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ECOTONE DYNAMICS: 2000 YEARS OF FOREST CHANGE IN THE LOWER PENINSULA OF MICHIGAN, USA

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ABSTRACT

ECOTONE DYNAMICS: 2000 YEARS OF FOREST CHANGE IN THE LOWER PENINSULA OF MICHIGAN

By

Christina Marie Hupy

The forests of the Great Lakes region are important biological, cultural, economic, and global resources. These forests are under pressure from a variety of forces, including land use change, logging, pests, disease, and global warming. In light of these pressures, we need to better understand their dynamics in order to successfully manage these forests today and in the future. By examining how forests have responded to similar pressures in the past, particularly climatic change, we will gain a better a perspective on their dynamics today as well as into the future.

Extensive paleoecological research has documented vegetation change in the Great Lakes region at coarse temporal (1,000's of years) and spatial scales (1,000's of km). While this research has proved invaluable, relatively little is known about vegetation change at finer temporal and spatial scales. The goal of this dissertation research was to examine forest dynamics in the Great Lakes region during the last 2,000 years. This research focused on the forest tension zone, an ecotone located in the central Lower Peninsula of Michigan, between the deciduous forests in the south and the mixed coniferous-deciduous forests in the north. The first objective was to generate a comprehensive quantitative baseline of forest community composition within the study area prior to Euro-

American settlement. This baseline was developed through statistical analysis of the Public Land Survey (PLS) data collected during the General Land Office Survey from 1815-1836. The second objective was to reconstruct vegetation change in the central Lower Peninsula during the last 2,000 years through fossil pollen analysis. High-resolution fossil pollen analysis was conducted on sediments from three lakes, Hicks Lake (Osceola County), Cowen Lake (Montcalm County), and Morrison Lake (Ionia County), all which represent different forest communities relative to the ecotone. The third objective was to assess the vegetation changes detected in the fossil pollen analysis in order to identify shifts of the ecotone over time and to compare the PLS data to the fossil pollen records. Several statistical techniques were utilized to identify ecotone shifts, over time, and compare the PLS data and fossil pollen records.

This research demonstrated that the presettlement forest ecotone was a complex and dynamic ecological phenomenon where species competed intensely forming a wide variety of diverse communities. The fossil pollen analysis documented the presence of the ecotone during the past 2000 years as well as revealed significant changes in forest vegetation around each of the three lakes. Further analysis identified three major ecotone transitions including a northerly shift during the Medieval Warm Period (1000-800 cal yr BP) and a southward shift during the Little Ice Age (800-300 cal yr BP). Thus, the vegetation identified from the analysis of the PLS data was a relatively new arrangement of species and forest communities and the geographic ranges of these forest types had only been stable for a few hundred years.

DEDICATION

I dedicate this PhD dissertation to the many generations of my family before me who did not have the opportunities that I have had.

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Chapter 1

Introduction

1.1 Introduction

The forests of the Great Lakes region are important biological, cultural, economic, and global resources. In the wake of a changing planet, these forests are under pressure from a variety of sources, both anthropogenic and non-anthropogenic, including land use change, logging, pests, disease, invasive species, and climatic change. The climate of the Great Lakes region is predicted to be 2 °C warmer and 15-20% wetter by the end of the 21st century (Sousounis and Bisanz 2000). These predicted changes will likely impact forest ecosystems in the Great Lakes region, especially because they already facing many other pressures (Solomon and Bartlein 1992; Walker et al. 2002). The composition, extent, and diversity of these forest communities are likely to change in response to future climatic variations (Walker et al. 2002). In order to better manage these important forest resources today and in the future, we must better understand their dynamics. Improving our understanding of how these forests have responded in the past to such pressures is of particular importance if we are to better monitor, predict, and manage for future vegetation change. Prediction of future forest change is often based on studies that document past forest change, a focus of this dissertation.

Increasingly, management of forest systems is based on the prediction of future vegetation changes, the responses of systems to recent pressures, as well as the emulation of system dynamics in the past, particularly before the onset of disturbance associated with Euro-American settlement (Cleland et al. 2004). Hence, historical data sets are key resources needed to advance knowledge about forest dynamics in the past, including community composition and disturbance regimes (Schulte and Mladenoff 2005), as well as to predict future changes. Obtaining historical data on the Great Lake region is especially difficult because the majority of the forests in the Great Lakes region were decimated with the onset of Euro-American settlement in the region beginning around 1800 (Hupy and WinklerPrins 2005). This has rendered other reconstructive tools, such as dendrochronology, generally inapplicable (Frelich 1995). Therefore, knowledge about the dynamics of forest ecosystems in the Great Lakes region prior to Euro-American settlement must be gained from either historical data, such as the U.S. General Land Office's (GLO) original Public Land Survey (PLS), or from environmental proxies, such as fossil pollen and preserved macrofossils.

The PLS data are the most detailed record of forest systems available for the time period just before Euro-American settlement (hereafter "presettlement"), available. The PLS data have been widely applied within the Great Lakes region in order to spatially reconstruct forest community composition, disturbance regimes, species competition, as well as to examine relationships between soils and vegetation (Barrett et al. 1995;Bourdo 1956; Hushen 1966; Whitney 1986; Medley and Harman 1987; Palik and Pregitzer 1992; Dodge 1995; Schaetzl and Brown 1996; Schulte and Mladenoff 2001, 2005; Cleland et al. 2004). Because the PLS data are spatially explicit and were collected at a relatively fine spatial grain within a standard system, they can be used to statistically reconstruct the species composition and distribution of presettlement forests communities (Delcourt and Delcourt 1996). The PLS data provide a record of both regional vegetation patterns as well as relatively detailed information about local conditions prior to Euro-American settlement. With appropriate analysis they are representative of the ecological characteristics of the historical landscapes at the time they were collected (Bourdo 1956; Grimm 1984; Delcourt and Delcourt 1996; Manies et al. 2001; Schulte and Mladenoff 2001).

While the PLS data provide a relatively detailed history of forest ecosystems in the Great Lakes region, they were typically collected over a few decades and were then compiled, providing a detailed forest history for a relatively narrow (10-30 yr) snapshot in time. Environmental proxies, such as fossil pollen, provide relatively less detailed information about forest ecosystem history than do the PLS data, but fossil pollen can be used to reconstruct the history of forest ecosystems over time. Fossil pollen has the advantage over PLS data that it can be used to reconstruct forests at multiple snapshots in time.

Plants produce pollen grains in abundance. Pollen grains released by plants become airborne and are mixed by the atmosphere. Pollen grains in the air, referred to as the pollen rain, are representative of the surrounding vegetation. The proportion of each pollen type in the pollen rain is a function of both the dispersal mechanism of the pollen, i.e. insect pollinated plants are under-represented in the pollen rain and wind pollinated plants are over-represented, and the abundance of each plant type in the surrounding vegetation. Airborne pollen grains are transported, deposited, and then preserved in anaerobic environments such as lakes, fens, bogs, as well as the ocean floor, for thousands of years. Over time, pollen accumulates in these aquatic environments and the buried pollen grains within these sediments provide a record of past vegetation. A sample of the pollen rain obtained from the analysis of these aquatic sediments contains a snapshot of vegetation history at a particular point in space and time (Bennett and Willis 2001). By collecting and analyzing samples of fossil pollen at different sediment depths and by collecting and dating sediments from multiple lakes in key geographic locations, vegetation history, over time and space, can be reconstructed (Lui 1990).

Extensive research, using paleo-environmental proxies such as fossil pollen, has been conducted in the Great Lakes region. Particularly, numerous fossil pollen studies have reconstructed the vegetation of the Great Lakes region throughout the late Quaternary Period (Potzger 1948; Brubaker 1975; Grimm 1983; Webb et al. 1983; Bartlein et al. 1984; Kapp et al. 1990; Graumlich and Davis 1993; Liu et al. 2001; Flakne 2003). A majority of this research has focused on vegetation change at 1,000-year intervals, and over relatively large geographic areas, i.e. at regional and continental scales (>500 km^2). Research conducted at these relatively coarse temporal and spatial scales, referred to here as the macro-scale domain, generally examines vegetation change at the formation or biome scale. These vegetation changes are generally associated with interglacial climatic and orbital cycles, or in other words long-term climatic trends. Macro-scale research has documented species migrations, the re-forestation of North America since deglaciation, and major biome shifts (Delcourt and Delcourt 1987). Moreover, this research has provided many insights into the dynamics of vegetation systems at temporal and spatial scales, where traditional ecological research is limited. While the contributions of paleoecological research to our understanding of Great Lakes forest dynamics are significant and have proved to be invaluable, gaps in the record still exist and many questions regarding the nature and details of these vegetation changes remain unanswered.

Very few studies conducted in the Great Lakes region have examined vegetation dynamics at intermediate temporal and spatial scales, i.e. the meso-scale domain (sub-regional changes at 10 to 100-yr intervals), resulting in a void in the paleoecologic record. However, research predicting the future of the Great Lakes forests is often conducted at the meso-scale domain and requires knowledge and data about vegetation responses to short-term fluctuations in climate. The few existing pollen studies conducted at the meso-scale domain have provided valuable insights into vegetation dynamics, have wide application, and have aided in management as well as modeling efforts to predict future forest change (Bernabo 1981; Davis et al. 1986; Solomon and Bartlein 1992). Results from meso-scale pollen research that investigates the responses of forest ecosystems to past climatic change has the potential to: 1) provide detailed data sets that measure changes at the same scales in which the models of future forest change operate; 2) fill a gap in the paleoecolgical record; and 3) provide valuable insight into vegetation dynamics at scales where relatively little pollen research has been conducted (Overpeck et al. 1991; Noss 2001; Jackson and Williams 2004; Saxon et al. 2005). When insights gained from meso-scale research are combined with knowledge of current or recent ecological systems, such as that from the study of the PLS data, a broader perspective over both time and space is gained. These new perspectives can be used directly to predict and manage for future shifts in plant community composition and structure (Scheller and Mladenoff 2005).

Plant communities are most sensitive to pressure, i.e. changes in their environment such as climate change and other types of disturbances, at their ecological limits or boundaries. Therefore, studying changes in ecological communities at their range limits, or ecotones, is useful because it is here that responses to environmental change are most likely to occur first. Ecotones are spatially measurable systems, sensitive to climate change, and thus provide an excellent opportunity to examine vegetation responses to climate change over time at the meso-scale domain (Neilson 1993; Baker and Weisberg 1995; Kupfer and Cairns 1996; Cairns 1999; Malanson et al. 2001). Several studies have successfully documented and quantified transitions in ecotones during the Holocene period in North America at the macro-scale domain (Liu 1990; MacDonald 1998; Camill and Clark 2000; Liu et al. 2001; Baker et al. 2002), but very few studies have examined ecotone *dynamics* at the meso-scale domain. Meso-scale domain research has the potential to answer questions about ecotone dynamics and the responses of vegetation to short term variations in climate such as: *How stable are temperate forest ecotones? Do ecotones* *become more diffuse or more defined as a result of climate change? Which species are most likely to respond to shifts in temperature and precipitation?*

Many tree species meet their climatic tolerances and thus their geographical limit at ecotones within the Great Lakes region, including the forest transition zone in the central Lower Peninsula of Michigan. The forest tension zone is a transitional zone between deciduous-dominated forests to the south and mixed coniferous forests that lie to the north. Several macro-scale paleoecolgical studies have documented significant change specifically within the forest communities of the Lower Peninsula of Michigan during the Holocene (Potzger 1948; Gilliam 1967; Ahearn 1976; Bernabo 1981; Webb et al. 1983; Kapp 1999). Although these studies have provided valuable knowledge about the long-term dynamics of these forests, relatively little is known about the dynamics of the forests, specifically the forest tension zone, at finer temporal and spatial scales.

The majority of vegetation models developed for the Great Lakes region predict a northward shift in the range of several species in the near future, as well as increased mortality of boreal species currently at their southern limit (Iverson and Prasad 1998; Sousounis and Bisanz 2000; Walker et al. 2002). Forests in the region may become increasingly depauperate and may even cease reproductive growth in the near future (Solomon and Bartlein 1992). For example, the STASH model, based on climatic tolerances of key species predicts that several species, including the economically important *Pinus strobus* (white pine) and *Betula lutea* (yellow birch) may become extinct in the region by the end of the century (Walker et al. 2002). While models such as STASH provide much insight into the impacts of climate change, many questions remain. *Can indicator species show early signs of global warming impacts on forest systems? How will complex forest systems, such as ecotones, respond to climate change?*

Current models may be improved with advances in understanding of meso-scale vegetation dynamics (Noss 2001; Sitch et al. 2003). This research will address these issues by investigating the ecotone dynamics, specifically the forest tension zone in the Lower Peninsula of Michigan, to recent climate fluctuations at the meso-scale domain

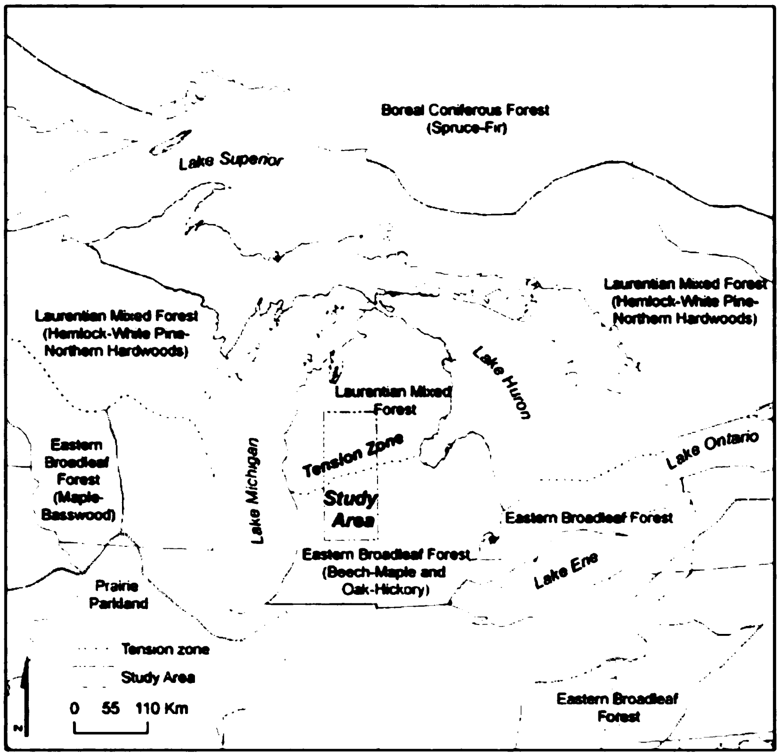

Figure 1.1 Major vegetation regions in the Great Lakes Region and the location of the tension zone (adapted from Bailey 1976).

1.2 Research Design

The goal of this research is to examine the dynamics of a mid-latitude forest tension zone at the meso-scale domain. Specifically, I examined the composition, spatial arrangement, and reconstructed changes within the forest tension zone in the central Lower Peninsula of Michigan during the past 2,000 yrs. The forest tension zone in the central Lower Peninsula of Michigan is an ecotone between the Laurentian mixed-forest north of the tension zone (dominated by hemlock-white pine-northern hardwood communities) and the eastern broadleaf forests south of the tension zone (dominated by beech-maple and oak-hickory communities) (Barbour and Billings 1988; Burns and Honkala 1990). North of the tension zone, coniferous species such as *Pinus strobus*, *Pinus rubra* (red pine), and *Tsuga canadensis* (hemlock) increase in abundance along with *Acer saccharum* and *Betula lutea* (yellow birch) forming a mixed coniferous-deciduous forest. South of the ecotone the dominant species include *Fagus grandifolia* (American beech), *Acer saccharum* (sugar maple), several species of *Quercus* (oak) and *Carya* (hickory). Also, several herbaceous taxa meet their southern or northern range limits in the central part of the Lower Peninsula (Voss 1972).

This research had three specific objectives each of which is discussed below:

- **The first objective of this research was to reconstruct presettlement forest composition based on the PLS data, for a study area within the central Lower Peninsula of Michigan.** The study area encompasses the forest tension zone, as well as forest communities immediately to the north and south. This research: 1) quantitatively described the various forest communities within the study area, including those that comprise the tension zone itself; 2) examined the spatial distribution of these communities within and near the tension zone, and 3) explored the relationships between species, the identified communities, and their distribution in regard to the tension zone. The PLS data were collected and analyzed using forest structural metrics, statistical clustering, and ordination analysis.

- **The second objective of this research was to reconstruct changes in the forest communities within the tension zone during the past 2,000 years at the meso-scale domain using high-resolution fossil pollen analysis of three representative study lakes.** High resolution fossil pollen analysis was conducted for three lakes all located within the PLS study area including: Hicks Lake in Osceola County (north of the tension zone), Cowden Lake in Montcalm County (within the tension zone), and Morrison Lake in Ionia County (south of the tension zone). Each lake is located in a different forest type with regard to the tension zone. The fossil pollen data were then statistically analyzed and interpreted in order to reconstruct changes in forest communities over the past 2,000 years.
- **The third objective of this research was to quantitatively assess changes in the forest tension zone in the central Lower Peninsula of Michigan during the past 2,000 years by correlation of the PLS and pollen data sets**. Both the fossil pollen data and the PLS data were

analyzed with multiple statistical techniques in order to assess the dynamics of the forest ecotone. Specifically, this research: 1) determined if and where the ecotone had shifted over the past 2,000 years; 2) assessed which communities had shifted; and 3) examined how species associations have reorganized over this time period. The detailed reconstruction of forest composition generated from the PLS data served as a baseline for which to compare changes in forest composition in the past.

1.3 Dissemination of Dissertation

This dissertation is composed of an introduction (Chapter 1), three main chapters (Chapter 2, Chapter 3, and Chapter 4), which address each of the three main objectives, and conclusions (Chapter Five). The three main chapters, Chapter 2, Chapter 3, and Chapter 4 are designed and written independently of each other such that they may be submitted separately for external peer-review, pending successful dissertation defense and committee approval. Thus, some of the background material within each chapter overlaps. Several target publications have been chosen and final decision will be made in concert with committee members.

Chapter 2, entitled "The forest tension zone in the central Lower Peninsula of Michigan, USA: A quantitative assessment of community composition before Euro-American settlement" is written to be submitted to the *Canadian Journal of Forest Research*. Chapter 3 entitled "The vegetation history of the forest tension zone in the central Lower Peninsula of Michigan, USA, during the past 2,000 years" is written to be submitted to either *Ecological Monographs* or *The Holocene*. The fourth chapter, titled "Meso-scale dynamics of the forest tension zone in the central Lower Peninsula of Michigan, USA: 2,000 years of change," is written to be submitted to the *Journal of Biogeography*. Chapter 5 is a conclusion chapter and summarizes my contributions to the field of biogeography and addresses avenues of future research.

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Chapter 2

The Forest Tension Zone, in the central Lower Peninsula of Michigan, USA: A Quantitative Assessment of Community Composition before Euro-American Settlement

2.1 Introduction

The forests of the Great Lakes region are under constant pressure from a variety of both anthropogenic and non-anthropogenic disturbances including: land use change, harvesting, invasive species such as *Pinus sylvestris* (Scotch Pine), pests such as *Agrilus planipennis* (emerald ash borer) and *Lymantria dispar* (gypsy moth), diseases including *Ophiostoma ulmi* (Dutch Elm), fire, windthrow, and climate change (Sousounis and Bisanz 2000). Successful management and monitoring is essential to ensure the longevity and health of forest systems under such pressures. Management of forest systems is increasingly based on both the responses of systems to recent pressures as well as the emulation of system dynamics in their "natural state" or before the onset of disturbance associated with Euro-American settlement (Cleland et al. 2004). Therefore, historical data sets are key resources needed to advance knowledge about past forest dynamics including community composition and disturbance regimes (Schulte and Mladenoff 2005). Detailed knowledge of forest community composition and disturbance regimes in the past is often difficult to obtain. Obtaining historical data in the Great Lake region proves especially challenging given that the majority of the forests were decimated after A.D. 1800 with the onset of Euro-American settlement in the region (Hupy and WinklerPrins 2005). This fact diminishes the utility of other reconstructive tools, such as dendrochronology, (Frelich 1995).

The U.S. General Land Office's (GLO) original Public Land Survey (PLS) is the most detailed record available for forest systems prior to Euro-American settlement (hereafter referred to as presettlement) (Schulte and Mladenoff 2001). The PLS data have been widely applied within the Great Lakes region in order to spatially reconstruct forest community composition, disturbance regimes, species competition, as well as to examine relationships between soils and vegetation (Barrett et al. 1995; Bourdo 1956; Hushen 1966; Whitney 1986; Medley and Harman 1987; Palik and Pregitzer 1992; Dodge 1995; Schaetzl and Brown 1996; Schulte and Mladenoff 2001, 2005; Cleland et al. 2004). While the PLS data have serious limitations, including surveyor bias (Bourdo 1956), they are an extremely valuable resource, with many advantages over early accounts by explorers and naturalists. They have greatly contributed to our understanding of forest systems (Manies et al. 2001). Because the PLS data are spatially explicit, quantitative, and were collected within a grid system, they can be used to reconstruct forest communities with statistical parameters (Wu 2005). Since the PLS data were collected over a broad spatial coverage, but implemented at a relatively fine spatial grain, both regional vegetation patterns as well as relatively detailed information about local conditions can be extracted (Delcourt and Delcourt 1996). Previous research has demonstrated that, with appropriate analysis, the PLS data are representative of the ecological characteristics of the historical landscapes at the time they were collected (Bourdo 1956; Grimm 1984; Delcourt and Delcourt 1996; Manies et al. 2001; Schulte and Mladenoff 2001; Wu 2005)). Because the PLS was implemented over large areas of the United States, analytical methods appropriate for these data have been developed and tested (Manies and Mladenoff 2000), and can be implemented by multiple researchers in different regions to facilitate comparison of historical landscapes across much of the United States (Wu 2005).

The PLS data have been used to reconstruct vegetation in several states, including Michigan, Wisconsin, Minnesota, and Missouri; similar historic data have been used in Ontario, Canada, as well (Comer et. al. 1995a; Cowell 1998; Batek et al. 1999; Jackson et al. 2000; Friedman 2001; Schulte et al. 2002; Suffling et al. 2003). Many of these early maps of regional forest types were constructed through qualitative interpretation of the PLS data based on the physical geography of the landscape in focus, including soils, climate, and topography (Veatch 1959). While the maps resulting from these immense efforts have been extremely valuable, they often lack detail and their accuracy is difficult to assess (Schulte and Mladenoff 2001). Quantitative methods, including ordination and geospatial interpolation (Delcourt and Delcourt 1996; Brown 1998; Friedman 2001), have been applied in order to reconstruct forest composition at sub-regional and local scales. More recently, cluster analysis has been successfully employed at regional scales in both Wisconsin and New England (Cogbill et al. 2002; Schulte et al. 2002).

While statewide qualitative vegetation maps have been constructed from the PLS data in Michigan (Vetach 1959; Comer et al 1995a), quantitative techniques have only been employed in individual counties or local sites (Barrett et al. 1995; Schaetzl and Brown 1996; Zhang et al. 2000). Completely lacking from this research is a quantitative reconstruction of the presettlement forest communities in the Lower Peninsula of Michigan at regional or sub-regional scales. Presettlement maps of the forests in the Lower Peninsula of Michigan would be valuable resources for monitoring and managing of forest ecosystems, as well as be useful for other scientific endeavors such as archeology. These maps would provide insight into the regeneration of forests after Euro-American settlement as well as aid in the successful management of forests ecosystem today and in the future.

The forests within the Lower Peninsula of Michigan as with most of the Great Lakes region, experienced intense anthropogenic disturbance associated with Euro-American settlement and associated logging. While existing research has provided insights into the impacts of logging on the regeneration of these forests (Whitney 1987; Barrett 1998) and the quality of forests today in comparison with those of the past (Donnelly and Murphy 1987; Scull and Harman 2004), the effects of this intense disturbance are still not fully understood. Today, remnant second and third generation forests exist in a mosaic of agricultural, urban, and suburban land uses and are faced with a wide variety of pressures, including urban sprawl, climate change, Emerald Ash Borer attacks, Dutch elm disease, and Gypsy moth infestations.

The tension zone, an ecotone between the mixed-coniferous forests in the northern Lower Peninsula and the deciduous forests in the southern Lower Peninsula of Michigan, has been of particular interest to many researchers (Andersen 2005). To date, the PLS data have been utilized to investigate relationships between soils and vegetation (Medley and Harman 1987; Dodge 1995; Schaetzl and Brown 1996) as well as to assess competition between species within the ecotone (Brewer 1982). But a quantitative baseline of forest communities within and surrounding the tension zone prior to Euro-American settlement and subsequent devastation has not yet been established. A quantitative assessment of the tension zone just prior to Euro-American logging could be used to measure the responses of these forest systems to pressures, especially climatic variations, in the past and into the future. Because many species reach their distribution limits within the tension zone within the Lower Peninsula of Michigan, these forests are particularly sensitive to changes in climate and other disturbances. Other ecotones, such as those in alpine areas, are sensitive to climate perturbations and have proved useful in studying the impacts of climate change on vegetation (Baker and Weisberg 1995; Kupfer and Cairns 1996; Stohlgren and Bachand 1997)

In this research, previously developed and tested quantitative methods (Schulte et al. 2002) were utilized to reconstruct presettlement forest composition based on the PLS data for a study area within in the central Lower Peninsula of Michigan (Figure 2.1). The objectives of this research were: 1) to quantitatively reconstruct the forest composition of the communities comprising the ecotone, as well as communities just outside the tension zone, prior to the onset of major disturbance associated with Euro-American settlement; 2) to examine the distribution of communities with regard to the ecotone itself; and 3) to explore the relationships between species, their cluster memberships, and the ecotone. This research does not attempt to address specific hypotheses in regards to the tension zone or its nature but instead uses multiple statistic techniques to reconstruct forest communities within the tension zone and explore the results. The data generated from this research will then be used in future research to ask specific questions with regards to the tension zone. The PLS data were collected and analyzed with forest structural metrics, statistical clustering, and ordination analysis. Relative importance calculated from both relative density and relative dominance of species within the study area was the primary input for all statistical analysis. Relative importance is a widely applied forest metric used to analyze PLS data which can measure tree distribution on the landscape (Schulte et al. 2002). Cluster analysis was utilized to identify groups of species, i.e. communities, on the landscape. Once communities were identified, maps of these communities were constructed at the grain of sampling, one PLS section (2.65 km^2) or one square mile. The results from the cluster analysis were then further analyzed with ordination.

The resulting map of forest community composition clearly demonstrated the presence of the forest tension zone and revealed new insights into the character of the tension zone. The insights include: the diffuse nature of the transition, the presence of transitional communities distributed primarily within the ecotone itself, and the complexity of individual species dominance on the landscape.

2.2 Study Area

The PLS data were collected from an rectangular area within the central portion of the Lower Peninsula of Michigan which encompasses the tension zone itself as well as communities immediately to the north and the south of the tension zone (Figure 2.1). The study area (Figure 2.1 and 2.2) was carefully delineated based on physical geography, climate and soils, as well as broad presettlement forest patterns. Areas adjacent to the Great Lakes, Lake Michigan and Lake Huron, were excluded from analysis due to the influence of lake-effect climate in the western Lower Peninsula of Michigan (Schaetzl and Isard 2002). Areas near Saginaw Bay in the east were excluded because of the dominance of fine-textured, organic (muck), and poorly-drained soils, both of which strongly influence forest composition (Barnes and Wagner 2004). The study area encompassed all established locations of the tension line or ecotone itself as (based on summaries by Schaetzl (1990) and Andersen (2005)) as well as communities north and south of the ecotone. The length and width of the study area rectangle were chosen on the basis of all these criteria. The study area covers approximately 15, 700 km^2, 6,060 sections, and more than 330,000 bearing trees.

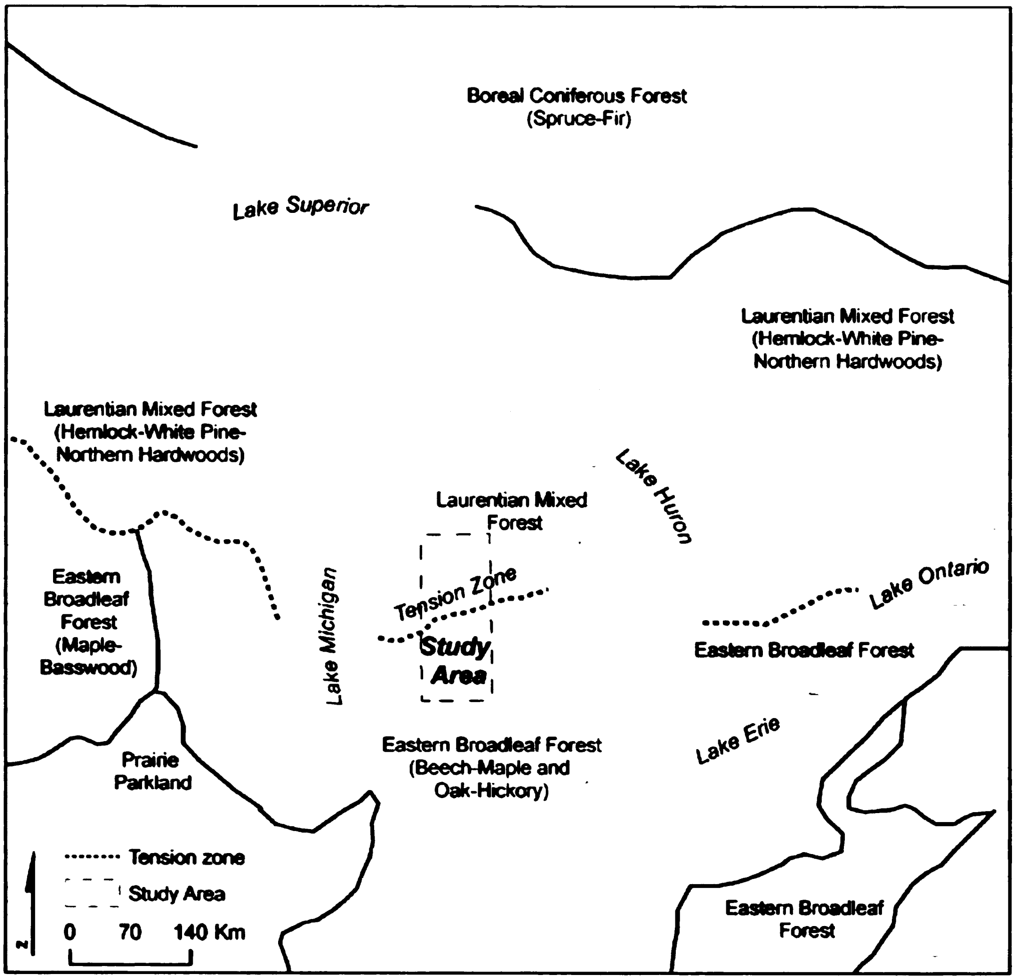

Figure 2.1 Major vegetation regions in the Great Lakes Region and the location of the tension zone. Adapted from Bailey 1976.

A regional landscape ecosystem classification system has been devised for all of Michigan based on the integration of climatic, landform, soil and vegetation factors (Albert et al. 1986; Albert 1995). The Lower Peninsula of Michigan is divided into two major regions and subdivided further into sections and sub-sections (Figure 2.2). The physical geography of the study area is described generally below and details regarding the different sections and sub-

sections within the landscape ecosystem classification system are provided in

Table 2.1.

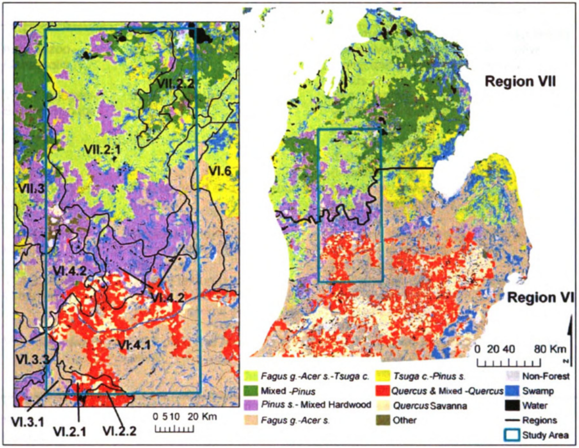

Figure 2.2 Regional Landscape Ecosystems of Lower Michigan (Albert et al. 1986; Albert 1995), presettlement vegetation (Comer 1995a), and the study area.

Table 2.1 Characteristics of the regional landscape ecosystems sub-districts within the study area (Comer et. al. 1995b, Albert 1995). Map of sub-districts is shown in Figure 2.2.

LTA*	Landform	Soils	Disturbance**
VI.2.1 Kalamazoo – Battle Creek	Outwash and ground moraine	Well or moderately well drained sands and loamy sands	Fire (lightening and Native American activity)
VI.2.2: Kalamazoo–Cassopolis	Coarse textured end moraine and ice-contact terrain	Well drained and excessively drained loamy and gravely sands	Fire (lightening and native activity)
VI.3.1: Allegan–Berrien Springs	End and ground moraine	Sandy loams underlain by clays or gravelly sands, moderately well drained or well drained	
VI.3.3: Allegan–Jamestown	Fine-textured end and ground moraine	Loamy with small areas of well drained outwash	
VI.4.1: Ionia–Lansing	Medium-textured ground moraine with outwash channels	Loamy with alternating well and moderately well drained	Windthrow and fire
VI.4.2: Ionia–Greenville	Coarse-textured end and ground moraine with outwash channels on low slope position	Well drained and excessively well drained sands and loams	Fire and windthrow
VI.6: Saginaw Bay	Lake plain and reworked till plain	Poorly drained mineral soils on lake plain and excessively drained sandy soils on till plain	Fire and water level fluctuations
VII.2.1: Highplains–Cadillac	Coarse textured end moraine	Sandy well to excessively drained	Fire and windthrow
VII.2.2: Highplains–Grayling	Outwash	Excessively drained sands or sands mixed with gravel	Fire (over 3% of land area burned), windthrows, blowdowns, frost pockets
VII.3: Newaygo	Outwash	Excessively drained sands	Fire (extensive)

*Land Type Associations

**Disturbances noted are those directly recorded in the original Public Land Survey notes within each sub-district (Comer et. al. 1995b).

2.2.1 Geology and Soils

Michigan's geomorphology is strongly influenced by numerous episodes of glaciation and interglaciation during of the Pleistocene Epoch (Schaetzl and Isard

2002). The major landform types found within the study area are end moraines, ground moraines, and outwash plains (Albert 1995). Several types of glacial sediment are found in the region, including glacial till composed of unsorted and unstratified sand, clay, gravel, and rocks; glacial outwash composed of primarily of sorted and stratified silt, sand, and gravel; lacustrine sediment composed of fine-grained sediments; and dune sand composed of wave-sorted sediments re-worked by wind (Schaetzl and Isard 2002).

Parent material, climate, and topography all exert strong influences on the soils within the region. The soils in the northern Lower Peninsula of Michigan are generally classified within the Spodsol order (Podzolic Order in Canadian System of soil classification) (Soil Classification Working Group 1998), while in the southern half of the Lower Peninsula soils are generally classified within the Alfisol order (Solonetzic or Luvisolic Order in Canadian System) (Schaetzl 1990). Soil development and distribution are determined largely by the parent material on which they have formed. Soils found on the moraines are generally fertile, while the soils found on outwash are generally very coarse textured, porous, dry, and relatively less fertile.

2.2.2 Climate

The climate of the Lower Peninsula of Michigan is classified as humid continental, although temperature and precipitation vary considerably. Major climatic controls include the state's continental location, latitude, and large-scale circulation patterns, as well as the Great Lakes themselves (Eichenlaub et al.

1990; Schaetzl and Isard 2002). A strong temperature gradient occurs within the state and the Lower Peninsula itself, where temperature decreases with increasing latitude. The annual mean temperature in the state ranges from 10° C in the Lower Peninsula to 4.4°C in the Upper Peninsula. Within the study area itself, the average maximum July temperature is 25.5 ° C and the minimum average January temperature is -11°C (data for Mount Pleasant, Michigan) (Hoare 2005).

The number of growing days (0°C, 32° F freeze free period) in the southern Lower Peninsula ranges from 160 to 170 days. The number of growing degree days declines in a northerly direction where the northern part of the Lower Peninsula experiences approximately 70 growing days (Van Der Brink et al. 1971; Barnes and Wagner 2004). In the Lower Peninsula mean annual precipitation ranges from 91.4 cm in the southwest to 68.5 cm in the northwest part of the Lower Peninsula. The presence of the Great Lakes has a moderating effect on local climates along shorelines. Areas slightly inland from the shorelines commonly experience increased winter snowfall in the form of lake-effect snow. Lake effect snowfall is due to unstable conditions in the atmosphere, caused by cold continental polar air masses moving over the Great Lakes. The snow showers produced by lake-effect snowfall can account for 30% to 60% of the total snowfall in areas that fit the criteria for lake effect conditions (Schaetzl and Isard 2002).

2.2.3 Vegetation

A variety of diverse and extensive forest communities dominated the landscapes of the Lower Peninsula of Michigan during the early 19th century before Euro-American arrival and subsequent disturbance. Mixed Laurentian forests dominated the northern half of the Lower Peninsula of Michigan while the eastern broadleaf forests dominated the southern half of the Lower Peninsula. The nature of this vegetation is best discussed within the context of the regional landscape ecosystem classification system developed by D. Albert (1995). In this system, the northern Lower Peninsula is designated as Region VII while the southern Lower Peninsula is designated as Region VI (Albert et al. 1986; Albert 1995) (Figure 2.2). The northern limit of Region VI is roughly delimited by a line running from Saginaw Bay on the east side horizontally across the state to Lake Michigan in Muskegon County on the west side (Figure 2.2), which also roughly approximates the general location of the forest tension zone. This line is also approximately at the 8.3 °C isotherm of mean annual temperature.

The forest tension zone, an ecotone where several taxa meet their distribution limits on the landscape (Andersen 2005), occurs between the broadleaf forests of eastern North America and Laurentian mixed forests at the boundary of Region VI and Region VII (Elliot 1953; Curtis 1959). This tension zone spans from southern Ontario westward to northern Minnesota. Along this geographic boundary between major forest associations, the nature of the tension zone changes in association with the different forests communities present in the Great Lakes region (Andersen 2005). In the Lower Peninsula of

Michigan, the tension zone is a gradual transition between deciduous forests in the south, including *Fagus-Acer* (beech-maple) and mixed *Quercus* (oak) forests, and the mixed coniferous-deciduous forests in the north, with dominants including *Tsuga canadensis* and various species of *Pinus* (pine). Several species reach both their northern and southern range limits in the Lower Peninsula of Michigan, and within the tension zone itself (Figure 2.3). *Abies balsamea*, *Picea mariana*, *Pinus strobus*, and *Tsuga canadensis* all are at their southern range limits, while *Quercus velutina*, *Quercus alba*, and *Carya ovata* reach their northern range limits in the central Lower Peninsula of Michigan (Voss 1972; Burns and Honkala 1990). While the delineation of the zone varies (Potzger 1948), the tension zone is typically described as a 95-km wide belt (Barnes and Wagner 2004) whose center may be broadly approximated by the 8°C (47°F) isotherm of mean annual temperature (Medley and Harman 1987; Barnes and Wagner 2004). Some authors refer to the tension zone as an abrupt ecotone (Elliot 1953; Brewer 1982) while others refer to it as diffuse (Medley and Harman 1987).

Region VI, dominated by the eastern broadleaf forests, experiences a warmer climate than Region VII, therefore communities of this southerly Region were predominately deciduous (Albert 1995). Communities in Region VI included *Quercus-Carya*, and *Fagus –Acer saccharum* forests, *Quercus* savanna, and deciduous hardwood swamps. *Quercus-Carya* communities were dominant mainly in the southern and eastern part of Region VI where the climate was warmer and drier than in the west near Lake Michigan. These communities thrived on xeric to dry mesic well-drained soils on sandy end moraines and outwash plains (Barnes and Wagner 2004). Fire was an important component of these communities, which allowed *Quercus* species to dominate compared to the other deciduous species, such as those found in the *Fagus -Acer* forests. Dominant species included *Quercus alba* (white oak), *Quercus velutina* (black oak*)*, *Quercus rubra (*red oak*)*, *Carya glabra* (pignut hickory), and *Carya ovata (*shagbark hickory*)*. *Fagus -Acer* forests, the second most common community in Region VI, were dominant on more mesic conditions and richer soils found on the upland portions of ground and end moraines. Dominant species in these forests included *Fagus grandifolia, Acer saccharum*, *Quercus rubra*, *Tilia americana (*basswood*)*, and *Fraxinus americana (*white ash).

Although much less extensive, *Quercus* savannas were also present in Region VI and were found on hot dry sites where frequent fire encouraged the growth of grasses. Dominant species included: *Quercus macrocarpa (*bur oak*)*, *Quercus velutina*, and *Quercus ellipsoidalis* (northern Pin oak) (Dickman and Leefers 2003; Barnes and Wagner 2004). In these *Quercus* savannas, trees grew out in the open as individuals surrounded by grasses and forbs, or in groves which often transitioned into pockets of prairie. True prairies, devoid of all trees with some shrubs, and brush prairies, where grasses were accompanied by shrubs as well as tree sprouts, were present in this southern region in selected locations (Barnes and Wagner 2004). Deciduous swamps, dominated by *Acer rubrum* (red maple), *Fraxinus nigra (*black ash*)*, *Ulmus americana (*American elm*)*, and *Betula alleghaniensis* (yellow birch) were found in low, wet areas in

Region VI, especially on the wet landscapes near Saginaw Bay and in extreme south east Lower Michigan.

The forest communities in Region VII, mainly coniferous or mixed coniferous-deciduous forests, were quite different from those in the southern part of the state. *Pinus* and northern hardwood communities dominated Region VII before Euro-American settlement. The *Pinus* communities, including dominant taxa *Pinus strobus*, *Pinus resinosa (*red pine*),* and *Pinus banksiana* (jack pine), were common in the central part of the region on sandy outwash plains and found on droughty, acidic, nutrient-poor soils, where fires occurred frequently. On excessively drained sandy ridges, *Quercus-Pinus* forests dominated and were comprised of either *Pinus resinosa* or *Pinus strobus* and *Quercus alba* (Dickman and Leefers 2003). In extremely xeric sites, where fire was frequent, *Pinus banksiana* dominated. *Pinus strobus* was more common in the dry-mesic sites, but would also be successful surrounded by other hardwoods on the more mesic, nutrient-rich sites.

Pinus species were perhaps the most impressive trees on the landscape at the time of Euro-American arrival. *Pinus strobus* could reach heights of up to 36 m and over 1 m in diameter at breast height (Barbour and Billings 1988; Burns and Honkala 1990). The northern hardwoods community, or northern mesic forest, the other dominant forest type in Region VII, was found predominately on the more fertile and mesic till soils often on moraines. Dominant species in the northern hardwood communities included *Acer saccharum*, *Fagus grandifolia*, *Betula alleghaniensis*, *Tsuga canadensis*, *Acer rubrum*, *Tilia americana*, *Abies* *balsamea,* and *Pinus strobus.* Fire and gap disturbance was frequent enough to maintain the presence of *Pinus strobus* in theses communities. Conifer swamps were found in low, wet areas which were dominated by *Picea glauca* (white spruce), *Picea mariana* (black spruce), *Larix laricina* (tamarack), and *Thuja occidentalis* (northern white cedar).

The spatial arrangement of and reasons for the forest tension zone in the Lower Peninsula of Michigan has been debated in the literature (McCann 1979; Medley and Harman 1987; Dodge 1995; Barnes and Wagner 2004). McCann (1979) attributed the boundary to a rapid change in the growing degree day gradient, which decreases in a northerly direction at the location of the transition. Alternatively, Brewer's (1985) research attributes the transition to competition between northern species, *Tsuga canadensis* and *Pinus strobus*, and southern species including *Quercus* spp. and *Carya* spp.. Medley and Harman (1985) concluded that the location of the tension zone was significantly correlated with the increase in abundance of coarse-textured soils in the north and the ability of coniferous species to dominate more than the deciduous species on these sites. Dodge's (1995) research in the "thumb" of the Lower Peninsula also demonstrated a relationship between vegetation, soil texture, and the location of the tension zone. However, soil geography only explained 50 percent of the variance in the relationship; thus Dodge (1995) stressed the importance of other factors including disturbance and climate. The general consensus from the literature is that climate is the broad-scale influence on the location of the tension zone, while at finer spatial scales edaphic controls are more important (McCann

1979; Brewer 1982; Medley and Harman 1987; Dodge 1995; Barnes and Wagner 2004). Coarse-textured soils are more common in the northern part of the Lower Peninsula, on which coniferous species are more successful, while in the southern part deciduous trees out-compete coniferous trees on loamy soils.

The presettlement vegetation composition of the Lower Peninsula of Michigan was driven mainly by species migration after deglaciation, physical factors (climate and soils), and biotic interactions (herbivory and competition) as well as disturbance regimes (fire, windfall, insect outbreaks, and disease). While it is now well established that Native Americans had a significant impact on the landscapes of North America (Doolittle 2000; Vale 2002), this impact appears to have been relatively minimal and localized (Lewis 2002; Lovis et al. 2005).

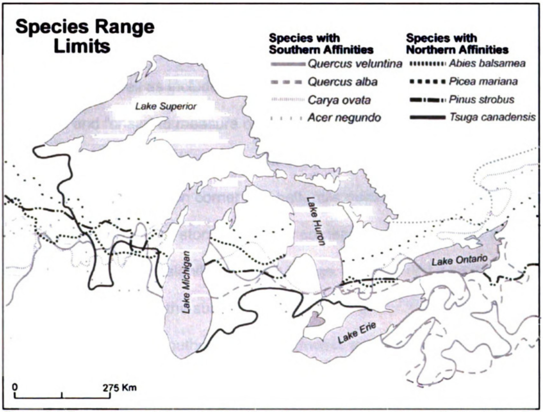

Figure 2.3 Range limits of aboreal taxa with both northern and southern affinities in the Great Lakes region. Adapted from Schaetzl and Isard (2002).

2.3 Materials and Methods

2.3.1 Public Land Survey

The U.S. General Land Office (GLO) original Public Land Survey (PLS) was initialized in 1785 and was conducted in Michigan between 1816 and 1856, prior to the onset of widespread Euro-American settlement (Comer et. al 1995b). Base and meridian lines had been established several years earlier. Therefore, the survey does provide a record of the landscape before the major disturbances associated with Euro-American settlement, subsequent logging, and other activities. Following the PLS standard survey system, the state was divided into thirty-six square mile grids, or townships, measuring 9.7 X 9.7 km (6mi X 6 mi) which were further divided into thirty-six sections measuring 2.6-km^2 (1-mi^2) (Figure 2.4) (Stewart 1935). While the surveyors' main task was to measure the landscape, they were also required to leave markers of the township and section boundaries, as well as include land resource information. The surveyors used a compass and "chain" to measure out the boundaries while noting features such as water, soils, topography, and vegetation that they encountered along each section line. Each section corner and half- mile point was marked with a wooden post, earthen mound, or stone. Meander corners were also marked where sections lines crossed significant water bodies. At each of the section, quarter, and meander corners, the surveyors marked two to four "bearing trees" at the northeast, northwest, southeast, and southwest quadrants of the intersections, which were intended to aid settlers in identifying parcels. As the surveyors marked "bearing trees", they recorded the species, diameter at breast height, and the bearing and distance of each bearing tree in relation to the corner post (Bourdo 1956).

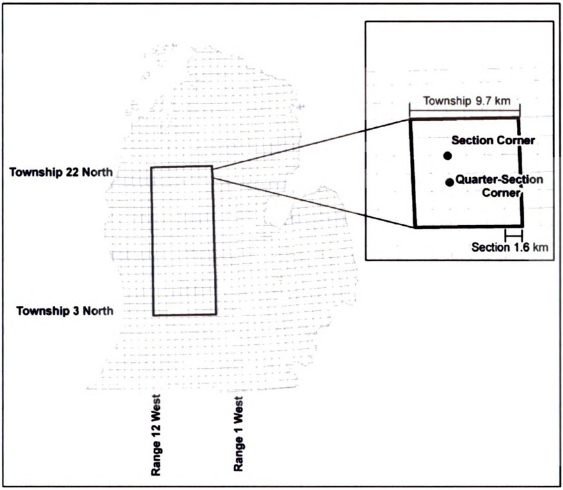

Figure 2.4 Diagram of the Public Land Survey (PLS) scheme and study area.

