RECONSIDERING THE PALEORANGE OF *FAGUS GRANDIFOLIA*

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The undersigned, appointed by the dean of the Graduate School, have examined the [thesis or dissertation] entitled

RECONSIDERING THE PALEORANGE

OF *FAGUS GRANDIFOLIA*

presented by Stephen P. Markley

a candidate for the degree of master of arts,

and hereby certify that, in their opinion, it is worthy of acceptance.

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LIST OF ABBREVIATIONS

ascii: American Standard Code for Information Interchange

BP and B.P: years before present, the year 1950 being defined as the present.

COHMAP: cooperative Holocene mapping project.

D.N.A: Deoxyribonucleic acid; a nucleic acid that carries a cell's genetic information and hereditary characteristics.

ka, kya: thousands of years ago.

mya: millions of years ago

NAP: Non Arboreal Pollen, pollen whose source is not from trees.

WDC: World Data Center

yBP and yr B.P: years before present, the year 1950 being defined as the present.

yr k and yka: thousands of years ago.

ABSTRACT

One of the major consequences of forecasted future climate change is the redistribution of plant life due to species migrations and extinctions in response to these changes. This has caused many scientists to look at the history of vegetation migrations to help understand future vegetation management strategies and biodiversity concerns. Our knowledge and understanding of past long-term species range changes is best understood from interpretations of the palynological record.

This study reexamines paleopollen data from the World Data Center in conjunction with a recent chloroplastic DNA study of one temperate woody vegetation species, *Fagus grandifolia*. The pollen percentage level of 0.5 percent of total pollen is used to infer the presence of *Fagus grandifolia* at palynological sites. The majority of the sites that meet this threshold limit are located south of 34° N latitude for the time period of 21k to 16k BP, suggesting a paleorange confined to the Gulf Coastal Plain. When assumptions about the suitability of this threshold are challenged, a different late-Pleistocene geography emerges for *Fagus grandifolia.*

A survey of all palynological sites in the North American pollen database for *Fagus grandifolia* pollen, in conjunction with supporting DNA evidence, indicates consistent patterns of more northerly refugial locations and different migration routes for *Fagus grandifolia* than currently accepted. Patterns of pollen deposition and DNA evidence reveal a possible refuge in the area of the northern Mississippi Embayment. There is as well evidence of refugia for and expansion of *Fagus grandifolia* mixed with boreal forest elements along the Appalachian Plateau, closer to the ice sheet margin than the Gulf Coastal Plain.

Chapter 1 *Fagus grandifolia* and Past Climate Change

Introduction

There are many climate models that show that the addition of greenhouse gasses to the atmosphere due to the burning of carbon based energy sources, deforestation, and other anthropogenic processes will tip the balance toward a climate that will be several degrees warmer than today. Over the next several decades as well as centuries, models forecast that further global surface temperature change, whether based on human induced causes or naturally occurring climate cycles, will be on the order of from 0 .4º C to 4.0º C (IPCC 2007, 14). This warmer climate will spatially shift the current environmental conditions of the Earth for both plants and animals, including humans. A look at past climate change and its effects on the environment may give insight into the future changes we might expect. This is important because "…changes in components of the Earth's biodiversity cause concern for ethical and aesthetic reasons, but they also have a strong potential to alter ecosystem properties and the goods and services they provide to humanity" (Hooper et al. 2005, 3). Perhaps by a better understanding of species response to past climate changes, management will be enhanced.

It has been hypothesized that during the last glacial maximum, or LGM [see appendix A for glossary], small pockets of temperate tree species may have survived in favorable environments whose micro-climates were less xeric and were perhaps topologically protected from the harshness of the general climate of the time (Rowe et al. 2004). "Deciduous tree pollen increases in abundance rapidly at many southern sites during the late-glacial period, suggesting that at least small populations of temperate trees such as *Fagus* grew nearby in very small, scattered refuges at the time of the glacial maximum" (Davis 1983, 553-54). These refugia may have been geographically small in area and perhaps due to the relative sparseness of palynological study sites and geographical extent of North America, evidence for these refugia simply may not have been discovered yet. The relevance of the study of these refugial areas of is that they give temporal insight into the processes of vegetation survival and biodiversity (Taberlet 2002).

The current method used in palynology to identify past species range limits is that pollen must reach a certain percentage of total pollen found at a site before its actual presence can be inferred. This study will utilize a modified method. It will look for accumulation and temporal patterns of pollen deposition rather than percentages of a species' pollen, thus eliminating false positives resulting from far-travelled pollen and false negatives due to such things as small pollen-producing populations or small catchment areas. Utilizing this method in conjunction with a genetic study done by McLachlan, Clark, and Manos (2005), the study will look for refugia and refine the paleorange limits of the temperate deciduous species *Fagus grandifolia* during the retreat of the Laurentide Ice Sheet from North America (Fig.1.1).

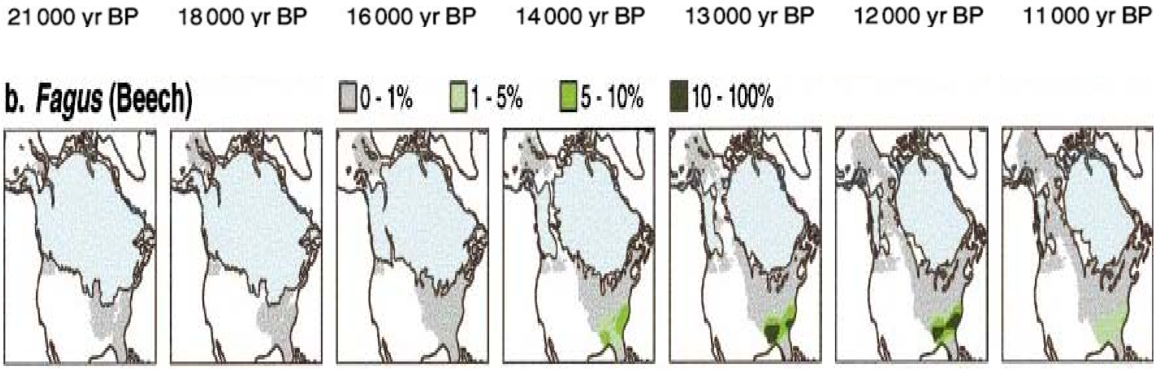

Figure 1.1 Fossil pollen percentages for *Fagus grandifolia* during the Laurentide Ice Sheet's retreat (adapted from Williams et al. 2004).

1.1 *Fagus grandifolia*

Fagus grandifolia (American beech; Fig. 1.2) is a mesophytic deciduous tree. It grows to a height of 25 meters on average but can reach 40 meters and has a lifespan up to 300 years (Coladonato 1991).

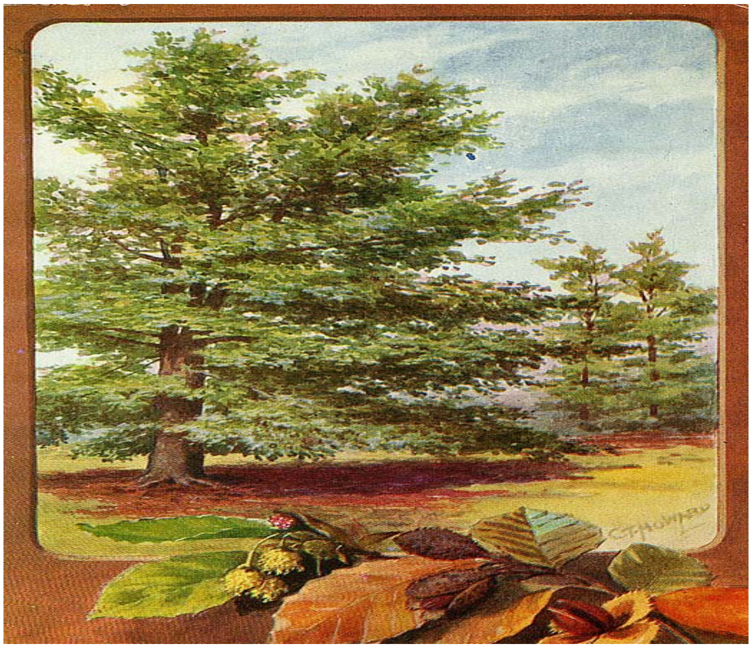

Figure 1.2 Profile of a mature *Fagus grandifolia* tree (Hatzigeorgiou 2009)

Soil moisture is a limiting factor for this species at the western extent of its range in North America (McLachlan and Clark 2004, Fig. 1.3). A temperature limit of -30º C to -45º C is *Fagus grandifolia's* freezing limit; below this is when intracellular damage starts to occur and -12º C is the minimum mean January temperature at its present day northern range limit in North America (Huntley, Bartlein, and Prentice 1989). *Fagus grandifolia* is often a dominant hardwood in the Appalachians, the Northeast, and the northern Midwest (Coladonato 1991).

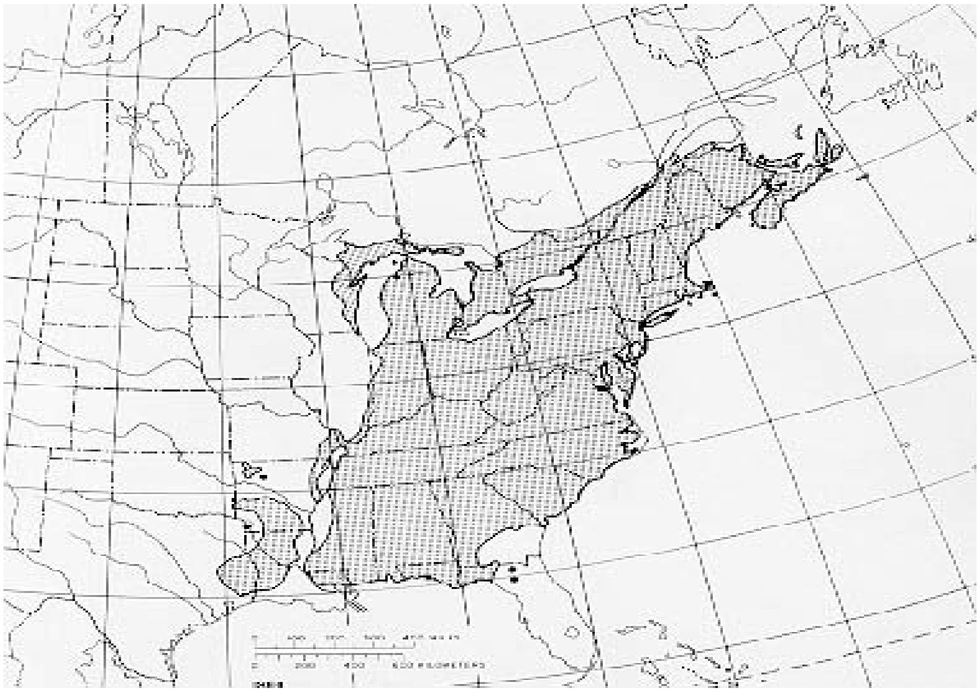

Figure 1.3 Current range of *Fagus grandifolia* in North America (Tubbs and Houston 1990)

Fagus grandifolia reproduces by both seed dispersal and root sprouts. Seed dispersal is thought to be assisted by blue jays (*Cyanocitta cristata L.*) and in the past, passenger pigeons (*Ectopistes migratorius*) as well as other seed predators (Delcourt and Delcourt 1987; Webb 1987; Huntley, Bartlein, and Prentice 1989). It is also thought that root sprouting is possibly *Fagus grandifolia's* response to severe climatic induced environmental conditions of its habitat such as precipitation amounts and/or temperature ranges (Held 1983; Kitamura and Kawano 2001). Reproduction by root sprouting has a large impact on the localized genetic profile of this species (Kitamura and Kawano 2001).

Fagus grandifolia has been reported to diffuse at rates of from 150 to 300 m yr^{-1} as inferred from its fossil pollen record (Bennett 1985; Delcourt and Delcourt 1987; Huntley, Bartlein, and Prentice 1989). This dispersal rate may decrease as less habitable environments for this species become the norm at the northern limits of its range (Bennett 1985).

The refugial centers for *Fagus grandifolia* as identified by palynologists Paul and Hazel Delcourt for the late Pleistocene/ early Holocene are in the central and eastern gulf coastal plain of North America (Delcourt and Delcourt 1987). The Delcourts extrapolated their refugia and inferred range from palynological study sites where a specific pollen percentage threshold was reached signifying the presence or absence of the species. These inferences based on pollen threshold limits can come into question, as modern pollen studies having revealed that "[o]nly 25% of sites in the southern half of beech's range exceeded the … threshold" limit currently defined for this species (McLachlan and Clark 2004, 142).

This study will reexamine the paleopollen record by mapping the World Data Center's (WDC) sites in eastern North America containing *Fagus grandifolia* pollen. A look at the temporal patterns of pollen evidence will be utilized so as to provide an alternative to the simple pollen thresholds limits that have previously been used to determine species range limits. Patterns of *Fagus grandifolia* DNA in eastern North America taken from McLachlan, Clark, and Manos' (2005) study will also be mapped due to the fact that their "… data indicate that divergent lineages of beech also persisted in interior refuges near the former ice margin" (McLachlan, Clark, and Manos 2005, 2095).

The goal of this mapping project is to see whether it can demonstrate possible refugial centers and migration routes better than those shown using traditional pollen thresholds. The results of this reexamination may contribute to a better understanding of past vegetation dynamics and response to climate change.

1.2.1 Past Climate Change

Climate is a constantly changing factor not only over relatively small temporal extents such as years, but also in much larger extents such as geological time frames. The paleoclimatic record indicates that at present, the earth is currently within a broader cycle of glacial/interglacial recurrence, "[t]he 100,000-year timescale in the glacial/interglacial cycles of the late Pleistocene epoch (the past ~700,000 years) is commonly attributed to control by variations in the Earth's orbit" (Huybers 2005, 491). Recurring variations such as obliquity and precession of the planet's orbit cause waxing and waning of the amount of solar radiation warming the Earth.

These orbital cycles sometimes resulted in the process of ice sheet formation over large areas of the northern continents. These orbital variations have determined the magnitude and timing of 100,000 year glacial periods for at least the past 1 million years (Kerr 1987; Muller and MacDonald 1997). There is further evidence of even shorter geological time scales involved when time spans as small as 10,000 years have seen the pace of climate change mimic the longer period glacial formation periods (Steig 1999).

The most recent glacial climate oscillation, the Wisconsinan, resulted in the formation of the Laurentide Ice Sheet which extended from approximately the continental divide in the west to the continental shelf in the east and the high Canadian Arctic in the north to roughly 39° N at its southern extent (Fig. 1.4).

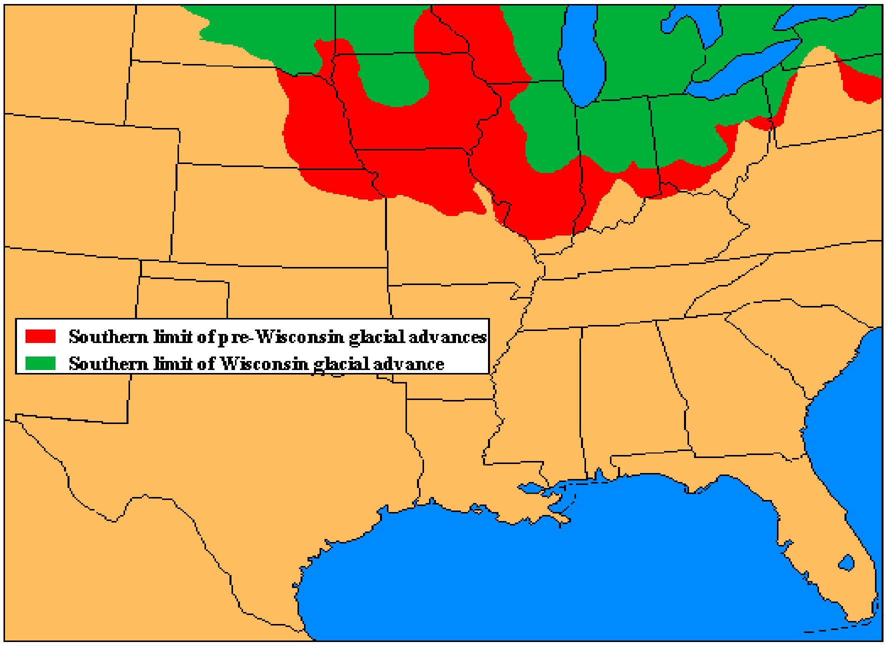

Figure 1.4 North American Pleistocene glacial extents in the Midwest (E.P.A. 2007).

1.2.2 Climate and Ecology

One of the foremost determinants of the ecology of a region is its climate. Average precipitation and temperatures greatly affect biome distributions. Climate change therefore has a large impact on the composition of vegetation in a region (Emanuel, Shugart, and Stevenson 1985). Changing temperatures during the Pleistocene (Fig. 1.5) caused large spatial shifts in the ranges of species such as *Fagus grandifolia*. “Over glacial-interglacial cycles, climatic and environmental changes have restructured biological systems, resulting in disassembly and reassembly of communities, individualistic migrations of species, and changes in genetic diversity resulting from alternate restriction and release of refugial populations” (Delcourt and Delcourt 1998, 923).

