fluctuated significantly during the period of record (Figure 38, Table 2). The minimum area occurred in 1967 (~31 acres) when the basin was a mosaic of 3 disjunct ponds (Figure 43). By 1995, the lake area was at a maximum (~180 acres) and was a continuous water body (Figure 43). Contrary to local popular opinion, airphoto interpretation indicates that the lake had not continuously risen since the construction of highway US 131 around 1960. Prior to that time, a ponded area occupied the position where the highway now crosses the west arm of the basin on a ~40 foot high artificial ridge (Figure 39). According to the aerial photographs, the lake area apparently decreased between 1950 and the late 1960s, when it attained the recorded minimum in 1967. Since the late 1960s, the net area of the lake has increased precipitously, by a factor of 5 in 28 years.

Lake area was co-plotted with mean RWID data for Fraxinus americana against time (Figure 93). The mean RWID data were fit to a 6th-order polynomial equation to show the general trend of the data. Although the direction and magnitude of lake area
Figure 92. Twin Lakes West: Historical Surface Water Area.

Sources of Data:
- P = aerial photograph
- M = topographic map
- O = observation
Figure 93. Twin Lakes: Lake Area and SEN-COM Ring-Width Index Difference, *Fraxinus americana*.
deviations between "snapshots" was unknown, a line can be visualized connecting the
data points to illustrate the general trend of hydrologic change. If the 1974 topographic
map data point is ignored, the lake area trend has a similar shape to that of the FAmm
RWID trend. The inflections in the RWID trend appear to lag 4 to 7 years behind
those of lake area. When lake levels were high, Sensitive Zone growth increased and
so did the SEN-COM RWID ratio. The *Fraxinus americana* DM histogram also
showed that Sensitive Zone growth increased in the mid- to late-1980s when the lake
margin migrated landward (Figure 85). These results suggest that increased lake levels
improved, rather than reduced, growth of upland *Fraxinus americana* trees living near
the margins, at least temporarily.

Sherriff's Marsh Precipitation-Growth Analysis

Total annual precipitation curves for the Gull Lake Biological Station and Battle
Creek were constructed for the period 1948-1994 (Figures 45, 46, 51). The upper end
of the range was more than double that of the lower end at each station and the
amplitude varied strongly from year to year. Moving averages of 5 and 10 years were
applied to the data. Each plotted point on the moving average curves represents the
average for the previous 5 or 10 years of data. The longer the moving average period,
the smaller the effect of extreme values on the plotted curve because central values in
the average function to attenuate the extremes. Application of moving averages to the
data produced curves that illustrated similar trends at the two stations. The 5- and 10-
year moving averages at both stations showed a pronounced precipitation low.
Comparison of the moving average low with the actual precipitation curve suggests
that the inflection was near 1960. The general trend appears to have been upward ever
since then.

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Polynomial regressions of orders 2 through 6 were applied to the Gull Lake Biological Station data, but a good fit was not possible in any case (low $R^2$s). The visual fit of the third-order polynomial appeared to approximate the general trend, indicating a period of relatively low precipitation in the early 1960s and a precipitation maximum in the 1980s (Figure 48). A cumulative departure from the mean plot showed an inflection in the mid-1960s (Figure 49). Following the beginning of a decline in precipitation rates in the early 1950s, it was not until the early 1990s that the cumulative departure from the mean returned to normal.

It is difficult to characterize the effect of annual precipitation swings on the elevation of the water table. The magnitude of water table fluctuations tends to be attenuated in response to climatic variations because much of the groundwater system is generally buffered from losses by the vadose zone. Similarly, recovery of the groundwater system generally lags behind the precipitation recharge events because of high plant demands following a dry interval and replenishment of hygroscopic water in the vadose zone. It is therefore reasonable to approximate the climatic effects on water table fluctuations by comparison of the statistical averages in annual precipitation. It is suggested here that, independent of human influence, the water table generally fluctuates in accordance with the moving average and cumulative departure from the mean curves. The timing of the statistical inflections probably lags behind the climatic pulses by one or more years and the changes in magnitude are relative. Attenuation of the magnitude of water table fluctuations in and near the wetlands of southwest Michigan is expected to be considerable because they are mostly groundwater discharge areas that are continually resupplied with water from upgradient sources.

The growing season is the frost-free period of the year (Cowardin, et al. 1979). For the purposes of this study, the growing season in southwest Michigan was designated as May 1 through September 30. October 1 through April 30 was
considered the dormant season. Comparison of monthly average precipitation for the 1948-1994 period at Gull Lake Biological Station shows that the growing season months, except for May, are generally wetter than the dormant season months (Figure 50). Annual precipitation at Gull Lake Biological Station was also differentiated into growing season and dormant season periods and graphically displayed (Figure 44). The 10-year moving averages for the growing season and dormant season were compared to that of the annual data (Figure 47). From the late 1960s through the early 1990s, the growing season and dormant season contributed equally to the total annual precipitation. However, because the dormant season is 7 months long, the average magnitude of precipitation per unit of time during the growing season was greater. Prior to the late 1960s, the growing season contribution to the total annual precipitation was relatively depressed.

