1-1-2008

The Impact Of Climate On The Leaf Characteristics Of Genus Fraxinus

Brian W. Craven
Eastern Illinois University

THE IMPACT OF CLIMATE ON THE LEAF CHARACTERISTICS OF GENUS FRAXINUS

CRAVEN

THESIS REPRODUCTION CERTIFICATE

TO: Graduate Degree Candidates (who have written formal theses)

SUBJECT: Permission to Reproduce Theses

The University Library is receiving a number of request from other institutions asking permission to reproduce dissertations for inclusion in their library holdings. Although no copyright laws are involved, we feel that professional courtesy demands that permission be obtained from the author before we allow these to be copied.

PLEASE SIGN ONE OF THE FOLLOWING STATEMENTS:

Booth Library of Eastern Illinois University has my permission to lend my thesis to a reputable college or university for the purpose of copying it for inclusion in that institution's library or research holdings.

Brian W. Ca[illegible] 3/10/08

Author's Signature Date

I respectfully request Booth Library of Eastern Illinois University **NOT** allow my thesis to be reproduced because:

Author's Signature Date

This form must be submitted in duplicate.

The Impact of Climate on the

Leaf Characteristics of Genus Fraxinus

(TITLE)

BY

Brian W. Craven

THESIS

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF

Biological Sciences

IN THE GRADUATE SCHOOL, EASTERN ILLINOIS UNIVERSITY
CHARLESTON, ILLINOIS

2008

YEAR

I HEREBY RECOMMEND THAT THIS THESIS BE ACCEPTED AS FULFILLING
THIS PART OF THE GRADUATE DEGREE CITED ABOVE

7 March 2008
DATE

Gordon C. Tucker
THESIS DIRECTOR

7 March 2008
DATE

Andrew S. McElwee
DEPARTMENT/SCHOOL HEAD

ABSTRACT

Fraxinus (ash) has six species across eastern North America, five of which are found in Illinois (*F. americana, F. pennsylvanica, F. nigra, F. quadrangulata, F. profunda*). It is also threatened by the emerald ash borer (*Agrilus planipennis*) (EAB). Are climate differences across a north-south distance of 600 km great enough to create differences in the morphological characteristics of *Fraxinus* species? Studying latitudinal variation in the species of *Fraxinus* would reveal the impact of climate on the leaf characteristics of a genus of trees which extend over a considerable portion of the continent. The objectives of this study were to determine if quantitative differences occur in leaf characteristics of the species found across Illinois, to determine if EAB is present at the sites visited, to determine if quantitative differences occur in leaf characteristics between variety and species for *F. americana and F. pennsylvanica*, and to define variation in leaf and twig characteristics for the 5 species in Illinois to see of there are any qualitative differences between the regions. Regions (northern, central, and southern Illinois) were defined using annual mean maximum and minimum temperature as well as mean total precipitation. Leaves and twigs were collected from 235 trees at 18 locations across Illinois. Materials were dried and then measured for length and width of all leaflets, leaf area and dry mass for all leaves. Data were collected for several qualitative characteristics as well. A multivariate analysis of variance and a principal components analysis were run on several characteristics for *F. americana, F. pennsylvanica, F. quadrangulata,* and *F. profunda*. Regional differences were found to be significant in *F. americana* and *F. pennsylvanica*, with total leaf area, L2 length, R2 length, T length, and L2 width, T width measurements being much larger in northern IL for white ash and leaf mass and leaf density being much

larger in southern IL for green ash. Varieties were tested and *F. americana var. biltmoreana* was found to have significant differences from white ash, while *F. pennsylvanica var. subintegerrima* was not found to have significant differences. Several trees with very large leaves were found, necessitating revisions in the upper size limit for leaves of *F. americana, F. nigra,* and *F. profunda*. Two trees matching descriptions of *F. caroliniana* were found in Illinois. The population is most likely artificial, having arrived via unintentional introduction anytime since 1848. No signs of EAB were found at the sites in 2006. Based on the specimens of blue ash collected having several characteristics which differed from the description of the species in the literature (adaxial and abaxial leaf surface colors, leaflet shape, leaflet tip form, range of most frequent number of leaflets, leaf thickness, twig thickness, lateral bud and leaf scar size), a variety of blue ash is proposed, *F. quadrangulata var. fuscopapyraceus*. Several abnormalities were observed, particularly in *F. americana*, indicating this species has a higher frequency of variability than previously indicated. Revised species descriptions have been provided to account for the variation seen, yet not previously described. Difficult to identify specimens were very common, with 24% having 1-2 characteristics not traditionally associated with the species it was identified to being and 8% being extremely hard to identify. These specimens refute all previously reliable wedge traits to differentiate between species (excluding samaras). The only reliable means of discerning species is to look at a suite of characteristics, not just one or two.

ACKNOWLEDGEMENTS

The assistance provided during the development, implementation, and composition of the thesis by thesis advisor Gordon Tucker and committee members Scott Meiners and Janice Coons should be acknowledged. Some funding for the thesis came from the Lewis Hanford Tiffany and Loel Zehner Tiffany Botanical Graduate Research Fund. Permits allowing collection of ash materials came from the Illinois Department of Natural Resources, the Illinois Nature Preserves Commission, the US Fish & Wildlife Service, and the Cook County Forest Preserve District. Assistance during collection at two sites was provided by Walter McCarthy. Finally, leaf and twig materials from hybrids created over three decades ago were provided by the University of Michigan-Ann Arbor.

TABLE OF CONTENTS

LIST OF TABLES AND FIGURES

Figures

INTRODUCTION

Illinois spans 640 km from north to south (5.6° of latitude) and has a continental climate (King 1981). Latitude is the primary factor affecting temperature and precipitation in Illinois (King 1981). The conditions in the northern part of the state and the southern part of the state differ noticeably in the summer and winter. While not as drastic a difference as going from one climate to another (e.g. taiga to tundra, temperate to tropical), Illinois occupies a considerable span of the temperate climate zone and has some species which do not reach further south than the northernmost counties of the state and some species which do not reach further north than the southernmost counties of the state. Is this difference in climate enough to generate differences in the populations of a species found across the entire state or to generate similar changes or trends in the species of a genus with different distributions across Illinois?

The genus *Fraxinus*, the ash, is one of the prevalent types of trees that comprise the temperate deciduous forests of the northern hemisphere. *Fraxinus* species are found in forests with many other common tree species in eastern North America, like *Quercus* (oak), *Acer* (maple), *Carya* (hickory), *Ulmus* (elm), *Salix* (willow), *Betula* (birch), *Fagus* (beech), *Pinus* (pine) (Griffith 1991; Gucker 2005a; Gucker 2005b). Though referring to white ash, the following statement from Schlesinger applies to all ashes: "Throughout its range it is a minor but constant component of both the understory and overstory of mature forests on suitable soils" (Schlesinger 1990). The genus tends to remain in the background of the forest associations in which it is a part.

Of the six species found in eastern North America, five are found in Illinois. White ash, *Fraxinus americana*, is found across most of the temperate zone east of the

Great Plains (fig. 1a). Green ash, *F. pennsylvanica*, has the broadest range of the six, spanning from the Atlantic Coast to the western edge of the Great Plains (fig. 1b). Black ash, *F. nigra*, has the most northerly range, being found north of the Ohio River to the limits of deciduous species in Canada (fig. 1c). Blue ash, *F. quadrangulata*, is found generally only in the central and southern sections of the Midwest (fig. 1d). Pumpkin ash, *F. profunda*, has a fragmentary range with three large components- the Carolinas, Florida, and the lands near the confluence point of the Mississippi and Ohio Rivers (fig. 1e). Carolina ash, *F. caroliniana*, is the only eastern Ash that is not found in Illinois. Its range is generally confined to the Gulf Coast and Atlantic Coast from the Carolinas southward (fig. 1f). Range maps by county for Illinois can be found with the Illinois Plant Information Network (Illinois Plant Information Network website). Two species (*F. americana, F. pennsylvanica*) are found statewide, three are limited to certain sections of the state, *F. nigra* to the northern part, *F. profunda* to the southern part, and *F. quadrangulata* generally to the central part.

The primary purpose of the study described in this thesis is to determine whether quantitative differences occur in the leaf and seed characteristics of the species of *Fraxinus* between northern, central, and southern Illinois. This genus was selected because it is a relatively common tree in forests and it was the only major type of tree (e.g. oaks, maples, elms, hickories, ashes, walnuts) with both multiple species in the state and species found only in northern Illinois generally (*F. nigra*), generally only in southern Illinois (*F. profunda*), and only across central Illinois primarily (though with a less widespread presence in northern Illinois) (*F. quadrangulata*) in addition to statewide (*F. americana, F. pennsylvanica*). In addition, the genus is in peril, perhaps even being in the process of becoming a ghost of forests past like the American chestnut, the passenger pigeon, or the Carolina parakeet.

The genus *Fraxinus* in North America is currently under threat from an invasive species. The emerald ash borer, *Agrilus planipennis* (hereafter abbreviated EAB), was first identified in July 2002 in Michigan and is estimated to have arrived around the mid 1990s. EAB has spread across several states via human transport, specifically by firewood or violations of a federal quarantine, since its flight range is only up to 5.2 km per year, not allowing it to cover the distances between confirmed infestations (Taylor et al 2004; Terrell and Bolger 2006). The EAB is native to northeast China, Japan, Korea, Taiwan, and the Russian Far East (OEPP/EPPO Bulletin 2005). Unlike most other invasive pests or diseases, the EAB kills 100 percent of all ash trees it infests (OEPP/EPPO Bulletin 2005).

This situation is worse than similar situations which have blighted the continent in the 20th century. The chestnut blight of the early 20th century eliminated one of the dominant trees of the eastern North American forests, the American chestnut (*Castanea dentata*) and Dutch elm disease dramatically reduced the population of the American elm (*Ulmus americana*) in the mid 20th century. Both of those only impacted one species, not up to half a dozen species. Ironically, after Dutch elm disease destroyed many elm trees across the US, many vacant spots in yards and parkways were replaced with ash trees (Sinclair 2004). This will have an economic impact as white ash is one of the more commercially valuable timber trees of North America (Fernald 1950; Gleason and Cronquist 1963; Brown 1975).

The EAB is currently infesting Michigan, Ontario, Ohio, Indiana, Maryland, Pennsylvania, Illinois, and was once found in Virginia (Fairfax Office of Public Affairs 2004; Terrell and Bolger 2006; Henrichs 2007). It has only been successfully eradicated in Virginia (Fairfax County, Virginia Website 2007). It was first reported in Illinois in June 2006 and is infesting portions of Kane, Cook, DuPage, and LaSalle Counties (Illinois Department of Agriculture 2006; Terrell and Bolger 2006; Illinois Department of Agriculture 2007a, Illinois Department of Agriculture 2007b; Schelkopf 2007). Ash trees comprise an estimated 130 million, or 6%, of the trees found in Illinois, 12% of street trees in Chicago, and 22% of street trees in Cook County (Nowak 1994; Terrell and Bolger 2006). To date, it has killed 25 million ash trees since its arrival in 2002 (Heinrichs 2007).

Some measures have been taken to isolate and destroy EAB wherever it is located, though efforts to contain it have had very limited success, though there has been some hope recently with the approval of three species of parasitoid wasps from China for use as a biocontrol for EAB in 2007 (Gould 2007). Based on the increased rate of discoveries of infestations in Illinois, it is clear EAB is a growing problem in the state of Illinois.

The purposes of this study were: 1) to determine if any differences, as determined by quantitative measurements of leaf and seed characteristics, occur between the northern, central, and southern sections of the state, 2) to assess the trees of these sites for the presence of the emerald ash borer, and 3) to determine if there are quantitative differences that would differentiate the varieties of *Fraxinus* besides the presence/absence of pubescence. As the project was running, it became apparent that descriptions of the variation within species would also need to be compiled due to several problem specimens defying easy classification. This added an additional purpose: 4) to define the leaf and twig characteristics of the species to identify diversity and variation within species and to see if any differences occur in these characteristics between northern, central, and southern Illinois.

The seed portion of the study would be dropped due to poor seed production by *Fraxinus* in Illinois in 2006.

LITERATURE REVIEW

History of *Fraxinus* in Illinois since the end of the Wisconsin Glaciation:

The land currently designated as the state of Illinois was significantly shaped by the Wisconsin Glaciation, a part of the last global Ice Age. Glaciations are considered the defining events in the recent geologic history of the state (Frye et al, 1965).

In northern Illinois, the pollen records from Volo Bog (McHenry County) indicate forest replaced the tundra around 11,070 BP (King 1981). Between 10,900- 10,300 BP, *Fraxinus* was a part of a group of genera (including *Betula, Pinus, Abies*) which dominated the forest composition, replacing *Picea* (King 1981). Ash pollen indicated the *Fraxinus* species involved was *F. nigra*, a species currently known for its northerly distribution relative to other ash species. *Fraxinus* was common during a cool, temperate climate. As temperatures got warmer, *Quercus* began to dominate (though it shared dominance with *Ulmus* and *Ostrya/Carpinus* until around 8000 BP) and the percentage of the pollen record that *Fraxinus* comprised diminished to present levels. The pollen assemblage indicates after *Fraxinus* dominated, the forest transitioned into a xeric oak-hickory forest, with a return to slightly cooler mesic conditions from 900-400 BP, which corresponds with the Little Ice Age (King 1981).

In central Illinois, the pollen records from Chatsworth Bog (Livingston County) indicate forest replaced the tundra around 14,700 BP, *Fraxinus* first appeared and came to dominate the forest between 13,800- 11,600 BP, taking over from *Picea*. Then it was then superceded by *Quercus* and *Ulmus*, and finally *Quercus* (King 1981). The pollen there indicates the species was either *F. quadrangulata* or *F. nigra*, most likely being *F. nigra* based on the climate at the time. *Fraxinus* dominated in cool temperature conditions. When *Quercus* and *Ulmus* took over, conditions were getting warmer, and *Quercus* came to dominate fully when conditions started to dry, forming the prairie (King 1981).

No comparable pollen record can be found for southern Illinois, but General Land Office (GLO) land surveys from 1805-1815 are the best data set available for pre-settlement forest composition of the region. These land surveys for southern Illinois, describing 38°50'N southward, indicate the general composition of the forests at this time were ~40% *Quercus* (29% Section *Quercus*, 11% Section *Lobatae*), 9% *Carya*, 7% *Ulmus*, 7% *Fraxinus*, 7% *Liquidambar*, and smaller percentages of *Acer, Betula*, and others. The habitat for the region broke down into 5 different types: mesic oak-hickory forest with a mix of mesophytic and xerophytic species (Shawnee Hills, Cretaceous Hills, limestone uplands along Mississippi River), mixed hardwood forest (Thebes Hills), lowland-depressional forest (Cache, Ohio, Saline, Wabash river valleys, upland sections lining river valleys, bottomlands), floodplain forest (Mississippi River Bottoms), and wet prairie (small locations on Mississippi River floodplain). *Fraxinus* was a major component in the lowland-depressional forest and floodplain forest comprising about 10% of trees in each of those habitat types (in contrast, they comprised only about 3% of trees in mesic oak-hickory forests & 4% in mixed hardwood forests) (Leitner and Jackson 1981). Overall, southern Illinois is described as an ecotone based on the mixture of species from different regions there (Leitner and Jackson 1981).

The Grand Prairie Division which occupies much of Illinois developed between 8500-7900 years ago, replacing the deciduous forest that was present. The oak-hickory forest association had established itself as the major forest type in Illinois by 7900 years ago based on pollen evidence indicating a shift towards drier conditions (Wright Jr. 1976).

At present in northern Illinois, *Quercus alba, Q. rubra, Q. macrocarpa, Carya ovata, C. cordiformis, Ulmus* rubra dominate upland locations, *Acer saccharum, Fraxinus americana, Tilia americana* dominate mesic locations, and *A. saccharinum, F. pennsylvanica, Ulmus* spp. dominate lowland locations (King 1981). Central Illinois had limited forests, with *Q. velutina, Q. marilandica* dominating dry, sandy upland sites, *Q. velutina, Q. alba, Q. rubra, C. ovata, A. saccharum, U. rubra* dominating dry-mesic sites, *Q. macrocarpa, U. americana, F. quadrangulata, Celtis occidentalis* dominating wet-mesic sites, and *Platanus occidentalis, F. pennsylvanica, A. saccharum, Populus deltoides* dominating floodplains (Adams and Anderson 1980). In southern Illinois, *Q. alba, Q. stellata, Q. velutina, Q. marilandica, Q. coccinea, C. ovata, C. glabra* dominate upland locations, *Q. rubra, F. americana, Juglans nigra, J. cinerea, Fagus grandifolia, A. saccharum, C. cordiformis, T. americana* dominate mesic locations, and *Taxodium distichum, A. rubrum, Fraxinus pennsylvanica, Nyssa aquatica, Liquidambar styraciflua* dominate lowland swamp locations (King 1981). Generally, Illinois is dominated by oaks, though sugar maple is noticeably increasing and eroding that historic dominance by oaks (Leitner and Jackson 1981).

Fraxinus usually receives little beyond mentioning in literature about Illinois' landscape. While it is commonly found in the state, it isn't a major component of forests like oaks. *Fraxinus pennsylvanica* is noted as one of the dominant trees of floodplains in central Illinois though and *F. quadrangulata* is noted as being commonly found in Illinois on limestone cliffs as well as in mesic wooded slopes or wet-mesic sites (Mohlenbrock 1973; Adams and Anderson 1980).

Profile of genus *Fraxinus* and its species:

The genus *Fraxinus* is a part of the family Oleaceae, which comprises around 30 genera of which the most well known are *Olea* (olives), *Syringa* (lilacs), *Forsythia* (forsythias), *Jasminium* (jasmine), and *Ligustrum* (privets). *Fraxinus* comprises roughly 40-60 species of trees or shrubs spanning across the temperate region of North America, Europe, and Asia, depending on the source (e.g. Oxford University, USDA Germplasm Resources Information Network, et al.) (Taylor 1945). In North America, 6 species are located in the eastern region and around 11-14 are located in the western region and Mexico. Only the 6 species found in eastern North America will be profiled here.

Ash trees have opposite, pinnately-compound leaves. The number of leaflets depends on the species and can vary between 1 and 13. The winter buds have all of the leaf primordia that will emerge during the following growing year (Kozlowski 1971). *Fraxinus* is among the genera that leaf out late into spring, alongside *Quercus* and

Juglans (Lechowicz 1984). Unlike other genera, which can generate additional flushes of leaves past the spring flush (e.g. *Quercus*) or additional individual leaves past the spring flush (e.g. *Populus, Betula*), *Fraxinus* only produces leaves in a spring flush, barring regeneration following defoliation (Lechowicz 1984).

The genus has wind-pollinated flowers which are generally dioecious. The seeds are located inside winged fruits called samaras. Samaras generally contain one embryo per seed, though polyembryony, a seed with two or more embryos, has been documented in a few species (Steinbauer 1943).

Six *Fraxinus* species are found in eastern North America. Five of these are found in Illinois, with two having statewide ranges, and three having ranges spanning half the state or less (Prasad 2002). *Fraxinus caroliniana* is included in the species descriptions for reasons that will become apparent later in this paper.

In section *Fraxinus* within genus *Fraxinus*, there are two subsections, *Melioides* and *Fraxinus* (Hardin and Beckmann 1982). In each subsection are grouped complexes, though researchers have noted the complexes are problematic (Hardin and Beckmann 1982). *Melioides* contains *F. americana, F. pennsylvanica, F. caroliniana, F. profunda, F. texensis* and *Fraxinus* contains *F. nigra, F. quadrangulata* (Hardin and Beckmann 1982). A more recent attempt to reorganize the genus recognizes three sections, *Dipetalae*, containing *F. quadrangulata* and some western North American ashes, *Ornus*, containing European species *F. ornus* and several Asian species, and *Fraxinus*, which contains several subsections, with three species of uncertain classification (Wallander 2001). Section *Fraxinus* contains four subsections, *Fraxinus*, containing *F. nigra, F. mandschurica*, and European species *F. excelsior* and *F. angustifolia*, *Melioides*, containing *F. americana, F. caroliniana, F. pennsylvanica, F. profunda, F. texensis*, and several western North American and Mexican ashes, *Pauciflorae*, containing a few Mexican ash species, and *Sciadanthus*, which contains Asian species (Wallander 2001).

Discerning between species in *Fraxinus* in eastern North America has been a challenge for many years. There are several mentions in the literature of ash species being difficult to tell apart aside from "a few well-marked forms," particularly between *F. americana* and *F. pennsylvanica* (Taylor 1945; Miller 1955; Santamour Jr. 1962; Petrides 1972). Several papers make mention of ash trees that could not be identified easily or which were later classified as a different species (e.g. Wright 1944a, Taylor 1945 as referred to in Santamour Jr. 1962, Santamour Jr. 1962, and the *Fraxinus profunda-tomentosa* naming controversy). Many keys say definitive identification can only come from the samaras or flowers (Taylor 1945; Petrides 1972). The difficulty stems from variability in morphological characteristics which overlap between species, resulting in difficulty in demarcating the boundaries between species (Taylor 1945). The variability within species is attributed to polyploidy and ecotypes; hybridization is not responsible for this confusion (Miller 1955; Hardin and Beckmann 1982). Identification is complicated by multiple ploidy levels within *F. americana* and *F. pennsylvanica* (Hardin and Beckmann 1982). Specifically, the overlaps between species tend to involve *F. americana* and *F. pennsylvanica*, *F. pennsylvanica* and *F. caroliniana*, and *F. profunda* with both *F. americana* and *F. pennsylvanica*.

Fraxinus americana L., White Ash

Fraxinus americana, the white ash, has a range which overlaps with much of the deciduous forests of eastern North America, extending from the Eastern Seaboard and Nova Scotia to eastern edge of the Great Plains, generally near the Missouri River, and from Ontario (and a small part of Quebec) to northern Florida (Schlesinger 1990). It is found in upland forests or on ridges along rivers and requires well-drained soils to thrive (Schlesinger 1990).

White ash has a dioecious flowering habit and the flowers appear in April to May. Samaras are produced in October to November and dispersed between October and December (Bonner 1974). White ash seeds have dormancy as a result of an impervious seedcoat and inhibitors (Dirr and Heuser Jr. 1987; Schlesinger 1990). They generally require either 2-3 months cold or 1 month warm followed by 2 months cold (to allow for after-ripening) to germinate properly, although the literature conflicts on the matter (Dirr and Heuser Jr. 1987).

White ash is the most commercially valuable ash on North America and one of the more valuable timber trees overall, being used to make a wide array of wood products (Fernald 1950; Gleason and Cronquist 1963; Brown 1975). Prior to the popularity of green ash as a yard tree, white ash was the most desirable choice of ash for planting in the late 1800s and early 1900s (Hough 1921; Dame & Brooks 1972). It was considered to have an impressive form, with Hough describing it as "one of the statliest representatives of its genus" (Hough 1921).

White ash has one variety, *Fraxinus americana var. biltmoreana*, the Biltmore ash. When it was originally considered a separate species, it was differentiated from white ash by its wider samaras, stouter twigs, pubescence, and clove brown buds (Beadle

1898). At the time, it was noted for its similarity to *F. americana* and for relating to white ash the same way *F. pennsylvanica* related to *F. lanceolata* (Beadle 1898). Since it was designated a variety, it has generally kept that classification, but some think it should not receive any distinction at all. Biltmore ash was thought to be a natural hybrid of *F. americana* and *F. pennsylvanica*, but an examination of the microscopic foliar features show a resemblance to *F. americana*, not to *F. pennsylvanica* and it does not resemble the diploid hybrid created by Sylvia Taylor in 1968 and 1970 at University of Michigan-Ann Arbor (Miller 1955; Santamour Jr. 1962; Hardin and Beckmann 1982). Miller maintained Biltmore ash should be considered a separate species since it has more characteristics distinguishing it from white ash than mere pubescence, such as the bud characters of red ash, though Santamour found tetraploid white ashes have leaf scars resembling those of *F. pennsylvanica*, removing Miller's grounds for maintaining a species-level division, however, Santamour maintains Biltmore as a separate species because it has tetraploid and hexaploid ploidy levels, but not a diploid level and had consistent combinations of characters: leaf scars with a truncate upper margin, reniform or round lateral buds, a difference in size of stomatal guard cells, and pubescence (Miller 1955; Santamour Jr. 1962).

White ash is known to have 3 possible total numbers of chromosomes: diploid (2n= 46), tetraploid (2n= 92), and hexaploid (2n= 138) (Wright 1944b; Santamour Jr. 1962). The diploids are found to occur throughout the range of the species while the tetraploids are found south of the 35°N latitude, and the hexaploids are found between 35°N and 40°N latitude (Schlesinger 1990). The diploids have stable DNA values, but the tetraploids and hexaploids have variation in their DNA values (Black and Beckmann

1983). Triploid and pentaploid embryos have been documented, though no triploids have been found to be viable (Clausen et al. 1981; Black and Beckmann 1983). Pentaploids have been reported in one article, specifically Clausen et al. 1981, though oddly the 7 individuals found were not treated in the article as being exceptionally unusual, nor do major works on white ash following this article (e.g. Schlesinger 1990) make note of these pentaploids.

It was thought these ploidy levels lacked any morphological distinction (e.g. Wright 1944b, Black and Beckmann 1983), but Santamour found differences, noting the original study relied only on 2 year old seedlings and not all morphological characteristics are apparent at that age (Santamour Jr. 1962). Diploids had triangular-shaped lateral buds and deeply notched leaf scars (the typical white ash features), tetraploids and hexaploids had reniform or rounded lateral buds and leaf scars with a truncate or slightly truncate upper margin (features traditionally affiliated with red ash) (Santamour Jr. 1962). Tetraploids were also observed to produce the longest leaf lengths out of all 3 ploidy levels while hexaploids (and pentaploids) had significantly longer samaras and wider seeds (Clausen et al. 1981). Variation in ploidy level accounts for different samara length, seed width, seedling height, and leaf fall date on plantations of seeds from various ploidy levels across the species range, while variation in seed length (not samara length) and wing length were found to vary along clines though (Clausen et al. 1981).

Ecotypes are individuals within a species adapted to survive better in a particular environment within the species' range than other members of that species (Spooner et al. 2003). Three ecotypes have been attributed to white ash, a northern ecotype found in

New England states, MI, OH, PA, an intermediate ecotype found in OH, PA, WV, and a southern ecotype found in AR, AL, MD, IN (Wright 1944b). The northern ecotype has a low frequency of discernable pubescence and lacks anthocyanin, which gives a reddish cast to petioles. The intermediate ecotype has a high frequency of pubescence and a lack of anthocyanin. The southern ecotype has a high frequency of pubescence, and anthocyanin present. This ecotype also had a glossier surface to its leaves as well as red petioles and midribs. Leaflet shape showed variability independent of ecotype (Wright 1944b). These ecotypes also had differences in cold-hardiness, upheld by additional research, and root system habitat, with northern and intermediate ecotypes having extensive shallow root systems while the southern ecotype had a taproot; resilience to northern winters varied from high (northern ecotype) to low (southern ecotype) (Wright 1944b; Alexander, Flint, and Hammer 1984). The ecotypes are thought to have originated before the polyploidy (Wright 1944b). However, some think the geographic ranges of polyploids accounts for the differences seen and therefore ecotypes don't exist (Schlesinger 1990).

Fraxinus pennsylvanica Marsh., Green Ash

A note of clarification: because the term green ash has been applied to different trees over time, separate terms will be used to refer to the different applications of green ash. "Original green ash" will refer to the type of tree that was once called *F. lanceolata* and was later classified as a variety of red ash and then merged entirely into red ash. "Modern green ash" refers to the current definition of green ash, which includes green ash and red ash as one species, *F. pennsylvanica*, without any varieties. "Red ash" will refer to the species that was once separate from original green ash and which bore the name *F. pennsylvanica* at the time the original green ash bore the name *F. lanceolata*.

Modern green ash has the most expansive range of all eastern North American ashes, extending across much of North America east of the Rocky Mountains where deciduous trees can be found. It is found from the Eastern Seaboard from New Brunswick and Nova Scotia down to northern Florida to the western edge of the Great Plains and from Ontario down to the Gulf of Mexico, with a presence in southern Saskatchewan and Manitoba as well (Kennedy Jr. 1990). It is found in lowland forests and in lands adjacent to rivers or streams (Kennedy Jr. 1990). It is shade-intolerant to somewhat tolerant in the northern part of its range and is shade-tolerant, becoming only somewhat tolerant as it ages in the southern part of its range (Kennedy Jr. 1990). When the division was maintained, red ash's range was said to span from the Northeast and lower ON, PQ down to the Gulf Coast and over to MI & WI and green ash's range spanned from the Northeast & lower ON, PQ down to the Gulf Coast and over to SK, MT (Hough 1921; Fernald 1950; Dame and Brooks 1972).

Green ash is dioecious and flowers from March to May, produces samaras in September or October and disperses them between October and the following spring (Bonner 1974). The seeds display some dormancy due to inhibitors and an impenetrable seed coat (Kennedy Jr. 1990). They require 2-3 months cold stratification or 2 months warm followed by 3 months cold stratification (Dirr and Heuser Jr. 1987).

Green ash is also one of the more commercially-utilized ashes. The original green ash became popular as a street tree for cities or a yard tree for suburbs in the latter half of the 20th century, particularly after the development of the cultivar Marshall's Seedless in

1946 by the Porter-Walton Co. of Salt Lake City, UT, which had the desirable attribute of not producing seeds (Santamour and McArdle 1983; MacFarlane and Meyer 2005). It was not widely used in landscaping in the early 20th century outside of the central US (Dame and Brooks 1972; Brown 1975).

Modern green ash has rather complicated origins. The full history can be found in Appendix I, though a shortened summary will be given here. It originally started as 2 separate species, red ash and (original) green ash based on whether pubescence was present or not and the primary form of margin, entire or crenate (red) or serrate (green); otherwise, they were similar. Reclassifying original green ash as a variety of red ash formally occurred in the mid 20th century. Original green ash, *Fraxinus lanceolata*, was reclassified as *F. pennsylvanica var. subintegerrima*. At this time, a different classification was proposed as well, one that recognized no varieties and removed the taxonomic rank of *F. lanceolata* entirely (Little Jr. 1953). Compounding the confusion, this consolidated species went by the common name green ash despite having the scientific name *F. pennsylvanica*, which went by the name red ash until that time. Both classifications floated around in the latter half of the 20th century, though the view which recognized no varieties grew more common towards the end of the century based on a survey of literature. No quantitative tests justifying either classification can be found in the literature.

No total surveys of all potential ecotypes were done across the modern green ash range; only studies from parts of the overall range exist. Three ecotypes were found in the Great Plains for original green ash, varying by drought-resistance and leaf color (Meuli and Shirley 1937). The further north and the further west a seedling was originally from, the greater its drought resistance (Meuli and Shirley 1937). These differences were deemed to belong to discrete types and not be a gradient because differences within regions were not statistically significant, nor were upland-lowland differences significant (Meuli and Shirley 1937). The three regions had varying lengths of time between heavy rains and the regions with longer lengths between rains had more drought-tolerant green ash (Meuli and Shirley 1937). Three ecotypes elsewhere on the continent were found as well, a northern, southern, and intermediate ecotype (Wright 1944a). The northern ecotype was found in MI, WI, MN, ME, ON and the southern ecotype was found in VA, NC, SC (Wright 1944a). The northern ecotype has green petioles and brown twigs, the southern ecotype had reddened petioles and midribs and green twigs (Wright 1944a). The northern ecotype also showed less stem dieback in a northern winter than the southern ecotype, though tended to grow slower than the southern ecotype. Oddly though, the southern ecotype had leaves which would not be killed by temperatures below 20°F, a feature not shared by the northern ecotype (Wright 1944a). The intermediate ecotype was only found around Ithaca, NY (in his sampling regime), which had cold-hardiness and growth rates between the other two ecotypes; leaf and twig features weren't noted (Wright 1944a).

Fraxinus nigra Marsh., Black Ash

Fraxinus nigra has a range spanning from the Atlantic Coast to eastern Iowa, Minnesota, and Manitoba, and from south to north, it extends from 40°N, around the middle of Indiana, Ohio, and Pennsylvania, up to the northern limit of deciduous forests, though it can also be found on parts of Newfoundland (Wright and Rauscher 1990). It resides in poorly drained areas (e.g. swamps, bogs, seeps, riversides) (Wright and Rauscher 1990). Despite the northerly range, it is well-known for having very frost-sensitive leaves.

Black ash has a dioecious flowering habit, though there is some evidence this trait can vary. While the species is most commonly reported as dioecious, there are accounts of individuals with perfect flowers or having male and female flowers in separate places on the same tree (Anderson and Nesom 2006). It flowers in May or June, produces samaras between June and September and disperses seeds between July and October (Bonner 1974; Wright and Rauscher 1990). Black ash seeds germinate naturally the second spring following their dispersal due to dormancy (Wright and Rauscher 1990). This dormancy is a result of a combination of an immature embryo, inhibitory enzymes, and an impermeable seedcoat (Wright and Rauscher 1990). The usual tactic for germination follows a period of warm stratification followed by cold stratification, usually set at 2 months warm then 3 months cold (Dirr and Heuser Jr. 1987).

While black ash grows in poorly drained areas, it is not as tolerant to standing water for long periods of time as pumpkin ash is. Black ash radial growth is affected positively by low-intensity floods, but is affected negatively by high-intensity floods (Tardif and Bergeron 1993). Other factors positively affecting radial growth were spring temperatures and summer and winter precipitation the previous year, while factors negatively affecting radial growth were spring and autumn precipitation (Tardif and Bergeron 1993).

Fraxinus quadrangulata Michx., Blue Ash

Fraxinus quadrangulata has an odd bow-shaped range, extending through MO, IL, IN, OH, KY, and TN with small isolated populations in AL, GA, WV, AR, OK, KS, WI, MI, ON as well (Fernald 1950). It is found generally on dry ridges and upland regions, though occasionally in moist bottomland forests (Hough 1921).

Blue ash has a perfect flowering habit and flowers in March or April, produces samaras between June and October (Bonner 1974). No detailed information is available on the samara dispersal time. Blue ash seeds contain immature embryos and require exposure to warm temperatures followed by cool temperatures. 2 months of cold stratification only has also worked well (Dirr and Heuser Jr. 1987).

Ecological research into blue ash has been strongly lacking in comparison to research into *Fraxinus americana, F. pennsylvanica*, and *F. nigra*. In a survey of literature, blue ash usually only received mention in broader studies looking at an entire forest system and was never the subject of research. In addition, an explanation for its unusual range in comparison to other eastern North American ashes remains absent nor is there any discussion on possible variation in the species across its range. Additionally, Silvics of North America, which covers most of the eastern ashes, does not mention blue ash. Other authors (e.g. MacFarlane and Meyer 2005) have also noted the literature is sparse for blue, pumpkin, and Carolina Ash.

Fraxinus profunda (Bush) Bush, Pumpkin Ash

Pumpkin Ash is one of the more unusual ashes. It was originally identified as a variety of white ash and later a variety of red ash before being given a species-level rank. It has a range unlike most of the other ashes. It has a few small extensive ranges and several isolated populations with very limited ranges. Its largest ranges are close to the Atlantic shore from southern Virginia to South Carolina, in the Florida Panhandle, and in southern Illinois, southeast Missouri, western Tennessee, and southwest Indiana (Harms 1990). Isolated populations can be found in Illinois, Indiana, Ohio, Maryland, Kentucky, Tennessee, North Carolina, South Carolina, Georgia, Florida, Alabama, Louisiana, as well as Michigan and Ontario (Harms 1990; McCormac, Bissell, and Stine Jr. 1995; Waldron, Gartshore, and Colthurst 1996). Its primary habitat is in bottomlands, swamps, and wetlands (Harms 1990).

Pumpkin ash's most distinguishing feature is the trunk's swollen base. Interestingly, while it is often submerged in water for significant amounts of time in its main habitat, it is documented as growing slowly in such conditions and grows faster where soil has better drainage (Harms 1990).

Pumpkin ash has a dioecious flowering habit. It flowers in April to May, produces samaras in September or October and disperses its seeds in October to December (Bonner 1974; Harms 1990). Data on how many years between large seed crops for this species are unknown, though it is "apparently not a prolific seeder" (Harms 1990). Guides which provide information on propagating seeds for other *Fraxinus* species (e.g. Dirr and Heuser Jr. 1987) do not list how to propagate pumpkin ash.

Much speculation over the nature of pumpkin ash, though there is general agreement that it doesn't have the standard origin the other five eastern species have. Most of this speculation circulates around whether it is a hybrid or an autopolyploid. Since early on, it was noticed pumpkin ash was similar to white ash and red ash, though had some characteristics they lacked, as evidenced by the taxonomic flux pumpkin ash had prior to being named *Fraxinus profunda*. It was also noticed pumpkin ash had "gigas" characteristics, which are common in polyploids. Miller thought pumpkin ash was an autopolyploid derivative of *F. pennsylvanica* due to its "gigas" characteristics, or it resulted from chromosome doubling in a hybrid of *F. americana* and *F. pennsylvanica* or of *F. pennsylvanica* and *F. caroliniana* (Miller 1955). In 1959, Wright described pumpkin ash as behaving like a true-breeding hexaploid derivative of a tetraploid white ash and a diploid green ash (Harms 1990; Schlesinger 1990). Evidence given to support this is the qualitative similarity between pumpkin ash's morphological characteristics and the characteristics of white and green ash in addition to its distribution (Kennedy Jr. 1990). Hardin and Beckmann thought pumpkin ash could not be of hybrid origin because the microscopic features on leaf surfaces of the artificial *F. americana x pennsylvanica* hybrid did not resemble pumpkin ash's microscopic foliar features (Hardin and Beckmann 1982). They instead supported pumpkin ash being an autopolyploid derivative of *F. pennsylvanica* based on the microscopic foliar features.

The origin of pumpkin ash remains mired in mystery. To date, no definitive genetic study has been done to compare its DNA to the DNA of white ash and modern green ash and determine which of these species is the parent if not both and which characteristics the ancestral parents of pumpkin ash had. It is known polyploids in general must face the minority cytotype exclusion principle, which describes the difficulty a rare cytotype (e.g. a polyploid) has in its finding another of its kind, mating, and producing an offspring capable of reproduction because of the superior numbers the dominant cytotype (e.g. a diploid) has, which makes it harder for rare types to find one another (Fowler and Levin 1984). The usual means for a rare cytotype to become established are: if the diploid population is very small, if the rare cytotype occupies a different niche from the diploid, or if the rare cytotype can outcompete the diploid and eventually replace it (Fowler and Levin 1984).

Ecological research into pumpkin ash has been strongly lacking in comparison to research into *Fraxinus americana, F. pennsylvanica*, and *F. nigra*. In a survey of literature, pumpkin ash rarely receives mention even in broader studies looking at an entire forest system and was never the subject of direct research. It is perhaps the most obscure of the six eastern ashes with regards to how much is known about it.

Fraxinus caroliniana Mill., Carolina Ash

Fraxinus caroliniana is found along the Coastal Plain reaching from VA to FL, and along the Gulf Coast states from FL to LA (Hough 1921). It resides in swamps and floodplains for rivers, usually being found either on land inundated for part of the year or directly adjacent to a body of water (Hough 1921).

Carolina ash takes the form of a shrub or small tree, growing to a maximum height of only 20-40 feet, much shorter than the maximum heights of the other ashes (Bonner 1974). Carolina ash has a dioecious flowering habit and flowers in February or March, produces samaras in August to October (Bonner 1974).

While detailed information has been compiled on the other ash species, Carolina ash has several gaps regarding seed data. There is no information on the range during which it disperses seeds. Sources which list information on propagating the seeds of the other ash species (e.g. Dirr and Heuser Jr. 1987) have no information on propagating

Carolina ash. No data are available for this species' minimum seed bearing age and at what interval it produces large seed crops. It has never been cultivated (Bonner 1974).