Because the bearing trees were collected for legal, not ecological, purposes, the surveyors chose the trees based on the following criteria: size and age of tree; species longevity; distance from corner; and conspicuousness in the stand. Therefore, the data are inherently biased for or against certain species and sizes (Grimm 1984). Moreover, the bearing tree data collected are of a coarser scale than typical vegetation survey data collected today. Because of the nature of the survey, the data may have variable quality, contain ambiguities, and may include error and, or, bias (Bourdo 1956; Grimm 1984; Comer et al. 1995b; Delcourt and Delcourt 1996; Manies et al. 2001; Schulte and Mladenoff 2001).

Specific areas of concern include the preference for certain tree species among surveyors and estimations, instead of exact measurements, of tree diameters. Although the PLS data cannot be used to directly calculate absolute density or tree size, they are still useful for determining indexes of density and documenting ecological conditions at a time in the past (Grimm 1984). Bias toward tree selection by individual surveyors has been detected by Manies (2001), but the error was variable and not consistent across the landscape. In Michigan, surveyors favored long-lived species, such as *Fagus grandifolia* and *Thuja occidentalis*, as well as several species of *Quercus*. Short-lived species, such as *Populus* and *Betula papyrifera,* were used less frequently than their actual presence on the landscape (Bourdo 1956; Comer et. al. 1995b). Hushen et al. (1966) tested for surveyor bias using methods established by Bourdo (1956), in Montcalm County, located within the study area for this research, and found no statistical bias in the PLS data. In Michigan, many bearing trees were identified only to the genus level, including "pine", "elm", "ash" and "maple". In some cases, common names have changed for tree species such that in the notes, "spruce pine" is actually "jack pine" while "yellow pine" is "red pine" (Comer et. al. 1995b).

Ambiguous entries are a common problem when analyzing the PLS data, particularly when the genus designation could potentially refer to several individual species whose geographical and habitat ranges overlap. In the Lower Peninsula of Michigan, this problem is most commonly encountered when bearing trees are noted as "pine", leaving open the interpretation of species to either "jack", "red", or "white". Other authors have employed three main approaches in order to account for these ambiguities. These include: 1) using known relationships between soil and phytosociological associations to assign the ambiguous entry a species designator (Grimm 1984; Barrett et al. 1995; Zhang et al. 2000); 2) employing a logistic regression model based on several criteria (e.g., tree diameter, mean tree density, associated tree species, and land type associations) in order to assign a species designator (Schulte and Mladenoff 2001; Mladenoff et al. 2002); or 3) grouping bearing trees at the genus level (Grimm 1984; Schulte and Barnes 1996; Radeloff et al. 1999; Cogbill et al. 2002). In this research, ambiguous trees were treated as individual species such that all "maple" entries were treated as "maple" without further attempt to distinguish the entry at the species level. This method was chosen because the overall percentage of ambiguous entries was small. Also, because of the nature of the study area in focus, an ecotonal boundary, the success of and confidence in methods relying on the typical ranges and characteristics of tree species is lower than within a broad geographical region or a study area well within regional forest association boundaries.

Albeit numerous bias and ambiguities, the PLS data remain a valuable resources for reconstructing forest communities present in late 19th century landscapes. This is especially the case within the Lower Peninsula of Michigan where the majority of forests were decimated shortly after the onset of Euro-American settlement, and few other historical records exist. The PLS data were collected at a scale slightly coarser, i.e. extent and grain, compatible, with contemporary vegetation and mapping analysis from which forest communities can be reconstructed and various aspects of landscape heterogeneity can be measured. The resulting maps and measurements of landscape conditions from analysis of the PLS data can be directly related to ecosystem properties, including ecotone characteristics (Delcourt and Delcourt 1996). Therefore, maps of the forest communities comprising the tension zone before Euro-American settlement in the Lower Peninsula of Michigan could be utilized to study the ecology of forest systems before the onset of massive anthropogenic disturbance. They can also serve as a quantitative baseline for studies of forest change in the past and into the future.

2.3.2 Data Collection and Processing

The PLS data utilized in this research were not collected directly from the original survey notes, but rather from a compilation of the original notes generated by Michigan Natural Features Inventory (MNFI), a branch of the Michigan State University Agricultural Extension Service. The survey notes for Michigan have not been entered into a publicly available digital database. MNFI compiled the original PLS data as part of a project to generate a map of Michigan's native vegetation prior to Euro-American settlement (Comer et. al. 1995b). All information from the original PLS data and the township plat maps were georeferenced and transcribed onto matte mylar attached to 7.5 minute U.S. Geological Survey topographic maps (scales of 1:24,000 and 1:25,000) for the entire state of Michigan (hereafter mylar-maps) (Figure 2.5). MNFI plotted each bearing tree in its relative position to each corner along with the tree species, diameter, bearing, and distance from each corner onto the mylar-maps. All surveyors' comments with regard to ecological features and conditions (rivers, streams, drainage, soil characteristics, and fire scars) were also georeferenced and recorded on these mylar-maps. Lengthy notes taken by the surveyors were transcribed in the margins of the mylar-maps.

MNFI then developed a vegetation community classification scheme. Vegetation community boundaries were interpreted, drawn onto the mylar-maps, and then digitized in order to generate a state-wide map of presettlement vegetation (Comer et. al. 1995b). While the resulting digital maps produced during these immense efforts are extremely useful and of high quality, they cannot be used in independent statistical analyses.

Figure 2.5 Photograph of a typical portion of a mylar-map generated by Michigan Natural Features Inventory (MNFI). (Photography by author)

In this research, all the bearing tree data were collected directly from the mylar-maps. Methods used to collect the bearing tree data are illustrated in Figure 2.6. First a geospatial data set of the PLS quarter-quarter sections was downloaded from the Michigan Center for Geographic Information (MCGI). All geospatial data in this research were projected into the Universal Transverse Mercator (UTM), NAD 1983, Zone 16N, coordinate system. Using ArcGIS ArcInfo 9 ™, nodes were added to all corners. The nodes were then offset by 1-meter in a south-east direction in order to ensure that witness trees at each survey corner were used only once even though section boundaries are shared. This method is based on a similar method used by He et al. (2000) to reconstruct forest communities from the PLS data in northern Wisconsin within a GIS framework. Then the X and Y locations in UTM were added to the associated attribute table for every node. A U.S. Geological Survey Index of all topographic quadrangles was acquired and intersected with the X and Y locations layer for reference purposes during the data collection process. A database was then developed using Microsoft Access ™ to store all bearing tree data, including species, diameter at breast height, distance, and bearing from corner. Then all bearing tree data from the mylar-maps were entered into the database.

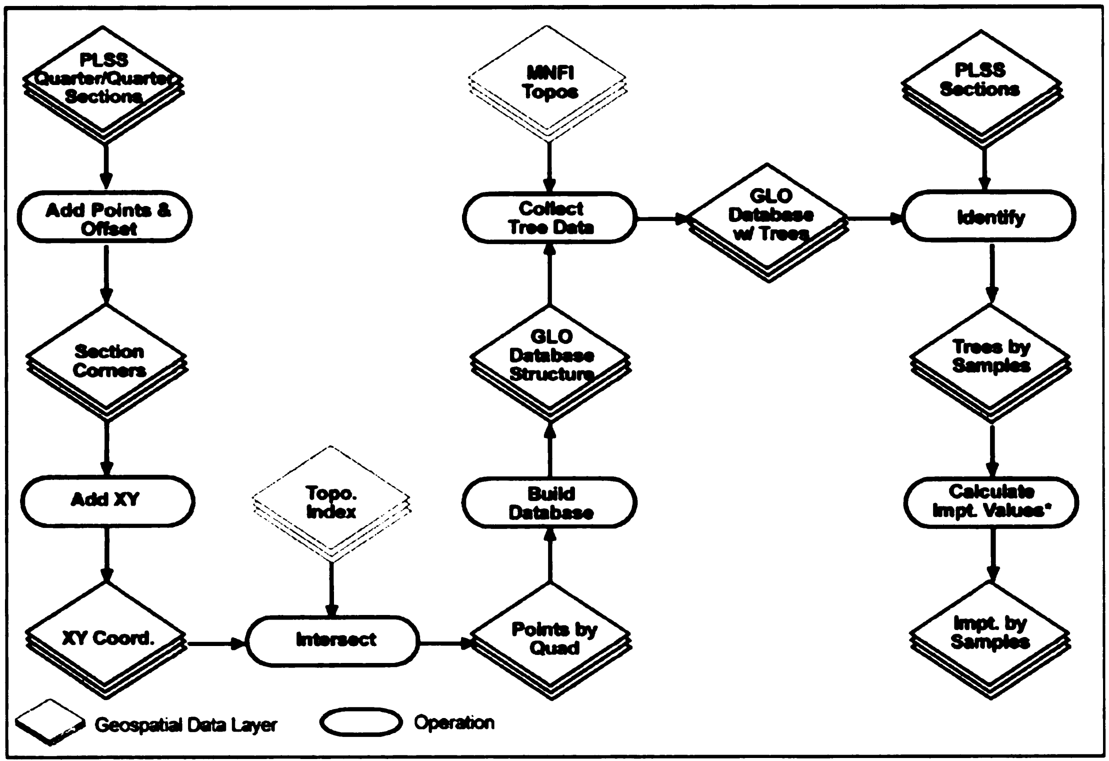

Figure 2.6 Flow chart of methods and data sets used to collect the PLS data from the mylar-maps and calculate importance values. * See equation page 44.

The PLS sections layer was also downloaded from MCGI and intersected with the bearing tree database. Sections were used as the sample unit for further processing. The bearing tree data were aggregated based on their associated survey location. Bearing tree data are commonly aggregated statistically because each survey point is considered to be analogous to a vegetation sample plot (He et al. 2000; Friedman et al. 2001). Aggregation also avoids problems associated with surveyor bias, including estimations of tree distance and azimuth from survey corners (Grimm 1984). The bearing tree data were sampled at the section level (1.6 X 1.6 km or 1 X 1 mi cell; 2.65 km^2 or 265 hectares). Delcourt and Delcourt (1996), in their evaluation of the grain of resolution of the PLS data, determined that a grid size of 1.29 X 1.29 km to 1.6 X 1.6 km (.5 X .5 mi to 1 X 1 mi) provides a conservative characterization of landscape properties and is appropriate for studies of historical landscape changes. Several other studies have used similar grains including: .01 km^2 (.1 hectare) (Cowell 1998); 2.65 km^2 (265 hectares) (Delcourt and Delcourt 1996; Schulte et al. 2002); 4.6 km^2 (460 hectares) (Schaetzl and Brown 1996); 15 km^2 (3884 hectares) (Bolliger et al. 2004); and 100 km^2 (1000 hectares) (Cogbill et al. 2002).

Within each section, relative dominance, relative density, and relative importance were calculated using ArcInfo ™. Relative measures were used because of the nature of bias within the bearing tree data set (Bourdo 1956). Dominance totals the basal area, specifically the diameter at breast height (1.4 m from the ground) of all trees of each species within a sample. Relative dominance expresses the dominance of each species with regards to all other species within the sample (Cottam and Curtis 1956). Relative dominance is calculated as follows:

$$RDOM\_Ci = \left(\frac{\sum\limits_{j=1}^{m} \text{basal area}ij}{\sum\limits_{i=1}^{n} \sum\limits_{j=1}^{m} \text{basal area}ij} \right) X\ 100$$

where *n* equals the number of species and *m* is the number of individuals of a given species in the samples. Basal area *ij* is the basal area of individual *j* of species *i*. High values of relative dominance indicate that a species is dominant in that it has a large proportion of the relative biomass in a sample.

Relative density of a species within each sample is calculated as follows:

$$RDen\_Ci = \left(\frac{\sum_{j=1}^{m} Cij}{\sum_{i=1}^{n} \sum_{j=1}^{m} Cij} \right) X\ 100$$

where again *n* equals the number of species and *m* equals the number of individuals and C_{ij} is individual *j* of species *i*. High values of relative density indicate that a particular species has a high proportion of all the stems within a sample. Relative density should not be used alone as a forest metric, because it does not provide a measure of biomass allocation (Schulte et al. 2002). Both relative density and relative dominance were used to calculate relative importance. Relative importance is calculated as follows:

$$RIV\_Ci = \frac{RDen\_Ci + RDom\_Ci}{2}$$

Both relative dominance and relative importance have been used as inputs to cluster analysis and have exhibited similar robust results (Schulte et al. 2002). Relative dominance tends to emphasize species which reach large diameters while relative importance tends to over emphasize species which grow in high densities, such as those of *Populus* or *Betula papyrifera*. The use of relative importance in previous research (Schulte et al. 2002) resulted in a higher number of significant classes. Relative importance was used for this analysis, because it has been shown by Schulte (2002) and others to provide significant results and does not exhibit as strong a bias towards trees with larger diameters, e.g. *Pinus strobus*. Relative importance was calculated for all species within each PLS survey section. These values were then exported for both ordination and cluster analysis in PC-ORD ™ software (McCune and Mefford 1997).

2.3.3 Clustering

Statistical clustering was used to group PLS bearing tree data and sample sections into forest communities based on the relative importance values of a total of 44 species and genera (Table 2.2) after the removal of rare types. In this context, a community is an assemblage of species which is repeated on a landscape. The assemblage of species and their relative importance values are relatively similar. Rare species, those species which were found only once or twice in the entire study area, were removed to avoid problems with outliers. Hierarchical clustering was performed in PC-ORD ™ software (McCune and Mefford 1997). Ward's (1963) minimum variance method was used as the hierarchical agglomerative clustering procedure. This commonly used method generally performs well with historical tree data and minimizes the variance among average group composition (Cogbill et al. 2002; McCune and Grace 2002; Schulte et al. 2002).

Table 2.2: List of species, common, and scientific names, and associated diameter at base height and percent of stems found in the study area.

Common Name	Scientific Name	Diameter (%)	Stems (%)
Ash (white, black or red)	*Fraxinus* spp.	0.530	0.564
Aspen (Quaking or Bigtooth)	*Populus* spp.	0.598	0.907
Balsam Fir	*Abies balsamea*	0.090	0.163
Basswood	*Tilia americana*	2.473	2.189
Beech	*Fagus grandifolia*	19.835	24.773
Big tooth Aspen	*Populus grandidentata*	0.005	0.005
Birch	*Betula* spp.	0.787	0.935
Black Ash	*Fraxinus nigra*	2.263	2.510
Black Cherry	*Prunus serotina*	0.006	0.007
Black Gum	*Nyssa sylvatica*	0.035	0.036
Black Oak (Pin Oak and N. Pin Oak)	*Quercus velutina*	2.117	1.938
Black Walnut	*Juglans nigra*	0.028	0.021
Blue Ash	*Fraxinus quadrangulata*	0.004	0.005
Blue Beech	*Carpinus caroliniana*	0.004	0.008
Bur Oak	*Quercus macrocarpa*	0.211	0.257
Butternut	*Juglans cinera*	0.043	0.046
Cherry	*Prunus* spp.	0.216	0.259
Chinkapin Oak	*Quercus muehlenbergii*	0.397	0.445
Cottonwood	*Populus deltoides*	0.014	0.021
Dogwood	*Cornus* spp.	0.001	0.003
Eastern Hemlock	*Tsuga canadensis*	10.935	10.857
Oak	*Quercus* spp.	0.062	0.068
Sugar Maple	*Acer saccharum*	8.655	8.761
Swamp White Ash	*Fraxinus americana*	0.033	0.036
Swamp White Oak	*Quercus bicolor*	0.086	0.073
Sycamore	*Platanus occidentalis*	0.107	0.057
Tamarack	*Larix laricina*	1.939	2.876
Tulip Tree	*Liriodendron tulipifera*	1.939	2.876
White Ash	*Fraxinus americana*	0.777	0.803
White Birch	*Betula papyrifera*	0.194	0.236
White Oak	*Quercus alba*	10.814	10.049
White Pine	*Pinus strobus*	17.381	11.329
Willow	*Salix* spp.	0.042	0.091
Yellow Birch	*Betula alleghaniensis*	0.192	0.244

The number of appropriate groups in the dendrogram (or level of pruning) was determined using the Indicator Species Analysis method, including average p-values, the number of significant species (Dufrene and Legendre 1997), and the 1% rule. First, an initial cluster analysis was performed without assigning groups. Then, the cluster analysis was repeated multiple times by defining groups ranging from 10 to 60, including 10, 15, 20, 25, 30, 35, 40, 45, and 60. The range of group numbers was decided by running preliminary statistics and based on previous research (Schulte et al. 2002). For each step of the clustering, Indicator Species Analysis was performed using the option for the Monte Carlo test. The Monte Carlo test for significance of observed maximum indicator values from each species was based on 1000 randomizations. The p-values from the Monte Carlo tests were then plotted against the number of clusters for each step of clustering. The lowest p-value then indicated the number of clusters or level in the dendrogram which provided the most information. The number of significant species for each step of clustering was also totaled and plotted against the number of clusters. The indicator species method assists in finding a balance between large groups with better within-group homogeneity and very small heterogenous groups (McCune and Grace 2002).

Based on the results from the indicator species analysis, 40 clusters provided the lowest p-value, while 15 clusters provided the maximum number of significant indicator species at 28 (Figure 2.7). The percentage of each cluster on the landscape was calculated for each range in the number of clusters. All clusters had more than 1% representation on the landscape at the 20 cluster step while several clusters had less than 1% at the 25 cluster step. Even though 40 clusters do produce the lowest significant p-value, the ranges of p-values for all tests vary by only .04. In this case, 20 clusters provided the most ecologically meaningful groups. Ecological meaningful groups are those which are represented on more than 1% of the landscape. A higher number of clusters, although significant, placed more emphasis on rare community types, those represented on less than 1% of the landscape. Therefore, a total of 20 clusters were used in the final classification. The dendrogram was pruned with 65% of the information remaining, providing a good balance between the amount of information remaining, the interpretability of the dendrogram, and the representation of clusters on the landscape. The resulting 20 clusters were then assigned back to each individual sample or section number and displayed using ArcMap ™ software.

The importance values of each species were averaged for all sections within each cluster and were ranked. Clusters were named based on the rank of each species using the following convention modified from Schulte et. al. (2002): 1) single species – the highest ranking species was 30% or higher, and was at least twice as dominant as the second ranking species; 2) two species –the two highest ranked species totaled at least 50%, while the third highest species was half as dominant as either of the first two highest; 3) mixed – the remainder of classes which did not meet the above criteria were labeled by the top four highest ranking species. In some cases, this naming convention resulted in clusters with the same name, requiring the addition of species to the name in parenthesis to qualify the differences. When identifying clusters by their individual names, species names are abbreviated. (See Table 2.2. for complete names for these abbreviations).

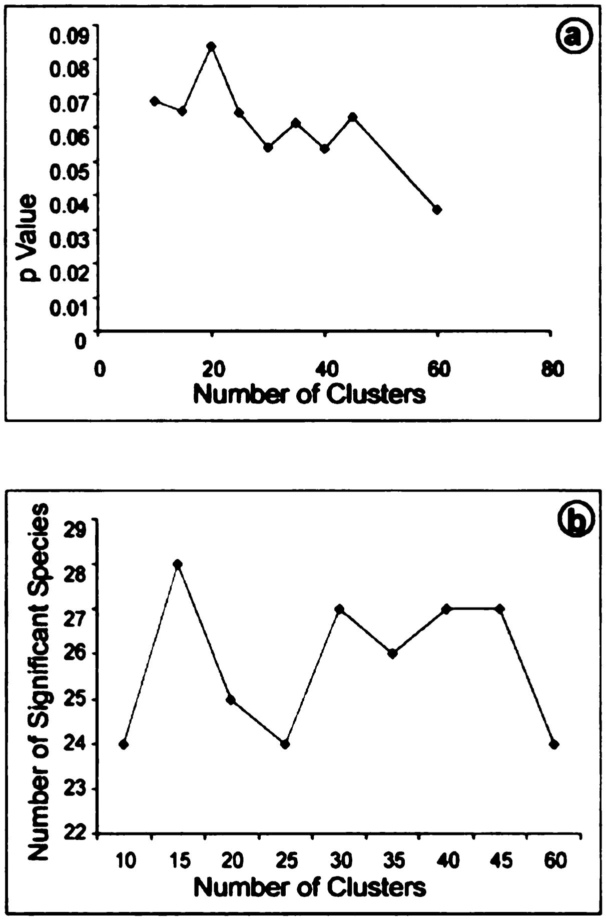

Figure 2.7 Results of indicator species analysis. For a) the number of clusters is plotted against p-values, for b) the number of clusters is plotted against number of significant species.

The results from the clusters analysis at the 40 group level were assigned back to each individual sample section number and displayed in ArcMap ™ Software. The results from the twenty grouping level and the forty grouping were compared and cross referenced in order to examine the further separation of clusters. The clusters were not named due limitations of the naming convention and because they are not discussed in depth as the twenty clusters. The forty clusters were numbered from 1 to 40 with a lowercase "a" to distinguish them from the twenty clusters.

2.4 Results

A total of 337,192 individual trees and 50 individual tree names, including species designations and genus designations, were recorded in the study area (Table 2.2). Of the 50 tree names, a total of four names identified trees only to the genera level and did not include species: "pine", "oak", "maple", "birch", and "ash". These taxa represent 11.5% of the total diameter for the entire study area. *Fagus grandifolia* was the most common tree recorded with 19.8% of the total diameter and 24.7% of all stems. The other most common trees measured in percent of stems and diameter, respectively, were *Pinus strobus* (17.3%, 11.3), *Tsuga canadensis* (10.9%, 10.8%), *Quercus alba* (10.8%, 10%), and *Acer saccharum* (8.6%, 8.7%). The least common species, which were removed from the cluster analysis (with less than 0.005% of stems and diameter each) were *Prunus* spp., *Sassafras albidum*, and *Cornus* spp. A total of 14 species were represented in more than 1% of the total diameter. The diameter of all 14 species totaled to more than 92% of the total diameter.

2.4.1 Cluster Analysis

A total of twenty classes were identified in the final cluster analysis of the PLS data (Table 2.3). All clusters identified were represented in at least 1% of the landscape. The majority of the classes identified were single species clusters. The single species clusters identified were: *Fagus g., Quercus a.* (*Quercus v.–Fagus g.*), *Pinus* (*Quercus a.–Fagus g.*), *Pinus s.* (*Fagus g.–Tsuga c.*), *Quercus a.* (*Quercus v.–Quercus m.*), *Thuja o.*, *Tsuga c.*, *Fagus g.* (*Acer s.–Tilia a.*), *Larix l.*, *Pinus b., Acer s.*, *Quercus a.* (*Pinus s.*), *Pinus s.*, and *Pinus r.*. Of all the single species clusters identified, the *Tsuga c.* cluster was the most common on the landscape at 11.6 % of all sections. The *Pinus s.* (*Fagus g.–Tsuga c.*) cluster was the second most dominant on the landscape with 9.9% followed closely by the *Fagus g.* cluster at 9.3%, and *Quercus a.* (*Quercus v.–Fagus g.*) at 9.2%. *Quercus a.* was the most important species in three clusters, which overall totaled to 15.2% of the landscape. The least dominant cluster on the landscape was the *Pinus b.* cluster at 1.04% of the landscape followed closely by the *Pinus r.* cluster at 1.07% of the landscape. Several clusters with two dominant species were identified: *Fagus g.–Tsuga c.*; *Fagus g.–Acer s.*; and *Fagus g.–Pinus s.* The most dominant of the two-species clusters was the *Fagus g.–Tsuga c.* cluster at 6.45%. Several multiple or mixed-species clusters were identified: *Ulmus–Fraxinus n.–Fagus g.–Quercus v.;* Acer–*Fagus g.–Pinus s.*; and *Fagus g.–Pinus–Tsuga c.*. The *Ulmus–Fraxinus n.–Fagus g.–Quercus v.* cluster was the most dominant of the mixed species clusters at 4.68% of the landscape. Overall, these clusters identified *Fagus g.* as the most dominant on species the landscape with a total of 33.08%.

The dendrogram illustrates the relationships of the cluster groups to one another (Figure 2.8). The strongest division within the dendrogram occurred between cluster 3 *Quercus a.* (*Quercus v.–Fagus g.*), cluster 5 *Quercus a.* (*Quercus v.–Quercus m.),* and the remaining clusters. The next largest division occurred based on the importance of *Tsuga c.* Clusters 16 *Quercus a.* (*Pinus s.*), 15 *Acer–Fagus g.–Pinus s.*, 17 *Pinus s.*, and 18 *Fagus g.–Pinus s.* all had lower average percentages of *Tsuga c.*. The length of the branch separating cluster 18 *Fagus* g.–*Pinus s.,* from cluster 4 *Pinus s.* (*Fagus* g.–*Tsuga c.*) illustrates the distinctiveness between the lower one third and upper two thirds of the dendrogram. The center of the dendrogram was split based on the importance of *Fagus g.* In cluster 2 *Fagus g.*, *Fagus* had an average importance of 66, while in cluster 6 *Pinus* (*Quercus alba – Fagus*), *Fagus g.* had an importance value of 7 (Appendix 1). In cluster 13 *Acer s.* and cluster 14 *Fagus g. -Acer saccharum,* *Fagus* g. had a relatively high average importance value of 18 and 46, respectively. Clusters 8 *Thuja o.*, 12 *Pinus b.*, and 11 *Larix l.* also had high importance values for *Fagus g.*, but were separated out based on the existence of the highest-ranking species for which they are named. Cluster 1 *Ulmus – Fraxinus n.–Fagus g.–Quercus v.* was distinguished from the rest of the dendrogram based on the comparatively low-average importance value of 8 for *Fagus g.* of 8.

Table 2.3: Cluster identification number, associated percents, and name of each cluster.

Cluster	Percentage	Name*
1	4.68	*Ulmus-Fraxinus n (nigra).-Fagus g. (grandifolia)-Quercus v.(velutina)*
2	9.38	*Fagus g.(grandifolia)*
3	9.22	*Quercus a .(alba) (Quercus v. (veluntina)-Fagus g. (grandifolia))*
4	9.91	*Pinus s. (strobus) (Fagus g.(grandifolia)-Tsuga c.(canadensis))*
5	4.42	*Quercus a. (alba) (Quercus v.(veluntina)--Quercus m. (muehlenbergii))*
6	4.82	*Pinus (Quercus a. (alba)-Fagus g.(grandifolia))*
7	6.45	*Fagus g.(grandifolia)-Tsuga c.(candadensis)*
8	1.35	*Thuja o. (occidentalis)*
9	11.61	*Tsuga c. (canadensis)*
10	6.91	*Fagus g. (grandifolia) (Acer s. (saccharum) -Tilia a. (americana))*
11	3.38	*Larix l. (laricina)*
12	1.04	*Pinus b. (banksiana)*
13	8.26	*Acer s. (saccharum)*
14	3.61	*Fagus g.(grandifolia) -Acer s.(saccharum) (Tsuga c. (canadensis))*
15	1.45	*Acer s.-Fagus g.-Pinus s.*
16	1.62	*Quercus a.(alba) (Pinus s. (strobus))*
17	4.07	*Pinus s.(strobus)*
18	3.94	*Fagus g.(grandifolia)-Pinus s.(strobus)*
19	2.79	*Fagus g.(grandifolia)-Pinus-Tsuga c.(canadensis)*
20	1.07	*Pinus r. (resinosa)*

*Species designators are abbreviated in text. Complete species designator is listed in parentheses.

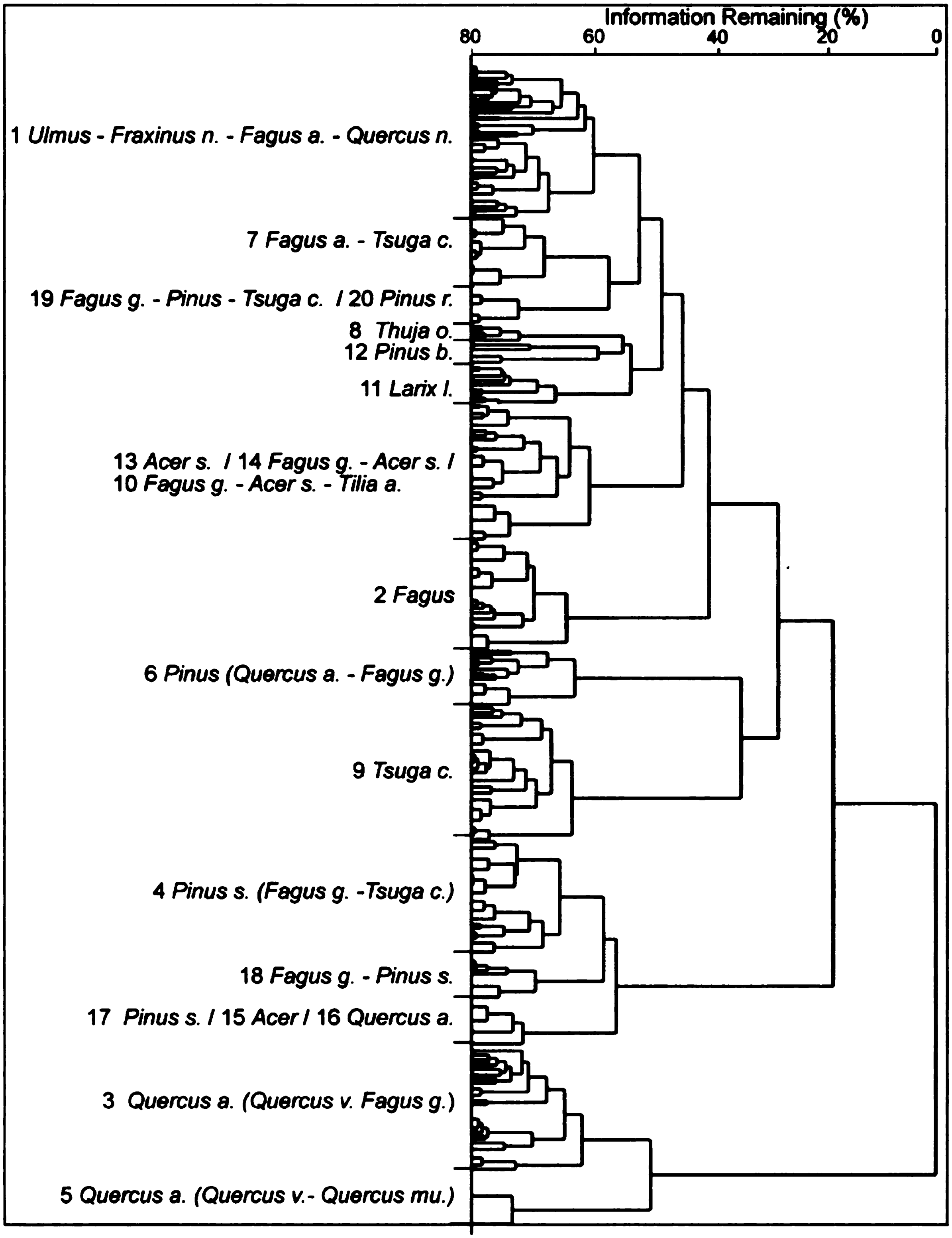

Figure 2.8 Dendrogram results from cluster analysis of Public Land Survey (PLS) data for study area. Several clusters are grouped together in the dendrogram for display purposes.

The spatial assignment of each section to its statistically identified cluster is illustrated in Figure 2.9. The distribution of clusters within the study area demonstrates the ability of cluster analysis to identify communities inherent in the landscape. Cluster 3 *Quercus a.–Quercus v.–Fagus g.* was predominant (over 98%) in the southern half of the study area. Cluster 5 *Quercus a.* (*Quercus v.–Quercus m.*), the second most dominant cluster in Region VI, was also predominately located in the southern half of the study area; all but three individual sections lie south of the ecotone. Cluster 10 *Fagus g.* (*Acer s.–Tilia a.*) was also found mainly within the southern half of study area but was also present within the tension zone itself. Cluster 13 *Acer s.* was distributed in both the southern and northern half of the study area but not within the tension zone or central portion of the study area. Cluster 14 *Fagus g.–Acer s.–Tsuga c.* exhibited a similar pattern to cluster 13, but with a slight presence within the ecotone.

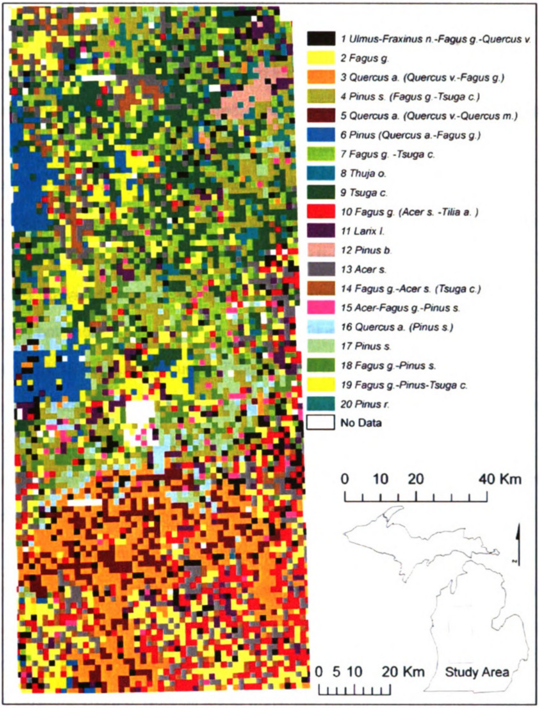

Figure 2.9 Map of the identified clusters for the study area. Map shows the assignment of each individual Public Land Survey section (2.65 km^2) to its assigned clusters based on the cluster analysis. Images in this dissertation are presented in color.

Several clusters were distributed throughout the study area including: cluster 2 *Fagus g.*; cluster 1 *Ulmus– Fraxinus n.–Fagus g.–Quercus v.;* and cluster 11 *Larix l.* Several clusters were located solely within the central or transitional portion of the study area. Cluster 18 *Fagus g.–Pinus s.* and cluster 16 *Quercus a.* (*Pinus s.*) were both highly transitional communities distributed predominantly within the transition zone itself. Cluster 17 *Pinus s.* and cluster 15 *Acer s.–Fagus g.–Pinus s.* were also distributed within the central portion of the study area, although they were not as strongly transitional as clusters 16 and 18. Cluster 15 was distributed mainly within the transition itself, but branched out slightly both north and south of the ecotone. Clusters 4 *Pinus s.* (*Fagus g.–Tsuga c.*), 19 *Fagus g.*–Pinus s.–*Tsuga c.,* and 6 *Pinus* (*Quercus a.–Fagus g.*) were located within the transition zone but were also located within the northern portion of the study area. Cluster 6 had a unique distribution in that it was distributed in two major contiguous areas in the northwestern and southeastern portions of the study area.

The remaining clusters were located solely or almost exclusively within the northern portion of the study area. Cluster 9 *Tsuga c.* was located primarily in the northern portion of the study area, with a few sections distributed within the ecotone. Cluster 7 *Fagus g.–Tsuga c.*, cluster 20 *Pinus r.*, cluster 12 *Pinus b.*, and cluster 8 *Thuja o.* were all found within the northern portion of the study area.

2.4.1.2 Rare and Additional Clusters

Comparison of the map resulting from twenty groupings and the map resulting from forty groupings of the hierarchical cluster analysis provides additional insights into the nature of forest communities within the study area and the tension zone itself. The purpose of dividing the data into forty clusters was solely to determine if rare communities were found primarily within the tension zone. Therefore, only the rare clusters are shown and the distribution of all forty clusters is not shown. The rare communities present in the Figure 2.10 are those present on less than 1% of the landscape. The clusters resulting from the forty groupings are not named because of limitations of the naming convention and because they are not discussed in detail.

The rare clusters are widely dispersed across the study area. In total, the rare clusters (Figure 2.10) are present on only 4% of the landscape. The remaining clusters in the map are present on over 1% of the landscape. The results from the comparison between the two maps are listed in Table 2.4.

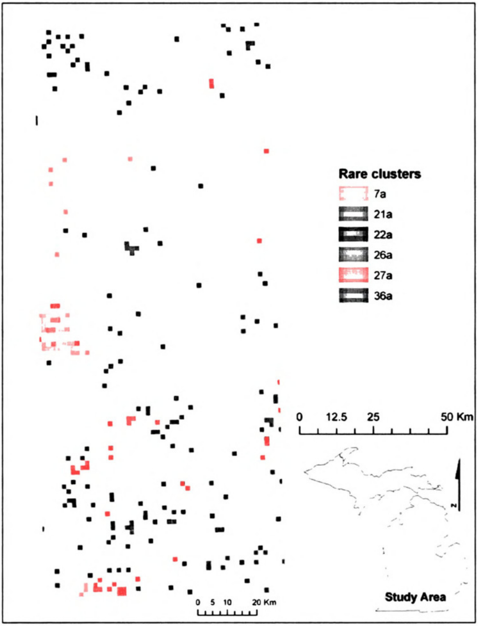

Figure 2.10 Map of rare clusters (found on less than 1% of the study area) resulting from the hierarchical cluster analysis with forty groupings. Clusters are not named, see table 2.4 for the names of the parent clusters.

Table 2.4 Results from the comparison between the results from the cluster analysis with twenty groupings and with forty groupings. The table shows how clusters at the twenty grouping level were divided into forty clusters. The percentage column shows the percent of the clusters at the forty cluster level on the landscape.

Clusters (20)	Clusters (40)	# Sections	Percent
1 *Ulmus-Fraxinus n.-Fagus g.-Quercus v.*	1a	107	1.76
	3a	117	1.93
	21a	29	0.48
	27a	31	0.51
2 *Fagus g.*	2a	473	7.80
	25a	96	1.58
3 *Quercus a .(Quercus v.-Fagus g.)*	4a	262	4.32
	17a	246	4.06
	36a	51	0.84
4 *Pinus s. (Fagus g.-Tsuga c.)*	5a	286	4.72
	34a	239	3.94
	40a	76	1.25
5 *Quercus a.(Quercus v.-Quercus m.)*	6a	268	4.42
6 *Pinus (Quercus a.-Fagus g.)*	7a	41	0.68
	37a	124	2.05
	38a	127	2.09
7 *Fagus g.-Tsuga c.*	8a	239	3.94
	33a	152	2.51
8 *Thuja o.*	9a	82	1.35
9 *Tsuga c.*	10a	132	2.18
	11a	389	6.42
	13a	82	1.35
	35a	101	1.67
10 *Fagus g.(Acer s.-Tilia a.)*	12a	219	3.61
	19a	86	1.42
	24a	114	1.88
11 *Larix l.*	14a	159	2.62
	26a	46	0.76
12 *Pinus b.*	15a	63	1.04

Table 2.4 Continued

Clusters (20)	Clusters (40)	# Sections	Percent
13 *Acer s.*	16a	127	2.09
	20a	123	2.03
	22a	46	0.76
	23a	205	3.38
14 *Fagus g.-Acer s.(Tsuga c.)*	18a	219	3.61
15 *Acer s.-Fagus g.-Pinus s.*	28a	88	1.45
16 *Quercus a.(Pinus s.)*	29a	98	1.62
17 *Pinus s.*	30a	247	4.07
18 *Fagus g.-Pinus s.*	31a	239	3.94
19 *Fagus g.-Pinus-Tsuga c.*	32a	169	2.79
20 *Pinus r.*	39a	65	1.07

2.4.2 Ordination

Detrended correspondence analysis (DCA) was utilized to further explore the relationships between the identified clusters and species importance values. The data matrix of sections and species (genera where indicated) importance values were reduced in the ordination to two axes arranged in relation to their similarity (Figure 2.10). DCA is an eigenvector ordination technique based on correspondence analysis which uses chi-square distance measures (McCune and Grace 2002). The proportion of variance represented by each axis was measured by the covariance between Euclidean distances among samples units in the ordination and the relative Euclidean distances in the original space (McCune and Grace 2002). The r-squared values are as follows: axis 1 (0.316), axis 2 (0.193), axis 3 (0.017). Cumulative variance for axis 1 and 2 as shown in Figure 2.10 is 0.509.

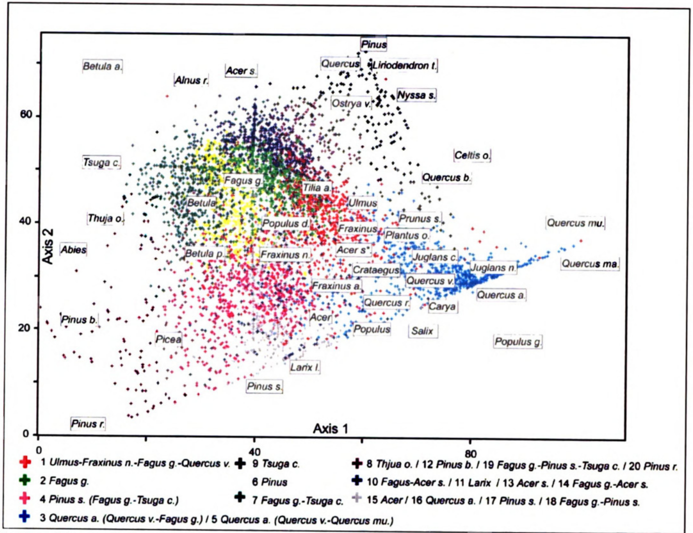

Figure 2.11 Ordination of the results from the cluster analysis of the Public Land Survey Data.

The ordination reiterates the strong differences in composition between the southern communities dominated by *Quercus* spp. and the northern communities comprised mainly of coniferous species, such as *Tsuga canadensis*, *Pinus resinosa*, *Pinus banksiana*, *Picea glauca,* and *Abies balsamea* (Figure 2.10*)*. Axis one separated the northern communities from the southern communities. The northern communities, i.e., clusters 12 *Pinus b.*, 9 *Thuja o.*, 20 *Pinus r.*, and 9 *Tsuga c.,* were aligned to the left of the diagram while the southern communities, i.e. clusters 3 *Quercus a.* (*Quercus v.–Fagus g.*), and 5 *Quercus a.* (*Quercus v.–Quercus m.),* were pulled to the right edge of axis one. Several species, characteristic of the *Quercus-Carya* communities located predominately south of the tension zone, including *Carya* spp.*, Quercus velutina, Quercus rubrum, Juglans cinera,* and *Juglans nigra,* were grouped around clusters 3 and 5 at the far right edge of axis one. In contrast to clusters 3 and 5, cluster 10 *Fagus g.–*Acer *s.,* also distributed mainly south of the tension zone, was dispersed in the center of the diagram due to the strong importance of *Fagus grandifolia*, *Acer saccharum*, *Tilia americana*, and *Ulmus* spp.. Clusters 17 *Pinus s.*, 15 *Acer s.–Fagus g.–Pinus s.*, and 16 *Quercus a.* (*Pinus s.*), were found predominantly within the tension zone, and were grouped together in the center of axis one along the bottom edge of axis two.

Axis two primarily separated communities within the study area based on the importance values of *Acer saccharum*, *Fagus grandifolia*, and *Pinus strobus*. *Acer saccharum* was at the top of axis two, *Fagus grandifolia* was positioned just above center, and *Pinus strobus* was placed at the very lower end of axis two.

These three species were all aligned vertically just to the left of center on axis one. The positioning of *Acer saccharum* at the pole of the second axis may be representing its ability to dominant on a narrow range of sites. Clusters found throughout the study area were spread throughout the center of the diagram as well.

Cluster 1 *Ulmus–Fraxinus n.–Fagus g.–Quercus v.* was found in the center of both axes. Species requiring mesic to wet-mesic sites were positioned near the center of this cluster, including *Acer saccharinum*, *Ulmus* spp., and *Populus deltoides*. Other species preferring mesic sites, such as *Tilia americana*, *Quercus rubrum*, and *Prunus serotina,* were positioned just out from the center of cluster 1. Cluster 2 *Fagus g.* was the most ubiquitous cluster in the study area, and one of the most dominant. Interestingly, it was not positioned directly in the center of diagram but was found just above center on axis two, and just below center on axis one. Its position illustrates the degree of importance of other species, i.e., *Acer saccharum*, *Ulmus* spp., and *Tsuga canadensis,* in the *Fagus grandifolia* community. Clusters with a biomodal distribution, clusters 13 *Acer s.* and 14 *Fagus* g.*–Acer s.,* were found in a relatively tight group in the very upper pole of axis two centered on axis one. The importance of *Acer saccharum* in both of these communities skews the distribution towards the upper pole. Clusters that were found mainly in the northern portion of the study area, which are characteristic of the Laurentian mixed forests, such as clusters 7 *Fagus g.–Tsuga c,*, 8 Thuja o., 9 *Tsuga c.* , 20 *Pinus r.*, and 12 *Pinus b.,* were all aligned to the left side of axis one. The sections within cluster 7 *Fagus g.–Tsuga c.* were relatively widely dispersed between the position of individual species, including *Fagus grandifolia*, *Tsuga canadensis*, and *Pinus strobus*. Cluster 12 *Pinus b.* was pulled far to the left pole of axis one and the lower pole of axis two, predominantly separated from all other communities.

2.5 Discussion

The results of this research are discussed below within several sections. First the nature of the forest tension zone is addressed. Then, the forest communities identified through the statistical analysis are discussed in context of their geographic distribution within the study area: bimodal distribution, ubiquitous distribution, ecotonal distribution, and northern and north central distribution. The results of the ordination are then compared with the spatial distribution of communities. The results from this research are also compared to other regional ecotones. This discussion utilizes the regional landscape ecosystems or land type associations (Figure 2.2. and Table 2.1) as a framework for summarizing and comparing differences in cluster distribution. While the examination of the relationships between physical geography and the tension zone was not a direct focus of this research, discussing the results within the framework of the regional landscape ecosystems, or land type associations, is useful because it provides additional insights into the nature of ecotone and poses future research questions.

2.5.1 Forest Tension Zone

The species composition and groupings of taxa (i.e. clusters), their spatial patterning, as well as the variations of species importance values within the communities, demonstrated the presence of a vegetation gradient, i.e. the tension zone in the study area. This overall gradient was exhibited by the transition from *Quercus*-dominated forests, in the southern portion of the study area to the *Pinus* spp. and *Tsuga canadensis* dominated forests, in the northern portion. The broad pattern of forest communities within this gradient and the location of the tension zone itself were generally similar to the classic description of the tension zone in the Lower Peninsula of Michigan by Curtis (1959) as well as others (Vetach 1959; Kuchler 1964; Comer et. al. 1995b).

This research provides a finer resolution map of the tension zone than has previously been generated (Figure 2.9). Furthermore, the cluster analysis revealed complexities in the character of the ecotone not previously noted, including variations within the regional forest associations. Several characteristics revealed in the cluster analysis results exemplify the complexity of the ecotone including: 1) the variability of species importance values across the study area; 2) the presence and diffuse nature of transitional communities; 3) the widespread distribution of communities across the regional landscape ecosystem sub-district boundaries; and 4) the contiguous nature of communities dominated by or having a strong *Quercus* component within Region VI, in contrast to the dispersed nature of most other communities. Each of these characteristics is elaborated on below.

Many of the important species, i.e. dominants in each of the regional forests types (Figure 2.1), exhibited variable gradients across the study area. For example, *Pinus strobus*, a dominant in the Laurentian forests, had high importance values (over 30%) in 4 of the 20 clusters (4, 16, 17, and 18), and had moderately high importance values (10 – 30%) in 5 clusters (7, 11, 12, and 15) (Appendix I). These clusters were widely dispersed across the study area and were represented in all of the sub-districts except for a few in the southeast corner (VI.3.1, VI.3.3) (Table 2.4). *Fagus grandifolia* had a distribution similar to *Pinus strobus* in that it was highly important (over 30%) in many clusters, (2,7,10,14,18,19) and moderately important (10-30%) in five clusters (4,9,11,13,15) (Appendix I). The *Fagus grandifolia* dominated clusters were the most widely dispersed, occurring in all of the sub-districts in both Regions (Table 2.4). In contrast, *Quercus alba* was limited to high importance values (over 30%) in only three clusters (3, 5, and 15) (Appendix I) which were dispersed predominately in southern sub-sections (VI). Except for cluster 15, which was found in several subsections of both regions (VI and VII) (Table 2.4). These examples illustrate the variable nature of species dominance across this landscape.