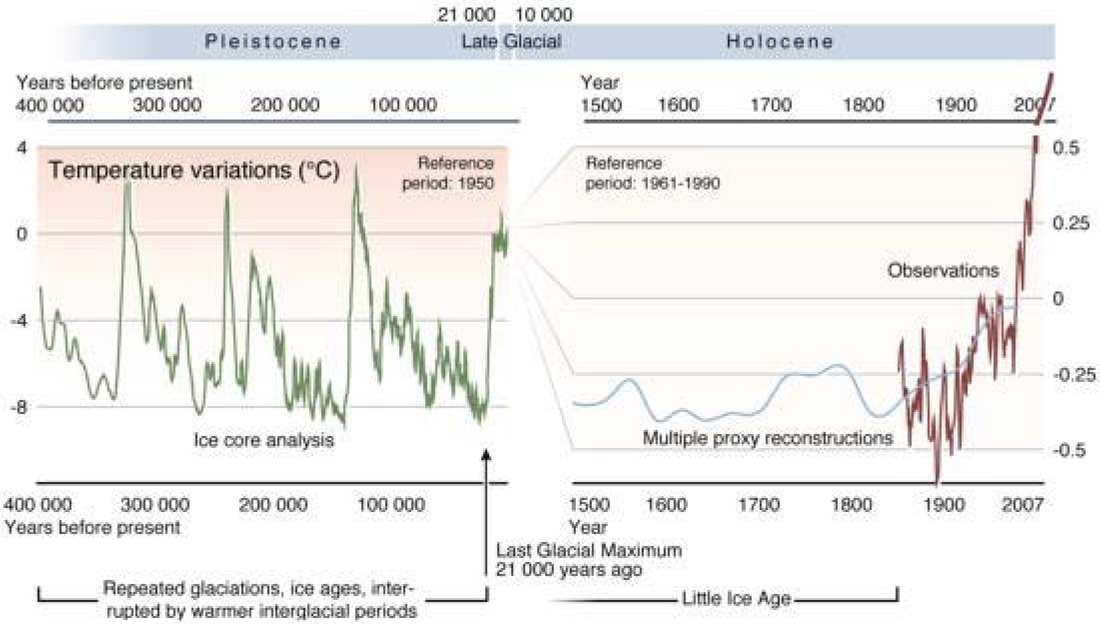

Figure 1.5 Global temperature oscillation during late Pleistocene/ Holocene Periods (adapted from U.N.E.P. 2007).

Plant populations have continually advanced and retreated across the North American landscape in response to complex and continuous changes in environmental conditions (Huntley and Webb 1989). “Ecologists and resource managers are recognizing that environmental variability at timescales of 10^1-10^4 years play a major role in governing spatial patterns and temporal dynamics of populations, communities and ecosystems” (Jackson and Overpeck 2000, 195).

An important question to ask is what effects a future global climate change, regardless of its cause, will have on both society and the earth’s ecosystems. For example, a change in climate can modify disturbance regimes and thus alter the biodiversity of a region (Gita 2002). The impacts of future climate change will have consequences for humans in the forms of agricultural practices and production because of climate’s influences on these ecosystems. These changes will be spatial in that, as the climate changes, so do environmental parameters relevant to particular locations where the growing of crops and husbandry are currently practiced. “The synergism of rapid temperature rise and other stresses, in particular habitat destruction, could easily disrupt the connectedness among species and lead to a reformulation of species communities, reflecting differential changes in species, and to numerous extirpations and possibly extinctions” (Root et al. 2003, 57).

A look at past climates through proxies such as glacial ice cores and their spatial and biological effects on plant and animal species as evidenced in the fossil record will give insights into future biogeographical distributions. This look back at past climate change and its effects will also enable us to fine tune climate models so as to forecast the extent and intensity of these future changes (Birks and Birks 2000). An understanding of the changing climate parameters and the consequent vegetation patterns changes in North America during the LGM have importance in the forecasting of future climate change (Jackson et al. 2000).

1.3 Interpretations of the Fossil Pollen Record

Climate cycles have had major impacts on the composition of plant life in the northern latitudes of North America. At the maximum extent of the Laurentide Ice Sheet at approximately 21,000 BP (approximately 18,000 ^{14}C dated years ago), the vegetation is characterized as one of steppe and tundra in the American Midwest, and boreal forest elements in much of the eastern part of North America (Jackson et al. 2000; Williams et al. 2000). "The fate of warm temperate biota of the eastern United States during a glacial maximum is one of the intriguing problems in Pleistocene biogeography" (Martin and Harrell 1957, 468). As the Laurentide Ice sheet waned at approximately 14k BP, pollen evidence of temperate vegetation appears relatively quickly. This perhaps suggests "that at least small populations of temperate trees such as *Fagus* grew nearby [(the glacial margin)] in very small, scattered refuges at the time of the glacial maximum" (Davis 1983, 554). The current understanding from the palynological record however shows that temperate deciduous species such as *Fagus grandifolia* were only found in the Lower Mississippi Valley (Jackson et al. 2000).

In 1987, Paul and Hazel Delcourt produced an exhaustive compilation of palynological records in the eastern United States (Delcourt and Delcourt 1987). They characterized the nature of arboreal species change at the time of the late glacial period as one of a transition from *Pinus banksiana* "through mixed hardwood northern forest with increasing contributions of oak *[Quercus]*, hickory *(Carya)*, beech *(Fagus grandifolia)* and sugar maple *(Acer saccharum)*, to mixed deciduous forest dominated by oak *[Quercus]*and hickory *[Carya]*" (Delcourt and Delcourt 1984, 1987, 22-3; Fig. 1.6, [see appendix B for common names of taxa metioned in this thesis]). With the retreat of the glacial climate from the Midwest, the Delcourts say that "… relatively stable full-glacial boreal forest was replaced by cool-temperate deciduous forest in the Holocene, after an interval of compositional instability and successive migrations during the late-glacial and early Holocene intervals" (Delcourt and Delcourt 1987, 22).

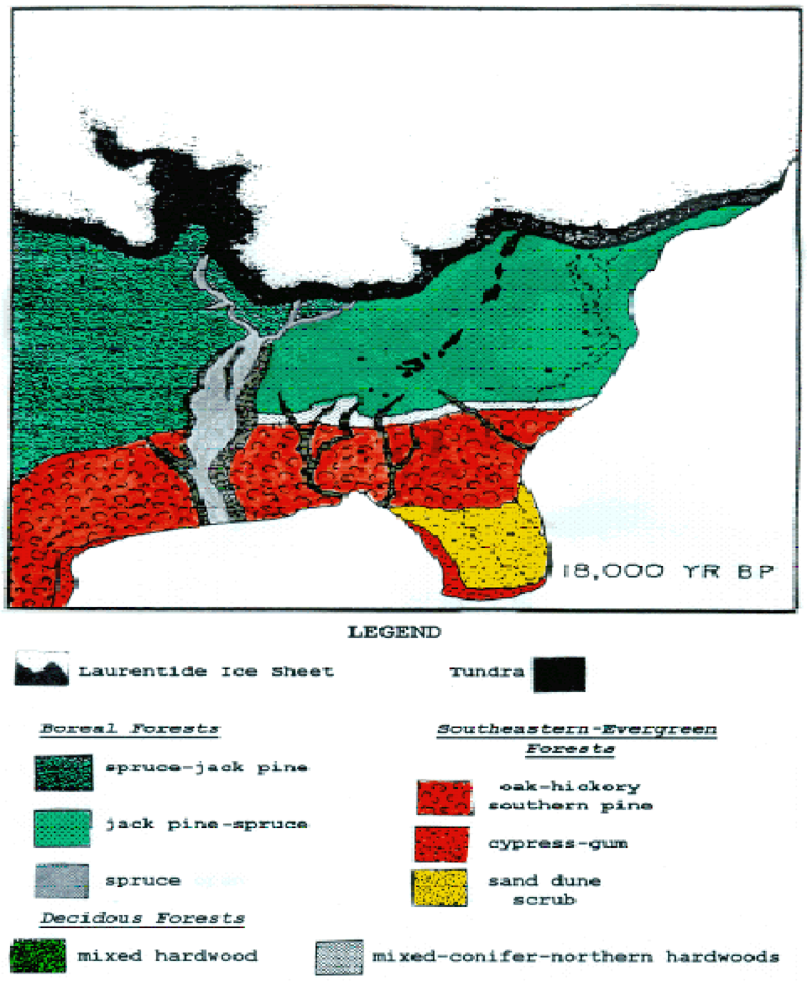

Figure 1.6 The Delcourt and Delcourt (1984) Paleovegetation Map for 18,000 yr BP.

In her seminal paper, "Development of the Eastern Deciduous Forests of North America (1947)," E. Lucy Braun describes the migrational strategies of arboreal plant life during the Pleistocene thusly, "[n]orthern plants migrated southward in advance of the ice (in response to climatic change), invading the established vegetation insofar as suitable habitats were available or weakened competition of more southern forms permitted; [t]o and fro migrations took place, not once, but with each advance of ice" (Braun 1947, 216). Braun thought that palynological studies showed that the deciduous forest was not driven to migrate far to the south of the Laurentide Ice Sheet's advance as the climate changed. She thought that, other than in a zone along the ice sheet's edge, the region was still temperate enough for survival of deciduous species. Braun believed that a mixed mesophytic forest existed on the Allegheny and Cumberland plateaus of the Appalachians and that this was the ancestral home of today's Eastern North American deciduous forests (Delcourt 2002).

This was contradicted by Edward Deevey who did not agree that plant communities had simply migrated a relatively short distance north and south as the climate oscillated. He put forth the theory that Pleistocene plants had diffused much further south with climate change than Braun believed. He theorized that northern deciduous forests retreated to refugia in peninsular Florida and the Gulf Coast region during the glacial maximum, with a band of *Picea*-dominated boreal forests to the north that had also shifted southward with the advance of the Laurentide Ice Sheet (Deevey 1949). As evidence for these more southerly refugial locations, Deevey cited *Picea* macrofossils and pollen grains found in the 1930s and 1940s in Louisiana, Texas and Florida as well as spruce pollen found in Mexico's central valley region (Delcourt 2002).

Paul and Hazel Delcourt say that at the beginning of the retreat of the Laurentide Ice Sheet, around 18,000 BP, and its accompanying climate change resulted in coniferous and deciduous hardwoods assemblages following the boreal forest northward as the ice sheet retreated (Delcourt and Delcourt 1987; Pielou 1991). As the Laurentide Ice Sheet's extent waned at the end of the Pleistocene into the early Holocene, the areas once dominated by boreal forest at 14k BP now at 10k BP were now colonized by a combination of prairie, deciduous forest, and a mixture of northern hardwoods (such as *Fagus grandifolia*) and conifer trees (Delcourt and Delcourt 1987).

More recently, after examining the data from over 700 North American fossil pollen sites, Williams described the vegetation and changes due to the Wisconsian glaciation of North America in the following terms, "[n]orthern populations of boreal taxa (e.g., *Picea*, *Pinus*, *Abies*, *Larix*, and *Betula*) expanded in areas vacated by the retreating ice sheets while southern populations declined. Temperate trees increased in abundance and their distributions shifted north from the southeastern United States" (Williams et al. 2004, 318).

1.4.1 Paleovegetation Migration

The migration of the vegetation is governed by the distance of range expansion during a certain time period (Clark and Fastie 1998). The migration capacity of arboreal taxa is based on an individual species' capacity to disseminate its pollen and seeds. The pace of migration of an individual species is difficult to resolve but, "[a]ccording to such reconstructions, species with a variety of life histories and dispersal mechanisms migrated northwards at rates of 102 to 103 m per year" (McLachlan and Clark 2004, 139). Dispersal capacity is used, by the proxy of the palynological evidence and macrofossils, to develop paleovegetational reconstructions of species range limits during the past.

The migration rates of paleovegetation that are derived from the fossil pollen record do not coincide necessarily with the expected dispersal rates as evidenced by present day vegetation; they are far too fast to coincide with the rate observed in modern studies (Clark and Fastie 1998). The creates difficulties in predicting future response to climate change because of the variability of vegetations response to climate changes that have occurred in the past have no modern analogues (Shaver et al. 2000).

The study of *Fagus grandifolia's* migration in relation to climatic patterns indicates that "[c]omparison of the [current] geographic ranges of Fagus … with climatic maps suggests that the ranges may be determined primarily by some combination of summer and winter temperatures" (Huntley, Bartlein, and Prentice 1989). "Although indices like the accumulated temperature over the growing season and the winter minimum temperature may be most directly related to plant growth, these indices are highly correlated with the monthly mean temperatures for July and January respectively" (Huntley, Bartlein, and Prentice 1989, 554).

The reconstruction of paleovegetation's range limits due to migration are too intricate to be just spatial displacements due to environmental change (Prentice, Bartlein, and Webb 1991). This raises the question that, if the paleorange limit of a species is based on paleoclimatic reconstructions derived from the fossil pollen record, does the pollen record *actually* indicate favorable climatic conditions for the species at the time or could the pollen record perhaps indicate evidence of a refugial location (Birks and Birks 2000)?

1.4.2 Paleovegetation Range Limits

It may be possible to refine certain paleorange limits and migration pathways. Characteristic problems that occur when inferring the spatial attributes of a species include such things as imprecise taxonomic identification and the limited overall spatial extent of palynological study sites; these factors sometimes cause the vegetation patterns evidenced in the past to be overlooked by today's ecologists (Odgaard 2001). Another factor to be considered is the temporally-constrained character of the paleopollen found in the stratigraphic record. This constraint results sometimes in palynological study sites that include only relatively small slices of time in that the core samples themselves often record only short and widely dispersed portions of time (Odgaard 1999). The accuracy of quantifying past pollen production by the current method of correlating its past production to present day production must also be considered. "The use of correction coefficients on fossil data requires that the coefficients for each taxon be relatively invariant through time. Evidence however often exists that the sampling site and its surrounding vegetation have changed through time, and these changes may require alterations to the coefficients" (Bradshaw and Webb III 1985, 721). It is therefore quite possible that past patterns inferred by examining paleopollen evidence might sometimes be inaccurate.

Another factor to be considered when looking at individual species such as *Fagus grandifolia* is that the paleopollen record has mainly been used to construct past vegetation assemblages rather than determine the presence or absence of one particular species (Odgaard 2001). Resolution becomes even coarser as increasing precision is attempted because the taxonomic identification to the species level can sometimes not be determined and this identification problem changes from sample to sample (Williams et al. 2000). Although the picture of past distributions is becoming clearer with the investigation and analysis of new palynological sites, the aforementioned factors and others sometimes result in a very broad picture of paleovegetation distributions.

Questions can therefore consequently arise as to species' ranges and geographical distributions that are inferred from the paleopollen record. "In order to understand the changing plant distributions and abundances of the postglacial, a flexible approach to the early stages of increase of pollen curves is needed. In some instances they may represent far-travelled pollen, but in others they may represent pollen from small local populations" (Bennett 1985, 149). This leads to uncertainty of how past climate affected the range limits of certain species, particularly those species whose evidence in the paleopollen record like *Fagus grandifolia* is scant due to biological factors inherent to the species such as low pollen production rates. In the case of *Fagus grandifolia*, it is classified as a K-migration strategist whose percent dominance in the fossil pollen record is miniscule and "… it is doubtful whether the interpretation of pollen records will ever be developed to be able to sense small isolated tree populations far outside a migrational front" (Odgaard 2001, 199). These factors call into question the accuracy the currently inferred ranges of species like *Fagus grandifolia* derived from its fossil pollen percentages.

1.5 Pollen Evidence Threshold Limits

It is a basic assumption of palynology that there is a definable correlation between a species abundance and the pollen it manufactures and distributes (Brown 1999; Birks and Birks 2000). The typical amount of pollen an individual species distributes is taken from modern pollen studies and used as a proxy in fossil pollen studies (Schwartz 1989). This amount of pollen is then correlated to other species pollen amounts to determine its hierarchal place in paleovegetation reconstructions (Prentice and Parsons 1983).

Typically a threshold is established by determining a level of a species pollen percentage that species/genera can not fall below and still be considered present at the locality being studied. "… [S]tudies depend on fossil pollen to provide evidence for the locations of species range limits in the past. It is therefore critical to define the pollen criteria that can be used to detect species presence or absence" (Davis, Schwartz, and Woods 1991, 653). The threshold used to determine the presence of *Fagus grandifolia* is 0.5 percent of the total pollen counted from the sample (Webb 1987; Davis, Schwartz, and Woods 1991; McLachlan and Clark 2004).

The mechanical aspects of the generation of pollen such as its release rate to the atmosphere as well as other environmental mechanical factors such as prevailing wind directions may have an effect on the amount recoverable from palynological study sites (Odgaard 1999). With this in mind, the 0.5 percent threshold limit for *Fagus grandifolia* pollen that is presently used as an indicator for this species paleovegetational presence is reexamined.

One problem with the pollen record is that not every kind of pollen locally present at the time of deposition will survive to the time of extraction, let alone be deposited at a study site. This could lead to gaps such as overlooking the presence of a species in vegetation reconstructions. “A logical problem with the rational limit, even assuming it is correctly determined, is that pollen percentages exceeding the rational limit provide evidence for the presence of nearby source plants, whereas percentages below the rational limit are *not* convincing evidence of the regional absence of source plants. For example, low values can be found in surface samples from unusual habitats well within the geographical range of a species” (Davis, Schwartz, and Woods 1991, 653).

It may be possible to dismiss low pollen percentages of *Fagus grandifolia* at a study site as an irregularity due to extraneous wind or waterborne deposition rather than indicating the species presence at a particular palynological studies’ location. “[T]he error associated with prediction of tree frequencies from pollen frequencies is shown … to preclude any assurance of accuracy with normal pollen count levels” (Schwartz 1989, 129). “When a pollen curve first becomes continuous and rises, this may represent continuing expansion of the taxon from earlier frequencies too low to be detected in the pollen counts” (Bennett 1985).

1.6 Conflicting DNA Evidence and Paleovegetational Reconstructions of *Fagus grandifolia*

The ranges of arboreal taxa have been most often interpolated from the presence and relative abundance of pollen in the sedimentary record. New phylogeographic reconstructions do not always agree with the geographic patterns of distribution derived from the fossil record; most often this is due to lack of palynological data (Comes and Kadereit 1998; Hewitt 2004; Lascoux et al. 2004; McLachlan, Clark, and Manos 2005).

The relatively slow rate of genetic mutation of the chloroplastic genome has allowed researchers to infer post-glacial patterns from modern genetic samples (Provan, Powell, and Hollingsworth 2001).

Genetic histories are proving instructive in the development of histories during the late Pleistocene (Rowe et al. 2004). “Recently, molecular biogeography or phylogeography has provided new sources of information on the glacial history of species and their range shifts as inferred from the geographical patterns of genetic variation” (Schonswetter et al. 2005, 3547). “ …[A]spects of demography and phylogeography can be discerned by nested clade analysis, and spanning haplotype networks can reveal both demographics and geographic history” (Hewitt 2000, 908). This “genetic data [can be used] to estimate the demographic history of a population, the dates of historical bottlenecks or expansions, the size of ancestral populations, the location of refugial areas, the dates of divergence, the extent of migration and gene flow, the extent of fragmentation, and the sequence of such events to produce the present geographic distribution of genotypes…” (Hewitt 2004).