Fernald called Carolina ash the "most variable species" (Fernald 1950). It can be pubescent or glabrous, have a serrated or entire margin, have an ovate, lanceolate, or elliptical shape to its leaflet, have acuminate, obtuse, or acute leaflet tips, have an acute or rounded leaflet base, and its samaras can vary widely in shape. While it has wide variability with regards to its leaf morphology, though at the microscopic level, its leaf surfaces display little variation (Hardin and Beckmann 1982).

Ecological research into Carolina ash has been strongly lacking in comparison to research into *Fraxinus americana, F. pennsylvanica*, and *F. nigra*. In a survey of literature, Carolina ash only received mention in broader studies looking at an entire forest or wetland ecosystem and was never the subject of direct research. Additionally, Silvics of North America, which covers most of the eastern ashes, does not cover Carolina ash.

The complete taxonomic history of these six *Fraxinus* species is given in Appendix I.

Description of the morphological characteristics of *Fraxinus* across the 20th century:

When looking at variation and diversity within species, it is helpful to have detailed descriptions of the characteristics affiliated with the species in the literature. This gives a frame of reference for the characteristics evaluated in the study and an index to compare observed characteristics to in order to discern if there are any characteristics not described in the literature or not described well. A summary of descriptions from five taxonomic keys or books about trees ranging from 1901 to 1963 can be found in Appendix II.

Hybridization in *Fraxinus*:

Reports of hybridization in *Fraxinus* are uncommon compared to other forest genera (e.g. *Quercus, Acer*) and are not well fleshed out. Compounding the matter of the frequency of occurrence of hybridization in the genus is the difficulty in distinguishing some of the species apart.

The earliest report of hybridization in the genus is in the 1930s with Anderson and Turill's work. They reported evidence of hybridization between *Fraxinus oxycarpa* and *F. pallisiae*, two European species considered closely related. They found a whole population where most ash trees showed characteristics of both species, although showed more characteristics from one species or the other (Anderson and Turrill 1938). The authors in the same publication determined *F. oxycarpa* and *F. angustifolia* belonged to the same species, a classification which has remained intact, though some still maintain the division. Former species *F. oxycarpa* and *F. pallisiae* are currently considered to be subspecies of *F. angustifolia* (Wallander 2001).

In a more recent discovery, *Fraxinus excelsior* and *F. angustifolia* are known to hybridize where their ranges overlap in the Loire valley, France (Gérard et al. 2006). The hybrid has not been given a formal scientific name yet.

Among the eastern North American ashes, *Fraxinus americana* and *F. texensis* are considered to intergrade (Schlesinger 1990). *Fraxinus profunda* is currently theorized to be a fertile reproductively-isolated hybrid of *F. americana* & *F. pennsylvanica* (Harms 1990; Schlesinger 1990).

The literature is peppered with accounts of unusual ash trees, though in most cases the authors are never able to conclusively identify them, thus nothing becomes of these sports. Wright found an unusual tree from near Ithaca, NY which seemed to be a hybrid of *Fraxinus pennsylvanica* and *F. profunda*, having samaras and stomatas resembling pumpkin ash and samara length and leaflet margin resembling red ash (Wright 1944a). Santamour found two trees from Indiana which were originally considered white ash which were diploid, but had bud and leaf scars associated with tetraploid white ashes and lacked the papillose condition on the lower surface of the leaf, something all white ashes have (Santamour Jr. 1962). He thought they might have been green ash, resulting from contamination of the seed lot by *F. pennsylvanica* seeds or a possible hybrid of *F. americana* & *F. pennsylvanica.* No mention is made of the leaf margin or complexion of the lower leaf surface, which would have offered more information on discerning to which species it belonged.

Artificial hybrids are known to exist. Hybrids of *Fraxinus pennsylvanica* and *F. velutina* have been created and two cultivars, 'Northern Treasure' and 'Northern Gem', cultivated hybrids of *F. mandshurica* and *F. nigra* have been made as well (Kennedy Jr. 1990; Davidson 1999). Sylvia Taylor created hybrids of *F. americana* and *F. pennsylvanica* at the University of Michigan in Ann Arbor in 1968 and 1970 (Hardin and Beckmann 1982). Both parent trees for the hybrids were diploids.

As iterated earlier, it can be difficult to tell *Fraxinus* species apart, so finding hybrids is a difficult task unless easy to discern species are involved. It is therefore important to find a reliable means of sifting through individuals, sorting them into specific species or into an unclassifiable category by such means, without variation within a species which overlaps with another species' characteristics impeding the process. Anderson and Turrill gauged the variation within a species using herbarium specimens, then using collections of leaves from two areas in Europe to examine correlations between leaflet width and degree of pubescence to differentiate between *F. oxycarpa* and *F. pallisae* and expanded coverage of other leaf characteristics. The specific characteristics they used were length: width ratios in mature lateral leaflets, type of pubescence, length of serrations along margin, number of leaflets per leaf, presence/absence of branched hairs, and petiolule length to discern the diversity within the species (Anderson and Turrill 1938).

METHODS

Defining Regions:

While Illinois is known for its diverse range of climates and terrains, defining the exact borders between the regions is problematic. Traditionally, the state is divided either into two or three parts: northern and southern Illinois or northern, central, and southern Illinois.

From north to south, based on firsthand experience living in and traveling around Illinois, northern Illinois is known for its colder winters, more abundant snowfall, terrain that is a mix of forest and agriculture, and cooler temperatures year-round, central Illinois is known for its extensive farmland and prairies, warmer temperatures year-round and less snowfall relative to the north, and southern Illinois is known for its forests and swamps, warmer temperatures and high humidity year-round, and warm winters relative to the rest of Illinois. Many tree species found in the southern United States have their ranges terminate in southern Illinois. Major species found only in southern Illinois are *Quercus falcata, Q. lyrata, Q. shumardii, Carya illinoensis, Fraxinus profunda, Liquidambar styraciflua, Ulmus alata* and some other species are found in the southern half of Illinois (e.g. *Q. stellata, C. lacinosa, C. tomentosa, Aesculus glabra, Sassafras albidum*) (Burns and Honkala 1990). Fewer species tend to be constrained to northern Illinois or further north, namely *Populus grandidentata, P. tremuloides, F. nigra* and some other species are found in the northern half of Illinois (*U. thomasii, F. quadrangulata*) (Burns and Honkala 1990). Many *Quercus, Acer, Carya, Juglans, Ulmus, Fraxinus* spp. are found all over Illinois though (Burns and Honkala 1990). These defining characteristics, in map form, would be useful to delineate the formal borders.

The defined borders for the regions encompassed by this study were composed by examining the differences in temperature, precipitation, and frost times. All maps which charted out such variables that were used for this study were made by the National Climatic Data Center (NCDC) of the National Oceanic and Atmospheric Administration (NOAA), accessible via their website (National Climatic Data Center website). The borders between ranges on these various maps were used to determine how many regions should exist in this study and where the formal borders between those regions (northern, central, and southern Illinois) would be (Figs. 2a-2d). The map image used for the final map was obtained from the Census Bureau, a part of the Economics and Statistics Administration in the U.S. Department of Commerce. It was modified to illustrate the borders between regions that were used in this project and marked with the 18 sites from which samples were collected (Fig. 3).

Illinois' mean daily maximum temperature falls into three separate temperature ranges (Fig. 2a). Northern Illinois has temperatures between 50-60°F, central Illinois has temperatures between 60-65°F, and southern Illinois has temperatures between 65-70°F. The northern dividing line roughly follows the course of Interstate 80 and the southern dividing line roughly follows the course of Interstate 70.

Illinois' mean daily minimum temperature falls into three separate temperature ranges as well, though the borders are different from the mean daily maximum temperature (Fig. 2b). In northern Illinois (excluding the city of Chicago), the temperature is 32-40°F, across most of Illinois (and Chicago) it is 40-45°F, and in far southern Illinois along with a few isolated pockets across southern Illinois it is 45-50°F.

Illinois' precipitation regime falls into two rainfall ranges with a border that is not roughly latitudinal, unlike the two temperature charts (Fig. 2c). The northern two-thirds of Illinois receives 30-40" rain/year while the southern third of Illinois receives 40-50" rain/year. The dividing line roughly follows the course of Interstate 70.

The portion of the year which is free of freezing in Illinois falls into two ranges (Fig. 2d). The northern half of Illinois receives 121-180 days/year free of frost on average and the southern half receives 181-240 days/year free of frost.

The mean daily maximum temperature graph was given the highest priority in determining the borders because average annual temperature, a result (generally) of latitude, plays a significant role in determining what the environment is. The graph given the second highest priority was mean total precipitation since yearly total rainfall is another factor which strongly defines species' ranges (e.g. separating forest from grassland from desert). Mean daily minimum temperature, length of freeze-free period, dates of last frost in spring and first frost in fall, and mean total snowfall were all given minor consideration. Natural divisions also contributed to defining the borders.

The northern-central border generally follows the northern-central border found in the mean daily maximum temperature map with the exception of eastern Illinois. The date of last 32°F temperature in spring was also used to reinforce the placement of this border, as were the borders for the natural divisions, though the Grand Prairie Division extends well into northern and northwestern Illinois, so using the northern limit of the prairie as the northern-central border became impossible since it extended north of where many of the other maps' borders lay. The determined border in western Illinois conforms exactly to the mean daily maximum temperature border because the border between the Western Forest-Prairie Division and the northwestern sections of the Grand Prairie Division is identical to border on that temperature map. The convergence of a line from two separate variable maps (temperature, natural division) in the same place was taken as strong confirmation of the validity of placing the border there.

The central-southern border generally follows the central-southern border found in the mean daily maximum temperature graph and an average for the dividing line on the mean total precipitation graph between the northernmost portion of its edge and the southernmost portion of its edge. The date of last 32°F temperature in spring was also used to construct this border. Additionally, the northern border for the Southern Till Plain natural division was also considered in the construction of the central-southern border.

Hardiness zones were also looked at to compare how well the different regions are defined relative to the limits on where plants can survive. Hardiness zones use the average annual minimum temperature to define which areas a plant can survive in since cold temperatures are one of the defining factors limiting a species' range. Virtually all of Illinois falls into 3 hardiness zones, zone 5a, zone 5b, and zone 6a. Zone 5a covers all of the northern region and about one-third of the central region, zone 5b covers the lower two-thirds of the central region and Cook County, and zone 6a covers southern Illinois (United States Natural Arboretum website 2007). A very small part of northwest Illinois (around Whiteside, Ogle, and Winnebago Counties) is classified as zone 4b. The hardiness zones generally fit where the delineated borders were placed in this project, though the 5a-5b border fell a little bit south of where the northern-central border was placed in this experiment.

Describing the regions in terms of natural division, northern Illinois contains the entirety of the Northeastern Morainal Division, the Wisconsin Driftless Section, the Rock River Hill Country Division, and the northern third of the Grand Prairie Division, central Illinois contains most of the Grand Prairie Division and all of the Western Forest-Prairie Division and Illinois River Bottomlands Division, and southern Illinois contains the entirety of the Southern Till Plain Division, the Shawnee Hills Division, the Coastal Plain Division, and most of the Wabash Border Division. Of the 14 natural divisions of Illinois, ash trees were sampled from 9 divisions and out of 34 sections, 13 were visited.

Site Selection:

Sites were selected which were publicly-owned land which was known to include forests as well as by examining ash distribution by county to pick counties which have multiple ashes in them. The general pattern which was sought was to have one site towards each corner of the region and one site in the center of the region. Some additional sites were added to supplement collection totals in northern and central Illinois.

General descriptions for each site along with information pertaining to where samples were collected are noted in Appendix III.

Collection permits were obtained from the Illinois Department of Natural Resources (IDNR), Cook County Forest Preserve District, Illinois Natural Preserves Commission, and the National Wildlife Refuges at Crab Orchard and the Illinois River.

Travel and Sampling Parameters:

Collection rounds were limited to about 3 sites per trip based on the storage capacity available for keeping the leaves cool in the heat of the summer and the amount of time available for abscised leaves to be pressed before they become difficult or impossible to properly press. One or more trails were walked at each site. Trail selection was based on recommendations made by park personnel or evaluating trail names. When a suitable ash tree was found (i.e. branches being within reach of pole pruner, tree is not a very young sapling), the GPS coordinates were recorded and the tree was tagged to make it possible to pinpoint the same tree for the seed collection. Efforts were made to avoid sampling planted trees.

Sample Collection:

When an ash tree was located, 4-8 leaves were collected from each tree along with a small segment of a branch using a telescoping pole pruner or a pair of hand clippers if the branches were low enough. Factoring in the maximum extended length of the pole pruner and the author's height, leaves were collected from 0- 4.75m. The most fully-developed leaves on the tree were collected and leaves with significant insect damage or wilting were avoided. GPS coordinates were also gathered for each sampled tree.

Sample Preparation:

Once collected, the bags containing the leaves were placed in a large Ziploc bag and then placed in styrofoam coolers loaded with ice. Samples were kept in this manner as long as they were being transported.

Samples were brought back to Eastern Illinois University (EIU) to be placed in plant presses within 3 days of being collected in most instances. During longer collection trips, samples were removed from the styrofoam cooler and placed in a refrigerator (still being kept in sealed or partially sealed Ziploc bags). Samples were usually processed and placed in standard plant presses within hours of arrival.

Standard plant specimen drying techniques were used. Newspapers were labeled with the sample code of the leaf. Between 1 and 3 leaves were placed in each sheet of newspaper, depending on the leaf size. The leaves were laid out flat and the newspaper was closed carefully to ensure no leaflets folded up or deformed when the leaves would go in press as the goal of the study was to measure the leaves and folding or crumpling interferes in recording length, width, and area.

One leaf or one leaflet (not taken from a sample measured in the data set) was reserved and stored separately to serve as a DNA sample in possible future studies of the genetics of the Illinois *Fraxinus* populations.

Data Compilation:

For each tree, four leaves were usually measured. Fewer leaves were measured (three leaves in most such instances) when collected leaves had too much damage (insect, disease, or damage during the collection process) on their leaflets, which would interfere with recording data or did not dry in the press properly, resulting in too much folding or crumpling. When such damage or disfiguring was limited, the leaves were still used.

Quantitative and qualitative data were gathered for each leaf. Quantitative data were comprised of numerical data while qualitative data were comprised of categorical data. Quantitative data included the length and width of each leaflet, total dry mass, total leaf area, and number of leaflets. Qualitative data included of leaflet shape, leaflet margin, leaflet base shape, petiolule length, leaflet thickness, leaflet underside color/complexion, pubescence and location of pubescence, twig color, twig shape, leaf scar shape, bud colors, terminal bud size, uppermost lateral bud position relative to terminal bud, presence of any uneven leaflet pairings, and any anomalous leaflet development around the leaf terminus.

Leaflet length and width were recorded in a consistent manner, keeping track of its position on the leaf. Data were collected for leaves which were overall intact save for one or two leaflets where damage impaired recording the length or width as well as for leaves missing one leaflet.

Length and width were recorded using a metric ruler, dry weight using an electronic balance, and leaf area was measured using a LiCor leaf area meter. Some leaves were too large to run through the leaf area meter. A paper facsimile of these leaves was constructed by tracing the leaf's parts onto paper and cutting these parts out and then running them through the leaf area meter. The petiole was included in the leaf area reading.

A system was used to ascribe a simple term to each leaflet which would be consistent across each leaf for all species. The abbreviations are indicated on the chart below (Fig. 4).

Data Analysis:

The quantitative data used to represent each tree in the analysis were the average of all the leaves measured from that tree. They were averaged to prevent natural variation in leaf morphology on a given tree from having an undue influence on the results as individual leaves on any given tree can vary widely from one another.

The data were entered into Microsoft Excel and imported to SPSS for analysis. Quantitative data were analyzed by a multivariate analysis of variance (MANOVA) and a principal components analysis (PCA) for the averaged leaf data for 4 species (the others had less than 10 trees representing the sample set). Each species was analyzed individually with region (northern, central, and southern) as the differentiating criterion for the MANOVA and PCA. Qualitative data were not quantified; it was catalogued to document the variation in each species as well as to provide support for identification.

Total leaf area, total leaf mass, leaf density, the length of L2, R2, and the terminal leaflet, and the width of L2, R2, and the terminal leaflet were selected as the variables to measure statistically because the first three are major characteristics for leaves in general and the leaflets selected showed the most consistency regarding anomalies or mutations. Pillai's Trace was used for all analyses.

Tree Identification:

Trees were identified to species by examination of the morphological characteristics of the leaf and twig in the lab. Trees that fit the published profile of a species (e.g. Hough 1921, Fernald 1950, Gleason and Cronquist 1963, Dame and Brooks 1972, Brown 1975) were labeled as that species. However, trees that mostly fit the profile of a species with one trait considerably out of line for that species' profile were labeled as that species, but marked with an (A) for anomaly for more discerning analysis in the characterization of the variation in the species. Trees that did not fit cleanly into any species profile (i.e. there were multiple anomalies) were labeled as unknown. Trees were labeled down to varietal level (e.g. Biltmore, green/red) to test whether the variety had more characteristics beside presence or absence of pubescence to discern it from the main species.

RESULTS

Collection Statistics:

Leaves and Twigs:

Leaf and twig samples were collected from 235 ash trees across Illinois with all 6 eastern species being found along with a number of trees which defied easy classification (Table 1). Each species was not found across all 3 regions. Only *Fraxinus americana* and *F. pennsylvanica* were found statewide.

There were 19 trees which could not be easily identified via their leaf and twig characteristics. These were labeled 'mystery'. They required extensive examination to formally identify them. Identification of these specimens is provided in Appendix IV. These trees were not included in the quantitative analysis of species.

There were 2 additional trees which could not be keyed to white, green, blue, black, or pumpkin ash. Both of these fit the description of *Fraxinus caroliniana* based on a comparison with specimens of that species in the EIU herbarium. The trees in question had twigs similar to Carolina ash, a distinctive, wine red, flat, twisted twig, and one had bright orange buds as well, which is generally found only in Carolina ash. Their other characteristics matched to Carolina ash as well.

Statistical Analyses:

Fraxinus americana:

The effects of region on leaf parameters of white ash were significant (Table 2). Total leaf area, L2 length and width, R2 length, and terminal leaflet length and width all differed significantly between regions (Table 3). In all characteristics, northern Illinois white ash had sharply higher values than central and southern trees (Figs. 5a-5f). Those two regions produced similar values across the board, with southern white ashes tending to have slightly higher estimated marginal means than central Illinois white ash with all characteristics except for total leaf area.

A PCA indicated 2 components had eigenvalues over 1 and accounted for 82% of variation observed in white ash. Total leaf area, total leaf mass, L2 length and width, R2 length and width, terminal leaflet length and width all showed significant positive correlation to component 1, leaf density showed significant negative correlation to component 1, and total leaf mass, leaf density, L2 length, R2 length showed significant positive correlation to component 2, while terminal leaflet width showed significant negative correlation to component 2 (Table 4).

A regression factor correlation graph indicated the white ashes from different regions overlap in ordination space with the exception of a few outliers (Fig. 6). Those outliers comprise 2 individuals from the Cook County Forest Preserve and 1 individual from Lowden State Park.

The regression factor correlation graph had more northern white ashes located on the positive side of component 1's axis, differing from central and southern white ashes, which tend to be located from the axis towards the negative side. Component 1 is associated with the lengths and widths of several leaflets as well as total leaf area and total leaf mass. These results conform with the MANOVA results, which indicated leaflet lengths and total leaf area were significantly greater in northern white ashes than white ashes from other regions.

Fraxinus pennsylvanica:

Regional divisions for green ash were significant (Table 2). Total leaf mass and leaf density had significant differences between regions (Table 5). Both characteristics feature significantly higher values for southern Illinois over northern and central Illinois, with central Illinois having the lowest values (Figs. 7a-7b).

A PCA indicated 2 components with eigenvalues over 1 accounted for 77% of variation in green ash. Total leaf area, L2 length and width, R2 length and width, terminal leaflet length and width all displayed significant positive correlation to component 1 and leaf density showed negative correlation to the component while total leaf mass, leaf density, L2 length, R2 length, terminal leaflet length all showed significant positive correlation to component 2 with terminal leaflet width showing negative correlation to the component (Table 6).

A regression factor correlation graph (Fig. 8) indicated green ash trees from different regions were generally a part of the same continuum within the ordination space, though southern trees were skewed towards the far end of component 2's axis. There were a few outliers from central Illinois, which were two trees from Momence Wetlands.

The regression factor correlation graph has more southern green ashes located around the axis for component 2 and they are skewed more towards the negative side of component 1 than green ashes from the other regions. Component 1 is negatively associated with leaf density. Northern and central green ashes tend to be spread out all over the graph along both axis (with the exception of northern green ashes along axis 1, which are skewed more towards the positive side). These PCA results agree with the MANOVA results.

Fraxinus quadrangulata:

Tests indicated there were no significant differences in leaf parameters between blue ashes of northern and central Illinois (Table 2). Between-subject effects for regions showed the only significant differences were in L2 length (Sig= 0.037) and R2 length (Sig= 0.045).

A PCA of blue ash indicated 2 components had eigenvalues over 1 and accounted for 85% of the variation. Total leaf area, total leaf mass, L2 length and width, R2 length and width, and terminal leaflet width all had a significant positive correlation with component 1 and leaf density showed a positive correlation with component 2 (Table 7).

A regression factor correlation graph indicates there is little difference between northern and central Illinois blue ashes, though central IL has a few outliers, two trees from Windfall Prairie (Fig. 9).

Fraxinus profunda:

Finally, for pumpkin ash, tests indicated a significant difference in leaf parameters between region (Table 2), however, all tested parameters were not significant. These results seem to indicate the sum of all parameters is different between regions.

A PCA of the data collected for pumpkin ash indicated 2 components had eigenvalues over 1 and accounted for 84% of the variation. Total leaf area, total leaf mass, L2 length and width, R2 length and width, and terminal leaflet length were positively correlated with component 1 significantly and total leaf mass and leaf density were positively correlated with component 2 significantly (Table 8).

A regression factor correlation graph (Fig. 10) indicated the central IL pumpkin ashes tended to have some outliers from the majority of the pumpkin ashes sampled (southern IL), though the small sample size from central IL (n=5) makes this less definitive. The one extreme outlier was the gigantic-leaved ash from Kickapoo State Park (CKP05).

Analyses of Varieties:

Modern green ash was once divided into two varieties which at present are no longer recognized by a majority of sources in the literature. White ash is presently divided into two varieties which are recognized by a majority of sources in the literature. They tend to be split or lumped together depending on opinion regarding qualitative characteristics. Quantitative comparisons seemed scarce. Thus, it seemed worthwhile to run a MANOVA and PCA on white ash and modern green ash measurements to test whether their varieties can stand on their own or not quantitatively.

Testing the validity of dividing white ash into two varieties (var. *americana,* var. *biltmoreana*) revealed a significant difference (Table 9). Out of all characteristics tested, only L2 length was significant (Sig= 0.022). Thus, quantitatively, white ash and Biltmore ash are generally indistinguishable though the aggregate of their characteristics indicates a difference.

A regression factor correlation graph indicates both varieties of white ash plot out similarly, with only a few anomalous white ashes occurring as outliers (Fig. 11).

Testing the validity of dividing green ash into two varieties (*var. pennsylvanica, var. subintegerrima*) revealed no significant difference quantitatively between trees classified by the standards that divide green ash from red ash (Table 9). The only characteristic which displayed a significant difference was leaf density (Sig= 0.044).

A regression factor correlation graph which differentiated between original green ash and red ash indicates both are generally a part of the same continuum (Fig. 12).

Survey for the Presence of Emerald Ash Borer at the Sites:

All sites but one were confirmed to lack any signs of EAB along the trails taken. Moraine Hills State Park had several dead Ash trees in two sections of the Fox River Loop. No signs of EAB were visible (crown dieback, epicormic shoots, D-shaped exit holes), but their presence could not be ruled out either. As of July 2007, no news reports had come out indicating EAB was discovered at these parks, preserves, or forests.

The ash trees at most sites were healthy and in good shape. Ash yellows struck ashes along the I-70 corridor, with ash trees near some roadsides in Red Hills State Park (SP) afflicted with it and some trees in Eldon Hazlet SP affected and killed as well.

Observations Regarding Qualitative Characteristics:

Observations regarding leaflet shape, leaf margin, leaflet tip, leaflet base, petiolule length, leaf thickness, leaf color (top/bottom), color and shape of new twig growth, leaf scar shape, bud color, uppermost lateral bud position, number of leaflets, presence of pubescence, and whether there is a split terminus or staggered leaf pairing can be found in Appendix V and a summary of the variation in these characteristics for each species can be found in the updated species descriptions located in Appendix VI.

DISCUSSION

General Discoveries:

There were several interesting discoveries made from the sampling of the 235 ashes, namely the discovery of *Fraxinus caroliniana* in Illinois and several trees with very large leaves, larger than the largest leaves mentioned in the literature.

Carolina Ash:

Two trees were discovered that did not fit the description of white, green, blue, black, or pumpkin ash, one from the Palos Division and one from Rock Cut State Park. Herbarium samples of other North American species were examined. Samples of Carolina ash from its native range resembled the leaves and twigs of the trees found in northern Illinois. Both trees were located within 1m of the edge of a body of water, which is the natural habitat of the species. Both trees were only 2-3m high. A subsequent visit to Saganashkee Slough in the Palos Division turned up another confirmed Carolina ash and an ash which may have been Carolina ash (due to the tree's position, a closer examination could not be attempted).

There are a few possible scenarios for how Carolina ash arrived in northern Illinois:

1.) Dispersal by hurricane or tropical storm remnants via upper-level storm winds. Long-distance dispersal by such storms is very unlikely, but not physically possible.

2.) Dispersal by canal traffic. In Cook County, there are a few canals which run less than 2 miles from the location the Carolina ash was found at- the Illinois &

Michigan Canal, opened in 1848, closed in 1933 and connecting the Great Lakes with the Mississippi River via the Chicago River and Illinois River, the Chicago Sanitary & Ship Canal, opened in 1900 to replace the I&M Canal, and the Calumet-Saginaw Channel (Cal-Sag Channel), opened in 1922 and connecting the Chicago Sanitary & Ship Canal to industrial sites in the southern suburbs (Baer and Andries 2007).

3.) Human-mediated point dispersal. This would entail individual introduction by humans. One possibility would be samaras stuck in equipment (e.g. boat, cooler, fishing gear) and transported from one lake or wetland to another. Another possibility is transport from the native range by being lodged beneath windshield wipers or in the vents near the base of the hood of a vehicle.

Based on the locations and their histories, it would seem canals were the most likely means of dispersal to the Palos Division but not to Rock Cut since there are no canals, nor rivers leading to the lake. Individual human transport (most likely by personal boat) seems most likely for Rock Cut, though both bodies of water the Carolina ashes were found along are frequented by fishermen. A DNA test of the Carolina Ash from the Palos Division (and nearby Carolina ashes) and of Carolina ashes found in Louisiana and Arkansas along the Mississippi River should reveal whether dispersal via canals was the most likely cause or not. It would also be interesting to check sites located along the Mississippi River in Missouri, Kentucky, and Illinois for Carolina ash along its banks or along any canals accessible from the Mississippi River in those states.

The trees seem unlikely to be natural isolated populations because of the proximity to major avenues of traffic, either in the past or the present (canals and interstates).

Some general information about flowering time and time of color change in leaves was also gathered. The Carolina ash in the Palos Division was visited in mid-October and it still appeared solid green, not showing the beginning signs of changing color (i.e. turning a spring green or yellow-green color). It was also visited in early June and it had produced flowers, which were green in color. Its foliage had developed, though some new, small, purple-colored foliage had just begun to emerge (newly emerged white ash leaves were also purple in color).

Gigantic Leaves:

Occasionally during this study, gigantic leaves were found on trees. These are leaves that appeared exceptionally large in length, width, or total leaf area.

First examining length, it seemed the point at which a leaf started to seem qualitatively 'big' was at 30 cm in length. Leaves that stood out lengthwise were measured from the base of the petiole to the tip of the terminal leaflet. In the event the leaf was bent or curved, a string was carefully laid along that same length and cut, with the length of the string then being measured. In the few instances width was measured, it was measured by a straight line perpendicular to the rachis that spanned from the tip of the longest leaflet on the left side to the tip of the longest leaflet on the right side. It was then necessary to look at the literature for size ranges for the leaves. Converting the statistics given for ash leaf lengths provided in the literature from inches to centimeters, the following ranges have been observed for leaf sizes: white ash- 15.0-38.0 cm, green ash- 18.0-30.5 cm, black ash- 25.5-40.5 cm, blue ash- 20.0-30.5 cm, pumpkin ash- 23.0-45.5 cm, Carolina ash- 18.0-30.5 cm. Width is rarely described in the literature.

Most of the gigantic leaves were from white ashes generally located in northern Illinois. Leaves from one tree in the Palos Division had the following measurements: 36.4 cm length (l.) x 29.3 cm width (w.), 38.4 cm l. x 35.4 cm w., 37.8 cm l. x 32.4 cm w., 38.4 cm l. x 32.8 cm w. A tree in Lowden State Park had a leaf which was an astounding 52.7 cm long; its width was 33.4 cm. Other large leaves were: 37.3, 40.0, 41.7, 43.6, 45.2, 45.5, 46.5, 46.7 cm in length (5 were from the north, 3 were from the south). These numbers blow away the old upper size limit, 38 cm. It is recommended the upper size limit be given as 53 cm.

Only one tree identified as green ash had leaves approaching the size of these other giant-leaved trees, and its largest leaf measured only 30.9 cm in length. It was from Moraine Hills State Park. This only marginally exceeds the upper limit given for green ash leaf size. It is recommended the upper size limit be given as 31 cm.

While black ash lacks a tendency for large leaves, some black ash trees had extremely long leaves. Leaves from one tree were 48.2, 47.3, 42.4, 48.8 cm long and leaves from a second tree were 37.4, 50.4, 42.9, 42.6 cm long. 2 leaves from a third tree were measured as being 38.0 cm long and 26.8cm wide and 44.9 cm long and 32.0 cm wide. The upper limit listed in the literature for its leaf size is 40.5 cm. These findings clearly indicate that value falls considerably short. The upper limit in the literature should be revised to 51 cm. The primary reason behind the tendency to be longer is having more leaflets. Some European species can have 11 or more leaflets and such leaves have considerably longer lengths than leaves with 7 or less leaflets.

Blue ash did not tend to have any leaves which stood out as being large.

A few pumpkin ashes were recorded with large leaves as well, specifically a tree from Red Hills State Park with a leaf 48.8 cm long and a tree from Dixon Springs State Park with a leaf 51.9 cm long. While it may seem like large leaves for pumpkin ash are scare, this finding may not be applicable because the majority of leaves from this study may not show gigantism because no pumpkin ashes in standing water or in soils inundated for several months a year were sampled, and that habitat is known to be the species' ideal habitat. It is recommended the upper limit should be revised to 52 cm.

Examining leaf area, it seemed the point at which a leaf seemed to be 'big' was around 300 cm^2. Data on ranges of size for leaf areas for the species in the literature were not available. Leaves with areas up to 850 cm^2 were observed.

Breaking down the 889 leaves collected, 730 leaves had leaf areas <300 cm^2 and 159 had areas greater than 300 cm^2 (Table 10). Big-leaved specimens of green ash and blue ash made up a smaller amount of the total sample set for their species than big-leaved specimens of white ash and pumpkin ash did for the total sample set of their species.

These leaf area totals indicate white ash and pumpkin ash occasionally develop large leaves and black ash can do so as well. Blue ash and green ash can get into the 300 cm^2 range but have difficulty exceeding 400 cm^2. While it may appear white ash is the most common ash with large leaves, that conclusion cannot be drawn due to the proportions of each species in the total collection, where white ash made up a significant amount, pumpkin ash a small amount, and black ash comprised only a small percentage of the total sample set.

Overall, these giant-sized leaves reveal white ash can easily match and exceed pumpkin ash in leaf length and leaf area. The ploidys of these leaves are unknown. It would be interesting to see if these large white ashes were all or mostly hexaploids or if they were divided among the three ploidys.

One tree in particular deserves a more detailed discussion. CKP05 is a tree found on a bluff overlooking a lake in Kickapoo SP. It was classified as pumpkin ash despite its habitat and limited pubescence (only on leaf veins) due to its gargantuan leaf size, big conical terminal bud, dark green color to its upper leaf surface and pale green color to its lower leaf surface. Its second most notable characteristic is its leaf color is a very dark shade of green. Several of its leaves' leaflets are 17-21 cm long and 8-11 cm wide, with one terminal leaflet being 25.5 cm, as large lengthwise as some other ashes' leaves are. The dimensions of its leaves are: 46.2 cm l. x 40.2 cm w. with leaf area= 849.04 cm^2, 35.7 cm l. x 36.0 cm w. with leaf area= 736.74 cm^2, and 34.5 cm l. x 22.5 cm w. with leaf area= 471.09 cm^2.

The quantitative values for this tree make it an extreme outlier (as seen on Fig. 10, for example). If it is said polyploids like tetraploids and hexaploids display 'gigas' characteristics relative to diploids, then CKP05 would best be said to display 'titan' or 'gargantuan' characteristics relative to diploids, with single leaflets as long as some ash leaves and leaf areas large enough to comprise three or four average-sized ash leaves. Besides its size, its color is also a very dark green color, darker than other leaves classified as dark green to the point its color might best be described as blackish green.

Based on all of these qualities, this author wonders if CKP05 has a ploidy level higher than a hexaploid; perhaps this tree is an octoploid. It should also be noted this tree was not that tall; it was not yet at maturity, being only about 4-6m tall. It also had an odd canopy, not a full canopy encompassing all the upper branches; instead, it resembled a palm tree or a bonsai plant, with a canopy directly above the trunk and two small clusters of leaves on larger side branches further down the tree.

Findings from Quantitative Analyses:

Analysis of the species' leaf measurements across the regions that were defined gave both significant correlations and non-significant correlations depending on the species, and in the cases of significant, what characteristics they were significant in differed.

Relationships between leaf characteristics and climate have been known about for a century (Wright, Reich, and Westoby 2004). In terms of how leaf dimensions are known to be affected by latitude and the variables generally associated with it (i.e. temperature, precipitation), leaf area, leaf length, and leaf width tend to decrease with decreasing mean annual temperature, mean annual precipitation, and soil fertility (McDonald et al. 2003). The leaf area of the species *Rhizophora mangle* for example, increases with decreasing latitude as well as with increasing precipitation (Rico-Gray and Palacios-Rios 1996). Samara length and fruit weight for *Acer rubrum* were correlated with latitude, with length and weight decreasing with increasing latitude. The specific properties associated with latitude that were attributed to this observation were the length of the freeze-free period, mean annual temperature, and mean January temperature

(Townsend 1972). This can provide a handy reference for *Fraxinus* since both genera have similar ranges in eastern North America and often are found together. The morphological characteristics of *Halesia carolina* were significantly associated with latitude as well (Fritch and Lucas 2000). Also, species which are found in forests tend to have larger leaf area than species found in savannas (Hoffmann et al. 2005). This would another variable in addition to latitude to consider.

Regional divisions for white ash were found to be significant, with trees from northern Illinois having sharply higher values for total leaf area, L2, R2, terminal leaflet length, and L2, terminal leaflet width than trees from central and southern Illinois had. In an ordination space, all of these characteristics (excluding terminal leaflet length, but including R2 width and total leaf mass) were positively correlated with the axis associated with the primary eigenvalue and leaf density was negatively correlated with the same axis. Trees from all three regions tended to load in the same general area in the ordination space, though the northern region had a long arm extended deeper into the positive side of the axis. The presence of several giant-leaved white ashes from northern Illinois, as indicated in the previous section, is this arm, as all of those leaves had greater leaf areas and leaflet dimensions than other ashes.

These findings for white ash are rather counterintuitive. Increasing leaf area is associated with increasing temperature and the largest leaves are found in the coolest part of the state. Northern Illinois has a cooler annual mean daily maximum and minimum as well as a later date of final frost in spring than central and southern Illinois have. Shade leaves are observed to have an increased leaf area relative to sun leaves, an adaptation to increase the surface area upon which sunlight can be received to maximize what is a limited resource in the shade (Ryser and Eek 2000). It has been observed in *Dactylis* species that a reduction of photosynthetic flux by 70-80% (associated with being in shade) doubles to triples the leaf area (Ryser and Eek 2000). It is unlikely shade is responsible for the large leaves as some of the large-leaved white ashes were growing in full sun, having greater light intensity readings than other white ashes at the same site and those trees did not have larger leaves. Another possibility is this may be an instance of a large-leaved population limited to northern Illinois through random genetics and not climatological factors (though it isn't known if this population is isolated or exists in a broad band further east and west along the 41°N latitude and northward) or the cooler temperatures in northern Illinois are more optimal for leaf development specifically for the white ash species. A third possibility is northern Illinois has a population of hexaploid white ashes, with hexaploids known as having 'gigas' features relative to lower ploidy levels.

Regional divisions for green ash turned out significant as well, with trees from southern Illinois having sharply higher values for total leaf mass and leaf density than their northern and central Illinois counterparts. In an ordination space, leaf density was negatively correlated on an axis with positive correlations for total leaf area, L2, R2, terminal leaflet length and width. Trees from northern and central Illinois were more positively loaded on this axis. Trees from southern Illinois were more positively loaded on the second axis, which was positively correlated with total leaf mass, leaf density, as well as L2, R2, and terminal leaflet length.

It has been observed species with higher leaf mass per area (LMA) values had thicker laminas, higher tissue density, and longer leaf lifespans (Westoby et al. 2002).

Also, leaf thickness generally increases with increasing aridity, with arid or semi-arid regions having plants with thick, leathery leaves (high LMA) as well (Wright, Reich, and Westoby 2004). High LMA requires more investment per unit of mass than lower LMA values and is associated with a longer leaf lifespan (Wright, Reich, and Westoby 2004). The greater leaf density found in southern Illinois would support the previous findings of higher LMA values being associated with longer leaf lifespan as southern Illinois has a longer freeze-free period and warmer temperatures than the rest of the state. Lower LMAs tend to be associated with higher photosynthetic capacity in leaves and a greater turnover rate in leaves. This is associated with greater flexibility in responding to spatial heterogeneity of light resources (Grime 1994). These results would reflect a lack of light being a limited factor in these systems. The only site where green ashes were found in southern Illinois was Wayne Fitzgerrell State Park, which tended to have ample availability of light; the other sites were all upland forests. The other variable southern Illinois has in greater value over northern and southern Illinois is precipitation. Green ash generally favors lowland areas and areas relatively close to bodies of water whereas white ash favors well-drained upland areas. Precipitation may be more conducive to leaf development in terms of mass and density than it is for development in white ash leaves. The higher temperature and precipitation values might allow for greater development of leaf tissues than in cooler regions with shorter growing periods, particularly with regards to the length of time between the final frosts and the peak of the growing season for ashes.

Blue ash is generally found along the bluffs overlooking rivers and rivers tend to moderate temperatures in their immediate vicinity due to the heat capacity of water.

There may not be enough of a difference to cause significant differences to develop over a north-south distance of ~320 km (~200 mi). However, there appear to be differences in species morphology on a longitudinal gradient based on some herbarium samples from states east of Illinois having a different set of traits than the Illinois blue ashes in this study and considerable differences between the observed morphology and the morphology described in the literature and based on these differences, a new variety is proposed. In an ordination space, northern and central region blue ashes were generally differentiated, with northern blue ashes being more positively loaded along the axis of the primary eigenvalue and central Illinois blue ashes being more negatively loaded along the axis, an axis positively correlated with total leaf area, total leaf mass, lengths of L2 and R2, and widths of L2, R2, and terminal leaflets. There was a large region of overlap though.

Pumpkin ash produced mixed results, with the difference between region being found significant, but none of the individual characteristics turned up significant. This may indicate while none of the measurements individually differ from one another enough to be considered statistically distinct, the aggregate of all measurements was statistically distinct. The small sample size from central Illinois (n=5), occupied by one far outlier (CKP05) may have led to central region pumpkin ashes being skewed away from the mean for the species in Illinois, producing such contradictory results. If the sample size was larger and more sites were sampled with pumpkin ash, the results would be clearer. It is suspected the sample size and extreme outlier caused the odd results.