The complexity exhibited in the importance values among the dominant species, as well as the widespread distribution of communities on the landscape, generally supports the individualistic (Gleason 1939), and later developed continuum models of vegetation (Curtis and McIntosh 1951; Whittaker 1956). In the continuum model, species vary on a landscape as a result of the chance interaction of a variety of factors, both stochastic and deterministic, within a continuously varying environmental context, forming associations. In the case of the forest tension zone, this precursory examination indicates that while edaphic factors were important, they are not the sole factor driving the distribution. Other factors must also be important including biotic interactions (competition), legacies of the past (disturbance regimes, species migrations), and climatic variations (Cogbill et al. 2002). It is apparent that the three dominant species (*Quercus alba, Fagus grandifolia, and Pinus strobus*), are found together over time across the landscape in a wide variety of site conditions, and a small difference in one of the site factors allows for one of the species to gain a slight competitive edge over the others. This shared dominance is demonstrated both in the existence and nature of the transitional clusters.

The *Quercus a. (Pinus s.)* (cluster 16), the *Pinus s.* (cluster 17), and the *Fagus g.-Pinus s.* (cluster 18) communities were all distributed solely within the central portion of the study area near the Region VI and Region VII boundary. The existence of these communities in and of themselves is evidence of the diffuse nature of the ecotone. If this ecotone was a sharp boundary on the landscape similar to that of an alpine ecotone or along fire-breaks in the prairie-woodland border (Grimm 1984), the northern clusters would abut the southern clusters along an identifiable boundary. In the forest tension zone, however, unique communities present on less than 10% of the landscape exist within the boundary area itself. The existence of these spatially transitional communities demonstrated the gradual, as opposed to sharp, nature of the tension zone. Of particular note, each of the transitional communities was dominated by a different species; *Pinus strobus*, *Fagus grandifolia*, and *Quercus alba*, all which were dominant in either of their respective regional forests types. These transitional communities represent the intermixing of species at the ecotonal boundary.

Table 2.5. Percent of each cluster type within regional land type associations. For names of the land type associations please see table 2.1.

Cluster	Name	VI.2.1	VI.2.2	VI.3.1	VI.3.3	VI.4.1	VI.4.2	VI.6	VII.2.1	VII.2.2	VII.3
1	*Ulmus-Fraxinus n.-Fagus g.-Quercus v.*	1.80	0.30	3.29	0.60	42.51	18.26	1.20	17.37	9.88	4.79
2	*Fagus g.*	2.11	0.00	4.21	1.62	44.73	10.86	0.49	34.36	0.97	0.65
3	*Quercus a. (Quercus v.-Fagus g.)*	7.56	2.52	0.16	0.47	69.76	17.17	0.00	1.10	0.31	0.94
4	*Pinus s. (Fagus g.-Tsuga c.)*	0.00	0.00	0.00	0.29	8.82	16.76	0.00	53.97	15.44	4.71
5	*Quercus a. (Quercus v.-Quercus m.)*	6.58	2.63	0.00	0.66	64.80	24.67	0.00	0.00	0.00	0.66
6	*Pinus (Quercus a.-Fagus g.)*	2.05	0.29	0.58	0.58	0.58	8.48	0.00	44.74	1.46	41.23
7	*Fagus g.-Tsuga c.*	0.00	0.00	0.71	0.24	4.76	2.14	0.24	81.19	7.14	3.57
8	*Thuja o.*	0.00	0.00	0.00	0.00	9.68	1.08	0.00	59.14	21.51	8.60
9	*Tsuga c.*	0.00	0.00	0.00	0.00	5.71	1.69	0.39	76.49	10.39	5.32
10	*Fagus g. (Acer s.-Tilia a.)*	2.21	1.11	3.54	1.33	71.24	9.07	1.11	9.07	0.22	1.11
11	*Larix l.*	2.14	0.85	0.43	0.00	36.32	17.52	0.00	21.79	16.67	4.27
12	*Pinus b.*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.08	95.38	1.54
13	*Acer s.*	1.32	0.00	1.88	0.56	45.20	6.21	0.94	42.00	0.56	1.32
14	*Fagus g.-Acer s. (Tsuga c.)*	0.87	0.87	2.62	0.44	35.37	5.24	0.00	53.28	0.44	0.87
15	*Acer s.-Fagus g.-Pinus s.*	0.00	0.00	1.00	0.00	26.00	29.00	0.00	34.00	3.00	7.00
16	*Quercus a. (Pinus s.)*	0.00	0.00	0.00	0.88	20.18	53.51	0.00	13.16	0.00	12.28
17	*Pinus s.*	0.00	0.00	0.00	0.69	9.00	29.07	0.00	45.33	4.84	11.07
18	*Fagus g.-Pinus s.*	0.00	0.00	0.00	0.00	19.35	34.05	0.00	42.65	1.43	2.51
19	*Fagus g.-Pinus-Tsuga c.*	3.78	0.00	5.41	1.62	4.32	5.41	0.00	69.73	0.00	9.73
20	*Pinus r.*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.85

Moreover, the transitional communities were dispersed throughout the boundary area within a variety of landscape sub-districts. For example, the *Pinus s.* community (cluster 17) was distributed throughout several sub-districts including: VI.4.2 (9%); VI.4.2 (29%); VII.2.1 (43%); and VII.3 (11%) (Table 2.4). Therefore, the *Pinus s.* community was found on a wide variety of substrates ranging from medium-textured and coarse-textured ground moraine to sandy outwash. The spatial patterning of these transitional communities indicated that the forest tension zone in the central Lower Peninsula of Michigan was diffuse in nature and was not directly or solely a function of physical boundaries, whether climatic or edaphic.

Communities with obvious spatial affinities for the northern or southern portions of the study area and ubiquitous clusters were also distributed across sub-district and regional boundaries (Table 2.4). For example, the *Acer s.* community (cluster 13) was widely distributed in the northern sub-Region VII.2.1 (42%), and the southern sub-Region VI.4.1 (45.2%). The *Fagus g.* community (cluster 2) was ubiquitous throughout the study area and found in all of the largest sub-Regions including: VI.4.1, (44.7%); VI.2 (10.8%); and VII.2.1 (34.3%). Thus, the transitional clusters, as well as the clusters with spatial affinities and ubiquitous distributions, were represented in relatively high percentages across the major sub-regions. This widespread distribution reiterates the complexity of both the species assemblages forming the communities, as well as the factors driving their distribution.

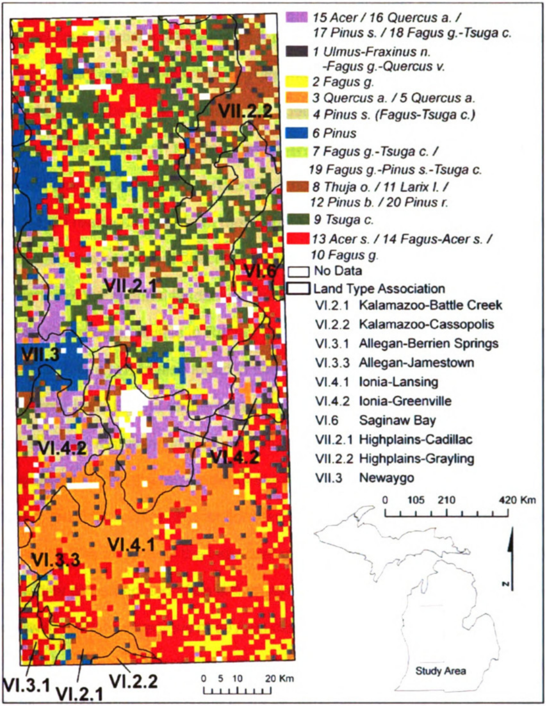

Figure 2.12 Map of the identified clusters for the study area. Map shows the assignment of each individual Public Land Survey section (2.65 km^2) to its assigned clusters based on the cluster analysis. Clusters are grouped based on the dominant species and place on the dendrogram.

The nature of the spatial arrangement (i.e. contiguous versus dispersed), of the individual sections within a cluster type varied considerably among clusters and surprisingly among the two main Regions. Figure 2.11 displays clusters grouped together based on the dominant species in each and the relative position of each cluster on the dendrogram (Figure 2.8). In Region VI, the two dominant *Quercus* communities (clusters 3 and 5) were found in a contiguous band (which reached its northern most extent south of the Region VI border) and then arched in a southward direction. This *Quercus* belt did not follow the boundaries of the regional landscape ecosystem Regions or sub-regions. The other dominant communities in Region VI, *Acer s.*, *Fagus g.-Acer s.*, and *Fagus g. (Acer s.-Tilia a.)* were also found in somewhat contiguous bands surrounding the *Quercus* belt. Except for the sections of the *Pinus (Quercus a.-Fagus g.)* community, the remaining individual sections of all other clusters exhibited a patchy distribution in the remainder of the study area. The difference in the nature of individual cluster distributions was most evident between Region VI and Region VII. The majority of the individual cluster sections found within Region VII were widely dispersed and often individual sections of a cluster type were intermixed with individual sections of several clusters types.

The contiguous distribution of individual sections of the *Quercus* clusters in Region VI suggested that some factor or combinations of factors, i.e. physical, biotic, or legacies of the past, allowed that particular assemblage of species to dominate over relatively widespread areas. Because the *Quercus* band in Region VI crossed multiple sub-district boundaries, other factors beside physical geography contributed to the conditions in which the *Quercus* communities were able to dominate. In contrast, the dispersed nature of individual cluster sections in Region VII suggested that competition over time was fierce between species, and that species abundance (i.e. response curves), importance values, and the overall role of species within a community varied over space. No one assemblage dominated for any considerable contiguous space. The disparity between the two Regions suggested that species inter-mixed more frequently in in Region VII, which may suggest stronger intra-species competition, compared to Region VI and that other factors, such as past disturbance and physical geography, were variable

2.5.2 Southern Communities (Region IV)

The presettlement vegetation of Region VI in the southern Lower Peninsula of Michigan was a mixture of forests dominated by either *Quercus alba* or *Fagus grandifolia* (Figures 2.9 and 2.11). *Quercus alba* dominated two different communities, *Quercus a.–Quercus v.–Fagus g.* (cluster 3) and *Quercus a.–Quercus v.–Quercus m. (*cluster 5), which covered the majority of Region VI, crossing all sub-district boundaries (Table 2.4 and Figure 2.11). Both of these communities were strongly dominated by *Quercus alba* (51% and 90%, respectively), but were quite different in composition (Appendix 1).

In the *Quercus a. (Quercus v.-Fagus g.)* community (cluster 3), *Quercus alba* was found with many other species, *Quercus velutina* (7.8), *Fagus grandifolia* (5.2), *Ulmus* spp. (4.7), *Quercus muehlenbergii* (3.9), *Quercus rubra*

(3), *Acer saccharum* (2.7), *Tilia americana* (2.5), and *Carya* spp. (2.32). These species included those found on more mesic and richer sites, such as *Tilia americana* and *Acer saccharum* (Appendix 1). This community represented the *Quercus-Carya* forests of Region VI, which often contained some species from the more mesic *Fagus grandifolia* communities. *Carya* spp. had a relatively low importance value in this community and was most likely under-represented due to a bias by the surveyors towards recording *Quercus* spp. and *Fagus grandifolia* (Comer et. al. 1995b). Overall, *Carya* spp. achieves a smaller diameter than *Quercus* spp. and *Fagus grandifolia*. The smaller diameter of Carya spp. compared to those of *Quercus* spp. may be reflected in the lower importance values of *Carya* spp., since diameter is a key parameter in the metric.

In contrast to the mixed *Quercus* community (*Quercus-Carya*), the other *Quercus* community, *Quercus a.–Quercus v.–Quercus m.* (cluster 5), was quite different in that *Quercus alba* strongly dominated with an importance value of over 90%. This community was representative of the '*Quercus* openings' and '*Quercus* savannahs' where *Quercus alba* was found with *Quercus velutina* and *Quercus muehlenbergii* on the driest sandy ridges in outwash channels. Further pruning of the dendrogram would likely result in the separation of communities dominated by *Quercus alba* and *Quercus velutina,* representing the *Quercus velutina* dominated forests, from the *Quercus* savannas dominated by *Quercus muehlenbergii*. *Quercus* dominated communities exhibited the most distinctive pattern in the study area, and were located in a relatively contiguous band arching across all of the sub-districts in Region VI (Figure 2.11). Fire played a significant role in the presettlement *Quercus* communities and their distribution on the presettlement landscape was most likely a function of both soil texture and legacies of the past, specifically with regards to fire frequency and extent. In the warm and dry areas of Region VI, fire would sweep through periodically. Although fire regimes have not been reconstructed for the *Quercus* forests in Region VI, reconstructions of fire history during early settlement (1840-1872) in similar areas in southeastern Wisconsin estimate that mean fire return intervals were 19.5 years (Wolf 2004). The thick bark of some *Quercus* species allowed individual trees to survive fires while most other mesic shade tolerant species were wiped out by the fire and excluded thereafter. *Quercus* and *Carya* sprout vigorously following fire. *Quercus* species are generally moderately shade intolerant or shade intolerant, and are able to re-sprout after top-kill which allowed them to quickly re-colonize burned areas (Barnes and Wagner 2004; Wolf 2004).

The other main community present on the presettlement landscapes in Region VI was the *Fagus g.–Acer s.-Tilia a.* community (cluster 10). This community was less dominant in Region VI and within the study area overall where it represented just under 7% of the total study area (Table 2.3). *Fagus grandifolia* was clearly the most dominant species within this community with an average importance value of 30 followed by *Acer saccharum* (12.5), *Tilia americana* (11.8), and *Ulmus* spp. (10.5). Other important species within this cluster included *Quercus alba* (6.1), *Acer* spp. (4.08), and several species of *Fraxinus* (Appendix 1). This assemblage was indicative of the *Fagus g. -Acer s.-*

Tilia a. forests found on moister sites within finer textured till soils where fire was less important. In contrast to both of the *Quercus* communities (clusters 3 and 5), the *Fagus g.-Acer s.-Tilia a.* (cluster 10) was also found within and north of the ecotone and was distributed in less contiguous patches than were the *Quercus* communities.

2.5.3. Biomodal Distribution of Communities

Two communities, the *Acer s.* (cluster 13) and *Fagus g.-Acer s. (Tsuga c.)* (clusters 13 and 14) exhibited a unique distribution (Figure 2.9 and 2.11). These communities were characteristic of the *Fagus grandifolia-Acer saccharum* forests of Region VI and the mixed northern hardwoods of Region VII. These two communities were distributed in both the northern and southern portion of the study area, across multiple sub-districts (Table 2.4), but were generally not present within the tension zone itself. The three most important species within the *Acer s.* community (cluster 13) were *Acer saccharum* (43.6), *Fagus grandifolia* (18.8) and *Ulmus* spp. (9.33), which are all species that prefer mesic-rich sites. These three species constituted 70% of the average importance values for this community, while other important species in this cluster included *Tsuga canadensis* (7.3), *Tilia americana* (3.4), *Fraxinus nigra* (2.6), *Acer* spp. (2), and *Ostrya* spp. (1.3) (Appendix 1). Further discrimination of this cluster (13) may result in the differentiation between those communities that would be sorted into the Laurentian northern hardwoods association and the southern forests or the eastern broadleaf forests.

Approximately half of the sections within *Acer s.* community were found in the southern half of the study area, south of the transition, while the other half were located in the very northern portion of the study area, far north of the transition. The bimodal distribution of this community reflects the habitat characteristics of *Acer saccharum,* which inlcude sites with fertile, mesic to wet-mesic drainage, and fine-textured soils, (Medley and Harman 1987; Barnes and Wagner 2004). The biomodal distribution was most likely an indication of the inability of *Acer saccharum* to be dominant similar sites within the tension zone.

The *Fagus g.-Acer s.* (*Tsuga c.*) (cluster 14) community also exhibited this unique distribution, although with a slightly higher presence in the transition zone than the *Acer saccharum* community. *Fagus grandifolia* and *Acer saccharum* were competing within this community as demonstrated by their similar average importance values of 46 and 35, respectively, followed by *Tsuga* (5.1), *Ulmus* spp.(3.4), *Pinus* spp. (2.1), and *Tilia americana* (1.86) (Table 2.3). The slightly higher presence of this community within the transition suggests that *Fagus grandifolia* was more dominant within the tension zone. Similar to the *Acer s.* community, further analysis would most likely separate the differences between the northern and southern clusters based on the presence of *Tsuga canadensis* and *Pinus* spp..

While both of these communities exhibited a bimodal distribution, they were more predominant in different sub-districts. The *Acer s.* community was distributed predominately in sub-district VI.4.1 (45%), and secondarily in sub-district VII.2.1 (42%), while the *Fagus g.-Acer s. (Tsuga c.)* community was found predominately in sub-district VII.2.1 (53%) and secondarily in sub-district VI.4.1 (35%) (Table 2.4). These differences again suggested a shared dominance between *Acer saccharum* and *Fagus grandifolia,* as well as indicated that slight differences in site characteristics allowed one species to be more successful then the others. Moreover, the dispersed nature of the individual sections within each community type suggested that the species abundances were quite variable across space. Thus, the advantages at certain sites, i.e. soil moisture or lack of competition, particular to either *Fagus grandifolia* or *Acer saccharum*, were not persistenct over space.

2.5.4 Ubiquitous Distribution of Communities

Several communities were present throughout the study area in both Region VI and II as well as within many of the sub-districts of these Regions. The most prevalent of these was the *Fagus g.* dominated community (cluster 2), ubiquitous throughout 9.38% of the landscape (Table 2.3). *Fagus grandifolia* strongly dominated this community with 66% of the average importance values followed by *Acer saccharum* (9.4) and *Ulmus* spp. (4). Other important species included *Tsuga canadensis* (3.3), *Acer* spp. (2.3), *Tilia americana* (2.2), *Quercus alba* (1.8), and *Pinus strobus* (1.6) (Appendix 1). The relatively high average importance value of *Fagus grandifolia* within this community may have been slightly inflated due to the bias by the surveyors towards *Fagus grandifolia.* Therefore, the importance of other species within this community may have been slightly diminished (Comer et. al. 1995b). This community was characteristic of the northern hardwoods, or northern mesic forests found in Region VII. It also was representative the variations of *Fagus grandifolia-Acer saccharum* forests in Region VI. The *Fagus grandifolia* community was found in three of the main sub-districts of this latter Region: VI.4.1 (44.7%), VI.4.2 (10.8%), and VII.2.1 (34.6%) (Table 2.4). This ubiquitous distribution indicated the ability of *Fagus grandifolia* to dominate and be more successful than other species on a wide variety glacial substrates, ranging from coarse textured end moraine (loamy sand) to medium and fine-textured end moraine.

Also ubiquitous in the presettlement forests of Region VI and Region VII were the wet deciduous forests and swamps, represented by the *Ulmus–Fraxinus n.–Fagus g.–Quercus v.* community, that were present on 4.68% of the landscape (Table 2.3, Figure 2.9). Both of the dominant species, *Fraxinus nigra* with an importance value of 16.7 and *Ulmus* spp with an importance value of 15.3, preferred wet sites. This community was widely dispersed within all of the sub-district boundaries (Table 2.1) and individual sections were dispersed within the other forests types, only rarely occupying adjacent sections. The distribution of these forests was predominately related to specific sites (Figure 2.9), i.e. low wet areas near rivers, lakes, wetlands, swamps, and marshes.

Although slightly less dominant at 3.38 % of the landscape (Table 2.3), the *Larix l.*-dominated community (cluster 11) was also distributed throughout the study area. Likewise this community was strongly related to soil moisture and predominately represented the wet coniferous forests. The average importance value of *Larix laricina* was 38.2 followed by *Fagus grandifolia* (15.7), *Pinus* *strobus* (11.56), and *Acer* spp. (4.9) (Appendix 1). The relatively high percentages of *Fagus grandifolia* and *Pinus strobus* indicate that further pruning of the dendrogram would separate the mono-specific *Larix laricina* swamp forests from the mixed deciduous-coniferous component found on wet-mesic and wet sites.

2.5.5 Ecotonal Distribution of Communities

Several communities existed primarily within the transition zone itself, and were hence strongly indicative of the presence of an ecotone (Figure 2.9 and Figure 2.11). These plant associations included: the *Fagus g.–Pinus s.* community (cluster 18), the *Pinus s.* community (cluster 17), the *Quercus a.* (*Pinus s.)* community (cluster 16), and the *Acer s.–Fagus g.–Pinus s.* community (cluster 15). While these communities were represented on a relatively small percent of the landscape (total of 11%) (Table 2.3), they were widely distributed across sub-district boundaries (Table 2.4) and represented the intermixing and potentially competition of species from the main forest types in Region VI and Region VII. Within the *Fagus g.-Pinus s.* community (cluster 18), the two dominants were competing strongly as indicated by their similar average importance values of 40.8 and 33.1 respectively (Appendix 1). Other species intermix within this transitional community, *Acer saccharum* (5.2), *Quercus alba* (3.5), *Acer* spp. (2.9), and *Tilia americana* (1.7), although they were much less important than the two dominants (Appendix 1).

In contrast, within the *Pinus strobus* transitional community (cluster 17, *Pinus strobus* (70) strongly dominated over *Fagus grandifolia* (7.8). While some species were similar, i.e. *Quercus alba* (6.2) and *Acer* spp. (3.9), other species were present in the *Pinus strobus* community, including *Quercus velutina* (1.7), *Larix larcinia* (1.06) and *Tsuga canadensis* (0.94). While this community was found within the ecotone itself, the dominance of *Pinus strobus* indicated that this community was not as strongly transitional as the *Pinus strobus-Fagus grandifolia* community.

The other two transitional communities, the *Quercus a.* (*Pinus s.)* (cluster 16) community and the *Acer s.-Fagus g.-Pinus s.* community, occupied a much lesser extent of the landscape at 3% collectively. Within the *Quercus a.* (*Pinus s.*) community, *Quercus alba* and *Pinus strobus* were both strongly dominate in this community as indicated by their almost equal importance values of 39.9 and 35.4, respectively (Appendix I). Several species present in the other transitional communities were also a component of the *Quercus a.* (*Pinus s.*) community including: *Fagus grandifolia (6.7)*, *Acer* spp. (6), *Quercus velutina* (1.6) and *Acer saccharum* (1.2). Similarly, the fourth transitional community, *Acer s.-Fagus g.-Pinus s.* was comprised of the same major dominant species with slightly different orders of importance and a few different lesser important species; i.e *Fagus grandifolia (*22), *Pinus strobus* (13.7), *Acer saccharum* (2.8), *Quercus alba* (2.2), *Ulmus* spp. (2.0), and *Tilia americana* (1.9).

As with many of the other communities, the individual sections within the transitional communities were dispersed among the other forest types and were not aligned in a contiguous pattern (Figures 2.9 and 2.11). The dispersed patterning of the individual sections of the transitional communities (for each community type), and similarities among the various important species (i.e. *Fagus grandifolia, Acer saccharum, Pinus strobus,* and *Quercus alba*), were indicative of the diffuse nature of the ecotone and the slight variations of species abundances in the ecotone. When the transitional communities were grouped together (Figure 2.11), they formed a slightly more contiguous pattern, but were still dispersed amongst the other communities. Thus, the dominant forest types in each Region (VI and VII) did not meet at a sharp boundary without intermixing. Instead, the important species from their respective communities were intermixed within the tension zone at the time of PLS surveys. The dispersed nature of these communities, at the time of the PLS survey and within the life-span of the trees present, species from Region VI and Region VII mingled within the tension zone. Individual trees had gained slight advantages, but only for a relatively limited geographic space until another species gained an advantage.

The dispersed distribution of the transitional clusters is most likely a factor of past legacies. Individual trees on a landscape at a snap-shot in time may be holding over or remnants from the past when the local environment may have been more suitable allowing individuals to gain and advantage. For example, small patches of *Fagus-Acer* forests may be remnants from the recent past when the environment was more suitable to mesic species. As the environment changed, primarily climate and moisture, other taxa may have increased in abundance within the tension zone, such as *Pinus strobus* or *Quercus alba,* and began to dominate while *Fagus grandifolia* and *Acer saccharum* trees remained but were not regenerating.

2.5.6 Northern and North-Central Distribution of Communities

The presettlement forests of Region VII were comprised of several different communities characteristic of the Laurentian mixed forests, dominanted by *Tsuga canadensis*, *Fagus grandifolia*, *Pinus strobus*, and *Acer saccharum* as the dominant species. Several of these communities were located primarily within the northern portion of the study area. The most prevalent community overall, distributed on 11.6% of the landscape (Appendix 1), was the *Tsuga c.* community (cluster 9) which was predominantly in the northern portion of the study area. The community occupied relatively few sections within the transition zone. *Tsuga canadensis* clearly dominated this forest with an average importance value of 47.7. This species was found with various other species including *Fagus grandifolia* (14.7), *Pinus strobus* (6.3), *Acer saccharum* (5), *Thuja occidentalis* (4.4), *Fraxinus nigra* (3.1), *Acer* spp. (3.1), *Pinus* spp. (2.7), *Larix larcinia* (2) and *Betula* spp (1.8). This community was clearly a northern community dominated by species preferring moist rich sites. The majority of this community was found in sub-district VII.2.1 (76.4%) and VII.2.2 (10.39%) with the remainder scattered in Region VI (Table 2.4). The individual sections within the *Tsuga canadensis* community exhibited a slightly more contiguous distribution than the other communities in Region VII, which reflected the site-specific needs of *Tsuga canadensis*. *Tsuga canadensis* requires moist cool sites to establish and is highly shade tolerant. Therefore, it is very sensitive to canopy openings. Nonetheless, the overall patterning was relatively dispersed.

Tsuga canadensis was also dominant in the *Fagus g.-Tsuga c.* community (cluster 7) which occupied 6.4% of the landscape, and was distributed predominately in the northern portion of the study area. *Fagus grandifolia* and *Tsuga canadensis* had similar importance values at 35.7 and 25 respectively and were found in this association with other species, such as *Pinus strobus* (10.5), *Acer saccharum* (8.1), *Acer* spp. (4.11), and *Thuja occidentalis* (2.62). This community was also predominately distributed in sub-district VII.2.1 (81.1%) with fewer than 8% found in Region VI. Individual sections of this community also exhibited diffuse patterning.

Pinus resinosa (cluster 20) dominated a community located completely within the very northern portion of the study area, occupying just over 1% of the landscape. Within this community, *Pinus resinosa* was clearly the dominant species with an average importance value of 54.2. Several other species were also found in the *Pinus resinosa* community including *Pinus strobus* (14.7), *Fagus grandifolia* (4.7), and *Tsuga canadensis* (4.07) as well as the less dominant *Pinus banksiana* (3.8).

Pinus banksiana dominated a community located in a contiguous patch in the northern portion of study area which occupied only 1% of the landscape. This community was characteristic of the *Pinus banksiana* barrens which were found on xeric soils formed in outwash, where fire was an important component of this system. A *Thuja o.* community (cluster 8) was also present in the very northern portion of the study area, typifying the *Thuja occidentalis* swamps characteristic of Region VII.

Several communities within Region VII were found both in the northern and central portions of the study area. The *Pinus s.* (*Fagus g.–Tsuga c.*) (cluster 4) community, the second most prevalent community in this Region which occupied 9.9% of the landscape and was distributed in both the northern and central portion of the study area in several sub-districts (Table 2.4). *Pinus strobus* dominated this community with an importance value of 42.8 followed by the other dominants in Region VII, *Fagus grandifolia* (14.2) and *Tsuga* canadensis (9.3). The individual clusters of this community were also widely dispersed among the other community types. The *Fagus g.–Pinus–Tsuga c.* (cluster 19) community was both a northern and transitional community, and occupied only a relatively small percentage of the landscape at 2.79%, but was widely dispersed across sub-districts (Table 2.4). *Fagus grandifolia* was the most important species in this community, with an average of 40.9% importance, followed by *Pinus* spp. (30.8), *Tsuga canadensis* (5.3), *Acer* spp. (4.2). The *Fagus g.–Pinus–*T*suga c.* (cluster 19) community differed from the *Pinus s.* (*Fagus g.–Tsuga c.)* community (cluster 4) in that *Pinus strobus* dominated cluster 4 whereas *Fagus grandifolia* dominated cluster 19. Coniferous species, such as *Tsuga canadensis*, *Pinus resinosa*, and *Larix laricina,* all had higher importance values in cluster 4 than in cluster 19, where only *Pinus* spp., *Tsuga canadensis*, and *Larix laricina* had high importance values.

In contrast, the *Pinus* (*Quercus a.–Fagus g.*) community (cluster 6) was distributed both in the center of the study as well as in the northern portion of the study area, but exhibited a unique distribution. It was found in contiguous areas in two major groupings. This cluster was located predominantly on the large glacial outwash plains found in the northwest section of the study area (Table 2.1, Figure 2.11). *Pinus* spp. was strongly dominant in this community with an importance value of 57, followed by *Quercus alba* (8.9), *Fagus grandifolia* (6.9), *Quercus velutina* (4.5), and *Tsuga canadensis* (4.32).

2.5.7 Additional and Rare Communities

The examination of the results from the forty cluster map provides further insight into the nature of the forest communities in the study area. The rare community types, those present on less than 1% of the landscape (Figure 2.10) are widely distributed across the study area. The rare communities were split from a total of four communities identified in the twenty cluster analysis (Table 2.4). Interestingly, the transitional communities identified in the twenty cluster results, which are characteristic of the tension zone, were not split further split into additional clusters in the forty cluster map. The integrity of the transitional clusters in the forty cluster analysis further reiterates the diffuse nature of the forest tension zone. If rare communities formed solely within the ecotone itself in an abrupt boundary (one or two sections wide), the cluster analysis at the forty grouping level would have split the transitional communities further. The communities which were split further in the forty cluster map are most likely those found within unique habitats. For example, the *Ulmus-Fraxinus n.-Fagus g.-Quercus v.* community was split into four different communities in the forty cluster map (Table 2.4). Two of these are represented only less than 1% of the landscape (Figure 2.10). These two communities (21a and 27a) are most likely very wet communities where *Ulmus* and *Fraxinus* were dominant and Fagus g. and *Quercus* were less dominant.

2.5.8 Ordination and Comparison with Cluster Distribution

The ordination analysis (Figure 2.10) further confirmed the diffuse nature of the tension zone. Clear boundaries between communities in ordination space were not evident. The individual sections within a community type were dispersed, as opposed to tightly centered, and often overlapped significantly. For example, the individual sections for the *Pinus* (*Quercus a.-Fagus g.*) (cluster 6) overlapped with those from the *Fagus g.* (cluster 2) community, as well as with the *Fagus g.-Tsuga c.* community (cluster 7). The only communities which did not overlap were the *Quercus* dominated communities, specifically the *Quercus a.* (*Quercus v.-Fagus g.*), and the *Quercus a.* (*Quercus v.-Quercus m.*) communities. These two communities were found in a contiguous band in Region VI (Figure 2.11). The apparent difference in the spread of the *Quercus* communities in ordination space in comparison to all of the other communities reflected differences in spatial patterning, i.e. contiguous versus dispersed, of communities on the landscape at the time of PLS.

In similar analyses, the ordination of presettlement tree data for the New England tension zone resulted in a clear and distinct boundary between the clusters confirming the "primacy of the division between the northern and the central hardwoods" (Cogbill et al. 2002:pg 1292). In contrast, within the 'tension zone' in the central Lower Peninsula of Michigan, the dominants from the Laurentian forests north of the tension zone and the eastern broadleaf forests south of the ecotone, specifically *Quercus alba*, *Pinus strobus*, and *Fagus grandifolia* formed continuous gradients. These communities and the distribution of dominant taxa did not exhibit distinct spatial boundaries for the snap-shot in time represented by the PLS data. Within these continuous gradients, one species gained an advantage and dominated for a limited amount of contiguous space until another species gained an advantage and dominated. If these species exhibited discrete gradients and formed distinct communities on the landscape with identifiable boundaries, the individual sections of each community type would be clearly separated in the ordination space. The only exception is the case where the *Quercus* dominated communities in Region VI were separated. Moreover, the individual clusters from the transitional communities (i.e. clusters 16, 17, 18) were dispersed in the center of the ordination diagram.

In contrast, species with strong latitudinal affinities, i.e. northerly or southerly, as well as species with specific site requirements, for example soil moisture, climate, or disturbance regimes, were clearly separated on the ordination diagram. For example, the species with southern affinities, *Carya* spp. and *Juglans* spp., were aligned to the very upper end of axis one, while the species with northern affinities, *Abies* spp. and *Picea* spp., are aligned to the very lower edge of axis one. Both *Quercus muehlenbergii* and *Quercus macrocarpa*, which thrive on very xeric sites in calcareous soils, were aligned to the very upper end of axis one. *Pinus banksiana*, a fire dependant species which thrives on xeric outwash plains and often grows in mono-specific stands, was aligned to the very lower end of axis one. *Quercus* species were less dominant on the xeric sites in the northern portions of the study area. Climatic factors, especially the number of growing degree days, which may be 70 days less in the northern Lower than in the southern Lower Peninsula (McCann 1979), may limit the ability of *Quercus* to be more dominant other xeric species in the north since *Quercus* is especially sensitive to frost damage (Barnes and Wagner 2004). Conversely, *Pinus* species which thrive in xeric conditions were not limited by growing degree days in the northern Lower Peninsula.

Common species with relatively wider habitat niches were positioned to the center of axis one, but pulled either to the upper end or lower end of axis two. For example, *Acer saccharum,* which prefers mesic sites with nutrient rich soils and is highly shade tolerant was aligned to the middle of axis one and the upper end of axis two. In contrast, Acer spp., which most likely refers to *Acer rubrum*, is positioned near *Pinus strobus* and the *Quercus* species. *Acer rubrum* has wide tolerance for different site conditions and occurs abundantly on both wet and dry sites (Hushen et al.1966). Species with a wide distribution were aligned to the middle of both axes, as was the case with *Fagus grandifolia,* which tolerates a wide variety of site conditions in Michigan (Hushen et al. 1966;

Medley and Harman 1987). Thus, the polar ends of each ordination axis represented the importance of site conditions, i.e. fire, soil texture, moisture, and climate (temperature or growing degree days), while the middle of either axes illustrated the wide tolerance ranges of the dominants from both Regions. Therefore, the forest tension zone was a gradual transition at the time of PLS. The dominants, *Fagus grandifolia*, *Pinus strobus*, and *Quercus alba*, all which have wide tolerance ranges, exhibited variable gradients over space, and were able to dominate in a variety of site conditions within both Regions which directly contributes to the diffuse nature of the ecotone.

As indicated above, the distribution of cluster members and individual species in the ordination diagram reflected the importance of time as well as physical and biologic factors. Specifically the role of fire and edaphic conditions were clearly identifiable in the ordination of individual species and the position of the communities in which these factors were important. Species were further separated out based on their climatic tolerances, which have been related to the growing degree gradient from the southern Lower Peninsula to the northern Lower Peninsula (McCann 1979). Here in this discussion, the individual axes were not specifically related to physical factors, such as soil moisture or texture because an indirect, as opposed to direct, ordination technique was used to identify and explore community composition. However, the results from this ordination indicated the importance of physical conditions, soil texture and climate, and recent disturbance regimes within the tension zone. The results suggested that direct ordination considering these factors may provide further insight into species gradients and the driving factors of the forest tension zone.

2.5.9 Comparison with Other Regional Ecotones

The findings of this research indicated that the forest tension zone in the central Lower Peninsula of Michigan, before the onset of massive Euro-American settlement and disturbance, was diffuse in nature and more complex than noted by previous researchers (McCann 1979; Medley and Harman 1987; Dodge 1995; Andersen 2006). This ecotone in Michigan shared several characteristics with other regional forest ecotones in eastern North American, including the tension zone in Wisconsin (Curtis 1959), surveyed in the mid 1950's, and the New England tension zone, also reconstructed from survey data (Cogbill et al. 2002). However, differences between the three tension zones were apparent. The two other forest ecotones exhibited regional species gradients, supported the continuum model of species abundance on the landscape, as did the tension zone in the Lower Peninsula of Michigan. But in the tension zones in Wisconsin and New England, sharp boundaries between the dominant communities were identified within the overall species gradients, unlike in the Michigan tension zone which was quite diffuse. For example, in the New England tension zone, the transition between the northern hardwood forests dominated by *Fagus grandifolia*, *Acer* spp., and *Betula* spp., and the central hardwood forests, dominated by *Quercus* spp., *Carya* spp., and *Castanea dentate* (American chestnut), was relatively abrupt and was coincident with the boundary of individual species abundances (Cogbill et. al 2002). In eastern Wisconsin, the tension zone is sharp; the xeric *Quercus* forests abut the xeric *Pinus* forests in a very narrow tension zone which "amounts to virtual replacement of one by the other" (Curtis 1959: pg 203). In western Wisconsin the tension zone is more gradual and mixed *Pinus* and *Quercus* forest are found. Small patches of pure *Pinus* forests are found on the rocky or sandy sites while pure *Quercus* forests are found on deeper soils (Curtis 1959).

Broad regional gradients of species abundances and community distributions were evident in the tension zone in the central Lower Peninsula. While distinct boundaries were evident for rare habitat specific associations, such as *Pinus banksiana*, distinct boundaries between the dominant communities and the majority of individual species abundances were not evident. Only the two *Quercus alba* communities, *Quercus a. (Quercus v.-Fagus g.)* and *Quercus a. (Quercus v.-Quercus m.)* exhibited distinct boundaries. Despite the distinctness of these boundaries, the dominant species in both, *Quercus alba*, was relatively abundant north of the *Quercus* band and had relatively high importance values in several other communities with more widespread distributions (Figure 2.9 and Figure 2.11).

Overall, a majority of the forest communities detected in the study area were widely distributed across sub-district boundaries (Table 2.4) and thus landform and soil type (Table 2.1). More importantly individual sections within the communities were widely dispersed, i.e. they did not form contiguous patches on the landscape. Moreover, the dominant species, *Fagus grandifolia*, *Pinus* *strobus*, and *Quercus alba*, all exhibited complex gradients on the landscape, dominating an assemblage for relatively small patches. Several of the less dominant species, i.e. *Acer saccharum,* also exhibited complex gradients. This was not generally the case within the presettlement New England tension zone, where the eight common genera showed "clear geographic patterns" and taxa abundances were coincidental with "distinct divisions" between the northern and southern vegetation types at the time the proprietary town surveys were collected (1770-1810) (Cogbill et al. 2002:pg 1295).

Further analysis is needed before specific conclusions can be drawn regarding the abundances of the most common species in the forest tension zone in the Lower Peninsula of Michigan. Upon further examination, more complex gradients may be evident in species abundances than is typical for the continuum model of vegetation (Collins and McIntosh 1993). Previous research has indicated that species gradients are often more complex than assumed within the continuum model and that species gradients often do not conform to one gradient model, but exhibit characteristics of several models (Hoagland and Collins 1997).

The presence of purely transitional communities at the location of the forest tension zone in the Lower Peninsula and the dispersed nature of communities on the northern side of the ecotone (Region VII), documents the diffuse nature of this ecotone, prior to Euro-American landscape disturbance. Therefore, this ecotone in the Lower Peninsula of Michigan was somewhat different from the two other regional forest ecotones in eastern Wisconsin and

New England. Transitional communities, representing the intermixing of dominants from their respective regions on each side of a tension zone, were identified within the tension zone in western Wisconsin but were limited primarily to the mixed *Pinus strobus* and *Quercus* forests (Curtis 1959). Transitional communities were not identified in the New England tension zone (Cogbill et al. 2002). However, a transitional community or 'buffer zone' was identified in the prairie-woodland ecotone in south-central Minnesota, comprised of fire-tolerant *Quercus* species and *Populus* spp. (Grimm 1984), although the ecotone in south-central Minnesota was quite different than the other regional forest ecotones.

Similar to the regional vegetation transitions in Wisconsin, New England, and Minnesota, the physical boundary of the forest tension zone in the Lower Peninsula, did not follow specific boundaries evident in the physical geography of the landscape, i.e. bedrock, substrate, climate, and topography (Table 2.1 and Table 2.4). For example, the distinct boundary between the northern and southern vegetation types within the New England tension zone was not correlated with any break in landforms or bedrock or gradients in environmental variables under examination (altitude or temperature). Instead, Cogbill et al. (2002) suggested that the abruptness of this boundary may be due to other factors such as soils or glacial substrates (not investigated), but was most likely a result of legacies of the past, especially of fire, which has been found to be a major factor in ecotone dynamics in other regional ecotones (Curtis 1959; Grimm 1984; Parshall and Foster 2002; Andersen 2005).

Based on the examination conducted in this research, the forest tension zone in the Lower Peninsula also did not follow the regional landscape ecosystem boundaries established on the basis of physical geography. At sub-regional scales the sub-district divisions are generally based on glacial substrates and soil texture, while the major division boundaries are based on regional climatic differences (Table 2.1, 2.4 and Figure 2.11). For example, the transitional communities are distributed within both Regions in 3 of the sub-districts which include several different soil types ranging from well to excessively drained sands and to well to moderately well drained loams (Table 2.1,2.4 and Figure 2.11). Therefore, while physical geography, specifically soil texture, has been documented as a significant driver in the location and character of the tension zone (Medley and Harman 1987), other factors, such as competition (Brewer 1982; Dodge 1995) and legacies of past disturbances, including both fire, other disturbances from storms, insects, and disease, as well as climatic change, must also be considered and evidently were important factors in determining the location of the tension zone in the Lower Peninsula. For example Dodge (1995) found relationships between conifer distribution and coarse textured soils in the tension zone in the "Thumb" of Michigan, soil geography explained only 50% of the variance in the relationship between the two variables (Dodge 1995).

The importance of fire, and specifically fire history, in relation to regional vegetation patterns and ecotone dynamics, has been demonstrated in other research. For example, fire and the fire tolerance of individual species were determined to be a significant factor in ecotone dynamics within the prairie-woodland border in south-central Minnesota (Grimm 1984) and within the tension zone of Wisconsin (Curtis 1959). The importance of fire in the historic (i.e. presettlement) landscapes in the northern Lower Peninsula of Michigan has been demonstrated in recent work (Cleland et al. 2004). The fire rotation interval for Region VII was as high as 47 years for the dry-mesic land type associations (sub-districts) dominated by *Pinus strobus-Tsuga canadensis* communities and 59 years for the extremely xeric land type associations dominated by *Pinus banksiana* communities (Cleland 2004). Other disturbances, especially wind throw may be particularly important and may contribute to the dispersed nature of communities. In the "Thumb" of Michigan surveyors noted numerous windfalls; the descriptions including "windfall entirely swept down", "tremendous windfalls", "windfall from tornado autumn 1832", confirm the role of wind as an agent of forest change and forest community distribution (Dodge 1995). Windthrow has been shown to have extensively impacted presettlement forests in Wisconsin (Schulte et al. 2005). Research specifically addressing the relationships of the forest communities and species abundances across the landscape studied here in relation to physical factors must be undertaken before conclusions regarding the driving factors of the ecotone can be made.

While differences in the nature of the tension zone in the Lower Peninsula of Michigan in comparison to tension zones elsewhere were clearly evident in the results from this research, the degree of difference may be impacted by the scale at which the research was conducted, i.e. the grain of a section (2.65 km^2)

compared to a town (100 km^2) (Cogbill 2002) or (6 km ^{2}) (Curtis 1959). Regardless, it is clear that distinct boundaries were not evident in the forest tension in the Lower Peninsula of Michigan, except in the location of the *Quercus* band within Region VI. Even when the clusters identified in the study area were grouped by dominant species and position on the dendrogram (Figure 2.11), only the *Quercus* community boundary was abrupt, while distinct spatial boundaries for the other dominant communities were not evident. While the diffuse nature of the forest tension zone was generally not similar to that of the other two tension zones, it appeared at precursory examination that the tension zone identified, especially in the case of the *Quercus* band, did not correspond to regional landscape ecosystem boundaries. Instead, legacies of the past, as with the other ecotones, were most likely a major influence on the character (both spatial distribution of communities and within species assemblages) of the tension zone in the Lower Peninsula of Michigan.

2.5.10 Public Land Survey Data as a Historical Baseline

The Public Land Survey data proved to be an invaluable resource in reconstructing the character of the forest tension zone in the Lower Peninsula of Michigan before Euro-American settlement and subsequent disturbance. The quantitative baseline of presettlement forest composition provided new insights into forest communities and their dynamics within the Lower Peninsula and the forest ecotone itself. The scale at which the PLS data were collected allowed for local details to emerge, which were not evident in previous qualitative studies

(Comer et al 1995). For example, the PLS data in this study revealed the complex gradients of several dominant species and the existence of purely transitional communities characteristics of the ecotone itself. Surveyor bias was evident in the data, especially in the case of the underestimated importance of *Carya* spp. and other taxa known to be important components of the *Quercus* forests in Region VI (Barnes and Wagner 2004). Also, the importance of long-lived, easily identifiable species, such as *Fagus grandifolia* and *Pinus strobus*, were most likely overestimated due to a well known surveyor bias (Bourdo 1956).

Overall, the lack of species designations for these clusters was not a major problem in this analysis. The lack of a species designator in 10% of the data set did affect the cluster analysis in that several clusters had dominant taxa without a species designation. Despite this fact, none of the clusters designated only to the genera level emulated the same importance values for the top ten dominants (Appendix I) of the other clusters with the same genus as the dominant, and were therefore evidently different communities. The use of historical data to examine the presettlement characteristics of the forest ecotone has been extremely useful, especially in light of the highly disturbed state of these systems today. Thus, as stated by Cogbill et al. (2002: pg.1298) "historical methods can also elucidate traditional questions".

2.6 Conclusions

The Public Land Survey (PLS) data were useful in reconstructing the forest tension zone in the Lower Peninsula of Michigan before the onset of Euro-

American settlement and subsequent disturbance. The quantitative baseline of presettlement forest composition was analyzed with both cluster analysis and ordination analysis in order to identify and map forest communities within the ecotone. The resulting map of forest communities provided new insights into the character of the presettlement forest ecotone in the Lower Peninsula of Michigan and provides a detailed snap-shot in time of forest characteristics. The methodologies employed here could be applied to ecotones in other regions where presettlement survey notes are available.

A broad regional gradient between the Laurentian forests north of the tension zone dominated by *Pinus strobus, Tsuga canadensis,* and *Fagus grandifolia,* and the eastern broadleaf forests south of the tension zone dominated by either *Quercus* spp. and *Carya* spp. or *Fagus grandifolia* and *Acer saccharum* was generally apparent in this analysis of the presettlement forests. This regional gradient was generally similar to those in other parts of eastern North America, i.e. the vegetation tension zone in Wisconsin (Curtis 1959) and the presettlement New England tension zone (Cogbill et al. 2002), and similar to previous descriptions of the tension zone in the Lower Peninsula of Michigan (Vetach 1959). However, this analysis revealed that the tension zone in the Lower Peninsula was much more complex and diffuse in nature at the time of the PLS than previously noted. The diffuse spatial distribution of different species and communities within the ecotone was revealed by the variability of species importance values. The identification of several transitional communities found only within the center of the study area along the border of two major land type associations (between Region VI and Region VII), also attests to the diffuse nature of ecotone. If this ecotone was sharp, northern communities would abut southern communities within the ecotone itself. Instead, this research documented that species from the dominant communities to the north and south of the ecotone intermixed in a complex nature, within a broad transition zone, forming communities which were not spatially contiguous on the landscape. This study demonstrates the importance of complexity within forest ecotones.