The Sensitive Zone minus Complacent Zone mean RWID for Fraxinus spp. at SM were co-plotted with total annual precipitation against year (Figure 94). During the period 1972-1994, Complacent Zone growth was generally favored when annual precipitation was relatively high. In the mid- to late-1960s, Sensitive Zone growth was relatively high when annual precipitation was relatively high. However, these comparisons are highly generalized and the very low coefficient of determination (1.5%) indicates that the two sets of data are poorly correlated. The reversal from dominant Complacent Zone growth to Sensitive Zone growth in 1979 in the DM histogram for Fraxinus spp. did not correlate with any pronounced shift in the precipitation records (Figure 86, 45).

Growth Ring Boundary Enhancement

The phloroglucinol staining technique was applied to selected diffuse-porous Acer saccharinum, Acer rubrum, Carpinus caroliniana, Tilia americana and Taxodium
Figure 94. Sherriff’s Marsh (SM), Annual Precipitation and Ring-Width Sensitivity Difference, *Fraxinus* sp.

Coefficient of Determination = 0.015
distichum cores using Patterson’s (1959) recommended procedure. Some improvement in ring boundary resolution was recognized, but not enough to permit continuous measurement of rings from the bark to the center of the cores. Variations in concentration and contact time were tried without success. The reason the stain had limited results was probably because the lignin:cellulose ratio did not vary much across the growth increment of the sampled species.

The high speed sanding technique of Fritz (1939) decreased the resolution of the rings as compared to the high speed planing technique developed in this study. Therefore, the dendrohydrological inferences of this study were almost entirely based on the growth-ring records of ring-porous tree species.
CHAPTER VIII

CONCLUSIONS

In the absence of hydrologic documentation, recognition of the relationships of the Cache River Floodplain growth data to streamflow or precipitation data was not possible. The tree-ring data did not support the idea of zoned growth on the CF floodplain as proposed in the model of Figure 53. Despite good streamflow data to compare to tree growth, no moisture-growth relationship could be established at the Kalamazoo River at Swan Creek site. Taxon-specific ring-width subchronologies and DM analyses at Twin Lakes and Sheriff's Marsh did not correlate with the image-based shoreline reconstructions and precipitation records, respectively. Some reasonable inferences about the impacts of soil saturation on the growth of individual trees were possible from the RW vs. RN and cumulative growth analyses.

The use of traditional sensitivity analyses and composite ring-width chronologies did not contribute significantly to the dendrohydrological interpretations. Sensitivity was low because the soil saturation/flooding signal was weak at the study sites. The composite and taxon-specific ring-width chronologies were incompatible with the hydrotopographic gradient concept because homogenization of the zones diluted the signal. Taxon-specific ring-width subchronologies were introduced in this study as an adaptation of traditional methods to the hydrotopographic gradient concept. These subchronologies were effective at recognizing shifts in dominant growth through time along the profile from wetland to upland, but did not compare well to the hydrologic documentation.
Deviation from the Mean Ring Width was introduced as new method of growth-ring analysis. It was used as an alternative to traditional standardization for filtering out noise related to ontogenetic changes and minor growth influences that compete with the targeted limiting factor. The composite DM histograms were useful for identifying broad changes in growth across a site, but were limited by the same problems as composite ring-width chronologies. Taxon-specific DM histograms prepared for the Sensitive and Complacent Zones were a conceptually appealing method of growth analysis along the hydrotopographic gradient, but the signal strength was generally too weak or variable to generate reasonable inferences.

This study differed from traditional dendrochronological studies in two primary ways. First, the growth-limiting factor was water-surplus stress, rather than water-deficiency stress. Second, the distribution of the limiting factor was variable across each sampling site. As a result of these differences, an important objective of this study was to apply traditional and innovative dendrochronological methods to acquiring and examining tree core time series. Much of the field, laboratory and data processing work of this study was focused on signal enhancement. In order to separate the water surplus stress signal from the other environmental noise that influenced the growth record, a carefully designed approach was necessary. The combined use of selective sampling and graphical noise filtering were the primary strategies used to enhance the signal-to-noise ratio.

Despite the use of multiple strategies for gathering and analyzing the data set, the hydrologic signal was often weak or uncertain in the growth-ring record. There are two probable explanations for these results. First, as forests develop and mature, the environmental conditions that influence growth vary temporally and spatially. Factors limiting to growth are constantly changing and their relative influence is not specifically labeled in the growth ring record. Reduced or accelerated growth may be attributed to
a complex combination of conditions. The growth of close tree neighbors occupying
the same hydrotopographic position could be regulated by different sets of
environmental conditions at any time. Attempts to reconstruct the historical spatial
distribution of limiting factors through time are overwhelming. Unless the imposition
of a particular limiting factor on tree growth physiology is outstanding compared to
other growth factors and is present for a sufficient duration of the growing season, its
signal could easily be diluted. In the absence of long-term site observations and
controls, it is difficult or impossible to sort out which environmental conditions most
influenced a particular growth increment in any tree. Second, trees appear to be well-
adapted to buffer the effects of short-term environmental stresses. As outlined in
Anaerobic Stress Model 2 (Figure 13), many trees are capable of compensating for soil
anaerobiosis in a variety of ways. Species well-adapted for life on saturated soils may
continue normal growth through a prolonged period of soil saturation or flooding. The
lag in the growth response of upland trees to water surplus stress can exceed the
residence time of the stress. This study demonstrated that even mixed mesophytic tree
assemblages appear to have considerable resilience to water surplus stress.