The findings from the PCAs for all species indicate a strong association among many of the characteristics studied. Total leaf area, total leaf mass, L2 length, L2 width, R2 length, R2 width, terminal leaflet length, terminal leaflet width were all associated with one another with a few single characteristics excluded in certain species (total leaf mass is excluded in *F. pennsylvanica*, terminal leaflet length excluded in *F. quadrangulata*, and terminal leaflet width excluded in *F. profunda*). The leaf characteristics of length and width of leaflets, total area, and total mass were interrelated, with a positive correlation such that, by increasing leaflet lengths area is increased and mass is increased. Leaf density did not group with this association and in fact has been negatively affiliated with components positively affiliated with this association in white ash and green ash. The associations between multiple leaf characteristics are known to be similar across all range of species and biomes (Reich, Walters, and Ellsworth 1997). Specific leaf area, leaf lifespan, and leaf nitrogen have been found to be linked, for example (Reich, Walters, and Ellsworth 1997). The linkage of leaf area, leaf mass, and various length and width measurements is not surprising in this regard.

The lack of consistent trends in multiple species across the state with the characteristics studied indicate there is no single factor which impacts *Fraxinus* universally in how large or small, how heavy or thin its leaves get. If factors do set up a gradient north-south through Illinois, those factors are species specific. With most species though, in an ordination space, most of the quantitative measurements ended up positively correlated with the first axis (the eigenvalue that explained the most variation). Total leaf area, total leaf mass, L2, R2, and terminal length and width all tended to be grouped together. It is rather logical for these to be correlated as the size of leaves affects its area and mass. Additionally, in some species, leaf density was negatively correlated on the first axis. This also makes sense when one considers density is dependent on area and mass, where if the leaf's length and width measurements are very large and its mass is only average, that leaf will have a very low density; density and leaf area tend to be inversely correlated.

Summary statistics for *Fraxinus americana, F. pennsylvanica, F. quadrangulata,* and *F. profunda* along with interpretation of those statistics can be found in Appendix VII.

Findings from Observations of Morphological Characteristics:

Observations made about the qualitative characteristics of *Fraxinus* can be found in Appendix V. This includes data and discussion of the number of leaflets per leaf for some species, composition of the leaf margin, notes on how Ash leaves are constructed, et al.

The morphological anomalies observed on *Fraxinus* leaves and twigs and the identification of the 19 Ash trees labeled as 'mystery' can be found in Appendix IV.

The observations made on the characteristics of *Fraxinus* leaves and twigs and the effort to classify the most challenging specimens helped clarify the specific causes of difficulty in identifying some individual ash trees to species. This discussion can be found in Appendix VIII. These observations also necessitated revising the species descriptions for the species studied, which can be found in Appendix VI.

Observations on Seed Production:

Out of 232 trees sampled in the summer (leaves from 3 additional trees were sampled without collecting twigs), 220 were revisited between mid-October and early-

November to collect samaras if the tree had produced seeds in 2006. Only 10 trees had produced seeds (7 Northern, 3 Central, 0 Southern; 9 green, 1 white).

2006 was an extremely sparse year for seed production among *Fraxinus* species in Illinois, with only 4% of sampled trees bearing seeds. The general interval documented for producing large quantities of seeds ranges from 1 in 3 years to 1 in 5 years usually, though 3 of the 6 species have no precise information on seed production. From what is known, the odds of any given species being fruiting in a single year is 33% or less. 2006 would be one of the majority years which have sparse seed production.

The Merits of *Fraxinus* Varieties:

The validity of existent *Fraxinus* varieties:

Biltmore ash and original green ash started out as full-fledged species before being demoted to varieties. Biltmore ash has managed to retain this status while red ash was relegated to a historical footnote. A reversal took place and green ash became the default member of *Fraxinus pennsylvanica* and red ash lost its taxonomic status in the mid 20th century based on the opinion of a handful of researchers, not on a quantitative review of their taxonomic status nor a thorough comparison of observed morphological characteristics.

Biltmore ash was originally considered a separate species upon its discovery in 1898. Fernald formally re-designated Biltmore ash as a variety in 1947 based on annotations by Wright (Miller 1955). This re-designation has stood unchanged to the present. Miller contended the original designation was valid, that Biltmore ash should be a separate species, because it has more differences from white ash than pubescence

(Miller 1955). The traits she listed Biltmore as having different from white ash, truncate upper margin to leaf scar, acute terminal bud, and reniform lateral buds. However, these are traits Santamour associates with tetraploid white ashes (Santamour Jr. 1962). Miller also contended Biltmore ash may be a hybrid of white and red ash, an idea which has been disproven (Hardin and Beckmann 1982).

The morphological characteristics for Biltmore ash and the former red ash were recorded in the same manner as given above for the main species for the purpose of determining how much Biltmore and white ash and green and red ash have in common versus have different to see if there are any morphological differences besides pubescence to support their status (whether current or former) as varieties (Appendix VIII).

The amount of data generated from this collection of ash materials should assist in examining the validity of merging original green ash and red ash into modern green ash and not recognizing any varieties. The qualitative data indicate green ash and red ash are virtually identical in every characteristic examined. Besides pubescence, which was used as the main means of segregation, there were only subtle differences between the two. The color of the bottom side of the leaf is most commonly light green in green ash, but medium green or dull green in Red ash and yellow-green is less common in red ash than it is in green ash. All the same colors were observed in both with only frequency varying, though green ash exclusively had the whitish-green underside occasionally. The color of new twig growth was generally gray in green ash while in red ash it tends to be a brown-gray color. The bud color is split between dark and medium brown in green ash while red ash is generally dark brown, with medium brown being uncommon. Additionally, the most common form for leaf tips in green ash is acuminate while red ash is split between acuminate and acute. The brighter green color on the underside of the leaves of green ash, the greater prevalence of acuminate apices in green ash were noted by Dame and Brooks in 1901 (Dame and Brooks 1972). The only characteristic from their description which clashed with the findings of this study is green ash tending to be more serrated than red ash. No difference was observed with leaf margins here.

Statistical analyses of leaf dimensions indicated there was no significant difference between green ash and red ash and when these trees were plotted in an ordination space, they overlapped. These analyses found the only characteristic with a significant difference between the two varieties was leaf density. Analyses for white ash and Biltmore ash found the distinction was significant, though the only individual characteristic which proved significant was L2 leaflet length. When plotted in an ordination space, both overlap, though white ash has several individuals that deviate from the norm. Sample size was very small for Biltmore ash (n=8), too small to draw definitive conclusions on this matter.

For *Fraxinus pennsylvanica*, the morphological data indicate there are subtle differences between its varieties observationally. Statistical tests indicate the quantitative aspects (e.g. leaflet lengths and widths) do not merit dividing the species into two varieties. Gathering similar data from across the species range and using statistical techniques to determine whether dividing green ash and red ash into varieties is supported or not should provide a definitive answer to this issue, but the Illinois data suggest a variety-level distinction does not exist. Quantifying qualitative characteristics and testing those findings for significance will help to definitively answer the question of do these trees merit being separate varieties.

The sample size for Biltmore ash was only 8 individuals, thus it is too small to draw definitive conclusions. In contrast, the red ash sample size comprised 1/4 the total sample size for *Fraxinus pennsylvanica*. The tentative conclusions that can be drawn are the only points of difference are Biltmore ash seemed polarized between short and long petiolules while white ash generally had long petiolules, with medium forms being less common and short forms being very uncommon and the twig color for new growth tended to be gray-brown or light brown in Biltmore ash and generally dark brown in white ash. When looking at quantitative data, differences are significant, though only one leaflet (L2) shows significant differences.

There is circumstantial evidence Biltmore ash has varying frequency across white ash's range and red ash has varying frequency across green ash's range. People who have worked out on the Eastern Seaboard and in the Midwest have noted red ash is more frequent in the Eastern states than it is in the Midwest and the same for Biltmore ash. In the early decades of the 20th century, Biltmore ash was thought to be limited to portions of the East Coast; only later was it found in the Midwest and South. Keys for trees found in the Northeast treat green ash as the less common form and note it is rare in the east but common in the Midwest (Hough 1921; Brown 1975). The webpage for the biology department at Ohio State University indicates white ash is common in northeastern Ohio while Biltmore ash is common in southwestern Ohio and red ash is more common in western and northern Ohio while Green ash is more common in eastern Ohio (Sydnor and

Cowen Year Unknown). If this can be confirmed quantitatively with collections from across the species' ranges, this would help support distinguishing them as varieties.

The difficulty with existing designations:

The lack of specific definitions for subspecies and variety seem to be fueling the lack of consensus in the categorization of certain species. For this thesis, the following definitions are used. A subspecies is a subset within a species which has a range geographically distinct from the species' range (though there may be some overlap), which intergrades with the species, and displays morphological characteristics not found in the species. A variety is a subset within a species which intergrades with the species and which displays a consistent suite of characteristics which are either not found in the general species population or which are not found together in the population. Varieties should have a range within the general species' range which does not encompass the entirety of the species' range. These differences, in range or morphological characteristics, should be testable.

Based on the results and findings of this project, *Fraxinus americana* var. *biltmoreana* would merit classification as a variety while *F. pennsylvanica* var. *subintegerrima* would not. Based on these definitions, the distinctive blue ashes found in Illinois would constitute a variety, *F. quadrangulata* var. *fuscopapyraceus*.

CONCLUSIONS

Revisiting the original question, is the climate difference across Illinois enough to create differences in species populations found across the state or create similar trends across the genus? These findings indicate 600 km of north-south distance is enough to generate differences in some individual species populations. Quantitative differences were discernibly found in the leaf morphology of white ash and green ash across the portions of their ranges encompassed by Illinois. Similar trends were not seen across the genus, with each species reacting to the 600 km gradient differently. This indicates the species of *Fraxin*us, at least the eastern North American species, react to broad environmental variables greater on an individual basis than on a collective basis. Their ecological behavior and occupation of different habitats may have a greater contribution to how they react to climatic variables than their shared identity as members of the *Fraxinus* genus, particularly as the upland-lowland segregation seems strong in defining where certain species are and are not found.

White ash had a population of large-leaved trees confined to northern Illinois which was unlikely to be the result of influence by light intensity levels and more likely a result of population genetics or some variable untested in this study. White ash has been observed to be significantly more variable in this study than the literature indicates and leaf size may be another such instance of that variability. Green ash had a population of trees with very thick leaves confined to southern Illinois. Lack of competition for light resources coupled with a longer growing season may be the variables influencing this finding. Higher precipitation may also be a factor as well.

On the final objective, there was considerable variation in several ash species, though variation among the traits observed for each characteristic did not vary discretely by region; several anomalous or unusual traits (e.g. red-colored petioles, tiny terminal buds, etc) did however. Ash leaves and twigs can develop many unusual traits. The ash leaf is a complex structure, with four separate leaflet components, and it seems the general adage, the more complicated a thing is, the more that can go wrong with it, holds.

White ash is a highly variable species, more than green ash is, the ash species previously known for being highly variable (whether it is more variable than Carolina ash is unknown). It displays several features thought to be limited to green ash, pumpkin ash, and even blue ash, in addition to several rare forms of characteristics. In planar dimensions, its leaves can even exceed pumpkin ash leaves. Biltmore ash as a variety is supported by the data, though the support does not conclusively end all doubts to the merits of its status.

Green ash is also a variable species, displaying several rare forms of characteristics. It lacks the major variability seen in white ash though. The differentiation of the species into varieties, green ash and red ash, is not supported by the data.

Pumpkin ash is also a fairly variable species. Some leaves significantly larger than size limits given in the literature were found. It seems to be able to inhabit upland sites, though this point needs confirmation. The species has several interesting properties, most notably its origin and the high rate of variation, which this thesis could not investigate in detail.

Blue ash is very consistent as a species, not displaying the anomalous traits or rare forms of characteristics at even remotely the same frequency as white, green, or pumpkin ash. The species does seem to display regional differences, enough to merit the designation of a variety to identify the dark-colored, thin-leaved, different-formed blue ashes of Illinois, *Fraxinus quadrangulata* var. *fuscopapyraceus*.

Black ash seems fairly consistent as a species, like blue ash, though there are hints of greater variation in it than the literature indicates.

There has been a historic difficulty in telling ash species apart in eastern North America. The characteristics of white, green, and pumpkin ash all overlap considerably. Tricky specimens are very common and prevail among the ash species that are hard to tell apart. With trees of white ash with several traditional traits of green ash being observed and trees of green ash with several of traditional traits of white ash being observed, the only reliable way to determine species among individual specimens is by looking at an entire suite of characteristics. All old conventions on using a certain characteristic to differentiate between species failed to divide the tricky specimens into their respective species. A set of several of the leaf characteristics and twig characteristics is reliable enough to identify specimens to species by visual assessment.

The general position in the literature regarding *Fraxinus* is that the only assuredly positive means of identification is by seeds. Variation in samaras was not observed in this study because they were very scarce in 2006, so this statement cannot be corroborated or refuted by observed evidence. However, since the genus is known for its irregular and infrequent fruiting periods, relying on samaras for formal identification in any study that is not a multi-year study is not a viable means for distinguishing the species from each other.

Some highly anomalous individuals were seen. One in northwestern Illinois (NAR02) may be a rare variety of a described species or an undescribed relict species. One in east-central Illinois (CKP05) has a form resembling pumpkin ash, except it is large enough to dwarf pumpkin ash, indicating this tree may have a ploidy level above hexaploid. It may be a higher ploidy of pumpkin ash or a higher ploidy of white ash, perhaps the result of chromosome doubling in the offspring of two tetraploid white ashes, chromosome doubling in the offspring of two hexaploid pumpkin ashes, or chromosome doubling in a hybrid of pumpkin ash and a white ash?

The genus *Fraxinus* contains several species which display a high degree of overlap in morphological characteristics and a very high rate of abnormalities in leaf development. Traditional keys and species descriptions only identify the easy to recognize members of many ash species. Some species in particular are a troublesome lock in which the taxonomic key does not work. *Fraxinus* is perplexing at best, frustrating at worst, though amid all the oddities and impersonators, virtually all specimens can be identified to species with an entire set of traits for a range of characteristics. The greatest advantages *Fraxinus* can provide to future research are the relatively small body of research into it, particularly among its ecological roles or for some species, even basic information, and there is a high probability of finding anomalies if a reasonable number of trees are sampled, making every project have a good chance of turning up something unusual.

FURTHER WORK

While it may seem like a significant quantity of information was gathered from this collection of materials from ash trees, there still remains much work to be done on the six species on this part of the continent.

Most of Illinois' natural divisions and less than half of its sections were visited and sampled. Four divisions dominate the state's geography- the Grand Prairie Division, the Southern Till Plain Division, the Northeastern Morainal Division, and the Western Forest-Prairie Division. The natural divisions that weren't visited were the Western Forest-Prairie Division, Illinois River and Mississippi River Sand Areas Division, Middle Mississippi Border Division, Lower Mississippi River Bottomlands Division, Ozark Division. The Western Forest-Prairie Division was the largest omission from this study because it is one of the four largest divisions in the state. It, especially the Galesburg Section, should have been a part of this study.

A few sections should have been visited as well due to their prominent size- Chicago Lake Plain Section (Northeastern Morainal Division), Springfield Section (Grand Prairie Division). The Ozark Division and the Cretaceous Hills Section of the Coastal Plain Division might have produced some interesting findings due to their high elevation relative to the rest of southern Illinois and the possibility of having been refugia during the last ice age. Having a larger sample size from the Wisconsin Driftless Section would have been better as well due to that area's unique history.

This thesis analyzed variation across a segment of the range of each species. Mapping out the variation within each species across its entire range should cease some of the taxonomic debate within the genus, such as the classification of Biltmore ash and the old varieties of green ash. It would also corroborate or refute the evidence indicating blue ash has a variety. While lacking any taxonomic tumult, variation among black ash and Carolina ash would perhaps be the most interesting to look at since their populations tend to be isolated from one another due to the uncommon frequency of wetlands and swamps across much of eastern North America. Variation among pumpkin ash's archipelago of isolated populations might also provide some interesting findings. Having the total range of variation for a species across something as broad as a section of a continent should also provide useful data for geneticists and ecologists, who could examine genetic differences and ecological differences of a broad-ranged species and compare the results to findings from other ash species to get an understanding of genus-level effects by genetics and the environment.

The bark of ash trees is not homogenous across all species; in fact, most species have relatively unique bark compared to the other five species in eastern North America. Bark was not examined as a part of the data collection. The bark of mature ash trees may help provide differentiation. With the advent of digital cameras, cataloging the appearance of bark is easier than it has been in the past. It may also be worthwhile to examine the bark on saplings to see if any species-specific characteristics can be observed which might help provide another means for differentiating similar species. The best scenario would be to photograph various ash trees as they age from saplings to mature trees to see how different patterns of bark develop and examine variation in bark morphology in each species.

White ash and green ash were known to have multiple ploidy levels. It would be interesting to see what effect ploidy has on leaf measurements (i.e. to get size ranges for the measurements for each ploidy level in each species). It would also be interesting to see if the other ashes where ploidy is not mentioned (e.g. black, blue, Carolina ash) have multiple ploidy levels or have only one level.

The origin of pumpkin ash has not yet been uncovered. A definitive genetic analysis of several members of the species from the main population centers as well as some of the isolated populations compared to white ash and green ash sampled from across their respective ranges, with samples collected from adjacent to isolated pumpkin ash populations as well, should provide an answer. The tools to answer this question may not have been around when it was first raised, but since they are available now, a researcher or even a graduate student who wants the credit of solving a mystery accomplished scientific predecessors couldn't solve, the puzzle of the pumpkin ash's progenitors remains open. Additionally, microscopic foliar analysis should be performed on upland trees classified as pumpkin ash to confirm the classification and thus whether the species' description needs revision. Such analyses should also reveal what the full range of morphological characteristics are that pumpkin ash could have and whether it is exclusively bound to bottomland and wetland habitat or it can reside on a habitat of higher ground.

Much remains unknown about the propagation of *Fraxinus profunda* and *F. caroliniana*. With the discovery of the emerald ash borer's presence in North America in 2002, all North American ash trees, especially the six species in the eastern forests, remain under threat of decimation comparable to the American chestnut or the American elm. Having such information would help to facilitate the preservation of these species and also to preserve details that would be valuable to have should the species be unfortunately pushed to extinction.

Flower color for *Fraxinus* species is inconsistent in the literature and webpages which profile the species. All eastern North American ashes have their color listed as green, purple (or reddish-purple), greenish-purple, or green to purple. Each species has one color given more consistently (i.e. purple for white, black, blue ash, green for green, Carolina ash), though the amount of contradictory information makes it impossible to state anything for certain on the matter. It is recommended that a comprehensive survey of flower color for these ashes be undertaken across the range to produce a definitive answer to the flower color for each ash species and whether that color varies or not.

Specific drop times for seeds of the various *Fraxinus* species are not known beyond the general earliest to latest limits for the species across their whole range. This is one area where information needs to be generated. In addition, the seed production time of the *F. caroliniana* individuals in northern Illinois is not known.

A worthwhile test of the potentially greater influence of habitat selectivity on response to climatic variation over similar taxonomy would be to take species of another genus that occupies a range of habitats, with similar differentiation as seen between white ash and green ash, that also extend statewide across Illinois, and determine if they vary in a similar manner as the ash species which has the same habitat preferences as them. Testing pumpkin ash populations from northern Illinois or other northerly island populations such as those in Michigan, Indiana, and Ohio against the Florida population and the Carolinas population against the population at the confluence of the Ohio and Mississippi Rivers may also produce some results relevant to this matter.

Finally, it is highly recommended seeds be gathered from CKP05, the ash with gigantic leaves from Kickapoo SP, with some being given to the Rose Lake ash preservation effort to preserve this unique individual and the rest being saved for cultivation. A large greenhouse or outdoor area of suitable climate not likely to be threatened by EAB (e.g. a different continent) could be used to grow this tree's seeds. More information should also be gathered from NAR02, the bizarre ash from Apple River Canyon SP, namely more leaves and twigs collected in addition to images taken of its bark and seeds gathered from it for preservation and for analysis. It is also recommended these areas be scouted for other such individuals as themselves. If NAR02 proves to be a distinct entity taxonomically, other forests and woodlands across the Driftless in Wisconsin, Iowa, and Minnesota should be visited to find if more individuals like this exist. Finally, it is recommended various woodlands located adjacent to bodies of water, particularly those along the Illinois Waterway be surveyed to determine how abundant Carolina ash is in the Palos-Sag Valley Division of the Cook County Forest Preserve and whether other Carolina ash exist in other counties along the canal and waterway.

BIBLIOGRAPHY

Adams, D.E. and Anderson, R.C. 1980. Species response to a moisture gradient in Central Illinois forests. American Journal of Botany 67: 381-392.

Alexander, N.L., Flint, H.L., and Hammer, P.A. 1984. Variation in cold-hardiness of *Fraxinus americana* stem tissue according to geographic origin. Ecology 65: 1087-1092.

Anderson, E. and Turrill, W.B. 1938. Statistical studies on two populations of *Fraxinus*. New Phytologist 37: 160-172.

Anderson, M.K. and Nesom, G. 2006. Plant Guides- Black Ash [Online]. United States Department of Agriculture, National Resource Conservation Service, National Plant Data Center and the Biota of North America Program. Available from: http://plants.usda.gov/plantguide/pdf/cs_fmi.pdf . Accessed 2007 Jun 25.

Baer, G. (Writer, Host) & Andries, D. (Producer). 2007. The Southwest Suburbs: Birthplace of Chicago. WTTW 11, PBS, Chicago, IL (Broadcaster, Distributor). Original Air Date: 2007 Mar 18.

Beadle, C.D. 1898. Notes on the botany of the southeastern states, II. Botanical Gazette 25: 357-360.

Black, C.L. and Beckmann, R.L. 1983. The variability of nuclear DNA and its implications for polyploidy in White Ash (*Fraxinus americana* L.: Oleaceae). American Journal of Botany 70: 1420-1423.

Bonner, F.T. 1974. *Fraxinus* Ash. *In* Seeds of Woody Plants. Schopmeyer, C.S. p. 411-416. U.S. Department of Agriculture. Agriculture Handbook No. 450. Washington D.C.

Brown, H.P. 1975. Trees of New York State Native and Naturalized. Dover Publications, New York, New York.

Burns, R.M. and Honkala, B.H. 1990. Silvics of North America Volume 2- Hardwoods. U.S. Department of Agriculture. Agriculture Handbook No. 654. Washington D.C.

Bush, B.F. 1894. Notes on a list of plants collected in southeastern Missouri in 1893. Missouri Botanical Garden Annual Report 5: 139-153.

Bush, B.F. 1897. Notes on the botany of some Southern swamps. Garden and Forest 10: 514-516.

Clausen, K.E., Kung, F.H., Bey, C.F., and Daniels, R.A. 1981. Variation in white ash. Silvae Genetica 30: 93-97.

Dame, L.L. and Brooks, H. 1972. Handbook of the Trees of New England with Ranges Throughout the United States and Canada. Dover Publications, New York, New York.

Davidson, C.G. 1999. 'Northern Treasure' and 'Northern Gem' hybrid ash. Hortscience 34: 151-152.

Dirr, M.A. and Heuser Jr., C.W. 1987. The Reference Manual of Woody Plant Propagation. Varsity Press. Atlanta, Georgia.

Fagerlind, F. 1958. Hip and seed formation in newly formed Rosa polyploids. Acta Horti Bergiani 17: 229-256.

Fairfax County, Virginia Website. 2007. Available from: http://www.fairfaxcounty.gov/dpwes/environmental/eab_general.htm. Accessed 2007 Jul 19.

Fairfax Office of Public Affairs. 2004 Jan 26. Emerald Ash Borer infests area of Fairfax County. Available from: http://www.fairfaxcounty.gov/news/2004/04027.htm . Accessed 2007 Jul 19.

Fernald, M.L. 1950. Gray's Manual of Botany. 8th Edition. American Book Company. New York, New York.

Foerste, A.F. 1897. Curious leaves. Botanical Gazette 23: 460-463.

Fowler, N.L. and Levin, D.A. 1984. Ecological constraints on the establishment of a novel polyploid in competition with its diploid progenitor. The American Naturalist 124: 703.711.

Fritch, P.W. and Lucas, S.D. 2000. Clinal variation in the *Halesia carolina* complex (Styracaceae). Systematic Biology 25: 197-210.

Frye, J.C., Willman, H.B., and Black, R.F. 1965. Outline of glacial geology of Illinois and Wisconsin. Pages 43-61 *in* H.E. Wright, Jr. and D.G. Frey, editors. The Quaternary of the United States. Princeton University Press, Princeton, New Jersey.

Gates, F.C. and Erlanson, C.O. 1925. Enlarged bases in *Fraxinus nigra* in Michigan. Botanical Gazette 80: 107-110.

Gérard, P.R., Klein, E.K., Austerlitz, F., Fernández-Manjarrés, J.F., and Frascaria-Lacoste, N. 2006. Assortative mating and differential male mating success in an ash hybrid zone population. BMC (BioMed Central) Evolutionary Biology 6: 96 [Online]. 2006. Available from: http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=1660552 . Accessed 2007 Mar 30.

Gleason, H.A. and Cronquist, A. 1963. Manual of Vascular Plants of Northeastern United States and Adjacent Canada. D. Van Nostrand Company. Princeton, New Jersey.

Gould, J. 2007. Proposed release of three parasitoids for the biological control of Emerald Ash Borer (*Agrilus planipennis*) in the continental United States. Environmental Assessment, April 2, 2007.

Griffith, R.S. 1991. *Fraxinus americana*. *In*: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Science Laboratory (Producer). Available: http://www.fs.fed.us/database/feis . Accessed 2007 Jun 29.

Grime, J.P. 1994. The role of plasticity in exploiting environmental heterogeneity. *In* Exploitation of Environmental Heterogeneity by Plants- Ecophysiological Processes Above- and Belowground. Caldwell, M.M. and Pearcy, R.W. p.1-19. Academic. New York, New York.

Gucker, C.L. 2005a. *Fraxinus nigra*. *In*: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Science Laboratory (Producer). Available: http://www.fs.fed.us/database/feis . Accessed 2007 Jun 29.

Gucker, C.L. 2005b. *Fraxinus pennsylvanica*. *In*: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Science Laboratory (Producer). Available: http://www.fs.fed.us/database/feis . Accessed 2007 Jun 29.

Halsted, B.D. 1888. Abnormal ash leaves. Bulletin of the Torrey Botanical Club 15: 212-213.

Hardin, J.W. and Beckmann, R.L. 1982. Atlas of foliar features in woody plants, V. *Fraxinus* (Oleaceae) of Eastern North America. Brittonia 34: 129-140.

Harms, W.R. 1990. *Fraxinus profunda* (Bush) Bush. Pumpkin Ash. *In* Silvics of North America Volume 2- Hardwoods. Burns, R.M. and Honkala, B.H. p. 355-357. U.S. Department of Agriculture. Agriculture Handbook No. 654. Washington D.C.

Henrichs, A.M. 2007 Jun 27. Destructive Asian insect found in Cranberry [Online]. Pittsburgh Tribune-Review. http://www.pittsburghlive.com . Accessed 2007 Jul 16.

Hoffmann, W.A., Franco, A.C., Moreira, M.Z., and Haridasan, M. 2005. Specific leaf area explains differences in leaf traits between congeneric savanna and forest trees. Functional Ecology 19: 932-940.

Hough, R.B. 1921. Handbook of the Trees of the Northern States and Canada East of the Rocky Mountains. 3rd edition. Self-published. Lowville, New York.

Illinois Department of Agriculture. 2006 (2006 Jun 21). Emerald Ash Borer discovered in Evanston [Online]. Illinois Department of Agriculture. Available from: http://www.agr.state.il.us/eab/ . Accessed 2007 Jul 17.

Illinois Department of Agriculture. 2007a (2007 Jul 11). Illinois Department of Agriculture finds new Emerald Ash Borer infestation [Online]. Illinois Department of Agriculture. Available from: http://www.agr.state.il.us/eab/ . Accessed 2007 Jul 17.

Illinois Department of Agriculture. 2007b (2007 Jul 16). Emerald Ash Borer discovered in DuPage County [Online]. Illinois Department of Agriculture. Available from: http://www.agr.state.il.us/eab/ . Accessed 2007 Jul 17.

Illinois Plant Information Network. 2007. Illinois Plant Information Network website [Online]. United States Forest Service. Available from: http://www.fs.fed.us/ne/delaware/ilpin/ilpin.html. Accessed 2007 Jul 16.

Jackson, S.T., Webb, R.S., Anderson, K.H., Overpeck, J.T., Webb III, T., Williams, J.W., Hansen, B.C.S. 2000. Vegetation and environment in Eastern North America during the last glacial maximum. Quaternary Science Reviews 19: 489-508.

Kennedy Jr., H.E. 1990. *Fraxinus pennsylvanica* Marsh. Green Ash. *In* Silvics of North America Volume 2- Hardwoods. Burns, R.M. and Honkala, B.H. p. 348-354. U.S. Department of Agriculture. Agriculture Handbook No. 654. Washington D.C.

King, J.E. 1981. Late Quaternary vegetational history of Illinois. Ecological Monographs 51: 43-62.

Kozlowski, T.T. 1971. Growth and Development of Trees vol. 1. Academic Press. New York, New York.

Lechowicz, M.J. 1984. Why do temperate deciduous trees leaf out at different times? Adaptation and ecology of forest communities. The American Naturalist 124: 821-842.

Leitner, L.A. and Jackson, M.T. 1981. Presettlement forests of the unglaciated portion of southern Illinois. American Midland Naturalist 105: 290-304.

Little Jr., E.L. 1953. Check List of Native and Naturalized Trees of the United States (Including Alaska). Agricultural Handbook No. 41. Forest Service. Washington D.C.

MacFarlane, D.W. and Meyer, S.P. 2005. Characteristics and distribution of potential tree hosts for Emerald Ash Borer. Forest Ecology and Management 213: 15-24.

McCormac, J.S., Bissell, J.K., and Stine Jr., S.J. 1995. The status of Fraxinus tomentosa (Oleaceae) in Ohio with notes on its occurrence in Michigan and Pennsylvania. Castanea 60: 70-78.

McDonald, P.G., Fonseca, C.R., Overton, J.M., and Westoby, M. 2003. Leaf-size divergence along rainfall and soil nutrient gradients: Is the method of size reduction common among clades? Functional Ecology 17: 50-57.

Meuli, L.J. and Shirley, H.L. 1937. The effect of seed origin on drought resistance of green ash in the prairie-plains states. Journal of Forestry 35: 1060-1062.

Miller, G.N. 1955. The Genus *Fraxinus*, the Ashes, in North America, North of Mexico. New York Cornell University Agricultural Experiment Station. Memoir 335. Cornell University. Ithaca, New York.

Mohlenbrock, R. H. 1973. Forest trees of Illinois. Illinois State Department of Conservation, Springfield, Illinois.

National Climatic Data Center. 2007. National Climatic Data Center website [Online]. National Oceanic and Atmospheric Administration website. Available from: http://gis.ncdc.noaa.gov. Accessed 2007 Jul 19.

National Resources Conservation Service, Plant Materials Center. United States Department of Agriculture. Plant Materials Program & National Ash Tree Seed Collection Initiative [Online]. Available from: http://www.mi.nrcs.usda.gov/programs/pmc.html . Accessed 2007 Mar 12.

Nowak, D.J. 1994. Urban forest structure: The state of Chicago's urban forest. U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station 186: 3-18.

OEPP/EPPO (Organisation Européenne et Méditerranéene pour la Protection des Plantes/ European and Mediterranean Plant Protection Organization). Data sheets on quarantine pests: Agrilus planipennis. 2005. OEPP/EPPO Bulletin 35: 436-438.

Petrides, G.A. 1972. A Field Guide to Trees and Shrubs Northeastern and north-central United States and southeastern and south-central Canada. 2nd edition. Houghton Mifflin. Boston, Massachusetts.

Prasad, A. 2002. Illinois Plant Information Network [Online]. U.S. Department of Agriculture, Forest Service, Northeastern Research Station (Website Manager). Available from: http://www.fs.fed.us/ne/delaware/ilpin/ilpin.html . Accessed 2007 Jun 27.

Reich, P.B., Walters, M.B., Ellsworth D.S. 1997. From tropics to tundra: global convergence in plant functioning. Proceedings of the National Academy of the Sciences 94: 13730-13734

Rico-Gray, V. and Palacios-Rios, M. 1996. Leaf area variation in *Rhizophora mangle* L. (Rhizophoraceae) along a latitudinal gradient in Mexico. Global Ecology and Biogeography Letters 5: 30-35.

Ryser, P. and Eek, L. 2000. Consequences of phenotypic plasticity versus interspecific differences in leaf and root traits for aboveground and belowground resources. American Journal of Botany 87: 402-411.

Santamour Jr., F.S. 1962. The relation between polyploidy and morphology in white and Biltmore ashes. Bulletin of the Torrey Botanical Club 89: 228-232.

Santamour Jr., F.S. and McArdle, A.J. 1983. Checklist of Cultivars of North American Ash (*Fraxinus*) Species. Journal of Arboriculture 9: 271-276. Available from: http://joa.isa-arbor.com/request.asp?JournalID=1&VolumeID=9&Issue=10 . Accessed 2006 Dec 8.

Schelkopf, E. 2007 Jun 29. Fermilab ash trees infested. Kane County Chronicle [Online]. Available from: http://www.kcchronicle.com . Accessed 2007 Jul 15.

Schlesinger, R.C. 1990. *Fraxinus americana* L. White Ash. *In* Silvics of North America Volume 2- Hardwoods. Burns, R.M. and Honkala, B.H. p. 333-338. U.S. Department of Agriculture. Agriculture Handbook No. 654. Washington D.C.

Sinclair, N. 2004 Oct 10. Ash borer battle: Resilient pests landed 5 years ago. The Detroit News [Online]. http://www.detnews.com/specialreports/2004/ashborer . Accessed 2007 Jul 16.

Spooner, D.M., van den Berg, R.G., Hetterscheid, W.L.A., Brandenburg, W.A. 2003. Plant nomenclature and taxonomy: An agricultural and agronomic perspective. Horticultural Reviews 28: 1-60.

Steinbauer, G.P. 1943. Frequency of polyembryony in *Fraxinus* seeds. Botanical Gazette 105: 285

Sydnor, T.D. and Cowen, W.F. Year Unknown. Ohio Trees Bulletin 700-00. *Fraxinus*-Ash. Ohio State University website. Available from: http://ohioline.osu.edu/b700/b700_63.html. Accessed 21 Jul 2007.

Tardif, J. and Bergeron, Y. 1993. Radial growth of *Fraxinus nigra* in a Canadian boreal floodplain in response to climatic and hydrological fluctuations. Journal of Vegetation Science 4: 751-758.

Taylor, H. 1945. Cyto-taxonomy and phylogeny of the Oleaceae. Brittonia 5: 337-367.

Taylor, R.A.J., Bauer, L.S., Miller, D.L., and Haack, R.A. 2004. Emerald Ash Borer flight potential. Emerald Ash Borer Research and Technology Development Meeting, Romulus, Michigan. October 5-6, 2004.

Terrell, C. and Bolger, K. 2006. It's here- The Emerald Ash Borer in Illinois [Online]. Morton Arboretum website. Available from: http://www.mortonarb.org/plantinfo/plantclinic.EAB.htm . Accessed 2006 Jul 9.

Townsend, A.M. 1972. Geographic variation in fruit characteristics of *Acer rubrum*. Bulletin of the Torrey Botanical Club 99: 122-126.

United States Natural Arboretum website. 2007. USDA Plant Hardiness Zone Map webpage. Available from: http://www.usna.usda.gov/Hardzone/ushzmap.html. Accessed 2007 Jun 30.

Waldron, G., Gartshore, M., & Colthurst, K. 1996. Pumpkin Ash, *Fraxinus profunda*, in southwestern Ontario. Canadian Field-Naturalist 110: 615-619.

Wallander, E. 2001. New classification of *Fraxinus*. Fraxigen. Ash for the future: defining European ash populations for conservation and regeneration [Online]. Oxford

Plant Systematics, Oxford University Herbaria. Oxford University, UK. Available: http://herbaria.plants.ox.ac.uk/fraxigen/ash/fraxinus_link.html . Accessed 2007 Jul 19.

Ward, J.S. and Parker, G.R. 1989. Spatial dispersion of woody regeneration in an old-growth forest. Ecology 70: 1279-1285.

Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A., Wright, I.J. 2002. Plant ecological strategies: Some leading dimensions of variation between species. Annual Review of Ecological Systematics 33: 125-159.

Wilhite, L.P. and Toliver, J.R. 1990. *Taxodium distichum* (L.) Rich. *In* Silvics of North America Volume 2- Hardwoods. Burns, R.M. and Honkala, B.H. U.S. Department of Agriculture. Agriculture Handbook No. 654. Washington D.C.

Wisconsin Department of Natural Resources. 2004. Southern forest communities. Ecological landscapes of Wisconsin- Ecosystem management planning [Online]. Handbook HB1805.1. Available from: http://www.dnr.state.wi.us/landscapes/community/page/sforest.pdf . Accessed 2007 Jul 3

Wright, H.E., Jr. 1976. The dynamic nature of Holocene vegetation. A problem in paleoclimatology, biogeography, and stratigraphic nomenclature. Quaternary Research 6: 581-596.

Wright, J.J., Reich, P.B., Westoby, M., et al. 2004. The worldwide leaf economics spectrum. Nature 428: 821-827

Wright, J.W. 1944a. Ecotypic differentiation in red ash. Journal of Forestry 42: 591-596.

Wright, J.W. 1944b. Genotypic variation in white ash. Journal of Forestry 42: 489-495.

Wright, J.W. and Rauscher, H.M. 1990. *Fraxinus nigra* Marsh. Black Ash. *In* Silvics of North America Volume 2- Hardwoods. Burns, R.M. and Honkala, B.H. p. 338-347. U.S. Department of Agriculture. Agriculture Handbook No. 654. Washington D.C.

Table 1. Number of ash trees by species sampled across each region.

Species	North	Central	South	Total
White	25	20	39	84
Green	29	37	16	82
Black	4	0	0	4
Blue	10	16	0	26
Pumpkin	0	5	13	18
Carolina	2	0	0	2
Mystery	5	13	1	19
Total	75	91	69	235

Note: If the species are broken down to varietal level, white ash would be as follows: North (24 white, 1 Biltmore), Central (18 white, 2 Biltmore), South (34 white, 5 Biltmore), while green ash would be as follows: North (23 green, 6 red), Central (26 green, 11 red), South (12 green, 4 red).

Table 2. Multivariate tests for differences in leaf characteristics in *Fraxinus americana, F. pennsylvanica, F. quadrangulata*, and *F. profunda* in northern, central, and southern Illinois.

Effect: Region

	White Ash	Green Ash	Blue Ash	Pumpkin Ash
Value	0.340	0.408	0.583	0.092
F	1.816	1.880	2.486	10.873
Hypothesis df	16.000	18.000	9.000	9.000
Error df	142.000	132.000	16.000	8.000
Sig.	0.034	0.023	0.054	0.001
Noncent. Parameter	29.063	33.835	22.370	97.861
Observed Power (a)	0.932	0.956	0.745	0.997

a: computed using Alpha= 0.05

Table 3. Tests of between-subject effects for the effect of region on various leaf characteristics in *Fraxinus americana*.

Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.	Noncent. Parameter	Observed Power(a)
Total Leaf Area	103871	2	51935.48	7.666	0.001	15.332	0.94
Total Leaf Mass	1.326	2	0.663	1.617	0.205	3.233	0.332
Leaf Density	1.80E-05	2	8.99E-06	1.693	0.191	3.385	0.346
L2 Length	63.127	2	31.564	8.668	0.000	17.336	0.964
R2 Length	42.285	2	21.142	5.906	0.004	11.812	0.864
T Length	102.478	2	51.239	8.51	0.000	17.02	0.961
L2 Width	11.164	2	5.582	4.513	0.014	9.027	0.755
R2 Width	6.913	2	3.457	3.069	0.052	6.138	0.577
T Width	35.994	2	17.997	9.716	0.000	-	-

Table 4. Pearson correlation for *Fraxinus americana* regression factors.