Additionally, the majority of the communities are widespread across regional landscape ecosystem sub-district boundaries, indicating the importance of factors besides those that are physical, such as biotic (competition) and legacies of the past (disturbance regimes, species migrations). While this research does not discount the importance of physical factors (Medley and Harman 1987) and competition (Dodge 1995) over time, it does suggests that legacies of the past also play a key role in the dynamics of forest tension zone in the Lower Peninsula of Michigan. Reconstructions of presettlement fire rotation intervals for Region VII indicate that fire occurred frequently on these landscapes, 47 years in dry-mesic forests dominated by *Pinus strobus* and *Tsuga canadensis* (Cleland 2004). Moreover, the spatial patterning of forest communities was clearly different in the northern portion of the study area (Region VII) in comparison to the southern portion of the study area (Region VI), as indicated by the presence of the Q*uercus* band, a large area of contiguous space dominated by *Quercus alba* communities. The communities present in the northern portion of the study exhibited diffuse patterning and generally did not occur in contiguous bands.

Fagus grandifolia, was the most dominant species within the presettlement forests of the Lower Peninsula. It was the most important species found in over a third of the landscape, in both the northern and southern portions of the study area. Communities dominated by *Quercus alba* and *Quercus velutina*, were the second most prevalent. *Quercus alba* was an important species both in the southern *Quercus* communities but also within the transition itself, as it was important in several of the transitional communities. *Pinus strobus* was the third most dominant species on the landscape and was found with both *Quercus alba* and *Fagus grandifolia* within the transition zone itself. The spatial distribution of *Acer saccharum* suggested that it was able to dominate at this point in time within the tension zone and was dominant only in the very southern and northern portions of the study area. *Tsuga canadensis*-dominated communities were the most abundant on the landscape, distributed primarily in the northern portion of the study area on just over 10% of the landscape.

The analyses of the Public Land Survey data provided new insights into the presettlement forests within the tension zone in the central Lower Peninsula of Michigan. Furthermore, this research emphasized the complexity of forest systems in the Great Lakes region. The results from this research can be used to further explore the nature of this ecological phenomenon with regard to its driving factors, i.e. physical geography, biotic interactions, and legacies of past disturbances. This research emulates other studies of regional ecotones in eastern North America (Curtis 1959; Grimm 1984; Cogbill et al. 2002) by suggesting the importance of legacies of the past, particularly with regard to disturbance including fire and potentially climatic variations, as well as physical and biological factors.

The complex nature of the forest ecotone and the importance of legacies of the past as a driver for ecotone dynamics have strong implications for the management and overall health of the ecotone today and in the future. This research provides a detailed baseline of presettlement forest composition in the study area which can be used directly to evaluate ecosystem reconstruction or restoration potentials (Bolliger et al 2004; Lunt 2005). Presettlement ecosystem reconstructions are useful tools for managers to asses the characteristics of presettlement landscapes including biodiversity, spatial extent of historical communities, boundaries between historical communities, ecological flows, biogeochemical cycling, as well as for providing a longer term perspective than is available through studies of current forests systems. Often, ecosystems managers aim to restore forests to presettlement conditions. Management strategies seeking to emulate presettlement forest ecosystems need to consider the variable nature of forest associations on the landscape. The results from this research will aid in these considerations. Management strategies should also consider the importance of historical legacies in these forest systems. By better understanding the dynamics of these systems in the past, new insights are gained on how to manage the ecotone today and in the future especially in the face of current threats to forest health in the Great Lakes region.

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Chapter 3

The Vegetation History of the Forest Tension Zone in the central Lower Peninsula of Michigan, USA, during the Past 2,000 Years

3.1 Introduction

The Late Quaternary history of Great Lakes region has been the focus of extensive paleoecological research (Potzger 1948; Brubaker 1975; Grimm 1983; Webb et al. 1983; Bartlein et al. 1984; Kapp et al. 1990; Liu 1990; Graumlich and Davis 1993; Flakne 2003). This research has provided many insights into the dynamics of vegetation systems over time and space, and at scales where traditional ecological research is limited. For example, paleoecological research conducted in the Great Lakes region, and elsewhere, has contributed to the overall understanding of forest systems by: 1) documenting the responses of vegetation to ecological processes, e.g. disturbance, over long time frames, 2) reconstructing the responses of vegetation to environmental changes of various magnitudes which occurred beyond the historic record, and 3) providing baseline knowledge of vegetation dynamics before major anthropogenic influences on the landscape. Also, the extensive data sets generated from this research can be used to test models and theories of past climatic and vegetation change (Foster et al. 1990; Davis 1994). While the contributions of paleoecological research to the understanding of Great Lakes forest dynamics are significant and have proved to be invaluable, especially in the modeling of past and future climate change (Sousounis and Albercook 1998; Walker et al. 2002), gaps in the record still exist and many questions regarding the nature and details of vegetation change remain.

A majority of the paleoecological research conducted in the Great Lakes region has focused on vegetation change that occurred over the entire Holocene Epoch (Brubaker 1975; Davis et al. 2000; Flanke 2003). Most of this research has focused on vegetation change at relatively coarse temporal and spatial scales. Coarse-scale paleoecological research, referred to as macro-scale research, typically investigates vegetation change at 1,000-year intervals, at regional and continental scales (>500 km^2). Macro-scale paleoecological research generally examines vegetation change in response to inter-glacial climatic cycles or long-term climatic trends at the formation or biome level. This research often documents species migrations, the re-forestation of North America after deglaciation, and major biome shifts (Delcourt and Delcourt 1987). The synthesis of existing macro-scale research has contributed to the understanding of long-term vegetation dynamics and has been particularly useful in answering questions about Late Quaternary climate change. For example*:* At what rates did species migrate northwards after deglaciation? Did vegetation assemblages of the past have modern analogs (Delcourt and Delcourt 1987; Webb et al 2004; Williams et al. 2004)?

Advancements in the field of paleoecology over the past few decades has allowed researchers to formulate specific questions and investigate vegetation dynamics at finer spatial (sub-regional 20-500 km^2) and temporal (decadal to centennial resolution) scales than previously thought possible, through fossil pollen and plant macrofossil analysis (Birks 1995; Bennett 2001). In contrast to macro-scale research, meso-scale research investigates vegetation change at 10 to 100-year temporal resolution, at the type, sub-type, and often individual stand scales. Meso-scale pollen research requires that sediment cores are sampled and analyzed for fossil pollen at close sampling intervals, e.g. 2-cm. This fine scale research also requires the study of multiple paleoecological study sites primarily lakes, in close proximity. Sites must also be correlated in order to assess changes within sub-regional vegetation formations. Knowledge gained by investigating meso-scale vegetation change, i.e. changes over the past few thousand years at higher temporal and spatial resolutions, can serve to fill a gap in the paleoecological record. Moreover, paleoecological research conducted at this scale will aid efforts to better predict future forest change, because often efforts to predict future changes are conducted within the meso-scale domain (Jackson and Williams 2004; Saxon et al. 2005). More importantly, meso-scale research will provide details regarding vegetation pattern and process at scales where both traditional ecological and paleoecolgical research are limited by spatial and temporal resolution (Delcourt and Delcourt 1987). For example, meso-scale paleoecological research has the potential to investigate the responses of forest species to medium frequency climatic oscillations, for example the Little Ice Age (from 600-150 cal yr BP), the role of past legacies (i.e. disturbance regimes) in forest dynamics, and the stability of the species associations (Gajewski 1987). When insights gained from meso-scale research are combined with knowledge of current ecological systems, a broader perspective over both time and space is gained. These new perspectives can be used directly to predict and manage for future changes (Scheller and Mladenoff 2005).

Of particular interest to paleoecological researchers in the Great Lakes region, and more broadly the Midwest, is the numerous ecotones between vegetation formations, types, and sub-types. Several macro-scale fossil pollen studies have documented the formation and subsequent shifts of Midwestern ecotones, during the late Quaternary. Existing macro-scale research has investigated the Holocene dynamics of the following ecotones: 1) between the boreal forest and the Great Lakes-St. Lawrence forest in northern Ontario (Liu 1990); 2) between eastern broadleaf deciduous forests and the Laurentian mixed-forests in the central Lower Peninsula of Michigan (Potzger 1948), 3) and the prairie-woodland ecotone in south-central Minnesota (Grimm 1983; Baker et al. 2002). Absent from existing research is an investigation into the meso-scale dynamics of these ecotones. While it is evident in the fossil record that these ecotones responded to climatic change associated with inter-glacial climatic cycles, there is a gap in our knowledge regarding the response of these ecotones to short-term climatic variations, such as the Little Ice Age or Medieval Warm Period, or to disturbances such as fire. Results from a limited number of meso-scale studies in the Great Lakes region (Bernabo 1981), the Midwest (Gajewksi 1987), and eastern North America (Russell and Davis 2001) suggest that forests systems are more dynamic than previously indicated in the paleoecological literature, and that forest systems do respond to short-term climatic variations and disturbances. Meso-scale research provides an opportunity to contribute to regional climatic histories, as well as document the responses of vegetation to short-term variations in climate, and disturbance with a higher degree of detail than the existing research.

Ecotones are particularly useful for investigating the responses of vegetation to meso-scale climate change because tree species which form regional ecotones are generally sensitive to climatic change. Therefore, responses to short-term variations in climate would be most evident at ecotonal boundaries (Neilson 1993). It is generally accepted that most vegetation systems follow the dynamic equilibrium model where lags between vegetation response and climate exist. This is especially true for long-term climatic change (millennial scale) examples, due to ice-sheet retreat and orbital forcing. However, this lag has been shown to be minimal (50-100 years) in pollen studies examining decadal and century scale climatic changes (Webb 1986). In ecotones where multiple species with different ecological relationships to climate intermix, most climatic changes should elicit an immediate vegetation response (50-80 year response time) by altering the competitive balance between the species (Webb 1986).

Because ecotones are spatially measurable systems, changes over time can be identified and measured (Baker and Weisberg 1995; Kupfer and Cairns 1996; Camill and Clark 2000). For this reason, efforts to model and predict the response of vegetation to future climate changes often focus on ecotones.

The purpose of this research was to investigate meso-scale vegetation dynamics by reconstructing changes in the 'forest tension zone', the ecotone between the mixed Laurentian forests and the eastern broadleaf forests in the central Lower Peninsula of Michigan, during the past 2,000 years. This research expanded on a fossil pollen study conducted by Bernabo (1981) at several lake sites within the Laurentian forests north of the tension zone. Bernabo's (1981) research will be used within this study for comparative purposes since it documented shifts in vegetation associated with several climatic variations during the past 2,000 years, including the Medieval Warm Period (MWP) (A.D. 1000 to 1300) and the Little Ice Age (LIA) (A.D. 1300 to 1850) (Bernabo 1981).

Specifically, in this study, changes in the forest tension zone were reconstructed through detailed fossil pollen analysis of sediments collected from three lakes along a north-to-south transect crossing the ecotone. Lakes sites, selected for this research are representative of forest communities known to exist before Euro-American settlement, and are located north of, south of, and directly within the tension zone itself. Distance between sites, individual lake basin characteristics, size of the pollen rain area (source of pollen), and glacial substrates were all considered in order to find optimal sites for detection of ecotone change. This research addressed the following questions: *Has the vegetation at each of the three sites changed over the past 2,000 years? If so, how have individual species changed in abundance across the ecotone for different time intervals? Are signals for either the LIA or MWP evident in the analysis of the fossil pollen record and vegetation reconstructions? If so, is the*

timing and pattern of vegetation change similar to those documented north of the study area (Bernabo 1981) and elsewhere in the Great Lakes Region (Kapp 1990)?

3.1.1 Holocene Forest History

A majority of the existing paleoecological studies for the Lower Peninsula of Michigan were conducted between 1948 and the late 1970's, when the focus of paleo-environmental science was at the macro-scale domain (Bryant and Holloway 1985; Kapp 1948,1999). Collectively, these studies have provided great insight into the vegetation history of Michigan since deglaciation. But many of them (Potzger 1948; Kapp et al. 1975; Aheran 1976; Lay 1979) often used methodologies considered inappropriate today and lack detailed descriptions of the methodology used. The lack of methodological detail is particularly a problem for chronological records in the central Lower Peninsula. Many of the chronologies were constructed from radiocarbon dates obtained from organic sediments or aquatic plant materials, both of which can provide erroneous dates without proper mediation (MacDonald et al. 1991). This includes the use of the *Ambrosia*-peak method or by correlating significant changes in the pollen abundances of specific taxa, i.e. hemlock decline, with other pollen records where reliable chronologies have been established (Webb et al. 1983; Grimm 1984). When using the *Ambrosia*-peak method, a spike in the percentage of *Ambrosia*-type pollen grains is related to a known date of Euro-American settlement. The bulk sediment at the location of the *Ambrosia*-type spike is radiocarbon dated and then the known date of that occurrence (based on local

Euro-American settlement) is used as a correction factor. In many studies (e.g. Kapp et al. 1975), no indication was given regarding attempts had been made to correct for errors in dates obtained from such sediments. In several cases, reference to the actual type of material dated was absent. Dates were commonly estimated based on correlation of pollen spectra with other sites (McMurray et al. 1978). Also, researchers often examined few samples and counted relatively low amounts of pollen grains (less than 200 grains) per sample. Additionally, several of the studies conducted in the central Lower Peninsula were part of student projects and were never officially published (Kapp et al. 1975; Ahearn 1976; Lay 1979). Despite the lack of detail in these studies, they have proved useful in reconstructing the vegetation history of Michigan since deglaciation, especially when they are synthesized with more recent research that has well documented and more appropriate methods (Bernabo 1981; Davis et al. 1986; Woods and Davis 1989; Davis et al. 2000; Booth and Jackson 2003; Flakne 2003). Nonetheless, details regarding specific events in the paleoecological history are often lacking for Michigan, particularly in the Lower Peninsula, where less recent research has been conducted in comparison with the Upper Peninsula.

The following summary of vegetation changes in Michigan since delgaciation is taken mainly from a synthesis of numerous Midwestern sites, by Webb et al. (1983, 2004), in which poor chronologies were adjusted when possible. Additionally, specific studies with reliable chronologies are referred to where appropriate and locations are shown in Figure 3.1. All dates are listed as calibrated calendar years before present (cal yr BP).

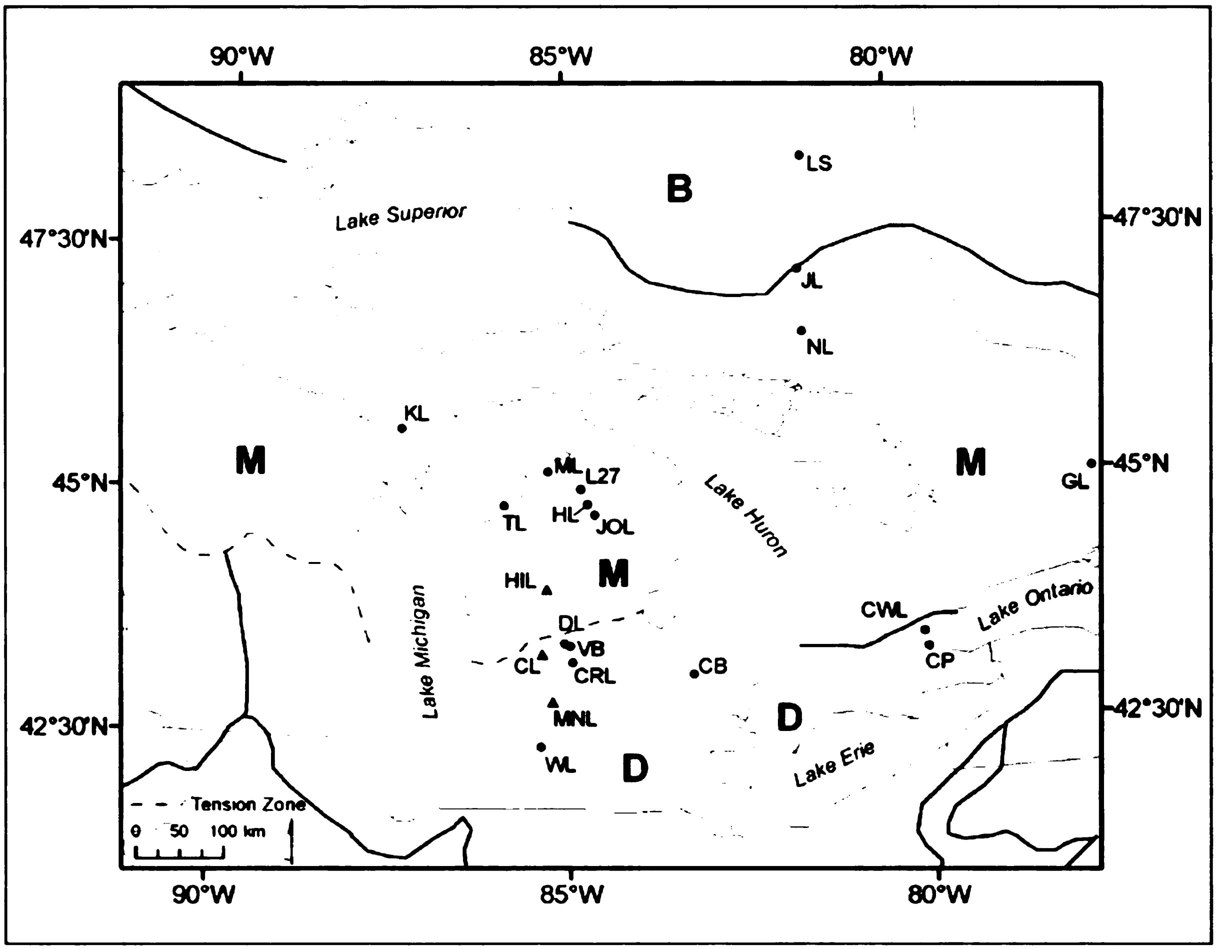

Figure 3.1 Major vegetation region within the Great Lakes Region: D = deciduous forests (eastern broadleaf forest), M = mixed forests (Laurentian forest), and B = boreal forest. Lake sites in this study (▲): HIL = Hicks Lake, CL = Cowden Lake, and MNL = Morrison Lake. Lake sites referred to in this study (●): LS = Lake Six, JL = Jack Lake, NL = Nina Lake (Lui 1990); GL = Graham Lake (Fuller 1997), CWL = Crawford Lake (Yu 2003); CP = Cootes Paradise (Finkelstein et al. 2005); ML = Marion Lake, L27 = Lake Twenty Seven, HL = Heart Lake, Jo. L = Jones Lake (Bernabo 1981); TL = Tamarack Lake (Davis 2000); DL = Demont Lake, VB = Vestaburg Bog, CRL = Crystal Lake (Kapp 1990), CB = Chippewa Bog (Bailey and Ahearn 1981); WL = Wintergreen Lake (Manny et al. 1978).

Michigan was ice free by 11,300 cal yr BP; while the southern third of the Lower Peninsula was mostly likely ice free several thousand years earlier (Farrand and Bell 1982; Schaetzl and Isard 2002). During deglaciation, Michigan's climate was much colder, approximately 10°C colder than today (Baker et al. 1986). Tundra-like vegetation first colonized Michigan as the Laurentide Ice Sheet receded. This vegetation was comprised of non-arboreal plants including Cyperaceae (sedges), Poaceae (grasses), *Artemisia* (wormwood), and *Salix* (Willow) (Kapp 1999). Tundra vegetation was evident as early as 18,000 cal yr BP in the southern Lower Peninsula. *Picea* migrated into the state by 13,800 cal yr BP, and *Picea*-Cyperaceae parklands, dominated primarily by *Picea glauca* (white spruce), formed in much of the Lower Peninsula south of the ice sheet (Wright and Porter 1983; Webb 1987; Webb et al. 2004). The *Picea*-Cyperaceae parkland phase was time-transgressive across the state.

The climate of Michigan changed rapidly from 13,000 to 11,000 cal yr BP as shifting orbital cycles resulted in increasing summertime solar radiation and corresponding decreased wintertime solar radiation (COHMAP 1988). As the climate warmed, *Pinus* displaced *Picea* northwards in the state. *Pinus banksiana/resinosa* (jack pine and/or red pine) arrived first, followed by *Pinus strobus* (white pine). *Pinus* first appeared in the southwestern Lower Peninsula during the *Picea* phase at 13,000 cal yr BP, and by 11,000 cal yr BP *Pinus* populations expanded, and dominated the forests of much of the Lower Peninsula (Manny et al. 1978; Kapp 1999). Several deciduous taxa also increased in abundance during the *Pinus* expansion and became significant components of the *Pinus* forests including: *Betula* (most likely *B. papyrifera*, paper birch), *Ostrya/Carpinus,* and *Ulmus* (elm). These species formed a mixed conifer and northern hardwood forest, dominated primarily by *Pinus*, in most of the southern Lower Peninsula. *Picea* remained dominant prior to 10,000 cal yr BP in most of the Upper Peninsula but shortly thereafter, the *Picea*-dominated forests transitioned to *Picea-Pinus* forests in the western half of the Upper Peninsula.

By 10,000 cal yr BP, two forest ecotones, or boundaries between major forest types, were present in the state. The northernmost ecotone resided between the *Picea-Pinus* forests in the western Upper Peninsula and the *Pinus*-dominated forests in the central portion of Michigan (Webb et al. 1983). The second, newly developed, ecotone lie in the southern Lower Peninsula, marked by the presence of deciduous taxa, such as *Quercus*, to the south of the *Pinus* forest (Webb et al. 1983).

Pinus spp. dominated forests persisted in the southern Lower Peninsula of Michigan for only a few thousand years as deciduous taxa, mainly *Quercus*, *Ulmus*, and *Ostrya/Carpinus*, increased in abundance (Manny et al. 1978). The climate continued to transition from a full glacial climate to an interglacial climate by 9,000 cal yr BP. *Quercus* became the dominant species in the southern Lower Peninsula by 9,000 cal yr BP. *Quercus*-dominated forests were prevalent in much of the southern Lower Peninsula while *Pinus* forests remained dominant in remainder of the northern Lower Peninsula and the Upper Peninsula (Woods and Davis 1989). After 9,000 cal yr BP, several new taxa migrated into Michigan, *Acer* spp. (maple), *Platanus* (sycamore), *Tilia* (basswood), *Juglans* (walnut), and *Celtis* (hackberry) and soon thereafter increased in abundance in the *Quercus*-dominated forests (Manny et al. 1978). At 7,800 cal yr BP, *Fagus* appeared in the southern Lower Peninsula of Michigan (Manny et al. 1978). Once established, it became an important component of the forests in the southern Lower Peninsula, and then began to migrate northward into the northern Lower Peninsula (Davis et al. 1986). *Fagus-Acer* forests with *Tilia, Ulmus*, and

Ostrya/Carpinus as sub-dominant taxa began to develop at this time, but were most likely limited to moist sites with fertile soils (Kapp 1999). Hardwood swamp forests comprised of species of *Fraxinus*, *Tilia, Acer*, and *Ulmus* formed in wet low lying areas (Bailey and Ahearn 1981). *Tsuga* also first appeared in the pollen records for both the Upper and Lower Peninsula around 7,800 cal yr BP but did not become established for at least 1,000 years (Davis et al. 1986).

Much of eastern North America and most of the Midwest experienced a period of increased warmth and dryness, referred to as the Hypsithermal or mid-Holocene warming, around 6,800 cal yr BP (Webb et al. 1983). In northern areas of the Midwest, including the Upper Peninsula of Michigan, this warming was experienced earlier (from 8,800 to 6,800 cal yr BP). During this time, Summertime insolation was about 5% greater than it is today by about 6,000 cal yr BP, causing temperatures from June to August to be 0.5 to 2°C warmer than present (Kutzbach et al. 1998) and 20% drier (Bartlein et al. 1984). During the mid-Holocene warming from 8,800 to 6,800 cal yr BP in the Upper Peninsula, the range of *Pinus* expanded and the *Pinus*-dominated forests became more prevalent.

After 6,800 cal yr BP, the Upper Peninsula experienced cooler and moister conditions, while the Lower Peninsula continued to experience increased warmth and dryness (Webb et al 2004). During this cool and moist period in the Upper Peninsula, *Tsuga* expanded its range and increased in abundance in the *Pinus*-dominated forests.

In contrast, the greater warmth and aridity evident in most of the Lower Peninsula by 6,000 cal yr BP caused patches of prairie and *Quercus* savanna to develop on the driest sites in the southwestern Lower Peninsula (Ahearn and Kapp 1990; Kapp 1999). Mixed *Quercus* forests dominated much of the rest of the Lower Peninsula and populations of *Fagus*, *Acer*, *Tilia*, and *Ulmus* declined in abundance correspondingly (Manny et al. 1978). The mesic *Fagus-Acer* forests were most likely limited to moist fine-textured soils on areas of ground moraine during this warm interval (Kapp 1999). Hardwood swamp forests comprised of *Ulmus* and *Fraxinus* were probably restricted to wet, low-lying sites near lakes (Kapp 1999).

During this warm/dry mid-Holocene interval, the forest tension zone shifted northward in the Lower Peninsula. The tension zone, reached its furthest northern extent by about 6000 cal yr BP (Webb et al. 1983). The tension zone is an ecotone between the mixed-*Quercus* forests and *Fagus-Acer* forests of the southern Lower Peninsula and the mixed coniferous-deciduous forests dominated primarily by *Pinus*, of the northern Lower Peninsula. Several paleoecological records for the Lower Peninsula document this northerly shift in the tension zone (Held and Kapp 1969; Jones and Kapp 1972; Ahearn 1976b; Kapp 1978; Manny et al. 1978; McMurray et al. 1978; Lay 1979; Kapp et al. 1990; Kapp 1999).

The warm dry interval ended by 3,200 cal yr BP in the Lower Peninsula, as the climate became more cool and moist. Meanwhile, the cool and moist climate in the Upper Peninsula continued. In response to the continued trend of increased moisture and cooler temperatures, several taxa including, *Betula*, *Tsuga*, *Acer* spp., and *Fagus* (in the eastern half) all increased in abundance in the Upper Peninsula (Woods and Davis 1989; Jackson and Booth 2002).

Mixed *Quercus* forests continued to dominate the southern two-thirds of the Lower Peninsula until 3,200 cal yr BP. At this time, the trend of northward deciduous forest expansion reversed in response to the cooler temperatures and increased moisture. The tension zone moved southward in the Lower Peninsula of Michigan (Webb et a.l 1983). *Fagus* and *Acer* increased in abundance as *Quercus* decreased in abundance. In much of the southern Lower Peninsula, *Quercus* forests became less common, but remained a significant forest type in the mosaic dominated by *Fagus-Acer* forests and, to a lesser extent, swamp hardwood forests of *Ulmus* and Fraxinus (Kapp 1999).

The expansion of the mesic *Fagus-Acer* forests and corresponding decline of the mixed *Quercus* forests after 3,200 cal yr BP has been documented in the pollen records from several sites in the Lower Peninsula, although the timing of this transition was variable. Mild conditions were documented in the northern Lower Peninsula at Lake 27, with the expansion of *Fagus*, *Tsuga*, *Acer* spp., and *Betula* after 3,200 cal yr BP (Bernabo 1981). This trend was evident later at Wintergreen Lake in the southeast Lower Peninsula where just after 2,000 cal yr BP, *Quercus* pollen percentages declined and *Fagus* pollen percentages increased. The increase in abundance of *Fagus* was interpreted as a response to increased precipitation, which encouraged the expansion of the mesic *Fagus-Acer* forests, including sub-dominants *Acer* and *Ulmus* (Manny et al. 1978). At

Chippewa Bog near Saginaw Bay, similar trends were evident, beginning at 1900 cal yr BP until 1150 cal yr BP, where *Fagus* and *Pinus* (Diploxyon) pollen percentages both increased concurrently, with decreased abundance of *Quercus* pollen (Bailey and Ahearn 1981). At Crystal Lake, located within the tension zone, *Pinus* pollen percentages began to increase and peak at 1450 cal yr BP, concurrent with a decrease in *Quercus* pollen percentages (Kapp et al. 1990).

Fluctuations in the location of the forest tension zone and evidence for widespread fire were detected much later, around 600 cal yr BP, at four sites: Demont Lake; Vestaburg Bog; and the "Olson" and "Tyler" sites, all located within the central Lower Peninsula (Kapp et al. 1975). Four main charcoal peaks were detected in the records from Demont Lake, as well as from the Olson and Tyler sites. A radiocarbon date of 640 ± 130 B.P was obtained from organic fibrous muck associated with the uppermost charcoal peak, although no mention was made of any corrections. An increase in the abundance of *Pinus* pollen was evident in the pollen records immediately after the charcoal peak and was concurrent with a decrease in the pollen percentages of mesophytic hardwoods such as *Acer* spp., *Fagus*, and *Ulmus*. This evidence suggests that forest fires occurred periodically in the Pine River watershed and had "sufficient ecological impact on the region to have caused vegetational changes which were recorded in pollen diagrams" (Kapp et al. 1975: pg 18).

It is evident that the forests within the tension zone have fluctuated greatly since the last documented shift of the ecotone south, at 3,200 cal yr BP, although relatively little is known about the nature of these changes. Further research into the changes within the forest tension zone since its last major documented shift, would not only fill a gap in the paleoecological record for the Lower Peninsula, but would provide details regarding the nature of ecotone change and forest dynamics.

3.1.2 Late Holocene Climatic Changes

Multiple proxy climate reconstructions provide the evidence for two climatic anomalies of 1 to 2°C variations in North American and Europe over the past 2,000 years (Bradley 1999; Bradley et al. 2003; Soon and Baliunas 2003). The first, known as the Medieval Warm Period or MWP (MWP) lasted from ~1000-800 cal yr BP (A.D. 1000-1200). This period of warm, dry summers, and mild winters was initially detected by Lamb (1965) mainly from analysis of historical anecdotes and paleoclimate data from Western Europe. Lamb (1965) estimated that the MWP was 1 to 2°C higher than average (1900 to 1939). The presence of a Medieval climatic anomaly is not evident in many records from Europe and elsewhere in the world, leaving its existence somewhat controversial (Bradley et al. 2003). This controversy is confounded by the lack of well-calibrated data sets with decadal or higher resolutions as well as inconsistencies among records (Bradley et al. 2003). Therefore, it is generally not known whether the MWP was a primarily local or North Atlantic phenomena, or whether it was experienced world-wide (Bradley 1999).

More extensive and geographically widespread evidence is present in a variety of climate proxies, including ice-cores, tree rings, and historical records, for the Little Ice Age (LIA) which lasted from about 600 to 100 cal yr BP (A.D. ~1400-1900). During this interval temperatures were 1 to 2°C colder on average than modern; it was one of the coldest periods in the last 12,000 years (Bradley 1999; Bradley et al. 2003).

Evidence for both of these climatic anomalies, the LIA and the MWP, has been detected in pollen records from the Great Lakes region and elsewhere in eastern North America (Russell et al. 1993; Pederson et al. 2005). Bernabo (1981) reconstructed the climate of the northern Lower Peninsula of Michigan over the last 2,700 cal yr BP based on pollen records from three sites located in the north-western corner of the Lower Peninsula (Bernabo 1981). Chronological control was established based on three radiocarbon dates, obtained from dating the organic sediment itself. These dates were corrected for the ancient carbon effect using the *Ambrosia* method. This research detected 1.5°C fluctuations in temperature over the past 2,700 years, including a slight warm interval, interpreted as the MWP, lasting several centuries between 1000-700 cal yr BP (A.D. 1000–1300) where average temperatures approximately reached the 1931-1960 mean. Bernabo's (1981) study also reconstructed a cool episode he interpreted as the LIA from around 700-150 cal yr BP (1300-1850 A.D.), in which the average temperatures were 1°C below the 1931-1960 mean.

A slight warming of around 0.5°C after the end of the LIA was also evident in the records (Bernabo 1981). The general timing and nature of climate change over the past 2,000 years, as detected for the northern Lower Peninsula of Michigan (Bernabo 1981), parallel climatic records from elsewhere in eastern

North America. Other research provides evidence of wetness in the Midwest for several centuries around the time of the MWP, at 900 cal yr BP, in contrast to dryness in the Great Plains and western North America during the MWP (Stine 1998; Soon and Baliunas 2003). Two climatic anomalies were detected in pollen records for the lower Hudson Valley in New York, one associated with the MWP from 1200-700 cal yr BP (A.D. 800-1300) and the second with the LIA from 600-150 cal yr BP (A.D. 1400-1850) (Pederson et al. 2005).

A limited number of meso-scale pollen studies in the Great Lakes region and eastern North America have detected changes in vegetation communities associated with these climate fluctuations during the past 2,000 years. Specific changes in vegetation are less evident in pollen records in the Great Lakes region, for the MWP than for the LIA. Bernabo (1981) found increases in the pollen abundance of *Pinus*, *Quercus*, and *Betula* pollen concurrent with declines in the abundance of *Picea* and *Tsuga* pollen, beginning around 1000 cal yr BP, at three lakes in the northern Lower Peninsula of Michigan. Gajewski (1987), using principal components analysis, detected coherent changes in the pollen records associated with the MWP (1200-1000 cal yr BP) from multiple lakes ranging from Maine to Minnesota.

Meso-scale pollen research has detected vegetation change associated with the LIA including: 1) expansion of *Fagus grandifolia* beyond its previous western limit in Upper Michigan (Davis and Botkin 1985); 2) population increase in *Tsuga canadensis* within the last few centuries in the northern Lower Peninsula of Michigan (Bernabo 1981); 3) increases in the abundance of *Tsuga* *canadensis* and *Betula lutea* in Wisconsin (Swain 1978); 4) development of the *Acer-Tilia* forests in southern Minnesota (Grimm 1983); and 5) a decline in *Fagus* at its northern range limit, a decline in *Pinus* at its northern limit and southward expansion, and peaks in *Betula* and *Populus* in between the decline in *Fagus* and rise in *Pinus,* all in central Ontario (Campbell et al. 1991).

Several vegetation changes have been detected in meso-scale pollen records for eastern North America, over the past 2,000 years. In the lower Hudson Valley of New York, Pederson et al. (2005) interpreted that *Pinus* and *Carya* increased in abundance while *Quercus* declined in abundance during the MWP from 1200-700 cal yr BP (A.D. 800-1300). At the same time, fire events increased dramatically concurrent with fluctuations in the abundances of drought-sensitive species (*Tsuga*, *Betula*, *Alnus*)(Pederson et al. 2005). Also in the lower Hudson Valley of New York, significant increases in the pollen percentages of *Picea* and *Tsuga* were associated with the LIA from 600-150 al yr BP (1400-1850 A.D.) (Pederson et al. 2005). In central and northern New England, *Picea* and *Pinus* pollen percentages increased consistently around 600-500 cal yr BP (1400 A.D.) during the LIA (Russell et al. 1993). From these records, it is evident that the MWP and LIA were experienced in eastern North America and were accompanied by significant vegetation changes.

Results from Bernabo's (1981) research and others (Stine 1998; Soon and Baliunas 2003) suggest that the climate during the past few thousands years varied at least within 1 to 2°C and that both the MWP and LIA were experienced in most of the eastern half of North America. Therefore, the Lower Peninsula of

Michigan should have also experienced similar climatic fluctuations, although research into climatic change during this time period has not been directly conducted in most of the Lower Peninsula of Michigan. Climatic variations of 1 to 2 °C should have resulted in shifts in forest communities, especially with regard to the forest tension zone in the central Lower Peninsula of Michigan.

Results from previous pollen studies which examined climatic change during the past few thousands years at decadal to centennial scale resolution, i.e. the meso-scale domain, have proved extremely useful. Results from such research have been applied in modeling efforts to predict future climatic change, have been used to compare current climate changes with those of the recent past, and predict responses of vegetation to global warming (Walker et al. 2002). The utility of these studies in such efforts emphasizes the importance of meso-scale pollen studies. More meso-scale research into vegetation and climate change is needed to better understand the magnitude of current climate change as well as to better predict the impact of future climate change. This type of research is particularly important in the Great Lakes region, a highly forested region, where the climate is predicted to change significantly, becoming 2 °C warmer and wetter, with 15-20% more precipitation, by the end of the 21st century (Sousounis and Bisanz 2000).

3.1.3 Study Area

Two major forest ecotones are present in the Great Lakes region today, the northern one is between the boreal coniferous forest and the Laurentian mixed forest, and the southern one is between the Laurentian mixed forest, and the eastern broadleaf forests (Figure 3.1). This southern ecotone, referred to as the tension zone, spans from southern Ontario to Minnesota (Andersen 2005). This research focused on this ecotone in the central portion of the Lower Peninsula of Michigan. In the Lower Peninsula, Laurentian mixed forest north of the tension zone dominated by hemlock-white pine-northern hardwood communities transitions into the broadleaf forest of Eastern North America which is dominated by beech-maple and oak-hickory communities (Barbour and Billings 1988; Burns and Honkala 1990). Dominant species south of the tension zone include *Acer saccharum* (sugar maple), *Fagus grandifolia* (American beech), and several species of *Quercus* (oak) and *Carya* (hickory). North of the zone, coniferous species such as *Pinus strobus* (white pine), *Pinus resinosa* (red pine), and *Tsuga canadensis* (hemlock) increase in abundance and with *Acer saccharum* (sugar maple) and *Betula lutea* (yellow birch) forming a mixed coniferous-deciduous forest. Many arboreal and herbaceous species meet their southern or northern range limits in the central part of the Lower Peninsula (Voss 1972).

The spatial arrangement and cause of the forest tension zone in the Lower Peninsula has been debated in the literature (McCann 1979; Medley and Harman 1987; Dodge 1995). While the delineation of the zone varies (Schaetzl 1991), the tension zone is typically described as a 95-km wide belt (Potzger 1948) whose center may be broadly approximated by the 8°C (47°F) isotherm of mean annual temperature (Barnes and Wagner 1981). Some authors refer to the tension zone as an abrupt ecotone (Medley and Harman 1987), while others refer to it as a diffuse vegetation boundary (Elliot 1953; Brewer 1982). Climate is assumed to be the broad-scale influence on the location of the tension zone, while at finer spatial scales edaphic controls are more important (Barnes and Wagner 1981; Medley and Harman 1987; Dodge 1995). Coarse-textured soils are more common in the northern part of the Lower Peninsula on which coniferous species are more successful, while in the southern part deciduous trees out-compete coniferous trees on loamy soils.

The climate of the Lower Peninsula of Michigan is classified as humid continental, although temperature and precipitation vary considerably. The annual mean temperature in the state ranges from 10°C in the Lower Peninsula to 4.4°C in the Upper Peninsula (Eichenlaub et al. 1990). Within the study area itself, the average maximum July temperature is 25.5 °C and the minimum average January temperature is -11°C (data for Mount Pleasant, Michigan) (Hoare 2005). The northern part of the Lower Peninsula experiences approximately 70 growing degree days while the southern Lower Peninsula experiences 160 to 170 days (Schaetzl and Isard 2002). Precipitation varies across the Peninsula as well; in the Lower Peninsula of Michigan annual mean precipitation ranges from 91.4 cm in the southwest to 68.5 cm in the northwest. The presence of the Great Lakes has a moderating effect on local climates along shorelines. Areas slightly inland from the shorelines commonly experience increased winter snowfall in the form of lake-effect snow. The snow showers produced by lake effect snowfall can account for 30% to 60% of the total snowfall in areas that fit the criteria for lake effect conditions (Schaetzl and Isard 2002).

3.2 Methods

3.2.1 Site Selection

The characteristics of a lake, i.e. size, shape, and landscape position, determine the level of detail that can be resolved in vegetation reconstruction through pollen analysis (Jacobson and Bradshaw 1981). Therefore, three lakes were chosen for the research based on the following criteria: 1) each lake must represent a different presettlement forest community relative to the forest tension zone as mapped by (Comer et al. 1995b) (Laurentian mixed (north), transitional (central), and broadleaf (south); 2) the lakes must follow a north-to-south transect, avoiding lake-effect climate to the west and the fine-textured, wet soils of the glacial lake plain to the east near Saginaw Bay; 3) the lakes must be between 60 and 100 km apart in order to minimize overlap of pollen rain sources (Jacobson and Bradshaw 1981), and yet be close enough (not more than 100 km apart) to document any shifts in the ecotone; and 4) the immediate area around the lakes must have similar soils because soil texture may directly influence forest composition at fine scales (Medley and Harman 1987) and the soil texture must be typical of those found in the tension zone. A similar site selection strategy was successfully utilized in a study detecting Holocene shifts of the Boreal-Great Lakes forest ecotone in northern Ontario (Lui 1990).

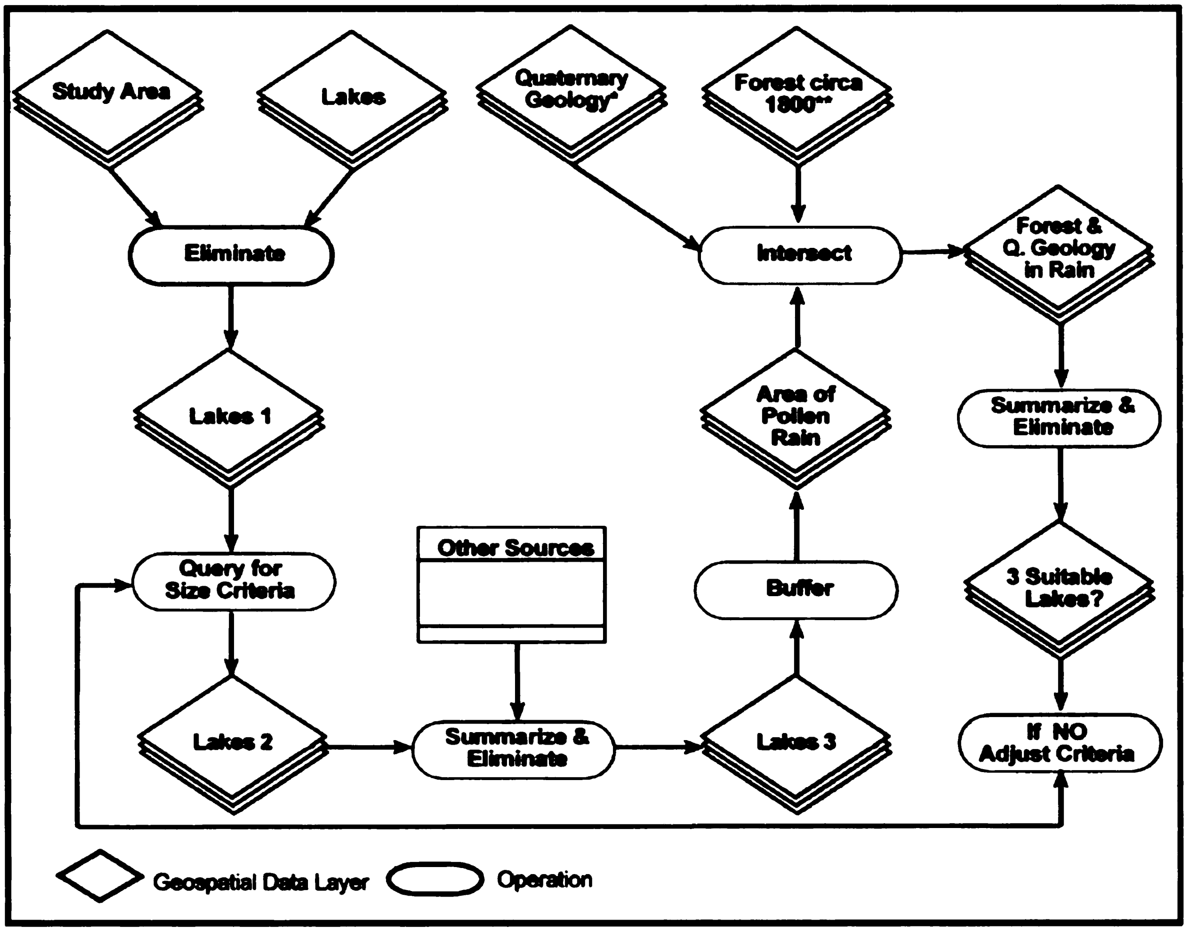

Figure 3.2 Flow diagram of data sets and methodology used to select three suitable lake sites. *Quaternary Geology (Farrand and Bell 1982); ** Forest ca 1800 (Comer et al. 1995b).

Additionally, the individual lake basins were chosen based on the following criteria: 1) lakes must be approximately 40 to 120 hectares in size to insure that the pollen grains collected represent a radius of approximately 27-km surrounding the lake (Jacobson and Bradshaw 1981; Bradshaw and Webb 1985; Sugita 1994); 2) the lakes must have no major inlets in order to minimize deposition of pollen grains from upstream areas; 3) the lakes must have similar bathymetry with a minimum depth of approximately 8 m, in order to minimize variation in pollen grain deposition, bioturbation, and sediment focusing; and 4) the lakes must not have experienced major anthropogenic disturbances, such as dredging, which would remove or disturb the pollen record. In several cases, local lake associations as well as the Department of Environmental Quality were contacted to determine the degree of disturbance at the lake site.

Because the criteria above involved the consideration of multiple spatial factors, a geographic information system (GIS) framework was utilized in order to analyze all possible lakes for the above criteria. The use of a GIS to select sites for paleoecological research was unique in this study and allowed for the selection of lake sites based on multiple spatial criteria. The procedure used to select the lake sites is outlined in Figure 3.2. All suitable lakes were then buffered based on their size to determine the area of pollen rain. Both the presettlement forest composition and Quaternary geology were calculated separately for each lake's pollen rain area. Forest composition was determined based on a spatial data set of the presettlement vegetation of Michigan developed by the Michigan Natural Features Inventory (MNFI) which was acquired from the Michigan Center for Geographic Information (MCGI) (Comer et al. 1995) (Table 3.1). Because these maps were generated through interpretation, not quantitative analysis of the Public Land Survey data by MNFI, the data presented in Table 3.1 are estimates. A spatial data set of Quaternary geology was also acquired MCGI (Farrand and Bell 1982) (Table 3.1). The lakes were then evaluated for both nearby presettlement forest composition and Quaternary geology. If three suitable lakes were not identified, the size criteria were adjusted and the procedure was performed again.

Following this methodology, three suitable lakes were chosen for: 1) north of tension zone: Hicks Lake in Osceola County (44°2'59.59N, 85°17'53.51W), 62.7 hectares with a maximum depth of 10.05 meters; 2) within the tension zone: Cowden Lake in Montcalm County (43°21'38.71N, 85°22'28.88W), 51.7 hectares with a maximum depth of 15.24 meters; and 3) south of the tension zone: Morrison Lake in Ionia County (42°51'35.11N, 85°12'36.26W), 131 hectares with a maximum depth of 10.9 meters. The three lakes are aligned in a north to south transect in the center of the study area and each lake represented different forest communities surrounded by similar parent material (Figure 3.3 and Table 3.1). The individual lake basins are illustrated in Figure 3.4.

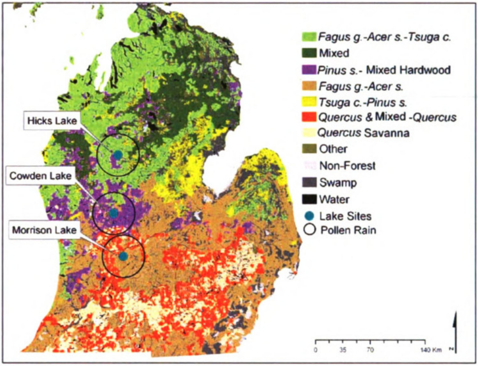

Figure 3.3 Location of three Lake sites, Hicks Lake, Cowden Lake, Morrison Lake, chosen for pollen analysis and forest composition in Lower Michigan circa 1800 (Comer et al. 1995).

Table 3.1. Quaternary geology (Farrand and Bell 1982) and forest types (ca A.D. 1800) (Comer et al. 1995) within the pollen rain area. Numbers listed are percentage of area.