The combination of recent genetic studies with that of currently inferred species presence and ranges can be used to evaluate species refugial locations and the consequent diffusion as well as the resulting genetic patterns (Magri 2006). With the advent of genetic examinations of present day deciduous taxa in relation to paleogeographic diffusions and range limits during the LGM, it is thought that “…divergent chloroplast DNA sequences from extant populations of several deciduous forest trees near the southern limit of the Laurentide ice sheet indicate the maintenance of separate lineages that may have persisted closer to the ice sheets than previously expected" (Rowe et al. 2004, 10355).

Incongruities in the paleoranges and diffusional routes presently inferred from the palynological record for *Fagus grandifolia* during the LGM and the genetic evidence of the present day range present a dilemma. "The data from the study of the cpDNA is based on modern material that may be precisely identified at the species level, and precisely located geographically. In contrast, whilst pollen studies provide thousands of years of vegetation history…[,] … the dispersal of the pollen grains limits the geographical precision of these studies" (Petit 2002, 51). Now however, cpDNA data can sometimes be used as an autonomous source in determining species past ranges (McLachlan, Clark, and Manos 2005). This is due to the fact that species "… colonization of new habitats occurs through seeds, chloroplast DNA (cpDNA) markers provide information on past changes in species distribution that is unaffected by subsequent pollen movements" (Petit 2003, 1563) and "[b]ecause it is likely that modern cpDNA haplotypes pre-date postglacial colonization (mutation rates in the chloroplast genome are low), and because there is little gene flow into established populations, the modern geographical distribution of cpDNA haplotypes can be used to infer past migration dynamics" (Pearson 2006, 112). Localities that were colonized after the retreat of the Laurentide Ice sheet are expected to have less evidence of genetic diversity due to founder effects than those areas that maintained a population throughout the glacial period (Hewitt 1996; Comps et al. 2001). The cpDNA molecular markers indicate that *Fagus grandifolia* may have been in evidence during the LGM in small refugial populations as close as 500 km to the edge of the ice sheet (McLachlan, Clark, and Manos 2005).

The presently inferred refugia for *Fagus grandifolia* during the LGM are located in the eastern and central gulf coast plain and northern Florida (Delcourt and Delcourt 1987). The Delcourts surmise that there were "limited populations of beech south of 34º N and east of 90º W" (Delcourt and Delcourt 1987, 176), but they also indicate that there were other outlying populations northwest of this range between 20k BP and 14k BP (Delcourt et al. 1980). It has been hypothesized by Bennett that *Fagus grandifolia* did not just exist in these coordinate ranges but had multiple refugia over a much larger area much closer to the ice sheet during the LGM (Bennett 1985) and then rapidly diffused into the recently deglaciated areas such as the upper Midwest (Williams-Linera, Rowden, and C.Newton 2003).

"American beech populations comprise a considerable amount of genetic variation throughout its geographic range" (Kitamura and Kawano 2001, 360). Recent studies of the genetic markers of present day *Fagus grandifolia* population (chloroplastic DNA haplotypes) suggest another route of expansion of this species from refugia farther west than the currently palynologically inferred routes originating in the Appalachians (McLachlan, Clark, and Manos 2005). This is also supported by genetic data that reveal a difference between current northern and southern *Fagus grandifolia* populations' isozyme markers (Kitamura and Kawano 2001; McLachlan, Clark, and Manos 2005). "This evidence suggests that the sharp differences detected between the northern-montane ('with' root sucker formation) and the southern-Piedmont-coastal ('without' root suckers) populations in the allele frequencies may reflect an extended period of isolation, i.e., genetic variations that differentiated at earlier stages during range extension are still conserved in these populations" (Kitamura and Kawano 2001, 360).

Studies of both fossil pollen and genetic data together in Europe have "… reveal[ed] new, unexpected perspectives on the history of [the related species of *Fagus sylvatica*], answering some questions concerning the relationships between the past geographic distribution of this species and its modern genetic distribution" (Magri 2006, 217). Is it possible to reach a better understanding of where *Fagus grandifolia* survived in North America during the LGM?

It is hoped that by mapping with a different method of data analysis of the paleopollen record in conjunction with modern cpDNA data that areas of refugia and possible diffusion areas for this species can be discovered. Areas of survival further north than 34º N latitude and further west than 90º W longitude which are the currently accepted range limits for *Fagus grandifolia* at the LGM.

Chapter 2 Methods

Data about paleovegetation assemblages is gathered by looking at fossil pollen that is preserved at select sites (Huntley 2001; Lui and Lam 1985; Davis 1983). This form of investigation has been the foremost method used in determining the climate and vegetation of the late Pleistocene/early Holocene (Faegri and Iversen 1975). By examining pollen grains that are present in the different layers of the soil, the presence and chronology of plant species can be inferred (Jackson et al. 2000).

2.1 Species Inference and Evidence Thresholds

The accumulation of fossil pollen grains is important in that the past presence of a taxon is often determined by a percentage level of its pollen in comparison to all the pollen found in a core (Brewer et al. 2002; McLachlan and Clark 2004). It has been generally accepted that this percentage threshold for the past presence of *Fagus grandifolia* in an area in close proximity to a palynological site be 0.5% of the total pollen found (Davis, Schwartz, and Woods 1991; McLachlan and Clark 2004). Fossil pollen is also used to provide evidence of a species paleorange limit (Davis, Schwartz, and Woods 1991). The focus of the methodology in this paper is a reexamination of *Fagus grandifolia* behavior during the late Pleistocene by not strictly using pollen percentages from the palynological record as an indicator of the species refugial locations but rather by examining recurring patterns of deposition, whether spatial or temporal in nature.

The currently accepted pollen analytical technique is based on statistical pollen amounts of species at palynological sites. A single probability threshold is developed for a species based on its pollen percentages found at other sites and modern studies of the species pollen production. This single probability threshold for a species pollen percentage is then assigned to a species and used to infer or reject a species' presence at all palynological sites (Brewer et al. 2002).

Species pollen percentages at individual sites, however, are developed from palynological sites that each have their own data sets. Each individual site has a different number and type of species present making up the total pollen count that an individual species percentage is derived from. Results could be skewed for a species that produces low amounts of pollen and is at a site with a species that produces copious amounts of pollen or a site that has a large number of species and therefore a large total pollen count.

This method could result in a statistical Type 2 error ("false negative") by accepting the hypothesis that pollen for a species has to reach a percentage threshold before its presence can be inferred when the species was actually present. This error would disallow the probability that certain sites and times actually had *Fagus grandifolia* present due to its low pollen levels. Perhaps by using a different method we may offer an alternative to the current understanding of the refugia during the LGM and migration paths used by this species during the late Pleistocene as the climate warmed.

This study examines different evidential criteria for the presence of *Fagus grandifolia* other than a threshold level of fossil pollen. No threshold is used at all. Pollen percentages are still used however so as to display different evidential levels and infer the past population of different sites.

This unconstrained level of examination is used to examine the patterns that may be revealed by mapping palynological sites that contain any pollen evidence. This method precludes either a Type 1 (“false positive”) or Type 2 statistical error by utilizing cpDNA data and the analysis of patterns of evidence rather than the statistical amount of a species pollen in relation to total paleovegetation pollen at a site.

In the case of *Fagus grandifolia*, “[m]oderate-sized lakes (30-150 ha) accumulate significant quantities of *Pinus* and *Quercus* pollen produced farther than 30 km away, but accumulate relatively few *Fagus* grains from >4.5 km …” (Bradshaw and Webb III 1985, 721). This reexamination is in order because, as Bennett put it in 1985, “[t]he spread of *F. grandifolia* across the continent was achieved at very low population densities. The detection and tracking of such a spread is only marginally possible with current pollen-analytical techniques” (Bennett 1985, 147).

To reexamine the paleorange of *Fagus grandifolia* in North America, two sets of data are examined, palynological study site’s fossil pollen finds and modern chloroplastic DNA samples of the species. The two sets of data are combined on maps of the eastern half of North America to determine if any patterns of evidence along with any associations between the two data sets might suggest a different geography of *Fagus grandifolia* refugia other than the one derived from prior interpretation of the palynological record.

2.2 Analysis of Soil for Pollen Evidence

Faegri and Iversen (1975) summarize conventional palynological analysis technique as follows. The sediment sample is first broken into pea size portions and immersed in 75 percent commercially available core analysis fluid and 25 percent dispersive household liquid detergent to deflocculate the sample (Faegri and Iversen 1975). The solution is then agitated and allowed to stand until the solids precipitate out from the liquid. The majority of the solution is then poured off to leave a sample that is then added to distilled water and boiled. The resulting solution is then placed in a centrifuge tube and spun to concentrate the sample further. This concentrated sample is treated with a number of chemicals to further refine it so as to leave only pollen. The resultant liquid sample is then added to a suspension medium of oil and placed on a microscope slide.

The microscope is used to count and identify the pollen on each of the slides produced from each portion of the soil sample that has been differentiated chronologically by stratigraphic, radio carbon or cosmogenic dating. At least 300 pollen grains are counted on each slide to identify the pollen by species if possible, and genus if not.

2.3.1 Fossil Pollen Data

The Paleoclimatology section of the World Data Center provides data about past climate and environment derived from a diverse range of proxies such as tree rings and ice cores as well as paleopollen studies (National Oceanic and Atmospheric Agency 2005). By examining the paleopollen data found by researchers, a picture of past species presence can be inferred for a particular location. These species assemblages presence are then assigned a time period by dating the layer of the soil the individual pollen grains were physically located in, typically with radiocarbon methods.

The WDC presents this data as raw species pollen counts for the stratigraphic layers of the soil sample core. These raw pollen counts were manipulated to separate out individual species counts at stratigraphically recorded time periods. The pollen counts from each species were converted to percentages of the total pollen count.

The *Fagus grandifolia* percentages were used, along with the spatial location of the palynological sites where it was found, to map the locations with the presence of any of its pollen. Several time bracketed maps of theses locations were made, each displaying sites where *Fagus grandifolia* pollen was found at the particular time period.

2.3.2 Parameters of the Pollen Data Used

Palynological study site pollen data were obtained from the WDC's North American Pollen Database at http://www.ngdc.noaa.gov/paleo/data.html. These data were categorized in the form of the 70 most common vegetation types as defined by the WDC. This categorization was used as opposed to the uncategorized total pollen counts that had differing numbers of species. This was done to allow for consistent spreadsheet mathematical manipulation and decrease the percentage variation due to the different pollen production parameters of species.

All sites between 25º N to 49º N latitudes and 75º W to 95º W longitudes were used in this analysis. The data were also temporally bracketed by the dates of 21k BP and 10k BP corresponding to the LGM and the beginning of the Holocene. These spatial and temporal extents were chosen because they encompass the likely eastern North American paleorange of *Fagus grandifolia* during the late Pleistocene.

Data from the 131 palynological sites in the database that met these spatial and temporal extents were then searched for evidence of *Fagus grandifolia* by the appearance of any of its fossil pollen at the study sites. A total of 70 sites included *Fagus grandifolia* pollen (Fig. 2.1).

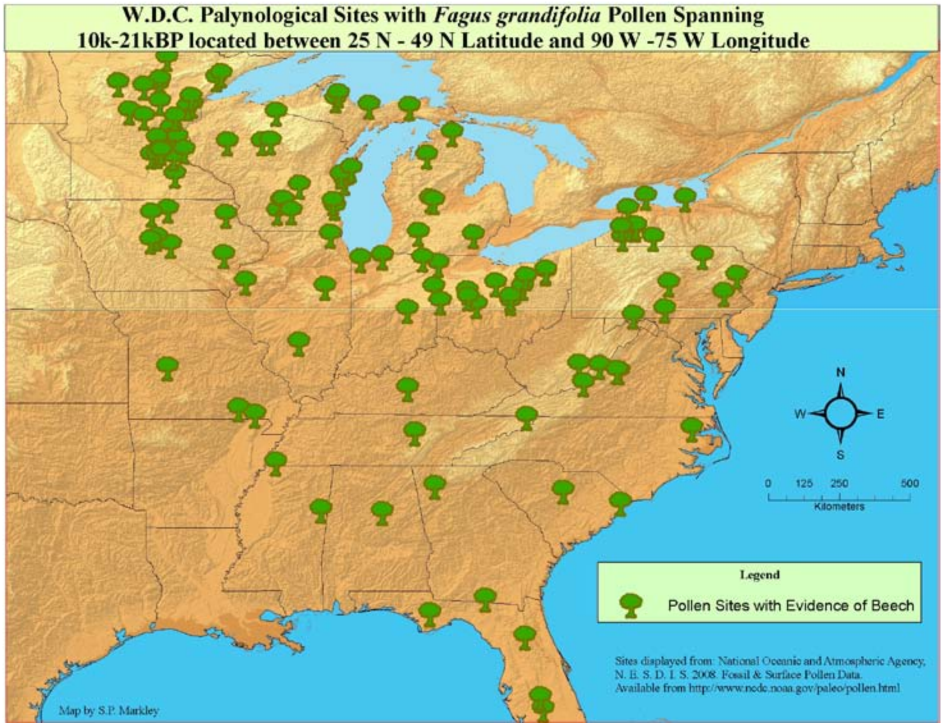

Figure 2.1 World Data Center Palynological Sites with *Fagus grandifolia* pollen.

2.4 Ordering of *Fagus grandifolia* WDC Palynological Data

Pollen counts in the form of asciii text data for the 70 selected study sites were imported one at a time into a simple data manipulation spreadsheet. The initial WDC data were displayed in rows that showed the raw pollen counts with their corresponding stratigraphic dates for the study sites in question. The 70 most common species were enumerated and then each study site had the pollen counts for each individual species displayed at their stratigraphic date.

All species pollen count rows were then added individually to get total pollen sums for the study site at the individual dates. The individual species pollen counts were then divided by the total pollen count of all species discovered at the site at the specific date to get the pollen percentage of each particular species.

These individual species percentages were displayed with their corresponding stratigraphic date. This operation resulted in the ability to examine individually each of the 70 species pollen percentages in relation to a particular stratigraphic date. This information was then transferred to a different spreadsheet (Table 1) to display all study sites with or without *Fagus grandifolia* pollen percentages at particular time periods at particular sites.

Table 1. WDC Palynological Sites

North American Pollen Database Site and Researcher	*Fagus grandifolia* pollen appears and reappears	Latitude	Longitude	21kBP	20.5kBP	20kBP	19.5kBP	19kBP	18.5kBP	18kBP	17.5kBPF	17kBP	16.5KBP	16kBP	15.5KBP	15kBP	14.5KBP	14kBP	13.5KBP	13kBP	12.5KBP	12kBP	11.5KBP	11kBP	10.5KBP	10kBP
Cupola Pond, Smith,E.N.,	**13k-10kBP**	-91.1	36.8																	0.218						0.374
Powers Fort Swale, Royall,P.	**18k-10kBP**	-90.58333	36.6							0.229					0.220		1.699	0.669	0.165	0.153	0.906		0.303		0.134	0.187
Chatsworth Bog, King,J.E.	**12k-11.5kBP**	-88.34333	40.675833																			0.305	0.590			
Pyle Site, Shane,L.	**12.5k-10.5kBP**	-84.88333	40.666667																		0.677	0.688	0.978	0.840	0.246	
Rhule Fen, Shane,L.	**13k-10kBP**	-85.74167	39.953611																	0.261			1.062	0.458		0.231
Battaglia Bog, SHANE, L.	**16k-10kBP**	-81.32861	41.143889											0.312						0.274		1.133		0.867		0.268
Brown Lake('s), SHANE, L.		-82.06	40.68																							
Bucyrus Bog, SHANE, L.	**14.5k-10.5kBP**	-82.93333	40.797222														0.267					0.275	0.524	0.284	0.232	
Carter Site, SHANE, L.	**14.5k-12kBP**	-84.68056	40.216667														0.427		0.219	0.455	1.023	0.694				
East Twin Lake, SHANE, L.	**11.5k-10kBP**	-81.33333	41.198611																				0.287	0.275	0.274	0.125
Fudger Lake, SHANE, L.	**13.5k-10kBP**	-83.53333	40.1																0.269	0.538			0.233	0.955		0.686
Ladd Lake, SHANE, L.	**11.5kBP**	-84.75	41.416667																				0.228			
Neville Marsh, SHANE, L.	**12.5k-11kBP**	-83.83333	40.545833																		0.261	0.911	0.637	0.262		
Smoot Lake Bog, SHANE, L.	**12.5k-11kBP**	-82.44583	40.205556																			0.229		1.087		
Stotzel-Leis Site, SHANE, L.	**14.5k-10kBP**	-84.68944	40.216667														0.229			0.254	0.259	0.198	2.344	1.538	0.556	0.851
Anderson Pond, Delcourt, H.	**18k-10kBP**	-85.5	36.033333							0.254			0.274			0.292	0.282	0.590	0.541	1.114	1.734	0.552		0.277		1.435
Nonconnah Creek, Delcourt, P.	**21k-13.5kBP**	-89.91667	35.083056	0.535												0.243		0.235	0.616							
Jackson Pond, Wilkins,G.	**17.5k-10kBP**	-85.71667	37.45								0.292													0.436	0.883	0.255
Cranberry Glades, Watts,W.	**12.5k-10kBP**	-80.28333	38.2																		0.309					0.210
Boney Spring, King,J.		-93.36694	38.111944																							
Browns Pond, Kneller,M.	**14k-12.5kBP**	-79.61639	38.154722															0.250		0.265	0.531					
Conklin Quarry, Ashworth,A.		-91.56389	41.694444																							
Crider's Pond, Watts,W.	**15k-10kBP**	-77.55	39.966667													0.332				0.671	0.340	0.342				0.581
Lake Mendota, Winkler,M.	**11k-10kBP**	-89.41667	43.1																					0.307		0.301
Rockyhock Bay, Whitehead,D.	**12k-10kBP**	-76.68333	36.166667																			0.272	0.812	0.878	0.853	4.129
Allenberg Bog, Miller,N.	**16k-10kBP**	-78.8825	42.251111											0.447	0.600	0.417	0.271	0.150		0.147	0.733	0.428			0.148	0.300
Belmont Bog, Spear,R.	**16.5k-10kBP**	-77.91667	42.25										0.716	1.902			0.242						0.115	0.709		0.268
Anderson Lake, Wright,H.		-92.71667	46.416667																							
Andree Bog, Cushing,E.		-93.25	45.725																							
Beckman Lake, Swain,P.		-93.18333	45.425																							
Big Pond, Watts,W.	**10kBP**	-78.55	39.766667																							1.351
Biggsville (Cessford Quarry), Baker,R.		-90.88	40.855556																							
Billy's Lake, Jacobson,G.		-94.58333	46.283333																							
Blackhoof Site, Wright,H.		-92.57333	46.503333																							
Blue Mounds Creek, Davis,A.		-89.86667	43.083333																							
Camp 11 Lake, Brubaker,L.		-88.01667	46.666667																							
Canyon Lake, Davis,M.		-87.92139	46.833333																							
Cedar Bog Lake, Cushing,E.		-93.19722	45.411111																							
Clear Lake, Bailey,R.	**10kBP**	-86.53	41.65																							0.449
Clear Lake, Baker,R.		-93.3500	43.1500																							
Colo Marsh, Baker,R.		-93.2700	42.0200																							
Demont Lake, Kapp,R.	**11k-10kBP**	-85	43.48																					1.327	0.552	0.444
Devils Lake, Maher,L.		-89.73194	43.418056																							
Disterhaft Farm Bog, Baker,R.	**11kBP**	-89.16694	43.916944																					0.482		
Disterhaft Farm Bog, Maher,L.		-89.16694	43.916944																							