The implementation of this study was further complicated by sample
limitations. The availability of a large number of trees from a variety of species at each
site that met the sample requirements was minimal, particularly when the
hydrotopographic gradient was compartmentalized for analysis. Two species that are
among the most common constituents of forested wetlands in the Midwest, Acer
saccharinum and Acer rubrum, have growth ring characteristics that are largely
indecipherable. Attempts at improving boundary resolution of diffuse-porous species
were unsuccessful. A combination of core characteristics and sample tree availability
generally favored one species or genus for the analyses at each site. Fraxinus spp. and
Quercus spp. were found to be the best-suited genera for dendrohydrological analysis of the wetland types examined in this study.

The hypothesis of this study was not supported by the data. The growth-ring records of the sampled trees were rarely comparable to the documented hydrologic records of the research sites. Observations of markedly reduced radial growth in relation to water surplus stress were infrequent. More commonly, upland trees subjected to water surplus stress appeared to function normally or slightly impaired for up to several years and died suddenly. Trees that established themselves on saturated soils appeared to experience water deficiency stress when the water table dropped, but functioned normally under saturated conditions. Floodplain trees appeared to be unaffected by marked annual variability in flood frequency. Therefore, tree-ring records alone were shown to be inadequate for reconstructing the hydrologic histories of wetlands and riparian environments.

From a practical viewpoint, the contributions of this study to day-to-day wetland delineation and characterization of temperate hardwood wetlands are minimal. However, the contributions of this study to the understanding of hardwood tree growth in and around temperate wetlands are significant. The hydrologic data processing methods that were developed, such as reconstruction of historical shoreline positions, stream stage frequency analysis and the application of moving averages to precipitation data, will be useful in other applications.
Appendix A

Plant Taxa Referenced in Text, Tables, Figures and Appendices
Appendix A. Plant Taxa Referenced in Text, Tables, Figures and Appendices. Indicator status is given as National range/Region 3 (Reed, 1988). Unlisted indicator status means the taxon is not observed in wetlands.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Common Name(s)</th>
<th>Abbreviation</th>
<th>Indicator Status</th>
</tr>
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<tbody>
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<td>Cryptogams</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Phytophthora spp.</td>
<td>fungus, undifferentiated</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gymnosperms</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cupressaceae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Thuja occidentalis L.</td>
<td>arborvitae, eastern white cedar</td>
<td>TOc</td>
<td>FACW/FACW</td>
</tr>
<tr>
<td>Juniperus procer</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pinaceae</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Abies concolor (Gord. and Glend.) Lindl.</td>
<td>white fir</td>
<td>LLa</td>
<td>FACW/FACW</td>
</tr>
<tr>
<td>Larix laricina (DuRoi) K. Koch</td>
<td>eastern larch, tamarack</td>
<td></td>
<td>FACW/FACW</td>
</tr>
<tr>
<td>Picea mariana (Mill.) B. S. P.</td>
<td>black spruce</td>
<td></td>
<td>FACW/FACW</td>
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<tr>
<td>P. schrenkiana Fisch. et Mey</td>
<td>Sitka spruce</td>
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<tr>
<td>P. sitchensis Bong. Carr</td>
<td>Colorado pinyon pine</td>
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<tr>
<td>Pinus edulis Engelm.</td>
<td>limber pine</td>
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<tr>
<td>P. flexilis James</td>
<td>Jeffrey pine</td>
<td></td>
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<tr>
<td>P. jeffreyi Grev. and Balf.</td>
<td>Great Basin bristlecone pine</td>
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<tr>
<td>P. longaeva D. K. Bailey</td>
<td>ponderosa pine</td>
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</tr>
<tr>
<td>P. ponderosa Dougl. ex Laws</td>
<td>red pine</td>
<td>PRe</td>
<td>FACU/FACU</td>
</tr>
<tr>
<td>Pinus resinosa Soland. In Ait.</td>
<td>eastern white pine</td>
<td>PST</td>
<td>FACU/FACU</td>
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<tr>
<td>P. strobus L.</td>
<td>Douglas fir</td>
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<tr>
<td>Pseudotsuga menziesii (Mirb.) Franco</td>
<td>eastern hemlock</td>
<td>TCa</td>
<td>FACU/FACU</td>
</tr>
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<td>Taxodiaceae</td>
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<tr>
<td>Taxodium distichum (L.) Rich.</td>
<td>bald cypress</td>
<td>TDi</td>
<td>OBL/OBL</td>
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Appendix A. Plant Taxa Referenced in Text, Tables, Figures and Appendices. Continued.