	Hicks L.	Cowden L.	Morrison L.
Quaternary Geology			
Coarse-textured glacial till	15	17	11
End moraines of coarse-textured till	39	43	12
End moraines of fine-textured till	2	3	6
End moraines of medium-textured till	0	2	16
Fine-textured glacial till	11	3	8
Medium-textured glacial till	0	2	26
Glacial outwash sand and gravel and postglacial alluvium	30	30	21
Ice-contact outwash sand and gravel	1	0	0
Lacustrine sand and gravel	1	0	0
Water	1	1	0
Forest Type circa A.D. 1800			
Fagus grandifolia–Acer saccharum	0	7	40
Fagus grandifolia–Acer saccharum-Tsuga canadensis	60	9	0
Pinus strobus-Mixed Hardwoods	10	43	0
Pinus strobus-Quercus	0	11	1
Quercus-Carya	0	4	30
Other *Quercus*	0	7	10

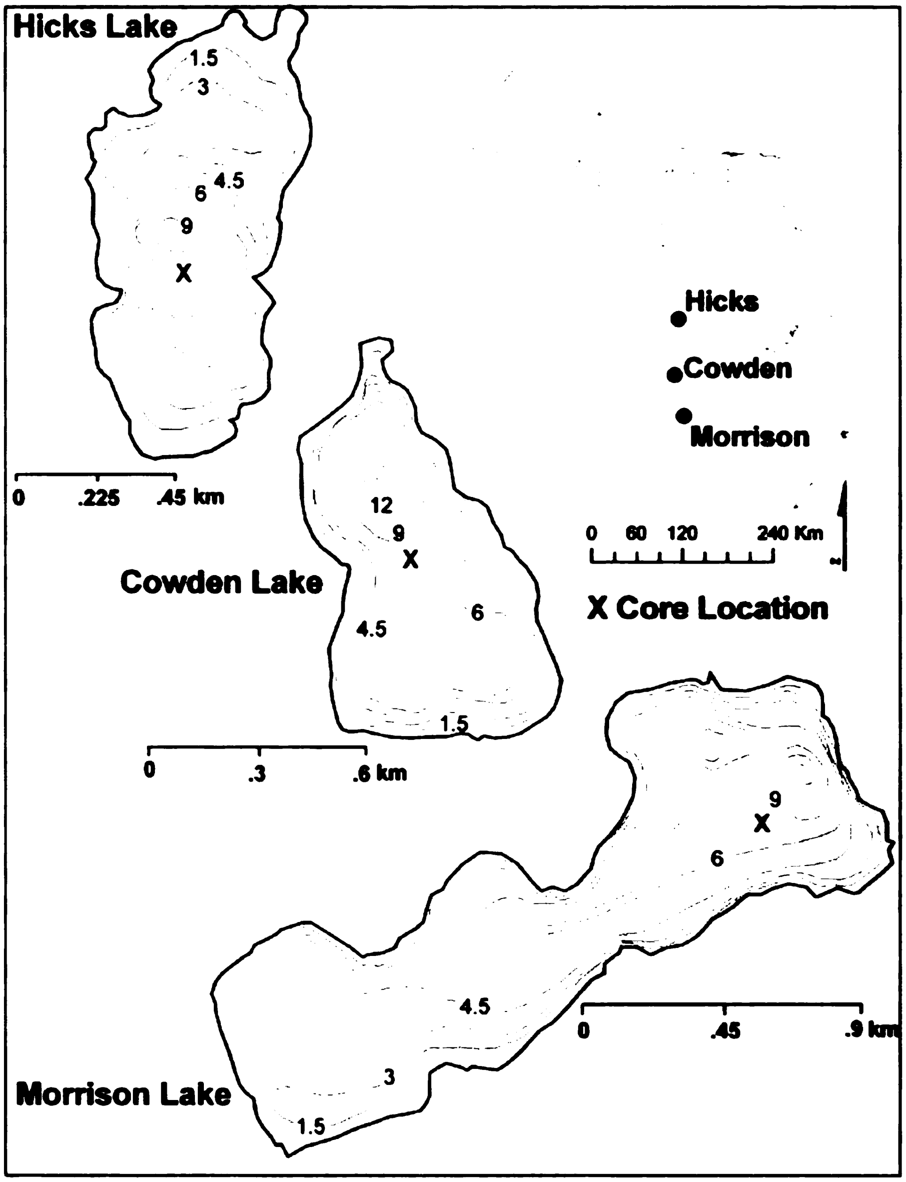

Figure 3.4 Maps of each individual lake basin showing bathymetry in meters and the specific coring location.

3.2.2 Field Sediment Coring

Lake sediments were collected from coring sites in the winter of 2004, using the ice surface as a coring platform. The actual site where the coring devices would be employed was based on examination of bathymetric maps of the individual lake basins upon arrival at the site. Coring sites were chosen which had a maximum depth of 8.5 m, the maximum obtainable depth of the coring device, and at a location with a relatively flat bathymetry. Areas with steep-sided rises were avoided because sediment on adjacent slopes can often become displaced and slough down. Also, because two different devices were used to retrieve the sediment, a site with consistent bathymetry, for at least a total of 7 m radius, was required to insure that both cores were taken from the same depth.

Once the chosen site was reached, several holes were drilled in the ice approximately 25 cm in diameter, and the water depth was measured at several locations surrounding the coring site. Then an appropriate coring site was chosen. Lake sediment cores were collected from Hicks Lake, Cowden Lake, and Morrison Lakes from the positions indicated in Figure 3.4. The upper 1 m of sediment was collected with a freeze-wedge coring device. The freeze wedge device was designed by myself and based on an earlier model (Huttunen and Merilainen 1978). It was constructed from welded steel. The device consisted of a rectangular box, approximately 1-m in length, 30 cm wide, and 5 cm deep, with a triangular keel at the bottom of the device which is the first part to cut into the sediment, and a lid attached to the top. At the coring site, the device was filled with dry ice pellets and left to chill on the ice for approximately 20 minutes while a hole of appropriate diameter (at least 60 cm) was drilled or chain sawed through the ice. The exact water depth was then measured. Ropes were attached to the lid of the device which was then released through the water column and stopped at the appropriate depth in the sediment where it was left for approximately 30 minutes while the sediment froze to the outer face of the box. The device was the then retrieved to the surface and sampled in the field.

The lower sediment (beyond one meter) was retrieved using a Livingston ™ coring device (Wright Jr 1967). The cores collected by the freeze core and the Livingston device were taken within 5 meters of each other where the depth to the sediment water interface was similar. A coring platform was placed on the ice over the coring site and multiple sections of aluminum casing (in 6 foot lengths) were coupled together and lowered through the water column. The casing, once lowered and secured to the platform, assured that the Livingston device was retrieving sediment from the same hole. Cores were collected from the same hole consecutively in one meter lengths until the device was not able to penetrate the sediment due a change in consistency (sand or till), or until all extension rods were in use. Therefore, the depth at which the core was taken was limited by the number of coring rods (total of 8.5 m).

3.2.3 Radiocarbon Dating and Chronology

The sediment cores were sampled for radiocarbon dating (^{14}C) at several depths along the cores. Core sediment was sieved through multiple mesh sizes ranging from 212 µm to 450 µm in order to obtain upland plant macrofossils or charcoal for radiocarbon dating. All retrieved macrofossils were taxonomically identified by Dr. Catherine Yansa in the Pollen Laboratory at Michigan State University, dried, and weighed. Because none of individual terrestrial materials recovered were not of sufficient mass for ^{14}C dating using the accelerator mass spectrometry (AMS) technique (Gillispie 1984), bulk organic sediment was dated using AMS.

When constructing radiocarbon chronologies, AMS dating of upland plant taxa macrofossils and/or charcoal is highly preferable over the dating of bulk sediment. However, in this case, the sediment did not contain enough upland plant macrofossils or charcoal for AMS dating. Therefore, AMS dates were obtained from the bulk organic sediment. Despite the numerous problems associated with the AMS dating of bulk organic sediment, dates obtained from bulk sediment can still be used to construct a chronology if the problems are addressed. The most problem is that the resulting dates are spuriously old because of the incorporation of ancient carbon into the bulk sediment (MacDonald et al. 1991).

Table 3.2 Radiocarbon dates (^{14}C) dates from cores taken at Hicks Lake, Cowden Lake, and Morrison Lake, Michigan. All dates reported in text are calibrated and in years B.P. The material dated for all samples was organic bulk sediment.

					Sedimentation	
Sample Depth (cm)	**Lab No.**	**^{14}C date (B.P. ± SD)**	**Correction Factor**	***Ambrosia* Corrected Date**	**Depth (cm)**	**Rate (cm/yr)**
Hicks Lake						
H/FW 65	195939	646 ± 40^{a}	492	154	0 – 65	.422
H/A/D1 91	114477	1349 ± 35^{b}	492	857	65 – 91	.036
H/A/D2 143	194252	3206 ± 40^{a}	492	2714	91 – 143	.028
Cowden Lake						
C/FW 65	195938	562 ± 40^{a}	408	154	0 – 65	.422
C/A/D1 91	1144776	1231± 35^{b}	408	823	65 – 91	.038
C/A/D2 140	194253	2954 ± 40^{a}	408	2546	91 – 140	.028
Morrison Lake						
M/FW/ 61	195937	644 ± 40^{a}	490	154	0 – 61	.396
M/B/D2 111	114475	2490 ± 35^{b}	490	2000	61 – 111	.027
M/B/D2 140	194251	2545 ± 40^{a}	490	2055	111 – 140	.52

.. [a] Dates obtained from Beta Analytic Inc. Miami FL, USA.

[b] Dates obtained from CAMS: Center for Accelerator Mass Spectrometry, Lawrence Livermore National Laboratory, USA.

In all, three radiocarbon AMS dates were obtained for each core from organic sediment samples (0.5 cm^3) (Table 3.2). Six samples were dated at the Beta Analytical Lab and three samples were dated at the Center for AMS, Lawrence Livermore National Laboratory (Table 3.2). The dates from Beta Analytical lab were reported as calibrated at their facility while the dates from Lawrence Livermore were reported without calibration; therefore I calibrated them using the CALIB 4.3 software (Stuiver and Reimer 1993; Stuiver and Braziunas 1998). All dates were rounded to the nearest decade and reported in calendar years before present (cal yr BP). Dates for individual pollen sub-samples were estimated by linear interpolation between the calibrated dates, with the top sediment considered to be 0 cal yr BP.

A common problem resulting from the dating of bulk organic sediment is that the resulting age is spuriously old (MacDonald et al. 1991; Bjorck and Wohlfarth 2001). This problem results from a deficiency in ^{14}C in the sediment relative to the proportion of the isotope in the atmosphere at the time of deposition. Sources of ^{14}C-deficient carbon in lake sediments includes detritus from older deposits, the dissolution of carbonate rocks, inputs of ancient ground water (the hard water effect), and gaseous emission of ^{14}C-free CO_2 from volcanoes (MacDonald et al. 1991). Errors may also be caused from living organisms assimilating ^{14}C-deficient carbon from environments (reservoir effect), which are in disequilibrium with atmospheric ^{14}C concentrations. Evidence from previous studies suggests that the ^{14}C reservoir deficiencies in limnic organics can be minimized by dating sediment samples with high organic content

(MacDonald et al. 1991). All of the samples used in this study had a high organic matter content.

In order to mediate the erroneously older dates resulting from the dating of bulk sediment, I employed the *Ambrosia* correction method (Grimm 1983). I adjusted all of the radiocarbon dates by the difference between the radiocarbon date for the sample depth containing the *Ambrosia* pollen percentage spike, which signifies the onset of Euro-American logging and agriculture in the area, and the known historic date of these events. The onset of this activity in the study area began around A.D. 1830 (175 cal yr BP) (Lewis 2002). The determined correction factor was 490 years for Morrison Lake and Hicks Lake, while the correction factor for Cowden Lake was 408 years. While this approach does assume that the correction was constant with sediment-core depth, which was most likely not the case, it is the best method available and has been used successfully in several other pollen studies (Manny et al. 1978; Bernabo 1981; Grimm 1983).

3.2.4 Pollen Analytical Method

Samples for pollen analysis (1 cm^3) were collected at 2-cm intervals from along the depths of both the freeze-wedge cores and the Livingston cores retrieved from the three lakes. The total numbers of samples used in the analysis from each lake were: Hicks (35), Cowden (26), and Morrison (32). Pollen grains were concentrated using a series of standard procedures (Faegri and Iverson 1975) with additional steps using sodium pyrophosphate rinses to remove the clay fraction (Bates et al. 1978) and sieving (140 μm) to remove coarse sand and any macrofossils prior to the hydrofluoric acid step (Shane c 1998). Each pollen sample was counted under a light microscope at X400 magnification in regularly spaced transverses. Between 350 and 500 grains of upland plant taxa were identified and counted for each sample. All other aquatic pollen and spores were also identified and counted. Identification of pollen grains was based on taxonomic keys developed for the Great Lakes region (McAndrews et al. 1973; Kapp 2000) and a modern reference collection housed in the pollen laboratory at Michigan State University.

3.2.5 Data Analysis

Pollen sums were calculated for each of the three lakes using *Tilia*™ software (Grimm 1993). Sums included all upland plant taxa and herbaceous species but did not include counts of spores and aquatics. Biostratigraphic diagrams were constructed using *Tilia*™ and *Tilia* Graph ™ software, based on percentages of each taxa and radiocarbon chronologies (Grimm 1993). The pollen data sets were then analyzed with stratigraphically constrained cluster analysis using no transformations and Euclidean distances with CONISS ™ software (Grimm 1987). The resulting dendrograms were then used as a basis for identification of vegetation zones for each site.

The data were also ordinated with principal components analysis (PCA), an indirect ordination method which reduced the dimensionality of the data, using PC-Ord ™ software (McCune and Mefford 1997). In preliminary analyses, the pollen data sets for each lake were ordinated with both detrended correspondence analysis (DCA) as well as PCA, in order to determine the more appropriate method. The first two axes for the PCA explained a higher percentage of the variance within the data set than the DCA, indicating that the data were linear and PCA was more appropriate for this analysis. The distortion associated with PCA was not a severe problem (McCune and Grace 2002). The ordination of the pollen data helped to establish pollen zones and explore changes in the diagrams over time. After elimination of rare types, a total of 21 pollen types were used for the ordination of data for Hicks Lake and Cowden Lake while 8 pollen types were used for the Morrison Lake data (Table 3.3).

Table 3.3 List of pollen types used in principal components analysis.

Pollen Type	Hicks L	Cowden L.	Morrison L.
Pinus undiff.	x	x	x
Picea	x	x	x
Abies	x	x	
Cupressaceae	x	x	x
Larix	x	x	
Tsuga	x	x	x
Acer undiff.	x	x	x
Alnus undiff.	x	x	
Betula	x	x	x
Ostrya	x	x	x
Carya	x	x	x
Fagus	x	x	x
Fraxinus undiff.	x	x	x
Juglans	x	x	x
Populus	x	x	x
Quercus	x	x	x
Salix	x	x	x
Tilia	x	x	x
Ulmus	x	x	x
Ambrosia	x	x	x
Poaceae	x	x	x
Chenopodaceae	x	x	x

3.3 Results

Three ^{14}C dates from each lake, Hicks Lake, Cowden Lake, and Morrison Lake, were used to generate chronological control for the paleoecological record (Table 3.2). The age-depth relationships are illustrated in Figure 3.5. The freeze-wedge core and the Livingston cores were correlated, for all three Lakes separately, using the depth down through the core from the sediment water interface which was identified on the freeze wedge. Sediment from all three lakes was consistently uniform, black, massive muck (sapric) with no visible laminations. After obtaining radiocarbon dates from all three cores, only the top two meters of the Livingston cores for each lake were used in this analysis, although several deeper cores were retrieved.

In the results and discussion sections of this dissertation all taxa are referred to by genus, unless the pollen taxa could be identified to species. In some cases, species within one genus are discussed together. For example, when all of the *Acer*-types are grouped the spp. designator is added to specify the grouping of genera.

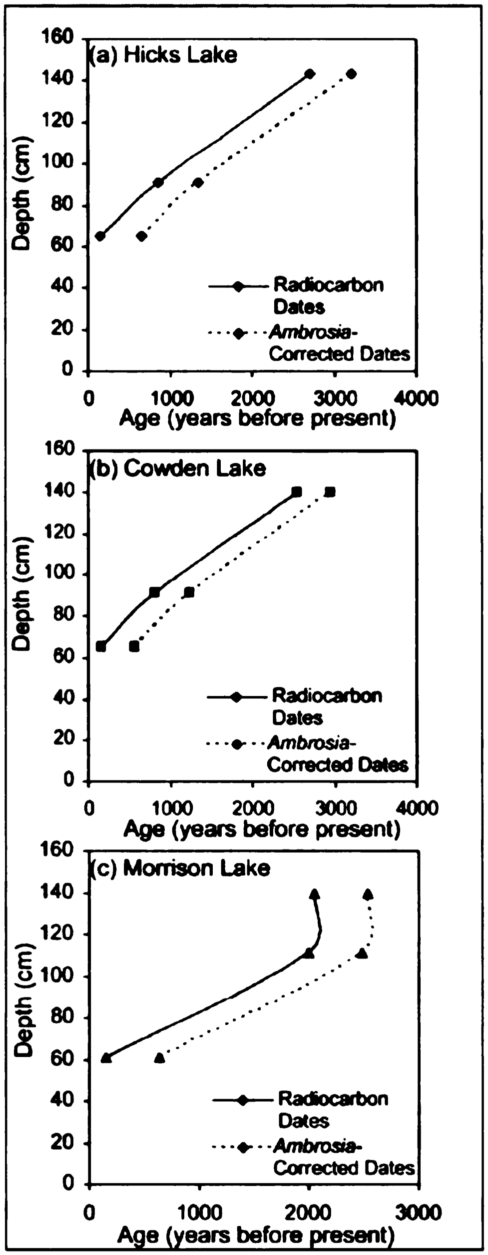

Figure 3.5 Age-depth relationships based on linear age model for the cores for the three study lakes (see text for detailed explanation).

3.3.1 Hicks Lake

The freeze core was 99 cm long and the Livingston core was 200 cm long. Sedimentation rates varied throughout the core, with the historic period having the highest rates (Table 3.2). The temporal resolution of the pollen samples varied throughout the core because of the various sedimentation rates. A total of

35 sub-samples were processed and analyzed based on the results from the radiocarbon dates and established chronology. The resolution at the top of the core, 0 – 50 cm, was 10 years between samples analyzed, while at the middle of the core, from 50 – 100 cm, the resolution was 50 – 100 years, and at the bottom from 100 to 200 cm, the resolution was 100 – 150 years.

3.3.1.1 Hicks Lake Pollen Zones

The pollen diagram for Hicks Lake was divided into a total of four total pollen assemblage zones (Figure 3.6).

H-I: 125 – 113 cm; *Pinus-Picea-Tsuga* (2100–1600 cal yr BP): This zone was characterized by relatively high pollen percentages of coniferous taxa. These taxa included both *Pinus* sections Haploxylon and Diploxylon, *Picea,* Cupressaceae, *Tsuga* (mostly likely *Tsuga canadensis*), and *Abies*; *Picea* and *Pinus* spp. had the highest values at approximately 30% and 15%, respectively. *Fagus* (most likely *Fagus grandifolia*) and *Quercus* had similar percentages. *Quercus* pollen percentages rose to slightly more than *Fagus* pollen percentages in the middle of the zone around 1950 cal yr BP. *Betula* pollen values slowly increased in this zone.

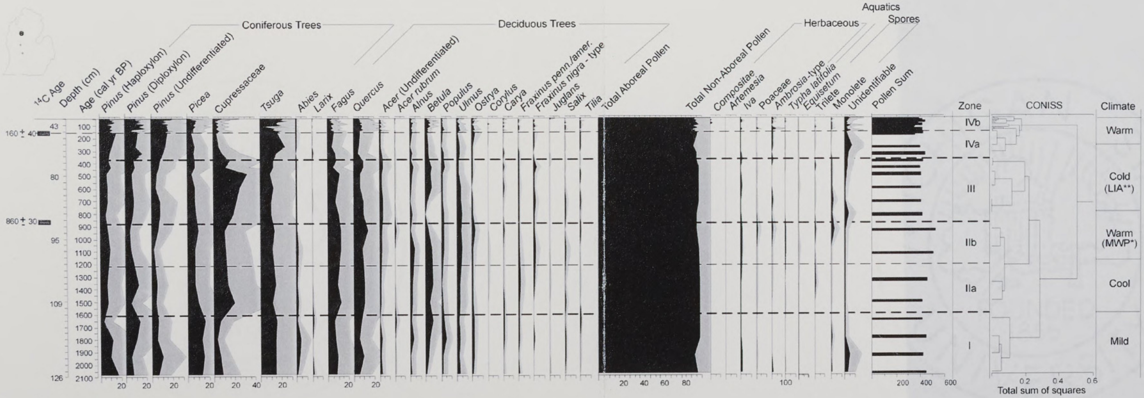

Figure 3.6 Fossil pollen diagram for Hicks Lake (north). Pollen percentages are plotted against depth.

H-II: 113 – 89 cm; (1600–880 cal yr BP):

H-IIa: 113 – 105 cm; *Pinus*-Cupressaceae-*Tsuga* (1600–1200 cal yr BP): In this sub-zone the pollen values of *Pinus* spp., *Picea*, *Tsuga*, and *Abies* decreased at the beginning of the zone. *Pinus* spp. pollen values increased again towards the end of the zone. Cupressaceae pollen percentages increased dramatically at the beginning of the sub-zone to 19% and then trailed off towards the middle of the zone. Both *Fagus* and *Quercus* pollen abundances increased to over 9% and then remained steady. *Betula* pollen values slightly decreased and then increased towards the end of sub-zone. *Ulmus* and *Fraxinus pennsylvanica/americana*-type pollen values increased slightly.

H-IIb: 105–89 cm; *Pinus-Tsuga*-Cupressaceae-*Quercus* (1200–880 cal yr BP): In this sub-zone *Pinus* spp. pollen percentages again began to decline while *Picea* pollen percentages remained steady. *Abies* pollen values also slightly decreased, while Cupressaceae and *Tsuga* pollen values both remained steady at approximately 11%. *Fagus* pollen values were relatively stable in this zone at approximately 12%. *Betula* pollen values remained relatively high while *Ulmus* and *Fraxinus nigra*-type pollen values steadily increased. *Acer rubrum* and *Acer* spp., *Ostrya*, *Alnus,* as well as Poaceae and *Ambrosia*-type pollen values also increased towards the end of the sub-zone.

H-III: 89–73 cm; *Cupressaceae-Pinus-Tsuga* (880–380 cal yr BP): *Pinus* spp. pollen slightly increased at the beginning of the zone and then began to decline towards the end while *Picea* pollen values remained relatively stable until the end of zone where values decreased. Cupressaceae pollen values dramatically increased throughout the zone and peaked towards the end at 31% followed by a slight decrease. *Tsuga* pollen values remained relatively stable at approximately 12% while *Abies* pollen values remained very low at less than 1%. *Fagus* pollen percentages were variable. *Quercus* pollen percentages exhibited trends exactly opposite to *Fagus* pollen percentages in that the values remained relatively high at the beginning of zone at approximately 11%, then decreased in the middle, and at the very end of the zone it rose again. *Acer* pollen values rose at the beginning of the zone and declined in the middle. *Betula* pollen percentages began to rise dramatically towards the middle of the zone and reached 6% and remained high throughout the rest of the zone while *Ulmus* pollen values began high at 4% and decreased steadily throughout the rest of the zone. Pollen values for *Ostrya*, *Carya*, *Populus*, and both *Fraxinus* types increased towards the end of the zone.

H-IV: 73–0 cm; (380–0 cal yr BP):

H-IVa: 380–65 cm; *Pinus-Tsuga* (380–150 cal yr BP): *Pinus* spp. pollen percentages increased in the zone to a collective 43% while *Picea* pollen values decreased to 4%. Cupressaceae pollen values dramatically declined at the beginning of the zone and then continued to decline to al low of 3%. *Tsuga* pollen percentages increased dramatically in this zone, peaked in the middle at 24%, and then began to decline. *Fagus* and *Quercus* pollen values began by exhibiting opposite trends but both increased towards the end of the zone. *Fagus* pollen values rose in the beginning to 8% while *Quercus* pollen percentages were low at 5% in the beginning but rose at the end. *Acer* spp. pollen values also declined at the beginning of the zone. *Betula* and *Populus* pollen values began to decline in the zone while *Ulmus* pollen values rose, peaked in the middle, and then began to decline. *Ostrya* and *Fraxinus nigra* type pollen values began to increase towards the end of the zone.

H-IVb: 65–0 cm; *Ambrosia* (type)-*Tsuga* (150–0 cal yr BP): This zone was characterized by a decrease in most pollen types slightly after the peak in *Ambrosia*-type at 4%. *Tsuga* pollen values decreased at the beginning of the zone, indicating deforestation, but recovered towards the end of the zone. The other pollen type values were quite variable throughout the zone. An initial drop in most values at the beginning of this zone indicated deforestation and subsequent rises indicated recovery. This zone was distinguished by a peak in *Ambrosia*-type and other herbaceous species at the beginning

3.3.1.2 Hicks Lake Ordination

The ordination of pollen types and samples summarized changes in the Hicks Lake pollen diagram and illustrated the dynamics between pollen types and vegetation assemblages over time (Figure 3.7). The proportion of variance represented by each axis was measured by the covariance between Euclidean distances among samples units in the ordination and the relative Euclidean distances in the original space (McCune and Grace 2002).Axis one explained 71% of the variance while the second axis accounted for 11%. Together the axes explained 82% of the variance. Axis one on the pollen type ordination diagram (Figure 3.7a) separated the deciduous taxa *Fagus*, *Quercus*, *Acer* spp., and *Ulmus* from the coniferous taxa found in the center of axis one, *Tsuga*, *Pinus*, *Abies*, and *Picea*. Cupressaceae was isolated to the far right corner of the diagram. Herbaceous taxa, such as Compositae, *Ambrosia*-type, and Poaceae, which increased in the more recent samples, were found in the lower end of axis one. Axis two, which accounted for much less of the variance, separated *Abies* and *Picea* with *Abies* placed at the top of axes two. Axis two also isolated *Juglans* to the bottom of the axis. In the ordination diagram of samples (Figure 3.7b) the level of separation on each axis represented shifts in vegetation. Axis one separated samples based on the percentages of coniferous types, specifically *Pinus* spp. and Cupressaceae. Axis two separated samples based on the percentages of *Picea*, *Tsuga*, and *Abies*. Zones H-I, H-II, and HIV were relatively distinct while H-III was spread out between two major clusters on axis one with a large gap in the center.

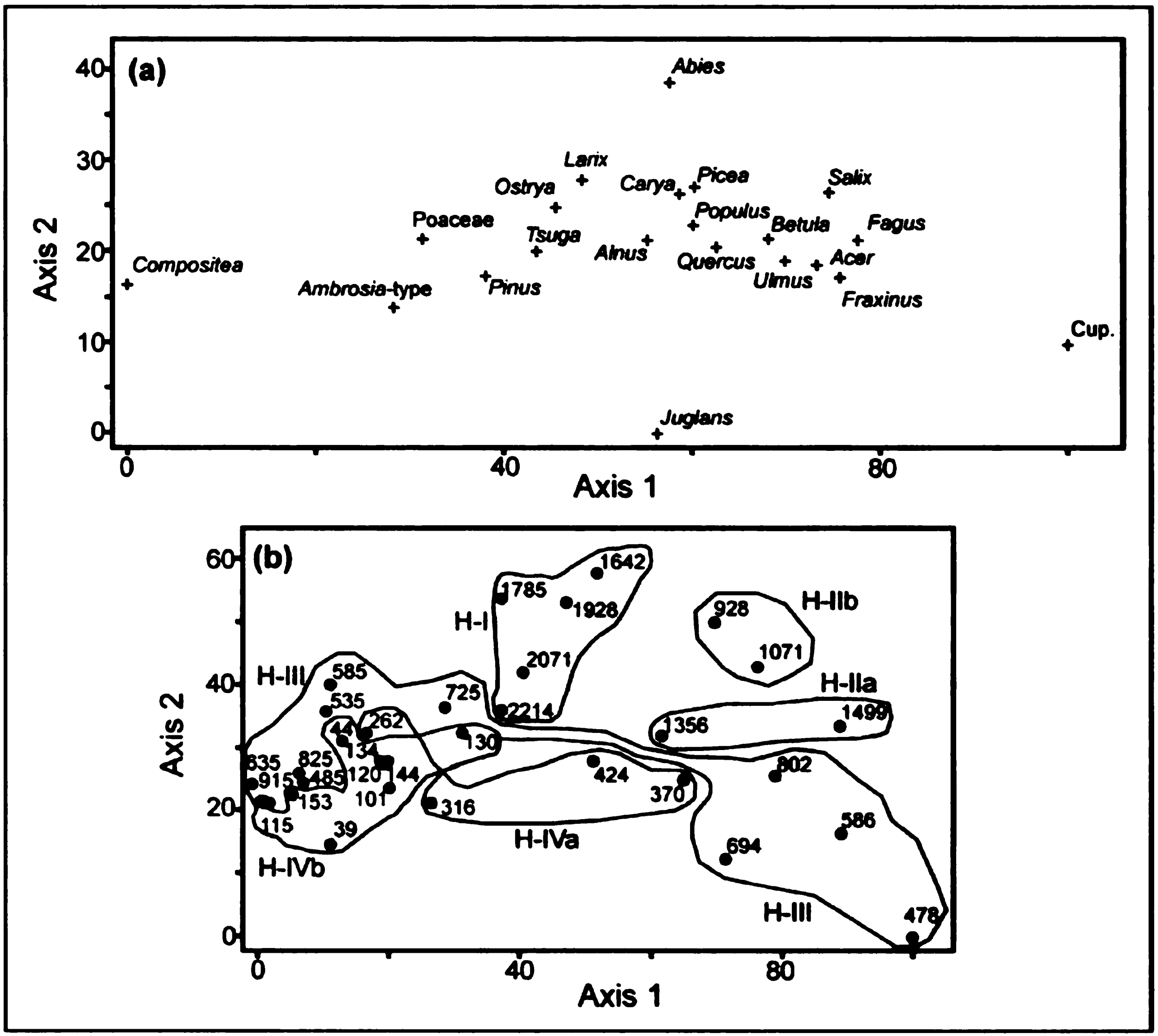

Figure 3.7 Principal components analyses of pollen data from Hicks Lake. Plot (a) shows the species placement while plot (b) shows the placement of individual sample age with outlines drawn around samples within each zone. Cup = Cupressaceae (most likely *Thuja occidentalis*)

3.3.2 Cowden Lake

The Cowden Lake freeze core was 72 cm long and the Livingston core was 200 cm long. The rates of sedimentation were variable throughout the core, with the historic period having the highest rates (Table 3.2). A total of 26 sub-samples were processed and analyzed based on the results from the radiocarbon dates and established chronology. Due to the variable sedimentation rates, the temporal resolution of the pollen samples varied throughout. The resolution at the top of the core from 0–150 cm was 10 years, while through the rest of the core 150 – 200 cm the resolution was 50–300 years.

3.3.2.1 Cowden Lake Pollen Zones

The diagram was divided into a total of 4 total pollen assemblage zones (Figure 3.8).

C-I: 129–117 cm; *Quercus-Pinus* (2100–1700 cal yr BP):

> **C-Ia: 129 – 125 cm; *Quercus-Pinus* (2100 – 1950):** This sub-zone was clearly dominated by *Quercus* pollen whose values rose steadily throughout the zone to 42%. *Pinus* spp. pollen values collectively reached 15%, the next most dominant type, and then declined slightly. Cupressaceae pollen abundance was also high in the zone at approximately 10%. *Picea* and *Tsuga* pollen percentages both reached a maximum of 3%. *Tsuga* pollen percentages decreased at the beginning of the zone. *Fagus* pollen percentages were quite low in this zone and reached only 5% while *Acer* spp. and *Ulmus* pollen values were both relatively high in this zone and reached 3% and 5%, respectively. *Populus* pollen abundance peaked in the center of the zone at 4%.

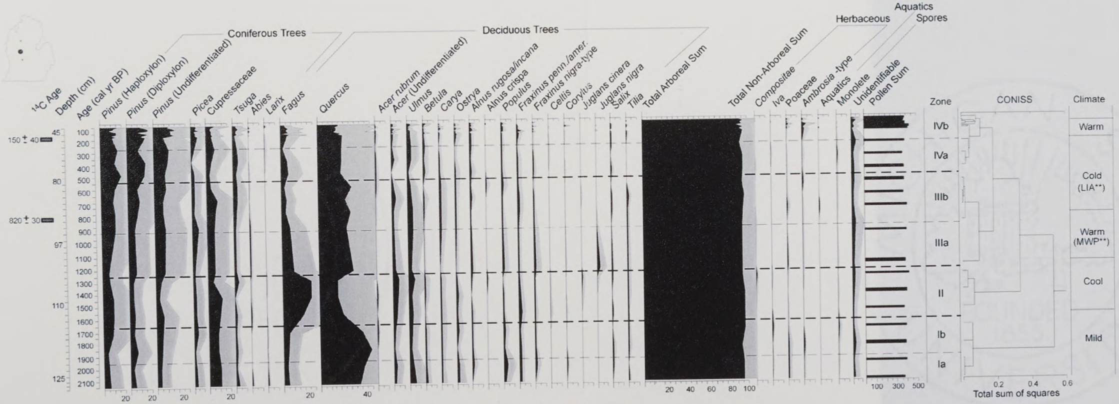

Figure 3.8 Fossil pollen diagram fro Cowden Lake (central). Pollen percentages are plotted against depth.

C-Ib: 125–117 cm; *Quercus-Pinus* (1950–1700): *Quercus* pollen abundance continued to rise in the zone and peaked at 48% and then decreased toward the end of the zone. *Pinus* spp. pollen values increased in this zone and collectively reached a total of 20%. Cupressaceae pollen abundance remained relatively stable in the zone at 9%. The pollen abundances of several deciduous taxa decreased at the same time as *Quercus* pollen abundance peaked; these included *Acer* spp., *Ulmus*, *Betula*, *Alnus*, *Populus*, *Fraxinus nigra,* and *Corylus*. *Picea* pollen abundance also declined at this time.

C-II: 117–105 cm; *Fagus* (1700–1300 cal yr BP): This zone was characterized by the dramatic shifts between pollen abundances of *Fagus* and *Quercus* pollen values. *Fagus* pollen percentages rose dramatically from a low of 6% in the previous zone to a high of 27% while *Quercus* pollen percentages declined dramatically from a high of 48% in the previous zone to 17% in this zone. The pollen abundances of several other taxa increased simultaneously with *Fagus*, including *Tsuga*, *Acer* spp., *Ulmus*, *Betula*, and *Tilia*. The pollen percentages of both *Pinus* and Cupressaceae declined concurrently.

C-III: 105–81 cm; *Quercus* (1300–550 cal yr BP):

C-IIIa: 105–93 cm; *Quercus-Juglans nigra* (1300–950 cal yr BP): This zone was characterized again by the dramatic shift between the pollen percentages of *Quercus* and *Fagus*. *Fagus* pollen percentages declined to 11% while *Quercus* pollen percentages rose sharply to 32% at 1250 cal yr BP. The pollen abundances of several taxa rose concurrently with *Quercus* pollen values including *Pinus* spp., which collectively reached 29%, and Cupressaceae, *Alnus rugosa/incana*, *Populus*, *Fraxinus nigra*, and *Juglans nigra*. The pollen percentages of several taxa also declined simultaneously with *Fagus* including *Tsuga*, *Acer* spp., *Ulmus*, *Betula*, and *Juglans cinera*.

C-IIIb: 93–81 cm; *Quercus* (950–550 cal yr BP): From 950-700 cal yr BP, pollen percentages for most taxa remained relatively stable. *Quercus* pollen percentages increased. At 700 cal yr BP, *Quercus* pollen values declined from 30% to 25% while *Fagus* pollen values rose (1%). The pollen abundances of several taxa also increased at 700 cal yr BP, including *Tsuga*, *Acer* spp., *Ulmus*, *Betula*, and *Tilia*. *Tilia* pollen percentages reached their maximum value at 1.4% just after 700 cal yr BP and then decreased and remained at less than 1%. Cupressaceae pollen abundances decreased significantly at 700 cal yr BP. *Quercus* pollen values peaked again by the end of the zone, just before 550 cal yr BP, at 32%.

C-IV: 81–0 cm; (550–0 cal yr BP):

C-IVa: 81–69 cm; *Pinus-Quercus* (550–250 cal yr BP): In this zone *Quercus* pollen percentages decreased from 32% in previous zone to 22% in this zone. *Quercus* pollen abundances remained steady throughout the remainder of the zone. *Fagus* pollen percentages increased in this zone, peaking at 7%, and then decreased slightly. *Pinus* spp. pollen values also increased to a collective 45%. The pollen abundances of Cupressaceae and *Tsuga* increased throughout the zone. *Acer* spp. and *Ulmus* pollen percentages also increased towards the end of the zone.

C-IVb: 65–0 cm; *Ambrosia (type)* (250–0 cal yr BP): At the beginning of this zone, *Pinus* (section Diploxylon), *Picea* and *Fagus* pollen abundances increased while most other types remained relatively stable. This zone was characterized by a spike in the *Ambrosia*-type pollen values at 4%. Directly after the spike in *Ambrosia*-type, the majority of pollen abundances declined, indicating deforestation, and then rose again towards the very end of the zone, a sign of subsequent recovery.

3.3.2.2 Cowden Lake Ordination

The ordination of pollen types and samples summarized changes in the pollen diagrams and illustrated the dynamics between pollen types and vegetation assemblages over time (Figure 3.9). Together, the two axes explained 96% of the variance in the data; axis one explained 71% of the variance while axis two explained 25% of the variance. In the ordination diagram illustrating pollen types (Figure 3.9a), axis one separated the coniferous species to the right from the deciduous species to the left. *Pinus* spp., *Tsuga* and *Picea* were pulled the right while *Abies* and Cupressaceae were nearer the center. *Tilia* was located on the very low end of axis one along with *Juglans*. Axis two mainly separated *Quercus*, just above center, and *Fagus,* which was at the very bottom of axis two.

In the ordination diagram of samples (Figure 3.9b) the level of separation on each axis represented shifts in vegetation. As illustrated in the pollen type diagram, axis one separated samples based on the percentages of coniferous types. Thus Zones C-Ia and C-Ib were found on the left end of axis one while Zones C-IVa and C-IVb were pulled to the right end of axis one. Zone C-II was closer to C-I while C-III is closer to C-IV. Axis two, again as illustrated in the pollen type diagram, separated samples based on the percentages of *Quercus* and *Fagus*. Zone, C-Ia and C-Ib, both of which have a strong *Quercus* component, were placed on the upper end of axis two. Zone C-II was very low on axis two, indicating the dominance of *Fagus* in this zone. Zone C-III was also dominated by *Quercus* and was placed on the upper end of axis two.

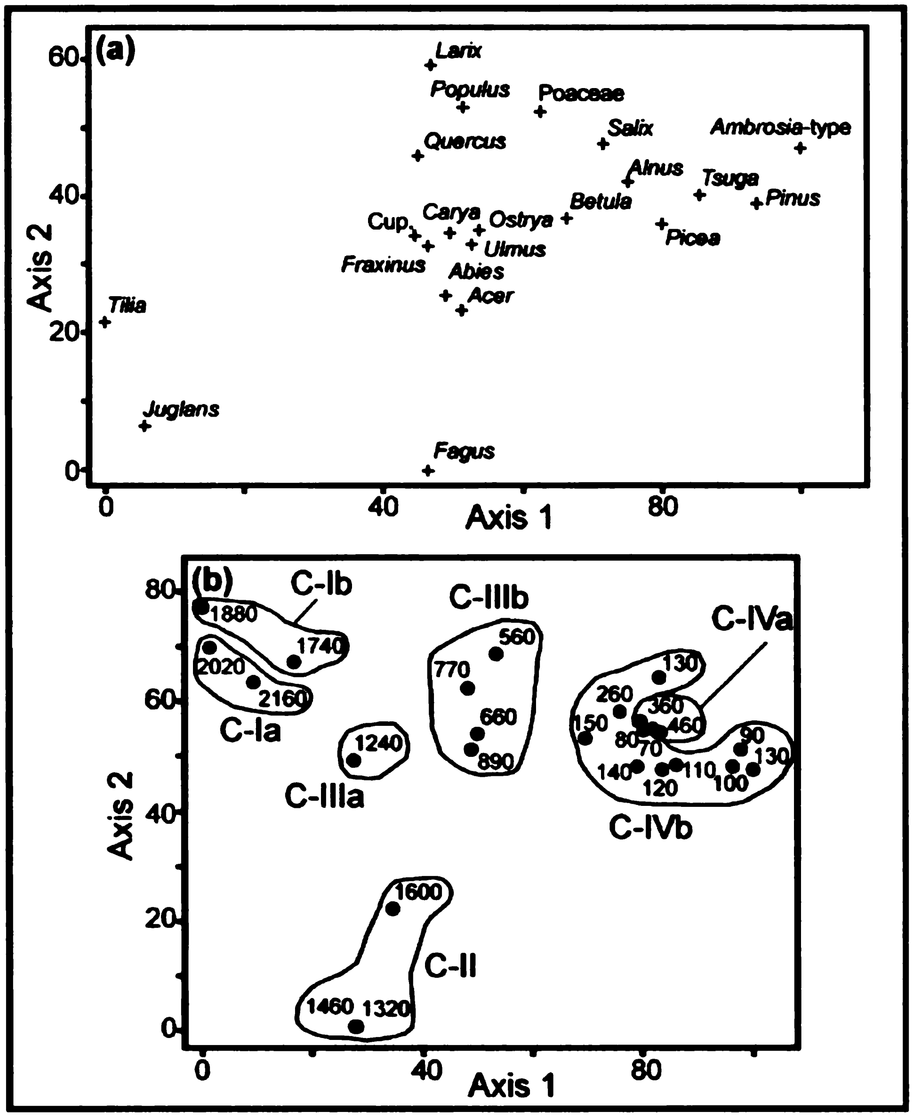

Figure 3.9 Principal components analyses of pollen data from Cowden Lake. Plot (a) shows the species placement while plot (b) shows the placement of individual sample age with outlines drawn around samples within each zone. Cup. = Cupressaceae (most likely *Thuja occidentalis*)

3.3.3 Morrison Lake

The freeze wedge core from Morrison Lake was 100 cm long and the Livingston core was in total 200 cm long. Sedimentation rates were variable throughout the core; the historic period and the very bottom of the core had relatively high rates (Table 3.2). A total of 30 sub-samples were processed and analyzed based on the results from the radiocarbon dates and established chronology. The temporal resolution of the pollen samples varied throughout the core because of the variable nature of the sedimentation rate. The resolution at the top of the core from 0 – 150 was 10 years, while throughout the rest of the core the resolution varied from 50 to 300 years at the very bottom.

3.3.3.1 Morrison Lake Zones

The diagram was divided into a total of four total pollen assemblage zones (Figure 3.10):

M-I: 141–105 cm; *Quercus-Fagus* (2100–2000 cal yr BP): This zone was characterized by relatively high percentages of both *Quercus* pollen, which peaked at 29%, and *Fagus* pollen which began off at a low of 9% and then slowly inclined to 21%. Cupressaceae and *Ulmus* pollen abundances were the next highest, both peaked slightly above 9%. In general, all other coniferous species exhibited low pollen abundances while several deciduous types such as, *Populus*, *Carya*, and *Ostrya,* had relatively high pollen abundances reaching 8%, 7%, and 3%, respectively.

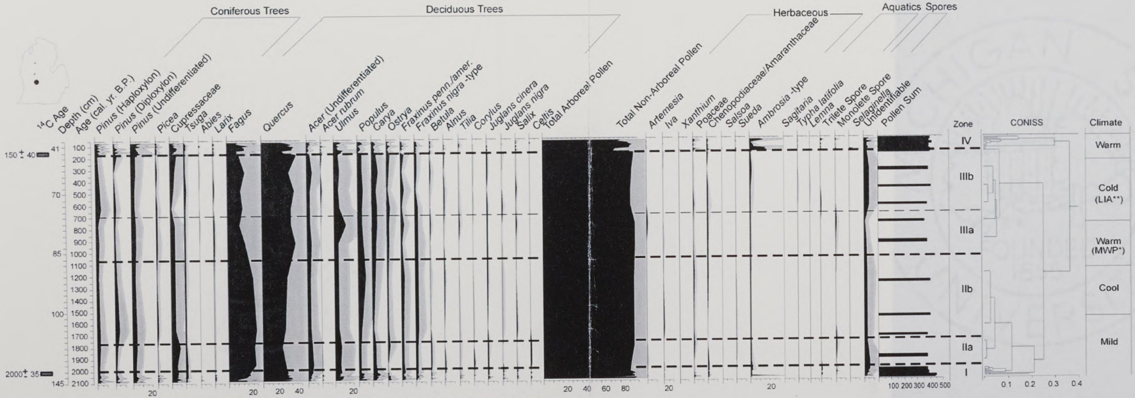

Figure 3.10 Fossil pollen diagram for Morrison Lake (south). Pollen percentages are plotted against depth.

M-II: 105–89 cm; (2000–1700 cal yr BP):

M-IIa: 105–89 cm; *Fagus-Quercus* (2000–1800): In this zone, F*agus* pollen percentages increased at the beginning of the zone to a high of 27%, while *Quercus* pollen values steadily declined to 23%. *Pinus* spp. pollen abundances rose slightly to 9%. Cupressaceae pollen values were the next highest type, and peaked in the middle of the zone at 9%, followed by *Ulmus* pollen values which peaked concurrently at 7%. The pollen abundances of other deciduous types, *Acer* spp., *Populus*, and *Carya,* remained relatively high. *Ostrya* pollen abundances increased toward the end of the zone.

M-IIb: 89–81 cm; *Fagus-Quercus* (1800–1050 cal yr BP): *Fagus* pollen percentages steadily declined from 28% to 25% while *Quercus* pollen percentages rose from 23% to 25%. The pollen values of most other taxa remained stable. *Pinus* spp. pollen values increased slightly to 12%. *Populus* pollen percentages also increased at 1200 cal yr BP to 8%, which was the overall high for *Populus*.

M-III: 81–57 cm; (1050–150 cal yr BP):

M-IIIa: 81–69 cm; *Quercus-Ulmus* (1050–700 cal yr BP): In this zone, *Quercus* pollen values steadily increased and peaked in 900 cal yr BP at 34%, while *Fagus* pollen values slowly declined to a low of 12% in 800 cal yr BP. *Ulmus* pollen percentages peaked in 800 cal yr BP at 13%. Concurrently, the pollen abundances of *Fraxinus* *pennsylvanica/americana*, *Betula,* and *Tilia* also rose to 3%, 1%, and 1%, respectively. *Pinus* spp. pollen values collectively reached just over 8%.

M-IIIb: 69 – 57 cm; *Quercus-Fagus* (700 – 150 cal yr BP): The pollen abundances of *Fagus* and *Quercus* fluctuated slightly and exhibited the same trends: *Quercus* pollen percentages increased while *Fagus* pollen percentages decreased. *Ulmus* pollen values decreased significantly to about 5%. *Pinus* spp. pollen percentages first declined and then increased back to 10% collectively. Cupressaceae pollen percentages rose steadily through the zone to a high of 7%. *Acer* spp. pollen abundances increased slightly toward the end of the zone to over 5%.

M-IV: 57–0 cm; *Ambrosia* (type)-*Quercus* (150–0 cal yr BP): This zone had high peaks in *Ambrosia*- type pollen values, one in 150 cal yr BP at 16% and then another at 50 cal yr BP at 14%. The pollen abundances of a majority of taxa declined dramatically at the same time as the spike in *Ambrosia*-type, indicating deforestation, and then increased to previous levels indicating subsequent forest recovery.

3.3.3.2 Morrison Lake Ordination

As with the analysis of pollen records from Cowden and Hicks Lakes, the ordination of pollen types and samples for Morrison Lake summarized changes in the diagrams and illustrated the dynamics between pollen types and vegetation assemblages over time (Figure 3.11). The two axes together explained 74% of the total variance while axis one accounted for 54% of the variance and axis two explained 23% of the variance. In the pollen-type ordination diagram (Figure 3.11a), axis one separated the herbaceous taxa, *Ambrosia-type*, Poaceae, Chenopodaceae, which were aligned to the left end of the axis, from *Fagus,* which was placed at the right end of the axis. Most of the deciduous species were placed in a clump just to the right center of axis one. *Pinus* spp., one of the coniferous taxa represented, was placed just to the right of center but on edge of the grouping of most species. Axis two separated *Quercus*, which was pulled to the upper end of axis two, from *Fagus* which was placed on the lower end of axis two. Most deciduous taxa were aligned in the center. *Ostrya* and *Carya* were both found close to *Quercus* while *Acer* spp. and *Tilia* were much closer to *Fagus*. In the ordination diagram of samples (Figure 3.11b) the level of separation on each axis represented shifts in vegetation. As illustrated by the pollen type diagram, axis one separated samples which had a higher percentage of herbaceous species. Thus, the majority of samples were aligned to the right of the diagram while samples from Zone M-IV were aligned to the left. Since axis two separated the samples based primarily on the percentages of *Quercus* and *Fagus* percentages, Zones M-IIa and M-IIb were aligned to the very bottom edge, while the other zones were aligned higher on axis two. In general, very little separation occurred between Zones M-I, M-III and M-IV.