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DATA *Not* Present 🟧

Table 1 (cont.). WDC Palynological Sites

North American Pollen Database Site and Researcher	*Fagus grandifolia* pollen appears and reappears	Latitude	Longitude	21kBP	20.5kBP	20kBP	19.5kBP	19kBP	18.5kBP	18kBP	17.5kBPF	17kBP	16.5KBP	16kBP	15.5KBP	15kBP	14.5KBP	14kBP	13.5KBP	13kBP	12.5KBP	12kBP	11.5KBP	11kBP	10.5KBP	10kBP
Ernst Brother's Pit, Maher,L.	**12kBP**	-88.04194	43.233056																			**0.939**				
Frains Lake, Kerfoot,W.		-83.63	42.33																							
Gass Lake, Webb,S.	**10.5kBP**	-87.73333	44.05																						**0.310**	
Green Lake, Lawrenz,R.		-85.11667	44.883333																							
Hack Pond, Craig,A.	**10kBP**	-78.99722	37.984722																							**0.323**
Hanson Marsh, Maher,L.	**11k-10kBP**	-89.675	43.433056																					**0.338**	**0.342**	**0.683**
Horseshoe Lake, Cushing,E.		-93.04778	45.460278																							
Houghton Bog, Miller,N.	**11.5k-10kBP**	-78.67028	42.541667																				**0.180**	**2.309**	**8.288**	**14.156**
Hudson Lake, Bailey,R.	**10kBP**	-86.53	41.67																							**0.137**
Irvin Lake, Cushing,E.		-93.64361	47.135556																							
Jacobson Lake, Watts,W.		-92.71694	46.416944																							
Jewell Site, Baker,R.		-93.7	42.26																							
Kellners Lake, Maher,L.		-87.84806	44.238056																							
Kellys Hollow 1, Heide,K.		-90.35	45.3																							
Kellys Hollow 2, Heide,K.		-90.35	45.3																							
Kirchner Marsh 1, Wright,H.		-93.125	44.270833																							
Kirchner Marsh 2, Wright,H.		-93.125	44.270833																							
Kotiranta Lake, Wright,H.		-92.62	46.72																							
Kylen Lake, Birks,H.	**10.5kBP**	-91.8	47.35																						**0.075**	
Lake Ann, Shane,L.		-93.6875	45.425																							
Lake Carlson, Wright,H.		-93.16389	44.822222																							
Lake Mary, Webb,T.		-89.9	46.25																							
Lake Mendota, Winkler,M.	**11k-10kBP**	-89.41667	43.1																					**0.307**		**0.301**
Lake Ontario, Mississauga Basin, McAndrews,J.		-78.15	43.556667																							
Lake Ontario, Rochester Basin, McAndrews,J.	**11.5k-10.5kBP**	-76.9	43.51																				**0.463**		**0.810**	
Lake Sixteen, Futyma,R.		-84.31667	45.6																							
Lily Lake, Eyster-Smith,N.		-92.825	45.05																							
Little Bass Lake, Swain,P.		-93.6	47.283333																							
Lockport Gulf Section, McAndrews,J.		-78.71667	43.166667																							
Longswamp, Watts,W.	**12.5k-10kBP**	-75.66667	40.483333																		**0.324**	**0.345**	**0.722**	**0.356**		**0.351**
Martin Pond, McAndrews,J.		-94.93333	47.183333																							
Myrtle Lake, Janssen,C.		-93.38333	47.983333																							
Nichols Brook Site 1, McAndrews,J.	**12.5k-10.5kBP**	-78.47889	42.544722																		**0.493**	**0.493**	**0.500**		**0.495**	
Nichols Brook Site 2, McAndrews,J.	**12.5k-10kP**	-78.47889	42.544722																		**0.490**	**0.451**			**0.248**	**0.267**
Panther Run Pond, Watts,W.	**10.5kBP**	-77.41667	40.8																						**0.334**	
Pilot Mound Site, Baker,R.		-93.9	42.16																							
Pittsburg Basin, Wright,H.		-89.1875	38.904167																							
Pogonia Bog Pond, Cushing,E.		-93.63333	45.033333																							
Portage Lake, McAndrews,J.		-94.11333	47.081389																							
Portage Marsh, Jackson,S.	**10kBP**	-87.2225	41.576111																							**0.110**
Potts Mountain Pond, Watts,W.	**11.5k-10kBP**	-80.13333	37.6																				**1.818**	**1.286**	**1.948**	**0.631**
Pretty Lake, Williams,A.	**13.5k-10kBP**	-85.25	41.583056															**0.342**								**0.047**
Protection Bog, Miller,N.	**10.5k-10kBP**	-78.46667	42.622222																						**0.161**	**0.340**

DATA Present 🟩 **DATA *Not* Present** 🟧

Table 1 (cont.). WDC Palynological Sites

North American Pollen Database Site and Researcher	*Fagus grandifolia* pollen appears and reappears	Latitude	Longitude	21kBP	20.5kBP	20kBP	19.5kBP	19kBP	18.5kBP	18kBP	17.5kBPF	17kBP	16.5KBP	16kBP	15.5KBP	15kBP	14.5KBP	14kBP	13.5KBP	13kBP	12.5KBP	12kBP	11.5KBPl	11kBP	10.5KBP	10kBP
Pyle Site, Shane,L.	**13k-10.5kBP**	-84.88333	40.666667																	**0.246**	**0.677**	**0.688**	**0.978**	**0.840**	**0.246**	
Quarles Pond, Craig,A.	**12k-10kBP**	-79.07222	37.995833																			**0.329**	**0.639**		**1.645**	**0.993**
Quillin Site, Shane,L.	**12.5k-10.5kBP**	-81.96667	41																		**1.090**	**0.310**	**0.515**	**0.723**	**1.156**	
Radtke Lake, Webb,S.		-88.1	43.4																							
Roberts Creek, Chumbley,C.		-91.50028	42.986111																							
Rockyhock Bay, Whitehead,D.	**12k-10kBP**	-76.68333	36.166667																			**0.272**	**0.812**	**0.878**	**0.853**	**4.129**
Rossburg Bog, Wright,H.	**11.5kBP**	-93.6	46.583333																				**0.382**			
Rutz Lake, Waddington,J.		-93.87	44.87																							
Seidel 1, Waddington,J.	**12kBP**	-87.51556	44.45																			**0.198**				
Seide 2, Maher,L.		-87.51556	44.45																							
Shady Valley Bog, Barclay,F.	**13k-10kBP**	-81.93333	36.525																	**1.974**	**0.645**		**0.699**	**1.290**		**0.667**
Silver Lake, Ogden,J.	**11k-10kBP**	-83.8	40.35																					**0.924**		**0.462**
Smoot Lake Bog, Shane,L.	**12k-11.5kBP**	-82.44583	40.205556																			**0.229**	**1.087**			
Spirit Lake, Davis,M.		-86.95833	46.47																							
Spring Lake, Nickmann,R.	**13k-10kBP**	-76.35	41.673889																	**0.185**		**0.249**	**0.978**	**0.503**		**0.905**
Stewart's Dark Lake, Peters,M.		-91.45	45.3																							
Stone Lake Tamarack Swamp, Swain,P.		-93.69167	44.891667																							
Stotzel-Leis Site, Shane,L.	**14.5k-10kBP**	-84.68944	40.216667														**0.229**			**0.257**	**0.254**	**0.198**	**2.344**	**1.538**	**0.556**	**0.851**
Tannersville Bog, Watts,W.	**14.5k-10kBP**	-75.26667	41.033333														**0.336**		**0.337**	**0.341**	**1.017**	**1.141**	**0.314**	**0.303**	**0.314**	**0.331**
Torren's Bog, Ogden,J.	**11.5-11kBP**	-82.46667	40.35																				**0.706**	**2.920**		
Vestaburg Bog, Gilliam,J.	**17.5k-10kBP**	-84.88333	43.416667								**0.985**										**0.476**					**1.020**
Volo Bog, King,J.		-88.18444	42.351111																							
Weber Lake, Fries,M.		-91.66	47.471667																							
White Lily Lake, Cushing,E.		-93.10278	46.086111																							
Winter Gulf Site, McAndrews,J.		-78.93389	42.561111																							
Wintergreen Lake, Bailey,R.	**11.5kBP**	-85.38333	42.4																				**0.654**			
Wolf Creek, Birks,H.	**20.5kBP**	-94.11667	46.116667		**0.068**																					
Wolsfeld Lake, Grimm,E.		-93.56667	45																							
Wolverine Lake, Futyma,R.		-85.66111	46.429167																							
Wood Lake, Heide,K.		-90.08333	45.333333																							
Zuehl Farm Site, Baker,R.	**12.5kBP**	-93.87	43.03																		**0.153**					
BL-Tombigbee, Whitehead,D.	**11.5k-11kBP**	-88.47444	33.563333																				**3.817**	**4.369**		
Bob Black Pond, Watts,W.	**19k-13.5kBP**	-84.86806	34.323611					**0.331**			**0.329**	**0.328**				**0.326**	**0.311**	**0.787**	**2.556**							
Cahaba Pond, Delcourt,H.	**12k-11kBP**	-86.53333	33.5																			**43.533**	**8.046**	**2.186**		
Camel Lake, Grimm,E.	**12k-11kBP**	-85.01667	30.266667																			**2.907**	**5.135**	**6.231**		
Clear Pond, Hussey,T.	**17k-11kBP**	-78.95361	33.798611									**0.264**	**0.269**	**0.268**							**21.508**	**20.603**	**22.332**	**18.710**		
Lake Annie, Watts,W.		-81.41667	27.2																							
Lake Louise, Watts,W.		-83.25833	30.725																							
Lake Louise 2, Watts,W.		-83.25833	30.725																							
Lake Tulane, Grimm,E.	**21k-11kBP**	-81.5	27.583333	**0.300**			**0.119**		**0.213**	**0.187**		**0.268**						**0.269**		**0.355**				**0.148**		
Quicksand Pond, Watts,W.	**18k-16kBP**	-84.86528	34.326389							**0.327**				**0.328**												
Sheelar Lake, Watts,W.	**21k-11.5kBP**	-82	29.516667	**0.806**	**0.514**																	**1.690**	**1.611**			
White Pond, Watts,W.	**14k-11kBP**	-80.775	34.166667															**0.278**	**0.304**		**2.663**		**7.395**	**10.947**		

DATA Present 🟩 **DATA *Not* Present** 🟧

All pollen percentages from the initial individual study site spreadsheet had myriad stratigraphic dates so the time periods were categorized into 500 year increments starting at 21k BP and ending at 10k BP. There were often several stratigraphically dated soil layers from a study site that are within these 500 year intervals and these were condensed by only using the stratigraphic layer with the highest percentage of *Fagus grandifolia* pollen that fell within a range of 250 years of the 500 year increments used. For example, if there were a stratigraphic date of 12,300 BP, which is within 250 years of the 12.5k BP category, it was thus categorized.

2.5 Pollen Data Mapping

These 500 year paleopollen percentages were mapped using ESRI's ArcMap GIS software. A total of 18 time referenced maps displaying study sites with *Fagus grandifolia* pollen were then made. These maps span five 2,000 year increments with one map showing a 1,000 year period. The maps cover a time period spanning 21k BP to 10k BP.

These study sites with evidence of *Fagus grandifolia* and their corresponding pollen percentages were overlain a Digital Elevation Model (DEM) of North America that was downloaded from http://edc.usgs.gov/products/elevation/gtopo30/gtopo30.html. The GTOPO30 is a global digital elevation model with a horizontal grid spacing of 30 arc seconds (approximately 1 kilometer). This topographic representation was used as a mapping base to determine if any pattern of relationship between possible *Fagus grandifolia* refugia and topographical locations could be inferred.

Paleodominance range limits inferred from pollen and macrofossil data for *Fagus grandifolia* by the Delcourts' were drawn on the maps (Delcourt and Delcourt 1987). These range limits were for the times of 10k BP, 12k BP, 14k BP, 16k BP, 18k BP and 20k BP and are the range limits below which the relative dominance of *Fagus grandifolia* falls below zero percent in the pollen record. These paleodominance range limits in the Delcourts' book (Fig. 5.14 b-g) were drawn on a paleo-representation of North America as opposed to the modern representation used in this paper's maps. This was resolved by georeferencing them to modern palynological site locations which were displayed in both this paper's maps and the Delcourts' maps.

Map layers of the Laurentide Ice Sheet boundary at 21k BP, 18k BP, 16k Bp, 14k BP, 12k BP and 10k BP were also developed. The 21k BP boundary layer was downloaded from http://geode.usgs.gov/. The other dates boundaries were developed by using jpegs displaying the time referenced Laurentide Ice Sheet limits imported from http://www.ncdc.noaa.gov/paleo/pollen/viewer/webviewer.html developed in conjunction with Williams et al. (2004). These jpegs were then georeferenced to the base map DEM of North America and the ice sheet limits traced on the map.

2.6 Chloroplastic DNA Data Mapping

Analysis of the cpDNA sample sites of *Fagus grandifolia* was done in an attempt to correlate palynological sites with pollen evidence of the species with the distribution of its modern day genetic markers (Fig.2.2). This cpDNA data of *Fagus grandifolia* is used to locate unique geographic ranges.

Chloroplastic genes have been little changed over the Quaternary period (Hewitt 2000). Late Pleistocene refugial areas and post glacial migratory paths are inferred using fossil pollen data in conjunction with this cpDNA data.

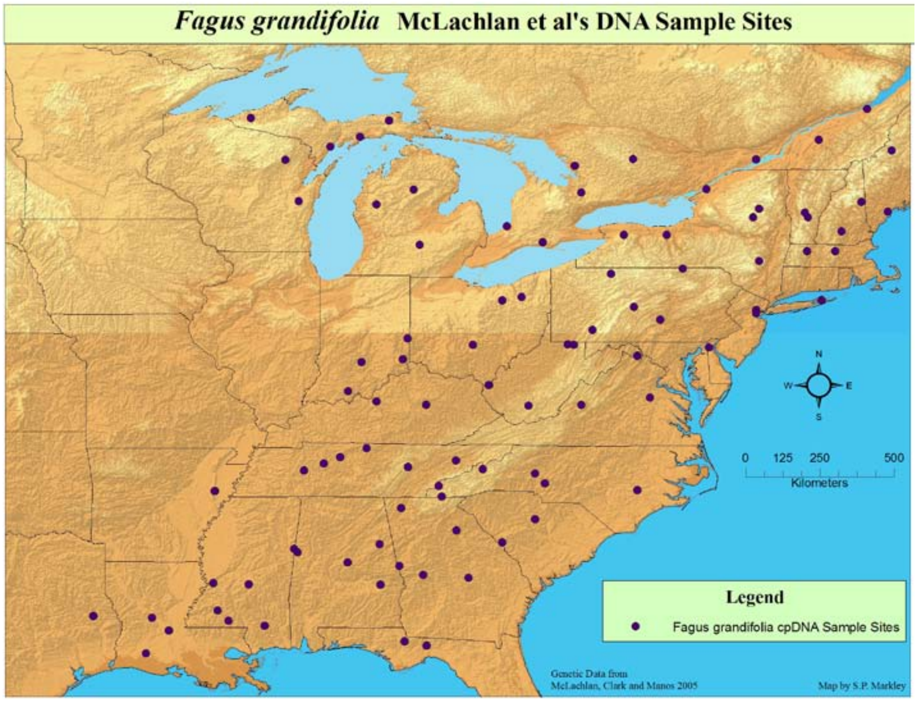


Figure 2.2. Chloroplastic DNA Sample Locations from McLachlan, Clark, and Manos (2005).

Sampling locations are examined as to their clade designations and the clade subsets of haplotypes. Of the four clades, A, B, C, and D, clade C is not analyzed because Mclachlan, Clark, and Manos describe the geographical origin of this clade as being indeterminable (McLachlan, Clark, and Manos 2005). Haplotype 10 in this clade is widespread in its distribution throughout the modern range of *Fagus grandifolia,* more so than any of the different clade's haplotypes. Due to this McLachlan, Clark, and Manos

(2005) say that haplotype 10 “[provides] little information about its late glacial distribution.” The geographic breadth of this clade’s predominant haplotype 10, it is of little use in determining refugial locations or migratory routes. The remaining haplotypes in clade C, haplotypes 7, 8 and 9 do hold promise in that they are few in numbers relative to the predominant haplotype 10 and possibly could perhaps define a migratory route due to their rarity. But none of these haplotypes were found below the maximum extent of the Laurentide Ice Sheet and thus cannot be used for inference of a refugial area during the LGM.

The analysis of *Fagus grandifolia’s* lineage in eastern North America was performed by downloading the cpDNA data from Mclachlan, Clark, and Manos’ (2005) study which was obtained from the *Ecological Archives* E086-110-S1 at the website http://esapubs.org/archive/ecol/E086/110/default.htm. These cpDNA data samples were then entered into a spreadsheet and manipulated to order the clade and haplotype designation location of each sample.

This cpDNA spatial data for *Fagus grandifolia* was imported into ArcMap. Three maps for each 2,000 year (and one 1,000 year) period are drawn, each showing a cpDNA clade. The lineage relationships between the haplotypes were drawn and the individual clades with their corresponding haplotypes mapped on the 2000 year paleopollen percentages maps. A map inset figure was also made showing all clades and their individual haplotypes and the relationship between each clade as shown in the McLachlan, Clark, and Manos (2005) article’s Figure 3B.