**Angiosperms**

<table>
<thead>
<tr>
<th>Family</th>
<th>Common Names</th>
<th>Abbreviation</th>
<th>Other Abbreviations</th>
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<tr>
<td><strong>Aceraceae</strong></td>
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<td><em>Acer</em> spp.</td>
<td>maples, undifferentiated</td>
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<td><em>A. saccharinum</em></td>
<td>silver maple</td>
<td>ASH</td>
<td>FAC/FACW</td>
</tr>
<tr>
<td><em>A. rubrum</em></td>
<td>red maple</td>
<td>ARu</td>
<td>FAC/FAC</td>
</tr>
<tr>
<td><em>A. saccharum</em></td>
<td>sugar maple</td>
<td>ASC</td>
<td>UPL/FACU</td>
</tr>
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<td><strong>Anacardiaceae</strong></td>
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<td></td>
<td></td>
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<tr>
<td><em>Toxicodendron</em></td>
<td>poison ivy</td>
<td></td>
<td>FACU;FACW/FAC+</td>
</tr>
<tr>
<td><em>radicans</em></td>
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<td></td>
</tr>
<tr>
<td><strong>Betulaceae</strong></td>
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<td></td>
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<tr>
<td><em>Betula</em> nigra</td>
<td>river birch</td>
<td></td>
<td>FACW;OBL/FACW</td>
</tr>
<tr>
<td><em>Carpinus</em></td>
<td>musclewood, American hornbeam</td>
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<td>FAC/FAC</td>
</tr>
<tr>
<td><em>caroliniana</em></td>
<td>hawthorns, undifferentiated</td>
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<td>FACU;FACU+/FACU-</td>
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<td><em>Walt.</em></td>
<td>eastern hop hornbeam, ironwood</td>
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<td><em>Crataegus</em></td>
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<td></td>
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<tr>
<td><em>spp.</em></td>
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<td><em>Ostrya virginiana</em></td>
<td>swamp dogwood</td>
<td></td>
<td>FAC;FACW/FACW-</td>
</tr>
<tr>
<td>(Mill.) Koch</td>
<td></td>
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<td><strong>Cornaceae</strong></td>
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<td><em>Cornus</em> foemina</td>
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<td>P. Mill.</td>
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<td><strong>Ericaceae</strong></td>
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<td><em>Diospyros</em></td>
<td>common persimmon</td>
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<td>FACU/FAC</td>
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<tr>
<td><em>virginiana</em></td>
<td></td>
<td></td>
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<tr>
<td>L.</td>
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Appendix A. Plant Taxa Referenced in Text, Tables, Figures and Appendices. Continued.

<table>
<thead>
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<th>Common Name</th>
<th>Code 1</th>
<th>Code 2</th>
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<td>Fagaceae</td>
<td>Fagus grandifolia Ehrh.</td>
<td>American beech</td>
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<td>FACU/FACU</td>
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<td>Quercus spp.</td>
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<td>QU</td>
<td>FACU-; FACU+/FACU</td>
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<td>Q. alba Wild.</td>
<td>white oak</td>
<td>QAi</td>
<td>FACW+; OBL/FACW+</td>
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<td></td>
<td>Q. bicolor Wild.</td>
<td>swamp white oak</td>
<td>QBi</td>
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<td>Q. imbricaria Michx.</td>
<td>shingle oak</td>
<td>QLy</td>
<td>FACU; FAC/FAC-</td>
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<td></td>
<td>Q. lyrata Walt.</td>
<td>overcup oak</td>
<td>QLy</td>
<td>FAC; FACW/FACW</td>
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<tr>
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<td>Q. macrocarpa Michx.</td>
<td>bur oak</td>
<td>QNi</td>
<td>FACW; OBL/OBL</td>
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<tr>
<td></td>
<td>Q. nigra L.</td>
<td>water oak</td>
<td>QNu</td>
<td>FAC; FACW/FACW</td>
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<td></td>
<td>Q. nuttallii Palmer</td>
<td>Nuttall oak</td>
<td>QPa</td>
<td>FAC; FACW/FACW</td>
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<tr>
<td></td>
<td>Q. palustris Muenchh.</td>
<td>pin oak</td>
<td>QPh</td>
<td>FAC+; FACW/FACW</td>
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<tr>
<td></td>
<td>Q. phellos L.</td>
<td>willow oak</td>
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<td>FACU-; FACU+/FACU</td>
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<td></td>
<td>Q. rubra L.</td>
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<td>Hamamelidaceae</td>
<td>Liquidambar styraciflua L.</td>
<td>sweetgum</td>
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<td>Juglandaceae</td>
<td>Carya aquatica (Michx. f.) Nutt.</td>
<td>water hickory</td>
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<td>OBL/OBL</td>
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<td>Juglans nigra L.</td>
<td>black walnut</td>
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<td>FACU/FACU</td>
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<td>Juncaceae</td>
<td>Juncus spp.</td>
<td>rushes</td>
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<td>mostly OBL or FACW</td>
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<td>Magnoliaceae</td>
<td>Liriodendron tulipifera L.</td>
<td>tulip tree, yellow poplar</td>
<td>LTu</td>
<td>FACY; FAC/FACU+</td>
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<td>Nyssaceae</td>
<td>Nyssa aquatica L.</td>
<td>water tupelo</td>
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<td>OBL/OBL</td>
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<td>N. sylvatica Marsh.</td>
<td>black gum, tupelo</td>
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<td>FAC/FAC</td>
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Appendix A. Plant Taxa Referenced in Text, Tables, Figures and Appendices. Continued.