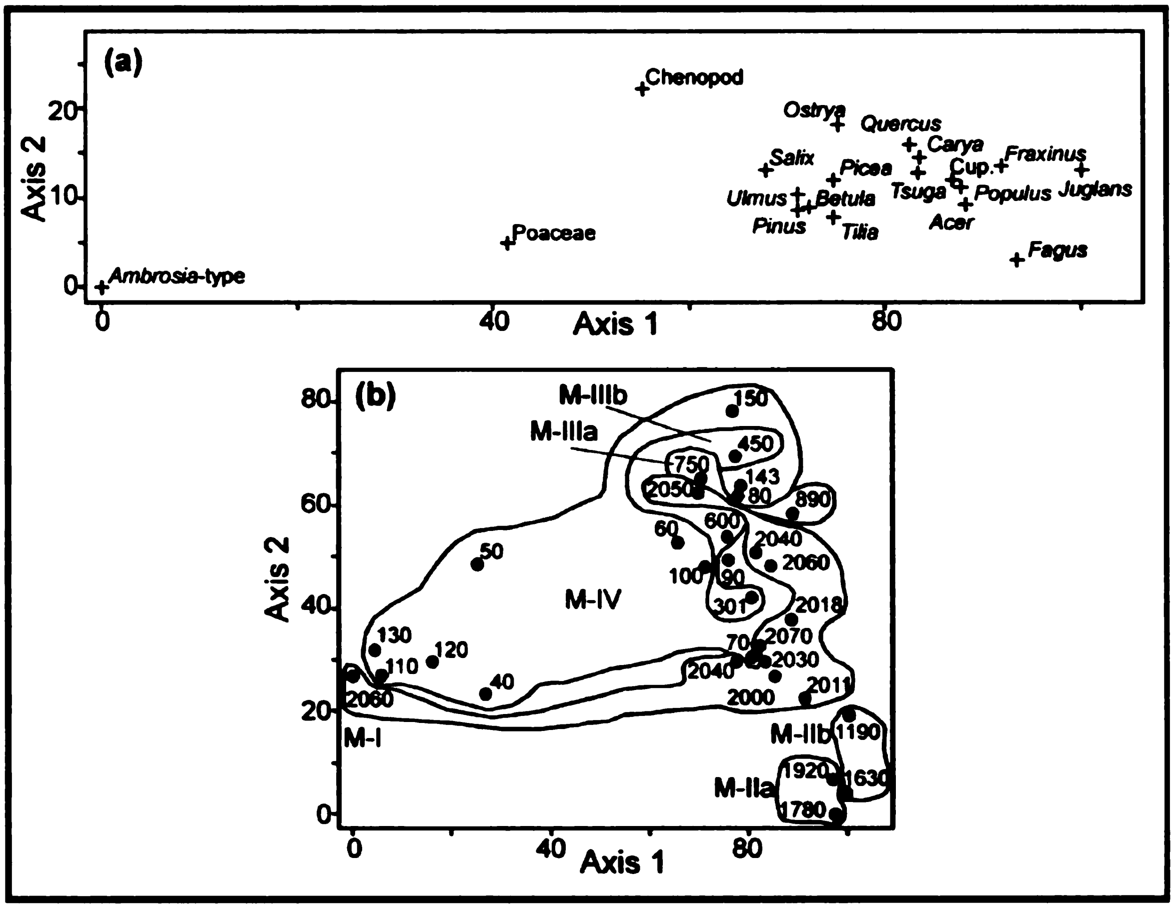

Figure 3.11 Principal components analyses of pollen data from Morrison Lake. Plot (a) shows the species placement and plot (b) shows the placement of individual sample age with outlines drawn around samples within each zone.

3.4 Interpretation

3.4.1 Vegetation History of Hicks Lake

<u>2100 – 1600 cal yr BP: Northern Mesic Mixed Coniferous Forest</u>

From 2100–1600 (Zone: H-I), the forests surrounding Hicks Lake were typical of the northern mixed-Laurentian forests. Several coniferous taxa were dominant while deciduous species were less important. The abundance of *Pinus* spp. and *Tsuga* indicated the presence of a northern mesic coniferous forest, while the abundance of *Picea* and *Abies* suggested a boreal-type mesic forest, most likely prevalent in the nearby lowlands. The presence of local stands of *Tsuga* and *Picea* suggests a cool and relatively moist climate for this time. This cool-mesic coniferous forest was prevalent throughout this zone. Because *Pinus* pollen tends to be over-represented in the record (Bernabo 1980), *Pinus* taxa were slightly less important than other coniferous species in the mixed coniferous forests. Early during this interval (2100-1800), a dry-mesic northern hardwoods forest was present dominated by *Pinus strobus* and *Quercus* spp. These forests were most likely prevalent on the sandier and slightly drier sites surrounding Hicks Lake and were less dominant than the northern mesic coniferous forests. Small pockets of a slightly moister northern mesic forest, with important species such as *Fagus* and *Acer* spp., were also present, most likely on the richer medium-textured soils. Although, as with *Quercus* and *Pinus strobus*, populations of both *Fagus* and *Acer* spp. declined by 1600 cal yr BP while both *Betula* and *Pinus resinosa/banksiana*-type expanded at 1700 cal yr BP. These shifts suggested that while the overall climate remained cool, a drying occurred around 1700 cal yr BP. The cool-mesic coniferous forests prevalent from 2100-1600 cal yr BP (zone: H-I), were quite different than the forests present in the area after 1600 cal yr BP.

1600-880 cal yr BP: Wet-Mesic Mixed Coniferous Forests

Beginning at 1600 cal yr BP, Cupressaceae, presumably *Thuja occidentalis* increased in local abundance while *Picea*, *Tsuga,* and *Pinus* declined in local abundance. These changes indicated a shift from the *Tsuga-Picea-Abies* mesic forests to wet-mesic coniferous forests dominated by *Thuja* and *Tsuga*. The dramatic expansion of Cupressaceae, most likely indicates the expansion of *Thuja occidentalis*, or northern white cedar, which tends to dominate in wet-mesic coniferous communities, especially in lowlands known as "cedar swamps". This expansion at 1600 cal yr BP (Zone: H-IIa) may have been a response to increased moisture that began a century earlier at 1700 cal yr BP. Despite the shifts in dominant taxa, the forest surrounding Hicks Lake at this time were primarily wet-mesic mixed coniferous forests. The consistently moderate abundance of important deciduous taxa, including *Fagus*, *Quercus* spp., and *Acer* spp., suggested that while the wet-mesic coniferous forests remained dominant, patches of dry-mesic and mesic northern hardwood forests were still prevalent.

The relatively high abundances of coniferous taxa and re-emergence of *Abies*, beginning at 1200 cal yr BP, suggests that a wet-mesic to mesic coniferous forest existed near Hicks Lakes at this time. The decrease in *Thuja* and the subsequent increase in both *Picea* and *Abies* may have been a response to a climatic cooling and drying beginning at 1500 cal yr BP which lasted until 1200 cal yr BP. This signal was also detected by Bernabo (1981) at Marion Lake and Lake 27 north of Hicks Lake. Again, the consistent abundances of several important deciduous taxa suggested that patches of dry-mesic and mesic northern forests with hardwoods were still prevalent. Overall, the forest communities reconstructed around 1600 cal yr BP remained relatively stable over the period from 1600 to 1000 cal yr BP.

At 1100 cal yr BP, *Tsuga* increased in abundance which may have been in response to a period of wetness associated with the onset of the MWP in the

Midwest (Soon and Baliunas 2003). After 1000 cal yr BP, several thermophilous taxa increased in abundance including *Quercus*, *Acer rubrum*, *Alnus*, *Populus*, *Ulmus* and *Ostrya-Carpinus*. Poaceae and *Ambrosia*-type became more common in local floras which coincided with a switch to dry conditions in the latter part of the Medieval Warm period after 900 cal yr BP (Soon and Baliunas 2003). Therefore, only a slight signal of the MWP, detected by Bernabo (1981) at a site 100 km north of Hicks Lake from 1000–800 cal yr BP, was evident around Hicks Lake. This signal at Hicks Lake was indicated by minimal increases in several thermophilous deciduous taxa and a decrease in *Abies*. The forests surrounding Hicks Lake at this time remained dominated by mesic coniferous species with local expansions of both the dry-mesic and northern mesic forests towards the end of the MWP. The major differences between the forests prevalent from 1600-880 cal yr BP (Zones: H-IIa and H-IIb) and those that existed earlier between 2100-1600 cal yr BP (Zone: H-I) was due to expansion of *Quercus* in the latter during the MWP. This contrasted greatly to the high importance of both *Abies* and *Picea* earlier.

880-380 cal yr BP: Wet-Mesic *Thuja* Forest

Beginning at 880 cal yr BP (Zone: H-III), *Thuja occidentalis* began to dominate the wet-mesic forests. Both *Picea* and *Pinus* spp. were relatively abundant within these forests while *Tsuga* declined in local importance concurrent with expansion of *Thuja*. Thermophilous taxa, including *Acer* spp., *Alnus*, and *Ulmus*, were relatively abundant in northern mesic forest surrounding

Hicks Lake, especially *Acer* (spp.) which is under-represented in the pollen record. At 450 cal yr BP, *Thuja* reached its highest abundance in the local flora, at the same time as *Picea*, *Tsuga* and *Quercus* declined in abundance. These patterns indicated a return to *Thuja* dominated wet-mesic coniferous forests, with a minimal decline in the mesic forests. The ordination diagram illustrated the polarity between the assemblages found both before and after the *Thuja* expansion and the assemblage during the *Thuja occidentalis* dominance. The expansion of *Thuja* began after the onset of the MWP and may have been a response to increased moisture which coincided with at least a 1°C decrease during the LIA, beginning at 600 cal yr BP and continuing as late as 250 cal yr BP in the region (Bernabo 1981; Soon and Baliunas 2003).

<u>380-0 cal yr BP: Mesic *Tsuga* Forests</u>

Beginning at 380 cal yr BP (Zone: HIVa), *Thuja occidentalis* declined significantly in abundance as both *Tsuga* and *Pinus* became the dominant taxa in the coniferous forests. *Tsuga* was mostly likely the dominant taxa in these forests, as *Pinus* spp. pollen is over-represented in the fossil records. Most of the deciduous taxa were relatively less abundant as this time, suggesting a decline in the deciduous component the mesic forests. The ordination diagram suggested that this assemblage was most similar to the one present from 2100-1600 cal yr BP (zone:H-I). Thus the forests at this time remained dominated by the mesic mixed coniferous type but with *Pinus* spp., *Tsuga* and *Picea* more important than *Thuja.* This assemblage was most likely the result of the cooling associated with the LIA. At 150 cal yr BP, most taxa declined significantly, indicating the disturbance associated with Euro-American settlement and subsequent logging of this area. This interval was also marked by the characteristic increase of *Ambrosia*-type pollen and herbaceous taxa, signifying the clearing of forests. After the logging disturbance, most taxa recovered and increased in abundance again. Several coniferous taxa, including *Pinus* spp., *Picea* and *Thuja*, regenerated after logging but were significantly less abundant on the landscape thereafter. Most deciduous taxa recovered and reached abundances similar to the pre-logging forests. The post-logging forests surrounding Hicks Lake had a significantly higher deciduous component but remained as a mixed coniferous-deciduous forest. *Tsuga* recovered to pre-logging levels and was the dominant coniferous taxa in these forests. Other species characteristic of a disturbed landscape, such as *Betula* and *Populus,* expanded and were present in higher abundances than in the pre-logged forests.

3.4.2 Vegetation History near Cowden Lake

<u>2100-1700 cal yr BP: Dry *Quercus*-mixed Forests</u>

From 2100-1700 (Zone: C-Ia) the forests surrounding Cowden Lake were primarily xeric deciduous forests dominated by *Quercus* with smaller patches of a more mesic deciduous forest. The relatively high pollen abundance of *Pinus* spp., which is generally over-represented in the pollen record due to both long-distance dispersal and high pollen grain production, suggests that some patches of mixed deciduous-coniferous forests, including *Pinus* spp., were present near

Cowden Lake. *Pinus* was clearly not the dominant species in this community. *Quercus* and *Pinus* were mostly likely the two dominants in the mixed coniferous-deciduous forests found on dry sandy soils near Cowden Lake. *Thuja* was also relatively abundant, and was most likely found on wet calcareous soils near swamps and rivers, as well as in mono-specific stands on poorly-drained sites. Other coniferous taxa, mainly *Tsuga* and *Picea*, were present in very low numbers within the mixed coniferous-deciduous forests. *Quercus* continued to increase in abundance until 1850 cal yr BP, when it reached it maximum abundance. Several taxa declined in abundance concurrent with the maximum expansion of *Quercus,* including: *Populus, Acer* spp., *Ulmus, Ostrya, Fraxinus nigra*-type, as well as *Pinus strobus* and *Picea.* These pollen data indicate a decline in the abundance of mesophytic deciduous forests as well as a decrease in the coniferous component of the mixed coniferous-deciduous forests.

After 1850 cal yr BP, *Quercus* began to decline in local abundance, but remained the most dominant species in the forests surrounding Cowden Lake. The relative prevalence of several types of taxa, i.e mesic and xeric deciduous species, as well as lowland coniferous species, are characteristic of a transition between forest regions, such as would be expected within a forest tension zone.

1700-1300 cal yr BP: Mesic *Fagus*-mixed Forests

The xeric *Quercus*-dominated deciduous forests declined significantly from 1700 to 1300 cal yr BP (Zone: C-II). As *Quercus* became much less dominant in all of the forest surrounding Cowden Lake, *Fagus* expanded dramatically in its local representation. The dominance of mesophytic taxa indicated the expansion of the mesic deciduous forests dominated by *Fagus* and *Acer* spp.. While *Quercus*-dominated forests were still present on the landscape, they were much less expansive, overall less prevalent than the mesic *Fagus-Acer* forests, and contained other taxa, such as *Juglans* and *Carya*. While most coniferous taxa did not expand and remained relatively stable, *Tsuga* expanded at 1350 cal yr BP concurrent with the *Fagus* expansion, suggesting the presence of *Tsuga* in the *Fagus-Acer* forests. There were probably also small pockets of mixed coniferous-deciduous forests with relatively low abundances of *Pinus* spp. Both *Thuja* and *Picea* were most likely found in very isolated instances within the mesic mixed coniferous-deciduous forests and lowlands, although some small mono-specific stands of *Thuja* may have remained but were less extensive.

This vegetation shift was the most dramatic of all changes around Cowden Lake and therefore suggests a significant change in climate, particularly the onset of moister conditions which favored mixed mesophytic forests. The ordination placed the assemblage from 1700-1300 cal yr BP (Zone: C-II) apart from all assemblages. The placement of these samples was strongly aligned with *Fagus* on the species plot. Bernabo (1981) suggested that the climate during this time, 1650 cal yr BP to 1250 cal yr BP, was generally cool in comparison to the previous 300 years. The shift from xeric *Quercus*-dominated forests to mesic *Fagus*-dominated forests, and expansions of other mesophytic taxa such as *Thuja*, *Tsuga,* and *Acer*, corroborates Bernabo's (1981) interpretation of a somewhat cool and moister climate during this time.

1300-550 cal yr BP: Dry *Quercus* Mixed-forests

Beginning at 1300 cal yr BP and continuing until 550 cal yr BP (Zone C-III), the forests surrounding Cowden Lake once again shifted dramatically, but this time from the mesic *Fagus-Acer*-dominated forests back to the drier *Quercus* dominated forests. The dominant taxa in the mixed mesophytic *Fagus-Acer* forests, including *Tsuga*, declined shortly after 1300 cal yr BP but still persisted on the landscape. *Quercus* increased in local abundance dramatically, as the xeric deciduous forests were once again dominant. Other taxa, including *Juglans nigra*, *Alnus rugosa/incana*-type, *Carya,* and *Populus,* were also present within the xeric deciduous forests, indicating that *Quercus* did not dominate these xeric forests as strongly as it did before (2100-1700 cal yr BP). The relatively high abundance of *Juglans nigra* at this time was unique, suggesting its increased importance in the *Quercus* forests and also potentially in the mesic *Fagus-Acer* forests.

The pollen data indicate the presence of mixed coniferous-deciduous forests near Cowden Lake with significant *Pinus* spp., although these forests were not prevalent and were most likely found in small patches. The expansion of the *Quercus*-dominated forests coincided with Bernabo's interpretation of the MWP beginning between 1200 to 1000 cal yr BP. The dramatic increase in abundance of *Quercus* at 1150 cal yr BP and the concurrent decline of *Acer* spp., *Ulmus*, and *Fagus,* and minimal increase of *Pinus resinosa/banksiana*-type, suggests that fire may have been have also been a factor.

After 1100 cal yr BP (Zone: C-IIIa), the xeric *Quercus* dominated deciduous forests experienced a decline. This decline, concurrent with an increase in the abundance of *Ulmus,* was most likely in response to the period of wetness at the onset of the MWP (Soon and Baliunas 2003).

By 700 cal yr BP (Zone: C-IIIb), the abundance of both *Quercus* and *Pinus* became variable just as the mesophytic forests of *Fagus-Acer* mixed-forests, and the decline of the *Quercus* forests. These moderate fluctuations reconstructed for Cowden Lake generally coincided with the onset of the LIA detected by Bernabo (1981) around 700 cal yr BP, as well as the dry conditions beginning at the end of the MWP around 800 cal yr BP (Soon and Baliunas 2003).

550-0 cal yr BP: Xeric *Quercus-Pinus* Mixed-forests

At 550 cal yr BP (Zone C-IVa) forests dominated by *Quercus* continued their decline. The decline in *Quercus* was once again accompanied by an increased abundance of *Fagus*. Interestingly, other taxa which expanded in the previous *Quercus* decline, such as *Acer* spp., *Ulmus*, *Betula*, *Populus*, and *Tsuga* decreased in abundance. The increased abundance of *Pinus* indicates an expansion of the *Quercus-Pinus* forests, present in the earlier forests. The increased dominance of *Pinus* in these forests may have been in response to temperature decreases associated with the LIA (700-150 cal yr BP) (Bernabo, 1981). The lower temperatures, of about 1°C, associated with the LIA may also explain why other deciduous taxa did not expand concurrently with the *Quercus* decline. The relatively high abundances of *Pinus, Quercus,* and *Fagus,* concurrent with population declines in other mesophytic taxa, suggest that a different mixed deciduous-coniferous forest was present on the landscape. *Pinus-Quercus* and mixed-forests with *Pinus* spp., with *Quercus* and *Fagus* present in significant abundances, dominated the landscape. Both *Thuja* and *Tsuga* became more common towards the middle of the LIA, around 350 cal yr BP, most likely in response to the associated cooling. These taxa likely became components of the mixed *Pinus-Quercus-Fagus* forests.

At 150 cal yr BP, most taxa declined significantly, indicating the disturbance associated with Euro-American settlement and subsequent logging of this area. The characteristic rise in *Ambrosia*-type signified the expansion of herbaceous species after the forests were cleared. Most taxa appeared again after the disturbance. The post-disturbance forests surrounding Cowden Lake were a mosaic of *Quercus*-dominated xeric forests and the more mesic *Fagus*-dominated mixed northern hardwoods forests. Most coniferous taxa were less abundant in the post-logging forests.

3.4.3 Vegetation History near Morrison Lake

<u>2100-1050 cal yr BP: Mixed *Quercus* and *Fagus* Forests</u>

From 2100 to 2000 cal yr BP (Zone: M-I), the forests surrounding Morrison Lake were a mixture of xeric *Quercus*-dominated forests and the more mesic *Fagus-Acer* dominated forests, both characteristic of the broadleaf forests of eastern North America. Of the two communities, the higher abundance of *Quercus* indicates that the xeric *Quercus* forests were more common on the landscape. *Carya*, *Ostrya*, and *Populus* were also relatively abundant and were a significant component of the *Quercus* dominated forests. All coniferous taxa were most likely not present in the forests near Morrison Lake, except in isolated spots. Beginning at 2000 cal yr BP until 1800 cal yr BP (Zone: M-IIa), *Fagus* and associated taxa, *Acer* spp., *Tilia*, *Ulmus*, *Ostrya*, and *Fraxinus* spp., slowly increased in the local flora indicating the dominance of *Fagus-Acer* mixed mesophytic forests near Morrison Lake. *Quercus* forests declined significantly at this time.

Beginning at 1800 cal yr BP and continuing until 1050 cal yr BP (Zone: M-IIb), the *Quercus*-dominated forests surrounding Morrison Lake slowly and steadily increased in abundance. Deciduous taxa associated with the *Quercus* dominated forest *Populus* and *Carya* also slowly became more common. There was a decline in the spatial extent of the *Fagus-Acer* mixed mesophytic forests. Despite the decline from 1800 cal yr BP to 1200 cal yr BP, the *Fagus-Acer* mixed mesophytic forests remained the dominate community on the landscape. The opposite trends exhibited by the *Quercus*-dominated xeric forests and the *Fagus-Acer* mixed mesophytic forests illustrate the competitive dynamics between the dominant species, *Quercus* and *Fagus*.

1050-700 cal yr BP: *Quercus* Forests

By 900 cal yr BP (Zone: M-IIIa), *Quercus* had once again became more common and the forests surrounding Morrison Lake were predominately mixed *Quercus* forests. *Carya* and *Populus* both remained relatively abundant and were still a significant component of the *Quercus* forests. By 750 cal yr BP the mixed mesophytic forests were dominated by *Ulmus, Fagus*, *Acer* spp., and *Fraxinus* spp..

After 700 cal yr BP (Zone: M-IIIb), *Fagus* dominated forests began to expand once again. Despite the *Fagus* expansion, the *Quercus* forests continued to be the dominant community on the landscape from 700 cal yr BP until 150 cal yr BP. The prevalence of *Quercus* was quite variable throughout this time period; it declined and then expanded in abundance. Concurrent with the variations in *Quercus* abundance, *Fagus* also exhibited variations, although in the opposite direction. When *Quercus* increased in abundance *Fagus* declined. This trend indicated the expansion and decline of both the mixed mesophytic forests and the *Quercus*-dominated xeric forests. This trend was most pronounced at 350 cal yr BP when *Fagus* expanded significantly as *Quercus* declined. Thus, the *Fagus–Acer* mixed-mesophytic and the mixed-xeric *Quercus* forests were present in a mosaic of relatively equal abundances. After 350 cal yr BP, the trend reversed again, as *Quercus* once again increased in abundance.

At 150 cal yr BP (Zone: M-IV), most taxa experienced a significant decline as a result of the dramatic disturbance associated with Euro-American settlement and subsequent logging. Concurrent with the decline in most taxa, *Ambrosia*-type expanded significantly, indicative of the dominance of herbaceous taxa immediately after logging. After 150 cal yr BP, most taxa returned to the landscape. And once again, the forests surrounding Morrison Lake were a mosaic of mixed-mesophytic forests dominated by *Fagus-Acer* and the more xeric forests dominated by *Quercus*.

3.5 Discussion

3.5.1 Forest Dynamics North of the Tension Zone

The pollen record from Hicks Lake generally corresponds to the pollen records from Marion Lake and Lake 27 (Figure 3.1), both of which are located approximately 100 km to the north (Bernabo 1981). From 2000 to 1600 cal yr BP, the forests at all three lakes were a mixture of the northern mesic forests dominated primarily by *Tsuga*, with *Fagus, Acer* spp. as subdominants, and the northern dry-mesic forests comprised of *Pinus* spp., with some *Quercus*. These assemblages correspond to relatively mild (Bernabo 1981) and mesic conditions. The low abundance of *Thuja* indicates that conditions were not moist enough to support *Tsuga* as a dominant.

A shift at around 1600 cal yr BP was evident all three lakes, characterized by increased abundance of *Pinus*, *Picea*, and *Ulmus*. *Tsuga* and *Quercus* declined at both Marion Lake and Lake 27. *Thuja* increased in abundance and *Tsuga* and *Pinus* declined in abundance near Hicks Lake. The differences between the timing of the changes in abundance of *Picea* and *Pinus* spp. surrounding Hicks Lake in comparison to Marion Lake and Lake 27 may be attributed to variations in chronologies, especially considering the use of the *Ambrosia* correction method in both. Bernabo (1981) did not report *Thuja* abundances at either Marion Lake or Lake 27. A decline in *Pinus* spp.

abundances at approximately 1600 cal yr BP was evident at Tamarack Lake (Figure 3.1), approximately 90 km to the northwest of Hicks Lake and near the shores of Lake Michigan (Davis et al. 2000). At Tamarack Lake, *Betula* was significantly higher than at the forests near Hicks Lake, Marion Lake and Lake 27. Also, because of the coarse temporal resolution in the Tamarack Lake pollen record, this record cannot be related to the specific nature and timing of the changes interpreted around Hicks Lake.

Just after 1600 cal yr BP, there was an increase in the amount of hardwoods (*Fagus* and *Quercus*) in the mesic and dry-mesic northern forests at Hicks Lake. This increase may be a delayed response to the previous mild period. The significant increase in *Thuja* after 1600 cal yr BP indicates that the shift to a cooler climate was also accompanied by increased moisture. The interpretation of increased moisture based on the expansion of Cupressaceae, probably *Thuja occidentalis*, surrounding Hicks Lake in the Lower Peninsula of Michigan is different than a previous interpretation of a *Thuja* expansion during the Hypsithermal (~6000 cal yr BP) in northern Ontario by Liu (1990). *Thuja occidentalis*, a species typical of the Great Lakes Laurentian forests, grows as far north as James Bay, in northern Canada and as far south as Tennessee and South Carolina. *Thuja occidentalis* grows best on calcareous soils and is often found in nearly pure stands in swamps, but is restricted from occupying deeper pools of water and acidic bogs; although its habitat characteristics vary considerably across the range (Barnes and Wagner 2004}. In northern Ontario, the location of Lui's (1990) research, *Thuja,* near its northern range limit, is restricted to the margins of streams, swamps, and nutrient rich fens where it comprises less than 3% of the trees in the boreal forests. In southern Ontario it is more prevalent (7%) in the Laurentian forests where it grows in both uplands and swamps.

Lui (1990) interpreted the *Thuja* expansion during the Hypsithermal as a response to a warmer and drier climate. In this manner, the drier climate lowered the regional water table and allowed *Thuja* to spread to the center of swamps. In the northern half of the Lower Peninsula of Michigan, *Thuja* is not limited to swamps, but is abundant on sites with calcareous soils and high water tables on the uplands as well as on the margins of most streams and swamps (Voss 1972; Barnes and Wagner 2004). In the vicinity of Hicks Lake, relatively low abundances of xeric taxa, i.e. *Pinus* spp. and *Quercus* as well as low abundances of *Tsuga*, were associated with the *Thuja* expansion. I interpreted the *Thuja* expansion as a response to increased moisture, and increased abundance of northern wet lowland and northern wet-mesic forest, in which *Thuja* is a dominant (Curtis 1959).

Bernabo (1981) estimated a shift to a cooler climate from 1500-1200 cal yr BP where *Pinus* and *Picea* remained relatively abundant while *Tsuga* was less dominant but slowly became more common in the vicinity of Marion Lake and Lake 27. At the same time, *Thuja* declined in the mixed coniferous forests surrounding Hicks Lake while *Pinus* spp. and *Tsuga* became more abundant. A decrease in Cupressaceae, presumably *Thuja occidentalis,* was also evident after 1400 cal yr BP at Jack Lake (Figure 3.1) in central Ontario (Liu 1990).

Between 1000 and 800 cal yr BP significant changes were evident in the forests at Marion Lake and Lake 27 which indicated a warming associated with the MWP. At Lake 27, these included a decline in the abundances of *Picea*, *Pinus* spp., and *Tsuga* and increased abundance of *Fagus*, and *Betula*. At Marion Lake, *Picea*, *Pinus* spp., *Betula* all declined in abundance accompanied by increased abundance of *Ulmus* and *Fraxinus* spp. Changes associated with the MWP occurred somewhat later around Hicks Lakes and were characterized by: 1) an initial increase in the abundance of *Quercus* at 1050 and then gradual decline, 2) a dramatic increase in the abundance of *Thuja* beginning at 1050 cal yr BP, which reached a maximum at 550 cal yr BP; and 3) declines in the local abundances of *Pinus* spp., *Picea*, *Tsuga*, *Fagus*, and *Betula* also at 1050 cal yr BP.

The dramatic expansion and dominance of *Thuja occidentalis* near Hicks Lakes suggests that the northern Lower Peninsula experienced increased moisture from 900-500 cal yr BP concurrent with the transition from the MWP to the LIA. Besides the dramatic increase in *Thuja* around Hicks Lake, the forests in the northern Lower Peninsula responded slightly to the MWP.

More significant changes were evident in the pollen records for all three lakes after 800 cal yr BP, during the onset of the LIA, which lasted until 150 cal yr BP. Vegetation shifts in the northern Lower Peninsula of Michigan during the LIA included: 1) significant increases in the abundances of *Picea* and *Pinus* spp. concurrent with moderate declines in the abundances of *Tsuga*, *Quercus*, *Fagus*, and *Acer* spp. after 700 cal yr BP at Lake 27, 2) increased abundance of *Picea*, *Pinus* spp., *Tsuga*, and declined abundance of *Quercus*, *Ulmus,* and *Fraxinus* spp. evident by 550 cal yr BP at Marion Lake; 3) a dramatic decline in the abundance of *Thuja*, and a moderate decline in *Fagus* while *Picea*, *Pinus* spp., and *Tsuga* expanded at 500 cal yr BP around Hicks Lake. This assemblage indicates an expansion of *Pinus* spp. in the dry-mesic forests and *Picea* in the lowland forests in most of the northern Lower Peninsula of Michigan with an overall decline in the deciduous components of the northern mesic and dry-mesic forests The decline in *Fagus* and increase in *Pinus* spp. and *Picea* after the onset of the LIA was evident in other records in the Great Lakes region, specifically within the mixed Laurentian forests in Ontario (Fuller 1997). The pollen record for Graham Lake (Figure 3.1), at approximately the same latitude as Hicks Lake in southern Ontario, documented a decline in *Tsuga* during the onset of the LIA (Fuller 1997).

All three records indicate that later, around 300 cal yr BP, *Tsuga* increased in abundance in the northern mesic as well as in the northern hardwood communities. This trend continued until Euro-American settlement and disturbance at 150 cal yr BP, but continued again afterward as *Tsuga* recovered.

Thus, several overall trends were evident in the pollen records for the Hicks Lake area. Throughout the record, a dynamic between *Thuja* and *Tsuga* and *Pinus* was evident. When *Thuja* dominated wet-mesic coniferous forests and wet-lowland forests near Hicks Lake, both *Tsuga* and *Picea* abundances were low. This pattern correlated with climatic reconstructions (Bernabo 1981) which suggested that *Thuja* displaces both *Tsuga* and *Picea* in slightly cooler and wetter conditions while *Tsuga* and *Picea* displace *Thuja* in mesic or slightly drier conditions. As illustrated in the ordination (Figure 3.7), the dynamics between *Thuja*, *Tsuga, Pinus*, and *Picea* were the main agents in determining the position of the zones on the ordination diagram (Figure 3.7).

3.5.2 Forest Dynamics within the Tension Zone

While the forest reconstruction for Cowden Lake contrasted greatly to that of Hicks Lake, as well as Marion Lake and Lake 27 (Bernabo 1981), the climatic interpretations are similar. *Quercus* dominated the forests surrounding Cowden Lake from 2100-1600 cal yr B. Other smaller pockets of mixed mesophytic forests were also present. The prevalence of *Quercus*-dominated xeric forests for this time period was also evident in the Crystal Lake (Figure 3.1) pollen record (Kapp et al. 1990), the closest lake, located approximately 33 km to the south east (Kapp et al. 1990). This paleovegetation reconstruction corroborated the interpretation of a mild and dry climate evident in the records from Hicks Lake, as well as Marion Lake and Lake 27 (Bernabo 1981).

A significant shift in forest composition was evident at 1600 cal yr BP in both the pollen records for Cowden Lake and Crystal Lake (Kapp et al. 1990). This shift was characterized by a dramatic decline in the extent of the *Quercus* dominated forests and an expansion of the mixed mesophytic *Fagus-Acer*-dominated forests, as well as an increase in the abundance of coniferous taxa, particularly *Pinus strobus*. The *Fagus-Acer* expansion was less evident in the record for Crystal Lake, primarily because of the coarse temporal resolution. These changes corroborated the interpretation of shift to a cooler and moister climate after 1600 cal yr BP evident in the records from Hicks Lake, Marion Lake and Lake 27.

At 1250 cal yr BP, mixed mesophytic forests declined around Cowden Lake as the *Quercus* forests became more common. A shift to *Quercus*-dominated forests was also evident in the Crystal Lake record but the timing of this evident is ambiguous (Kapp et al. 1990). The expansion of the *Quercus*-dominated forests is interpreted as a response to a warmer climate, which is correlated to the MWP. At this time, the mesic taxa, including *Fagus, Acer* spp., *Tilia*, and *Ulmus,* remained relatively abundant, moreso than in the previous mild period (2100-1600 cal yr BP) at Cowden Lake. This trend may reflect the increased moisture associated with the onset of the MWP contributing the persistence of the mixed mesophytic *Fagus-Acer* forests. This trend also indicates that the climatic change associated with the MWP was not significant enough to generate the decline of the *Fagus-Acer* forests. Changes associated with the MWP occurred slightly earlier at Cowden Lake than around Hicks Lake, Marion Lake and Lake 27, although these differences may be attributed to imprecision resulting from the dating of organic sediment and associated *Ambrosia*-correction method. The pollen record for Crawford Lake (Figure 3.1) (Yu 2003), located at approximately the same latitude as Cowden Lake in southern Ontario, also indicated a significant change *Quercus*-dominated forests during the MWP. Prior to the MWP, *Quercus* pollen percentages were relatively low at Crawford Lake but increased thereafter. In contrast to Cowden Lake, *Pinus* spp. pollen percentages increased significantly concurrent with the increase in *Quercus* in the pollen record from Ontario (Yu 2003).

The changes associated with the LIA (600-150 cal yr BP) around Cowden Lake occurred at 550 cal yr BP and included significant increases in the abundances of *Pinus* spp. and *Fagus,* concurrent with decreases in the abundances of *Quercus*, *Acer* spp., *Ulmus*, and *Carya*. Prior to 600 cal yr BP, *Thuja* dominated wet forests were relatively abundant but then declined at 550 cal yr BP corresponding to a much sharper decline of *Thuja* surrounding Hicks Lakes. This indicates a drier climate associated with the onset of the LIA. While the *Quercus*-dominated forests around Cowden Lake declined significantly, they persisted. This persistence suggests that while the *Quercus*-dominated forests did decline, they were not in direct equilibrium with the climate (Sprugel 1991). The dominate forest type was most likely a dry-mesic northern hardwoods forest dominated by *Pinus strobus* and *Fagus*. The Cowden Lake pollen record documented a *Tsuga* expansion corresponding to the *Tsuga* expansion at 300 cal yr BP around Hicks Lake, Marion Lake, and Lake 27 (Bernabo 1981).

Despite the lack of detail in the Crystal Lake pollen record, several patterns are shared between both the Crystal and Cowden Lake records. These trends included a strong relationship between the abundances of *Quercus* and *Fagus*. Both records documented opposite but concurrent patterns between the abundances of the two pollen types. Within this pattern, *Quercus* became less common and *Fagus* became more common. The increased abundance of *Pinus* spp. was documented in both records as well. The dominance of *Quercus* before this transition was also evident in both records. This evidence suggests that the rise in the importance of *Pinus* spp. in the *Pinus–Quercus* forests was a relatively new phenomenon, most likely a result of the cooling associated with the onset of the LIA. Thus in the 1300 years before the LIA, *Quercus* dominated the *Pinus-Quercus* xeric forests in the transition zone.

Records from Chippewa Bog (Figure 3.1), located within the tension zone but further east, documented similar shifts between *Quercus* and *Fagus* (Bailey and Ahearn 1981). The Chippewa Bog pollen record documented *Quercus* dominated forests before 2,000 cal yr BP, a subsequent decline with a concurrent expansion of *Fagus*-dominated forests, followed by a return to *Quercus*-dominated forests. The dynamics between *Quercus* and *Fagus* were not as evident in the Chippewa Bog record as around Cowden Lake but the record demonstrated similar variations over the past 2,000 years. The Chippewa Bog record also documented an increase in the abundance of *Pinus* spp. toward the end record, after 1000 cal yr BP. Again this record cannot be specifically correlated with the Cowden Lake record because of poor chronological resolution.

3.5.3 Forest Dynamics South of the Tension Zone

The forests around Morrison Lake were more stable over the past 2,000 years than those around Hicks Lake and Cowden Lake. The forests prior to 2000 cal yr BP were dominated by *Quercus* with relatively high abundances of other taxa such as *Carya*, *Ulmus* and *Populus*. After 2000 cal yr BP and until 1200 cal yr BP, mixed mesophytic *Fagus-Acer* forests were dominant near Morrison Lake. This trend contrasted greatly to the forest reconstructions around Cowden Lake, which were strongly dominated by *Quercus* from 2000 to 1600 cal yr BP.

A pollen record from Wintergreen Lake (Figure 3.1) (Manny et al. 1978), located approximately 60 km southeast of Morrison Lake, corroborated the dominance of *Quercus* prior to 2000 cal yr BP, as well as the expansion of the *Fagus-Acer* mixed mesophytic forests after 2000 cal yr BP. The Morrison Lake and Wintergreen Lake records indicate mild conditions, which correspond to other paleoclimatic estimations from pollen records (Bernabo 1981), but also indicate relatively high moisture, which was not evident in the other records for the Lower Peninsula. *Quercus* forests began to dominate after 1200 cal yr BP for several centuries at both Morrison Lake and Wintergreen Lake, which is attributed to in both cases the onset of MWP. *Quercus* forests remained dominant for several centuries. At 900 cal yr BP, *Quercus* abundances declined concurrent with an increased abundance of *Ulmus* more pronounced in the Morrison Lake records than in the record for Wintergreen Lake. This difference was most likely due to the coarse sampling resolution of Wintergreen Lake pollen record. The expansion of *Ulmus* at 900 cal yr BP corresponded to the dramatic increase of *Thuja* around Hicks Lake. Both indicate significant increased moisture during the MWP. The pollen record for Cootes Paradise, a coastal wetland in the western end of Lake Ontario (Figure 3.1), at a latitude between

Morrison Lake and Cowden Lake, also indicated the dominance of *Fagus* after 2000 cal yr BP (Finkelstein et al. 2005). This record also documented a subsequent decline of *Fagus* and expansion of *Quercus* which occurred approximately during the MWP, although a complete chronology was not reported by Finkelstein et al. (2005).

In contrast to the pollen signal of both Hicks Lake and Cowden Lake, major changes in the forests around Morrison Lake were not evident at the onset of the LIA. At Morrison Lake, the *Fagus-Acer* mesophytic forests expanded minimally. The *Fagus-Acer* forests may have been limited by the relatively drier conditions associated with the onset of the LIA, as indicated around Hicks Lake and Cowden Lake by decreases in the abundance of *Thuja*. A more significant decline in *Quercus* was evident at Wintergreen Lake although this decline was not accompanied by increased abundance of *Fagus* or *Acer* spp. (Manny et al. 1978).

Overall, less change occurred near Morrison Lake than around Cowden or Hicks Lake, over the past 2,000 yrs. These changes documented competition between the *Quercus*-dominated xeric forests and the mesic *Fagus-Acer* forests. The gradual nature of these changes suggests that climatic variations, as opposed to more dramatic disturbance events, such as fire or storms, were the main drivers of forest change around Morrison Lake. The general patterns of change over this period were corroborated by the nearest comparable paleoecological record from Wintergreen Lake (Manny et al. 1978).

3.5.4 The Forest Tension Zone within a Regional Context and Beyond

The results from this research generally parallel those from other regions within the eastern half of North America, although sub-regional differences are apparent. Several major trends in the fossil pollen records for Hicks Lake, Cowden Lake and Morrison Lake are also evident in other fossil pollen records.

Because relatively few studies have documented meso-scale vegetation change in response the MWP, the responses of the forests in the central Lower Peninsula of Michigan cannot be directly compared to most other pollen studies in eastern North America. In the Hudson Valley of New York, fossil pollen records document increased abundance of *Pinus* and *Carya* concurrent with declines in *Quercus* during the MWP (Pedersen et al. 2005). In contrast *Quercus* forests expanded during the MWP at both Morrison and Cowden Lake. The disparities between these trends suggest that the climatic changes associated with the MWP, i.e. increase or decrease in precipitation, was variable across North American (Stine 1998).

In contrast to the MWP, many studies document vegetation change associated with the LIA in the eastern half of North American. During the LIA the increases in the local abundance of *Tsuga* evident at Hicks Lake and more subtlety at Cowden Lake was also evident in pollen records in northern Wisconsin (Swain 1978) but not for the northeast (Gajewski 1987; Russell et al. 1993). An increase in local abundance of *Tsuga* during the LIA was also detected in the Hudson Valley of New York (Pedersen et al. 2005). Increases in the local abundances of *Picea* were also noted during the LIA in New York

(Pedersen et al. 2005) and the northeast United States in general (Gajewski 1987; Russell et al. 1993) although this trend was not as pronounced at Hicks Lake or Cowden Lake. *Pinus* populations expanded during the LIA at both Hicks and Cowden Lake but this trend was only evident at limited locations in the eastern United States (Russel let al. 1993). An increase in the population of *Pinus* was also noted in the southern portion of its range in Ontario, Canada (Campbell and McAndrews 1991). In southern Minnesota, the big woods, dominated by mesophytic taxa, such as *Ulmus*, *Tilia americana* and *Acer saccharum,* expanded after the onset of the LIA (Grimm 1983). This trend contrasts to the pollen records for Morrison Lake where *Quercus*-dominated forests were more prevalent than the mixed mesophytic forests of *Fagus*, *Acer*, *Ulmus* and *Tilia* during the LIA.

The increased abundance and range expansion of *Fagus* that was evident during the LIA in the Upper Peninsula of Michigan (Davis et al. 1986; Woods and Davis 1989) was not evident at Hicks Lake or at Cowden Lake. In contrast to the Upper Peninsula of Michigan, a decrease of *Fagus* during the LIA was noted in the northeast (Gajewski 1987; Russell et al 1993). A decline in the abundance of *Fagus* at its northern limit was noted in Ontario, Canada at this time as well (Campbell and McAndrews 1991).

3.6 Conclusions

Pollen records from three lakes, Hicks Lake, Cowden Lake, and Morrison Lake were used to reconstruct the vegetation history of the forest tension zone, an ecotone in the Lower Peninsula of Michigan between the mixed Laurentian forests and the eastern broadleaf forests during the past 2,000 years. The pollen records provided evidence of significant vegetation change at all three sites as well as indicated the presence of the 'tension zone' during the past 2,000 years. The ordination analysis of the pollen data from each site demonstrated that forests changed in terms of species dominance at all three lakes over time. Ordination diagrams displaying Holocene pollen records commonly document progression for one vegetation assemblage to another, i.e. spruce-fir to pine transition (Yu 2005). Oscillations between vegetation assemblages, particularly shifts back to previous vegetation assemblages, are usually not evident in coarse-scale (millennial resolution) vegetation reconstructions. In contrast, the ordination from this study demonstrated short-term oscillations between forest assemblages at all three lakes.

Several overall trends are evident in the forest dynamics at each of the lakes. These include:

1) At Hicks Lake, the pollen records documented strong competition between Cupressaceae, presumably *Thuja occidentalis,* and *Tsuga* and *Picea*. This competition indicates fluctuations between mesic coniferous forests dominated primarily by *Tsuga* and wet-mesic coniferous forests dominated by *Thuja occidentalis*.
2) Before 400 cal yr BP, *Pinus* spp. was a less significant component of the forests around Hicks Lake; after 400 cal yr BP both *Tsuga* and

Pinus spp. increased significantly and dominated the forests around Hicks Lake.

3) Competition between *Quercus* and *Fagus* was reconstructed for the pollen data from Cowden Lake. Thus, the forests near Cowden Lake were quite variable, transitioning relatively quickly from the xeric *Quercus*-dominated forests to the more mesic mixed *Fagus-Acer* forests.
4) Overall, less dramatic changes were evident in the forests around Morrison Lake during the past 2,000 years, compared to the other two study sites, although competition between *Quercus* and *Fagus* remained evident. Except for a period from 1650 to 1250 cal yr BP when the mesic *Fagus-Acer* forests were dominant, the forests near Morrison Lake were predominately mixed *Quercus* forests.

The pollen records from all three lakes documented significant changes in forests composition in association with several medium frequency climatic oscillations variations over the past 2,000 years, including the MWP from 1000-800 cal yr BP and the LIA from 600-150 cal yr BP. These changes include:

1) A shift from relatively mild and dry conditions to relatively cool and relatively moist conditions at 1700 cal yr BP. This shift was characterized by: the increased abundance of Cupressaceae, mainly *Thuja occidentalis*, and decline of *Pinus* spp. and *Picea* around Hicks Lake; a dramatic expansion of *Fagus*, *Acer* spp. and *Ulmus* concurrent with a decline in *Quercus* at 1650 cal yr BP near Cowden Lake; and

the dominance of *Fagus-Acer* spp. forests near Morrison Lake for several centuries after 1700 cal yr BP.

2) A period of increased warmth and greater moisture interpreted as a vegetation response to the MWP from 1000-800 cal yr BP is characterized by: a dramatic expansion of *Thuja* at 900 cal yr BP around Hicks Lake; a dramatic expansion of *Quercus* and decline of *Fagus* beginning at 1250 cal yr BP around Cowden Lake; and a shift to *Quercus*-dominated forests followed by the decline of *Fagus-Acer* forests beginning at 1200 cal yr BP.
3) A period of cooling and decreased moisture at the time of the LIA from 600-150 cal yr BP was interpreted from the pollen data which indicate: a dramatic decline in *Thuja* and expansions of *Pinus* spp. and *Tsuga* beginning at 550 cal yr BP around Hicks Lake; a decline in *Quercus* and expansion of *Pinus* spp., *Tsuga*, and *Fagus* around Cowden Lake began also at 550 cal yr BP; and increased abundance of *Fagus* and *Acer* spp. accompanied by a decline in *Quercus* beginning at 500 cal yr BP.

The fossil pollen records from all three sites generally indicate that vegetation responded to climatic variations within a relatively short time period similar to lags identified in other studies (Webb 1986). For example, the *Fagus-Acer* forests remained relatively abundant on the landscape after the onset of the MWP near Cowden Lake. This prevalence indicates a lags between climate change and the response of the Fagus-Acer forests suggesting that the forests in the central Lower Peninsula of Michigan were not in direct equilibrium with climate. Other types of disturbances e.g. from fire and wind storms, as well as the legacies of past disturbances, play a role in vegetation change, further complicating the responses of forests to climatic change and identification of time lags (Sprugel 1991; Perry 2002).

This research contributes to the paleoecological history of the Lower Peninsula of Michigan by providing a detailed reconstruction of forest history during the past 2,000 years. The fossil pollen record from the Hicks Lake, Cowden Lake, and Morrison Lake demonstrated the dynamic nature of the forests in the Lower Peninsula of Michigan. Vegetation change in response to three separate medium frequency climatic oscillations, including the MWP and LIA, was detected. The results from this research also show that these forests responded quickly to climatic change in the past, and suggest that these forests would respond as quickly to climatic change associated with global warming.