	PCA Axis I			PCA Axis II		
	Pearson C.	Sig (2-tailed)	N	Pearson C.	Sig. (2-tailed)	N
T. Leaf A	0.927(**)	0.000	80	0.108	0.342	80
T. Leaf M	0.506(**)	0.000	80	0.805(**)	0.000	80
Leaf Density	-0.446(**)	0.000	80	0.840(**)	0.000	80
L:L2	0.857(**)	0.000	80	0.238(**)	0.034	80
L:R2	0.872(**)	0.000	80	0.268(**)	0.016	80
L:Trml	0.802(**)	0.000	80	-0.066	0.561	80
W:L2	0.904(**)	0.000	80	-0.138	0.223	80
W:R2	0.912(**)	0.000	80	-0.156	0.168	80
W:Trml	0.804(**)	0.000	80	-0.312(**)	0.005	80

** Correlation is significant at the 0.01 level (2-tailed).
* Correlation is significant at the 0.05 level (2-tailed).

Table 5. Tests of between-subject effects for the effect of region on various leaf characteristics in *Fraxinus pennsylvanica*.

Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.	Noncent. Parameter	Observed Power(a)
Total Leaf Area	421.578	2	210.789	0.161	0.852	0.321	0.074
Total Leaf Mass	2.106	2	1.053	5.288	0.007	10.576	0.821
Leaf Density	0.000	2	5.56E-005	4.9	0.010	9.801	0.79
L2 Length	3.58	2	1.79	0.79	0.458	1.580	0.18
R2 Length	4.152	2	2.076	0.859	0.428	1.717	0.192
T Length	15.114	2	7.557	1.885	0.159	3.769	0.38
L2 Width	0.258	2	0.129	0.277	0.759	0.554	0.092
R2 Width	0.064	2	0.032	0.076	0.927	0.151	0.061
T Width	2.367	2	1.184	1.081	0.345	2.161	0.233

Table 6. Pearson correlation for *Fraxinus pennsylvanica* regression factors.

	PCA Axis I			PCA Axis II		
	Pearson C.	**Sig (2-tailed)**	**N**	**Pearson C.**	**Sig. (2-tailed)**	**N**
T. Leaf A	0.878(**)	0.000	76	0.14	0.229	76
T. Leaf M	-0.041	0.726	76	0.832(**)	0.000	76
Leaf Density	-0.631(**)	0.000	76	0.677(**)	0.000	76
L:L2	0.624(**)	0.000	76	0.660(**)	0.000	76
L:R2	0.544(**)	0.000	76	0.650(**)	0.000	76
L:Trml	0.761(**)	0.000	76	0.282(*)	0.013	76
W:L2	0.891(**)	0.000	76	-0.190	0.100	76
W:R2	0.863(**)	0.000	76	-0.179	0.122	76
W:Trml	0.863(**)	0.000	76	-0.391(**)	0.000	76

** Correlation is significant at the 0.01 level (2-tailed).
* Correlation is significant at the 0.05 level (2-tailed).

Table 7. Pearson correlation for *Fraxinus quadrangulata* regression factors

	PCA Axis I			PCA Axis II		
	Pearson C.	Sig (2-tailed)	N	Pearson C.	Sig. (2-tailed)	N
T. Leaf A	0.936(**)	0.000	26	-0.024	0.907	26
T. Leaf M	0.818(**)	0.000	26	0.377	0.058	26
Leaf Density	-0.016	0.940	26	0.942(**)	0.000	26
L:L2	0.959(**)	0.000	26	0.152	0.460	26
L:R2	0.957(**)	0.000	26	0.153	0.454	26
L:Trml	0.825(**)	0.000	26	0.041	0.842	26
W:L2	0.950(**)	0.000	26	-0.184	0.370	26
W:R2	0.930(**)	0.000	26	-0.224	0.271	26
W:Trml	0.794(**)	0.000	26	-0.27	0.182	26

** Correlation is significant at the 0.01 level (2-tailed).

* Correlation is significant at the 0.05 level (2-tailed).

Table 8. Pearson correlation for *Fraxinus profunda* regression factors.

	PCA Axis I			PCA Axis II		
	Pearson C.	Sig (2-tailed)	N	Pearson C.	Sig. (2-tailed)	N
T. Leaf A	0.942(**)	0.000	18	0.044	0.864	18
T. Leaf M	0.790(**)	0.000	18	0.571(**)	0.013	18
Leaf Density	-0.105	0.680	18	0.947(**)	0.000	18
L:L2	0.924(**)	0.000	18	0.153	0.544	18
L:R2	0.869(**)	0.000	18	-0.138	0.586	18
L:Trml	0.802(**)	0.000	18	-0.255	0.307	18
W:L2	0.948(**)	0.000	18	0.072	0.776	18
W:R2	0.932(**)	0.000	18	-0.033	0.897	18

** Correlation is significant at the 0.01 level (2-tailed).
* Correlation is significant at the 0.05 level (2-tailed).

Table 9. Multivariate tests for *Fraxinus americana* and *F. pennsylvanica* by variety.

	F. americana	F. pennsylvanica
Value	0.473	0.257
F	2.517	0.983
Hypothesis df	16.000	18.000
Error df	130.000	120.000
Sig.	0.002	0.484
Noncent. Parameter	40.277	17.694
Observed Power(a)	0.988	0.665

a Computed using alpha = .05

Table 10. Total leaf area (cm^2) by species.

Total Leaf Area	Total	Percent	White	Green	Blue	Black	Pumpkin	Other
<100.00	90	10.1	9	60	17	0	2	2
100.00-199.99	393	44.2	104	216	53	4	13	3
200.00-299.99	247	27.8	145	50	26	7	16	3
300.00-399.99	105	11.8	69	1	5	6	23	1
400.00-499.99	37	4.2	24	0	0	0	12	1
500.00-599.99	12	1.3	7	0	0	1	3	1
600.00-699.99	3	0.3	3	0	0	0	0	0
>700.00	2	0.2	0	0	0	0	2	0

Note: Other includes leaves from trees identified to Carolina ash or the one tree that defied classification.

Table 11. Terminal bud color by percentage of total population for *Fraxinus americana* and *F. pennsylvanica*.

Species	L. Brown	M. Brown	D. Brown	Mix
White	17%	47%	26%	9%
Green	13%	29%	54%	4%

Table 12. Observed frequency of number of leaflets per leaf in *Fraxinus americana*.

Region	3 leaflets	5 leaflets	7 leaflets	9 leaflets	11 leaflets	Split-t.
N	0%	3%	64%	24%	1%	8%
C	0%	8%	51%	28%	3%	10%
S	0%	11%	54%	28%	0%	7%
IL	0%	8%	56%	27%	1%	8%

Note: Sample sizes are n=102 (north), n=109 (central), n=148 (south), n=359 (total).

Table 13. Observed frequency of number of leaflets per leaf in *Fraxinus pennsylvanica*.

Region	3 leaflets	5 leaflets	7 leaflets	9 leaflets	11 leaflets	Split-t.
N	0%	18%	65%	6%	0%	11%
C	1%	9%	63%	18%	0%	9%
S	0%	10%	55%	28%	0%	7%
IL	<1%	13%	62%	16%	0%	9%

Note: Sample sizes are n=113 (north), n=58 (central), n=158 (south), n=329 (total).

Table 14. Observed frequency of number of leaflets per leaf in *Fraxinus quadrangulata*.

Region	3 leaflets	5 leaflets	7 leaflets	9 leaflets	11 leaflets	Split-t.
N	0%	24%	70%	3%	0%	3%
C	0%	31%	47%	9%	0%	13%
S	x	x	x	x	x	x
IL	0%	29%	55%	7%	0%	9%

Note: Sample sizes are n=37 (north), n=64 (central), n=101 (total).

Table 15. Observed frequency of number lf leaflets per leaf in *F. profunda*.

Region	3 leaflets	5 leaflets	7 leaflets	9 leaflets	11 leaflets	Split-t.
N	x	x	x	x	x	x
C	0%	4%	40%	40%	0%	16%
S	2%	6%	37%	44%	2%	9%
IL	1%	6%	38%	42%	1%	11%

Note: Sample sizes are n=25 (central), n=46 (south), n=71 (total).

Table 16. Petiolule length of *Fraxinus* species, expressed as a percentage of the total population. Abbreviations: short (S), medium (M), long (L), extra long (XL).

Species	S	M	L	XL
White	13%	22%	51%	14%
Green	61%	25%	12%	2%
Blue	67%	25%	8%	0%
Pumpkin	43%	24%	32%	0%

Table 17. Descriptive statistics for *Fraxinus americana*.

	Mean	St. Dev	Min	Max	Range
T. Leaf Area	264.8	95.9	105.5	600.4	494.9
T. Leaf Mass	1.93	0.68	0.53	4.01	3.48
Leaf Density	0.008	0.0023	0.004	0.014	0.010
L:L1	9.1	2.13	3.6	17.2	13.6
L:R1	9.1	2.04	3.8	18.0	14.2
L:L2	12.2	2.07	5.7	18.2	12.5
L:R2	12.2	2.03	6.2	19.0	12.8
L:L3	12.5	2.22	7.8	18.9	11.1
L:R3	12.5	2.21	7.4	17.9	10.5
L:L4	11.1	1.65	8.1	15.4	7.3
L:R4	11.5	1.77	8.0	15.2	7.2
L:T	14.7	2.82	9.0	23.4	14.4
W:L1	4.5	1.02	2.2	9.0	6.8
W:R1	4.4	0.95	2.4	7.9	5.5
W:L2	5.5	1.22	2.4	9.4	7.0
W:R2	5.5	1.13	3.3	9.2	5.9
W:L3	5.3	1.20	3.0	8.9	5.9
W:R3	5.4	1.18	3.2	8.9	5.7
W:L4	4.3	0.95	2.6	7.3	4.7
W:R4	4.5	0.99	2.6	7.1	4.5
W:T	6.2	1.49	3.2	11.0	7.8
# Leaflets	7.5	1.01	5.5	10.5	5.0

Note: The units for each metric for Tables 17-21 are as follows: total leaf area (cm^2), total leaf mass (g), leaf density (g/cm^2), length & width (cm).

Table 18. Descriptive statistics for *Fraxinus pennsylvanica*.

	Mean	St. Dev	Min	Max	Range
T. Leaf Area	146.2	39.4	29.0	238.0	209.0
T. Leaf Mass	1.40	0.48	0.38	2.56	2.18
Leaf Density	0.010	0.0035	0.004	0.017	0.013
L:L1	6.7	1.47	1.4	9.3	7.9
L:R1	6.8	1.44	3.0	10.4	7.4
L:L2	9.9	1.62	4.5	14.1	9.6
L:R2	9.8	1.64	5.0	13.6	8.6
L:L3	10.4	1.69	3.4	13.9	10.5
L:R3	10.5	1.70	4.3	13.6	9.3
L:T	12.5	2.02	8.3	17.5	9.2
W:L1	3.0	0.61	1.7	4.9	3.2
W:R1	3.0	0.56	1.7	4.8	3.1
W:L2	3.9	0.70	2.2	5.6	3.4
W:R2	3.9	0.68	2.0	5.2	3.2
W:L3	4.0	0.78	1.7	5.8	4.1
W:R3	4.0	0.79	1.5	5.8	4.3
W:T	4.7	1.05	2.7	7.2	4.5
# Leaflets	7.0	0.83	5.0	9.0	4.0

Table 19. Descriptive statistics for *Fraxinus quadrangulata*.

	Mean	St. Dev	Min	Max	Range
T. Leaf Area	169.6	67.0	81.0	303.9	222.9
T. Leaf Mass	0.96	0.45	0.40	1.84	1.44
Leaf Density	0.006	0.0004	0.004	0.014	0.010
L:L1	7.9	1.75	5.7	11.7	6.0
L:R1	7.8	1.56	5.2	11.0	5.8
L:L2	9.6	1.73	7.4	13.1	5.7
L:R2	9.5	1.65	7.1	12.7	5.6
L:L3	9.4	1.77	6.5	12.2	5.7
L:R3	9.2	1.66	6.7	12.2	5.5
L:T	11.3	1.93	8.0	14.1	6.1
W:L1	4.2	0.89	3.0	6.1	3.1
W:R1	4.2	0.76	3.2	6.1	2.9
W:L2	4.7	0.78	3.2	6.2	3.0
W:R2	4.6	0.65	3.4	6.1	2.7
W:L3	4.4	0.75	2.9	5.5	2.6
W:R3	4.2	0.69	2.8	5.3	2.5
W:T	5.3	0.75	3.6	6.6	3.0
# Leaflets	6.5	1.00	4.8	8.5	3.7

Table 20. Descriptive statistics for *Fraxinus profunda*.

	Mean	St. Dev	Min	Max	Range
T. Leaf Area	337.0	120.8	154.0	685.6	531.6
T. Leaf Mass	1.91	0.82	0.81	4.48	3.67
Leaf Density	0.006	0.0017	0.003	0.010	0.007
L:L1	8.9	2.38	5.0	13.7	8.7
L:R1	8.8	2.35	4.8	13.2	8.4
L:L2	12.5	2.50	8.3	18.6	10.3
L:R2	12.3	2.56	7.8	16.4	8.6
L:L3	13.6	1.92	9.9	18.5	8.6
L:R3	13.5	1.99	9.1	18.1	9.0
L:L4	11.6	1.65	9.0	14.0	5.0
L:R4	12.3	1.74	9.4	15.7	6.3
L:T	15.9	2.64	11.4	21.2	9.8
W:L1	4.9	1.56	2.6	8.3	5.7
W:R1	4.9	1.39	2.5	8.0	5.5
W:L2	6.1	1.41	3.6	10.2	6.6
W:R2	6.2	1.43	3.7	9.6	5.9
W:L3	6.1	1.28	4.0	9.5	5.5
W:R3	6.1	1.30	3.6	9.4	5.8
W:L4	5.0	1.11	3.2	6.9	3.7
W:R4	5.2	0.94	3.6	6.5	2.9
W:T	6.8	1.41	4.1	9.9	5.8
# Leaflets	7.8	0.83	6.0	9.0	3.0

Table 21: Averages for length and width for all leaflets across all species.

	Mean	St. Dev	Min	Max	Range
T. Leaf Area	215.3	100.1	29.0	685.6	656.6
T. Leaf Mass	1.58	0.67	0.38	4.48	4.10
Leaf Density	0.008	0.0031	0.003	0.016	0.013
L:L1	8.0	2.13	1.4	17.2	15.8
L:R1	8.0	2.05	3.0	18.0	15.0
L:L2	11.0	2.22	4.5	18.6	14.1
L:R2	10.9	2.24	5.0	19.0	14.0
L:L3	11.5	2.29	3.4	18.9	15.5
L:R3	11.4	2.28	4.3	18.1	13.8
L:L4	10.7	1.77	7.4	15.4	8.0
L:R4	11.2	2.05	5.6	15.7	10.1
L:T	13.6	2.79	8.0	23.4	15.4
W:L1	3.9	1.13	1.7	9.0	7.3
W:R1	3.9	1.06	1.7	8.0	6.3
W:L2	4.8	1.25	2.2	10.2	8.0
W:R2	4.8	1.22	2.0	9.6	7.6
W:L3	4.8	1.23	1.7	9.5	7.8
W:R3	4.8	1.23	1.5	9.4	7.9
W:L4	4.2	0.97	2.6	7.3	4.7
W:R4	4.5	1.02	2.1	7.1	5.0
W:T	5.6	1.46	2.7	11.0	8.3
# Leaflets	7.2	0.07	2.5	10.5	8.0

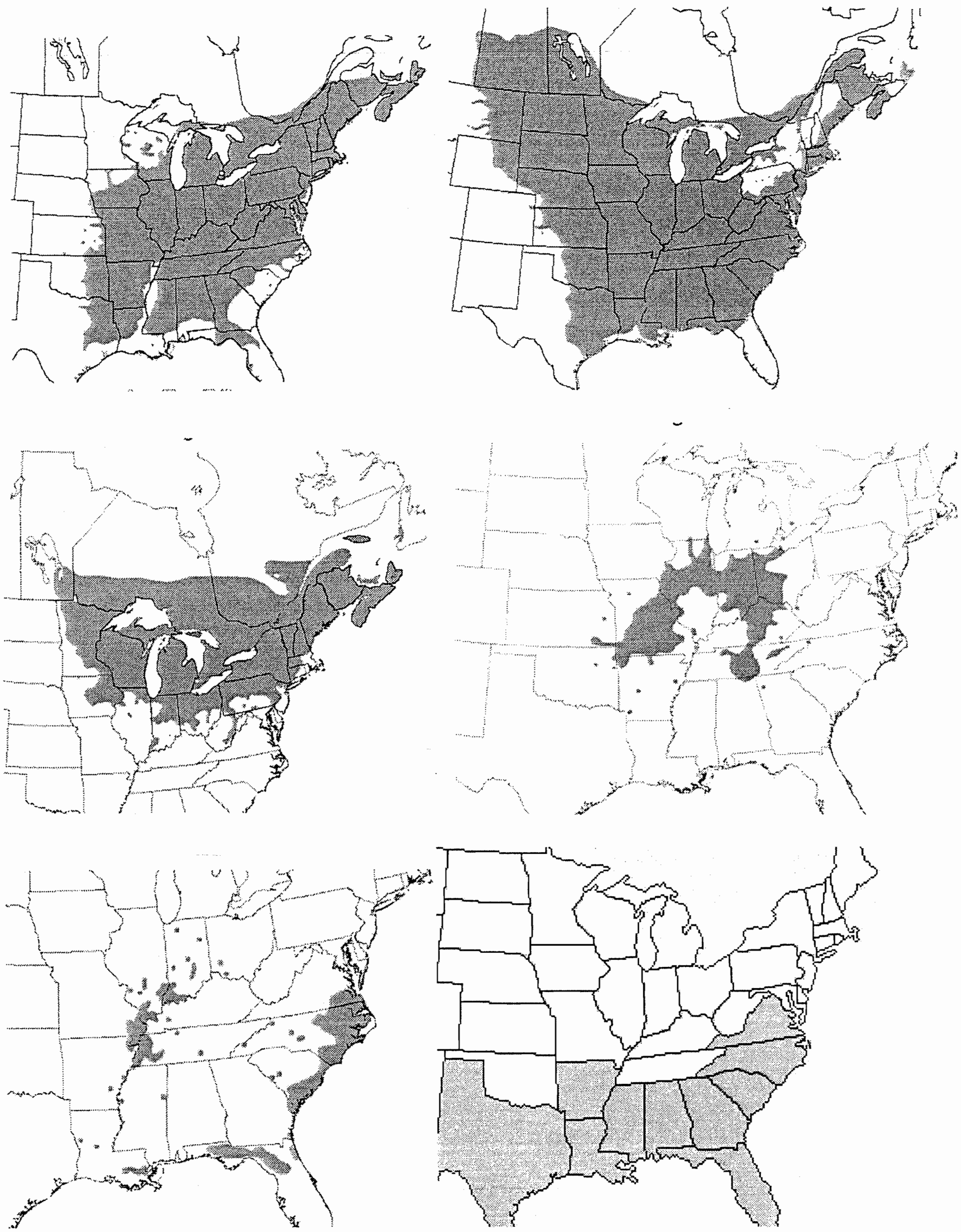

Fig. 1. Distribution of *Fraxinus* species in North America: a) *F. americana* (upper left), b) *F. pennsylvanica* (upper right), c) *F. nigra* (center left), d) *F. quadrangulata* (center right), e) *F. profunda* (lower left), f) *F. caroliniana* (lower right).
Fig 1a-1e images courtesy of the U.S. Forest Service, available from http://www.na.fs.fed.us/fhp/eab/index/shtm (accessed 2007 Jul 16). Fig 1f image courtesy of PLANTS Database, NRCS, http://plants.usda.gov (accessed 2007 Jul 16).

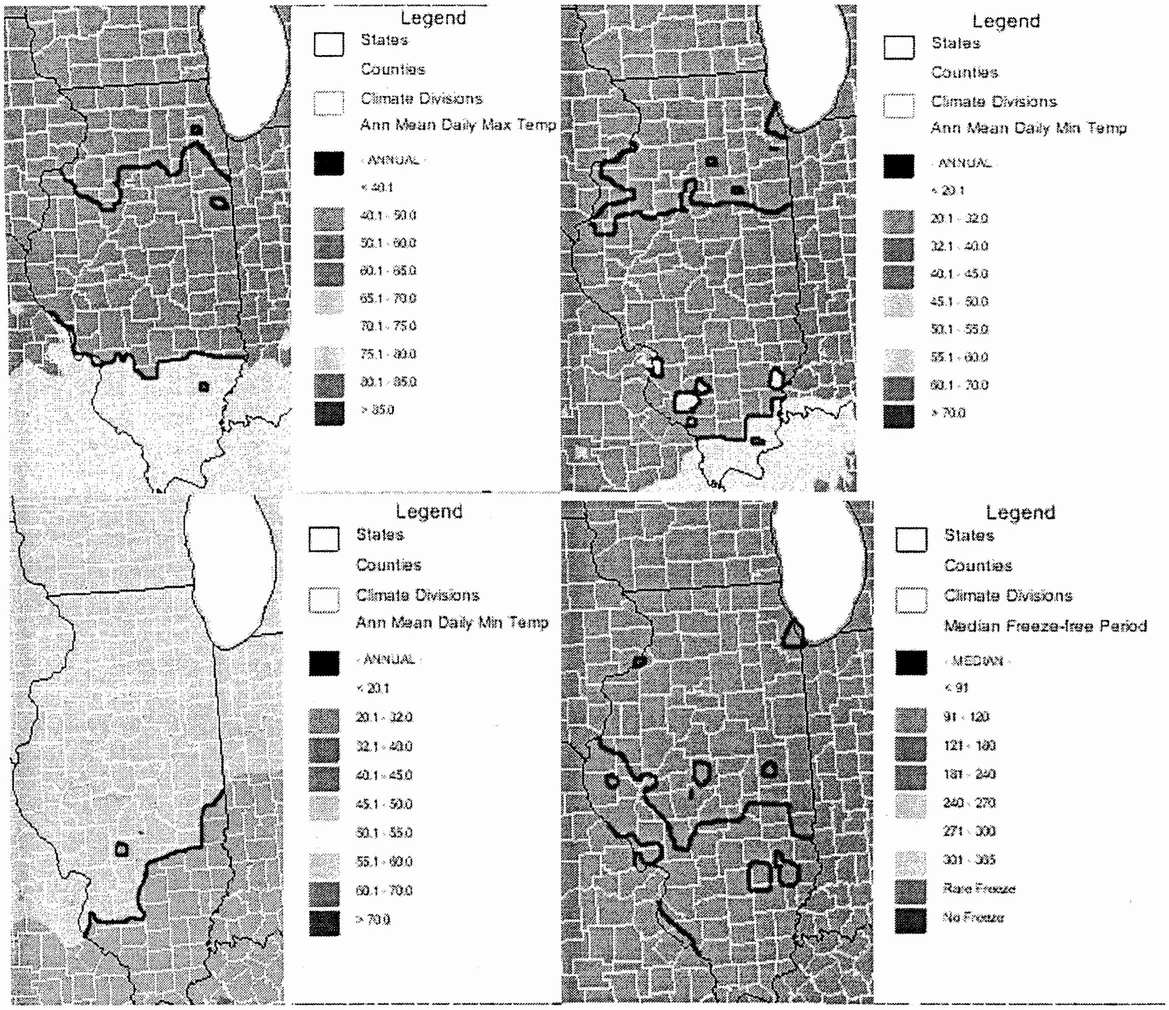

Fig 2. Climatic variables for Illinois: a) annual mean daily maximum temperature (upper left), b) annual mean daily minimum temperature (upper right), c) mean total precipitation (lower left), d) length of freeze-free period (lower right).
Note: Temperature is in Fahrenheit, precipitation is in inches, and freeze-free period is in number of days. All figures were modified to darken the boundary between divisions.

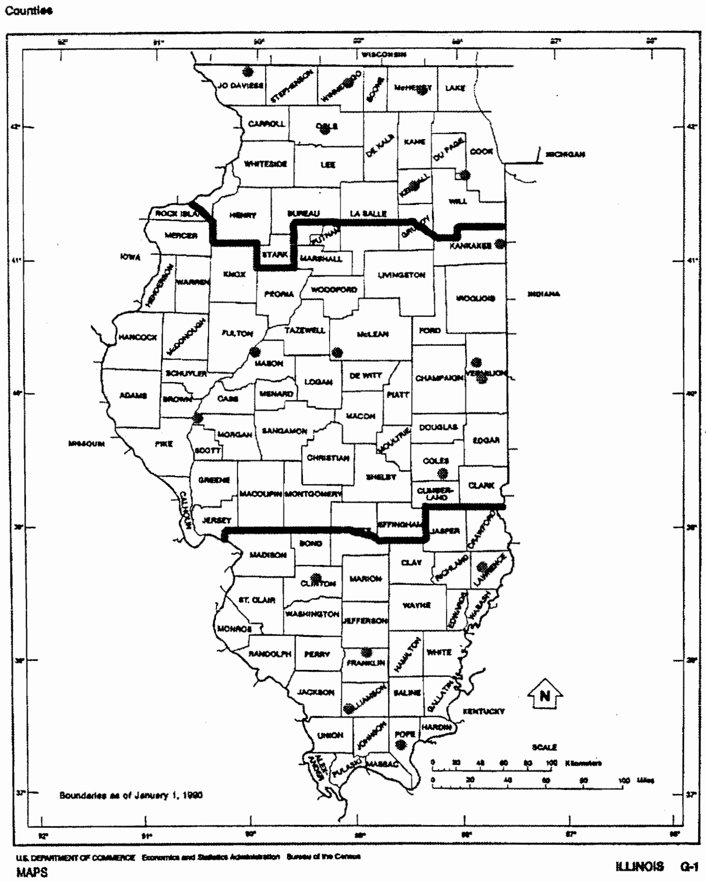

Fig. 3. Northern, central, and southern regions in Illinois along with sampled sites marked.

	Distal	
	Terminal	
L5		R5
L4		R4
L3		R3
L2		R2
L1		R1
	Proximal	

Fig. 4. Description of abbreviations for leaflets on a *Fraxinus* leaf.
Note: The abbreviations are encoded by the positions of the leaflets when the leaf is face up.

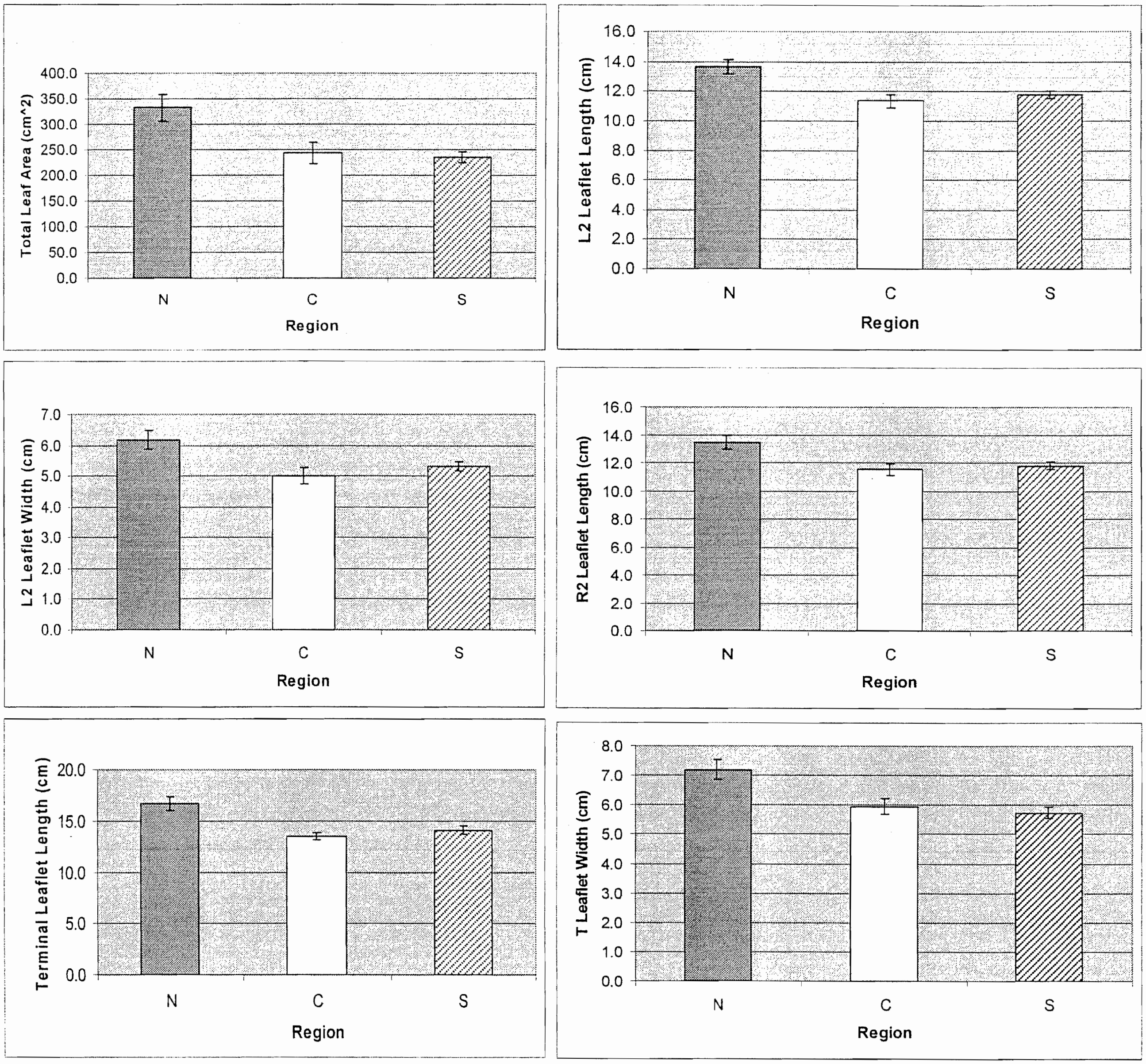

Fig. 5. Characteristics of *Fraxinus americana* which differed significantly by region: a) mean total leaf area (upper left), b) mean L2 leaflet length (upper right), c) mean L2 leaflet width (center left), d) mean R2 leaflet length (center right), e) mean terminal leaflet length (lower left), f) mean terminal leaflet width (lower right).

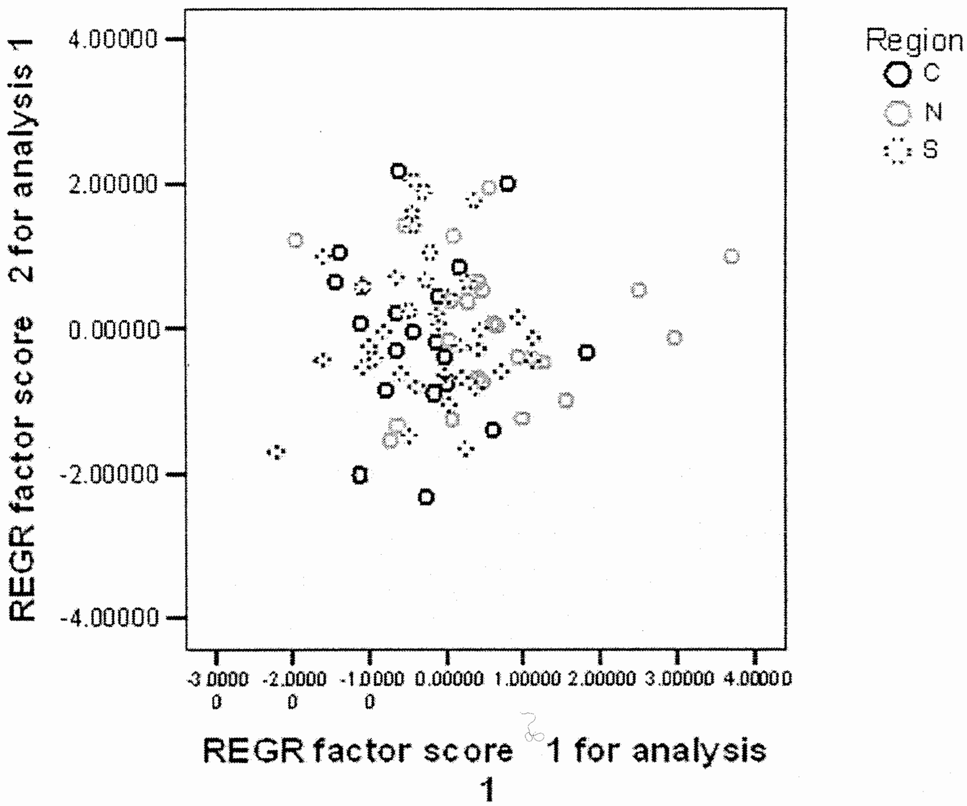

Fig. 6. Regression factor correlation graph for *Fraxinus americana* by region.

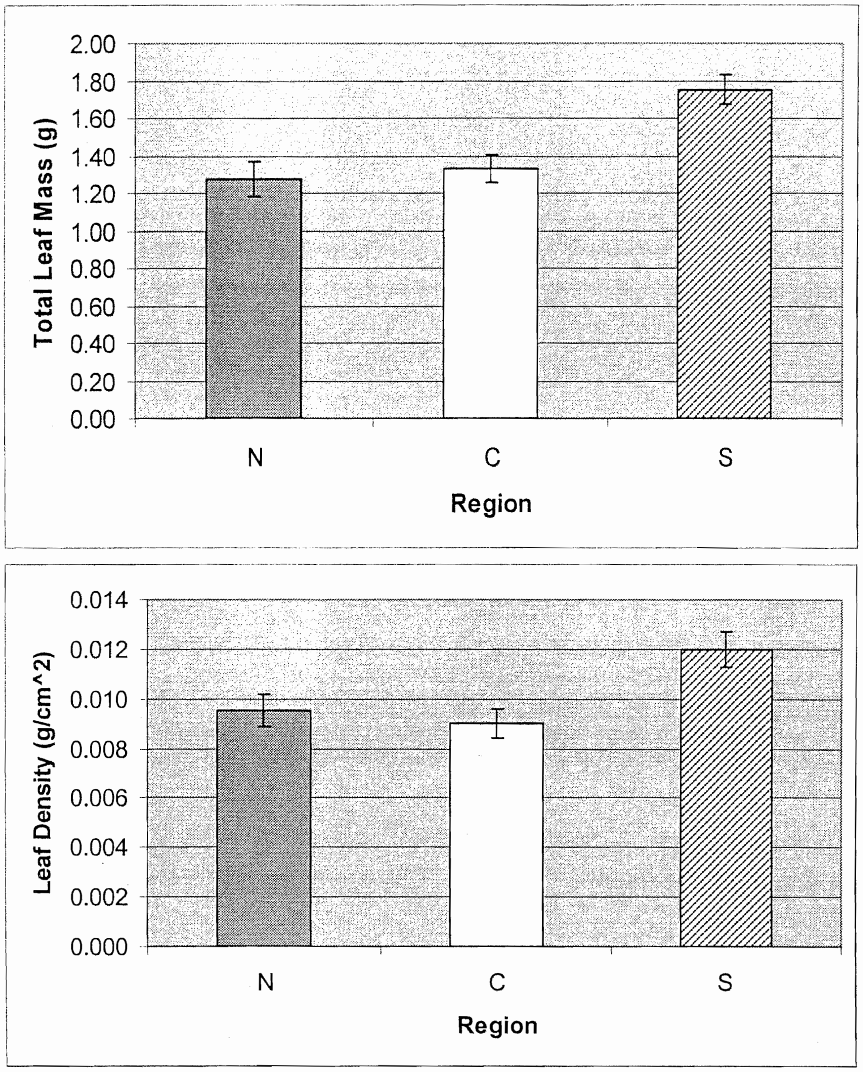

Fig 7. Characteristics of *Fraxinus pennsylvanica* which differed significantly by region: a) mean dry total leaf mass (top), b) mean dry leaf density (bottom).

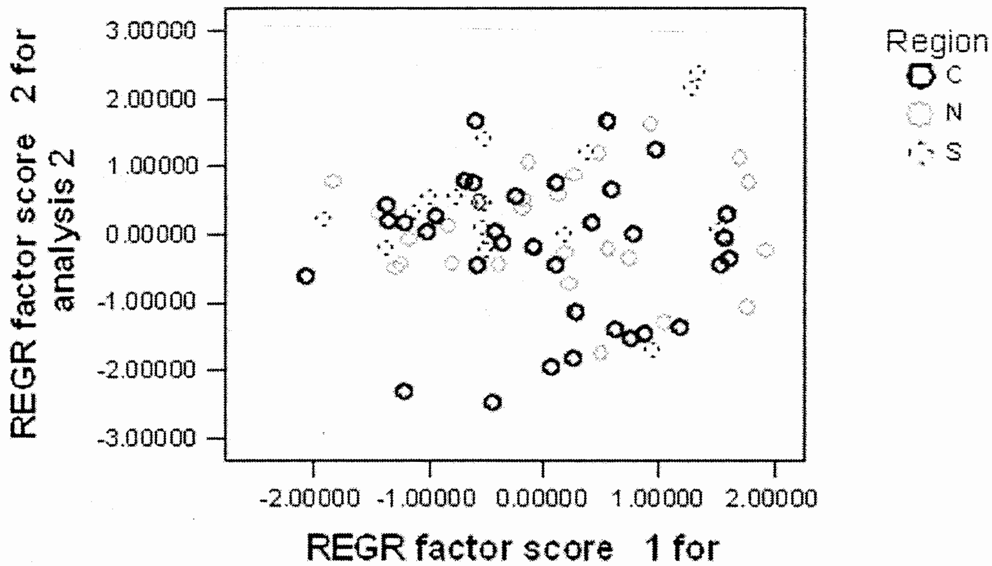

Fig. 8. Regression factor correlation graph for *Fraxinus pennsylvanica* by region.

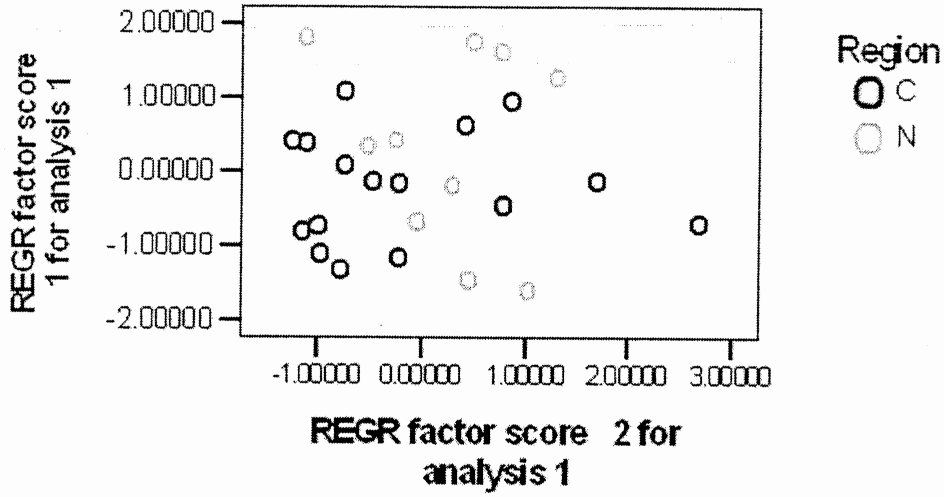

Fig. 9. Regression factor correlation graph for *Fraxinus quadrangulata* by region.