<table>
<thead>
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<th>Common Name</th>
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<tr>
<td>Oleaceae</td>
<td><em>Fraxinus</em> spp.</td>
<td><em>F. americana</em> L.</td>
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<td><em>F. pennsylvanica</em> Marsh.</td>
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<td><em>Ligustrum</em> spp.</td>
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<td><em>Prunus</em> serotina Ehrh.</td>
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<td>Rubiaceae</td>
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<td>buttonbush</td>
<td>OBL/OBL</td>
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<td>Salicaceae</td>
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<td><em>Salix</em> spp.</td>
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<td><em>S. exigua</em> Nutt.</td>
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<td>sandbar willow</td>
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<td><em>S. nigra</em> Marsh.</td>
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<td>black willow</td>
<td>OBL/OBL</td>
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<td>Tiliaceae</td>
<td><em>Tilia</em> americana L.</td>
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<td>American basswood, linden</td>
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<td>Ulmaceae</td>
<td>* Celtis laevigata* Willd.</td>
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<td>sugarberry</td>
<td>FACW/FACW</td>
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<td><em>C. occidentalis</em> L.</td>
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<td>hackberry</td>
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<tr>
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<td><em>Ulmus</em> spp.</td>
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<td>elms, undifferentiated</td>
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</tr>
<tr>
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<td><em>Ulmus americana</em> L.</td>
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<td>American elm</td>
<td>FACU/FACW</td>
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</tbody>
</table>
Appendix B

Ring Width vs. Ring Number Core Plots,
Cache River Floodplain
CFC 1 RING WIDTH DISTRIBUTION (*Quercus nuttallii*)

\[ y = -0.0003x^2 + 0.0138x + 0.1758 \]

\[ R^2 = 0.4349 \]
CFC 3 RING WIDTH DISTRIBUTION (Quercus phellos)

\[ y = 0.1322e^{0.022x} \]

\[ R^2 = 0.5792 \]
CFC 6 RING WIDTH DISTRIBUTION (Quercus nuttallii)

\[ y = -0.0002x^2 + 0.0114x + 0.0143 \]

\[ R^2 = 0.4512 \]
CFC 9 RING WIDTH DISTRIBUTION (Quercus nuttallii)

\[ y = 0.1083e^{0.0238x} \]

\[ R^2 = 0.4609 \]
CFC 10 RING WIDTH DISTRIBUTION (Quercus lyrata)

\[
y = 0.0432e^{0.0187x} \\
R^2 = 0.374
\]
CFC 13 RING WIDTH DISTRIBUTION (Taxodium distichum)

\[ y = -0.05x^2 + 0.0029x + 0.0573 \]

\[ R^2 = 0.0733 \]
CFC 17 RING WIDTH DISTRIBUTION (*Taxodium distichum*)

\[ y = 0.1185e^{-0.0145x} \]

\[ R^2 = 0.2126 \]
CFC 20 RING WIDTH DISTRIBUTION (*Quercus phellos*)

\[ y = 0.124e^{0.0179x} \]

\[ R^2 = 0.2832 \]
CFC 21 RING WIDTH DISTRIBUTION (*Celtis laevigata*)

\[ y = 0.0034e^{0.0818x} \]

\[ R^2 = 0.8553 \]
CFC 22 RING WIDTH DISTRIBUTION (*Quercus phellos*)

\[ y = 0.2088e^{0.0265x} \]

\[ R^2 = 0.6141 \]
CFC 23 RING WIDTH DISTRIBUTION (Quercus phellos)

Ring Width (inches)

Ring Number (from bark)

\[ y = 0.1576e^{0.0288x} \]

\[ R^2 = 0.4681 \]
CFC 24 RING WIDTH DISTRIBUTION (*Taxodium distichum*)

\[ y = 6E-06x^3 - 0.0004x^2 + 0.0084x + 0.1147 \]

\[ R^2 = 0.0418 \]
CFC 26 RING WIDTH DISTRIBUTION (Quercus sp.)

\[ y = 0.0951e^{0.014x} \]

\[ R^2 = 0.1153 \]
CFC 28 RING WIDTH DISTRIBUTION (*Quercus nigra*)

\[ y = 0.2191e^{0.0128x} \]

\[ R^2 = 0.1298 \]
CFC 29 RING WIDTH DISTRIBUTION (*Quercus nigra*)

\[ y = 0.3054e^{0.0003x} \]

\[ R^2 = 5E-05 \]
CFC 30 RING WIDTH DISTRIBUTION (Quercus lyrata)

Ring Width (inches)

y = 0.1109e^{0.0008x}

R^2 = 0.1003
CFC 31 RING WIDTH DISTRIBUTION (*Quercus nuttallii*)

\[ y = 0.1356e^{0.015x} \]

\[ R^2 = 0.4547 \]

Ring Width (inches)

Ring Number (from bark)
CFC 32 RING WIDTH DISTRIBUTION (*Quercus nigra*)

\[ y = 0.1737e^{0.019x} \]

\[ R^2 = 0.4759 \]
CFC 33 RING WIDTH DISTRIBUTION (Quercus phellos)

\[ y = 0.02846^{0.0791}x \]

\[ R^2 = 0.6804 \]
Appendix C

Ring Width vs. Ring Number Core Plots,
Kalamazoo River at Swan Creek
KSC 1 RING WIDTH DISTRIBUTION (*Fraxinus* sp.)

\[ y = 0.0213e^{0.0221x} \]

\[ R^2 = 0.3638 \]
KSC 2 RING WIDTH DISTRIBUTION (*Fraxinus* sp.)

\[ y = 0.02256 e^{0.0281x} \]

\[ R^2 = 0.634 \]
KSC 5 RING WIDTH DISTRIBUTION (*Quercus bicolor*)

\[ y = 0.0001x^2 - 0.0097x + 0.2672 \]

\[ R^2 = 0.5348 \]