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ECOTONE DYNAMICS: 2000 YEARS OF FOREST CHANGE IN THE LOWER PENINSULA OF MICHIGAN, USA

VOLUME II

By

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Chapter 4

Meso-scale Dynamics of the Forest Tension Zone in the Central Lower Peninsula of Michigan, USA: 2,000 Years of Change

4.1 Introduction

The climate of the Great Lakes region is predicted to be 2 °C warmer and wetter, with 15-20% more precipitation, by the end of the 21st century (Sousounis and Bisanz 2000). These predicted changes will greatly impact forest ecosystems in the region, especially because many dominant tree species in these forests are at the edge of their geographical ranges, and are thus sensitive to climate change (Solomon and Bartlein 1992; Walker et al. 2002). The composition, extent, and diversity of forest communities are likely to change in response to future climatic variations (Walker et al. 2002). For example, by 2025 *Pinus resinosa* (red pine) may no longer grow in the Lower Peninsula of Michigan, where today it is a dominant species today (Sykes et al. 1996). Forests are already stressed from a variety of disturbances in addition to global warming, including harvesting, pests (Emerald ash borer), disease (Dutch elm disease), and land use change. Since these forests are important resources, not only for commercial reasons but for ecosystem health, as well as recreation (Sousounis and Bisanz 2000), we need to manage for their longevity and health. Successful management requires detailed knowledge about current forests ecosystem. It also requires knowledge regarding how forest systems change over time in response to a wide variety of pressures, such as climate change and disturbance.

Much of our current understanding of the impacts of climate change on forest ecosystems is based on the responses of forests to climate change during the Holocene (Solomon and Bartlein 1992). The majority of research on Holocene vegetation change has been conducted at relatively coarse temporal (past 10,000 yrs at 1,000-yr intervals) and spatial scales (1000's km), i.e. at the macro-scale domain. This research has offered many insights into the nature of long-term vegetation change as well as provided a strong ecological basis for predicting future change (Foster et al. 1990; Davis 1994). Specifically, insights gained from macro-scale research into Holocene vegetation dynamics include: (1) species responses were generally at a dynamic equilibrium with climate change (Webb 1986); (2) species responded individualistically to environmental change; (3) the vegetation assemblages present today may not have had analogs in the past; and (4) the ranges of many species shifted northward during the early Holocene (Davis et al. 1986; Webb 1986; Prentice et al. 1991; Overpeck et al. 1992).

Very few studies in the Great Lakes region have examined vegetation dynamics at intermediate temporal and spatial scales, i.e. the meso-scale domain (sub-regional changes at 10 to 100-yr intervals), resulting in a void in the paleoecologic record. However, models attempting to predict future responses of vegetation to global warming, such as the STASH model which predicts the decline of *Pinus resinosa* in the Lower Peninsula of Michigan by 2025 (Sykes et al. 1996), are often conducted at intermediate scales and require knowledge and data collected at meso-scales. The few existing studies conducted at the meso-scale domain have: 1) provided valuable insights into vegetation dynamics; 2) wide application; and 3) aided in forest management; and 4) aided in modeling efforts to predict future forest change (Bernabo 1981; Davis et al. 1986; Solomon and Bartlein 1992). Results from meso-scale research investigating the responses of forest ecosystems to climate change will aid efforts to better predict future forest change by providing detailed data sets measuring changes at the same scales in which the models are predicting change, by filling a gap in the paleoecolgical record, and by providing valuable insight into vegetation dynamics at scales at which relatively little research has been conducted (Overpeck et al. 1991; Noss 2001; Jackson and Williams 2004; Saxon et al. 2005).

Ecological communities are most sensitive to changes in their environment, i.e. climate change and disturbance, at an ecotone. A tension zone is a type of ecotone, a boundary between plant communities, where plants species reach their distributional range limits on the landscape (Anderson 2005). Tension zones are spatially measurable systems, sensitive to climate change, and thus provide an excellent opportunity to examine vegetation responses to climate change over time at the meso-scale domain (Neilson 1993; Baker and Weisberg 1995; Kupfer and Cairns 1996; Cairns 1999; Malanson et al. 2001; Anderson 2005). Several studies have successfully documented and quantified transitions in ecotones during the Holocene period in North America at the macro-scale domain (Liu 1990; MacDonald 1998; Camill and Clark 2000; Baker et al. 2002), but very few studies have examined ecotone dynamics at the meso-scale domain. Meso-scale domain research has the potential to answer questions about ecotone dynamics and the responses of vegetation to short-term variations in climate such as: *How stable are temperate forest tension zones? Do tension zones become more diffuse or more defined as a result of climate change? Which species are most likely to respond?*

Many tree species are located at the edge of climatic tolerances and thus their geographical limit falls within the forest tension zone of the Great Lakes region. This tension zone spans from southern Ontario westward to northern Minnesota. Along this geographic boundary between major forest associations, the nature of the tension zone changes in correspondence with the different forests communities present in the Great Lakes region (Andersen 2005). In the central Lower Peninsula of Michigan, the tension zone is a transition between deciduous forests in the south, which include *Fagus-Acer* (beech-maple) and mixed *Quercus* (oak) forest communities, and the mixed coniferous-deciduous forests in the north, with dominants such as *Fagus, Acer, Tsuga* (hemlock), and various species of *Pinus* (pine). Several macro-scale paleoecolgical pollen studies have documented transitions in the forest tension zone in the Lower Peninsula of Michigan during the Holocene (Potzger 1948; Gilliam 1967; Ahearn 1976; Bernabo 1981; Webb et al. 1983; Kapp 1999). Although these studies have provided valuable knowledge about the long-term dynamics of these forests, relatively little is known about the dynamics of the forest tension zone at finer temporal and spatial scales.

The purpose of this research was to assess changes in the forest tension zone in the central Lower Peninsula of Michigan during the past 2,000 years. Specifically, the objectives of this research were 1) to determine if the tension zone has shifted over the past 2,000 years, 2) to determine which communities have shifted, and 3) to examine how species associations have reorganized over this time period. This study is unique because it integrates two different types of biogeographic data, fossil pollen records and historical survey data, collected at different temporal and spatial scales, in order to address these objectives. Fossil pollen data from three lakes, which lie along a north-to-south transect crossing the tension zone, were used to assess shifts in the tension zone. The Public Land Survey (PLS) data, collected just prior to Euro-American settlement in the area around 1836, was utilized as a detailed baseline of the vegetation that existed at that time. Correlation of the PLS data and the fossil pollen data sets allowed for the examination of the reorganization of species within forest communities and between communities both north, within, and south of the tension zone, during the last 2000 years.

This study is also unique because it examines forest ecotone dynamics at the meso-scale domain before the onset of Euro-American settlement in the region, as well as the changes in these forests during the past 2,000 years. While Native American activity prior to Euro-American settlement has been documented in the Lower Peninsula of Michigan, the impact of this activity appears to have been relatively minimal and localized within the study area itself (Lewis 2002; Lovis et al. 2005). Therefore, the PLS and fossil pollen data provide detailed records of forest composition before the onset of massive Euro-American disturbance in the study area.

In order to determine if the tension zone has shifted over time, as well as which communities have changed in species composition and dominance, the fossil pollen data and PLS data were analyzed with multiple statistical techniques. The fossil pollen data were analyzed with discriminant analysis, which compares fossil pollen data to sets of existing modern pollen data from known vegetation types (Liu and Lam 1985). This analysis has been successfully employed to identify shifts in other ecotones in the Great Lakes region during the Holocene and has identified coherent movement of vegetation communities in space, i.e., ecotonal shifts (Liu 1990; Liu et al. 2001). Several studies have investigated ecotone changes over the entire Holocene at the macro-scale domain using this technique (Lui 1990; Liu et al. 2001; Baker et al. 2002). However, this method has not been applied at the meso-scale domain to high-resolution fossil pollen data, in any locale, or to the forest tension zone in the Lower Peninsula of Michigan.

4.1.1 Study Area

Within the Great Lakes region, the broadleaf forests of eastern North American in the south transition into the Laurentian mixed forests in the central portion of the region. The mixed Laurentian forests then transition into the boreal forests in the north. Thus between these two transitions lie two major forest ecotones (Figure 4.1). This research focused on the tension zone, the ecotone between the Laurentian mixed forests and the eastern broadleaf forests in the central Lower Peninsula of Michigan (Potzger 1948; Elliot 1953; Curtis 1959). This tension zone spans from central Minnesota to southern Ontario (Andersen 2005). In the Lower Peninsula of Michigan, the tension zone is where the southern distributional limit of the *Tsuga-Pinus strobus* (white pine)-northern hardwood communities meets the northern distributional limits of the *Fagus-Acer* and *Quercus-Carya* (hickory) communities of the broadleaf forests (Figure 4.1) (Barbour and Billings 1988; Burns and Honkala 1990). Also, several herbaceous taxa meet their southern or northern range limits in the central part of the Lower Peninsula (Voss 1972).

The tension zone is typically described as a 95-km wide belt (Potzger 1948). The center of this ecotone may be broadly approximated by the 8°C (47°F) isotherm of mean annual temperature (Barnes 1981), but the exact delineation of the zone varies (Schaetzl 1991). The spatial arrangement of the forest tension zone in the Lower Peninsula of Michigan and the environmental factors responsible for this ecotone has been debated in the literature (Medley and Harman 1987; Andersen 2005). Various authors describe the tension zone differently; some characterize it as an abrupt ecotone (Medley and Harman 1987), while others refer to it as a diffuse ecotone (Elliot 1953; Brewer 1982). McCann (1979) concluded that the boundary is best associated with a steepening in the gradient of growing degree days, decreasing in a northerly direction, at the location of the transition. Alternatively, Brewer's (1985) research attributes the transition to competition between northern taxa, *Tsuga canadensis* and *Pinus strobus*, and the southern taxa of *Quercus* and *Carya*. Medley and Harman (1985), the last in the series of such research, concluded that the location of the tension zone was significantly correlated with the increase of coarse-textured soils in the north and the ability of coniferous species to outcompete deciduous species on these sites. Currently, the general consensus is that the broad scale influence of the location of the tension zone is assumed to be climate, while at finer spatial scales, edaphic controls are more important (Barnes 1981; Medley and Harman 1987; Dodge 1995). Coarse-textured soils are more common in the northern part of the Lower Peninsula on which coniferous species are more successful, while in the southern part, deciduous trees out-compete coniferous trees on fine-textured loamy soils.

The Lower Peninsula of Michigan experiences a humid continental climate regime. But within the Lower Peninsula itself, temperature and precipitation vary considerably. The annual mean temperature in the state ranges from 10° C in the Lower Peninsula to 4.3° C in the Upper Peninsula. Within the study area itself, the average maximum July temperature is 25.5 ° C and the minimum average January temperature is -11° C (data for Mount Pleasant, Michigan) (Hoare 2005). The northern part of the Lower Peninsula experiences approximately 70 growing days while the southern Lower Peninsula experiences 160 to 170 days (Schaetzl and Isard 2002). Precipitation varies across the Peninsula as well; in the Lower Peninsula of Michigan, annual mean precipitation ranges from a 91.4 cm in the southwest to 68.5 cm in the northwest Lower Peninsula.

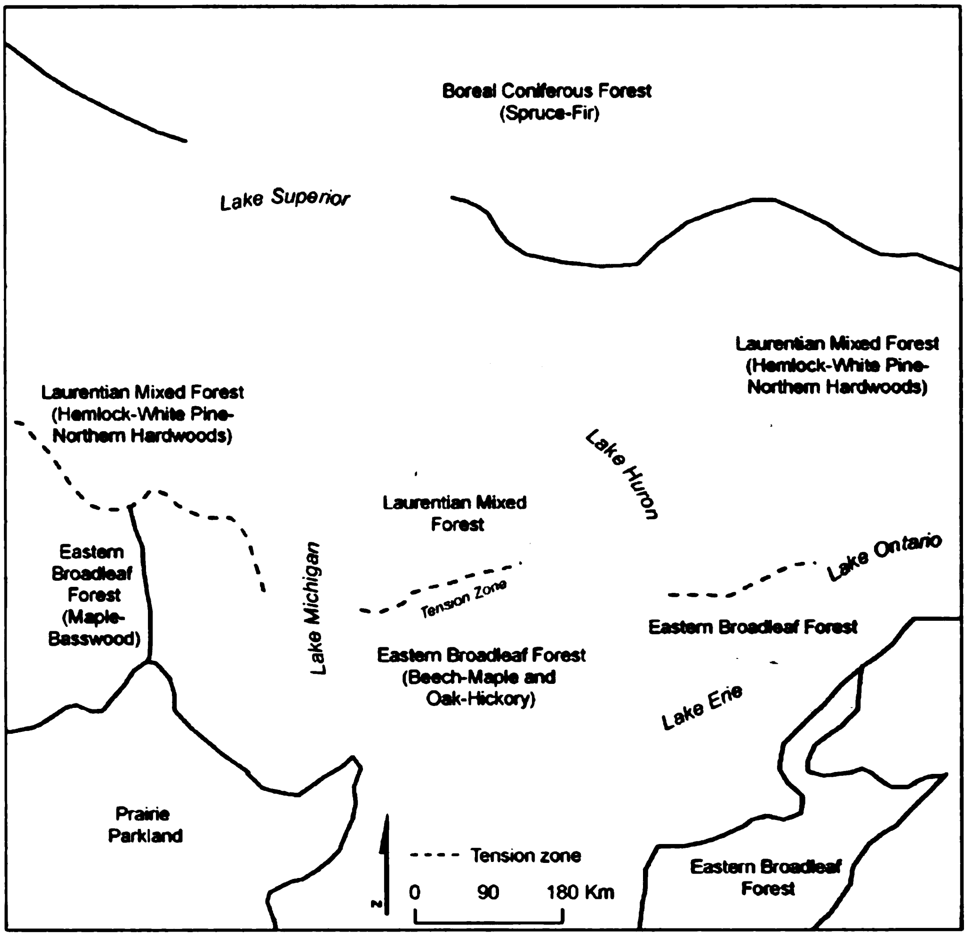

Figure 4.1 Major vegetation regions in the Great Lakes region and the location of the tension zone (Bailey 1976).

4.2. *Methods*

4.2.1 *Fossil Pollen Analysis*

Fossil pollen analysis was conducted on sediment cores taken from three lakes sites which lie along a north-to-south transect across the tension zone: Hicks Lake in Osceola County (north of), Cowden Lake in Montcalm County (within), and Morrison Lake in Ionia County (south of) (Figure 4.2). Sediments were sampled for fossil pollen analysis (1 cm^3) at every 2 centimeters along the length of the cores. Fossil pollen was concentrated using a set of standard lab procedures (Faegri and Iverson 1975), slightly modified by Shane (c1998). Between 300 and 500 grains of upland taxa were identified and counted for each sample. Because the terrestrial materials (upland plant and/or charcoal), recovered from sieving (using 212 μm to 450 μm mesh opening sieves) were not of sufficient mass for ^{14}C for dating by the accelerator mass spectrometry (AMS) technique (Gillispie 1984), organic sediment ($1 cm^3$) was dated using AMS. In all, three radiocarbon dates were obtained for each core in order to establish radiocarbon chronologies. In order to mediate the erroneously older dates which may result from the dating of organic sediment, mainly due to the incorporation of ancient carbon from geologic materials in the sediments, I employed the *Ambrosia* correction method which is described by Grimm (1983) (Table 4.1).

Pollen sums were calculated for each of the three lakes using Tilia™ software (Grimm 1993). Sums include all upland taxa and herbaceous species, but do not include spores and aquatics. Biostratigraphic diagrams were produced based on the percentages of each taxa and the ^{14}C chronology also using Tilia™ and Tilia Graph ™ (Grimm 1993). The pollen data sets were then analyzed with stratigraphically constrained cluster analysis in CONISS ™ software (Grimm 1987) using no transformations, or Euclidean distances. The resulting dendrograms were then used as a basis for identification of vegetation zones within each lake. For additional details of methods used in fossil pollen analysis, see Chapter 3.

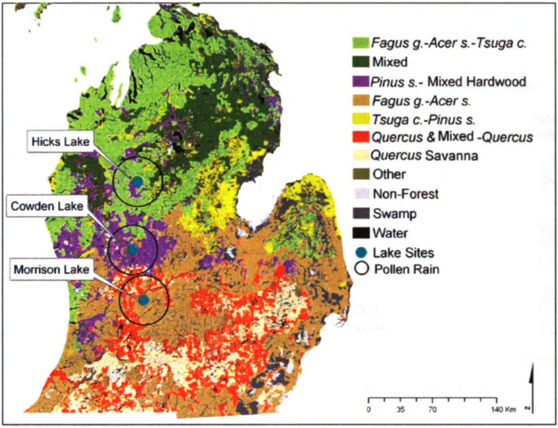

Figure 4.2 Location of three lake sites, Hicks Lake, Cowden Lake, and Morrison Lake, chosen for pollen analysis. The map also displays the forest composition in Lower Peninsula of Michigan circa 1800 (Comer et al. 1995).

Table 4.1 Radiocarbon dates (^{14}C) dates from Hicks Lake, Cowden Lake, and Morrison Lake, Michigan. All dates reported in text are calibrated and in years B.P. The material dated for all samples was organic bulk sediment.

					Sedimentation	
Sample Depth (cm)	**Lab No.**	**^{14}C date (B.P. ± SD)**	**Correction Factor**	***Ambrosia* Corrected Date**	**Depth (cm)**	**Rate (cm/yr)**
Hicks Lake						
H/FW 65	195939	646 ± 40[a]	492	154	0 – 65	.422
H/A/D1 91	114477	1349 ± 35[b]	492	857	65 – 91	.036
H/A/D2 143	194252	3206 ± 40[a]	492	2714	91 – 143	.028
Cowden Lake						
C/FW 65	195938	562 ± 40[a]	408	154	0 – 65	.422
C/A/D1 91	1144776	1231± 35[b]	408	823	65 – 91	.038
C/A/D2 140	194253	2954 ± 40[a]	408	2546	91 – 140	.028
Morrison Lake						
M/FW/ 61	195937	644 ± 40[a]	490	154	0 – 61	.396
M/B/D2 111	114475	2490 ± 35[b]	490	2000	61 – 111	.027
M/B/D2 140	194251	2545 ± 40[a]	490	2055	111 – 140	.52

.. [a] Dates obtained from Beta Analytic Inc. Miami FL, USA.

[b] Dates obtained from CAMS: Center for Accelerator Mass Spectrometry, Lawrence Livermore National Laboratory, USA.

4.2.2 Public Land Survey Data Analysis

The U.S. General Land Office's (GLO) original Public Land Survey (PLS) was initialized in 1785 and was conducted in Michigan between 1816 and 1856, prior to the onset of massive Euro-American settlement in the Lower Peninsula (Comer et. al 1995a). Therefore, the PLS data provide a record of the forests before the major disturbance associated with Euro-American settlement and subsequent activities. The original PLS data have not been entered into a digital public data base, as in some other states. Michigan Natural Features Inventory (MNFI), a branch of the Michigan State University Agricultural Extension Service, georeferenced and transcribed the original GLO survey notes onto matte mylar attached to 7.5 minute U.S. Geological Survey topographic maps (scales of 1:24,000 and 1:25,000) (hereafter mylar-maps) for the entire state of Michigan.

In this research, the PLS data bearing tree data were collected directly from the mylar-maps.

The PLS bearing tree data were analyzed with forest structural metrics, and statistical clustering. Relative importance of species within the study area, calculated from both relative density and relative dominance, was the primary input for all statistical analysis. Relative importance is a standard metric used to analyze PLS data, and it provides readily interpretable measures of tree distribution on the landscape (Schulte et al. 2002). All metrics were calculated for each individual species within a sample, one PLS section (1 mi^2 or 2.65 km^2). Cluster analysis was utilized to identify groupings of species, i.e. communities, on the landscape. Once communities were identified, maps of these communities were constructed at the spatial grain of sampling, one PLS section. A separate cluster map was generated for the area of pollen rain, 27 km radius, surrounding each of the three lakes (Figure 4.3). The estimated area of pollen rain was based on the relationships of modern pollen rain and lake size established by previous research (Jacobson and Bradshaw 1981; Bradshaw and Webb 1985). The pollen rain layer was then intersected with the map of forest composition. The clusters maps for each of the three lakes were then used as input for the further analysis addressed below. For detailed methods of this analysis see Chapter 2.

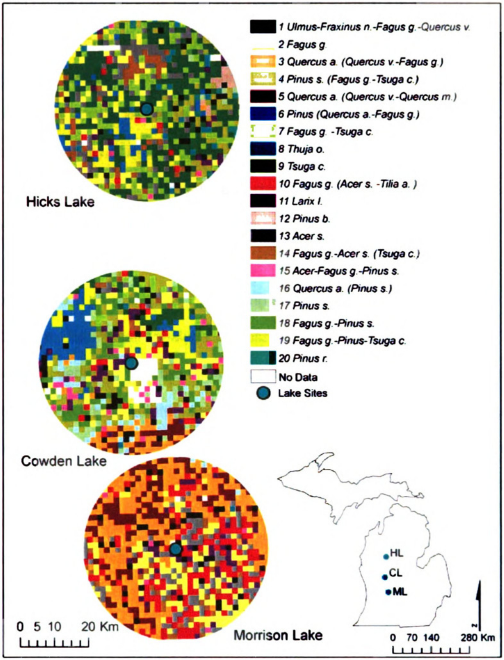

Figure 4.3 Map of clusters generated from clusters analysis of Public Land Survey Data (PLS) for the area within each pollen rain (27 km radius) for the three study lakes in relation to the tension zone: Hicks Lake (HL-north), Cowden Lake (CL-center), and Morrison Lake (ML-south).

4.2.3 *Discriminant Analysis*

Discriminant analysis was used to classify the fossil pollen samples from the three study lakes into vegetation types (deciduous, mixed, boreal) based on the fossil pollen percentages of various taxa within each of the samples. A set of modern pollen samples located within known vegetation types was used as the basis for this classification. This technique quantitatively assigned a probability of group membership for each sample into the three different vegetation types as well as a probability of modern analog. The results from the discriminant analysis were then used to detect major changes the type of vegetation at each site over time, further allowing ecotone change to be quantified.

Discriminant analysis is a method for differentiating samples into known groups based on probabilities. First, using samples with a known group membership, discriminant analysis establishes linear combinations of independent variables referred to as discriminant functions. These functions ensure maximum separation between the a-priori group samples (Liu and Lam 1985). The discriminant functions are then used to assign the unknown samples into one of the existing groups. The validity of the discriminant functions is tested by using the existing groups as new members, and then assigning their group membership. The use of discriminant analysis in palynology was first discussed in Birks and Peglar (1980), and later refined and developed by Lui and Lam (1985). Lui (1990) used discriminant analysis to identify ecotonal shifts in the forests of northern Ontario during the Holocene. This technique has been used to detect ecotonal shifts in other ecosystems as well (MacDonald 1987; Liu et al. 2001a).

Relationships between modern pollen spectra and vegetation patterns were used to establish the discriminant functions. The modern pollen spectra from a total of 196 sites from Michigan and Ontario were used as inputs for the discriminant analysis (Figure 4.4). The pollen data for the sites were obtained from the North American Pollen Database (NAPD 2005). The 196 sites lie along a broad transect from 54.4 °N to 41.5 °S and from 94.8°W to 75.6°W. The data were downloaded and imported into *Tilia*™ in order to calculate pollen percentages. Each site was then assigned to its respective modern vegetation assemblage based on its spatial location (Kuchler 1964; Schaetzl and Isard 2002).

This study encompasses three major vegetation regions including (1) deciduous forest, (2) Great Lakes-St. Lawrence Forest (mixed-forest), and (3) boreal forest. Among the sites chosen for analysis, 39 sites are located within the deciduous region, 106 within the mixed-forest region, and 51 were located within the boreal region (Figure 4.4). In both the modern and fossil pollen samples, a total of 18 taxa were used for the discriminant analysis. These include: *Pinus (*Haploxylon-type), *Pinus (*Diploxylon-type), *Picea, Abies,* Cupressaceae (*Thuja occidentalis*), *Tsuga, Acer* spp., *Alnus, Betula, Carya, Fagus, Populus, Quercus, Salix, Ulmus, Artemisia,* and Poaceae. The discriminant analysis was conducted using the discriminant function in SPSS™ software (2005). The fossil pollen assemblages were then ordinated along each of the discriminant functions.

Discriminant analysis produces two separate parameters: probability of group membership and probability of modern analog. Probability of group membership was used to establish a Vegetation Zone Index (VZI) following Lui and Lam (1985). The zonal nature of vegetation allows the establishment of the VZI. In all cases, the second most probable group is always one of the groups, which is geographically closest (Liu and Lam 1985). For example, if a sample is classified as deciduous then the most probable group is always mixed-forest as opposed to boreal forest. Because of this zonal nature, the probabilities of group membership can be transformed into the VZI. Typical samples, i.e. 100% probability of group membership, are classified and assigned their respective value of 1 for deciduous, 2 for mixed, and 3 for boreal. Transitional samples with intermediate probabilities are assigned values relative to the two perspective group memberships. A sample with an 83% probability of mixed-forest but 27% deciduous forest would be a 1.83 VZI. Samples classified as deciduous range from 1.0 to 1.5, mixed from 1.5 to 2.5, and boreal from 2.5 to 3.5. (Liu and Lam 1985). In this manner, shifts in vegetation type can be interpreted from the VZI. The VZI value was determined for each of the fossil pollen samples at all three lakes, plotted for each lake in chronological order, and then interpreted to detect shifts in forest composition at each of the sites.

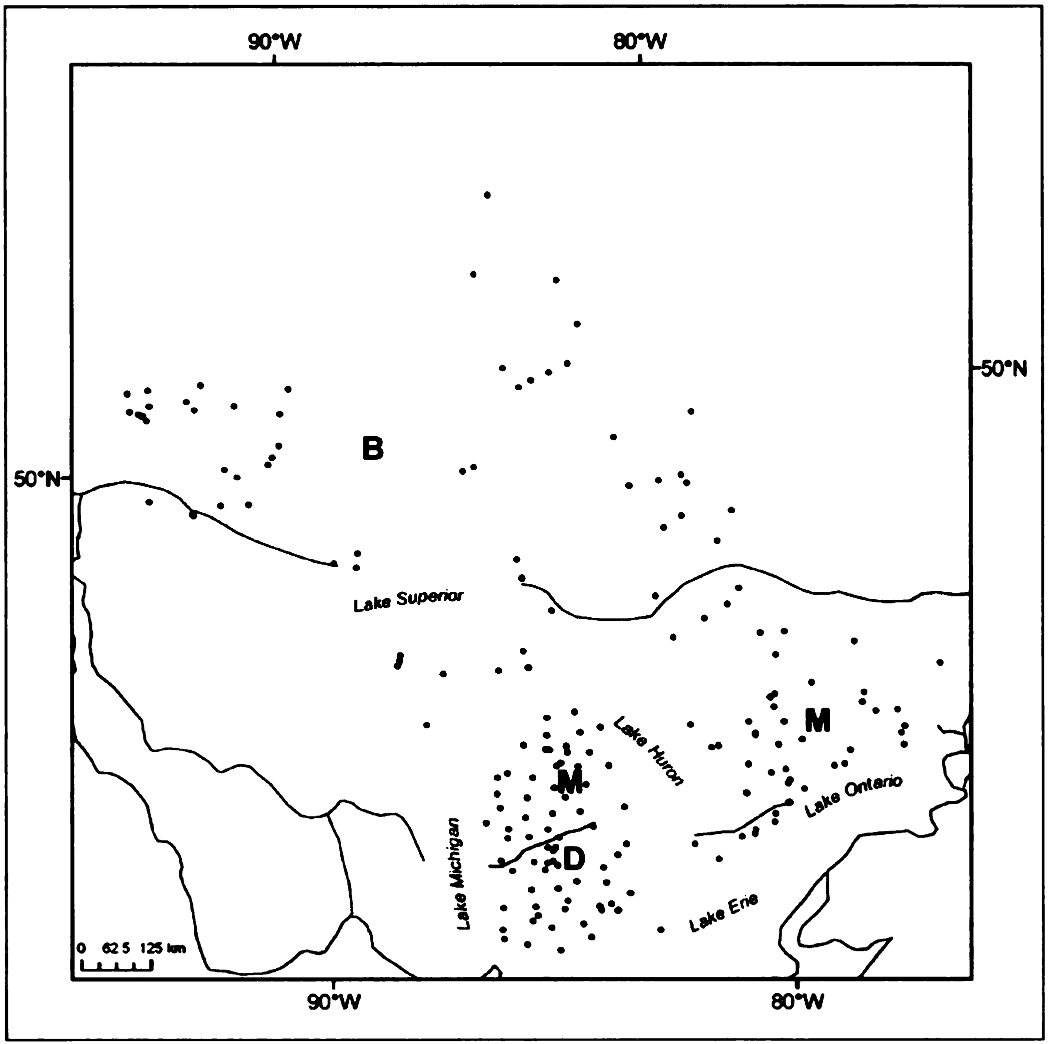

Figure 4.4 Distribution of the 196 modern pollen sites in relation to vegetation regions; D = deciduous (eastern broadleaf), M = mixed forest (Laurentian), and B = boreal. Source NAPD 2005.

4.2.4 Squared Chord Distance

The results from the fossil pollen analysis were further analyzed with dissimilarity analysis. Squared-chord distances were calculated between temporally paired samples in order to examine the similarities between forests around each lake over time. Squared-chord distance is a multivariate measure of dissimilarity between pollen assemblages. The equation for squared-chord distance is as follows: $Dij = \sum_k (p_{ik}^{0.5} - p_{jk}^{0.5})^2$ where D_{ij} is the distance between sample *i* and sample *j*, and p_{ij} and p_{jk} are the proportion of pollen type *k* in samples *i* and *j*, respectively. This quantitative technique has been used to successfully identified changes in forest communities over similar distances (Fuller 1997; Flakne 2003). While several studies have used this technique to investigate forest change during the entire Holocene at relatively coarse resolutions (Lui 1990; Liu et al. 2001b; Baker et al. 2002), this technique has not yet been applied to relatively finer-resolution data or with regards to the tension zone in the central Lower Peninsula of Michigan.

In this study the pollen percentage data for the samples from each lake were averaged for each time segments of 100 years per lake. The averages were then correlated based on the interpolated calibrated ages, and compared for each 100-year time interval, for example 200-100 cal yr BP per lake. A total of 45 samples, 15 from each lake, were used in the final analysis. A total of 18 pollen types were compared between samples from the three lakes: *Pinus (*all types*), Picea, Abies,* Cupressaceae, *Tsuga, Acer* (all types)*, Alnus, Betula, Carya, Ostrya, Fagus, Fraxinus* (all types)*, Juglans, Populus, Quercus, Salix, Tilia,* and *Ulmus*. The squared-chord distance for each pair of samples, i.e. Morrison versus Hicks, Hicks versus Cowden, and Morrison versus Cowden, was plotted for each time period.

4.2.5 *Comparison of PLS and Pollen Data*

Forest composition based on the analysis of the Public Land Survey (PLS) data was compared to the pollen percentages for the same time period. First, the location of each of the three lakes was entered into a geographic information system. A spatial layer of the estimated pollen rain area was then generated by buffering the lakes at a distance of 27 km^2. The percentage of each community within the pollen rain for each lake is listed in Table 4.2 and the maps for each of the lakes are shown in Figure 4.3.

In order to compare the PLS data to the fossil pollen records, both data sets were transformed to represent tree abundance. The pollen data for each of 15 taxa were transformed into tree abundance values based on their regional calibration coefficients (Table 4.2). The regional calibration coefficients were taken from Bradshaw and Webb (1985) and from Delcourt and Delcourt (1987). In order to transform the PLS data, the total diameter at breast height (DBH) for all the tree species was calculated for each section within the pollen source area (Figure 4.3), for each of the three lakes. Rare species, those represented in less than 1% of the sections within the pollen source area for each lake, were then eliminated from the data set. Both the DBH data set and the calibrated pollen data set were analyzed with detrended correspondence analysis. While the DBH data set and the calibrated pollen data set were not directly statistically compared here, comparison of the ordination diagrams was used in providing additional insights into the dynamics of the forest communities and species assemblages surrounding each lake. A similar approach has been used to analyze detailed data on forest succession within the context of the last 2,000 years of change in a Danish temperate forest (Bradshaw et al. 2005).

Table 4.2 Percentage of each cluster within the pollen rain for the three lakes with reference to the tension zone: Hicks Lake (north of the tension zone); Cowden Lake (within the tension zone); and Morrison Lake (south of the tension zone).

Cluster #	Cluster Name	Hicks Lake	Cowden Lake	Morrison Lake
1	*Ulmus - Fraxinus nigra - Fagus – Quercus velutina*	2.4	4.8	4.0
2	*Fagus*	6.7	6.5	12.6
3	*Quercus alba (Quercus veluntina - Fagus)*	0.2	6.7	32.2
4	*Pinus strobus (Fagus - Tsuga)*	9.4	15.1	0.2
5	*Quercus alba (Quercus veluntina – Quercus muehlenbergii)*	0.0	4.2	15.7
6	*Pinus (Quercus alba - Fagus)*	4.8	9.1	0.0
7	*Fagus - Tsuga*	14.8	3.5	0.0
8	*Thuja*	1.8	0.3	0.1
9	*Tsuga*	29.7	5.0	0.0
10	*Fagus (Acer saccharum - Tilia)*	1.0	2.3	14.6
11	*Larix*	1.9	4.4	3.4
12	*Pinus banksiana*	2.2	0.0	0.0
13	*Acer saccharum*	9.1	0.8	10.7
14	*Fagus - Acer saccharum (Tsuga)*	5.2	0.9	3.9
15	*Acer - Fagus - Pinus strobus*	0.7	2.6	0.6
16	*Quercus alba (Pinus strobus)*	0.0	5.7	1.1
17	*Pinus strobus*	1.0	11.2	0.8
18	*Fagus - Pinus strobus*	1.3	11.3	0.0
19	*Fagus - Pinus - Tsuga*	5.3	5.4	0.0
20	*Pinus resinosa*	2.3	0.0	0.0

Table 4.3 Calibration coefficients for aboreal taxa and source.

Aboreal Taxa	Slope	Intercept	Source
Pinus undiff.	2.9	10.03	Bradshaw & Webb (1985)
Picea	0.52	0.22	Bradshaw & Webb (1985)
Abies	0.11	0.02	Bradshaw & Webb (1985)
Cupressaceae	1.31	-1.4	Delcourt & Delcourt (1987)
Tsuga *	3.95	0.46	Bradshaw & Webb (1985)
Acer spp. undiff.	0.24	0	Bradshaw & Webb (1985)
Alnus undiff.	1.59	6.8	Delcourt & Delcourt (1987)
Betula	1.6	2.52	Bradshaw & Webb (1985)
Carya	0.45	0.56	Bradshaw & Webb (1985)
*Fagus***	1.5	0.85	Bradshaw & Webb (1985)
Fraxinus undiff.	0.66	-0.61	Bradshaw & Webb (1985)
Populus	0.09	0	Delcourt & Delcourt (1987)
Quercus	1.4	5.17	Bradshaw & Webb (1985)
*Tilia****	0.25	0	Delcourt & Delcourt (1987)
Ulmus	0.86	0.74	Bradshaw & Webb (1985)

*Most likely *Tsuga* canadensis within study area based on modern ranges.

** Most likely *Fagus* grandifolia within study area based on modern ranges.

4.3 *Results*

4.3.1 *Fossil Pollen Analysis*

The results of the fossil pollen analysis for each of the three lakes are summarized in Figures 4.5, 4.6, and 4.7. A summary of the vegetation zones within each of the lakes is provided in Tables 4.3, 4.4, and 4.6. Detailed discussion of these results are in Chapter 3.

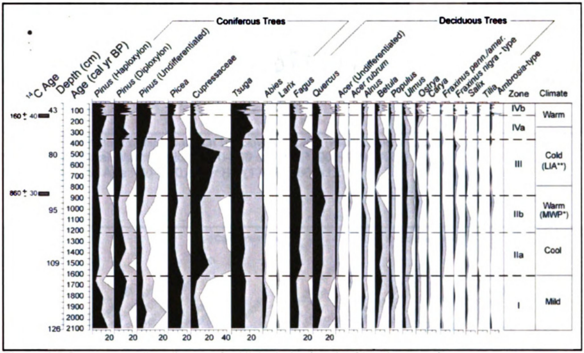

Figure 4.5 Summary pollen diagram for Hicks Lake (north of tension zone).
*MWP = Medieval Warm Period 1110-800 cal yr BP (900-1200 A.D.)
**LIA = Little Ice Age 700–150 cal yr BP (1300-1850 A.D.)

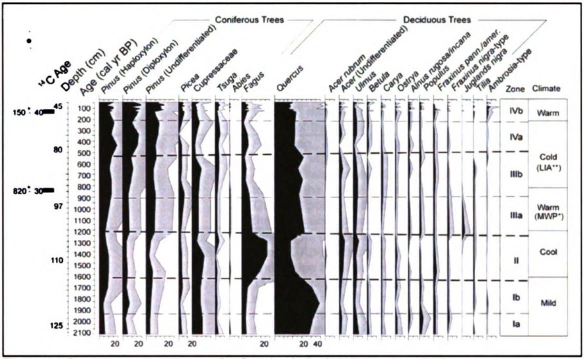

Figure 4.6 Summary pollen diagram for Cowden Lake (within tension zone).
*MWP = Medieval Warm Period 1110-800 cal yr BP (900-1200 A.D.)
**LIA = Little Ice Age 700–150 cal yr BP (1300-1850 A.D.)

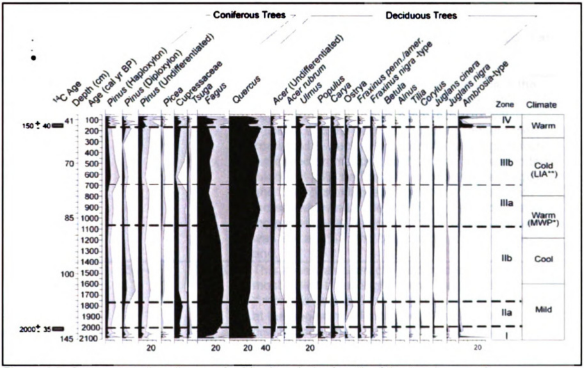

Figure 4.7. Summary pollen diagram for Morrison Lake (south of the tension zone).
*MWP = Medieval Warm Period 1110-800 cal yr BP (900-1200 A.D.)
**LIA = Little Ice Age 700–150 cal yr BP (1300-1850 A.D.)

Table 4.4 Pollen assemblages zones and descriptions for Hicks Lake (north of the tension zone).

Zone/Sub -zone	Depth (cm)	Age (^{14}C BP)	Description
H-I: *Pinus-Picea-Tsuga*	125 –113	2100 – 1600	This zone had high percentages of *Pinus* spp. (15%), *Picea* (30%) *Thuja*, *Tsuga*, and *Abies*. *Fagus* and *Quercus* had similar percentages with *Quercus* rising to slightly more than *Fagus* in the middle of the zone.
H-IIa: *Pinus*-Cupressaceae-*Tsuga*	113 –105	1600 - 1200	*Pinus* spp., *Picea*, *Tsuga*, *Abies* decreased initially. *Pinus* spp. rose near the end of the zone. *Thuja* pollen increased to 19% and then trailed off towards the middle of the zone. Both *Fagus* and *Quercus* pollen both increased to over 9% and then remained steady.
H-IIb: *Pinus*-Cupressaceae-*Tsuga*	105 – 89	1200 – 880	*Pinus* spp. began to decline while *Picea* remained steady. *Abies* also slightly decreased, while *Thuja* and *Tsuga* both remained steady at approximately 11%. *Fagus* was relatively stable in this zone at approximately 12% while *Quercus* increased slightly at the end of the zone. *Betula* pollen remained relatively high and then decreased slightly. *Ulmus* and *Fraxinus nigra*-type steadily increased.
H-III: Cupressaceae-*Pinus-Tsuga*	89 – 73	880 – 380	*Pinus* spp. pollen slightly increased and then declined while *Picea* remained stable. *Thuja* pollen dramatically increased and peaked towards the end at 31%. *Tsuga* pollen remained stable at 12% while *Abies* remained low at less than 1%. *Fagus* pollen percentages were variable. *Quercus* pollen exhibited trends exactly opposite to *Fagus* in that it remained high at the beginning of zone at 11% and then decreased in the middle and at rose at the end.
H-IVa: *Pinus-Tsuga*	380 – 65	380 – 150	*Pinus* spp. pollen increased in abundance in the zone to a collective 43% while *Picea* pollen decreased to 4%. *Thuja* pollen dramatically declined and the beginning of the zone and then continued to decline to a low of 3%. *Tsuga* pollen increased dramatically in this zone, peaking in the middle at 24% and then began to decline. *Fagus* and *Quercus* exhibited opposite trends but both increased towards the end. *Fagus* abundance increased in the beginning to 8% while *Quercus* was low at 5% in the beginning but rises at the end.
H-IVb: *Ambrosia*	65 – 0	150 – 0	This zone was characterized by decreases in most pollen types slightly after the peak in *Ambrosia*-type at 4%. *Tsuga* decreased the most at the beginning of the zone. This zone was distinguished by a peak in *Ambrosia*-type and other herbaceous species.

Table 4.5 Pollen assemblage zones and descriptions for Cowden Lake (within the tension zone).

Zone/Subzone	**Depth (cm)**	**Age (^{14}C BP)**	**Description**
C-Ia: *Quercus-Pinus*	129 – 125	2100 – 1950	This sub-zone was dominated by *Quercus* pollen which steadily rose to 42%. *Pinus* spp. reaches 15%. *Thuja* values were also high at 10%. *Picea* and *Tsuga* both reached a maximum of 3%. *Fagus* percentages were quite low in this zone reaching only 5%. *Acer* spp., and *Ulmus* were both relatively high reaching 3% and 5%.
C-Ib: *Quercus-Pinus*	125 – 117	1950 – 1700	*Quercus* continued to rise in the zone peaking at 48% and began to decrease towards the end. *Pinus* spp. pollen increased this zone and collectively reached a total of 20%. *Thuja* pollen remained stable in the zone at 9%. Several deciduous species decreased at the same time as *Quercus* including; *Acer* spp., *Ulmus*, *Betula*, Alnus, *Populus*, *Fraxinus nigra*, and *Corylus*.
C-II: *Fagus*	117 – 105	1700 – 1300	*Fagus* and *Quercus* shifted dramatically. *Fagus* rose dramatically from a low of 6% in the previous zone to a high of 27%. *Quercus* declined dramatically from 48% in the previous zone to 17%. Several types increased at the same time as *Fagus*, including *Tsuga*, *Acer* spp., *Ulmus*, *Betula*, and *Tilia*.
C-IIIa: *Quercus*	105 – 93	1300 – 950	This zone was characterized again by the dramatic shift between *Quercus* and *Fagus*. *Fagus* declined to 11% while *Quercus* rose sharply to 32% at 1250. Several species rose concurrently with *Quercus* including *Pinus* spp., reaching 29%, *Thuja*, *Alnus rugosa/incana*, *Populus*, *Fraxinus* nigra, and *Juglans nigra*.
C-IIIb: *Quercus*	93 – 81	950 – 550	From 950 to 700 most pollen types remained relatively stable. At 700, *Quercus* declined from 30% to 25% while *Fagus* rose slightly (1%). Several species also increased at 700, including *Tsuga*, *Acer* spp., *Ulmus*, *Betula*, and *Tilia*. *Thuja* was the only other species which decreased significantly at 700. *Quercus* peaked just before 550, at 32%.
C-IVa: *Pinus-Quercus*	81 – 69	550 – 250	*Quercus* decreased from 32% in previous zone to 22% in this zone. *Fagus* increased and peaked at 7% and then decreased. *Pinus* spp. increased to a collective 45%.
C-IVb: *Ambrosia*	65 – 0	250 – 0	At the beginning *Pinus* Dip., *Picea* and *Fagus* slightly increased while most other types remained stable. *Ambrosia*-type spikes at 4%. Afterwards, the majority of pollen types declined and then increased again during the 20th century

Table 4.6 Pollen assemblages and zones for Morrison Lake, Ionia County Michigan. (south of the tension zone)

Zone/Sub-zone	Depth (cm)	Age (^{14}C BP)	Description
M-I: *Quercus-Fagus*	141 – 105	2100 – 2000	This zone was characterized by relatively high percentages of both *Quercus* which peaked at 29% and *Fagus* which began off at a low of 9% and then slowly increased to 21%. *Thuja* and *Ulmus* were the next highest and peaked slightly above 9%. In general all other coniferous species were low while several deciduous types, *Populus*, *Carya*, and *Ostrya*, were relatively high reaching 8%, 7%, and 3%, respectively.
M-IIa *Fagus-Quercus*	105 – 89	2000 – 1800	*Fagus* increased at the beginning of the zone to a high of 27% while *Quercus* steadily declined to 23%. *Pinus* spp. rose slightly to 9% while *Thuja* was the next highest type, and peaked slightly in the middle of the zone at 9% followed by *Ulmus* which peaked concurrently at 7%. Other deciduous types, *Acer* spp., *Populus*, and *Carya*, remained relatively high. *Ostrya* increased slightly toward the end of the zone.
M-IIb *Fagus-Quercus*	89 – 81	1800 – 1050	*Fagus* declined slightly and steadily from 28% to 25% while *Quercus* values rose slightly and steadily from 23% to 25%. Most pollen types remained stable. *Pinus* increased slightly to 12%. *Populus* also slightly increased at 1200 to 8%.
M-IIIa *Quercus-Ulmus*	81 – 69	1050 – 700	This zone was characterized by a steady increase in *Quercus* which peaked in 900 at 34% while *Fagus* slowly declined to a low of 12% in 800. *Ulmus* peaked in 800 at 13%. Concurrently, *Fraxinus penn./amer. Betula* and *Tilia* also rose slightly to 3%, 1%, and 1% respectively. *Pinus* collectively reached just over 8%.
M-IIIb: *Quercus-Fagus*	69 – 57	700 – 150	*Fagus* and *Quercus* fluctuated slightly and exhibited the same trends of an increase in *Quercus* and a decrease in *Fagus*. *Ulmus* decreased significantly back to just over 5%. *Pinus* spp. first declined and then increased back to 10%. *Thuja* roses steadily through the zone to a high of 7%. *Acer* spp. roses slightly towards the end of the zone to over 5%.

4.3.2 *Public Land Survey Data*

The hierarchical clusters analysis of the PLS data set for the entire study area resulted in the identification of a total of 20 clusters (Figure 4.3). The percentages of each cluster within the pollen source area for each lake are summarized in Table 4.2. A total of 18 clusters were present in the pollen source area for Hicks Lake. The dominant clusters (i.e. community type) were *Tsuga c.* at 29.7% and *Fagus g.-Tsuga c.* at 14.8%. A total of 18 clusters were also present within the Cowden Lake pollen rain. The most dominant cluster was the *Pinus s. (Fagus g.-Tsuga c.)* cluster at 15% followed by the *Pinus s.* and *Fagus g.-Pinus s.* clusters both at 11%. Only 13 clusters were present in the pollen rain for Morrison Lake. The most dominant was *Quercus a. (Quercus v.-Fagus g.)* at 32.2% followed by the *Quercus a. (Quercus v.-Quercus m.)* cluster at 15%.

4.3.3 *Discriminant Analysis*

The descriptive statistics for the modern pollen samples, including the percent of each taxon in each forest type, are listed in Table 4.7. The standardized canonical discriminant function coefficients calculated in the discriminant analysis for each species are listed in Table 4.8. These coefficients accounted for a total of 100% (78.7% for function 1 and 21.3% for function 2) of the variance within the modern samples. The discriminant scores for the 196 surface samples were plotted along the first two discriminant functions (Figure 4.8). The plot shows the separation between group centroids. The positions of the un-classified pollen samples were plotted in their respectively. The results from the classification of the modern pollen samples are listed in Table 4.9. Overall, 88% of all of the modern pollen samples were correctly classified with only 22 samples out of 196 misclassified. For each forest type, the percent of correctly classified samples were deciduous forests, 87.8%, mixed-forest, 86.9%, and for boreal forest, 94.1%.