Chapter 3 Results

There are six different areas in North America that exhibit relatively continuous deposition patterns of *Fagus grandifolia* fossil pollen between 21k BP and 10k BP. The first of these areas is the Delcourts' traditionally identified refuge of the Gulf and southern Atlantic Coastal Plains interpreted from 162 published and unpublished paleoecological site pollen records (Delcourt and Delcourt 1987). The remaining five areas that display deposition are the northern Mississippi Embayment, in both northern and southern areas of the Appalachian Plateaus province, and two areas in the Interior Plains Region.

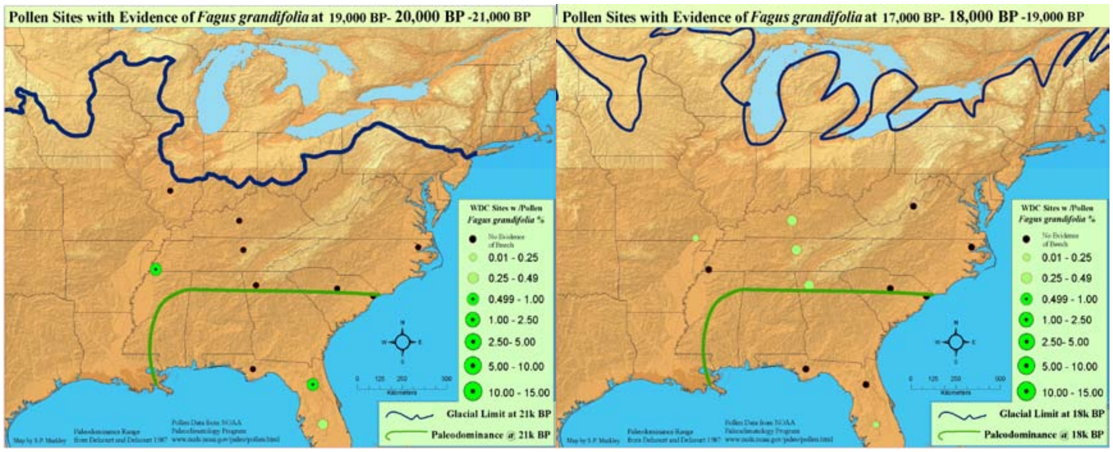
The five aforementioned physiographic areas are excluded from the currently specified range limits for *Fagus grandifolia* at different times because they do not meet a pollen percentage threshold limit. These areas are interpreted as potential refugia or areas along migrational pathways for *Fagus grandifolia* as the ice sheet retreated. The location of refugial areas north of the standard range boundary is supported by the spatial distribution of samples taken of the cpDNA of *Fagus grandifolia*.

3.1.1 Northern Mississippi Embayment, 21k BP to 19k BP

At Nonconnah Creek, Tennessee, near Memphis, the Delcourts found the earliest LGM evidence of a macrofossil of *Fagus grandifolia* (21,807 BP carbon dated) as well as pollen in surrounding sediment layers (Fig. 3.1A, Delcourt et al. 1980). Currently the latitude of 35º N is recorded as the northernmost latitude at which hard evidence for

Fagus grandifolia has been located at the LGM. Only nine sites in the entire study area have pollen records for this time.

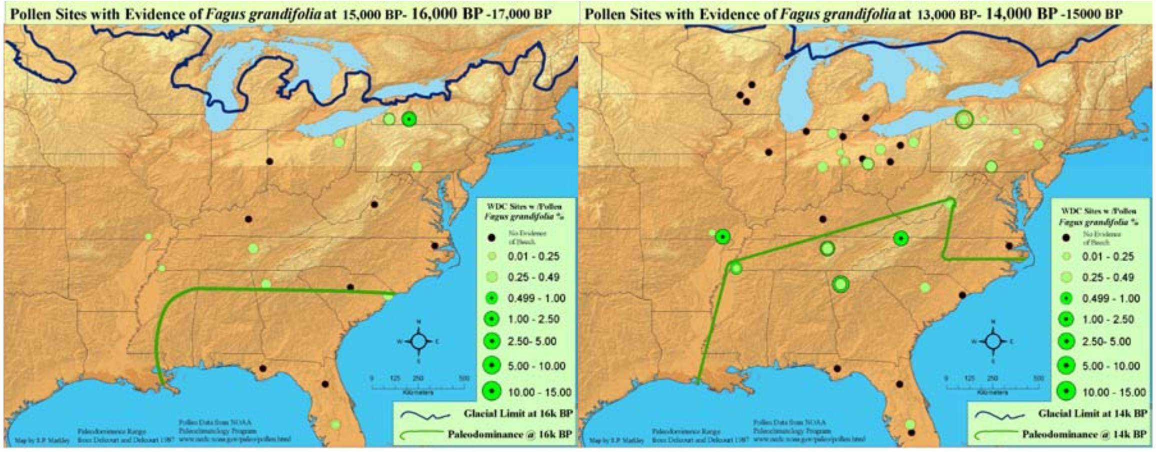
The amount of *Fagus grandifolia* pollen found at Nonconnah Creek is 0.53 percent of total pollen found. It is on the eastern side of the northern Mississippi Embayment in the Coastal Plain province where the topography starts to rise from the Mississippi Alluvial Plain. This site is located approximately 150km to the northwest of the Delcourts' range limit for this time. The Florida sites with evidence of *Fagus grandifolia* pollen at this time period of 21k BP to 19k BP sites are not discussed as they are within the Delcourts' range limit for the time.



A. 21k BP to 19k BP

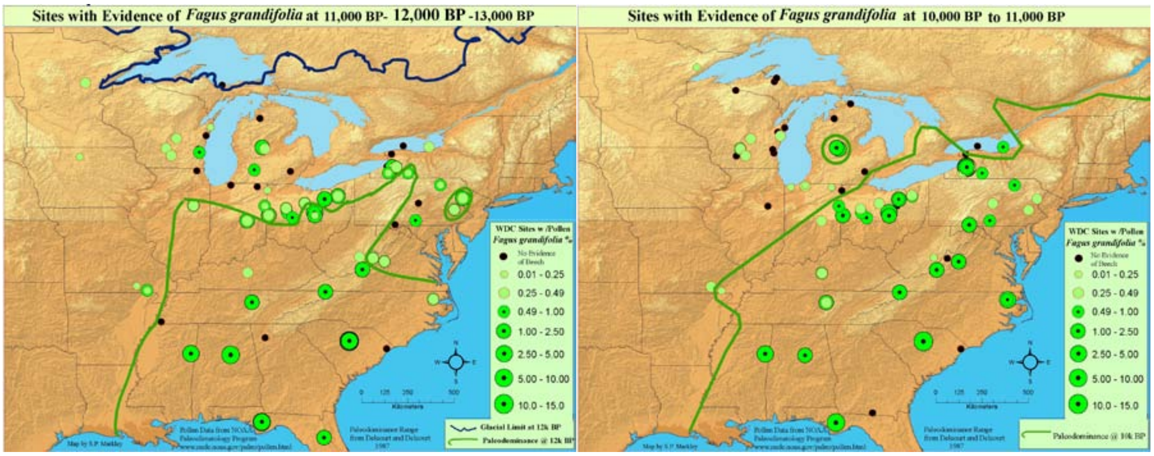
B. 19k BP to 17k BP

Figure 3.1. WDC Sites at times indicated with pollen and the Delcourts' Range Limits.



C. 17k BP to 15k BP

D. 15k BP to 13k BP



E. 13k BP to 11k BP

F. 11k BP to 10k BP

Figure 3.1 (contd.). WDC Sites at times indicated with pollen and the Delcourts' Range Limits.

The Noncannah Creek site is not included within the Delcourts' range limit for this time period, even though it meets the percentage threshold limit of 0.5 percent for the species. Noncannah Creek's percentage of *Fagus grandifolia* pollen at 21k BP is defined as a sporadic peak value (Delcourt and Delcourt 1987). When mapping range limits, any sporadic peak values of a species percent dominance are defined as outlier values from the lower mean values by the Delcourts and are not included in the range limits. This site is within approximately 475 km of the ice sheet.

3.1.2 Southern Portion of the Appalachian Plateaus Province, 19k BP to 17k BP

Eleven WDC sites record pollen during the time period bounded by the dates 19k BP to 17k BP (Fig. 3.1B). Six of these eleven sites have *Fagus grandifolia* pollen during the time period; two of which are just on the northern edge of the Delcourts' range limit and three that are well outside of it.

Bob Black Pond in the southernmost portion of the Appalachian Highlands region in northern Georgia is on the northern edge of the Delcourts' range limit for *Fagus grandifolia* at 18k BP. *Fagus grandifolia* pollen was found at this site at 17k BP, 17.5k BP and 19k BP in the amounts of approximately 0.33 percent of total pollen for all three time periods. Pollen is also found in the same amount at the Quicksand Pond site a few kilometers distant from Bob Black Pond at 18k BP. At both of these sites, pollen percentages exhibit an average of 0.33 percent of the total pollen found of the seventy important Northern Hemisphere species types used by the WDC.

Moving northward on the Cumberland Plateau, *Fagus grandifolia* fossil pollen is found at 18k BP at Anderson Pond in central Tennessee. This site is 190km to the northwest of the other two Appalachian Plateaus sites at this time. The Cumberland Plateau is hypothesized to be a refuge by the Delcourts but is approximately 200km to the north of their range limits at 18k BP (Delcourt 1979).

Jackson Pond, Kentucky has pollen evidence of *Fagus grandifolia* at 17.5k BP in the amount of 0.29 percent. This site is 150 kilometers to the north on the Lexington

Plain of the Interior Low Plateaus province adjacent to the northerly reach of the Cumberland Plateau. This site is the northernmost at which *Fagus grandifolia* pollen is found during this time period and is within approximately 425 km of the ice sheet at this time period.

At a northern Mississippi Embayment site in southeastern Missouri, at Powers Fort Swale, fossil pollen is found at approximately 18k BP in the amount of 0.23 percent. It is of interest to note that this site is located in the bluffs along the northwestern edge of the Mississippi Embayment, 185km north, northwest of Noncannah Creek and this area's pollen deposition pattern, albeit in small amounts, continues from the 21k BP to 19k BP period.

All the sites where pollen occurs for 19k BP to 17k BP except the Lake Tulane site are on the western side of the Appalachians and all sites excepting Bob Black and Quicksand ponds and the aforementioned Florida site are outside the Delcourts' range limit for this time period.

3.1.3 Northern Portion of the Appalachian Plateaus Province, 17k BP to 15k BP

In the north of the Appalachian Plateaus province, *Fagus grandifolia* pollen appears in the Southern New York section during this time slice. At Belmont Bog, New York, *Fagus grandifolia* pollen is in evidence at the times of 16.5k BP in the amount of 0.72 percent and at 16k BP with 1.9 percent (Fig. 3.1C). It also appears at Allenberg Bog approximately 83 kilometers to the west of Belmont Bog from the times of 16k BP to 12k BP.

Fagus grandifolia pollen at Allenberg Bog occurs continuously from 16k BP to 12k BP (it does not show at 13.5k BP). Though the pollen threshold limit was met 75 km to the east at Belmont Bog, for the times of 16.5 k BP and 16k BP, it was only met at 15.5k Bp for Allenberg Bog. However, dates that bracket 15.5k BP at Allenberg Bog, 16k BP and 15k BP, have pollen in the amounts of 0.45 percent and 0.42 percent respectively. Results in this section of the Appalachian Plateaus province show a presence of *Fagus grandifolia* at this time with the Delcourts' range 930 km to the south.

Anderson Pond in central Tennessee on the Cumberland Plateau again has pollen evidence at the times of 16.5k BP and 15k BP. *Fagus grandifolia* pollen is found at the 0.3 percentage level at Battaglia Bog at 16k BP, approximately 50km to the south of Lake Erie in northeastern Ohio. This site is 240km to the west of the Southern New York section sites. A site in southern Pennsylvania, Crider's Pond, shows pollen of at a 0.3 percent level at 15k BP. Crider's Pond being the first site to have evidence of *Fagus grandifolia* east of the Appalachians. Battaglia Bog and Crider's Pond pollen deposition during the 17k BP to 15k BP time period is perhaps evidence of an expansion of the species to the east and the west from the Appalachian Plateaus province.

Pollen was again found at the northern edges of the Mississippi Embayment. Powers Fort Swale shows a level of 0.22 percent and the site of Nonconnah Creek with a level of 0.24 percent. The now recurring pollen deposition evidence at these sites from the initial appearances at 21k BP at Noncannah Creek and 18k BP at Powers Fort Swale bolsters the case for this area being a possible refugial one.

3.1.4 Central Lowlands Province, 15k BP to 13k BP

The period from 15k to 13 k BP has WDC **s**ites with *Fagus grandifolia* pollen increase from nine sites with pollen evidence during the past 17k to 15k BP period to over twice that number (Fig. 3.1D). The most significant area of expansion during this time period is seen in the Till Plains section of the Central Lowland Province, just to the southwest of Lake Erie. In this region there are eight different sites containing pollen evidence for this time period (Rhule Fen, Pretty Lake, Carter Site and Pyle Site in eastern Indiana to Stotzel-Leis Site, Fudger Lake, Bucyrus Bog and Battaglia Bog again in Ohio) that appear in the eastern portion of the Till Plains section. *Fagus grandifolia* pollen deposition occurred from14k to 13k BP at percentages ranging from 1.13 percent (at Battaglia Bog) to 0.25 percent (at Pyle Site). An increase in the number of sites with pollen in the Till Plains appears to expand westward from patterns appearing in the southern New York sites at this time.

The Southern New York physiographic section sites of Allenberg Bog and Belmont Bogs in western New York continue their pattern of pollen deposition for *Fagus grandifolia* at 15k BP to 13k BP. The range limits for *Fagus grandifolia* at the time of 14k BP now include Allenberg Bog as an outlier, but as an outlying range that is approximately a full 400 km to the north of the main paleodominance line still in the southern and eastern portion of the continent.

The main range limit line is approximately 800 km from the ice sheet’s edge at this time but this outlying range is only approximately 400 km away. An additional site 150 km to the southeast but still in the same physiographic section with a pollen percentage of only 0.18 is found at Spring Lake in northeastern Pennsylvania which also may be an expansion from southern New York but in an easterly direction or a northern migrational pathway site along the Appalachians.

Sites with pollen evidence for *Fagus grandifolia* at the times spanning 15k BP to 13k BP now appear both to the east and the west along highlands of the Appalachians, from the southern tip of the range in the Southern section of the Blue Ridge province north to the Piedmont Lowlands in eastern Pennsylvania. The sites in this region are the aforementioned Spring Lake, Tannersville Bog in far eastern Pennsylvania with 0.34 percent at both 13.5k BP and 13k BP, and Criders Pond in southernmost Pennsylvania with 0.67 percent at 13k BP. Other sites in the Appalachian Highlands with *Fagus grandifolia* pollen that are now included in the Delcourts' range limits are Brown's Pond in western Virginia, Shady Valley Bog in the easternmost tip of Tennessee, and Bob Black and Quicksand Ponds in northern Georgia.

To the west, the sites along the northern edges of the Mississippi Embayment continue to show evidence of *Fagus grandifolia*. Nonconnah Creek displays pollen at 13.5k BP, 14k BP, and 15k BP with only the 13.5k BP layer however reaching the rational pollen threshold. Two more sites in the northern Mississippi Embayment are found in southeastern Missouri at Powers Fort Swale starting with 1.7 percent at 14.5k BP and decreasing to 0.15 percent at the time of 13k BP. The other Missouri site, Cupola Pond, not a few kilometers from Powers Fort Swale, has 0.22 percent at 13k BP; these two sites are still outside the Delcourts' range limit for this time period.

3.1.5 Eastern Lakes Section, Central Lowlands Province, 13k BP to 11k BP

Sites with *Fagus grandifolia* pollen make a first appearance to the northwest of the Till Plains section, in the Eastern Lakes section of the Central Lowland province between 13k and 11k BP. There are eight sites surrounding Lake Michigan (Wintergreen Lake, Vestaburg Bog, and Demont Lake in Michigan and Ernst Brother's Pit, Seidel Site, Lake Mendota, Devil's Lake, and Hanson Marsh in Wisconsin). These sites around the Lake Michigan are also now the closest to the retreating ice sheet at approximate average of 350 km. Despite their number, these Eastern Lakes section sites are not included in the Delcourts' range limit for 12k BP.

At Rossburg Bog in the Superior Upland province of the Laurentian Upland region. This site in northern Minnesota has a 0.38 percentage of Fagus grandifolia pollen at 11.5k BP. This site is only approximately 60 km from the12k BP ice sheet's edge and is notable due to its proximity. This is not considered a possible refugial area for *Fagus grandifolia* in this study due to the absence of both a temporally recurring pattern at the site or the relatively close proximity of other sites. There is also a site in northern Iowa, Zuehl Farm, that has 0.15 percent of *Fagus grandifolia* pollen at 12.5k BP that also has the aforementioned lack of corroborating evidence.

During this time period, there is an increase of pollen sites with evidence of *Fagus grandifolia* in the southern New York section of the Appalachian Plateaus province (Fig. 3E). This increase is in number of sites and the abundance of pollen they exhibit. The Delcourts include this section in their range limit for *Fagus grandifolia* at 12k BP. An area of approximately 130 km in diameter in this section saw an increase to four sites from two, with three of the four sites reaching the threshold pollen limit. This is out of a total of seven sites in or close to this physiographic section (a far northeastern site, Lake Ontario Rochester Basin, occurs on the southeastern shore of Lake Ontario).

The Till Plains section of the Central Lowlands province also shows a marked increase in both number of sites and *Fagus grandifolia* pollen percentages. During the period of 13k BP to 11k BP, an increase of from seven to thirteen sites display *Fagus grandifolia* pollen evidence in the eastern half of this section. The range limit for this time period runs from west to east in this section. The range includes Chatsworth Bog, Illinois, Rhule Fen, Indiana and Smoot Lake Bog and Torren's Bog in Ohio but excludes the remaining eleven, marginally more northern sites, in the Till Plains section.

The Appalachian Highlands region shows an increase in the number of sites from six to nine. Two sub-areas along the Appalachians, one in the Northern section of Blue Ridge province and one in the Middle section of the Valley and Ridge province are noted for patterns of both the increase in number of sites with evidence and pollen percentages at the sites. The Valley and Ridge province's sites in far eastern Pennsylvania are also now included in the range limit for 12k BP as an outlier from the Delcourts' main range limit.