Ring Width (inches)

Ring Number (from bark)
KSC 6 RING WIDTH DISTRIBUTION (*Celtis occidentalis*)

\[ y = 0.0531e^{0.0681x} \]

\[ R^2 = 0.6948 \]
KSC 7 RING WIDTH DISTRIBUTION (*Ulmus americana*)

\[
y = 0.0805 \cdot e^{0.0552x} \\
R^2 = 0.6881
\]
KSC 9 RING WIDTH DISTRIBUTION (*Fraxinus* sp.)

\[ y = 0.0806e^{-0.0021x} \]

\[ R^2 = 0.0126 \]
KSC 10 RING WIDTH DISTRIBUTION (*Fraxinus* sp.)

\[ y = -2 \times 10^{-6}x^3 + 0.0002x^2 - 0.0044x + 0.1264 \]

\[ R^2 = 0.3813 \]
KSC 11 RING WIDTH DISTRIBUTION (*Fraxinus* sp.)

\[ y = -1E-06x^3 + 0.0002x^2 - 0.0052x + 0.15 \]

\[ R^2 = 0.2065 \]
KSC 12 RING WIDTH DISTRIBUTION (*Fraxinus* sp.)

\[ y = -0.0001x^2 + 0.0073x + 0.0245 \]

\[ R^2 = 0.4843 \]
KSC 13 RING WIDTH DISTRIBUTION (*Fraxinus* sp.)

\[ \gamma = 0.0704e^{0.017x} \]

\[ R^2 = 0.4884 \]
KSC 14 Ring Width Distribution (Quercus bicolor)

\[ \gamma = 0.1035e^{0.0056\times} \]

\[ R^2 = 0.1871 \]
KSC 15 RING WIDTH DISTRIBUTION (Quercus bicolor)

\[ y = 3 \times 10^{-5}x^2 - 0.0024x + 0.1289 \]
\[ R^2 = 0.2296 \]
KSC 16 RING WIDTH DISTRIBUTION (*Quercus rubra*)

\[ y = 0.0407e^{0.0203x} \]

\[ R^2 = 0.7594 \]
KSC 17 RING WIDTH DISTRIBUTION (Quercus rubra)

\[ y = 0.114e^{0.0132x} \]

\[ R^2 = 0.6116 \]
KSC 18 RING WIDTH DISTRIBUTION (Quercus rubra)

\[ y = 0.1207e^{-0.0028x} \]

\[ R^2 = 0.0282 \]
KSC 19 RING WIDTH DISTRIBUTION (*Quercus rubra*)

\[ y = -3E-05x^2 + 0.0024x + 0.0361 \]

\[ R^2 = 0.3438 \]
KSC 21 RING WIDTH DISTRIBUTION (*Fraxinus* sp.)

\[
\begin{align*}
y &= 0.0521e^{0.0074x} \\
R^2 &= 0.2928
\end{align*}
\]
KSC 23 RING WIDTH DISTRIBUTION (Fraxinus sp.)

\[ y = 5E-05x^2 - 0.0038x + 0.1413 \]

\[ R^2 = 0.4525 \]
KSC 24 RING WIDTH DISTRIBUTION (*Fraxinus* sp.)

\[ y = 7 \times 10^{-5}x^2 - 0.0064x + 0.2068 \]

\[ R^2 = 0.6747 \]
KSC 26 RING WIDTH DISTRIBUTION (*Fraxinus* sp.)

\[ y = 0.0433e^{0.001x} \]

\[ R^2 = 0.0032 \]
KSC 27 RING WIDTH DISTRIBUTION (Fraxinus sp.)

\[ y = 0.0001x^2 - 0.0057x + 0.1498 \]

\[ R^2 = 0.53 \]
KSC 28 RING WIDTH DISTRIBUTION (Fraxinus sp.)

\[ y = 0.0397e^{0.0361x} \]

\[ R^2 = 0.8537 \]
KSC 29 RING WIDTH DISTRIBUTION (Fraxinus sp.)

\[
y = 0.0428e^{0.0456x}
\]

\[
R^2 = 0.8203
\]
KSC 30 RING WIDTH DISTRIBUTION (*Fraxinus* sp.)

\[
y = 0.0779e^{-0.0028x}
\]

\[
R^2 = 0.0111
\]

Ring Width (inches)

Ring Number (from bark)
KSC 31 RING WIDTH DISTRIBUTION (*Fraxinus* sp.)

\[ y = 0.06376^{0.0203x} \]

\[ R^2 = 0.4447 \]
Appendix D

Ring Width vs. Ring Number Core Plots,
Twin Lakes
TLC 3 RING WIDTH DISTRIBUTION (Acer rubrum)

\[ y = -1E-06x^3 + 0.0001x^2 - 0.0023x + 0.072 \]

\[ R^2 = 0.2802 \]
TLC 4 RING WIDTH DISTRIBUTION (*Acer rubrum*)

\[
y = -5E-07x^3 + 2E-05x^2 + 0.001x + 0.0531 \\
R^2 = 0.2212
\]
TLC 5 RING WIDTH DISTRIBUTION (*Fraxinus* sp.)

\[ r = 0.0303 e^{0.0313x} \]

\[ R^2 = 0.783 \]
TLC 6 RING WIDTH DISTRIBUTION (*Quercus rubra*)

\[ y = 2 \times 10^{-6}x^3 - 0.0002x^2 + 0.0026x + 0.1257 \]

\[ R^2 = 0.3702 \]
TLC 7 RING WIDTH DISTRIBUTION (Fraxinus sp.)