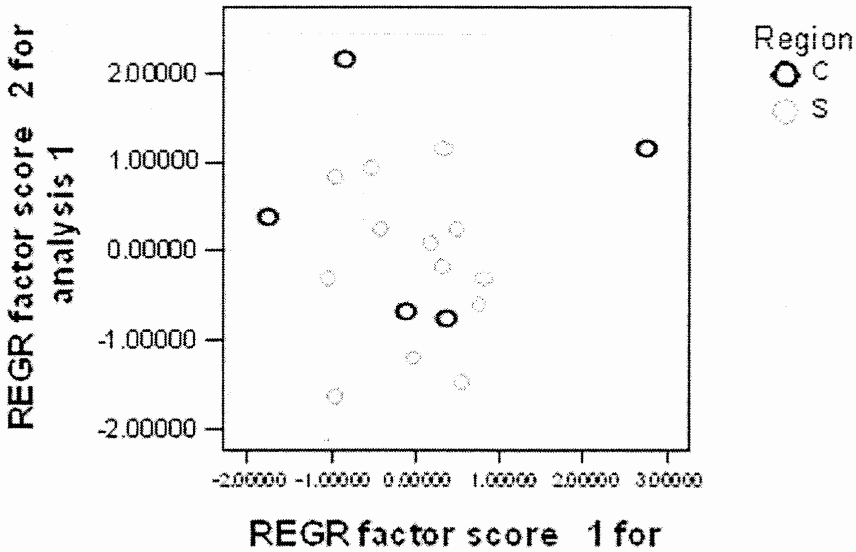

Fig. 10. Regression factor correlation graph for *Fraxinus profunda* by region.

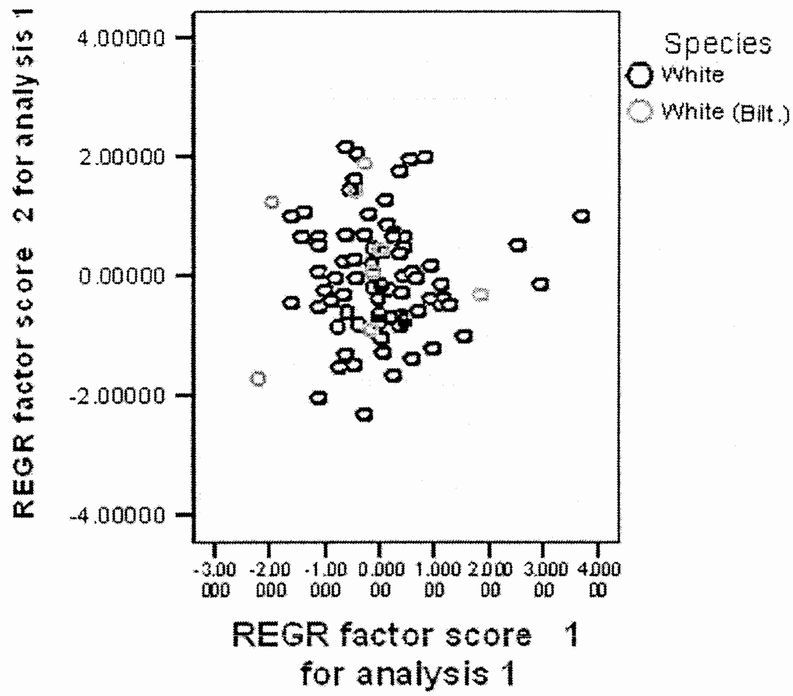

Fig. 11. Regression factor correlation graph for potential varieties within *Fraxinus americana* with individuals with anomalous leaf characteristics noted.

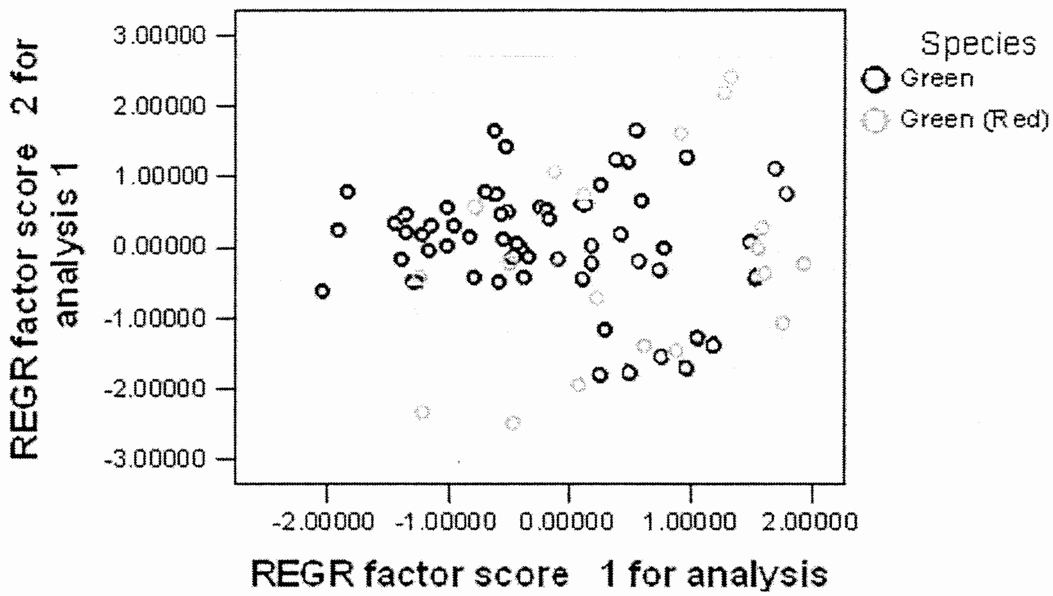

Fig. 12. Regression factor correlation graph for potential varieties within *Fraxinus pennsylvanica* with individuals with anomalous leaf characteristics noted.

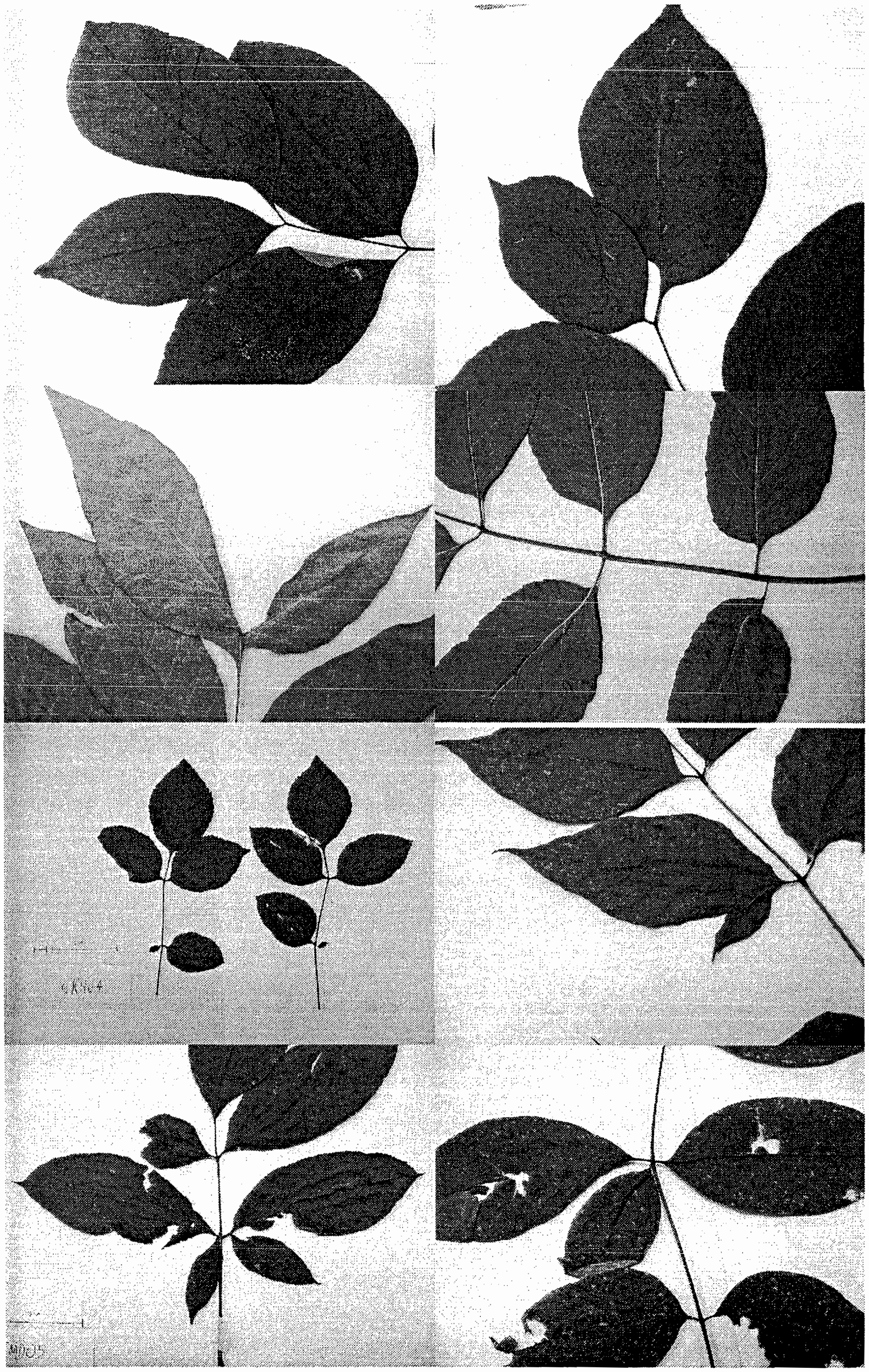

Fig 13. Examples of abnormal morphology in *Fraxinus* leaves- a) split-terminus on an ash leaf, b) split-terminus on a different ash leaf, c) white ash from Kickapoo State Park with an unusual terminal leaflet, d) staggered leaflet pairing on an ash lead, e) stunted leaflets on a blue ash's leaves from Windfall Prairie Nature Preserve, f) abnormal leaflet on a white ash from the Shawnee Hills, g) abnormality in a green ash leaf from Meredosia National Wildlife Refuge, h) abnormality in a white ash leaf from Dixon Springs State Park.

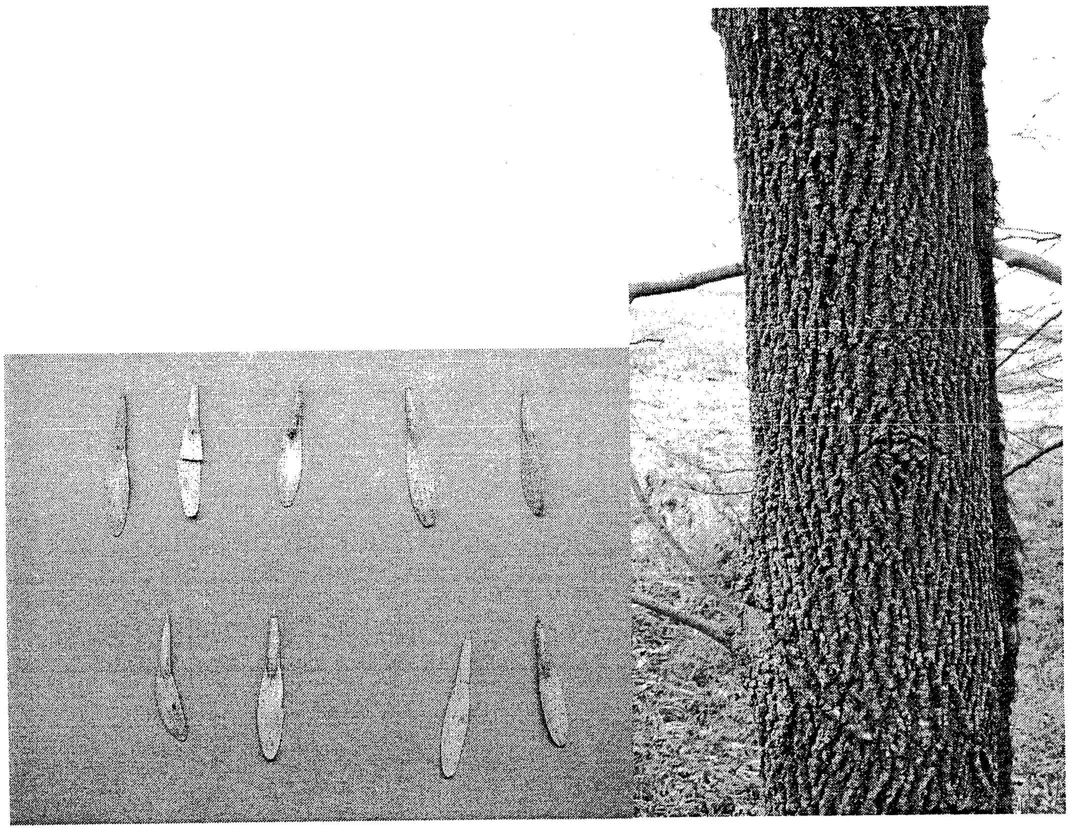

Fig 14. Images taken of CSG15: a) samaras (left), b) bark (right).

Fig 15: Comparison of the bark of CSG22 with a positively-identified white ash: a) bark of CSG22, b) bark of white ash.
Note: Identification of the white ash was confirmed by examination of leaf and twig. This ash was not a part of the study. It was located in Waterfall Glen Forest Preserve in DuPage County, IL.

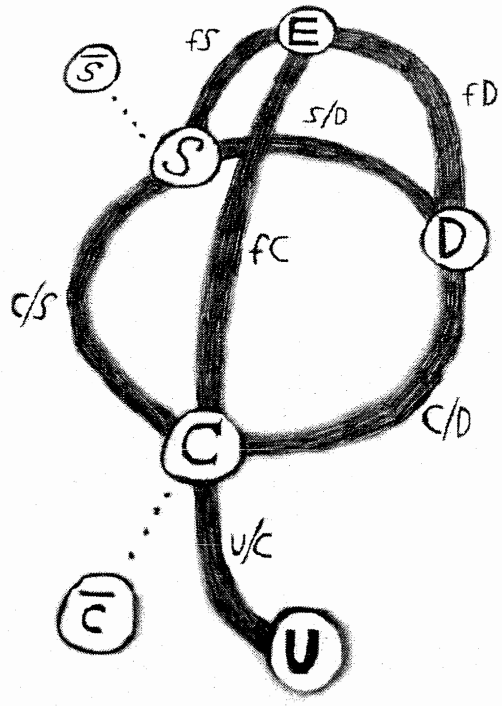

Fig. 16. Observed relations of all leaf margin types in *Fraxinus*.

Abbreviations: entire (E), crenate (C), serrate (S), dentate (D), undulate (U), fS (faintly serrate), fC (faintly crenate), fD (faintly dentate), C/S (crenate-serrate), S/D (serrate-dentate), C/D (crenate-dentate), U/C (undulate-crenate), s-bar (serrulate), c-bar (crenulate). Note: revolute margins are not depicted, but have been seen with entire, faintly serrate, faintly dentate, undulate.

Fig. 17. Base of a pumpkin ash in Momence Wetlands.

Appendix I: Taxonomic History of *Fraxinus*

Taxonomic history of *Fraxinus* species:

The genus *Fraxinus* was first named by Carolus Linnaeus in Species Plantarum, published in 1753, deriving from the Latin word for ash tree, though was first described in scientific format decades earlier, by Joseph Pitton de Tournefort in 1719 (Little Jr. 1953; Miller 1955). *Fraxinus* is a part of family Oleaceae. Only the six species found in eastern North America will be profiled here.

Fraxinus americana L., White Ash

Fraxinus americana was the first North American ash to be identified, being first identified in Species Plantarum by Carolus Linnaeus, published in 1753 (Little Jr. 1953). Its common name, white ash, likely originates from the distinctive pale lower surface on its leaves.

White ash had one additional scientific name in the literature. *Fraxinus juglandifolia* Lam. was first used by John-Baptiste de Lamarck in Encyclopédie Méthodique Botanique 2: 548. 1788 (Little Jr. 1953). D.J. Browne tried to make it a variety, *F. americana var. juglandifolia* [(Lam.)] Browne in the 1846 work, Trees of America, p. 348 (Little Jr. 1953) (Note: this appears to be the proper name, though a *F. americana var. juglandifolia* (Lam.) Rehd. exists in the literature as well).

The historic literature is littered with archaic varieties. *Fraxinus americana var. crassifolia* Sarg. first received mention in 1922 by C.S. Sargent in Manual of Trees of North America (Exclusive of Mexico) 2: 841 (Little Jr. 1953). It was supposedly found in OH, MO, and TX. There was also another which began as another species, *F. curtissi*

Vasey, first identified in 1876. It was later rendered as a variety, *F. americana var. curtissii* (Vasey) Small (sometimes seen with Sudw. as the author). It is unclear when these varieties were no longer recognized, though they received no mention in the numerous keys and guides of the early 20th century (e.g. Hough 1921, Dame and Brooks 1972, Brown 1975). One variety did receive mention in some 20th century guides though, *F. americana var. microcarpa* A. Gray. This variety was first identified by Asa Gray in 1878 in Synoptical Flora of North America 2: 75 (Little Jr. 1953). It was distinguished by its small seeds and ranged from AL to VA primarily and could be found, albeit rarely, from that range to southern Canada (Fernald 1950).

One ash originally identified as a separate species and later as a variety of white ash merits more discussion. The Biltmore ash was first identified as *Fraxinus biltmoreana* Beadle in 1898 in Botanical Gazette 25: 358 (Little Jr. 1953). It was discovered on the Biltmore forest estate of George Vanderbilt in North Carolina and named after the estate (Hough 1921). Its range extends from NJ to southern IL & MO southward to AL & GA (Fernald 1950). The similarity in how it related to *F. americana* when compared with how *F. pennsylvanica* related to *F. lanceolata* had been documented since its discovery (Beadle 1898). Biltmore was originally differentiated from white ash by the wider samaras, stouter twigs, pubescence, and clove brown buds (Beadle 1898). Eventually, it was relegated to a variety after research found pubescence can occur in the progeny of two glabrous parents (e.g. white ashes) (Wright 1944b). It was formally switched to *F. americana var. biltmoreana* (Beadle) J. Wright ex Fern. in 1947 (Little Jr. 1953). Most sources upheld the distinction, but some thought it should not receive any taxonomic rank at all. In the years following this reclassification, some researchers have speculated Biltmore ash may be a natural hybrid of *F. americana* and *F. pennsylvanica*, but evidence from microscopic foliar features and an artificially created hybrid between the two species challenge this claim (Miller 1955; Santamour Jr. 1962; Hardin and Beckmann 1982). Miller maintained Biltmore ash as a separate species based on morphological characteristics differentiating it from white ash besides pubescence, though the same characteristics she affiliates with Biltmore ash were found to be common in tetraploid white ashes, refuting her grounds for a species-level rank (Santamour Jr. 1962). Santamour maintained Biltmore ash as a separate species based on the absence of a diploid ploidy level and the presence of multiple ploidy levels and a consistent combination of characters, as well as pubescence (Santamour Jr. 1962). Pubescence among *F. americana* is very rare in the northern states and is more common in the southern states (Wright 1944b).

Fraxinus pennsylvanica Marsh., Green Ash

Note: The terms used in this section, original green ash, modern green ash, and red ash, are defined in the Profile of *Fraxinus* and its Species section on p.30.

Fraxinus pennsylvanica was first identified in 1785 by Humphry Marshall in Arbust Americanum: The American Grove, or, an Alphabetical Catalogue of Forest Trees, Shrubs, Natives of the American United States, Arranged According to the Linnaean System, p. 51 (Little Jr. 1953). It was named after Pennsylvania, the state where it was first discovered. *F. pennsylvanica* went by the name red ash from the 18th century to the late 20th century. *Fraxinus lanceolata* was first identified in 1800 by Moritz Balthasar Borkhausen in Theoretisch-praktisches Handbuch der Forstbotanik und

Forsttechnologie 1:826. (Little Jr. 1953). It was named after the lanceolate shape of its leaflets. *Fraxinus lanceolata* went by the name green ash from the turn of the 19th century to the late 20th century. Its common name originates from the reddish color on some of its branches (Hough 1921). No source explicitly states the name origin for green ash, but it most likely comes from the green color on the underside of its leaves.

Modern green ash has the most convoluted taxonomic history of the six eastern North American ashes. It was originally classified as two separate species, red ash and original green ash. The features segregating these species were the presence or absence of pubescence and often the margin, entire or crenate vs. serrate. All tree guides and taxonomic keys in the early 20th century listed red and green ash as separate species. The first effort to give *Fraxinus lanceolata* a taxonomic rank within the *F. pennsylvanica* species was in 1894 by Charles Sargent in Silva of North America 6:50. He gave it the designation *F. pennsylvanica var. lanceolata* (Borkh.) Sarg. Evidently, Sargent's interpretation was not widely accepted for decades as several tree guides (e.g. Brown 1921/1975, Hough 1921) continued to classify them as separate species until around 1950. The next effort came half a century later, with *F. lanceolata* being renamed *F. pennsylvanica var. subintegerrima* (Vahl) Fern. and *F. pennsylvanica* being renamed *F. pennsylvanica var. integerrima* (Vahl) Fern. by Merritt Fernald in Rhodora 49: 145-159 (1947). The name selected originated from an earlier classification attempt to move original green ash into white ash as a variety, *F. juglandifolia var. subintegerrima* Vahl in 1804 in Enumeratio Plantarum 1:50 by Martin Vahl. This interpretation stuck and *F. lanceolata* became an obsolete name for an entity that was now a variety, however, a second interpretation would also arise. This view, originating with Elbert Little Jr. in

1953, classified *F. lanceolata* entirely within *F. pennsylvanica* (Little Jr. 1953). These 2 interpretations would both be used over the next few decades, with Fernald's view being most dominant in the 1960s and 1970s and Little's view being the most dominant in the 1980s and 1990s based on a survey of literature focusing on modern green ash and whether they use *F. pennsylvanica* or mention *var. subintegerrima.* It was also observed when Little's interpretation was more accepted, the name red ash faded from the literature and green ash became the primary common name of the species. Probably the most clear-cut case of the abandonment of Fernald's view in favor of Little's view is with Santamour's work, best known for his research into white ash. Santamour rejected the classical distinction between original green ash and red ash as well as Fernald's effort to designate those two *var. subintegerrima* and *var. integerrima* respectively, opting to follow Little's classification of both as *F. pennsylvanica* under the common name green ash (Santamour Jr. and McArdle 1983). Some tree guides, most notably Petrides, maintain red and green ash as separate species (though noting intermediate specimens do occur); however, they are in the minority (Petrides 1972). The consolidated species inherited the scientific name of red ash, *F. pennsylvanica* and the common name of *F. lanceolata*, green ash.

The historical literature available for green/red ash is cluttered with several archaic species which have been folded into it. *Fraxinus darlingtonii* Britt. was first identified by Nathaniel Britton in Manual of the Flora of the Northern States and Canada, p. 725, published in 1901 (Little Jr. 1953). It went by the common name Darlington ash and was found in NY and PA. *Fraxinus campestris* Britt. was first identified by Nathaniel Britton in North American Trees, p. 799, published in 1908 (Little Jr. 1953). It went by the common name prairie ash and was found in MT, WY, KS, and MB. There was also *F. smallii* Britt., also identified by Nathaniel Britton in North American Trees, p. 805 (Little Jr. 1953). It was found in the South (from GA to LA) and up to MO. These species receive little mention in the literature or in tree keys. Hough mentioned *F. darlingtonii* as a "little known species" differentiated from *F. pennsylvanica* by the shape of the samara; the twigs and foliage could be glabrous or pubescent (Hough 1921). It is unclear when *F. darlingtonii* and *F. smallii* were dropped as separate species, though *F. campestris* lost its status as a species after Meuli and Shirley's work with original green ash in the Great Plains was published (Meuli and Shirley 1937).

There was also one obsolete variety, *Fraxinus pennsylvanica var. austinii* Fern., first identified in Rhodora 40: 452. 1938. It was found in New England and the eastern seaboard down to VA, parts of the Midwest (OH, IL, IA), and in Canada (from MB to NS) (Little Jr. 1953; Fernald 1950). It was described as having serrated leaf margins and long, narrow samaras with spatulate wings (Fernald 1950).

Modern green ash also had a few alternate scientific names now considered obsolete. *Fraxinus pubescens* Lam. was first used by John-Baptiste de Lamarck in Encyclopédie Méthodique Botanique 2: 548. 1788 (not 1790 as listed in Miller) (Miller 1955). It was considered an obsolete name for red ash. *Fraxinus viridis* Michx. f. was first used by Francois Michaux in Histoire des Arbres Forestiers de Amérique Septentrionale 3: 115. 1813 (Little Jr. 1953). It was considered an obsolete name for original green ash.

Fraxinus nigra Marsh., Black Ash

Fraxinus nigra was also first identified by Humphry Marshall in Arbust Americanum: The American Grove, or, an Alphabetical Catalogue of Forest Trees, Shrubs, Natives of the American United States, Arranged According to the Linnaean System, 51 (1785) (Little Jr. 1953). Its name presumably comes from the black color of its terminal and lateral buds, which are unlike the colors of any other Ash in eastern North America though similar to the bud color of *F. excelsior*.

Black ash has no documented varieties nor are their any archaic varieties found in the literature. One obsolete scientific name exists for black ash. *Fraxinus sambucifolia* Lam. was first used by John-Baptiste de Lamarck in Encyclopédie Méthodique Botanique 2: 549. 1788 (not 1786 as listed by Little) (Little Jr. 1953).

Fraxinus quadrangulata Michx., Blue Ash

Fraxinus quadrangulata was first identified by André Michaux in Flora Boreali-Americana 2: 255 (1803) (Little Jr. 1953). Its name derives from its 4-sided twigs. Blue ash is the only ash in eastern North America which has never had any alternate scientific names, obsolete varieties, or any other nomenclatural confusion in its history.

Fraxinus profunda (Bush) Bush, Pumpkin Ash

Pumpkin ash is a bit of an oddity out of the six eastern species. For the first 10 years it was known about, it underwent taxonomic flux as a variety of various species before it was finally determined to be a separate species. Pumpkin ash was first identified in 1894 by Benjamin Franklin Bush as *Fraxinus americana var. profunda* Bush in the 5th Annual Report of the Missouri Botanical Garden, p.147. He found it in the swamps of

Dunklin and New Madrid Counties in Missouri in 1893 (Bush 1894). When others looked at it, they thought it was a variety of red ash and as a result, it was re-designated *F. pennsylvanica var. profunda* Sudw. in USDA Division of Forestry Bulletin 14: 329. 1897. B.F. Bush later determined it was different from all available *F. americana* specimens and merited a separate species designation, *F. profunda*, in Garden and Forest 10: 515.1897 (Bush 1897). When Nathaniel Britton published his book in 1901, Manual of the Flora of the Northern States and Canada, 1st edition, he kept B.F. Bush's classification of pumpkin ash as a separate species and the name *F. profunda*, but in the 2nd edition, published in 1905, he renamed it *F. michauxii* Britt. out of tribute to Francois Michaux, who appeared to identify pumpkin ash 80 years earlier as *F. tomentosa* Michx. f. in Histoire des Arbres Forestiers de Amérique Septentrionale 2: 112. 1813 by Francois Michaux (Little Jr. 1953). This name was rejected because nomenclature rules give precedence to the earliest name used for a species. Conventional wisdom indicates at this point *F. tomentosa* Michx. f. became the scientific name for pumpkin ash, however Little attributes *F. tomentosa* to Fernald in 1938, but documents discussing pumpkin ash in years prior to Fernald's article use *F. profunda* as the scientific name, indicating Little's research was erroneous on this point (Hough 1921; Little Jr. 1953). It was later discovered the type specimen for *F. tomentosa* was a red ash, not a pumpkin ash, and the scientific name reverted back to *F. profunda*. Many guides and publications from the middle decades of the 20th century listed *F. tomentosa* as the species name (e.g. Fernald 1950, Miller 1955, Santamour Jr. 1962, Gleason and Cronquist 1963, Petrides 1972). All publications after 1980 referring to pumpkin ash call it *F. profunda*. The scientific name, meaning "deep", relates to the habitat in which it is generally found, swamps (Little Jr.

1953). The common name derives from the tree's swollen base which gives it stability in the inundated soil, which resembles a pumpkin and was used by locals in Arkansas long before pumpkin ash ever received a taxonomic designation (Bush 1897, Hough 1921).

One variety was briefly recognized, *Fraxinus profunda var. ashei* E.J. Palmer, first reported in 1932 in Arnold Arboretum Journal 13: 417 (Little Jr. 1953). No reference to this variety is made in any keys from the 1950s onward, so it most likely was never considered to exist or was dropped in the 1930s or 1940s.

Fraxinus caroliniana Mill., Carolina Ash

Fraxinus caroliniana was first identified by Philip Miller in Gardeners Dictionary, 8th edition, no. 6. 1768 (Little Jr. 1953). The name derives from its original location of discovery, the Carolinas. Its common name has changed over the years, with water ash being the most frequent name used across the literature (e.g. Hough 1921, Fernald 1950, Gleason and Cronquist 1963, Petrides 1972). Carolina ash was not even listed as an alternate common name in such sources. The first guide of significance to use the name Carolina ash was Elbert Little's in 1953 (Little Jr. 1953). At some point in the last few decades of the 20th century, Carolina ash became the common name, replacing water ash. Pop ash appears to be a less common name for the species as well (e.g. Fernald 1950).

Carolina ash had 2 alternate scientific names floating around from the 19th century to the early 20th century. *Fraxinus platycarpa* Michx. was first used in Flora Boreali-Americana 2: 256, published in 1803 by André Michaux (Little Jr. 1953). *F. pauciflora* Nutt. was first used in 1849 in The North American Sylva, or a Description of Forest

Trees, of the United States, Canada, and Nova Scotia, Trees Not Described in the Work of F. Andrew Michaux... 3: 61, by Thomas Nuttall (Little Jr. 1953).

Carolina ash had 3 varieties that are not recognized any longer. *Fraxinus caroliniana var. cubensis* (Griseb.) Lingelsh. was first described in Botanishe Jahrbücher für Systematik Pflanzengeschichte und Pflanzengeographie 40: 221. 1907 (Little Jr. 1953). It had been originally described as a separate species, *F. cubensis* Griseb. by August Grisebach in 1866 in Catalogue Plantarum Cubensium Exhibens Collectionem Wrightianam, p. 170. It was found in Florida and Cuba (Fernald 1950). *Fraxinus caroliniana var. oblanceolata* (M.A. Curtis) Fernald & B.G. Schub was first described as *F. platycarpa var. oblanceolata* M.A. Curtis in American Journal of Science and Arts, Ser. 2, 7: 408. 1849 and renamed by Fernald in Rhodora 50: 188. 1948 (Little Jr. 1953). It was found from Florida to southern Virginia (Fernald 1950). Both were distinguished by their seed shape. There was *F. caroliniana var. pubescens* (M.A. Curtis) Fern., originally described as *F. platycarpa var. pubescens* M.A. Curtis, identified in the same article as *var. oblanceolata* in 1849, and renamed by Fernald in Rhodora 39: 442. 1937. It was distinguished by pubescence on the leaf and twig.

Lumping and splitting in genus *Fraxinus*:

As with many other genera, it appears that the ash trees of North America have undergone periods of splitting the species into more species or more varieties or lumping the species together more and doing away with infra-species ranks. An overall assessment of the creation and dissolution of *Fraxinus* species and varieties indicates in the 19th century, ash trees currently recognized as distinct species found in the West and Southwest were classified within *F. americana* or *F. pennsylvanica*. *F. acuminata*, *F.*

berlanderiana, F. oregana, and *F. pubescens* were all originally classified as varieties of white ash before being spun off as separate species. *Fraxinus latifolia* and *F. velutina* originally were classified as subspecies of *F. pennsylvanica*. This changed by the first decade of the 20th century, where several species no longer recognized were named. *Fraxinus darlingtonii, F. campestris,* and *F. smallii* appeared, all of which were no longer recognized by the middle of the 20th century. The trend since the mid-20th century has been towards consolidation, as has been described in detail in earlier sections.

Earlier, pubescence was considered an important character in defining species. A non-pubescent population similar to *Fraxinus pennsylvanica* was classified as *F. lanceolata* and a pubescent population similar to *F. americana* was classified as *F. biltmoreana*. By the mid 20th century, there was 'conflict' over how useful pubescence was in defining species in *Fraxinus* (Wright 1944b). In studies of white and green ash, Wright found both glabrous white ash and original green ash could produce at least a small percentage of offspring with pubescence, meaning pubescence alone was not enough of a reason to divide each of those species into glabrous and pubescent varieties (Wright 1944a; Wright 1944b). After this point, original green ash was demoted to a variety and eventually failed to be recognized in any form by some.

Appendix II: Descriptions of the Morphological Characteristics of the *Fraxinus* Species (and Former Species) of Eastern North America across the 20th Century

When looking at variation and diversity within species, it is helpful to have detailed descriptions of the characteristics affiliated with the species in the literature. This gives a frame of reference for the characteristics evaluated in this study and an index to compare the observed characteristics to in order to discern if there are any characteristics not described in the literature or not described well.

There are a few points of note with the data gathered here. First, while it may appear there is an inconsistency in the species headings, whether common name or scientific name is used, it is done because some species had their scientific name or common name fluctuate across the 20th century and this section includes historical species (e.g. *Fraxinus lanceolata, F. biltmoreana*) now consolidated into other species. For example, pumpkin ash was almost always the common name for the species, but its scientific name was in nomenclatural flux between *F. profunda* and *F. tomentosa* for several years. The common names green ash and red ash have also had varying applications over the 20th century while their scientific names have been fairly consistent. Second, "-" indicates the listed source did not include a description for that morphological characteristic. It is included to show the source did not discuss that characteristic. Third, the Dame and Brooks source, dated 1901 below, was from a 1972 reprint by Dover Publications, Inc. The notes prior to the preface indicate the only changes were the deletion of a 4 page list of authorities that have become obsolete and the addition of a table of changes in nomenclature (Dame and Brooks 1972). The book was originally published in 1901. Because the changes made for the 1972 edition appeared negligible, the source is listed as 1901 to provide a chronological context for the information given in that source and to allow any changes to the species descriptions over time to be observed. The Brown source, dated 1921, was from a 1975 reprint by Dover Publications, Inc. The notes prior to the preface indicate there were slight corrections, but the work is otherwise unabridged (Brown 1975). The book was originally published in 1921. Based on the list of revisions given, the source is listed as 1921 to provide chronological context for its information as well. These works are listed properly in the Bibliography and everywhere else they are referenced in this paper.

A. *Fraxinus americana*, White Ash

Common Name: Always white ash (Dame and Brooks 1901, Hough 1921, Brown 1921, Fernald 1950, Gleason and Cronquist 1963)

Scientific Name: Always *F. americana* (Dame and Brooks 1901, Hough 1921, Brown 1921, Fernald 1950, Gleason and Cronquist 1963)

Location: Rich or moist woods, fields and pastures, near streams (Dame and Brooks 1901), rich bottomlands of the lower Ohio River basin, usually in rich slopes and bottomlands (so long as they aren't too moist) (Hough 1921), rich, moist, well-drained woods, common in rolling country in fields, pastures, along fence rows and stream courses (Brown 1921), rich upland to lowland woods (Fernald 1950), moist (not wet) woods (Gleason and Cronquist 1963)

Leaf Length: Leaves 6-12" long, leaflets 2-5" long (Dame and Brooks 1901), leaves 8-15" long (Hough 1921), leaves 8-15" long, leaflets 3-5" long (Brown 1921), - (Fernald 1950, Gleason and Cronquist 1963)

Number of Leaflets: 5-9 leaflets (Dame and Brooks 1901, Fernald 1950), 5-11 leaflets (Hough 1921, Brown 1921), 5-9 leaflets, usually 7 (Gleason and Cronquist 1963)

Leaf Appearance, Topside: Deep green, smooth above (Dame and Brooks 1901), subcoriaceous, glabrous, dark green above (Hough 1921), dark green, glabrous, somewhat lustrous (Brown 1921), glabrous (Gleason and Cronquist 1963), - (Fernald 1950)

Leaf Appearance, Underside: Pale and smooth or slightly pubescent (Dame and Brooks 1901), whitish below, glabrous or pubescent (Hough 1921), pale white and glabrous or pubescent below (Brown 1921), whitish or pale below, glabrous or sparsely pilose (Fernald 1950), paler and papillose beneath (Gleason and Cronquist 1963)

Petiolule Length: Short leaflet stalks (Dame and Brooks 1901), petiolulate leaflets (Hough 1921), slender petiolules (Fernald 1950), - (Brown 1921, Gleason and Cronquist 1963)

Leaflet Margin: Entire to somewhat toothed (Dame and Brooks 1901), entire or crenate-serrate margin (Hough 1921), obscurely crenulate-serrate (Brown 1921), entire, undulate, or serrate margin (Fernald 1950), crenulate to entire (Gleason and Cronquist 1963)

Leaflet Shape: Oblong-lanceolate or ovate (Dame and Brooks 1901, Fernald 1950), oblong-lanceolate, ovate, or obovate shape (Hough 1921), ovate, ovate-lanceolate, falcate (Brown 1921), oblong, ovate, or obovate (Gleason and Cronquist 1963)

Leaflet Base: Obtuse, rounded, occasionally acute base (Dame and Brooks 1901), rounded or cuneate at base (Hough 1921), rounded, cuneate, unequal at base (Brown 1921), - (Fernald 1950, Gleason and Cronquist 1963)

Leaflet Apex: Pointed apex (Dame and Brooks 1901), long-acuminate or acute leaflet apex (Hough 1921), attenuate apex (Brown 1921), acuminate to blunt (Fernald 1950), usually abruptly acuminate (Gleason and Cronquist 1963)

Petiole: Petiole smooth and grooved (Dame and Brooks 1901), petioles & rachises glabrous (Fernald 1950), wingless petiole (Gleason and Cronquist 1963), - (Hough 1921, Brown 1921)

Twig Appearance: Twigs grayish-green, new growth olive green (Dame and Brooks 1901), glabrous or lustrous, grayish-brown twigs, having scattered pale lenticels, semi-orbicular leaf scars (Brown 1921), smooth gray glabrous branchlets (Fernald 1950), branchlets/twigs glabrous, leaf scars commonly have concave upper margin (Gleason and Cronquist 1963), - (Hough 1921)

Terminal Bud: Short, prominent buds that are smooth, dark or pale rusty brown (Dame and Brooks 1901), rusty-brown to brownish-black terminal bud (Brown 1921), rust-colored buds (Fernald 1950), terminal bud generally blunt (Gleason and Cronquist 1963), - (Hough 1921)

B. Biltmore Ash

Dame and Brooks as well as Brown do not describe Biltmore ash.