Sites in southeastern-most Missouri on the northern edge of the Mississippi Embayment continue to receive pollen. A high of 0.9 percent is reached at Powers Fort Swale but this area is still considered just to the west of the presumed range limit at this time.

3.1.6 End of the Pleistocene/ Early Holocene, 11kBP to 10k BP

Patterns remain essentially the same for the next 1,000 years (Fig. 3F). The addition of more sites in the same regions also displays a decrease oftentimes in the pollen percentages of *Fagus grandifolia* in these sites' pollen counts.

In the Eastern Lakes section, the Demont Lake site in central Michigan meets the pollen threshold limit at both 10.5k and 11k BP and is now included in the range limits for 10k BP as an outlier. The Hanson Marsh site in south central Wisconsin also reaches the pollen threshold limit but is still outside the currently established range.

Fourteen sites are in evidence in the Till Plains section of both central and northern Indiana and Ohio. The percentages of *Fagus grandifolia* pollen found at these sites ranges from 2.9 percent at Torren's Bog in Ohio to 0.04 percent in northern Indiana at Pretty Lake. Of these Till Plains sites, half of them reach the 0.5 percent threshold limit.

The eastern side of the Appalachians in the Piedmont province, Piedmont lowlands section started out with three sites in the 15k BP to 13k BP time period, then the number of sites went to four in the next time slice of 13k BP to 11k BP and the sites' percentages of *Fagus grandifolia* pollen increased. In the last time period of 11k to 10k BP, these Piedmont Lowlands sites increased in number to five but only two sites reached above 0.5 percent of *Fagus grandifolia* pollen in the paleobotanical record.

In the southern New York section of the Appalachian Plateaus province, pollen continues to be deposited during this time period. It is noted that at the Allenberg Bog, Protection Bog and the Nichol's Brook that these sites never reach the threshold pollen limit but at Houghton Bog not 40 km distant or less from the aforementioned sites has one of the highest percentages of *Fagus grandifolia* pollen in this study at 14.0 percent. Belmont Bog and one other site in the Rochester Basin of Lake Ontario meet the pollen threshold limit. The sites in the southern New York section are located inside the range limit at 10k BP although the Lake Ontario, Rochester Basin site is excluded. All sites in this section are within 140 km radius of each other.

From 11k BP to 10k BP, the number of sites does not increase in the alluvial plain of the northern part of Mississippi Embayment. The two sites of Cupola Pond and Powers Fort Swale actually show a decrease in percentage of *Fagus grandifolia* pollen from 11k BP to 10k BP. The northernmost Mississippi Embayment is now just within the western edge of the range limits at this time as defined by the Delcourts. This area has shown evidence of *Fagus grandifolia* pollen since the LGM.

3.2.1 Clades and the cpDNA of *Fagus grandifolia*

Modern genetic data from *Fagus grandifolia* displays evidence of the species' range that differs from those based on pollen. Differences between genes within a species (clades) may be spatially differentiated, suggesting potential patterns of isolation. A representation of a clade diagram may therefore be informative about a species' past distributions and the geographical relationships among its different clades (Crisci 2001).

A recent study by McLachlan, Clark, and Manos (2005) of cpDNA patterns in North America offers separate evidence of migrational rates and refugial areas since the LGM from that shown in the paleoecological record. The modern spatial patterns of the clade and haplotype categories of a species determined from its cpDNA correspond to potential ancestral refugia and migrational paths the species utilized.

Members of a species can be differentiated by having morphologically distinct features classified by the taxonomic term clade. Clade designations are further subdivided by the genetic attribute of a haplotype. A haplotypes consists of a group of distinct genes that are found together on a single chromosome and inherited together. Four different clades of *Fagus grandifolia* with their accompanying subsets of haplotypes are found in North America. The relationship between the clades and their haplotypes (see map inset) and ranges of these clades are found in Figure 3.2.

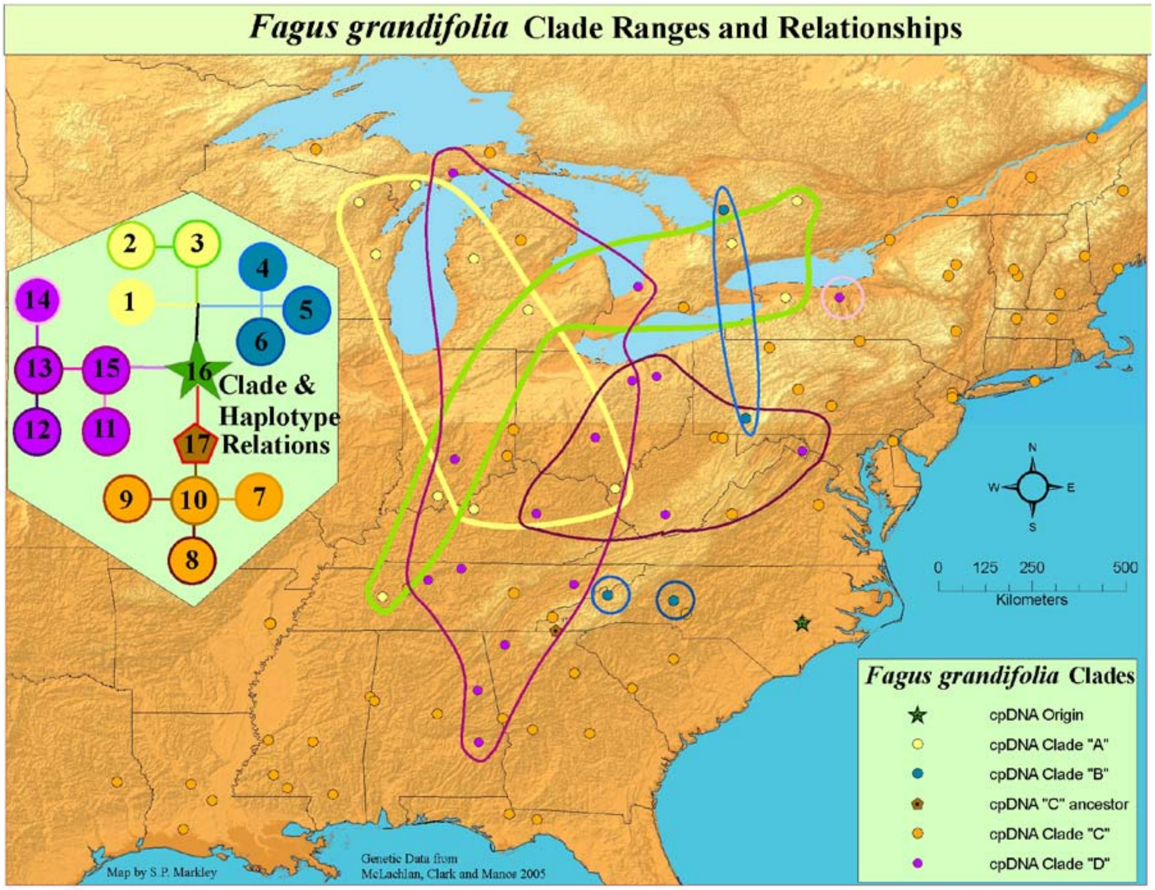


Figure 3.2 *Fagus grandifolia* Clades A (green and yellow), B (blue), and D's (purple and magenta) ranges found by McLachlan, Clark, and Manos (2005).

McLachlan, Manos and Clark (2005) sampled for *Fagus grandifolia* clades throughout the species range because "modern haplotypes almost certainly predate postglacial colonization and the modern geographic distribution of cpDNA haplotypes corresponds to the migration routes of expanding populations" ((McLachlan, Clark, and Manos 2005, 2089). One of the four clades' geographic distribution, A, is not within the Delcourts' range limits at the LGM. Clade B remains to the east of the Appalachians until it reaches more northerly latitudes and can be interpreted as a coastal migration route for *Fagus grandifolia.*

The haplotypes of clade A stretch northward from the Interior Low Plateau to the Central Lowland sections of the Interior Plains region (Fig. 3.2). Most of clade A's haplotypes are clustered in the Till Plains and Eastern Lakes section with exception of the southernmost and progenitor of this clade found in western Tennessee.

Two of the four widely spaced haplotypes of clade B are present in the Blue Ridge Province of the Appalachian Highlands (Fig. 3.2). A haplotype of clade B is the closest to the cpDNA progenitor haplotype 16 found in east central North Carolina along the Atlantic Coastal Plain. Of the remaining haplotypes samples of clade B, one is in the Appalachian Plateaus in southwestern Pennsylvania and one in the far western Eastern Lakes section on the eastern shore of Lake Huron.

The clade designated "C" by McLachlan, Manos, and Clark (2005) is not examined due its ubiquitous distribution throughout *Fagus grandifolia's* modern range. This clade as has no descendant linkages to the other three clades found in North America other than sharing a descent from the founding haplotype, number 16, which has no clade designation.

Clade D samples are observed from the Gulf Coastal Plain in southeastern Alabama north to the Upper Peninsula of Michigan in the Eastern Lakes section (Fig. 3.2). The haplotypes of clade D also extend to the western side of the Appalachians except for one haplotype sample to the west of this mountain range in easternmost West Virginia. This clade is observed beginning in the southern Appalachians (haplotype number 15) and stretching northward along the range and expanding into the Till Plains and the Eastern Lakes section.

3.2.2 Clade A Haplotypes

The only sample of haplotype 3 taken from clade A is found in central western Tennessee not far from the pollen site found in southwestern most Tennessee (Fig. 3.3).

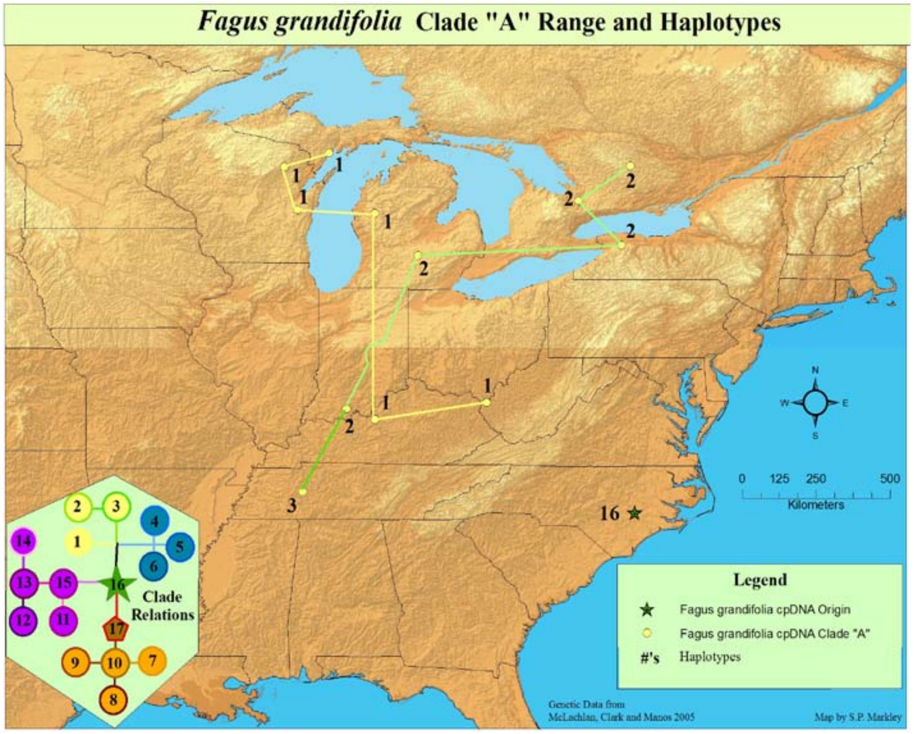


Figure 3.3 *Fagus grandifolia* Clade A and its Haplotypes.

One of the other haplotypes in this clade, number 2, is found north of the northern Mississippi Embayment from haplotype 3. This northward expansion of clade A from this area, coupled with southwestern Tennessee's Nonconnah Creek paleoecological evidence at the LGM, point to a northward and eastward expansion from a refuge in this area. Haplotype 3 does not appear within the traditional range limit for *Fagus grandifolia* from 21k BP to 14k BP. This means that unique, genetically distinct examples of *Fagus grandifolia* appeared outside the range limits defined for this species for 7,000 years.

Haplotype 2 is the easternmost manifestation of the three haplotypes in clade A and most of this haplotype is found in the Eastern Lake section of the Central Lowland. Haplotype 1 also expands northward from the Till Plains into the Eastern Lakes section. The observed patterns of pollen deposition beginning in the Till Plains at approximately 14.5k BP and then appearing in Eastern Lakes section at approximately 12k BP correspond to clade A's spatial distribution.

3.2.3 Clade B Haplotypes

Clade B is differentiated from clade A by two of its three haplotypes appearing on the eastern side of the Appalachian Mountains (Fig. 3.4). The two southernmost haplotypes of this small but widespread clade, numbers 5 and 6, are found in western North Carolina in the Piedmont Uplands and, 140km to the west in the Blue Ridge province. Similar to clade A, clade B is also outside the ranges drawn for *Fagus grandifolia* for the times of the 21k BP until 14k BP. An eastern Appalachian palynological site that may be associated with clade B is Shady valley Bog, 129 km from haplotype 5 and 90 km from haplotype 6.

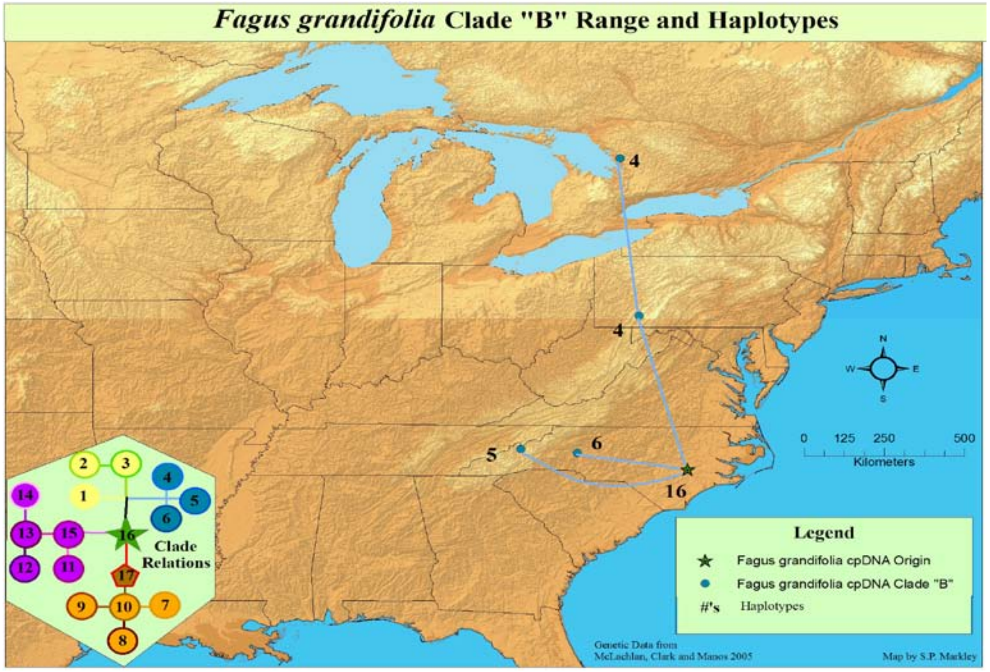


Figure 3.4 *Fagus grandifolia* Clade B and its Haplotypes.

Two northern haplotypes samples of this widespread clade, both of haplotype 4, were taken from the western side of the Appalachians. One haplotype 4 sample is found in the Appalachian Plateaus province approximately 250 km to the south of the southern New York section sites. This sample is approximately 535 km north of haplotypes 5 and 6. The other northern example of this haplotype is found another 550 km north in southern Ontario.

3.3.4 Clade D Haplotypes

Clade D has distribution similar to clade A in that is most of its haplotypes are found to the west of the Appalachians (with the exception of haplotype 13 with one example discovered on the east side of the range, Fig 3.5). This clade's progenitor haplotype 15 is however exhibited further south than clade A and B haplotypes. Haplotype 15 is found in the Southern section of the Blue Ridge province, 40km from the Bob Black and Quicksand Pond sites.

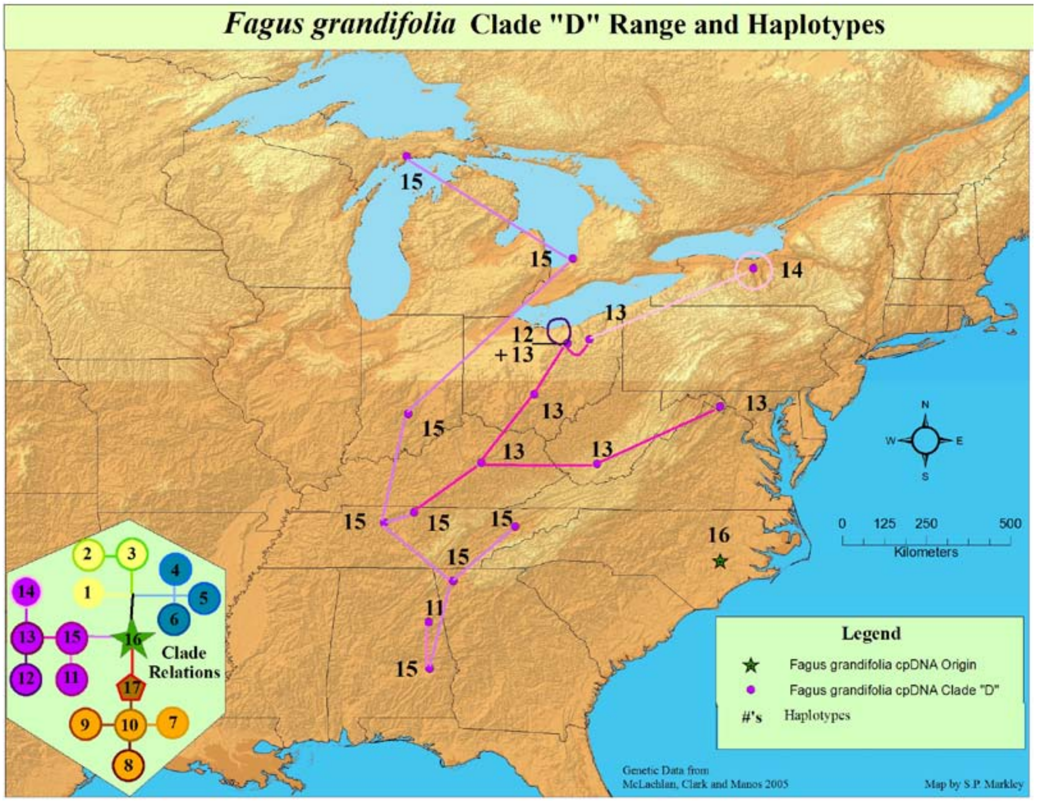


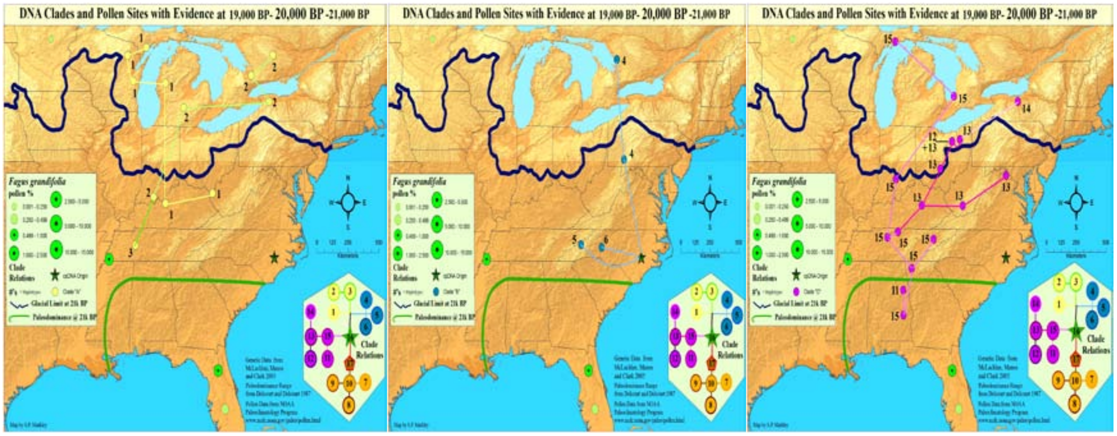
Figure 3.5 *Fagus grandifolia* Clade D and its Haplotypes.