\[ y = 0.031e^{0.0316x} \]

\[ R^2 = 0.5932 \]
TLC 8 RING WIDTH DISTRIBUTION (*Fraxinus* sp.)

\[ y = 0.0332e^{0.286x} \]

\[ R^2 = 0.4259 \]
TLC 9 RING WIDTH DISTRIBUTION (Fraxinus sp.)

\[ y = 0.0546e^{0.0184x} \]
\[ R^2 = 0.5486 \]
TLC 10 RING WIDTH DISTRIBUTION (Quercus rubra)

\[ y = 0.1239e^{0.0384x} \]

\[ R^2 = 0.8224 \]
TLC 11 RING WIDTH DISTRIBUTION (Quercus rubra)

\[ y = 0.1275e^{0.032x} \]

\[ R^2 = 0.6005 \]
TLC 12 RING WIDTH DISTRIBUTION (Quercus rubra)

\[ y = 0.1921e^{-0.0048x} \]

\[ R^2 = 0.0345 \]
TLC 14 RING WIDTH DISTRIBUTION (Quercus rubra)

\[ y = 0.1344e^{0.029x} \]

\[ R^2 = 0.3977 \]
TLC 15 RING WIDTH DISTRIBUTION (*Fraxinus* sp.)

\[ y = -0.0002x^2 + 0.0063x + 0.0758 \]

\[ R^2 = 0.2312 \]
TLC 16 RING WIDTH DISTRIBUTION (Fraxinus sp.)

\[ y = 0.0796^{0.0227x} \]

\[ R^2 = 0.605 \]
TLC 17 RING WIDTH DISTRIBUTION (*Fraxinus* sp.)

\[ y = 0.0993e^{0.0428x} \]

\[ R^2 = 0.7477 \]
TLC 22 RING WIDTH DISTRIBUTION (*Fraxinus* sp.)

\[ y = 0.0281 e^{0.0899x} \]

\[ R^2 = 0.7233 \]
TLC 23 RING WIDTH DISTRIBUTION (Fraxinus sp.)

Ring Width (inches)

\[ y = 0.1111e^{0.0373x} \]

\[ R^2 = 0.4631 \]
TLC 24 RING WIDTH DISTRIBUTION (Fraxinus sp.)

\[ y = -0.0002x^2 + 0.0104x + 0.0312 \]

\[ R^2 = 0.5077 \]
TLC 25 RING WIDTH DISTRIBUTION (Fraxinus sp.)

\[ y = 2 \times 10^{-5}x^3 - 0.0012x^2 + 0.0236x + 0.1025 \]

\[ R^2 = 0.1665 \]
TLC 26 RING WIDTH DISTRIBUTION (Fraxinus sp.)

\[ y = 6 \times 10^{-6}x^2 - 0.0006x^2 + 0.0139x + 0.0413 \]

\[ R^2 = 0.3532 \]
TLC 27 RING WIDTH DISTRIBUTION (*Fraxinus* sp.)

\[ y = 0.0839e^{0.0131x} \]

\[ R^2 = 0.4803 \]
TLC 30 RING WIDTH DISTRIBUTION \textit{(Fraxinus sp.)}

\[
y = 0.0596e^{-0.0084x} \\
R^2 = 0.0563
\]
TLC 31 RING WIDTH DISTRIBUTION (Fraxinus sp.)

\[ y = 5 \times 10^{-5} x^2 - 0.0036x + 0.098 \]

\[ R^2 = 0.8359 \]
TLC 32 RING WIDTH DISTRIBUTION (*Fraxinus* sp.)

\[ \gamma = 5 \times 10^{-5}x^2 - 0.0045x + 0.1292 \]

\[ R^2 = 0.3262 \]
TLC 34 RING WIDTH DISTRIBUTION (*Fraxinus* sp.)

\[ y = 1E-05x^3 - 0.0009x^2 + 0.0162x + 0.0257 \]

\[ R^2 = 0.5509 \]

Ring Width (inches) vs. Ring Number (from bark)
Appendix E

Ring Width vs. Ring Number Core Plots,
Sheriff's Marsh
SMC 1 RING WIDTH DISTRIBUTION (*Fraxinus* sp.)

\[
y = 0.2226e^{-0.0323x} \\
R^2 = 0.4373
\]
SMC 2 RING WIDTH DISTRIBUTION (Fraxinus sp.)

\[ y = 0.0468e^{0.0191x} \]
\[ R^2 = 0.6713 \]
SMC 3 RING WIDTH DISTRIBUTION (Quercus rubra)

\[ y = 5 \times 10^{-5} x^2 - 0.0031x + 0.1659 \]
\[ R^2 = 0.2792 \]
SMC 4 RING WIDTH DISTRIBUTION (*Fraxinus* sp.)

\[ y = 0.0534e^{0.0037x} \]

\[ R^2 = 0.0051 \]
SMC 6 RING WIDTH DISTRIBUTION (*Fraxinus* sp.)

\[ y = 0.0477e^{0.0113x} \]

\[ R^2 = 0.3201 \]
SMC 7 RING WIDTH DISTRIBUTION (*Fraxinus* sp.)