Common Name: Always Biltmore ash (Hough 1921, Fernald 1950, Gleason and Cronquist 1963)

Scientific Name: *F. biltmoreana* (Hough 1921), *F. americana var. biltmoreana* (Fernald 1950). Treated as a species of hybrid origin or as a variety of *F. americana*, which it often occurs with (Gleason and Cronquist 1963)

Location: Rich well-drained soil of slopes, banks of streams, occasionally lowlands in the foothills of the Appalachians (Hough 1921), rich woods (Fernald 1950), - (Gleason and Cronquist 1963)

Leaf Length: Leaves 10-15" long (Hough 1921), - (Fernald 1950, Gleason and Cronquist 1963)

Number of Leaflets: 7-9 leaflets (Hough 1921), - (Fernald 1950, Gleason and Cronquist 1963)

Leaf Appearance, Topside: Dark green above (Hough 1921), - (Fernald 1950, Gleason and Cronquist 1963)

Leaf Appearance, Underside: Paler below, pubescent (esp. on the veins) (Hough 1921), strongly whitened beneath (Fernald 1950), - (Gleason and Cronquist 1963)

Petiolule Length: Long petiolulate leaflets (Hough 1921), slender petiolules (Fernald 1950), - (Gleason and Cronquist 1963)

Leaflet Margin: Entire or obscurely denticulate margin (Hough 1921), - (Fernald 1950, Gleason and Cronquist 1963)

Leaflet Shape: Ovate or ovate-oblong to lanceolate shape, falcate? (Hough 1921), - (Fernald 1950, Gleason and Cronquist 1963)

Leaflet Base: Obtuse or rounded at base (Hough 1921), - (Fernald 1950, Gleason and Cronquist 1963)

Leaflet Apex: Acuminate apex (Hough 1921), - (Fernald 1950, Gleason and Cronquist 1963)

Petiole: Velvety pubescent branchlets (Hough 1921) [no mention of petiole & rachis pubescence], branchlets, petioles, rachises velvety-tomentulose (Fernald 1950), - (Gleason and Cronquist 1963)

Twig Appearance: No mention of branchlet color (Hough 1921)

Terminal Bud: - (Hough 1921, Fernald 1950, Gleason and Cronquist 1963)

C. *Fraxinus pennsylvanica*

Common Name: Red ash (Dame and Brooks 1901, Hough 1921, Brown 1921, Fernald 1950, Gleason and Cronquist 1963), brown ash (Dame and Brooks 1901) [secondary name], river ash (Dame and Brooks 1901) [secondary name]

Scientific Name: *F. pennsylvanica* (Dame and Brooks 1901, Hough 1921, Brown 1921, Fernald 1950, Gleason and Cronquist 1963), *F. pubescens* (Dame and Brooks 1901, Brown 1921) [as synonym]

Location: Riverbanks, swampy lowlands, stream and pond margins (Dame and Brooks 1901), low, rich bottomlands, swamp margins, stream margins (Hough 1921), "swampy situations along sluggish rivers and lakes", lands usually inundate part of year, occasionally at higher elevations along stream courses (Brown 1921), low grounds and river banks (Fernald 1950), moist, often wet woods (Gleason and Cronquist 1963)

Leaf Length: Leaves 9-15" long, leaflets 3-5" long (Dame and Brooks 1901), leaves 7-12" long (Hough 1921), leaves 7-12" long, leaflets 3-5" long (Brown 1921), - (Fernald 1950, Gleason and Cronquist 1963)

Number of Leaflets: 7-9 leaflets (Dame and Brooks 1901, Hough 1921, Brown 1921), 5-9 leaflets (Fernald 1950), 5-9 leaflets, usually 7 (Gleason and Cronquist 1963)

Leaf Appearance, Topside: Light green and smooth above (Dame and Brooks 1901), lustrous, yellow-green above (Hough 1921), light yellow-green glabrous (Brown 1921), - (Fernald 1950, Gleason and Cronquist 1963)

Leaf Appearance, Underside: Paler and more/less downy beneath (Dame and Brooks 1901), paler yellow-green, tomentose below (Hough 1921), pale silky-pubescent below (Brown 1921), lower leaf surface fulvous-pubescent (Fernald 1950), densely pubescent, less often glabrous, not papillose beneath (Gleason and Cronquist 1963)

Petiolule Length: Short, grooved, downy leaflet stalks (Dame and Brooks 1901), petiolulate (Hough 1921), short petiolule (Fernald 1950), decurrent onto short petiole or subsessile (Gleason and Cronquist 1963), - (Brown 1921)

Leaflet Margin: Entire or slightly toothed (Dame and Brooks 1901), entire or obscurely serrate margin (Hough 1921), obscurely serrate (Brown 1921), entire or undulate, rarely toothed (Fernald 1950), serrate, crenulate, or subentire (Gleason and Cronquist 1963)

Leaflet Shape: Extremely variable outline: ovate, narrow-oblong, elliptical, sometimes obovate (Dame and Brooks 1901), oblong-lanceolate or ovate shape (Hough 1921, Brown 1921, Fernald 1950), oblong or elliptic (Gleason and Cronquist 1963)

Leaflet Base: Acute or rounded base (Dame and Brooks 1901), unequally cuneate at base (Hough 1921, Brown 1921), gradually narrowed at base (Fernald 1950), acute or broadly cuneate at base, often inequilateral (Gleason and Cronquist 1963)

Leaflet Apex: Acute to acuminate apex (Dame and Brooks 1901), usually acuminate apex (Hough 1921), attenuate apex (Brown 1921), taper-pointed (Fernald 1950), acuminate to blunt or acute (Gleason and Cronquist 1963)

Petiole: Short downy petiole elongated at base (Dame and Brooks 1901), petiole and rachis velvety pubescent (Hough 1921), stout, pubescent petioles (Brown 1921), petioles & rachises fulvous-pubescent (Fernald 1950), - (Gleason and Cronquist 1963)

Twig Appearance: Branches grayish, new growth greenish-gray with rusty-velvety pubescence lasting into 2nd year (Dame and Brooks 1901), velvety branchlets, can become glabrous by end of 1st season (Hough 1921), ashy-gray, pale reddish-brown, densely velvety-pubescent, conspicuous semi-circular lead scars (Brown 1921), velvety-tomentose branchlets, inner face of branches red or cinnamon color (Fernald 1950), twigs densely pubescent, leaf scars have truncate or barely concave upper margin (Gleason and Cronquist 1963)

Terminal Bud: Rounded dark reddish-brown bud, downy to some degree. Bud smaller than White Ash (Dame and Brooks 1901), ovate, acute, rusty-brown terminal bud (Brown 1921), acute terminal bud (Gleason and Cronquist 1963), - (Hough 1921, Fernald 1950)

D. *Fraxinus lanceolata*

Common Name: Green ash (Dame and Brooks 1901, Hough 1921, Brown 1921, Fernald 1950, Gleason and Cronquist 1963)

Scientific Name: *F. pennsylvanica var. lanceolata* (Dame and Brooks 1901, Brown 1921), *F. lanceolata* (Hough 1921), *F. pennsylvanica var. subintegerrima* (Fernald 1950)

F. lanceolata (Brown 1921) [considered synonym], *F. viridis* (Brown 1921) [considered synonym]

Gleason and Cronquist do not describe it. The implication with Fernald is it is identical to *F. pennsylvanica*. Dame and Brooks describe it as identical to red ash except it lacks pubescence on young twigs, leaves, or petioles, is bright green above and below, has a more acuminate apex, and "usually more distinct serratures above the center".

Location: Banks of streams (Fernald 1950), river valleys and wet woods (Dame and Brooks 1901), streambanks, lakeshores, bottomlands (Hough 1921), similar habitat to red ash, "damp situations along stream courses, lake shores and bottom-lands" (Brown 1921)

Leaf Length: Leaves 8-12" long (Hough 1921), leaves 8-12" long, leaflets 3-5" long (Brown 1921), - (Dame and Brooks 1901, Fernald 1950)

Number of Leaflets: 5-9 leaflets (Hough 1921, Brown 1921), - (Dame and Brooks 1901, Fernald 1950)

Leaf Surface, Topside: Glabrous, bright green above (Hough 1921), bright green, glabrous, somewhat lustrous (Brown 1921), green on both sides (Fernald 1950), - (Dame and Brooks 1901)

Leaf Surface, Underside: Glabrous, bright green or slightly lighter below (Hough 1921), bright green, glabrous, somewhat lustrous (Brown 1921), green on both sides (Fernald 1950), - (Dame and Brooks 1901)

Petiolule Length: Petiolulate leaflets (Hough 1921), - (Dame and Brooks 1901, Brown 1921, Fernald 1950)

Leaflet Margin: Usually sharply serrate (Hough 1921, Brown 1921), toothed (Fernald 1950), - (Dame and Brooks 1901)

Leaflet Shape: Oblong-lanceolate to ovate shape (Hough 1921), lanceolate to ovate-lanceolate (Brown 1921), - (Dame and Brooks 1901, Fernald 1950)

Leaflet Base: Cuneate at base (Hough 1921, Brown 1921), - (Dame and Brooks 1901, Fernald 1950)

Leaflet Apex: Acuminate apex (Hough 1921), attenuate apex (Brown 1921), - (Dame and Brooks 1901, Fernald 1950)

Petiole: Petiole and rachis glabrous or nearly glabrous (Hough 1921, Fernald 1950), stout, glabrous petioles (Brown 1921), - (Dame and Brooks 1901)

Twig Appearance: Not pubescent (Dame and Brooks 1901), Branchlets gray, terete, glabrous with white lenticels (Hough 1921), glabrous twig, ashy-gray, marked with lenticels, semi-circular leaf scars (Brown 1921), branchlets/twigs glabrous (Fernald 1950)

Terminal Bud: Ovate, acute, rusty-tomentose (Brown 1921), - (Dame and Brooks 1901, Hough 1921, Fernald 1950)

E. Black Ash

Common Name: Black ash (Dame and Brooks 1901, Hough 1921, Brown 1921, Fernald 1950, Gleason and Cronquist 1963), hoop ash (Dame and Brooks 1901, Hough 1921) [secondary name], swamp ash (Dame and Brooks 1901) [secondary name], basket ash (Dame and Brooks 1901) [secondary name], brown ash (Dame and Brooks 1901) [secondary name]

Scientific Name: *Fraxinus nigra* (Dame and Brooks 1901, Hough 1921, Fernald 1950, Gleason and Cronquist 1963), *F. sambucifolia* (Dame and Brooks 1901, Brown 1921) [as synonym]

Location: Wet woods, river bottoms, and swamps (Dame and Brooks 1901), low banks of streams, cold swamps, often with arbor-vitae, balsam, tamarack, silver maple, black spruce; can sometimes form a considerable portion of forest tracts (Hough 1921), low wet woods on bottomlands or sluggish rivers, cold mountain streams, deep, poorly drained swamps (Brown 1921), swamps and shores (Fernald 1950), wet woods and swamps (Gleason and Cronquist 1963)

Leaf Length: Leaves 12-15" long, leaflets 3-5" long (Dame and Brooks 1901), leaves 10-16" long (Hough 1921), leaves 10-16" long, leaflets 3-5" long (Brown 1921), - (Fernald 1950, Gleason and Cronquist 1963)

Number of Leaflets: 7-11 leaflets, frequently 9 (Dame and Brooks 1901), 7-11 leaflets (Hough 1921, Brown 1921, Fernald 1950, Gleason and Cronquist 1963)

Leaf Surface, Topside: Green and smooth both sides (Dame and Brooks 1901, Fernald 1950), glabrous, dark green above (Hough 1921, Brown 1921), - (Gleason and Cronquist 1963)

Leaf Surface, Underside: Lighter beneath, hairy on the veins (Dame and Brooks 1901), slightly paler dark green below, glabrous with rufous hairs along the midrib (Hough 1921, Brown 1921), green and smooth both sides, when young, rusty beneath (Fernald 1950), - (Gleason and Cronquist 1963)

Petiolule Length: Sessile (Dame and Brooks 1901, Brown 1921, Gleason and Cronquist 1963), sessile leaflets, but terminal leaflet petiolulate (Hough 1921), sessile lateral leaflets (Fernald 1950)

Leaflet Margin: Serrate (Dame and Brooks 1901, Fernald 1950), sharply serrate margin (Hough 1921), remotely serrate (Brown 1921), conspicuously serrate (Gleason and Cronquist 1963)

Leaflet Shape: Variable outline: oblong-lanceolate usually (Dame and Brooks 1901), oblong to lanceolate shape (Hough 1921, Fernald 1950, Gleason and Cronquist 1963), oblong-lanceolate (Brown 1921)

Leaflet Base: Obtuse or rounded at base (Dame and Brooks 1901, Fernald 1950), rounded or cuneate and unequal at leaflet base (Hough 1921, Brown 1921), broadly acute at base (Gleason and Cronquist 1963)

Leaflet Apex: Acuminate apex (Dame and Brooks 1901), long-acuminate at leaflet apex (Hough 1921), acute apex (Brown 1921), tapering to point (Fernald 1950), - (Gleason and Cronquist 1963)

Petiole: Petioles stout and pale (Brown 1921), - (Dame and Brooks 1901, Hough 1921, Fernald 1950, Gleason and Cronquist 1963)

Twig Appearance: Olive-green twigs, stout, flattened at apex, with small black vertical dots (Dame and Brooks 1901), terete, glabrous branchlets/twigs (Fernald 1950, Gleason and Cronquist 1963), - (Brown 1921, Hough 1921)

Terminal Bud: Rounded, pointed, very dark (Dame and Brooks 1901), - (Hough 1921, Brown 1921, Fernald 1950, Gleason and Cronquist 1963)

F. *Fraxinus quadrangulata*, Blue Ash

Note: Dame and Brooks in addition to Brown do not include blue ash in their works as their works were limited to New England trees and blue ash is not found in that region.

Common Name: Always blue ash (Hough 1921, Fernald 1950, Gleason and Cronquist 1963)

Scientific Name: Always *F. quadrangulata* (Hough 1921, Fernald 1950, Gleason and Cronquist 1963)

Location: Dry limestone ridges and uplands, usually in association with white ash, Texas oak, chinquapin oak, other oaks, woolly bumelia, redbud, many hickories, etc (Hough 1921), dry or moist rich woods (Fernald 1950), moist woods (Gleason and Cronquist 1963)

Leaf Length: Leaves 8-12" long (Hough 1921), - (Fernald 1950, Gleason and Cronquist 1963)

Number of Leaflets: 7-9 leaflets (Hough 1921), 7-11 leaflets (Fernald 1950, Gleason and Cronquist 1963)

Leaf Appearance, Topside: Glabrous, dark yellow-green above (Hough 1921), green both sides (Fernald 1950), - (Gleason and Cronquist 1963)

Leaf Appearance, Underside: Paler dark yellow-green, glabrous below, hairy-tufted in the axils of the veins beneath (Hough 1921), green both sides (Fernald 1950), - (Gleason and Cronquist 1963)

Petiolule Length: Short petiolulate leaflets (Hough 1921), short stalked (Fernald 1950), - (Gleason and Cronquist 1963)

Leaflet Margin: Closely serrate margin (Hough 1921), sharply serrate (Fernald 1950), - (Gleason and Cronquist 1963)

Leaflet Shape: Ovate-oblong to lanceolate shape (Hough 1921, Fernald 1950), commonly lanceolate (Gleason and Cronquist 1963)

Leaflet Base: Rounded or obtuse at base (Hough 1921), broadly cuneate to subrotund, usually inequilateral at base (Gleason and Cronquist 1963), - (Fernald 1950)

Leaflet Apex: Long-acuminate at leaflet apex (Hough 1921, Gleason and Cronquist 1963), pointed (Fernald 1950)

Petiole: No mention of petiole and rachis appearance (Hough 1921, Fernald 1950, Gleason and Cronquist 1963)

Twig Appearance: 4-angled twigs (Hough 1921), branchlets square and glabrous (Fernald 1950), sharply 4-angled twigs or narrowly 4-winged twigs (Gleason and Cronquist 1963)

Terminal Bud: - (Hough 1921, Fernald 1950, Gleason and Cronquist 1963)

G. Pumpkin Ash

Note: Dame and Brooks as well as Brown do not include pumpkin ash in their works as their works were limited to New England trees and pumpkin ash is not found in that region.

Common Name: Pumpkin ash (Hough 1921, Fernald 1950, Gleason and Cronquist 1963), red ash (Fernald 1950)

Scientific Name: *F. profunda* (Hough 1921), *F. tomentosa* (Fernald 1950, Gleason and Cronquist 1963)

Location: Swampy bottomlands of AR and MO as well as the Apalachicola River valley in FL; deep swamps, slough banks, streambanks, areas inundated for much of the year. Found with bald cypress, cotton gum, water gum, planer-tree, swamp poplar, water locust (Hough 1921), inundated swamps and bottoms (Fernald 1950), swamps and wet woods (Gleason and Cronquist 1963)

Leaf Length: Leaves 9-18" long (Hough 1921), Leaflets 0.9- 2.0dm long (Fernald 1950), - (Gleason and Cronquist 1963)

Number of Leaflets: 7-9 leaflets (Hough 1921, Fernald 1950), 5-9 leaflets, usually 7 (Gleason and Cronquist 1963)

Leaf Appearance, Topside: Dark green, nearly glabrous above (Hough 1921), subcoriaceous, lustrous above (Fernald 1950), - (Gleason and Cronquist 1963)

Leaf Appearance, Underside: Pubescent below, no mention of color (Hough 1921), rufescent-tomentulose to glabrate (Fernald 1950), hairy beneath (Gleason and Cronquist 1963)

Petiolule Length: slender petiolules (Fernald 1950), - (Hough 1921, Gleason and Cronquist 1963)

Leaflet Margin: Entire or almost entire margin (Hough 1921, Gleason and Cronquist 1963), entire or undulate (Fernald 1950)

Leaflet Shape: Lanceolate or ovate-lanceolate shape, usually inequilateral (Hough 1921), elliptic to ovate-lanceolate (Fernald 1950), lanceolate, oblong, or elliptic (Gleason and Cronquist 1963)

Leaflet Base: Rounded or cuneate base (Hough 1921), broadly acute to rounded, often inequilateral at base (Gleason and Cronquist 1963), - (Fernald 1950)

Leaflet Apex: Acuminate apex (Hough 1921), long-acuminate (Fernald 1950, Gleason and Cronquist 1963)

Petiole: Petiole is inferred to be pubescent (Hough 1921), petioles and rachises velvety-tomentulose (Fernald 1950), hairy twigs (Gleason and Cronquist 1963)

Twig Appearance: Branchlets and all new growth densely pubescent (Hough 1921), branchlets velvety-tomentulose (Fernald 1950), - (Gleason and Cronquist 1963)

Terminal Bud: - (Hough 1921, Fernald 1950, Gleason and Cronquist 1963)

H. *Fraxinus caroliniana*

Note: Dame and Brooks in addition to Brown do not include Carolina ash in their works as their works were limited to New England trees and Carolina ash is not found in that region.

Common Name: Water ash (Hough 1921, Fernald 1950, Gleason and Cronquist 1963), pop ash (Fernald 1950)

Scientific Name: Always *F. caroliniana*, at least in the 20^{th} century (Hough 1921, Fernald 1950, Gleason and Cronquist 1963)

Location: Deep swamps, streambanks inundated much of the year, usually with bald cypress, cotton gum, water gum, overcup oak, laurel oak, water oak, red maple, swamp bay, white cedar (Hough 1921), inundated swamps, bottomlands, wet shores (Fernald 1950), swamps and bottomlands on the coastal plain (Gleason and Cronquist 1963)

Leaf Length: Leaves 7-12" long (Hough 1921), Leaflets 4-12cm long (Fernald 1950), - (Gleason and Cronquist 1963)

Number of Leaflets: 5-7 leaflets (Hough 1921, Fernald 1950, Gleason and Cronquist 1963)

Leaf Appearance, Topside: Dark green above (Hough 1921), - (Fernald 1950, Gleason and Cronquist 1963)

Leaf Appearance, Underside: Paler green below, glabrous or tomentose (Hough 1921), green beneath (Fernald 1950), - (Gleason and Cronquist 1963)

Petiolule Length: Elongated petioles, remote long petiolulate leaflets (Hough 1921), slender petiolules (Fernald 1950), petiolulate (Gleason and Cronquist 1963)

Leaflet Margin: Closely serrate or entire margin (Hough 1921), serrate-dentate or entire (Fernald 1950), - (Gleason and Cronquist 1963)

Leaflet Shape: Ovate to ovate-lanceolate shape (Hough 1921, Fernald 1950), oblong or roundish (Fernald 1950), lanceolate to elliptic (Gleason and Cronquist 1963)

Leaflet Base: Cuneate or rounded leaflet base (Hough 1921), acute at base (Fernald 1950), - (Gleason and Cronquist 1963)

Leaflet Apex: Acute or acuminate apex (Hough 1921), acute or obtuse at apex (Fernald 1950), abruptly acuminate to obtuse (Gleason and Cronquist 1963)

Petiole: No mention of petiole & rachis appearance (Hough 1921, Gleason and Cronquist 1963), petioles terete (Fernald 1950)

Twig Appearance: No mention of branchlet color or appearance (Hough 1921), branchlets terete (Fernald 1950), branchlets terete or nearly terete, glabrous or thinly hairy (Gleason and Cronquist 1963)

Terminal Bud: - (Hough 1921, Fernald 1950, Gleason and Cronquist 1963)

APPENDIX III: Site Information

The following are descriptions of the sites visited and the general composition of their forest based on first-hand observations during collection.

Information about the composition of the forests along the trails came from a firsthand description of the trail made while searching for ashes. Information about the geography of the parks or their history comes from the pamphlets put out by the Illinois Department of Natural Resources containing the park's map and information about the park.

Apple River Canyon State Park:

Location: Jo Daviess County

Natural Division: Wisconsin Driftless Section (1)

Apple River Canyon State Park is consists of upland forest, rocky bluffs, and some lowland forest located adjacent to the Apple River. It is established on land where a town no longer in existence, Millville, once stood. Established as a sawmill town, it declined over the latter half of the 19^{th} century until devastated by a flood in 1892. The town was not rebuilt and the land was abandoned.

The trail taken was the Pine Ridge Trail, located on the south side of the Apple River on a large hill. The main trail runs in a giant circle from the parking lot to the roadside with a few unmarked side trails running off at various points.

The Pine Ridge Trail is an upland site dominated by oaks and pines. A few sugar maples are also found at the site.

Cook County Forest Preserve: Palos Division:

Location: Cook County

Natural Division: Northeastern Morainal Division- Morainal Section (3a)

The Palos and Sag Valley Divisions of the Cook County Forest Preserve are an expansive forested area consisting of a wide range of habitats- upland forest, lowland forest, wetland, and grassland. The land was never developed, being set aside in the early 20^{th} century to preserve remaining forestland in Cook County. For simplicity, the whole area is called Palos Division.

Trees were sampled from three locations primarily: a network of trails near Bullfrog Lake, a network of trails near Horseshoe Lake, and trees lining the north shore of Saganashkee Slough. One tree was sampled from Pulaski Woods.

Bullfrog Lake is a system of trails through an upland forest nearby a lake which is surrounded by a dense thicket. The upland forest slightly further back from the thicket is dominated by oaks and hickories, with many elms and white ashes also present. Sugar maples are difficult to find there.

Horsetail Lake is a system of trails through an upland forest. It is strongly dominated by oaks, with a large percentage of the canopy being oak. A few elms and hophornbeams are also found in this forest. A few sugar maples can be found in the understory though. A rough visual estimate of the canopy finds about 95% of the canopy trees are oaks.

Pulaski Forest is an upland forest which is dominated by oaks. In the western portion it lacks trails.

Saganashkee Slough is a forest surrounding a lake. It is dominated by silver maple, green ash, and willows. Oaks do not have a presence outside of the outskirts of the location. Some cottonwoods are found here. It is located immediately by the Cal-Sag Channel.

Lowden State Park:

Location: Ogle County

Natural Division: Rock River Hill Country Division- Freeport Section (2a)

Lowden is a state park situated atop a bluff running along the east side of the Rock River. It was evidently never developed into farmland and was used as an artists' colony from the turn of the 20th century to the mid-20th century due to its natural scenery and scenic view from atop the bluff.

The trail taken was the Black Hawk Trail, which runs north-south along the Rock River with some paths being located atop the bluff, near one of the park's roads and some paths run right along the shoreline of the river. The trail is easily located by the giant Black Hawk statue and the lengthy flight of stairs down the bluff to the river's edge.

The Blackhawk Trail is dominated by sugar maples, though oaks are still common. There are many blue ashes here, particularly on the steep slopes. A few elms are also present.

Lyon Forest Preserve:

Location: Kendall County

Natural Division: Grand Prairie Division- Grand Prairie Section (4a)

Lyon Forest Preserve contains a wooded upland section, a prairie section, and lowland seep section. It is located near the Fox River, with the lowland portion closer to the river and the upland portion farther from the river.

Trees were sampled from the lowland section, near Lyon Fen and Hepatica Hill. The section trees were collected from is where a few small wooden bridges cross the stream running through the preserve.

The forest is dominated by elms. There are also many sugar maples, but they don't dominate like they do in other forests; they are merely common here. There are some hickories and only a few oaks. Along Van Emmon Road, the road from which Lyon Forest Preserve is accessible, which runs alongside the Fox River, there is a significant quantity of sugar maples.

<u>Moraine Hills State Park</u>:

Location: McHenry County

Natural Division: Northeastern Morainal Division- Morainal Section (3a)

Moraine Hills State Park is an area of land filled with forest, wetlands, and grasslands. It contains a few natural lakes and has the Fox River run along part of the park.

Trees were sampled from the Fox River Loop, a trail system located near the Fox River away from the main body of the park.

The Fox River Loop trail in Moraine Hills is half-forest, half-prairie. The forested half is closer to the Fox River and the prairie portion is further from the river. The forested portion generally is filled with boxelders and elms, with some silver maples and pines as well. A small portion of the forest which exists further in, by the prairie section was dominated by oaks.

Rock Cut State Park:

Location: Winnebago County

Natural Division: Northeastern Morainal Division- Winnebago Section (3d)

Rock Cut State Park is an area filled with woodland and prairie. It has two lakes within its borders, both artificial.

Trees were sampled along a trail by Olson Lake, which consists of a small area of trees, a thicket, and a prairie between the Interstate 90 and private land. It is the only part of the park east of I-90. No ash trees were found on the trails in the northern part of the park, where the main entrance is.

Olson Lake has some forest located along part of its shore and tall grasses along other parts of its shore, with grassland sections located past the edge of the forest opposite from the manicured, recreational portion of the site. The forests here are dominated by oaks and some other tree genera which were not identified at the time (not hickory, ash, maple, or willow).

Chautauqua National Wildlife Refuge:

Location: Mason County

Natural Division: Upper Mississippi River and Illinois River Bottomlands Division- Illinois River Section (5a)

Chautauqua National Wildlife Refuge is a natural area devoted to creating/restoring a large wetland, Lake Chautauqua to draw back wildlife. The refuge also contains woodland and seeps. It contains upland and lowland sections. It is located just east of the Illinois River.

The trees were sampled from a trail which starts just across from the refuge's main office. Some trees were accessible from on the trail while others were collected down in the lowlands off the trail between the edge of the hill on which the trail runs and the tall grasses bordering the marsh.

The upland portion is dominated by various oaks and hickories and has a higher amount of sassafras trees than other sites. The lowland portion is dominated by various willows and silver maple.

Fox Ridge State Park

Location: Coles County

Natural Division: Grand Prairie Division- Grand Prairie Section (4a)

Fox Ridge is a forest with upland and lowland sections containing a lake and sharing a border with the Embarras River. The lowland portion commonly had oaks with some silver maples and ash trees.

The trail samples were collected from is the No-Name Trail located by the south canoe access and Riverview Trail.

The trees along the trail are primarily oaks, with some hickories and silver maples present. There are few sugar maples along the river's edge.

Kennekuk Cove County Park + Windfall Prairie Nature Preserve:

Location: Vermilion County

Natural Division: Wabash Border Division- Vermilion River Section (10c)

Kennekuk Cove and Windfall Prairie are located close to the Middle Fork of the Vermilion River and near Kickapoo State Park. Kennekuk Cove County Park is dominated by Lake Mingo, an artificial lake, and is generally a forested upland site which extends between farmland and the steep bluffs along the eastern side of the Middle Fork. Windfall Prairie is an assemblage of various habitats, prairie, upland forest, lowland forest, and seep. It has a slope going down to the river that varies from being a steep hillside to a near-vertical cliff. It has prairie located upland, near farmland and on a steep hillside heading down to the Middle Fork. Forest is located upland, lowland, and on the steep hillside. The seep is located in some low-lying lands near the river. In the sandy, bare portions of the steep hillside, water can easily be seen trickling out and down the slope.

Although Horseshoe Bottoms was the site intended to be visited, due to misinterpretations regarding the nature preserve's location, the seep visited was actually the seep within the Windfall Prairie Nature Preserve (located downstream from Horseshoe Bottoms). This was determined by overlaying the GPS coordinates of the ash trees sampled on a topographic map available from the IDNR website by using an analogous map from the Topozone website, which allows for precise GPS coordinates to be obtained on a topographic map. The description of the terrain (the grassy hills, the lowlands by the river, the slopes and ravines) visited matches the IDNR website's description of Windfall Prairie (e.g. sugar maple, oak, hickory, prairie dock being present).

Trees were sampled from Kennekuk Cove on the trail system running from the western shores of Lake Mingo, along the spillway, into the woods which leads to Windfall Prairie. Trees were sampled from Windfall Prairie near its southern entrance (marked by barbed wire and a 4ft. high wooden entrance) along the bluff overlooking the river. One tree was sampled from a seep near the river and further north than the other samples.

Kennekuk Cove's forest has many oaks and sugar maples and some elms and hickories. In Windfall Prairie's associated forests, sugar maples dominate the upland portion and the wooded sections of the slopes. Blue ash is very common in the understory along the slopes and in some sections of the upland portion. Silver maple and green ash are common in the lowlands and along the river. Oaks are also present here, though in a lesser quantity than maples. Additionally, sugar maples dominate the wooded portions of southern Vermilion County which can be found further downstream of the river. This can easily be discerned during autumn.

Kickapoo State Park:

Location: Vermilion County

Natural Division: Wabash Border Division- Vermilion River Section (10c)

Kickapoo State Park is located in a hilly, forested area with several lakes and rocky outcrops. It is generally upland forest. It is used as a major recreation center in summer and fall, more so than all other sites visited for this thesis. It isn't known if all of the lakes are natural or if some are artificial, though at least one is natural based on its steep shoreline (artificial lakes tend to have a high portion of its shoreline low-lying, easily accessible land since the lakes are mostly created for recreational purposes).

The trees were sampled around a trail system near High Lake and another lake. Most were on the main trail system, but a few were on a small gravel path to a muck-filled pond (No Name Pond) and some were on a small side trail.

The forest around High Lake is dominated by oaks and sugar maples, with neither seeming more prevalent than the other.

Meredosia National Wildlife Refuge:

Location: Morgan County

Natural Division: Upper Mississippi River and Illinois River Bottomlands Division-Illinois River Section (5a)

Meredosia National Wildlife Refuge is an area dominated by wetlands and forests near the Illinois River. The wetlands are located by Meredosia Lake.

Samples were collected from Toe Head Trail, which is located some distance away from the main body of the refuge. It is a narrow strip of trees located on a narrow hill bordered by a creek on one side and farm fields on the other side. The trail is merely a wide grassy strip which vehicles are used to drive down.

Toe Head Trail is filled with willows and a few other trees not identified at the time were commonly located there.

Momence Wetlands Nature Preserve:

Location: Kankakee County

Natural Division: Grand Prairie Division- Kankakee Sand Area Section (4e)

Momence Wetlands Nature Preserve consists of lowland forest located near the Kankakee River. It lacks any trails through it. It was the most difficult site to navigate through, taking the longest time to cover any distance of all the sites (seep portions of Windfall Prairie excluded).

The portion where trees were sampled was on the north side, closer to the northern edge, located near farmland than to the southern edge, along the river. It was accessible from the Blackhawk Trail road.

The section where samples were collected is dominated by oaks and silver maples with a strong presence of elms. Pumpkin ash and green ash (red) is common in the understory.

Sugar Grove Nature Preserve:

Location: McLean County

Natural Division: Grand Prairie Division- Grand Prairie Section (4a)

Sugar Grove Nature Preserve is a forest with little variance in elevation. It seems to be a lowland site and not an upland site based on how moist the soil is relative to upland sites in dry weather. It also contains a restored prairie section. It is located near Historic US Route 66 and Interstate 55. Historically, there was maple syrup production in the area.

Trees were sampled on the trails through the forest north of the prairie restoration which surrounds the main office. Most trees were located on the paths while a few were located off the trail in the woods between the trail and the road into the nature preserve.

The forest is overwhelmingly dominated by sugar maples. Blue ash and pawpaws are common understory trees. A few oaks do exist in the forest though.

Crab Orchard National Wildlife Refuge:

Location: Williamson County

Natural Division: Shawnee Hills Division- Greater Shawnee Hills Section (13a)

Crab Orchard National Wildlife Refuge is an extensive preserve of land containing forests, lakes, and wetlands. The section of the park where samples were collected, Devil's Kitchen, is dominated by Devil's Kitchen Lake, an artificial lake created by impounding waters from the Big Muddy River. The area was only cleared for farmland in the early 19^{th} century. The unsuitability of the terrain to agriculture led to the land being abandoned not long after it was cleared.

The trail most samples were collected from was Rocky Bluff Trail, located in the Devil's Kitchen area of the preserve. The trail is mostly upland forest, filled with rocky bluffs and descending hills, and a small portion lining Devil's Kitchen Lake is lowland. Two trees were sampled along the roadside in the Devil's Kitchen area of the preserve.

The forest along the Rocky Bluff Trail of Crab Orchard is strongly dominated by oaks. Very few sugar maples were present, though a few other types of maples could be found through the woods.

Dixon Springs State Park:

Location: Pope County

Natural Division: Coastal Plain Division- Bottomlands Section (14b)

Dixon Springs State Park is a hilly, rocky, upland forest which was once the site of a small town, Dixon Springs, due to the presence of springs in the area.

The trail taken was the Oak Tree Trail. Trees were sampled from where the trail meets up with Pine Tree Trail at the western edge to the point where the trail begins to turn north at the far eastern side. A few trees were collected from the Ghost Dance Trail, which runs near a small creek.

The forest of Dixon Springs State Park was dominated by oaks, pines, and one other conifer which was not identified at the time. Very few sugar maples were present.

Eldon Hazlet State Park:

Location: Clinton County

Natural Division: Southern Till Plain Division- Effingham Plain Section (9a)

This state park is situated along the west side of Carlyle Lake. It contains forest and prairie. Carlyle Lake is a creation resulting from an artificial impoundment of the Kaskaskia River. It was created in 1967. It is the largest artificial lake in Illinois and the largest lake in the state besides Lake Michigan.

The trail taken was the Cherokee Trail, Loops 2 & 3. These trails run from inland to along the lakeshore.

The Cherokee Trail is dominated by oaks with a sizeable presence of hickories and elms. Some walnuts and sycamores are found there as well. Very few maples were present.

Red Hills State Park:

Location: Lawrence County

Natural Division: Wabash Border Division- Bottomlands Section (10a)

Red Hills State Park is an extensively forested piece of land with woodland, hills, springs, and a lake. It is the highest point of land found between St. Louis and Cincinnati. It is an upland forest.

Trees were collected from two locations in the park. Some were collected along the Valley Springs Trail, located in the half of the park north of US Route 50. Some were collected along the southeastern shore of the Red Hills Lake, from trees lining the road or trees found between the road and the lake. The lake is artificial, having been created by damming a tributary of the Embarras River in 1953.

The forest along the Valley Springs Trail was a mix of sugar maples and oaks at the canopy level. The entire understory, though, was sugar maple. A few elms, hickories, and sycamores were present as well. In autumn, the dominance is strikingly apparent as the entire forest looks yellow, with only a few patches of red in the canopy, indicating oaks.

Wayne Fitzgerrell State Park:

Location: Franklin County

Natural Division: Southern Till Plain Division- Mt. Vernon Hill Country Section (9b)

This state park is situated along the Southeast side of Rend Lake on a small peninsula. It is an area filled with forests and grasslands. Rend Lake is an artificial reservoir created by damming the Big Muddy River in 1970. Much of the land comprising the park was farmed. Small patches of original woodland still exist in the park.

No specific trail was taken. Samples were collected from along a hiking/biking trail in the segment of that trail that runs through a large loop of a road, the road that leads to Lake View, Shady Rest, and several other points. It is the only road that looks like a giant hand, with a single road connected the road network to the main north-south road through the park and a large loop with five roads branching off it at various points. The trail taken runs through that loop.

The area where trees were sampled is a mix of oak and maple. Most of the maples are silver maple and one other type of maple which wasn't identified. There were a few sugar maples there.

Additionally, three trees were sampled from a private property in the forests of the Shawnee Hills of southern Illinois. This property was located in Jackson County in the Shawnee Hills Natural Division- Greater Shawnee Hills Section.

Appendix IV: Abnormalities of *Fraxinus* Morphology

Anomalies Observed in *Fraxinus*:

Fraxinus appears to be particularly prone to develop abnormalities in its leaves and twigs at a fairly high rate. The literature contains many references to abnormal features on trees or even trees that are difficult to identify to species and in compiling data for this project, many abnormalities were observed and several trees were hard to identify.

Historic Observations of Leaf Abnormalities:

Significant abnormalities in *Fraxinus* leaf formation have been noted occasionally and are not considered uncommon (Miller 1955). Leaves collected from a white ash in Ohio in 1896 showed a cleft leaflet tip on several leaflets and one panduriform leaflet (Foerste 1897). Leaves from a green ash of unknown location had a pair of leaflets substitute in for a single leaflet on the 1st and 2nd nodes (Halsted 1888). This included all manner of combinations: one leaflet on one side with a pair of leaflets on the opposite side and a pair of leaflets on both sides. Another leaf had an entire leaf emerging from one side of the 1st node where a single leaflet should be (Halsted 1888). Reported observations on this matter note trees with opposite leaves rarely have only one leaf show an abnormality; both leaves across from one another tend to show the same abnormality (Foerste 1897). This generalization does not seem to apply to *Fraxinus*, as Halsted's oddities included some leaves where only one in a pair of leaves displayed an anomaly and many observed abnormalities in this study were not seen in both pairs of leaves. The only abnormality observed in opposite pairs of leaves were on CKH04, where one had a stunted leaflet at L1 and the other leaf had a stunted leaflet at R1 and with SDS16, where two leaves had 3 leaflets at the 2^{nd} node.

Some extreme oddities have also been observed. Wright found a green ash originally from Maine which produced mostly regular offspring and 7 seedlings that he called "hardly recognizable as belonging to the genus *Farxinus*" (sic) (Wright 1944a). The seedling height was only 5" after 2 years of growing, nodes were located very close together, leaves were simple and only 1-3" long and 0.25-0.50" wide, with wavy irregular outlines (instead of serrate margins like the normal offspring). Compound leaves only developed after 2 years and only had 3 leaflets. Three leaves per node has been observed with *Fraxinus* previously, though it was only noted as being found on shoots coming up from the stump of a cut down ash tree (Foerste 1897).

In examining ash leaves from all over Illinois as well as the hybrids created by Sylvia Taylor in Michigan in 1968 and 1970, the only time leaflets with very irregular, wavy outlines was observed was with Taylor's hybrids. It is possible Wright's odd seedlings were green-white hybrids though Taylor's hybrids managed to develop into regular-sized trees. Another possibility might be a triploid (or haploid?) individual, either a green ash or a hybrid, which happened to be viable. Triploid and pentaploid embryos, generally non-viable, were mentioned in Black and Beckmann 1983 and there is a report of pentaploids that grow to normal heights and have nothing apparently odd about them, though there is a surprising lack of follow-up on this significant find (Clausen et al 1981).

Anomalies Regarding the Leaf Terminus:

The most common abnormality with the terminus involves a malformed terminal leaflet developing in place of a lateral leaflet. 80 leaves belonging to 66 trees had numerical oddities relating to their uppermost pair of leaflets and the terminal leaflet. 29 leaves had a normal uppermost pair of leaflets but had no terminal leaflet. 51 had an abnormality during leaflet differentiation resulting in a terminal leaflet replacing one of the 2 lateral leaflets in the uppermost pair. Such leaflets are abnormally wider than the lateral leaflet across from them and they resemble a terminal leaflet except that they are asymmetric towards the node. 22 of these misplaced terminal leaflets replaced the left lateral leaflet while 29 replaced the right lateral leaflet. Examining which node number the node is with this abnormality, 3 instances were with the 2nd node, 21 instances were with the 3rd node, 27 instances were with the 4th node, and 0 instances were with the 5th node. Left-right breakdowns for node were relatively even- 2nd node (1 left, 2 right), 3rd node (9 left, 12 right), 4th node (12 left, 15 right). This anomaly would appear to best be described as a split-terminus (Figs. 13a, 13b). Split-termini were observed in all 6 eastern species, with 25 white ash, 25 green ash, 7 blue ash, 6 pumpkin ash, 1 black ash, and 2 Carolina ash having a leaf with a split-terminus.

A white ash had a leaf with a very bizarre terminal leaflet (CKP08B). This leaflet appeared like a terminal leaflet that had subdivided into two standard leaflets (Fig. 13c). It can best be described as resembling a fish's tail. This was not a case of a split-terminus where the terminal leaflet was missing as this odd leaflet's blade extended past the base of each sub-leaflet and down the petiolule. A lateral leaflet on a different tree (CMD08), specifically the left leaflet at the 2nd node, had been observed subdivided in a similar manner.

One leaf of a green ash (CFR03B) had a terminal leaflet which was noticeably smaller in size relative to other terminal leaflets. It was not abnormally small or stunted, but it was unusually small for the type of leaflet it was.