Clade D's haplotype 13 appears to the west of the Appalachians and then transects the mountains to east with a single sample found to the east of the range. This eastern example is approximately 75km from the Crider's Pond site in Valley and Ridge province of the Appalachian Highlands. Clade D's haplotype 13 and clade B, haplotypes 4, 5, and 6 are the only samples found in the Appalachians other than clade C's widespread ones.

Haplotype 14 from clade D is found in the southern New York section that contains Belmont and Allenberg Bogs (Fig. 3.3C). Of the 16 different sample locations of this clade, the location where this haplotype was found is the most easterly of this clade. Haplotype 14 developed from haplotype 13 which shows up both to the south on the east side of the Appalachians in the Piedmont Uplands as well as in the Southern New York section.

The spatial pattern revealed by haplotype D locations is the most widespread other than Clade C's. It appears as though the haplotypes of this clade start from a Gulf Coastal Plain refuge origin and expand from the southern Appalachians to the Cumberland Plateau before expanding into the Till Plains. It is noted that clade D at the same time continues in a northern direction directly along the Appalachians.

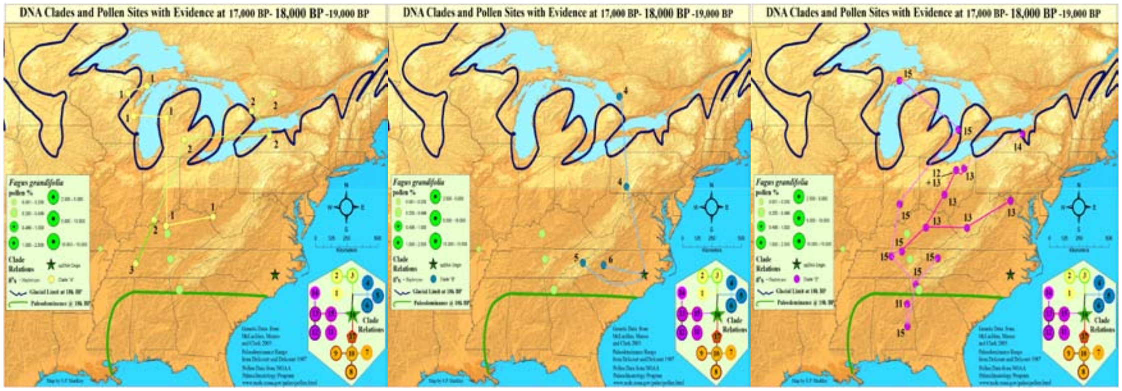
These genetic data, by nature of cpDNA's slow mutation rate and unique spatial arrangement, suggest that *Fagus grandifolia* did occur north of the Delcourts' range limit for thousands of years (Fig. 3.6).


DNA Clades and Pollen Sites with Evidence at 19,000 BP- 20,000 BP -21,000 BP
DNA Clades and Pollen Sites with Evidence at 19,000 BP- 20,000 BP -21,000 BP
DNA Clades and Pollen Sites with Evidence at 19,000 BP- 20,000 BP -21,000 BP

Clade A Clade B Clade D

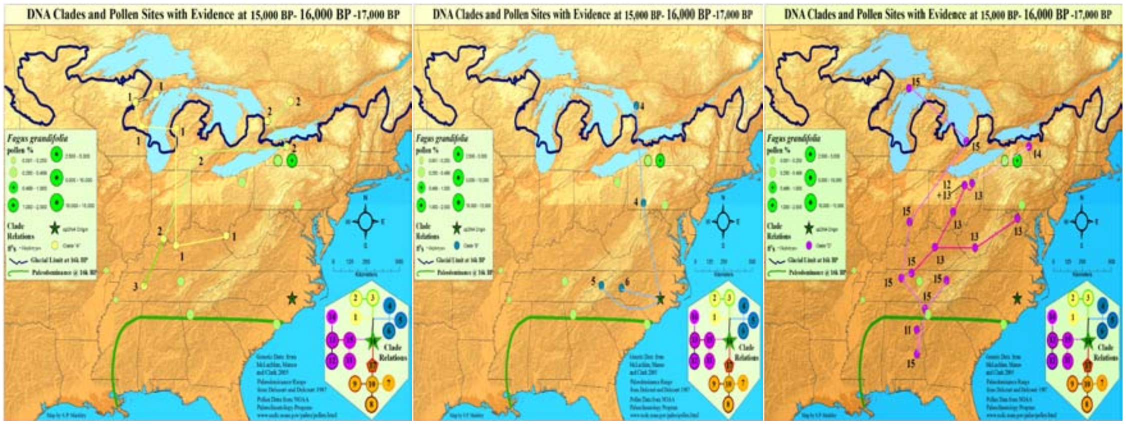
A. Palynological sites with evidence at 21k to 19k BP and Clades.

Figure 3.6. Palynological Sites and cpDNA Clade and Haplotype Sample Sites.



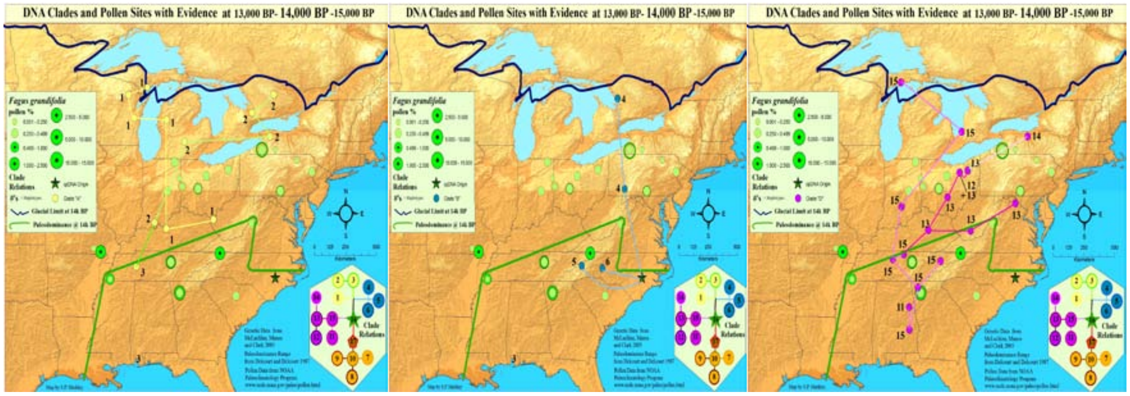
Clade A Clade B Clade D

B. Palynological sites with evidence at 19k to 17k BP and Clades.



Clade A Clade B Clade D

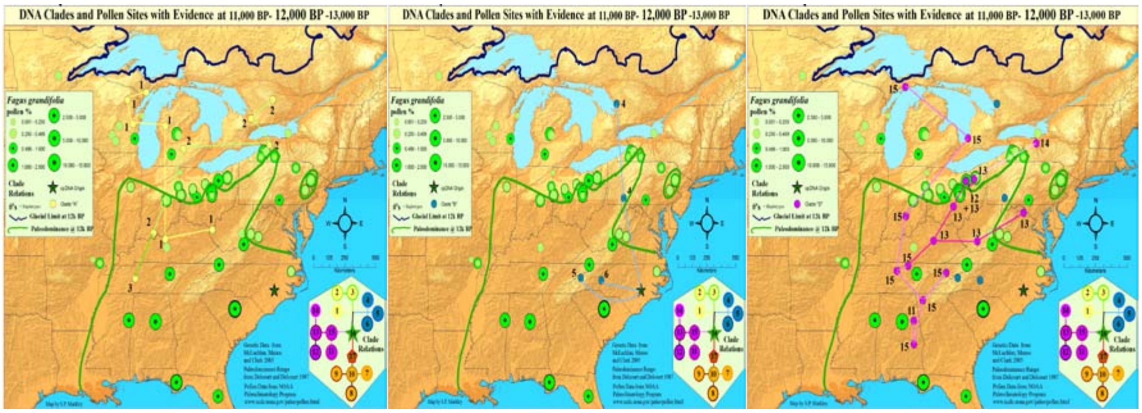
C. Palynological sites with evidence at 17k to 15k BP and Clades A, B and D.



Clade A Clade B Clade D

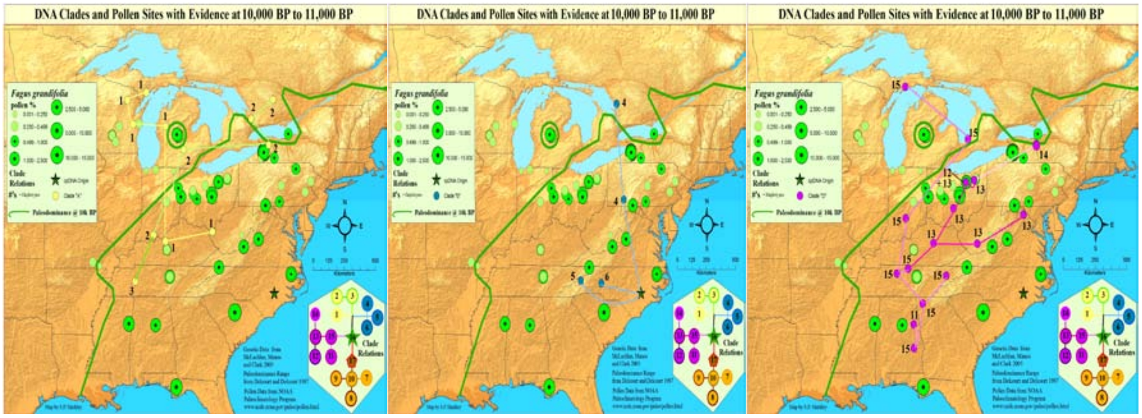
D. Palynological sites with evidence at 15k to 13k BP and Clades A, B and D.

Figure 3.6 (cont.). Palynological Sites and cpDNA Clade and Haplotype Sample Sites.



Clade A Clade B Clade D

E. Palynological sites with evidence at 13k to 11k BP and Clades A, B and D.



Clade A Clade B Clade D

F. Palynological sites with evidence at 11k to 10k BP and Clades A, B and D.

Figure 3.6 (cont.). Palynological Sites and cpDNA Clade and Haplotype Sample Sites.

3.4 Modified range limits

In this study, five different areas outside of the Delcourts' range limits show patterns of continuous pollen deposition or an increased density of sites with *Fagus grandifolia* pollen. These areas, depending on the time of their appearance, can be interpreted as either refuges or expansion of the range along migrational pathways.

The first area is the northern Mississippi Embayment, with evidence starting from 21k BP suggests *Fagus grandifolia's* presence there during the LGM. Pollen and macrofossils from the Nonconnah Creek site in westernmost Tennessee and pollen evidence from the sites of Cupola Pond and Boney Springs in the northern tip of the embayment located in southeastern Missouri lend support to this area as a refugial one for this time period.

Additionally, the phylogeographic distribution of clade A occurs in this area, suggesting a possible refuge as opposed to just a migratory route. A sample taken of haplotype 3 of this clade is within approximately 180 km of the Nonconnah Creek, Tennessee site.

The second area outside the Delcourts' range limits with evidence is the southern portion of the Appalachian Plateaus province in the unglaciated dissected plain that runs along western edge of the Appalachians. This relief of this area may have afforded refugia for *Fagus grandifolia*. The Appalachian Plateau that stretches from northern Georgia to western New York may have sheltered the species as it migrated northward along the western edge of the Appalachian Mountains.

The patterns displayed at the southern Appalachian Plateaus province sites in Georgia lend credence to the Gulf Coastal plain refuge hypothesis of the Delcourts (Delcourt and Delcourt 1987). Genetic cpDNA evidence also supports the Delcourts theory as haplotype 15 of clade D is found in the Gulf Coastal plain extending into the southern Appalachians and westward.

Evidence further north at Tennessee and Kentucky sites can also be interpreted as being a result of a migration from a refuge perhaps in the Cumberland Plateau rather than from the Gulf Coastal plain. South facing gorges of the Cumberland Plateau were theorized as possible refugial locations for deciduous trees by the Delcourts during the full glacial. (Delcourt 1979; Delcourt and Delcourt 1987).

A third area for consideration as time advances during the late Pleistocene is located in southern New York. This northward migration along the Appalachians may have been the cause of the persistent pattern of *Fagus grandifolia* pollen in the northern portion of the Appalachian Plateau province starting at the date of 16.5k BP. The Delcourts' range limit for *Fagus grandifolia* does not reach this area until 14k BP an then is included as an outlier approximately 400 km to the north of their main range limit. These patterns of evidence begin in 16.5k BP and stretch almost unbroken till 10k BP at sites in this area.

The sites in this southern New York section of the Appalachian Plateaus province displaying *Fagus grandifolia* pollen are approximately only 110 km from the retreating ice sheet at 16k BP. The closeness of these sites in the dissected plains of the northern Appalachian Plateaus province to the ice sheet perhaps points to these areas having microclimates that were able to support *Fagus grandifolia* at this time. It is noted that the Delcourts' include Allenberg Bog in this area in their range limit for 14k BP when it is about 400 km distant from the edge of the ice sheet. This could be extrapolated to conjecture that it is accepted that *Fagus grandifolia* could survive at least this close to the ice sheet given the proper topographical relief and environmental parameters.

The fourth area for consideration is just to the west of these dissected plain sites in the northern portion of the Appalachian Plateaus province. A pattern of increasing number of sites with evidence of Fagus grandifolia appears beginning at 14.5k BP in northern Ohio/eastern Indiana in the Till Plains section.

Starting with three sites at 14.5k BP, pollen sites with positive result for the species increase steadily to nine sites by 13k BP. These sites are all within an area of approximately 250km radius of each other. This spatial pattern bears consideration when determining Fagus grandifolia’s actual presence in this area as it is unlikely that so many false positive results would be in evidence in the number of sites in this area. It is also noted that these Till Plain sites are approximately 250km north of the range limits for 14k BP and within approximately 410km to 500km of the 14k BP ice sheet edge.

The Delcourts’ inclusion of the Appalachian Plateaus province site at Allenberg Bog, New York for their range limits at 14k BP but not the seven sites in the Till Plain section of the Central Lowland province in northern and central Ohio point out deficiencies in using the percentage threshold limit method. Why, though there are numerous sites with pollen evidence in the Till Plains at 14k BP, is the paleodominance range limit for *Fagus grandifolia* at 14k BP approximately 275 km to the south of the closest site in this area?

I hypothesize that the Till Plain section’s sites might have been developed from the Southern New York section of the Appalachian Plateaus province. This migratory route is conjectured due to the temporal patterns of northern sites on the west side of the Appalachians. Pollen evidence of *Fagus grandifolia* begins in the east in this area, and as time advances, moves to the west to the Till Plains.

As time approaches the beginning of the Holocene at 10k BP, a fifth area reveals temporal and deposition site patterns that are not included in the range limits for *Fagus grandifolia* at 12k BP. *Fagus grandifolia* starts to appear in the Eastern Lakes section of the same Interior Plains province as the Till Plains section. Starting with an increase from a single site at 12k BP to eight sites by the beginning of the Holocene at 10k BP, evidence suggests that this area developed out of the northern migration from the Till Plains section. This is theorized due to the first appearance in this section being in the Michigan Peninsula directly to the north of the Till Plains sites. As time advances, positive evidence sites occurring in Michigan expand to include ones to the west in Wisconsin.

There has been discussion concerning whether the migrational path taken was from the east side to the west side when crossing Lake Michigan into Wisconsin or a southern to northern route from areas in the Till Plains to the south and southeast of the state (Webb 1987). The actual migrational path is not readily apparent from this study's maps though the western edge of the Till Plains section south of Wisconsin only has one site with pollen evidence at this time as opposed to the three sites in central and southern Michigan.

The range limits for *Fagus grandifolia* interpreted from the pollen record by the Delcourts' for the time periods of 21k BP, 18k BP, 16k BP, 14k BP, 12k BP and 10k BP do not include the areas identified in this study at the times that their sites record *Fagus grandifolia* pollen. This calls into question the validity of range limits that are based strictly on percentages of *Fagus grandifolia's* pollen in a site's record. The patterns revealed of recurring deposition of pollen and, increases in the number of sites with this deposition in areas outside the traditionally held range limit, may point to new refuge areas for the species that were disregarded by relying only on the pollen percentage method.