\[ y = -0.0006x^2 + 0.0201x + 0.0194 \]

\[ R^2 = 0.6103 \]
SMC 8 RING WIDTH DISTRIBUTION *(Fraxinus sp.)*

\[ y = 0.0421e^{0.0121x} \]

\( R^2 = 0.0993 \)
SMC 9 RING WIDTH DISTRIBUTION (Carpinus caroliniana)

\[ Y = 0.0391e^{0.067x} \]

\[ R^2 = 0.5033 \]
SMC 10 RING WIDTH DISTRIBUTION (*Prunus serotina*)

\[ y = 0.0286e^{0.0128x} \]

\[ R^2 = 0.2144 \]
SMC 12 RING WIDTH DISTRIBUTION (Fraxinus sp.)

\[ y = -0.006x^2 + 0.0155x + 0.1055 \]

\[ R^2 = 0.7099 \]
SMC 14 RING WIDTH DISTRIBUTION (*Quercus bicolor*)

\[
y = -1E-06x^3 + 0.0002x^2 - 0.0081x + 0.0796
\]

\[
R^2 = 0.5926
\]
SMC 15 RING WIDTH DISTRIBUTION (*Fraxinus sp.*)

Ring Width (inches)

\[ y = 2 \times 10^{-5}x^2 + 0.0001x + 0.0492 \]

\[ R^2 = 0.4235 \]
SMC 16 RING WIDTH DISTRIBUTION (Quercus bicolor)

\[ y = 0.0284e^{0.0147x} \]

\[ R^2 = 0.3685 \]
SMC 17 RING WIDTH DISTRIBUTION (Fraxinus sp.)

\[ y = 5 \times 10^{-6}x^3 - 0.0004x^2 + 0.0089x + 0.0385 \]

\[ R^2 = 0.4201 \]
SMC 18 RING WIDTH DISTRIBUTION (*Prunus serotina*)

\[ y = 5E-06x^3 - 0.0003x^2 + 0.0076x + 0.0476 \]

\[ R^2 = 0.2096 \]
SMC 19 RING WIDTH DISTRIBUTION (Fraxinus sp.)

\[ y = 0.0869e^{0.0123x} \]

\[ R^2 = 0.1517 \]
SMC 20 RING WIDTH DISTRIBUTION (*Prunus serotina*)

\[ y = 0.1043e^{0.0073x} \]

\[ R^2 = 0.0625 \]
SMC 21 RING WIDTH DISTRIBUTION (Fraxinus sp.)

\[ y = 2E-06x^3 - 0.0002x^2 + 0.0076x + 0.1016 \]

\[ R^2 = 0.0722 \]
SMC 22 RING WIDTH DISTRIBUTION (Quercus rubra)

\[ y = 0.1964e^{0.0135x} \]

\[ R^2 = 0.1731 \]
SMC 23 RING WIDTH DISTRIBUTION (*Quercus alba*)

\[ y = 0.033e^{0.035x} \]
\[ R^2 = 0.6944 \]
SMC 25 RING WIDTH DISTRIBUTION (*Fraxinus* sp.)

\[ y = 0.286e^{-0.0134x} \]

\[ R^2 = 0.3343 \]
SMC 26 RING WIDTH DISTRIBUTION (*Fraxinus* sp.)

\[ y = 0.1835 \cdot e^{0.0231x} \]

\[ R^2 = 0.2801 \]
SMC 27 RING WIDTH DISTRIBUTION (Fraxinus sp.)

\[ y = 0.0002x^2 - 0.0044x + 0.1443 \]

\[ R^2 = 0.2202 \]

Ring Number (from bark)
SMC 28 RING WIDTH DISTRIBUTION (Fraxinus sp.)

\[ y = 0.0332e^{0.0408x} \]

\[ R^2 = 0.8277 \]
Appendix F

Abbreviations
APPENDIX F. Abbreviations

The following list of abbreviations were introduced and used throughout the text.

Core Analyses
CN: Core Number
CW: Cumulative Ring Width
DM: Deviation From the Mean
MA: Mature Tree Age
MN: Mean Tree Age
MTA: Minimum Tree “Age”
RN: Ring Number
RW: Ring Width
RWC: Ring-Width Chronology
RWI: Ring-Width Index
RWID: Ring-Width Index Difference
RWS: Ring-Width Subchronology
AV: Time Interval Before Present

Government Agencies
ASCS: Agricultural Stabilization and Conservation Service
COE: U.S. Army Corps of Engineers
FWS: U.S. Fish and Wildlife Service
MDEQ: Michigan Department of Environmental Quality
MDNR: Michigan Department of Natural Resources
NRCS: U.S.D.A., Natural Resources Conservation Service
SCS: U.S.D.A., Soil Conservation Service
USGS: U.S. Geological Survey
WES: Waterways Experiment Station

Site and Core Identification (followed by “C##” if used in reference to a particular core, e.g. CFC 21)
CF: Cache River Floodplain
KS: Kalamazoo River at Swan Creek
TL: Twin Lakes
SM: Sherriff’s Marsh

Miscellaneous
BLH: Bottomland Hardwood Forest
DBH: Diameter at Breast Height
HTG: Hydrotopographic Gradient
HTP: Hydrotopographic Position
NWI: National Wetland Inventory
WT: Water Table
WY: Water Year
REFERENCES