Anomalies Regarding Lower Nodes:

Another type of anomaly which occurred frequently was observed in ash leaves. At the lowermost leaflet node, the leaflets were not attached oppositely, they were attached alternately (Fig. 13d). The leaflets can be out of alignment by between 1-5mm (measurements below 1mm are nearly imperceptible without magnification). In most instances where the disjunct was visible, it was usually 2-3mm; 4-5mm was not uncommon to observe though. This anomaly can be best called staggered leaflet pairs or a disjunct node. 204 leaves belonging to 124 trees had this stagger.

This type of stagger has been observed in white ash, green ash, and pumpkin ash. It seems to be extremely common in white ash. Out of 84 trees sampled, 61 had at least 1 leaf displaying a stagger out of 3-5 leaves collected. It is common in green ash as well, with out of 82 trees sampled, 36 had at least 1 leaf displaying a stagger; the percentage was considerably lower though. Trees which would have been identified as Biltmore ash or red ash also displayed the stagger. Out of 18 trees sampled for pumpkin ash, 15 had 1 or more leaves displaying a stagger. None of the leaves collected from blue ash or black ash displayed a stagger. The sample size of black ash is too small to draw a conclusion though. The remaining 12 trees that displayed the stagger were 10 of the hard to identify trees and 2 Carolina ash.

This anomaly was also seen in some twigs with leaves, where one lateral bud and leaf scar was located higher or lower than the lateral bud and leaf scar it would normally be paired with. Staggered leaves are much less frequent than staggered leaflet pairs though.

Additionally, on some leaves, the leaflets at the 1st node were not located 180° apart; they were located 90° apart or even nearly side by side on the same side of the petiole.

Other Anomalies on *Fraxinus* Leaves:

The most frequent abnormality aside from staggered leaflets or split-termini was stunted leaflets. Certain leaflets on leaves tended to be considerably smaller by length and width dimensions than other leaflets on the same leaf (Fig. 13e). Such leaves could aptly be described as miniature. These were observed at the 1st node (L1: CMW07C, CMW12D, CKH04C; R1: CMW10D, CKH04B, CSG12A), the 2nd node (R2: NPF02A, CMW16C), and the 3rd node (L3: CKP04B; R3: CSG09D). This anomaly was observed in white, green, and blue ashes.

A white ash had a leaf (SMP03B) had the leaflet L2 shaped like a mitten (Fig. 13f). It appeared as if it tried to subdivide into two leaflets, but the division was incomplete and one of the sub-leaflets was noticeably smaller than the other sub-leaflet, which was of average size for a leaflet.

One leaf of a green ash (CMD05B) had 4 leaflets at the 1st node, 2 larger (the upper ones) and 2 smaller (the lower ones) (Fig. 13g). There appeared to be one petiolule on each side, with the smaller leaflet emerging from the larger leaflet's petiolule. This leaf had only 2 nodes and the 1st node's main leaflets look decidedly unlike lower leaflet pairs and like middle leaflet pairs (see Appendix V).

Two leaves on a white ash (SDS16B, SDS16C) had 3 leaflets at the 2nd node instead of the standard 2 (Fig. 13h). This third leaflet was located 90° between the other leaflets. One leaf of a green ash (CFR09C) had 3 leaflets at the 1st node. Unlike the Dixon Springs tree, however, 2 of these leaflets were on the same side (right side). Each leaflet had a petiolule and the leaflet angled towards the terminal end of the leaf was of standard size whereas the leaflet angled towards the basal end of the leaf was much smaller.

Two trees, a green ash and a white ash, had leaves (NMH06A, SWF18C) where the L1 leaflet was missing. The leaflet never developed. This fact could be discerned from the absence of a circular hole in the side of the petiole which is created when a leaflet is broken off at the base of the petiolule. The side of the petiole in these leaves was entirely smooth over the spot where the leaflet should be and showed no blemishes or other unusual signs.

Some oddities were observed with blue ash as well. One was observed with leaves that were faintly serrate, undulate (NLP21). It did have square twig, indicating it was a blue ash.

Twig Anomalies:

Several oddities were observed in the twigs collected. All species showed at least a few peculiarities. This excludes standard characteristics found on species not traditionally associated with those characteristics.

One white ash (SDS06) was observed with a black and light gray terminal bud. The color wasn't a result of a fungus, frost damage, or cobwebs covering parts of the bud since the visual texture of the bud was identical to other ash terminal buds. Only the color differed. No other trees were observed with such an odd bud color, though it isn't surprising this was found in white ash since the species displays greater variation in its bud color than other species.

2 white ashes (CKP07, NPF02) had light brown-orange or orange-brown colored buds. Orange or orange-brown is one of the common colors for Carolina ash's buds.

On one white ash (NLP09), the uppermost lateral bud position was observed to be variable from one side of the twig to another. The skew was similar to the staggered pairing in the lowermost node of some leaves.

A few white ash twigs in Sugar Grove felt like a cross between a round twig and a square twig, with all sides roughly equal in length, but one set of sides being round and the other set of sides being flat.

The general terminal bud size for green ash is small to medium, though a few have been observed with a big cone-shaped bud similar to pumpkin ash.

One blue ash (CKH06) was observed with a terminal bud that was a mix of tan and brown instead of the usual tan-gray mix.

The blue ashes from Lyon Forest (NLP05, NLP06, NLP07) were very odd. They had long petiolules, unlike the rest of the specimens from northern and central Illinois.

Ash Trees Labeled as "Mystery":

There were 19 ashes that could not be easily classified or even identified after a moderate level of scrutiny; these required extensive scrutiny, more than was given the other 216 trees, to decide which species they were and even then, in many cases, the confidence in the identification is not absolute, as it is with all easier to identify samples.

From personal experience in doing this project, there seems to be three tiers of difficulty for ash leaves. The first grouping of leaves is very easy to identify. These lack anomalous traits and have several traits traditionally associated with the species. An example of this would be a white ash leaf with a pale underside, entire margin, and crescent-shaped leaf scars. There is no difficulty in identifying these to species. The second grouping cannot be identified by a casual examination of its leaves and twigs; it requires careful scrutiny, checking several characteristics to arrive at a positive identification. These tend to have one or two anomalous traits and the key identifying traits which would indicate the species are only weakly present or are absent. An example of this would be a white ash with a cuneate leaf base, a dull light green leaf underside, and half-round or reniform leaf scars. Finally, there is the third grouping of leaves, which are incredibly difficult to identify to species. These have multiple anomalous traits in the absence of any defining traits. These require the highest level of scrutiny and can only be identified by looking at several characteristics, and even then, there isn't total confidence in the identification. These leaves cannot be identified with absolute certainty by the naked eye, requiring a microscopic examination or a DNA test. An example of this would be most of the trees labeled as "mystery".

CMW02, 98, 99

These three have sharply serrated leaflet margins and pale green or pale white-green leaf undersides. The green ashes which had similar colored undersides were either faintly serrate or had other margins with one or two exceptions. They fit the profile for green ash (red ash under the old classification) with the exception of their pale underside. Their petiolules were medium or short, their leaflet bases tended to be cuneate, though one had some acute leaflets. Their leaves also tended to be smaller (by average weight and average total leaf area) than pumpkin ash from that site but similar to the other green ashes from this site. 2 had light gray twigs, 1 had a light brown twig (gray is the prevalent color for green ash).

CMW11

This one is similar to the above three in that it had serrated margins, but a pale green color to its leaf underside. It would likewise be green ash (red ash in the classic description based on its extensive pubescence), though has the abnormality of a terminal bud that is nearly black, a trait common in black ash but uncommon in all other eastern North American ashes. Its leaf averages were within the range of the green ashes at the site.

CMW15

This one had some slightly large leaves, though had a margin which was a mix of serrate and crenate. Its underside was a dull light gray-green. This led to some confusion over whether it was green ash or pumpkin ash and to its designation as “mystery”. Its other distinctive characteristics are a short petiolule, cuneate leaflet base, green leaf surface. Based on its leaf averages compared to the identified species of the site and the fact some green ashes from the site had pale complexions on the bottom of their leaves, this would be another green ash. In addition, pumpkin ash tends to have dark green leaves.

CMW18

This one has characteristics generally fitting green ash. The inclusion of this one in the list appears to be an oversight caused by the difficulty in trying to classify the previous 17 ashes from this site (this tree is the last primary specimen from this site).

CMW07, 16

These two have serrated leaflet margins, though one has only faintly serrated margins and the other has some leaves with faintly serrated margins and some leaves with regularly serrated margins. They both have pubescence, short petiolules, and cuneate leaflet bases. Based on the size of their leaves relative to the green ashes from the site and they generally stood out from the other mysterious ashes from this site in average leaf area and average leaf mass, they would seem to be pumpkin ash. Some of the leaves from this tree had high leaf area totals ($425cm^2$, $355cm^2$, which the green ashes at the site don't even come close to) as well. One had a big conical terminal bud. Both had dark green leaf surfaces and the leaf underside was either a dull green or dull gray-green.

Pumpkin ash traditionally does not have a serrated margin. Faintly serrated would be plausible for a non-serrated leaf since mixed margins of serrated and crenate content have been found. The leaves with regular serrations would run contrary to pumpkin ash's traditional description. It may be possible that these isolated pumpkin ashes stem from a different combination of white and green ash, still a hexaploid, but with different features from the main pumpkin ash which dominates the core of the range and the species descriptions.

SDS05

This one generally fits the profile of white ash except for its black and gray terminal bud and its dull green leaf underside. The dark brown twig, long petiolule, and entire margin, slightly revolute support this classification. It also has shield-shaped leaf scars (along with reniform scars), which are a rare occurrence in white ash. It does have some pubescence along its leaf veins. Based on all of these characteristics, it is simply a white ash which has collected in it a few odd traits.

CSG07, 10, 21

These three trees have twigs where their shape is a cross between round and square. It is different from the flattened oval form. In those instances, the shape is an oval where the long axis has flattened edges and the short axis has rounded edges. This twig has all sides of equal length, only one pair is rounded and the other pair is flat. Of all trees sampled, these are the only ones with such unusually shaped twigs. The twig colors were generally olive or green. All three had crenate or faintly crenate margins (one had slightly revolute margins as well). The most common type of leaf scar was shield-shaped, with reniform & crescent shapes occurring as well. The leaves were all papery or thin in their thickness. The petiolules tended to be long and all had acute leaflet bases that were asymmetric as well. Bud color was light brown or medium brown. The color of the leaf underside was a pale gray-green or pale white-green. Leaflet tips tended to be acuminate, occasionally caudate. Leaflet shape tended to be elliptical or ovate. Pubescence was variable among them, ranging from being absent to having slightly pubescent main leaf veins and petiole. The color of the surface of the leaves varied as well, ranging from medium green to dark green.

These trees are hard to characterize. Their twig shape suggests a mix of a white or green ash and a blue ash, but the twig color tends to be different from the general color of all three species. The leaflet margins favor white ash and are not seen in blue ash. The shield-shaped leaf scars are occasionally seen in white ash and green ash (more frequent in white than green though), with one of the 26 blue ashes observed having shield-shaped scars. About half of their characteristics belong to white ash and about half are either shared characteristics or characteristics which are a mix of a white & blue ash characteristic.

Based on looking over what species their characteristics tend to be affiliated with, these appear to be white ash who have some characteristics which resemble blue ash. The lack of major blue ash characteristics like tan-gray buds, serrated margin and the presence of major white ash characteristics like long petiolules, crenate margin, supports this classification and overrides the confounding characteristics.

CSG15

This tree's twigs have a square shape, like blue ash, though it is dark brown, unlike blue ash, and lacks any sort of ridges. It also has crenate margins on some of its leaves and serrate margins on other leaves. It has a long petiolule and medium thickness to its leaves, which are traits affiliated with white ash more often. Its lower leaf surface is pale green. The leaf scars are crescent, horseshoe-shaped, or U-shaped, similar to white ash. Seeds collected were identical to white ash (Fig. 14a). The furrowed bark also is typical white ash bark (Fig. 14b). Based on all available information, this is a white ash with an extremely unusual characteristic (square-shaped twig) and very uncommon characteristic, serrated margins. The majority of its characteristics are standard white ash characteristics though. The odd shape may be an extreme form of the occasionally observed characteristic of white ashes having twigs that don't feel rounded, but have more sides than a square, such as a 10, 12, or more-sided figure (e.g. NPF02).

CSG22

This tree has a round green-brown twig with new growth taking the shape of a flattened oval and a light brown terminal bud. The leaf underside is pubescent, with a pale light green color. It has a green upper surface to its leaves which are papery in thickness. The margin is crenate, petiolules are of medium length, and the leaflet base is a mix of acute and cuneate. This tree generally fits the profile of white ash with a few oddities. The papery consistency is rare in white ash, though abounds in the blue ash which are common to Sugar Grove. The color is a bit unusual for a twig as well. The leaves' general appearance deviates from the standard for white ash, leading to its classification here. Based on the evidence, this tree is a white ash.

Its bark (Fig. 15a) is rather unlike white ash's furrowed bark at maturity. There is a point of development where ash bark becomes furrowed, though has not taken on its fully matured form. The bark looks somewhat similar to blue ash bark images posted on the biology department websites of various universities which do not resemble the mature 'shingled' appearance blue ash bark takes on. However, it has been observed some white ash at this stage of development can have bark resembling CSG22's bark (Fig. 15b). This reinforces the assessment CSG22 is a white ash.

NAR02

This one is perhaps the most perplexing of all the mysterious trees. The overall form of its leaves is unlike any of the documented species in the east. If one were to judge it solely on the traditional characteristics used to identify species, it would be green ash because of the serrated margin, green color to the leaf underside, and lack of pubescence. Its habitat is decidedly unlike green ash, being found in a section of the woods high up on a hill, away from the river and in the section of the woods filled with pines. It isn't a hybrid either because the handful of leaves and twigs from Taylor's ash did not look remotely like this. Bud color and twig shape, medium brown and flattened oval, don't assist in identifying it since both green and white ash share those characteristics.

The leaf's measurements are rather odd. Its average leaf area is 407.92cm^2 (range: 224-551cm^2) and its average weight is 1.59g (range: 0.88-2.12g). Looking at all ash trees with averages over 400cm^2, none are green ash; virtually all are white ash or pumpkin ash (plus 1 black ash leaf), and this one is the remaining one. Additionally, its average weight is much lower than the others, which averages 2.10-4.48g. In essence, it is the odd one out in the giant leaf club.

The best verdict that can be given with morphological and habitat information is this tree is either a strange, very geographically limited variety of green ash which can thrive in upland, pine-filled forests, a similar variety of white ash which happened to converge on some of green ash's defining traits albeit taking on an appearance unlike either species, or a relict species of ash distinct from the 6 eastern species. The area in which it is found, the Driftless Area, was left unscathed by the last Ice Age. Some of the theories which came up in discussions about pumpkin ash's range centered on glacial refugia and pumpkin ash failing to expand its range outside of those refugia in southern Illinois to Arkansas and the Carolinas. The Driftless area, once thought to have been only taiga or tundra, is now considered to have contained deciduous forests at least in some parts based on examining fossil pollen in peat bogs, most notably *Quercus* pollen (Wisconsin Department of Natural Resources 2004; Jackson et al 2000). Anomalous white ashes are common, though none look remotely like this individual. Based on all the characteristics observed for this tree's leaves, this tree is not white ash, green ash, pumpkin ash, black ash, blue ash, or Carolina ash.

Other possibilities include NAR02 being an introduced species despite it seeming rather unlikely due to the remoteness of the location (far northwest Illinois in a sparsely settled area some distance from cities [Dubuque, Rockford, and the Quad Cities are the nearest cities]). Its appearance is decidedly unlike the three European species (*Fraxinus excelsior, F. angustifolia, F. ornus*).

Based on the available data, this tree may belong to an undescribed species or undescribed variety. Collecting seeds from it and examining its microscopic foliar features (i.e. in the manner of Hardin and Beckmann 1982) should provide a formal classification of this individual. Regardless of whether it is its own species or a bizarre variety, its scientific name should bear the name of its location, the Driftless, in it.

NLP01, 07, 10

These trees are also a bit hard to classify. They are grouped together because 2 of the 3 share in common a trait for several traits, though which 2 varies from trait to trait. 2 have sharply serrate margins and 1 has a mix of serrate and crenate. 2 have long petiolules, 1 has short petiolules. 2 have leaves which are papery thin, 1 has medium thickness leaves. 2 have dark brown terminal buds, 1 has a medium brown terminal bud. 2 had reniform leaf scars, 1 had half-round and shield-shaped leaf scars. 2 had twigs with a flattened oval shape and green-brown color, 1 had a rounded twig and a blue-green color. All had slight pubescence on the main leaflet vein or all leaflet veins. Their leaflets all bear the same traits, elliptical shape, acuminate tip, acute base. Additionally, NLP01 and NLP10 have fairly large leaves by leaf area.

Based on assessing their qualitative traits and comparing those traits to the formally identified white, blue, and green ashes from Lowden, which have several anomalous individuals as well, it appears all three of these trees are very anomalous white ashes. They have characteristics in common with the anomalous white ashes from the area in addition to a very odd trait which creates paradoxical mixes (like serrated margins with long petiolules and papery thickness) that lack any key characteristic which could confidently identify them to species. Of all the "mystery" ash classifications, these three are the ones the author has the least confidence in.

Both Lowden SP and Sugar Grove NP have populations of white ash and blue ash. Both have white ashes displaying very peculiar traits (such as serrate margins, square-ish or partially squared twigs), traits which are common in blue ash. It is not clear why this occurs, if there was a chance hybrid between blue ash and white ash in the past which backcrossed with white ash, introducing some blue ash traits into the population (unlikely since both species belong to different sections of the genus), a chance convergence on the same traits, or some other mechanism at work here.

NLF01

This tree generally resembles black ash, particularly in its leaf form. It had several notable differences though. While it has a rounded, tan twig, it has a light brown bud. It lacked petiolules, though the leaflet tapered to a very narrow width when it attached to the petiole, unlike what sessile tends to be. Other black ashes were observed with this narrow sessile trait, though not this narrow. The color of the leaf underside was a bright light green. None of its other traits are distinctive enough to assist classification (i.e. leaf scars, leaflet tips). While the light-colored bud and light complexion to the underside of the leaf is an anomaly and blue ash exist in close proximity to black ash here, this tree lacks traits that one would affiliate with blue ash (square-twig or twig with evidence of cubing, papery thin leaves). Based on the available information, it is black ash.

Only a limited number of black ashes were found in the collection expeditions. As a result, any potential variation in its traits is not well documented. While it traditionally has black buds, a dark complexion to the underside of the leaf, and sessile leaflets, this tree may be evidence of some of the variation that exists in black ash. Other ashes have shown extensive variation, so it would be a logical assumption that black ash should show at least some variation.

Appendix V: Observations Regarding Qualitative Characteristics

Leaflet Shape:

The literature tends to commonly describe the shape of ash leaflets as lanceolate. Based on the 889 leaves that have been analyzed in this study, very few have been lanceolate. Unless there is a geographic decline in the prevalence of the lanceolate shape from the eastern states to Illinois, the more accurate term to describe the shape of most ash leaflets would be elliptical. Lanceolate describes a shape which is relatively narrow at the base (compared to other shapes), though the base is the widest part and as the shape extends from the base to the tip, it tapers to a point. Elliptical describes a shape which is relatively narrow overall (compared to other shapes) with the widest portion of the leaflet at the middle. If a line is drawn through the middle of the leaflet perpendicular to the central axis and one half folded over the other, both halves would be generally the same size, though asymmetric leaf bases and the shape of the leaf apex would affect this. A lanceolate leaflet with a line drawn perpendicular to the main axis midway along its length which then has one half folded onto the other would show two unequal halves.

Leaflet Bases:

Some leaves have uneven (asymmetric) leaflet bases. Usually it is only slight, but some have an asymmetry as much as elms (asymmetry to this degree is very uncommon though). Asymmetry is found with acute and nearly obtuse leaflet bases. It is more common in the lower leaflets than the higher leaflets. Miller noted white ash "often" had unequal leaflet bases (Miller 1955). Across species, it seemed in all of the occurrences of asymmetric leaflet bases, northern Illinois had strongly asymmetric bases, central Illinois only slightly asymmetric, and southern Illinois was slightly asymmetric as well, though there were a few southern individuals with strongly asymmetric bases.

Composition of Leaf Margins:

In recording data for the type of leaf margin for each tree sampled in this study, it was apparent there was an entire gradient of margin types, not a set of discrete margins. Finding leaves with mixed margins was not hard. Serrate-crenate mix, serrate-dentate mix, and crenate-dentate mix have been observed, as well as entire or undulate margins with the beginnings of serration or crenation, which can be considered entire-serrate, entire-crenate, undulate-serrate, and undulate-crenate mixes. In place of calling the leaf margin types 'discrete margins', it would be more accurate to call them 'defining marginal forms'.

The types of leaf margins, at least in *Fraxinus*, can be arranged in a progressive gradient linking all margins, albeit in a complicated diagram (Fig. 16).

Observations indicate it is not a bipolar gradient with entire and serrate margins at opposite ends; rather, there are five 'defining marginal forms' which can transition into most of the others. While it has not been observed widely, it is suspected transitions between undulate and serrate and dentate exist. Additionally, a faintly undulate margin should be indicative of a transition between an entire margin and undulate margin. Prominence of undulation was not examined in this project. That variable would likely segregate undulate from faintly undulate margins.

Each form also displays some variability within itself. The serrate form is perhaps the most obvious case, where the margin can appear anywhere on a gradient from dully serrate to sharply serrate. Such variation is likely to exist in other margins (e.g. dentate, crenate), with it being difficult to detect because it is easier to detect 'sharpness' or 'dullness' in a serrate margin than it is to detect how much a crenate margin protrudes from the base of the margin, for example.

Some of these 'defining marginal forms' can be modified into a different though similar form. Crenulate and serrulate appear to be modifications to crenate and serrate margins which are both variations on the same theme, creating the defining form of the margin (i.e. a half-circle or a curved point) at a finer resolution than is found in the discrete margin type.

The diagram (Fig. 16) has difficulty displaying slightly revolute, which would link to entire, crenate, undulate, faintly crenate, faintly serrate in what has been observed from the ashes of Illinois. The slightly revolute margin can be considered as a modification of the leaf margin and not a discrete margin type because it is observed on leaves of various discrete or transitional margins. Strongly revolute margins were only observed in white ash at Crab Orchard. This high intensity of revolution in leaves may be limited to white ash, with faintly to slightly revolute margins existing in white, green, and pumpkin ash.

Leaflet Attachment:

With regards to leaflet attachment, from observing the characteristics of hundreds of leaflets, it became clear there are not discrete categories for attachment (e.g. stalked, sessile, tapering to base), rather, there is a spectrum from stalked (which can be long, medium, or short) to tapering to the base to sessile. Trees definitively identified as

Fraxinus nigra (NLF02, 03) by twig and bark characteristics had leaflets that weren't sessile. They had leaflets which tapered to the base (the rachis), but they had a much wider area of green than leaflets that usually taper to the base (i.e. *F. pennsylvanica* leaflets). Leaflets that taper to the base have the green portion of the leaflet stop before reaching the rachis or have only a barely perceptible (with the naked eye) sliver of green at the base with the base of the leaflet vein being brown. These *F. nigra* leaflets looked to be a cross between sessile and tapering to the base, being best described as "wide-tapered", whereas all leaflets normally described as tapering to base are "narrow-tapered". Some leaflet bases were observed that looked like a mix of acute and cuneate, likewise there were leaflets with nearly obtuse bases, which would be weakly acute.

<u>Terminal Buds:</u>

The percentage of various tints or shades of brown for terminal buds in the populations of white ash and green ash differed noticeably (Table 11). White ash tended to have medium brown-colored terminal buds, with both light brown and dark brown being rather common. Green ash tended to have dark brown terminal buds with medium brown and light brown being rather common. The frequencies of color vary widely depending on geographic area (See Appendix VI).

Some terminal buds have been seen that are a mix of two colors. While this is common in blue ash, which has beige or tan and gray terminal buds, it is very uncommon in other species. Mixed color terminal buds tend to not be described in *Fraxinus* species outside of blue ash. Terminal buds were observed that were a mix of light brown and medium brown or dark brown. Lateral buds on the same twig were only one color and tended to be the lighter tone of brown. This trait is very uncommon outside blue ash, with less than a dozen individuals being found. Most of the individuals were white ash (3 light/medium brown, 3 light/dark brown, 1 light gray/black), some were green ash (3 light/dark brown). This trait tended to be more common in northern Illinois and was particularly concentrated in the Palos Division forests.

Certain terminal buds also have a reddish coloration to them, as if the brown color was given a reddish tint. 17% of white ashes sampled had red-tinted terminal buds and 4% of green ash had red-tinted buds. Two-thirds of pumpkin ashes sampled had a reddish tint, though based on the small sample size of the species, that number is dubious. The reddish tint is visible on light and medium brown buds. It was not checked whether there was any correlation between red-tinted terminal buds and reddish coloration on leaves and petioles.

Abnormally small terminal buds have been observed as well. These are tiny terminal buds that look unusually small for the twig they are on (i.e. they are being found on average-sized twigs, not slender, small twigs). Several trees (12 total) with tiny terminal buds were observed in Wayne Fitzgerrell SP and Fox Ridge SP. All but one of these trees were green ash (one was a white ash).

Lateral Buds:

There was some observed variation in the size of lateral buds, but this characteristic was not recorded with great detail in this study. The literature occasionally mentions ashes with large lateral buds. In Illinois, the most common size for ash buds is medium or small. Large lateral buds are somewhat uncommon, though not rare. Notes indicate they are most common in white ash, green ash, and Carolina ash, slightly common in pumpkin ash, and rare in blue ash (2 individuals out of 26, NLF05 and NLF07, were observed with large lateral buds), and occurs in samples collected from northern and southern Illinois, but not central Illinois. Some northern sites were dominated by large lateral bud ash trees (e.g. Moraine Hills, Rock Cut) while others had trees with average-sized and large-sized lateral buds at the same site in about equal numbers (e.g. Lowden, Palos Division). No southern site was dominated by large lateral bud trees, but a few sites had populations with equal numbers as standard-sized lateral bud trees (e.g. Dixon Springs, Crab Orchard).

Number of Leaflets:

The range and frequency of the number of leaflets per leaf for each species was observed (Tables 12-15).

The most common number of leaflets for *Fraxinus americana* was 7 with 9-leaflet leaves occurring at a moderate frequency (Table 12). The frequency of occurrence of 5-leaflet leaves in northern Illinois is noticeably lower than the frequency in other regions and the frequency of 7-leaflet leaves is higher than the frequency of occurrence in other regions. Central and southern Illinois have about even frequencies for all number of leaflets. Overall, 9-leaflet leaf frequency is relatively static across Illinois while 5-leaflet leaves and 7-leaflet leaves appear to have inverse proportional frequencies to one another.

The most common number of leaflets for *Fraxinus pennsylvanica* was 7, with 5-leaflets and 9-leaflets being somewhat common (Table 13). Northern Illinois has a higher frequency of 5-leaflet leaves and lower frequency of 9-leaflet leaves than other regions have and southern Illinois has a lower frequency of 7-leaflet leaves and a higher frequency of 9-leaflet leaves than other regions have. Thus, the frequency of 9-leaflet leaves increases the further south one gets in Illinois.

The most common number of leaflets for *Fraxinus quadrangulata* leaves was 7 (Table 14). The frequency of occurrence of 7-leaflet leaves in northern Illinois is considerably higher than the frequency found in central Illinois. The frequency of 9-leaflet leaves is also higher in central Illinois than northern Illinois. Central Illinois blue ashes also have a considerably higher frequency of split-termini than blue ashes of northern Illinois have.

The most common number of leaflets for *Fraxinus profunda* was generally a tie between 7 and 9 (Table 15). The frequencies of the various numbers of leaflets are about even across central and southern Illinois with only a slightly higher value for 9-leaflet leaves and lower value for 7-leaflet leaves in southern Illinois than in central Illinois.

The combined totals for all four species extensively studied reveals what the species have in common for number of leaflets and in what regards they differ. For all species, 3-leaflet leaves are extremely uncommon, with only 0-1 leaves of this type being found in an entire set, and 11-leaflet leaves are rarely occurring in white ash and pumpkin ash populations, though they are likely to be more common in black ash populations, which have 11 frequently reported in the literature. Split-termini are found in about 10% of all leaves regardless of species. Frequency of 7-leaflet leaves is at a little over 50% in all species' populations excluding pumpkin ash. Frequency of occurrence for 5-leaflet leaves and 9-leaflet leaves varies based on species and are generally inversely related; the higher the frequency of 5-leaflet leaves in a species, the lower the frequency of 9-leaflet leaves in the species. Pumpkin ash has the highest occurrence of 9-leaflet leaves, at about 40%, even with the frequency of 7 leaflet leaves, and has the lowest occurrence of 5-leaflet leaves, and percentages get progressively lower for 9-leaflet leaves and higher for 5-leaflet leaves from white ash to green ash to blue ash, with green ash having an almost even frequency between both numbers.

The number of leaflets per leaf, ignoring split-termini, can vary on the same tree with all 6 species. In fact, it is somewhat uncommon to, out of a set of 4 leaves per tree, have all 4 leaves with the same number of leaflets. Out of a set of 4 leaves per tree, 3:1, with 3 being the higher number and 1 the lower number or 3 the lower number and 1 the higher number has the highest frequency, though a 1:1 division between higher and lower numbers is not uncommon.

Since most trees have a dominant number, the variability in the number of leaflets per leaf may be due to a defect in the gene that determines the number of leaflets when cells are being replicated for the leaf primordia. What can be determined from the observations of this study is it is relatively random and can vary on the same tree.

It is unknown if 3-leaflet leaves can occur in white, black, pumpkin, and Carolina ash, if 5-leaflet leaves can occur in black ash, if 9-leaflet leaves can occur in Carolina ash, if 11-leaflet leaves can occur in green ash, or if 13-leaflet leaves can occur in black ash (some European spp. can have up to 13 leaflets).

Petiole Characteristics:

Notes were taken on the petiole shape and color for all species. All color descriptions for petioles are the color observed in dried specimens. There seem to be 4 types in *Fraxinus*: round, flat-topped (ungrooved or with a faint groove), flat-grooved (a deep groove with a flat floor), and deep-grooved (V-shaped groove). The most frequent form across the genus is flat-grooved, with flat-topped being less common, albeit the second-most common form, and deep-grooved and round being uncommon. Grooved petioles in the literature tend to be described as channeled or canaliculate.

White ash is most frequently flat-grooved, though flat-topped is common. Deep-grooved isn't too common, though is more frequent with V-shaped leaf scars. The most common color is a dull green color on the upper surface and a dull yellow color on the lower surface, though brown and yellow-green have been observed on the topside as well. Petioles can have a reddish tint occasionally as well. *Fraxinus americana* is typically described as having a deep U-shaped or V-shaped notch on the upper edge of the leaf scar, but the depth of this notch is said to commonly vary in *F. americana* and other *Fraxinus* species (Petrides 1972).

Green ash is most frequently flat-grooved, though flat-topped is common. The most common color for the petiole is a dull green or light green upper surface with a yellow to dull yellow lower surface.

Blue ash is most commonly flat-topped; flat-grooved has been observed, though was very uncommon. The most common color for the petiole is greenish-brown on the topside and yellow-brown to dull yellow on the underside. Petioles entirely greenish-brown have been observed. It is rare to find a description of the leaf scar for *Fraxinus* *quadrangulata*. The few references in the literature describe it as having a shallowly-notched upper edge (Petrides 1972).

Pumpkin ash is most commonly flat-grooved, though flat-topped is not infrequent. The most common colors are green-brown to dull green on the topside and dull green to dull yellow on the underside.

As for the other ashes, black ash has been observed with rounded and flat-topped petioles that have tended to be brown or green-brown on the topside and brown or green-brown on the underside (occasionally, color is consistent on both sides, occasionally it is different) and Carolina ash has been observed with rounded and flat-grooved petioles that have been green-brown or yellowish-green on the topside and yellow or yellowish-green on the underside. *Fraxinus nigra*'s leaf scar is only described as not deeply notched (Petrides 1972).

It has also been observed that the color of the petiole on fresh leaves, either on the tree, or recently fallen, in autumn are the color the leaf blade turns that season. Green, black, blue, and pumpkin ash were observed with dull yellow-colored petioles and white ash was observed with purple or wine red-colored petioles.

Petiolule Length:

Examining the frequency of different lengths of petiolules in the populations of the various *Fraxinus* species shows there to be considerable variation in all species, lacking any decisive dominance by one length, which the literature tends to paint (Table 16). Green ash and blue ash had similar numbers overall, with the short length being the most prevalent form and medium comprising one-quarter of the population, and the remainder being the long form. White ash and pumpkin ash had less decisive dominances by one length, with white ash having its most prevalent form being long, with medium being fairly frequent and extra long occurring more frequently than in any other species. Pumpkin ash has a more even spread than the other species.

The numbers reflect casual observation where green ash and blue ash tend to have short petiolules while white ash and pumpkin ash have a greater frequency in variation, with long dominating the former and the latter tending towards the short length.

Composition of Leaves:

In assessing the 889 leaves in this study, a pattern was observed in how the ash leaf is constructed. Ash leaves are more than lateral leaflets and a terminal leaflet on a petiole; they have multiple 'parts'. In gathering data on the various morphological characteristics of ash leaves, it appeared like various pairs of ash leaflets were 'behaving' differently relative to other pairs on the same leaf. Qualities such as leaflet shape and petiolule length varied among leaflet pairs on the same leaf and how they varied was relatively constant between leaves and species. Just as slope and X, Y, and/or Z coordinates as well as their relativity to one another can define lines and differentiate lines from one another, certain morphological characteristics can define and separate categories of leaflets from one another.

Based on the observations made during this study, dividing ash leaves' leaflets into lateral leaflets and the terminal leaflet is too simple; there are subdivisions within lateral leaflets. Terminal leaflets are distinct and tend to be wider than lateral leaflets, tend to take on a different shape (usually tending towards ovate or obovate), and are longer than lateral leaflets by virtue of the fact that they have a longer petiolule and measuring from node to leaflet apex will include that increased length. Lateral leaflets fall into three types: lowermost pair, uppermost pair, and middle pairs. The lowermost pair tends to be smaller than the other lateral leaflets in length and width dimensions and tends to be more ovate or oval shaped than other leaflets on the same leaflet. This pair is also the most prone to a disjunct in the leaflet pairing, with that node appearing alternate instead of opposite due to the growth rate differing on each side of the rachis. The uppermost pair tends to have very short petiolules, even in species which are known for having long petiolules and even on leaves where the lower and middle leaflets have long petiolules. If one were to only look at the petiolule length and leaflet base of these leaflets and disregard all others, they would classify all white ash as green ash since green ash is known for having shorter petiolules relative to white ash. These leaflets also tend to be angled slightly upward relative to the leaf axis, not the perpendicular (or as is commonly seen, somewhat close to perpendicular) angle the rest of the lateral leaflets take on. The angle they take on moves them closer towards the leaf axis. The middle pairs tend to be the longest and widest of the lateral leaflets. These are what would be deemed the 'standard' leaflets of an ash leaf, displaying all the traits considered normal for a leaflet (shape, petiolule length). They also tend to be the least prone to anomalies relative to the other types.

The question that arises from identifying the different types of leaflets is- how do these types plug into the varying number of leaflets ashes have? The most prevalent number of leaflets for ash leaves to have in this study was 7. These leaves have one lowermost lateral pair, one middle lateral pair, one uppermost lateral pair, and one terminal leaflet. Ash leaves with 9 and 11 leaflets simply add additional middle pairs. The measurements gathered bear this out as the 2nd, 3rd, and in the case of 11-leaflet leaves, 4th pairs of leaves tend to be more similar to one another than they are to the uppermost and lowermost leaflets. In the case of leaves with 5 leaflets, which leaflet type is omitted seems to vary. In some, it appears to be the uppermost leaflet pair since the 2nd pair of leaflets show average length petiolules and the 1st pair in such leaves tend to be smaller, like the lowermost pair tends to be. In others, the 2nd pair has very short petiolules and bears the angular change while the 1st pair resembles the middle pair of leaflets. The other combination (lowermost and uppermost, with a middle pair excluded) may be possible.

And generally for all *Fraxinus* species, it is extremely common for ash trees to have at least one leaf with a split-terminus out of a dozen leaves (See Appendix IV). The common frequency of this anomaly was indicated by the data and when walking through the woods on other occasions besides the collection expedition, a leaf with a split-terminus was very easy to find on the trees. This also extends to close-up photos taken of ash trees. On almost every photo the author took on forest walks, at least one leaf with a split-terminus could be easily seen in the photograph.

Effect of Leaflet Position on Leaflet Characteristics:

Leaflet position has some effect on the shape the leaf takes or the form its base takes on based on patterns observed while collecting data on the leaves' characteristics. First, it tends to be uncommon for any leaflets above the bottom pair (excluding the terminal leaflet) to be ovate. White, blue, and pumpkin ash tend to be the only ones to display ovate leaves among non-first pair lateral leaflets. Second, uppermost lateral leaflets tend to be slightly obovate compared to lower lateral leaflets, though they are never as obovate as terminal leaflets if the terminal leaflet is obovate on the same leaf. Third, terminal leaflets tend to be obovate, ovate, or oval. Finally, most cases where the leaflet base is nearly obtuse are in the bottom pair of leaflets.

Leaflet position also affects petiolule length. Excluding the terminal leaflet, all leaflets except for the uppermost lateral leaflet pair have petiolules of a similar length. It is this length that is referred to when describing the petiolule length of a leaflet in the literature. However, the uppermost pair of lateral leaflets commonly have short petiolules compared with the rest of the leaflets. Even in leaves with long to extra long petiolules in lower lateral leaflets, the uppermost pair has short petiolules. Regardless of what length the lower lateral leaflets have, the uppermost pair's length tends to range from short to non-existent.

Observations on Habit:

Out in the field, it became apparent mature ash trees which became canopy trees took on a few different forms. As with most canopy trees, the lowermost branches tended to be out of reach of the pole pruner extended to its fullest extent, but the spread of the canopy seemed to vary. Many canopies of ashes took what would best be described as a standard shape for a canopy, a relatively broad spread of branches out from the trunk. This form is the most common for tree canopies to take. Some ashes took a form similar to palm trees, however. These trees had a tall trunk with no branches lower down and a small globe of branches and leaves at the top, lacking the spread out canopy that trees tend to take when they reach such heights. The contours of the forest canopy at the time the ash tree was developing may be behind this, with little competition for light resources allowing for the ash tree to spread its canopy outward while with only a small opening of light in the canopy, an ash tree would have very little room for lateral development and take on a more confined vertical form.

Appendix VI: Updated Species Descriptions

In going over the data for morphological characteristics, it is apparent several ash species have great variability and overlap on many characteristics. The difficulty in differentiating certain ash species was always referred to ambiguously, but the specific points of overlap can be seen now. This is discussed at length in Appendix VIII. Based on the observations made here, the detailed descriptions for the ash species should be revised to note the variation various traits can have. The descriptions for the species tend to be simple and only note the most common form for a characteristic and tend to avoid mentioning the other forms they might have, forms which are the prevalent forms for other species. This omission of convenience creates the false impression that certain species (i.e. white ash, green ash) only have a narrowly defined range of variation and leaves the mystery of the difficult to identify individuals to continue further.

Note: The colors described here are the color specimens take when dried in a drying cabinet. General observation of fresh material of ash species versus dried material indicates the color of the upper surface of leaves does not change nor does its shade or intensity of green. The color of the lower surface of the leaves cannot be confirmed to remain the same or change. The color of new growth on twigs does tend to change though. It is common for any twig colored green or bluish-green to lose its green color in drying.

Fraxinus americana

<u>Number of Leaflets</u>: 5-11 leaflets. 7 leaflets is the most common form. 9 is fairly common, 5 is slightly uncommon, 11 is very rare.

Leaf Size: Can get up to 53cm in length.

Leaflet Shape: Most commonly elliptical. Oval and ovate are occasional. Oblong, narrow oblong, nearly oblong are uncommon. Obovate, panduriform, cordate have been observed.