Chapter 4 Discussion

Results from this mapping of primary evidence suggest that interpretation of spatial patterns of pollen deposition may be a more reliable alternative to the use of a fixed percentage to set species' paleorange limits. Small values that appear in the fossil pollen record at a site, and nearby sites, over hundreds and thousands of years may point to a species' presence at a site rather than just being anomalous outliers, particularly in the case of poorly dispersed pollen like that of *Fagus grandifolia*.

Spatial patterns are already used in palynology. Patterns of increase of pollen percentages between palynological sites are used to interpret the migrational strategy of a species. The use of pollen deposition patterns would reduce Type II error on the basis of small amounts of pollen's percentage in the paleobotanical record. The patterns of continuing pollen appearance, an increase in sites with positive evidence and genetic evidence of unique populations of *Fagus grandifolia* reveal possible refugial areas and migrational pathways. This species is defined as a K-migration strategist meaning that it is possible for small populations to be hundreds of kilometers ahead of a migrational front defined solely by the fossil percentages in the pollen record.

Analysis resulting from the mapping of pollen evidence pattern, in conjunction with mapping genetic marker locations, suggests refugial locations for *Fagus grandifolia* in North America other than just the traditionally defined Gulf Coastal and Southeastern Coastal Plains. The widely cited migration rate of *Fagus grandifolia* in the paleorecord of between 172 and 214 m/yr cannot be reconciled with the times of the appearance of pollen evidence at the sites in this study if a Gulf Coastal Plain is interpreted as its only refuge area without long-distance dispersal events (Delcourt and Delcourt 1987; Clark 1998).

4.1 Tree Pollen Production

Fagus grandifolia's limited display in the paleobotanical record may not simply be due to its pollen's very low or nonexistence at palynological sites. This lack of evidence may be due to the methods and fundamental assumptions currently used by palynologists.

Correction factors are used to account for different species' pollen production and dispersal rates. The correction factors for different species' are based on modern pollen rain or a statistical interpretation of their appearance at multiple sites in the paleorecord. A correction factor is used for each species pollen percentage to determine if it was actually present at the site or its pollen was the result of some other factor. These corrections do not take into account such things as the different methods of reproduction of species based on environmental conditions of the time or one species pollen overwhelming other species pollen due to its greater production capability resulting in samples that may be highly dominated by a few pollen types (Odgaard 2001).

For example, *Pinus* is a genus that produces copious amounts of pollen relative to species such as *Fagus grandifolia* and would display much more pollen in a site's record. The record of a site in the *Picea* and *Pinus banksiana* forest that prevailed over much of the eastern portion of North America at the LGM would have much *Pinus banksiana* pollen that would drive down the percentage of the relatively smaller number of deciduous trees' pollen at the site. McLachlan and Clark (2004) found that in the modern southern range of *Fagus grandifolia*, that 75 percent of modern sites never reach 0.5 percent of its pollen due to the abundance of *Pinus* in southern forests.

The problem associated with the detection of a species that produces relatively little pollen makes it difficult to identify its refugial areas during the LGM. "[It] is doubtful whether the interpretation of pollen records will ever be developed to be able to sense small isolated tree populations far outside a migrational front" (Odgaard 2001). It may be possible to overcome these problems by looking at the patterns a species pollen displays in the paleorecord and its genetic markers rather than just using a percentage threshold it must meet to say whether it was present or not. While the same methods were not used of pollen deposition pattern combined with genetic data, similar studies combining pollen percentages and genetics have been done in Europe which also point out the limitations of using pollen percentage alone to infer refugia and range.

4.2 European Studies Using Pollen and DNA Data

In Europe, researchers have been able to refine the interpretation of macrofossil and paleopollen data by the utilizing the unique genetic markers of a species. European studies of *Fagus sylvatica* (European beech), have been done that combine paleobotanical evidence and genetic data to answer questions such as whether the species survived the late glacial in a single refuge or multiple refugial areas (Magri 2006).

The problems manifested by using pollen percentages to infer a species also occur in this study. "In many European regions, pollen values below 2.0 percent [the pollen percentage threshold used for this species] occur throughout long sections of the postglacial profiles before actual expansion of beech takes place, suggesting that small populations of beech were unable to increase their role in forest communities for thousands of years” (Magri 2006, 205). This is supported by macrofossil evidence that shows the presence of *Fagus sylvatica* when the pollen record shows sub-threshold percentages and discontinuous evidence. Similar patterns of low pollen values and discontinuous deposition are observed in North America for *Fagus grandifolia* in this study. The European researchers deduced from their data that *Fagus sylvatica* did not immediately expand from refugial areas as the European Ice Sheet began to recede but slowly and at later dates.

Questions that Margri’s (2006) study attempted to answer are similar to this study. If it did survive in multiple locations, can these areas be identified? Did the postglacial spread of *Fagus sylvatica* emanate from multiple areas in Europe? What European physiographic features controlled migration routes of this species in the post-glacial? The European study also used datasets with the same type of data as this study’s to answer these questions.

Two different palynological datasets, one composed of fossil pollen from the WDC, European Pollen Data set and fossil pollen studies from published literature, as well as macrofossils also from established literature were used. These two datasets were complemented by cpDNA and nuclear markers (allozymes) dataset of *Fagus sylvatica* derived from data gathered by the Institute of Forest Genetics in Germany and various university studies.

By using these datasets the Magri (2006) found that Bohemia was the main source for population expansion into more northerly areas of Europe and not from southern populations based in Mediterranean areas (a parallel to this finding in North America from this study is patterns and genetic data suggesting more northerly refugial areas than the Gulf and Southeastern Coastal Plains). Researchers concluded that this finding confirmed more northerly refugial areas for temperate trees in Europe and called into question earlier inferences of refugial areas based on limited pollen and DNA data.

A finding the researchers made that also mirrors this study's findings is that *Fagus sylvatica* expanded along hilly and mountainous terrain in central Europe and later into surrounding plains. This finding is not unlike *Fagus grandifolia's* late appearance in the fossil record in the northern Appalachian Plateaus province in North America and later expansion into the Till Plains.

The paleobotanical data's findings were enhanced by the genetic data in that difference in populations appearing in the fossil record could be shown. "In some cases, the genetic data considerably refine inferences based on the paleobotanical record" (Magri et al. 2006, 215). Researchers were able to delineate the edge of western expansion along the Alps from populations in the east and distinguish between different populations living in adjacent mountain ranges in the Balkans. Sparse populations that barely show in the fossil pollen record, but are demonstrated by the genetic record, occur in northern Spain. Genetic data identified unique populations of *Fagus sylvatica* in this area that were not identified by the pollen record. This corresponds to the findings of this study's interpretation of the northern Mississippi Embayment population as being separate from Gulf Coastal Plain's by its spatial association with haplotype 3 of clade A.

4.3 Incongruity with Established Range Limits

The areas revealed by this study call into question the Delcourts' range limits and time of appearances for *Fagus grandifolia* based on a pollen threshold percentage (Delcourt and Delcourt 1987). Models predict that long distance dispersals are rare, although not impossible, and do not coincide with modern dispersal rates (McLachlan, Clark, and Manos 2005). An additional consideration is the tendency of *Fagus grandifolia* to reproduce asexually, rather than with seeds, under harsh environmental conditions such as might have been found at the northern edge of its range during the LGM (Morris 2004). K.D. Bennett extrapolated that since "*Quercus* was a prominent component of the full-glacial coniferous forest at least as far north as southern Illinois" that a species such as *Fagus grandifolia* would have been able to survive in the same environment as both species survive in the same northern range limits today (Bennett 1985). Bennet's extrapolation and the migration rate dissimilarity between modern rates and rates determined from paleopollen studies raise the question of possible refugial locations farther north than the Gulf Coastal Plain.

4.4 Pattern as an Alternative to Percentage

Mclachlan and Clark (2004) report that "[t]he 0.5 percent threshold that is often used to delineate the range of beech in fossil assemblages does not correspond to the modern range limits of American Beech" (McLachlan and Clark 2004, 142). They found that by lowering this threshold limit that false positives outside the modern range began to occur. The refugia and migration pathways revealed by the results of this study avoid these false positives because a single time referenced pollen value at a palynological site is not used.

The problems of false negatives due to *Fagus grandifolia* pollen's underrepresentation in the fossil record is nullified by looking for repeating chronologically and spatially dependent patterns of evidence rather than pollen evidence percentage thresholds. A more in-depth examination of the palynological record from more sources, using the alternative method of pollen pattern recognition, coupled with cpDNA evidence, would perhaps reveal refugial locations and consequently a new paleorange for *Fagus grandifolia* that are overlooked by solely using percentage threshold limits.

Chapter 5 Conclusion

Genetic data coupled with patterns of temporally-continuous pollen deposition and the increase of the number of palynological sites where *Fagus grandifolia* pollen was found leads to a conclusion that refugial areas and migration pathways for this species should be reinterpreted. Some of these palynological sites with evidence of the species are in areas that could have sheltered *Fagus grandifolia* during the LGM due to their dissected topography. The northern portion of the Mississippi Embayment has pollen evidence at the time of the LGM, and sites in the Appalachian Plateau region indicate *Fagus grandifolia* occurrence at a time when the range limit inferred by palynologists is 900km to the south of this area.

Modern DNA samples of *Fagus grandifolia* lend credence to the hypothesis that *Fagus grandifolia* was present in areas outside the traditionally drawn range limits for the late Pleistocene. The cpDNA sample data is observed to correlate with the spatial patterns of appearance of the pollen of this species. Clades A and B of this species are not found within the southern coastal plain range limits interpreted from the pollen threshold limit. Additionally, it was also found that the cpDNA of northern populations of the species is different from the cpDNA of populations within the southern range limit (McLachlan, Clark, and Manos 2005). The combination of these two data sets bolsters the case for a reinterpretation of *Fagus grandifolia's* paleorange other than current paleorange derived solely from pollen percentages of this species found at palynological sites.

This study has focused on the spatial patterns of evidence of *Fagus grandifolia* that appear from a combination of the palynological record correlated with the modern genetic record. Previous inferences of the paleorange of *Fagus grandifolia* derived exclusively from fossil pollen are reexamined in this context. Recent European studies of *Fagus sylvatica* show that discontinuous patterns of pollen evidence occur below the standard pollen threshold limits but in conjunction with macrofossils (Magri 2006). These studies can be extrapolated to conjecture *Fagus grandifolia's* presence nearer the North American glacial ice margin than currently thought.

Five areas in North America north of the currently accepted range limits have evidence for the occurrence of *Fagus grandifolia.* The northern edges of the Mississippi Embayment are a possible refugial area. The evidence for inferring this area as a refuge is the macrofossil found by the Delcourts, a consistent pattern of appearance of pollen evidence starting at the time of the LGM of 21k BP, and cpDNA evidence of clade A in the area (clade A only being found above 34º N). Four other areas also display significant pattern of fossil pollen evidence of *Fagus grandifolia.* These are the northern and southern sections of the Blue Ridge, the southern New York section of the Appalachian Plateaus, and the Till Plains and the Eastern Lakes sections of the Central Lowland. All of these regions accrue increasing patterns of pollen evidence at times that are outside the dates of the currently defined range limits times.

These currently defined range limits are taken from the Delcourts' *Long-Term Forest Dynamics of the Temperate Zone* (1987). It must be stressed that the Delcourts' inferred range limits for *Fagus grandifolia* are from a period approximately 18 years prior to the updated pollen dataset used in this study. The genetic data was also unavailable to the Delcourts during their inference of range limits. They also mention that *Fagus grandifolia* was “present locally in outlier populations [that were] northwest of its mapped range between 20k BP and 16k BP” (Delcourt and Delcourt 1987 ,176). This paper is a refinement of previous work based on new genetic evidence and the use of a pattern of accrual of pollen evidence rather than relying solely on statistical levels of fossil pollen evidence.

No inference of new range limits are made in this study due to the need for the scope of the data to be greater (more sites, dating confirmation). However the combination of recent phylogeographic data for *Fagus grandifolia* and the use of evidential patterns rather than fixed pollen threshold limits, point to a reconsideration of possible refugial areas of *Fagus grandifolia* in the past. A more in-depth mapping including these new data and methodology should be performed so as to better understand questions of species biodiversity in relation to climate change and the future management of the species *Fagus grandifolia*.

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Appendix A

Glossary:

alleles: Any of the possible forms in which a gene for a specific trait can occur. In almost all animal cells, two alleles for each gene are inherited, one from each parent.

biome: regional or global biotic community, such as a grassland or desert, characterized chiefly by the dominant forms of plant life and the prevailing climate.

biotic: of or relating to living organisms.

biostratigraphic: geology dealing with the differentiation of sedimentary rock units on the basis of the fossils they contain.

boreal: of or relating to the forest areas of the northern North Temperate Zone, dominated by coniferous trees such as spruce, fir, and pine.

calving: The process of a glacier shedding portions of ice into the sea.

chloroplastic: any of various small particles in the cytoplasm of the cells of plants that contain chlorophyll.

chronostratigraphy: refers to that aspect of the field of stratigraphy dealing with temporal relations and ages of rock bodies.

clade: a taxonomic group of organisms classified together on the basis of homologous features traced to a common ancestor.

cosmogenic dating: The dating of minerals by examining the decay rates of certain isotopes formed by the mineral's exposure to cosmic rays.

dissected plain: often an uplifted plain, cut by irregular valleys and hills due to erosion.

ecotone: the transition zone between two different plant communities, for example that between forest and prairie.

edaphic: pertaining to or conditioned by soil; indigenous.

erosional unconformity: A surface between successive strata representing a missing interval in the geologic record of time, and produced either by an interruption in deposition or by the erosion of depositionally continuous strata followed by renewed deposition.

Farmdalian interval: This period lasted from approiximately 28– 22 kya. A cool interstadial geostratigraphic substage of the Pleistocene in upper North America.

ferriargillans: a soil surface consisting of a mixture of clay minerals and iron oxides.

founder effect: loss of genetic variation when a new population is established from a small number of individuals.

genera: a group of species exhibiting similar characteristics.

geologic unconformity: Reflects tectonic activity that has turned a layer of rock "on end," and then more recent layers have formed right beside it. Appears as a vertical stratification next to a horizontal stratification.

haplotype: a group of alleles of different genes on a single chromosome that are closely enough linked to be inherited usually as a unit.

heterozygous: Possessing two different forms of a particular gene, one inherited from each parent. A person who is heterozygous is called a heterozygote or a gene carrier. Heterozygous is in contrast to homozygous, the possession of two identical copies of the same gene.

heterozygosity: The two measures of genetic variation examined by Allendorf (1986) were heterozygosity (proportion of individuals heterozygous at a locus) and allelic diversity (the actual number of alleles present at a locus). The expected heterozygosity following a bottleneck lasting a single generation is expressed as a proportion of the original heterozygosity.

Holocene: The more recent of the two epochs (the other being the Pleistocene) of the Quaternary Period, beginning at the end of the last major Ice Age, about 10,000 years ago.

in-situ: in the actual sediment, not the atmosphere

interstadial: a period of temporary retreat of ice during a glacial stage; a warming period.

isopol map: a map showing the spatial variations of pollen distribution.

isozyme or allozymes: nuclear genetic marker. Isozymes are isoforms (closely related variants) of enzymes. In many cases, they are coded for by homologous genes that have diverged over time.

kettles: A depression left in a mass of glacial drift, formed by the melting of an isolated block of glacial ice.

mesic: of, pertaining to, or adapted to an environment having a balanced supply of moisture.

mesophytic forest: a forest growing under a well-balanced moisture supply.

Mississippi embayment: a geologic trough that runs from eastern Arkansas down to mid-Louisiana formed by subsidence after the area had been uplifted by a hotspot plume during the mid-Cretaceous.

obliquity: the angle between the plane of the earth's orbit and that of the earth's equator, equal to 23°27′; the inclination of the earth's equator.

outlier: A value far from most others in a set of data: That which lies, or is, away from the main body which is in this case *Fagus grandifolia's* Gulf Coastal Plain refuge.

paleodominance: in the context of this paper, the relative dominance of taxa in the past.

phylogeographic: the study of genetic relationships patterns to determine the spatial distribution of species.

pine parkland: grassland region with isolated or grouped *Pinus*, usually in temperate regions.

Pleistocene: here defined as the epoch from approximately 1.8 million years ago to 10,000 years ago, time of glacial advances and retreats.

pollen influx: number of grains of a pollen type(s) deposited on a unit surface area in a given time, commonly grains cm-2 year, different taxa have different accumulation rates.

pollen rain: windborne pollen that falls from the atmosphere.

precession: conical motion of the earth's axis of rotation, caused by the gravitational attraction of the sun and moon, and, to a smaller extent, of the planets, on the equatorial bulge of the earth.

Quaternary: period that covers approximately from 1.8 mya to the present, includes both Pleistocene and Holocene epochs.

refugia: an area where special environmental circumstances have enabled a species or a community of species to survive after extinction in surrounding areas.

Reid’s paradox: past **r**apid rates of plant migrations are far too high to have been produced by present day dispersal mechanisms

speleothem: speleothems are formed from secondary deposition of calcite, aragonite, or other minerals in caves, common speleothems are stalagmites and stalactites.

stadial: a cold period during an interglacial period.

stratigraphic: the method of study of rock strata.

taiga/forest ecotone: transitional zone between northern coniferous forest and more temperate forest with deciduous elements that contains the characteristic species of each.

taxa: A taxonomic category or group, such as a phylum, order, family, genus, or species.

thermohaline circulation: process whereby ocean currents driven by the sun's heat absorbed by tropical oceans and impacted by variations in salt content in the water ciculate.

thermophilous: description for organisms that are predisposed to warm conditions.

Woodfordian: main Wisconsin glacial stage, from approximately 25,000 to 12,500 BP.

xeric: of, pertaining to, or adapted to a dry environment.

Appendix B

Latin/Common Names:

Abies fir

Acer maple

Alnus alder

Ambrosia ragweed

Artemisia sagebrush

Betula birch

Carya hickory

Celtis hackberry

Chenopodium-Amaranthus (cheno-am) goosefoot/pigweed type pollen.

Compositae certain flowering plants, examples are sunflowers, daisys etc.

Cornus dogwood

Cyperaceae sedges

Fraxinus (nigra) ash (black)

Graminae grasses

Juglans walnut

Larix larch

Ostrya/Carpinus hornbeam

Picea spruce

Pinus pine

Poaceae grasses

Poplus poplar

Quercus oak

Salix willow

Ulmus elm