Leaflet Margin: Most commonly crenate or faintly crenate. Undulate is somewhat common. Entire is slightly uncommon. Crenate/serrate mix, undulate/crenate mix have been observed. Entire, undulate, and faintly crenate have all been observed with slightly revolute margins on several occasions. Revolute margins are not uncommon. Serrated margins have been occasionally observed.

Leaflet Tip: Most commonly acuminate. Aristate, acute are less common. Rare forms (obtuse, caudate, emarginate, cuspidate, cleft) are not uncommon in general, though each individual type is infrequent.

Leaflet Base: Most commonly acute. Cuneate, nearly obtuse to obtuse not infrequent. Asymmetry is rather common.

Petiolule Length: Most commonly long. Medium and extra long are less frequent, though not uncommon. Short is somewhat uncommon.

Leaf Thickness: Most commonly thick or medium. Thin is less common, papery is very uncommon.

Leaf Color (top): Most commonly green, occasionally bright green. Light green is infrequent, dark green is very uncommon. This clashes with the literature, which indicates dark green is the prevailing color.

Leaf Color (bottom): Pale white-green, pale green, or pale light green most common. Dull green is uncommon. Yellow-green has been occasionally observed as have slightly dark-tinted undersides.

Pubescence (where): Main leaf veins, leaf veins, leaf underside, petiole. Only slight. Very uncommon in northern Illinois, slightly uncommon in central Illinois, and more common in southern Illinois, reinforcing previous indications pubescence becomes more frequent in the southern part of the species' range.

New Twig Growth Color: Most commonly dark brown. Some are dark brown on one side and light brown on another. Brown-gray (light, medium, or dark) is occasional. Light gray, dark gray, and light brown are uncommon, but not rare. Some are an olive color. Some can retain their green color after drying. Literature indicates twigs can have pale lenticels.

New Twig Growth Shape: Most commonly a flattened oval, though round is not uncommon.

Leaf Scar Shape: Crescent very common. V-shaped, reniform, half-round somewhat common. U-shaped infrequent. Shield-shaped, horseshoe-shaped, oval have been observed.

Bud Color: Frequency of color seemed to vary between regions. Some may have a reddish tint.

Northern IL- Medium brown or dark brown very common. Light brown very uncommon.

Central IL- Light brown very common. Dark brown, medium brown less common.

Southern IL- Medium brown very common (dark brown seemed to be the dominant color at Dixon Springs though), dark brown slightly common, light brown very uncommon.

The literature (e.g. Fernald 1950, Brown 1975) indicate the primary color of buds are rusty-brown or rust-colored, so bud color may vary along a longitudinal axis as well. One tree was observed with orange colored buds and another with orangish-brown colored buds. Orange tones are extremely uncommon though.

Lateral Bud Position: Most commonly beside the terminal bud. Being set slightly back is occasional.

White ash's highly variable leaflet shapes were previously noted by Miller (Miller 1955). Of all the species, anomalous leaflet shapes (e.g. panduriform, cordate) and other odd characteristics (e.g. shield-shaped or horseshoe-shaped leaf scars, various leaflet tips) occur at a higher frequency in white ash than in the other species of ash. While Carolina ash is known for its considerable variation and green ash for a fairly wide range of variation, white ash should be known to have considerable variation as well.

Wright categorized leaflet shape of white ashes in one of his studies into 3 categories, defined by the length: width ratios, broad, normal, narrow, and found most of the trees from AL & MD had broad leaflets, the vast majority from across the entire study range (encompassing parts of the Midwest, New England, and the South) had normal leaflets, and a few individual trees from MA, NY, ON had narrow leaflets (Wright 1944b). Length: width ratio was a measurement not used in this study, though general observation can confirm narrow-leaved white ashes were not found in Illinois.

Many trees which fit the overall description of white ash but which have serrated margins were observed in the Palos Forest Preserve and Lowden Park. Faintly serrated margins on white ash were occasionally observed elsewhere (e.g. Sugar Grove, Eldon Hazlet). Serrated white ashes run contrary to general descriptions of the species. The geographic localization of it is particularly interesting. This trait may be common only in the northwestern part of the species' range. Most of the historic descriptions were generated from trees located out in the eastern states and as a result may have overlooked characteristics on the fringe of the range (the Midwest, Great Plains). Another possibility is such trees may have not been selected for seed harvesting for experiments conducted by the Forest Service growing seeds from all across a species' range in one location because they were confused for green ash. It would be interesting to see if comprehensive surveys of white ash in Wisconsin, Iowa turn up serrated margin white ashes.

When the white ashes sampled in Illinois are compared with the three ecotypes previously observed, most would fall into the northern ecotype. Only 8 pubescent individuals were observed, with 5 of those being in southern Illinois. A reddish coloration to the petioles and leaf veins was observed in 8 trees. There is no overlap between the two characteristics linked with the southern ecotype. Outside of a somewhat common occurrence in Southwestern Cook County forest preserves, the red pigmentation was very rare across the state. While it may be common in southern populations, a similar gradient of more red coloration in white ash towards the southern side of Illinois was not observed, much the opposite in fact.

White ash is generally described as having fall colors of yellow or burgundy to purple. In Illinois, virtually all white ashes encountered were entirely purple (or burgundy) or purple with yellow coloration around the veins. Only one individual was encountered which had yellow foliage in the fall. There may be some geographic variation in the dominant secondary pigment (xanthophylls or anthocyanins). Gathering data on the fall color of natural white ashes from across the range should reveal whether this is the case or not.

Fraxinus pennsylvanica

(This description describes what was traditionally considered *Fraxinus pennsylvanica* var. *subintegerrima*)

Number of Leaflets: 3-9 leaflets. Most commonly 7 leaflets, occasionally 5 or 9. 3 leaflets very rare.

Leaf Size: Can get up to 31cm in length.

Leaflet Shape: Most commonly elliptical, narrow elliptical or oval occasionally, ovate or lanceolate infrequently. Obovate, oblong, obcordiform, panduriform can occur. Some leaflets can be falcate.

Leaflet Margin: Faintly serrate, serrate, and sharply serrate are the most common forms. Serrulate, crenate, undulate, entire or nearly entire are uncommon. Serrate/crenate mix and serrate/dentate mix has been observed, as well as dentate or faintly dentate. Some leaves with entire margins were slightly revolute.

Leaflet Tip: Most commonly acuminate. Occasionally acute, aristate. Obtuse, cuspidate, cleft, emarginate have been observed.

Leaflet Base: Cuneate in most instances. Acute is somewhat common. Cuneate/acute mix, obtuse, nearly obtuse have been observed. Asymmetric leaf bases are uncommon.

Petiolule Length: Most commonly short, medium not infrequent. Long is uncommon, a few can be extra long.

Leaf Thickness: Most commonly thick, medium common though. Thin and papery uncommon.

Leaf Color (top): Most commonly green, dark green somewhat common though. Bright green infrequent. The literature indicates leaf color ranges from yellow-green to green, so regional differences may exist.

Leaf Color (bottom): Light green seems most common, though dull green and yellow-green are very common as well. Pale green, pale white-green, pale light green has been seen occasionally. Dark green was observed very rarely.

Pubescence (where): Main leaf vein, leaf veins, petiole (only slight).

New Twig Growth Color: Most commonly light gray. Light brown-gray or gray-brown is uncommon, but not rare. Dark brown, yellow-brown has been observed as well. Some seem to retain their green color even when dried. Literature denotes twigs can have white lenticels.

New Twig Growth Shape: Almost all are round. Some have a flattened oval shape.

Leaf Scar Shape: Half-round, reniform most common. Crescent is somewhat uncommon but occurs more often than the obscure forms. Shield-shaped, U-shaped, triangular have been observed.

Bud Color: Dark brown, medium brown about equally common. Light brown somewhat uncommon. Reddish tint very uncommon.

Lateral Bud Position: Most commonly beside, being set far back is not infrequent. Being set slightly back is the least common of the three.

When observing drought resistance among green ash on the Great Plains, it was observed there were 3 different ecotypes. In addition to drought resistance, there were different shades of green associated with these ecotypes. The color of the upper surface of the leaves was as follows: most drought-resistant- 10% light green, 90% dark green, intermediate drought-resistance- 36% light green, 64% dark green, least drought-resistant- 52% light green, 48% dark green (Meuli and Shirley 1937). Across Illinois, the most common color was medium green, with dark green somewhat common. Bright green was infrequent. While it isn't clear where medium green fell in their spectrum as they only differentiated green into 2 categories, the color spectrum in Illinois is shifted towards the darker side of the green, indicating the green ashes may be slightly adapted to drought conditions. Illinois historically was a mix of prairie and forest, which indicates the climate regime that created conditions in the eastern Midwest, Appalachians, and the Northeast which favored forests weakens over Illinois. If Meuli and Shirley's work applies across the whole range of green ash, one would expect bright green to be the prevailing leaf color in the South and on the East Coast.

When the green ashes sampled in this thesis are compared to the other ecotypes, the majority of the trees fit the northern ecotype, having green petioles and 'brown twigs' (though most were gray or brownish-gray). Reddish petioles were found in 5 green ashes. Green-toned twigs were found in 15 trees, most commonly in central Illinois. Only 1 tree fit the classic southern ecotype. This indicates the northern ecotype extends into Illinois and either the southern ecotype may intergrade with the northern ecotype across the entire state, albeit having a low presence in the state overall or the traditional division described breaks down in Illinois.

Many trees which fit the overall description of green ash but have been observed some of the following characteristics: undulate or entire margins, acute leaflet bases, pale green or pale white-green leaf underside, and medium, long, or extra long petiolules. These run contrary to the description of the species. There were a high number of anomalous green ashes at Meredosia NWR, with only a handful of anomalous green ashes scattered across the rest of the sites.

Some dentate margins were observed, a characteristic very rarely reported in descriptions of the six ash species of eastern North America. Miller had noted the possibility of dentate margins in some ashes (Miller 1955).

Fraxinus nigra

Number of Leaflets: 7-11 leaflets. Most commonly 9 leaflets, occasionally 11 leaflets. 7 leaflets uncommon.

Leaf Size: Can get up to 51cm in length.

Leaflet Shape: Elliptical or narrow elliptical. Lowermost pair can be ovate. Literature indicates shape tends to be oblong to lanceolate.

Leaflet Margin: Serrate (1 observed crenulate).

Leaflet Tip: Aristate or acuminate, occasionally caudate, cuspidate.

Leaflet Base: Sessile or narrow sessile, can be uneven, occasionally obtuse or cuneate. Literature denotes base can be asymmetric as well.

Petiolule Length: Non-existent for lateral leaflets.

Leaf Thickness: Most commonly medium, occasionally thick or thin.

Leaf Color (top): Dark green, green, or olive green.

Leaf Color (bottom): Dull dark green, occasionally a dull gray-green or a dull pale green.

Pubescence (where): Rust-colored hairs around junctions of leaf veins occasionally.

New Twig Growth Color: A tan-light gray color, light gray, or light brown. Literature indicates twigs may be covered with black lenticels as well.

New Twig Growth Shape: Round or flattened oval shape.

Leaf Scar Shape: Reniform or half-round commonly, occasionally crescent.

Bud Color: Commonly black, occasionally dark brown.

Lateral Bud Position: Commonly set slightly back, occasionally set far back.

Black ash seems to display some characteristics that clash with its traditional set (i.e. crenulate margin, cuneate and narrow sessile leaflet bases), but the small sample size (n=4) prevents a broad picture of the variation within the species from being constructed.

Some black ashes have been described as having a swollen-base similar to pumpkin ash. These trees were found in swamps and bogs in the upper part of Michigan's Lower Peninsula (Gates and Erlanson 1925). The frequency of this characteristic is not known.

Fraxinus quadrangulata

Number of Leaflets: 5-11 leaflets. Most commonly 5 or 7 leaflets. 9 leaflets uncommon. 11 leaflets not seen in Illinois.

Leaf Size: Can get up to 31cm in length.

Leaflet Shape: Commonly elliptical, wide ovate to ovate is not uncommon. Oval is somewhat uncommon though usually restricted to the lowermost pair of leaflets.

Leaflet Margin: Serrate or sharply serrate. Rarely serrulate, dentate or a serrate/dentate mix.

Leaflet Tip: Most commonly acuminate, occasionally acute. Rarely aristate. Caudate, cuspidate, obtuse can also occur.

Leaflet Base: Most commonly acute, but cuneate or nearly obtuse can also occur. Asymmetric leaf base is not uncommon.

Petiolule Length: Most commonly short, occasionally medium, rarely long.

Leaf Thickness: Most commonly papery, occasionally thin, rarely medium, never thick.

Leaf Color (top): Most commonly dark green, uncommonly green or blue-green. This account clashes with the literature.

Leaf Color (bottom): Most commonly a dull gray-green or dark dull gray-green. Rarely dull pale green or dull light green. This account clashes with the literature.

Pubescence (where): On all leaf veins or main leaf vein only. Usually only slight. Rare individuals can have the entire leaf underside pubescent though.

New Twig Growth Color: Commonly tan-gray, tan, light brown, or light brown-gray.

New Twig Growth Shape: Rectangular. Thin woody ridges rise up from the corners of the square. Length can vary.

Leaf Scar Shape: Commonly reniform or half-round, oval-shape uncommon. Rare instances of crescent, shield-shaped, and U-shaped leaf scars noted.

Bud Color: Tan/bluish-gray mix.

Lateral Bud Position: Most commonly beside terminal bud, but not uncommon for them to be set slightly back. In rare cases they can be set entirely back.

Some points worth noting with blue ash are the width of the wings on the corners of the twigs can vary from being wide and thin or very narrow, resembling crown molding on the 4-sided twig and the margins have always been toothed in some form, nearly always serrate, though occasionally dentate. The variation in wing width has been noted previously (Gleason and Cronquist 1963).

Blue ash may be a commonly occurring member of sugar maple forest associations. One study in east-central Indiana studying regeneration in an old growth forest involved a forest strongly dominated by *Acer saccharum*. The other trees in this forest with large numbers of trees were *Ulmus rubra, Carpinus caroliniana, Aesculus glabra, Ulmus americana*, and *Fraxinus quadrangulata* (Ward and Parker 1989). Blue and white ash were the only ash trees found in this forest, but blue ash had nearly four times a presence as white ash (Ward and Parker 1989). Blue ash and white ash have been found together many times in this study (e.g. Sugar Grove NP, Lowden SP, Kennekuk Cove/Windfall Prairie), though it is commonly found near green ash if a river is nearby (e.g. Lowden SP, Windfall Prairie NP) and has been observed by black ash (e.g. Lyon FP). In the sugar maple forest, *F. quadrangulata* had a very high regeneration density under the secondary canopy, trees and shrubs under 15 feet tall (Ward and Parker 1989).

Among the oddities observed that deviate from the general range of characteristics of the species are dentate margins and a fully pubescent leaf underside. Additionally, the upper surfaces of some leaves have a bluish-gray tint to them. This characteristic has not been seen described in the literature. The compound which gives blue ash's sap its blue-dying properties (the source of its common name) may be found in the tree's leaves too. One blue ash was observed with a brown/tan terminal bud. This may indicate other bud colors are possible in blue ash (both blue ash and black ash tend to have little variation in bud color).

There are several differences between the description of characteristics for blue ash and the characteristics observed in blue ash in Illinois. The number of leaflets seen in Illinois is most commonly 5 or 7, with 9 being rare. Descriptions in literature indicate 7-11 leaflets is the range observed (Hough 1921; Fernald 1950; Gleason and Cronquist 1963). The leaf appearance is starkly different as well. The description of the upper surface is described as dark yellowish-green or simply green and the lower surface is described as a pale dark yellow-green or green (Hough 1921; Fernald 1950). The Illinois blue ashes are mostly dark green or a dark bluish-green on their upper surface and a dull gray-green, which is usually dark-tinted, on the lower surface. The sampled trees showed no signs of lighter green tints or of a yellowish color. The leaf shape is described as commonly lanceolate (Hough 1921; Fernald 1950; Gleason and Cronquist 1963). Common leaflet shapes observed in the state were elliptical, ovate, and wide ovate. The leaflet tip was said to be long-acuminate (a category called aristate in this study) (Hough 1921; Gleason and Cronquist 1963). In this study, acuminate was most common and acute was occasional; aristate was rare. Some samples in the EIU herbarium from outside the state fit the traditional description of blue ash. These have also had thicker leaves than the blue ashes in the state, which have tended to be very thin, thin to the point where they crumble easily when handled after drying.

There were some additional characteristics described that were found in only one source. Miller described the twig as dark orange in color and covered in rufous-colored pubescence early on (Miller 1955). No other descriptions of the species from the 20th century described the twig color (since the shape is considered sufficient for identification). This completely clashes with the observed color. Twigs tend to be a light woody brown to cream color when dried and when fresh tend to be bluish green with a light woody color to the wings. Miller also describes the twigs as stout, something which clashes with the observed properties of blue ash twigs in Illinois (e.g. relatively slender). Miller also describes the leaf scars as large; observed leaf scars were average.

This clash of descriptions may indicate two separate varieties, one found in the western part of the range (at least, in Illinois) and one found in the eastern part of the range, where traditional descriptions of eastern North American species originated. The high number of characteristics which differ between observed specimens and literary descriptions support a distinction rising to the level of variety. Illinois blue ashes can be described as having 5-7 leaflets, occasionally 9, darker green leaves (with a bluish or grayish cast occasionally), elliptical or ovate leaflet shape, and acuminate or acute tips. Leaf scars are of average size, not large, and twigs are slender to medium-size in diameter. Eastern blue ash can be described as having 7-11 leaflets, lighter green leaves (with a yellowish cast occasionally), lanceolate shape, occasionally ovate, and aristate tips often. Large leaf scars and stout twigs may also occur with this type. Based on the available information, this author would designate the blue ashes common in Illinois a variety, *Fraxinus quadrangulata var. fuscopapyraceus* ("dark paper-like", after its dark color and papery texture which tends to contrast with the color and texture of the eastern blue ashes), though the level of support for this designation is limited by the lack of analysis of blue ash across its entire range and a scarcity of presence in the literature by the species. If differences in frequency of these traits are found across the range with little deviation from the described set of characteristics among samples collected, then the division into varieties would be supported. If the suites of characteristics indicated are not shown to widely exist, with all these described traits not being found in association with the other traits attributed to the varieties, then this variety should go unrecognized. The contrast between collected specimens from Illinois and preserved specimens from more easterly states is very striking, particularly when considering Biltmore ash is defined by a far smaller set of characteristics than this proposed variety.

Fraxinus profunda

Number of Leaflets: 3-11 leaflets. Most commonly 7 or 9 leaflets. 5 leaflets rare. 3 or 11 leaflets have been observed.

Leaf Size: Can get up to 52cm in length.

Leaflet Shape: Elliptical or wide elliptical common, oval and ovate somewhat common, wide ovate, obovate occasional. Some leaflets can be falcate. The literature denotes leaflets can be oblong.

Leaflet Margin: Undulate or entire commonly, occasionally faintly to distinctly crenate. One tree observed with a faintly serrated margin though. Slightly revolute margins have been observed with undulate, entire, and crenate forms and are somewhat common.

Leaflet Tip: Commonly acuminate, occasionally acute. Caudate, cuspidate, obtuse are uncommon.

Leaflet Base: Acute or cuneate, though oddities like a wide cuneate base or a base that looks like a cross between acute and cuneate can be observed. Asymmetric bases are not uncommon. The literature indicates the base can be rounded as well.

Petiolule Length: Short, medium, or long.

Leaf Thickness: Commonly thin or medium, occasionally thick or papery.

Leaf Color (top): Most commonly dark green, occasionally green, rarely slightly light green.

Leaf Color (bottom): Dull pale green, dull green, dull gray-green, or pale green common, a dull white-green color or simple green color are rare.

Pubescence (where): Leaf veins, leaf underside, petiole, twig. Can range from slightly pubescent to densely pubescent. Traditionally densely pubescent though. Some individuals may entirely lack pubescence, though they appear to be infrequent.

New Twig Growth Color: Light brown-gray or brown-gray common, light brown or light gray can also be seen.

New Twig Growth Shape: Round or flattened oval.

Leaf Scar Shape: Oval and reniform commonly, half-round occasionally, very rarely U-shaped or crescent.

Bud Color: Medium brown to dark brown, a reddish tint is common regardless of the shade of color.

Lateral Bud Position: Beside or set far back, occasionally set slightly back.

It has been observed pumpkin ash tends to have darker colored leaves relative to the 'average' green seen in the genus (particularly in white ash and green ash). It was noted that *Rosa* polyploids, which had gigas characteristics, also had darker green leaves (Fagerlind 1958). This darker coloration has been documented in pumpkin ash leaves previously (i.e. Hough 1921). Pumpkin ash is known to be hexaploid, so this may be a reliable characteristic to use in conjunction with a few others to confirm identification of members of this species

The asymmetric bases in pumpkin ash were noted previously, being described as inequilateral (Gleason and Cronquist 1963).

The pumpkin ashes in Momence Wetlands lacked the flared-out base, but had 'feet', roots that connected to the trunk above the soil surface (Fig. 17). While occasionally the bases of a tree's roots are visible at the base of the tree, it is very uncommon to see so much exposed. This has not been seen in white, green, or blue ash. There most likely possibility that explains this is this may be the common form the flared-out base takes in landscapes that are not inundated for a portion of the year. It has been noted with bald cypress (*Taxodium distichum*), another species known for its swollen base, that the presence of such a base only occurs in sites which are inundated nearly year-round or have a very high water table; cypresses on sites that remain dry or only experience intermittent flooding lack the swollen bases (Wilhite and Toliver 1990). The buttressed base allows for trees to stand upright in soft, muddy soils, even when experiencing hurricane-force winds (Wilhite and Toliver 1990).

Some trees had leaf sizes and characteristics as well as twig characteristics resembling pumpkin ash except for the complete absence of pubescence. Such trees were also found in upland habitat and lacked the buttressed base, though it is unlikely such a form would occur in an upland habitat due to the lack of standing water. If these trees' identities can be corroborated by microscopic foliar analysis or DNA analysis, then the species description of a densely pubescent species limited to bottomlands and swamps would need to be revised. If these trees are simply hexaploid white ash, then species descriptions should indicate hexaploid white ash can imitate pumpkin ash to the extent they are indistinguishable with the naked eye and require microscopic analysis to differentiate. Of the pumpkin ashes that don't conform to the traditional definition, Dixon Springs SP and Crab Orchard NWR trees are the ones with the least confidence in their classification and the Red Hills pumpkin ashes have the most confidence in their classification.

Pumpkin ash occupying a different habitat than expected is plausible as it is theorized to be a hexaploid hybrid of white ash and green ash. As a result of not arising via traditional speciation, pumpkin ash could experience multiple originations over time and space. White ash and green ash are very genetically diverse species based on the high amount of anomalies and variation (and overlap) seen in both species. One is an upland tree, the other a lowland tree. It would seem improbable for pumpkin ash to display the same habitat preferences or overall characteristics at each place it originates (excluding 'gigas' characteristics associated with being a hexaploid, the ploidy being a necessity in its ability to speciate). For the most widespread pumpkin ash, green ash's habitat preference took dominance over white ash's and among plants in general, pubescence tends to be a dominant trait. If non-pubescent white and green ash produce a hybrid offspring which underwent chromosome doubling, the result would be a glabrous pumpkin ash. It is also not inconceivable that one of these originations could produce a pumpkin ash which would reside in upland habitats.

Fraxinus caroliniana

The current description cannot be revised based on the minor presence of Carolina ash in the sample collection. The presence of isolated individuals in northern Illinois should be noted on its range, though the presence is highly likely to be the result of an introduction.

The existing varieties of *Fraxinus* were given a similar treatment.

Fraxinus americana var. *biltmoreana*

Number of Leaflets: 5-9 leaflets were observed.

Leaflet Shape: Elliptical in almost all cases. Narrow elliptical, oblong, ovate, oval have been observed.

Leaflet Margin: Commonly crenate or faintly crenate, undulate. Occasionally entire or serrate. Some leaves with crenate, undulate, or entire margins have been observed with the margins slightly revolute as well.

Leaflet Tip: Most commonly acuminate. Acute, aristate are not uncommon. Cleft, cuspidate have been observed.

Leaflet Base: Most commonly acute. Cuneate, nearly obtuse have also been observed. Asymmetry is somewhat uncommon.

Petiolule Length: Commonly long or short. Medium was uncommon. Some petiolules were extra long.

Leaf Thickness: Thick, medium, thin have been observed. Sample size was too small to determine which one was most frequent.

Leaf Color (top): Light green, green, bright green have been observed. Slightly dark green or olive green have been seen as well.

Leaf Color (bottom): Pale green, pale light green, pale white-green were the only colors observed.

Pubescence (where): Leaf veins, leaf underside, petiole, twig. Can vary from slight to dense.

New Twig Growth Color: Brown-gray, gray-brown, light brown, dark brown, light gray have been observed

New Twig Growth Shape: Most commonly a flattened oval. Sometimes round

Leaf Scar Shape: Crescent, half-round, reniform, U-shaped have been observed

Bud Color: Medium brown, dark brown, and light brown have been observed. Some may have a reddish tint

Lateral Bud Position: Incomplete information

Fraxinus pennsylvanica

(This description describes what was traditionally considered *Fraxinus pennsylvanica*, red ash, and not what was known as the variety at the time, green ash)

Number of Leaflets: 5-9 leaflets observed. Similar frequencies to green ash.

Leaflet Shape: Most commonly elliptical, occasionally oval, ovate, narrow elliptical or wide lanceolate. Obovate, Oblong can occur.

Leaflet Margin: Most commonly serrate. Occasionally faintly serrate, sharply serrate, crenate. Serrulate, undulate, crenate/serrate mix has been observed. Some of the crenate and undulate leaves were slightly revolute.

Leaflet Tip: Acuminate, acute most commonly. Obtuse, caudate, aristate, emarginate, cleft have been observed.

Leaflet Base: Cuneate in most instances. Occasionally acute. Nearly obtuse has been observed.

Petiolule Length: Most commonly short, occasionally medium. Long is uncommon, a few can be extra long.

Leaf Thickness: Most commonly thick, medium common though. Thin and papery very uncommon.

Leaf Color (top): Green to dark green portion of spectrum common. Both green and dark green share about the same frequency. Any other color not observed.

Leaf Color (bottom): Most commonly dull green or green. Yellow-green is slightly common. Dark gray-green, gray-green, light reddish-green have been observed. Some of these colors can appear bright compared to the average color for leaf bottoms.

Pubescence (where): Leaf veins, leaf underside, petiole, twig, ranging from slight to dense on any part.

New Twig Growth Color: Commonly light brown-gray, brown-gray. Light gray or light brown rarely. Some seem to retain their green color even when dried.

New Twig Growth Shape: Almost all are round. Some have a flattened oval shape

Leaf Scar Shape: Reniform, half-round most common. Crescent, U-shaped has been observed.

Bud Color: Most commonly dark brown. Medium brown uncommon. Light brown rare. Reddish tint rare as well.

Lateral Bud Position: Most commonly beside, but being set far back is not infrequent.

Based on the data collected during this project and a survey of the literature, the genus *Fraxinus*, at least so far as the species found in eastern North America, would be reclassified as such:

Fraxinus americana (synonym: *F. juglandifolia, F. americana var. juglandifolia, F. americana var. crassifolia, F. curtissi, F. americana var. curtissi, F. americana var. microcarpa*)- A species with one subspecies, *Fraxinus americana subsp. texensis* (synonym: *F. texensis*), and one variety, *Fraxinus americana var. biltmoreana* (synonym: *F. biltmoreana*).

Fraxinus pennsylvanica (synonym: *F. pubescens, F. viridis, F. lanceolata, F. darlingtonii, F. campestris, F. smallii, F. pennsylvanica var. austinii, F. pennsylvanica var. subintegerrima, F. pennsylvanica var. integerrima*)- A species with no subspecies or varieties.

Fraxinus nigra (synonym: *F. sambucifolia*)- A species with no subspecies or varieties.

Fraxinus quadrangulata (synonym: none)- a species with one variety, *Fraxinus quadrangulata var. fuscopapyraceus*.

Fraxinus profunda (synonym: *F. michauxii, F. tomentosa, F. profunda var. ashei*)- A species with no subspecies or varieties.

Fraxinus caroliniana (synonym: *F. platycarpa, F. pauciflora, F. caroliniana var. cubensis, F. caroliniana var. oblanceolata, F. caroliniana var. pubescens*)- A species with no subspecies or varieties.

Appendix VII: Summary Statistics for *Fraxinus* Species

Some general data summarizing the data collected for the various characteristics of the species of *Fraxinus* may be helpful in determining what quantitative differences, if any, might exist between species as well as to have data for leaf characteristics so in the event the species are driven to endangerment or extinction, at least some comprehensive information about them is available. Data were compiled from averages for each tree which are then compiled into an average for each species (Tables 17-20). Pumpkin ash's numbers should be considered less accurate than the other displayed species due to its sample size being small (n=18). Black ash and Carolina ash are excluded due to their sample size being too small (n=4, n=2 respectively). Higher numbered sets of leaflets for all species are excluded when sample size is insufficient.

Compiled Averages for All Sampled *Fraxinus*:

The average values for all measurements utilized in this study compiled from all 235 ashes may have some value in providing information for the genus, so it is included below (Table 21).

Notes on Summary Statistics for *Fraxinus*:

Some findings from comparing the results of each species' quantitative averages aren't surprising while others are (Tables 17-20). Unsurprisingly, pumpkin ash has the highest mean and overall range for total leaf area and the ranges for other characteristics are shifted towards higher values than the other ashes. Interestingly though, white ash can equal or exceed pumpkin ash in some areas. Despite having a smaller leaf area than pumpkin ash, white ash's mean leaf mass is slightly greater than pumpkin ash. Pumpkin ash also had a mean leaf density identical to blue ash, where the thinness of leaves is a common feature. Pumpkin ash's range was also lower than blue ash's range, 0.003-0.010 g/cm^2 and 0.004-0.014 g/cm^2 respectively. These findings may be a result of the small sample size of pumpkin ash relative to the other ashes. A sample size comparable to the other species should bring less counterintuitive numbers for some of these values. White ash's range of lengths can exceed pumpkin ash's range, though the size of the range for widths is about comparable, with pumpkin ash tending to be wider. The important piece of information that can be gleaned from this is white ash can approach the size or weight of pumpkin ash on the high end and a significant part of the ranges for their values overlap.

Green ash's and blue ash's values were all lower relative to white and pumpkin ash. Outside of number of leaflets, all of green ash' minimum values fell below all other species' minimum values. Its means exceed blue ash's means in most areas though. So while these two species produce comparable measurements relative to white and pumpkin ash, green ash's tendency to have thicker leaves and blue ash's tendency to have papery leaves produces some differences in mean values. Additionally, blue ash displays less variability in the minimum and maximum value ranges (i.e. the smallest minimum to greatest minimum recorded for various lateral leaflets and the smallest to greatest maximum recorded for lateral leaflets) in its leaflets. This correlates with the lack of significance in the defined regions for blue ash. Green ash's greater tendency for variability in its morphology relative to blue ash accounts for this greater fluidity of value ranges. Blue ash had far less abnormalities or rare morphological characteristics observed than in other species.

The compiled average for a leaf across the entire genus in eastern North America (Table 21) produced some interesting findings. Despite wide variability in leaflet shapes, particularly with the lowermost pair of leaflets compared to higher pairs and even left leaflets versus right leaflets in the same pair, the values for length and width among leaflet pairs are nearly identical for most leaflets. The 1st pair had identical length and width values. The leaflets in the 2nd and 3rd pairs had identical width values. This corroborates the observation that in the middle pairs, they are very similar to nearly identical, particularly among width as they are sandwiched between different types of leaflet pairs and all middle pairs are generally copies of one another. The length values for the 2nd pair and 3rd pair were different, with the 3rd pair being slightly longer than the 2nd pair. General observation of all middle pairs finds the length tends to increase compared to previous middle pairs on the same leaf. The lengths for the left and right leaflets in the 2nd and 3rd pair were within 0.1cm of each other. The terminal leaflet tended to be longer and wider than any other leaflet pair, which fits general observations. Only the length and width values for the 4th pair produced differences exceeding 0.1cm between the left and right leaflets. This may be due to a greater variability among the uppermost pair or the values may be skewed by split-termini. Split-termini with the terminal leaflet replacing the right lateral leaflet were slightly more common on the right side and there were several instances of split-termini noted at the 4th node. Measurements for the 5th pair of leaflets were excluded since only a small number of leaves had 5 pairs of leaflets. So, despite wide variability in leaflet shape, number of leaflets, and occasionally asymmetry in length/width values between the left leaflets and right leaflets on the same leaf, average values for *Fraxinus* are surprisingly close between the left and right sides and between categories of leaflet pairs.

Appendix VIII: Causes of Difficulty in Identifying *Fraxinus* Species

With the effort to identify trees to species for the original purpose of this study, it became apparent there were dozens of individuals which were hard to place; they didn't fit nicely into the mould sculpted by the species descriptions in the literature. These either had one or two traits affiliated with another species or had several major differences from the classic examples of the species as painted by their descriptions. These tricky specimens comprised one-third of all trees sampled. From what has been seen in the collection compiled for this study, black ash and blue ash are easy to tell apart from all species; telling white ash, green ash, and pumpkin ash apart from one another, however, can be a challenging task.

Difficulty in discerning white ash from green ash has resulted in use of arbitrary rather than deliberate classification of trees. It has been noted many inventories of forests identify ash trees as white ash or green ash based solely on their position in the habitat, whether they are upland or lowland, or they don't differentiate between the two species at all (MacFarlane and Meyer 2005). This may have contributed to the cluttering of the species' identities, leading to further confusion via mislabeled specimens or specimens labeled without proper scrutiny.

Two of the characteristics that are traditionally used to distinguish white ash and green ash are white ash doesn't have a serrated margin, has long petiolules with an acute or rounded leaflet base, and has a pale underside (either a whitish-green or a white underside) while green ash has a serrated margin (usually), has short petiolules with a cuneate leaflet base, and has a green underside. Trees that otherwise fit the white ash profile except for having serrated margins have been seen. These problem ashes are fairly frequent in certain forests (e.g. Palos Division forests, Lowden SP, Sugar Grove NP). White ashes with cuneate bases are not infrequent, and ones with short petiolules are uncommon, but not rare. White ashes with dull green colors to the underside of their leaves have been seen occasionally as well. Green ashes with crenate, undulate, or entire margins have been observed. Ones with acute leaflet bases are not uncommon. Some green ashes have pale green to pale whitish-green undersides to their leaves. A few green ashes were also observed with long or even extra long petiolules; both species overlap with medium length petiolules as well.

A few other characteristics have been traditionally used to differentiate these species. Miller thought the best means of sorting the two species were the presence of concave leaf scars, ovoid terminal buds, and triangular lateral buds (white ash) and truncate leaf scars, conical terminal buds, and reniform lateral buds (green ash) (Miller 1955). Leaf scars have been shown to vary in white ash depending on ploidy, where the tetraploid's and hexaploid's leaf scars overlap with the shape of green ash's leaf scars. Lateral bud size and shape and terminal bud shape aren't reliable in discerning the species either. Another characteristic commonly used, the position of the 1st pair of lateral buds is also not reliable. White ash does have its lateral buds beside the terminal bud in most cases, but green ash commonly has its lateral buds besides the terminal bud as well. Only the frequency of occurrence is lower than with white ash.

One characteristic that was not commonly described but which appeared to easily differentiate the two was likewise unreliable. The shape of new growth in the twig was commonly a flattened oval shape in white ash and rounded in green ash. While green ash's twigs are rounded in most cases and the cases of a flattened oval shape are infrequent, the round shape in white ash is not uncommon.

The habitat they are located in can help. White ash is traditionally upland, found in drier forests or isolated woods and green ash is traditionally found in lowland forests or in riparian corridors. However, like with most other traits, there is a matter of frequency of occurrence. Green ashes have been observed on dry land in large numbers some distance from, but in general proximity to, a large lake or major river (e.g. Rend Lake, Fox River) and they have been observed on upland portions bordering a slope down to a river. White ashes have been observed near shallow creeks running through woods. It works in general, though there are some forests where the species overlap (e.g. Fox Ridge).

From what this author sees, there is no one reliable trait in white or green ash that occurs in all its specimens which can be used to differentiate it from the other species. All of the traditional wedge traits occur in both species at a frequency ranging from common to uncommon, but all tend to occur at a higher rate than truly rare traits (e.g. very odd leaflet tips, unusual leaf scar shapes, etc). The most reliable means to differentiate these species is to look at a whole set of characteristics. Most of the leaves or twigs of one species which impersonate the other species only do so with one or two characteristics; the suite of characteristics that separates species from species remains intact overall. A set of the following characteristics should be able to differentiate the impersonators from the genuine species: Leaf form, color of the leaf underside, petiolule length, margin type, leaflet base, lateral bud position, twig color (dried), new twig shape.

An examination of the anomalous characteristics and what other characteristics they appear with shows these individuals are mostly either white ash or green ash. First, looking at white ash, serrate or sharply serrate margins have been seen with medium, long, or extra long petiolules, pale white-green leaf undersides, and acute leaflet bases (all traditional white ash traits). Short petiolules have been seen with undulate or crenate margins, pale or dull white-green leaf undersides. Dull green or yellow-green leaf undersides have been seen with entire or undulate margins (and occasionally faintly serrate or mixed serrate-crenate margins) and medium to long petiolules. Cuneate leaflet bases as well as the first lateral bud pair being set back have been seen with traditional white ash characteristics too. In green ash, entire or slightly crenate margins have been observed with medium or long petiolules, cuneate leaflet bases, dull green leaf undersides, and lateral buds either beside or set back. Long petiolules have been observed with serrate, sharply serrate, or entire margins, dull green or pale light green leaf undersides, and cuneate leaflet bases (or leaves which have some cuneate and some acute leaflet bases). Pale green or pale light green leaf undersides have been observed with serrate or slightly crenate margins, short, medium, or long petiolules, and cuneate leaflet bases. Margins that are a mix of crenate and serrate have been seen as well.

Complicating the matter, there have been trees observed which resemble pumpkin ash with many characteristics (large conical terminal buds, large leaves, entire or undulate margins only), however, they have minimal pubescence (usually on leaf veins only or petiole only, but occasionally entirely absent) and are found in upland forests. The classic description of pumpkin ash is with its twigs, petioles, and leaf undersides densely pubescent, and found in swamps or lowland forests. Semi-reliable characteristics seem to be a dark green color to the leaves, a big conical terminal bud. Pumpkin ash helps compound identification even further as it has many characteristics common to white ash and green ash aside from the polyploid-related characteristics.

There are 76 tricky specimens in this collection, encompassing all of the individuals listed as anomalous or as "mystery". Breaking down the specimens into species (including keying those out designated as "mystery" to species), 46 are white ash, 16 are green ash, 11 are pumpkin ash, 1 is black ash, 1 is blue ash, and 1 is unknown (NAR02). The high number of white ash (nearly half of all collected specimens) reinforces the emerging portrait of white ash as a highly variable species. Green ash and pumpkin ash also have high numbers compared to their overall sample size (though pumpkin ash's high number of anomalous individuals is due to lack of pubescence or upland location and not due to the level of variability seen in white and green ash). There is no consistent suite of characteristics in these tricky specimens that would merit any of these impersonators being given a variety within their respective species.

While some species are hard to distinguish from one another even when well-versed in *Fraxinus* species, it does not seem likely *Fraxinus* is a compilospecies though. A compilospecies is a loosely defined 'species' able to take a wide range of forms, often considered species in their own right, usually having multiple ploidy levels and being of multiple hybrid origins and backcrosses (Spooner et al 2003). Compilospecies are known to obfuscate the boundaries of species. It seems unlikely due to the difficulty in finding hybrids between white and green ash; a compilospecies would have easy to find hybrids and ample evidence of hybridization and backcrossing. The possible role of hybridization in the classification confusion was ruled out in previous research as well (e.g. Miller 1955, Hardin and Beckmann 1982).