Table 4.7 Summary statistics of modern pollen samples within each vegetation region (data from NAPD 2005)

Pollen Taxon	**Deciduous Forest**		**Mixed Forest**		**Boreal Forest**	
	Mean %	St. Dev.	Mean %	St. Dev.	Mean %	St. Dev.
Pinus (Haploxylon)	0.13	0.84	3.82	8.75	1.22	2.20
Pinus (Diploxylon)	0.00	0.00	3.39	9.84	13.82	19.16
Picea	0.28	0.63	2.52	3.90	30.54	14.76
Abies	0.10	0.31	1.43	1.90	1.89	2.49
Thuja	0.52	0.50	1.58	2.49	0.38	1.10
Tsuga	0.68	1.17	4.19	4.62	0.08	0.18
Acer	2.53	1.41	2.80	2.08	0.13	0.25
Alnus	0.93	0.87	2.66	2.57	7.31	4.69
Betula	2.55	1.99	15.35	11.34	12.49	9.94
Carya	2.16	1.44	0.43	0.63	0.01	0.05
Fagus	3.28	2.86	2.35	2.63	0.03	0.09
Populus	1.24	1.28	0.91	1.54	0.26	0.41
Quercus	26.85	8.24	9.31	7.42	0.81	0.77
Salix	1.59	1.46	0.70	0.91	0.45	0.59
Ulmus	5.73	4.26	2.83	2.53	0.25	0.35
Artemisia-type	0.52	0.46	0.51	0.62	1.14	1.33
Poaceae	7.06	4.27	4.26	5.54	1.04	0.94

Table 4.8 Discriminant function coefficients determined from modern pollen samples.

Pollen taxon	**Function 1**	**Function 2**
Pinus (Haploxylon)	-0.23	-0.10
Pinus (Diploxylon)	0.33	0.28
Picea	0.75	0.47
Abies	0.05	0.10
Thuja	0.00	-0.10
Tsuga	0.00	-0.23
Acer	-0.15	-0.20
Alnus	0.41	0.16
Betula	-0.05	-0.04
Carya	-0.13	0.37
Fagus	-0.01	0.04
Populus	0.05	-0.04
Quercus	-0.28	0.55
Salix	-0.10	0.14
Ulmus	-0.09	0.40
Artemisia-type	0.13	0.06
Poaceae	-0.03	0.05

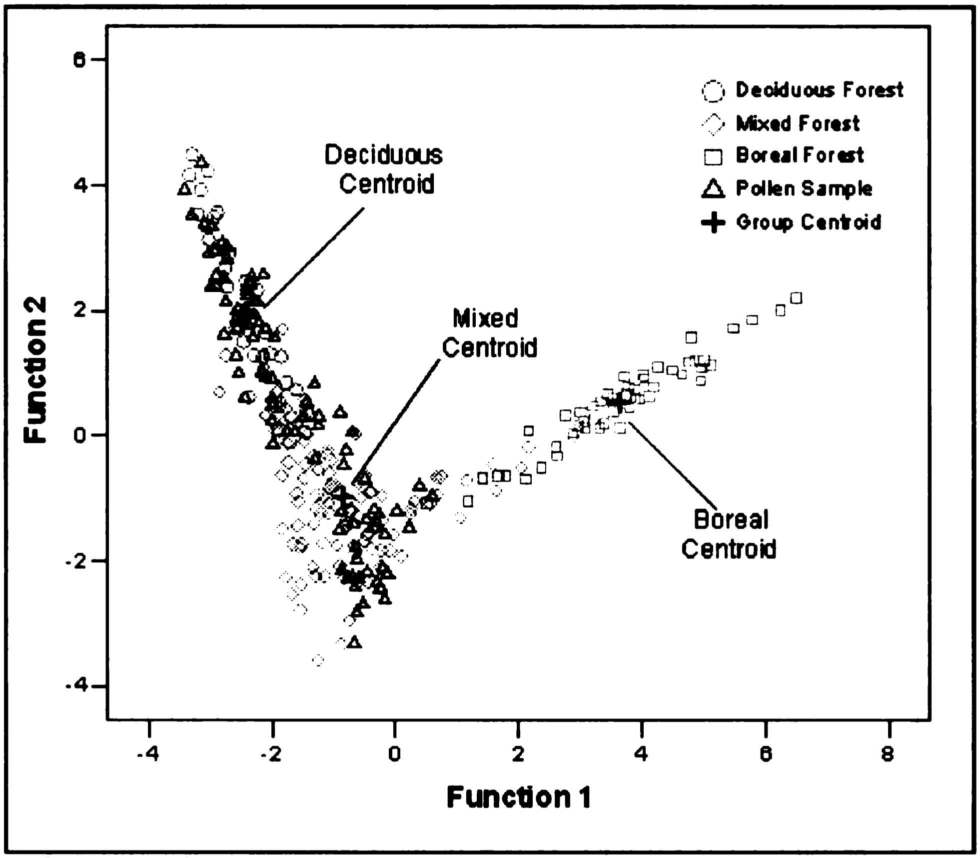

Figure 4.8 Ordination of 196 pollen samples categorized by their respective vegetation type (deciduous, mixed coniferous-deciduous, and boreal), the centroid of each group, and the distribution of the fossil pollen samples from all three study lakes (Hicks Lake, Cowden Lake, and Morrison Lake) along discriminant functions 1 and 2.

Table 4.9 Classification results from the discriminant analysis of 196 modern pollen samples (source NAPD (2005).

	Deciduous Forest	Mixed Forest	Boreal Forest	Number of Samples
Deciduous Forest				
Count	34	5	0	39
Percent	87.18	12.82	0.00	
Mixed Forest				
Count	9	92	5	106
Percent	8.49	86.79	4.62	
Boreal Forest				
Count	0	3	48	51
Percent	0.00	5.88	94.11	

Total number of samples: 196

Number of miss-classified samples: 22

Percentage of samples correctly classified: 88.8%

The VZI and probability of modern analog are summarized in Figures 4.9, 4.10, and 4.11. All samples from Hicks Lake were classified as mixed-forest and had a VZI of 2. All of the samples from Hicks Lake also had a high probability, above 99% of a modern analog.

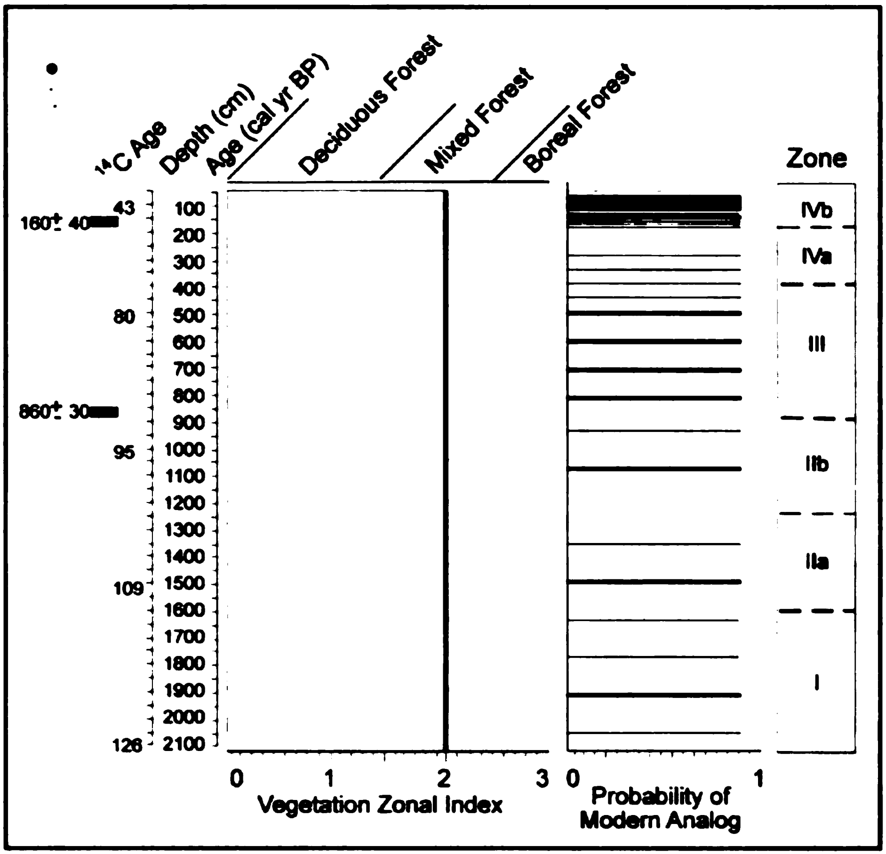

Figure 4.9 Results of the discriminant analysis of the pollen stratigraphy for Hicks Lake.

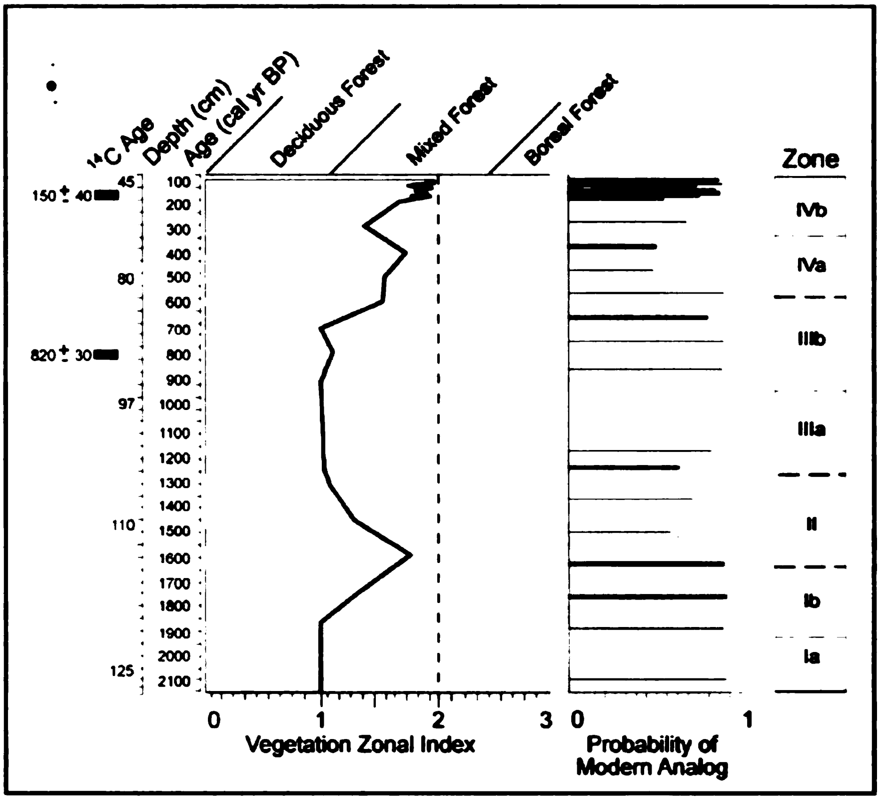

Figure 4.10 Results of discriminant analysis of the pollen stratigraphy for Cowden Lake.

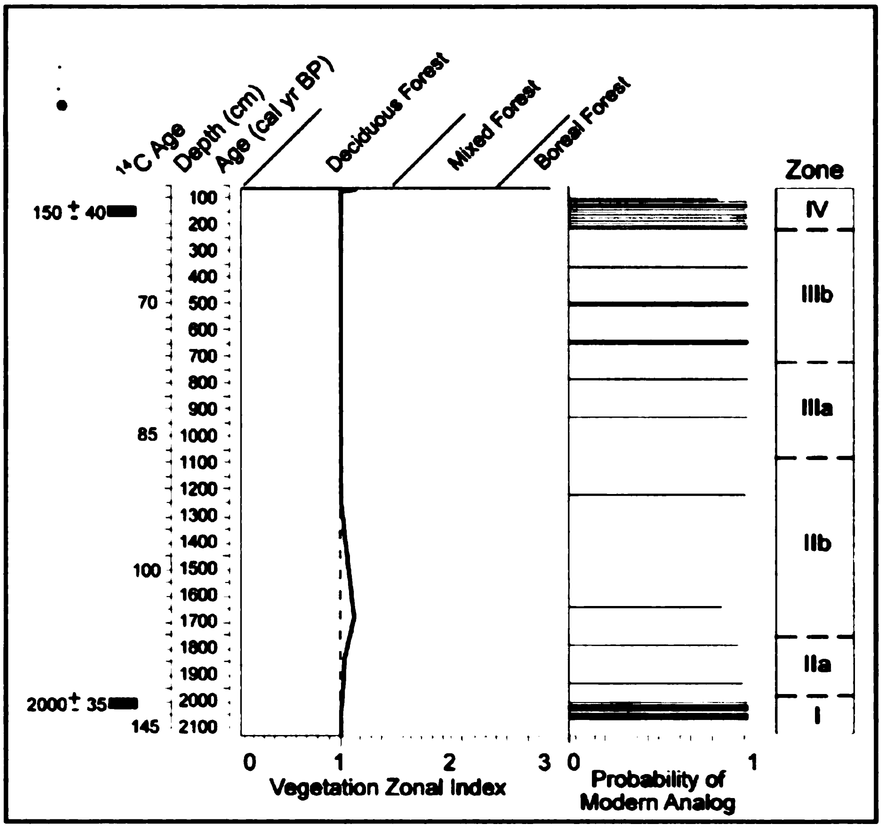

Figure 4.11 Results of discriminant analysis of the pollen stratigraphy for Morrison Lake.

In contrast, the VZIs for the samples from Cowden Lake were quite variable. The samples from 2100-1850 cal yr BP had a VZI of 1, or deciduous forest. The VZI value then changed at 1600 cal yr BP to 1.85 indicating a transition to mixed-forest. The VZI then dropped back down to 1 or slightly above from 1250 to 700 cal yr BP. After 700 cal yr BP, the VZI increased to over 1.5, indicating a transition back to mixed-forest. The VZI then declined to 1.4 at 300 cal yr BP and then rose to its maximum of almost 2 for the remainder of the record. The probability of modern analog for the Cowden Lake samples was also quite variable. Most of the samples remained above 99% probability of a modern analog; several samples had a probability of less than 70%.

The VZIs for Morrison Lake were much more stable than those for Cowden Lake. The VZI for Morrison Lake was 1 or slightly above within the range of deciduous forest for the entire record. The VZI rose slightly at 1700 cal yr BP to 1.2 and then quickly dropped back to 1. All of the samples had a very high probability of modern analog, over 99%, except for the sample at 1700 cal yr BP which had a slightly lower probability but still remained over 90%.

4.3.4 *Squared Chord Distance*

The results from the squared-chord distances between sites within each time periods are shown in Figure 4.12. As expected, samples from Hicks Lake and Morrison Lake, the northern-most and southern-most lakes respectively, had the highest squared-chord distance. Squared-chord distance between these two samples had a maximum of 1.75 at 250 cal yr BP and lowest (1.25) at 750 cal yr

BP. Samples from Hicks Lake and Cowden Lake reached a top squared-chord value of 1.30 at 500 cal yr BP. These samples were most similar at 250 cal yr BP when the squared-chord value was just above .75. The samples from Morrison Lake and Cowden Lake were most different just before 500 cal yr BP with a squared-chord value of 1.25; but they were most similar at 1250 cal yr BP with a squared-chord value just below .75.

Several overall patterns are evident in the variations of the squared-chord values over time. The values for Hicks Lake compared to Morrison Lake, and Hicks Lake compared to Cowden Lake exhibit very similar patterns. All three comparisons exhibit the same general trend, decreasing squared-chord values from 2000-1500 cal yr BP, after which the Morrison Lake versus Cowden Lake comparison increased in value. In contrast, the other two comparisons (Cowden Lake versus Hicks Lake) did not increase in value until about 1100 cal yr BP. The Morrison Lake versus Cowden Lake comparison and the Hicks Lake versus Morrison Lake comparison reached their highest squared-chord value at 500 cal yr BP, but then decreased.

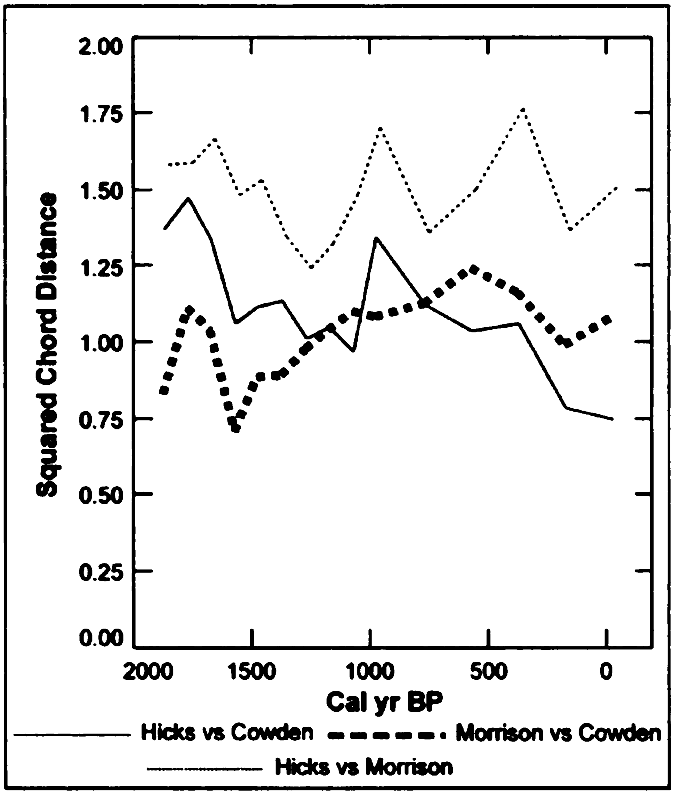

Figure 4.12 Squared-chord distances (dissimilarity) between temporally paired fossil pollen samples from Hicks Lake (north of the tension zone), Cowden Lake (within the tension zone), and Morrison Lake (south of the tension zone).

4.3.5 Pollen and Public Land Survey Comparison

The results for the ordinations of the pollen data and the PLS data are shown in Figures 4.13, 4.14, and 4.15. The variance captured by each ordination axis is summarized in Table 4.10. Here, the DBH of all species with each sample section within the buffered area of around each lake (Figure 4.3), are ordinated and related to changes in the pollen data for each lake. This method allows the detailed DBH data to be related to changes in forests composition over time. The results from the pollen and PLS data (DBH by section) comparison are listed and discussed in reverse chronological order from 150 cal yr BP back in time to 2000 cal yr BP, in contrast to the typical chronological order, of older to younger presented in pollen studies. The results are listed and discussed in reversed chronological order because the objective of this analysis was to compare the detailed PLS data to the pollen data specifically in order to examine how the forest communities identified in the cluster analysis in the early 19th century have changed at times in the past.

Table 4.10 Axis length from the ordination analyses shown in Figures 4.12, 4.13, and 4.14. Data sets are as follows: DBH is the diameter at breast height determined from the Public Land Survey data; all others (H-I etc.) are for the individual vegetation zones reconstructed from the pollen data.

Lake	Data	Axis	Increment	Cumulative
Hicks	DBH	1	0.375	0.375
		2	0.119	0.494
	H-I	1	0.599	0.599
		2	0.262	0.861
	H-II	1	0.617	0.617
		2	-0.015	0.601
	H-III	1	0.15	0.15
		2	0.811	0.962
	H-IV	1	0.714	0.714
		2	0.003	0.718
Cowden	DBH	1	0.337	0.337
		2	0.201	0.538
	C-I	1	0.59	0.59
		2	0.137	0.727
	C-II	1	0.545	0.545
		2	0.297	0.843
	C-III	1	0.949	0.949
		2	-0.1	0.938
	C-IV	1	0.457	0.457
		2	-0.041	0.415
Morrison	DBH	1	0.526	0.526
		2	0.091	0.617
	M-I	1	0.428	0.428
		2	0.269	0.696
	M-II	1	0.162	0.62
		2	0.773	0.934
	M-III	1	0.158	0.158
		2	0.742	0.899
	M-IV	1	0.267	0.267
		2	0.119	0.386

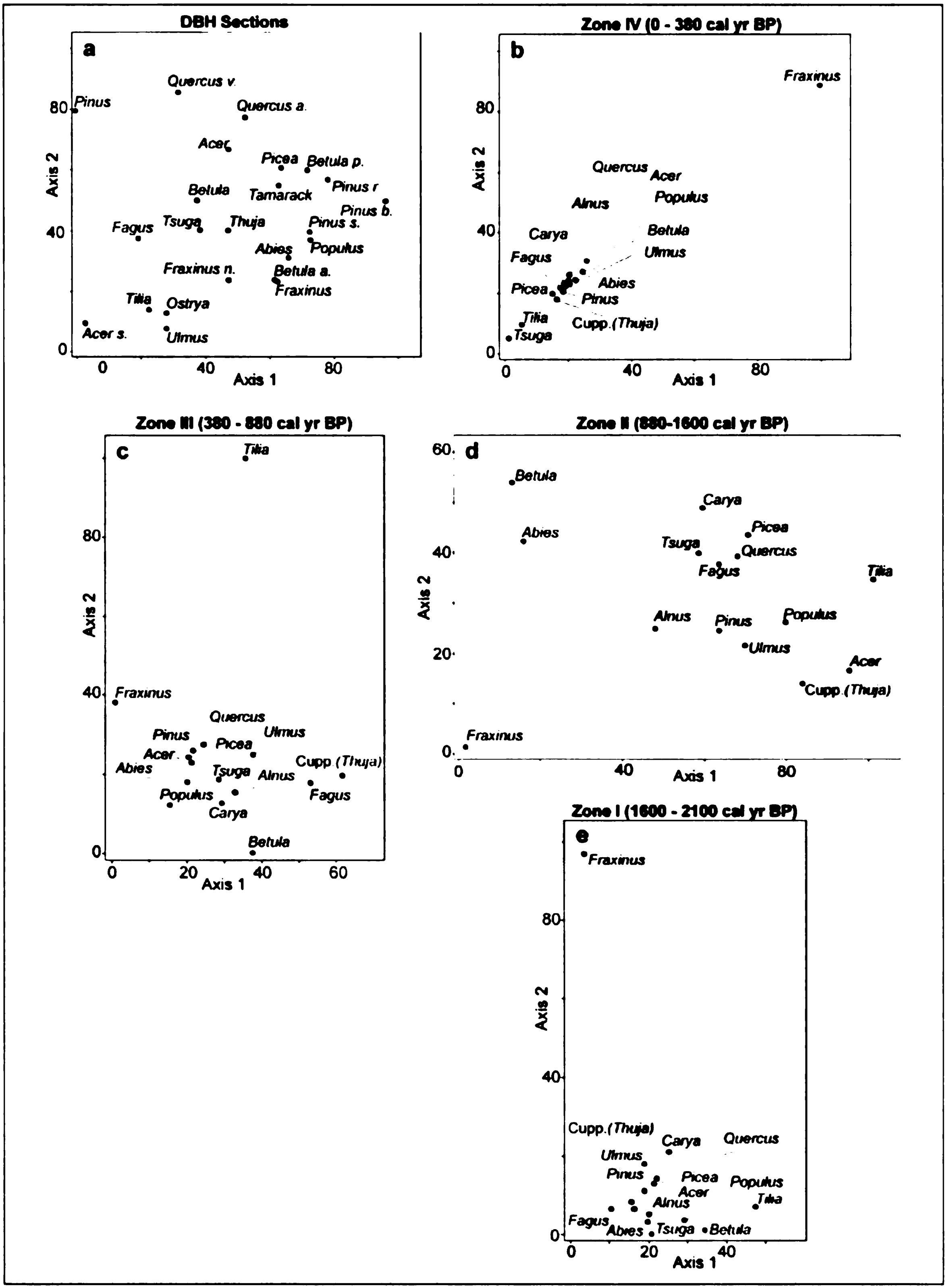

Figure 4.13 Ordination of data from Hicks Lake (north of the tension zone); (a) = ordination of diameter at breast height (DBH) based on the Public Land Survey data (PLS) within the pollen rain area; and (b) through (e) = ordination of the fossil pollen data for each of the vegetation zones based on the fossil pollen data.

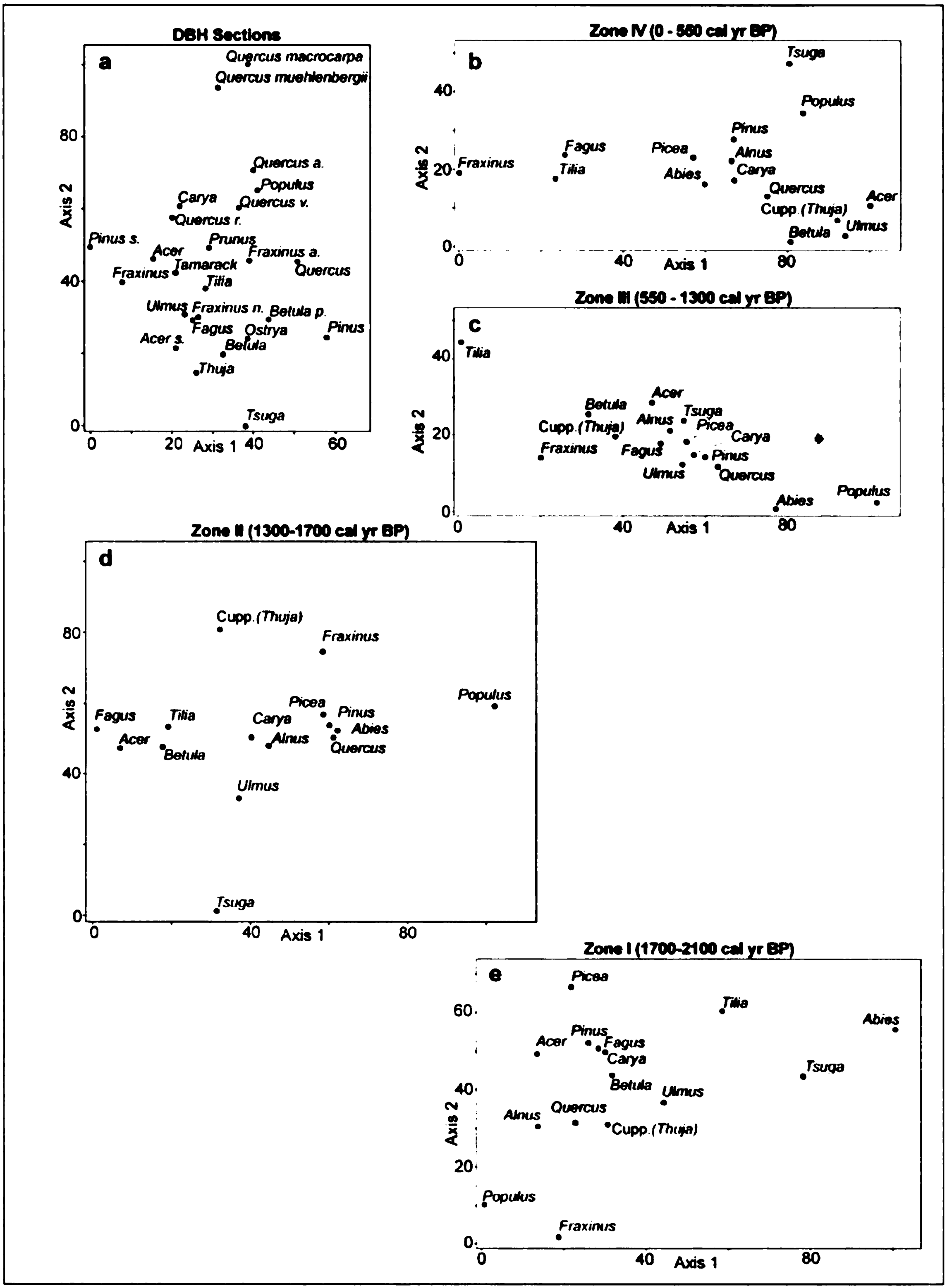

Figure 4.14 Ordination of data from Cowden Lake (within the tension zone); (a) = ordination of diameter at breast height (DBH) based on the Public Land Survey data (PLS) within the pollen rain area; and (b) through (e) = ordination of the fossil pollen data for each of the vegetation zones based on the fossil pollen data.

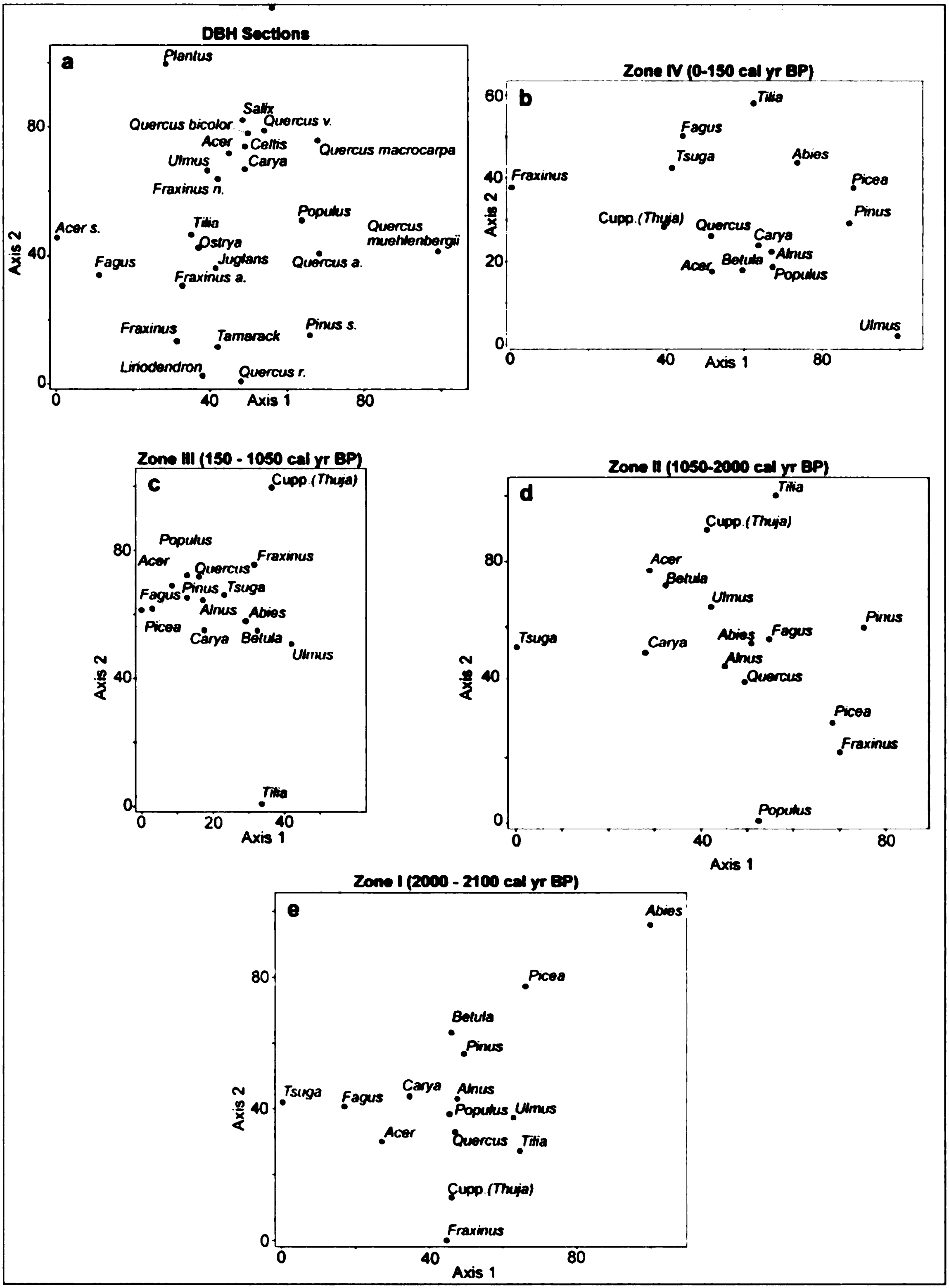

Figure 4.15 Ordination of data from Morrison Lake (south of the tension zone); (a) = ordination of diameter at breast height (DBH) based on the Public Land Survey data (PLS) within the pollen rain area; and (b) through (e) = ordination of the fossil pollen data for each of the vegetation zones based on the fossil pollen data.

4.3.5.1 *Hicks Lake*

The ordination of the PLS survey data (DBH) for the area within the pollen rain of Hicks Lake (Figure 4.3) illustrates the importance of individual species as well as ecological groupings found in each of the clusters (Figure 4.13a). Particularly evident are the relationships between *Tsuga*, *Fagus, Pinus,* and *Thuja* through time, as well as their dynamics, i.e., competition. The first axis separated *Fagus grandifolia*, *Tsuga canadensis*, *Thuja occidentalis* (Cup.), *Abies balsamea,* and *Pinus strobus*. Axis one was centered on *Tsuga canadensis,* which was the most dominant species within forests communities found within the pollen source area of Hicks Lake. The *Tsuga canadensis* community constituted almost 30% of the forest types at Hicks Lake. *Fagus grandifolia*, the next most important species, also the dominant species of the second most common community, *Fagus g.-Tsuga c.,* comprised about 15% of the pollen rain area around at Hicks Lake. *Fagus grandifolia* was aligned just to the left of *Tsuga canadensis* on axis one. All of the *Pinus* species were arranged to the right end of axis one. Axis two separated the less important, mainly deciduous species from the other dominant species, which were all centered at 40% on axis two. *Quercus velutina* (black oak) and *Quercus alba* (white oak) were aligned to the upper end of axis two and the center of axis one. In contrast, mesophytic deciduous species, such as *Tilia americana*, *Ostrya* spp., *Acer saccharum*, and *Ulmus* spp., were all aligned to the lower end of both axes near the dominants, *Fagus grandifolia* and *Tsuga canadensis*, which also prefer moister sites. The grouping of these species in the lower end of both axes represents the *Acer* *saccharum* community (Figure 4.3) in which *Ulmus* spp., *Tilia americana*, and *Ostrya* spp. were all within the ten most dominant species. Species that were more likely to be found within the *Pinus* communities, such as *Betula* spp., *Picea* spp., *Larix laricina*, and *Abies balsamea,* were aligned to the upper end of axis one and slightly above the dominants on axis two.

The ordination of the pollen data from Zone H-IV (0 – 380 cal yr BP) (Figure 4.13b) overlaps in time with the ordination of the PLS data based on DBH sections (Figure 4.13a). But the resulting diagram (Figure 4.13b) differs significantly from Figure 4.13a. Most of the species were grouped tightly together at the lower ends of both axes (Figure 4.13b). *Tsuga*, clearly the most dominant pollen type in this zone, was separated out in the lower left corner with *Tilia*, while *Fraxinus* was pulled out far from the community to the upper ends of both axes. In Figure 4.13b, the dominant species were aligned in linear fashion from the lower left corner out to the upper right corner in a diagonal direction. This pattern corresponds to a similar pattern evident in the alignment of the dominants in the DBH section data in Figure 4.13a. The main species were aligned in the same general order with *Fagus* and *Tsuga* on the lower end, and *Pinus* spp. on the upper end, such that species most associated with each of the dominants were closely grouped with their respective dominants.

The major vegetation changes which occurred between Zones H-IV (0 – 380 cal yr BP) and H-III (380 – 880 cal yr BP) are evident in the ordination diagram (Figure 4.13b, c). Near the end of zone H-III Cupressaceae pollen percentages, mainly representing *Thuja occidentalis*, increased dramatically and pulled the location of *Thuja*, towards the upper end of axis one. *Tsuga* and *Fagus* remained dominants in this zone. *Fagus* was aligned closer to *Thuja* while *Tsuga* was closer to the center of axis one. *Pinus* spp. was again located at the opposite end from the other dominants. This ordination positioned the dominant taxa in the same order as in the ordination of the PLS data in Figure 4.13a, in the order of *Fagus, Tsuga*, and *Pinus* spp.. In Zone H-III, *Tilia* abundance was comparatively low and was separated from all the other species. *Quercus* was again aligned close to *Pinus* spp. *Acer* spp. remained near both *Pinus* spp., and *Quercus* in Zones H-III, as in H-IV.

The increases in Cupressaceae near the end of zone H-III mostly likely indicate an increased abundance of the *Thuja occidentalis* dominated communities. *Thuja occidentalis* most likely increased in importance in the *Tsuga* dominated forests signaling a an expansion of the northern wet-mesic forests. *Thuja occidentalis* had relatively high importance value, 4%, in the *Tsuga* dominated forests. This change is demonstrated in the ordination by the placement of both *Tsuga* and *Thuja* at the same position on axis two (Figure 4.13b, c). This change suggests a drier climate after 380 cal yr BP, with wetter conditions prior (380-880 cal yr BP). *Betula, Fraxinus,* and *Ulmus* all had relatively high values in zone H-III, suggesting an expansion of the *Ulmus-Fraxinus n.-Fagus* g. communities in which *Betula* was a significant component.

The ordination of pollen data from Zone H-II (880 – 1600 cal yr BP) (Figure 4.13d) is evidently different from the previous ordinations and illustrates the major changes which occurred between Zones H-II and H-III. Overall, the most separation between species occurred in axis one compared to any of the other axes in the other ordinations. The dominant taxa reordered in this zone and *Tsuga* was once again aligned at the one end of axis one, *Fagus* is in the middle and then *Pinus* spp. at the other end. *Tsuga* was aligned to the lower end of axis one and the middle of axis two. *Tsuga* and *Fagus* were pulled closer together in Figure 4.13d than in the Figure 4.13e. *Thuja* was again aligned far to the upper end of axis one separated from most other species. *Quercus*, which reached its highest pollen percentages in Zone H-II, was aligned closer to both *Fagus* and *Tsuga* in Zone H-II than in the previous ordinations.

In zone H-II, *Tsuga* and *Fagus* were aligned closer together while the position of *Thuja* was shifted out from the center indicating that *Thuja* was less prevalent. This shift signals the decline of the *Thuja* dominated forests and overall decline of *Thuja* in the mixed coniferous wet-mesic forests; while *Fagus* and *Tsuga* dominated mesic-forests (*Fagus g.–Tsuga c.* and *Tsuga c.)* became more prevalent.

In the ordination of the pollen data from Zone H-I (1600 – 2100 cal yr BP) (Figure 4.13e) taxa were positioned closer together than in the ordination for Zone H-II. *Tsuga*, *Fagus*, and *Pinus* were tightly aligned, separated slightly by each axis. *Thuja* had comparatively low pollen percentages in Zone H-I but continued to be aligned at the end of the general species groupings. *Quercus* was placed closer to *Pinus* spp. than in Zone H-II. *Fraxinus* was once again displaced far from the groupings of other species. In zone H-I, all species were drawn closer together. *Pinus* was positioned closer to the center and near *Tsuga* and *Fagus* indicating an expansion of the northern mesic and dry-mesic forest types with a significant *Pinus* spp. component including communities similar to *Pinus s.* (*Fagus g.–Tsuga c.*), *Pinus s.*, both *Fagus g.–Pinus s.* and *Fagus g.–Pinus–Tsuga c.*

The oscillation between the *Thuja occidentalis*, *Tsuga canadensis*, and *Pinus* spp. dominated communities are evident in the ordinations and suggests that moisture is a significant driver of forest change near Hicks Lake. Both the *Tsuga canadensis* dominated communities and the *Thuja occidentalis* dominated communities identified in the analysis of the PLS data were most likely located primarily on coarse-textured soils. Because both *Tsuga canadensis* and *Thuja occidentalis* are generally not fire tolerant, changes in moisture, due to medium frequency climatic change, rather than disturbance from fire, best explains the oscillations between these two dominants. When the climate was slightly drier from 2000-1600 cal yr BP and again during the latter part of the LIA (400-150 cal yr BP), *Pinus* expanded.

4.3.5.1 *Cowden Lake*

The ordination of the PLS survey data (DBH of all species for each sample section) for the area within the pollen rain area of Cowden Lake (Figure 4.3) demonstrated the importance of individual taxa as well the natural groupings within the clusters (Figure 4.14a). In this ordination, both axes separated out the dominant taxa surrounding Cowden Lake. *Pinus strobus* was the most important species surrounding Cowden Lake at the time of the PLS survey. The most prevalent cluster within the pollen rain of Cowden Lake was *Pinus s. (Fagus g.-Tsuga c.)* community which was found on 15% of the landscape followed closely by the *Pinus s.* and *Fagus g.-Pinus s.* communities both at just over 11% (Figure 4.3). *Pinus strobus* was aligned to the lower end of axis one but in the middle of axis two while *Fagus grandifolia* was aligned on the center of axis one and positioned at about 30% on axis two. All of the *Quercus* species were aligned to the center of axis one but towards the upper end of axis two. Species of *Quercus* were the third most dominant taxa in the forests surrounding Cowden Lake.

The ordination of the pollen data from Zone C-IV (0 – 380 cal yr BP) (Figure 4.14b) corresponded most closely in time with the ordination of the PLS data (Figure 4.14a). Some similar patterns are evident in both ordinations. *Fagus* and *Pinus* spp. were separated on axis one but were aligned on axis two. *Tsuga* and *Fraxinus* were both isolated in the ordination of Zone C-IV. *Quercus* was aligned closer to *Pinus* spp., in this diagram but was not separated from the majority of the other deciduous species in Figure 4.14b. *Acer* spp., *Ulmus,* and *Betula* were placed closer together in Figure 4.14b than in Figure 4.14a. Overall, less variance was explained with this ordination, specifically within axis two than in the PLS ordination.

Most of the taxa in the ordination of zone IV, (0-380 cal yr BP) (Figure 4.14b) were aligned more tightly together, suggested a mixed-forest composition, which corresponds to the VZI, also indicating a mixed-forest type in association with the LIA (600-150 cal yr BP). While the ordination of the PLS data (Figure

4.14a) were not as tightly aligned, the species are relatively close together, with mesic species aligned on the right and the more xeric species aligned on the left. Three clusters comprised just fewer than 40% of the area within the pollen rain area for Cowden Lake (Table 4.2), all which have either *Pinus strobus* or *Fagus grandifolia* as their dominant species whereas *Quercus* dominated forests were much less prevalent.

The ordination of the pollen data from Zone C-III (550 – 1300 cal yr BP) (Figure 4.14c) illustrated the changes which occurred between this Zone and the previous Zone. Overall, less separation between species was evident in the Zone C-III ordination. Again relatively little variance was explained by the second axis. *Fagus* was aligned closer to the center of axis one, *Pinus* spp. and *Quercus* were pulled closer together but remain separate from *Fagus*, although less so than in Zone C-IV (Figure 4.315b). *Quercus* was the most dominant pollen type in this Zone, followed by *Pinus* spp. and then *Tsuga*. *Thuja*, *Populus*, *Fraxinus* and *Acer* spp. all remained on the fringes of the axes in a pattern similar to Zone C-IV.

In zone C-III (Figure 4.14c) the forests at Cowden Lake transitioned to a deciduous forest type. Despite the change (as indicated by the VZI), the ordination diagram for zone C-III shows most species clustered together and does not clearly show deciduous domination. *Pinus* spp. pollen was less abundant in zone C-III (380-880 cal yr BP) than in C-IV (0-380 cal yr BP) and several in deciduous species had higher percentages including *Acer* spp., *Ulmus*, *Carya*, and *Tilia*. This pattern suggests that communities dominated by *Pinus* or with a strong *Pinus* spp. component, similar to the *Pinus s.* (*Fagus g.* – *Tsuga c.*), the *Pinus* (*Quercus* a.-*Fagus g.*) and the *Pinus* s. communities for example, were less prevalent in zone C-III. While communities with strong deciduous components, particularly those dominated by *Quercus* such as the *Quercus a.* (*Quercus v.-Fagus g.*) community were more prevalent. This shift was a result of the warming which occurred during the MWP (from 1000-800 cal yr BP)

The major changes which occurred between Zones C-III and C-II are evident in the ordination of Zone C-II (1300 – 1700) (Figure 4.14d). Overall much more separation between species was apparent than in the other two ordinations (Figure 4.14b and Figure 4.14c). *Fagus* increased dramatically in Zone C-II at the same time *Quercus* decreased. *Fagus* and *Quercus* were pulled apart in the ordination diagram for Zone C-II. *Fagus* was aligned to the lower end of axis one and the center of axis two, while *Quercus* was at the upper end of axis one but slightly below *Fagus* on axis two. *Pinus* spp. and *Quercus* remained closely grouped. *Acer* spp., *Tilia*, and *Betula* were all clustered around *Fagus*. Other deciduous species, such as *Carya*, *Alnus*, and *Ulmus,* were also pulled between *Quercus* and *Fagus,* and were aligned in the center of the both axes. *Populus*, *Fraxinus*, *Tsuga,* and *Thuja* remain on the fringes of the ordination diagram, although all are more isolated in this Zone than in the Zones C-III and C-IV.

A clear difference is evident in the ordinations for zone C-III (Figure 4.14c) and C-II (Figure 4.14d). In zone C-II (880-1600), the forests near Cowden Lake were again dominated by mixed-forests and although many coniferous species did increase. *Fagus* dominated forests rapidly expanded as indicated by a increase in the percentages of *Fagus* pollen. *Fagus*, *Acer* spp., *Tilia,* and *Betula* were all aligned to the left of the ordination while *Quercus* was pulled to the right side and *Ulmus* was isolated in the center. These trends suggest that *Fagus-Acer* dominated forests, akin to those of the *Fagus g.,* and *Fagus* g. (*Acer* s.-*Tilia a.*) communities, were more prevalent in zone C-II while the *Quercus* dominated forests were less prevalent.

The ordination of Zone C-I was also different than the other two zones. *Quercus* dominated this zone while *Fagus* abundance had declined dramatically. This change was evident in the ordination diagram as *Quercus* and *Fagus* were aligned close together on axis one but separated by axis two (Figure 4.14e). *Pinus* spp. abundance was also lower in this Zone. The ordination shows that it was pulled closer to *Fagus* than to *Quercus* illustrating different relationship between *Quercus* and *Pinus* spp. as compared to all other Zones. *Acer* spp., *Carya,* and *Betula* were closer to *Fagus* whereas *Ulmus* were a steady distance from the *Fagus* grouping. *Fraxinus*, *Populus*, and *Tsuga* remained on the fringes of the grouping while *Abies, Picea,* and *Tilia,* were also separated from the core species. *Thuja* was drawn closer into the center of the ordination diagram than it was in Zone C-II.

The changes between zone C-I and C-II corresponds to a climatic change detected by Bernabo (1981) from relatively mild conditions prior to 1600 cal yr BP, to relatively cool and moist conditions after 1600 cal yr BP. Zone C-I was again dominated by *Quercus*. *Fagus* and *Quercus* were pulled closer together on the ordination diagram, indicating the strong competition between the two communities.

The ordination diagrams for Cowden Lake (Figure 4.14) illustrate the dynamics between *Quercus* and *Fagus* over time. The forests around Cowden Lake oscillated between the more xeric *Quercus*-dominated forests with sub-dominants including *Carya* and *Populus*, and the mesic *Fagus-Acer* dominated forests with sub-dominants including *Tilia, Ulmus*, and *Fraxinus* spp. Overall, the species in the ordinations for Cowden Lake were less clustered than at Hicks Lake. The dispersed nature of species in ordination space, through time, indicates that the communities around Cowden Lake were generally less similar in species composition to those at Hicks Lake. The dispersed nature also indicates that species arrangements on the landscape were more variable near Cowden Lake than at Hicks Lake, which is expected for a transition zone between forest types.

4.3.5.3 *Morrison Lake*

The ordinations of the PLS data (DBH of each species for all sections) from the buffered area surrounding Morrison Lake (Figure 4.3) also illustrate the dynamics between *Quercus* and *Fagus* (Figure 4.15a). Axis one separated the dominant taxa, *Fagus* and *Quercus*, found within the pollen rain area of Morrison Lake. Axis two mainly separated the different species of *Quercus*. *Quercus rubrum* (red oak) was aligned to the lowest end of axis two. *Quercus alba* and *Quercus muehlenbergii* were aligned in the center of axis two, while *Quercus* *velutina* and *Quercus macrocarpa* were aligned at the upper end of axis two. The most dominant forest type surrounding Morrison Lake was the *Quercus a. (Quercus v.–Fagus g.)* community (Figure 4.3). This community was strongly dominated by *Quercus alba*. Consequently, *Quercus alba* was ordinated near the center of both axes. *Acer* spp. and *Fagus* were grouped together on the lower end of axis one and the center of axis two. Species that may be found in either the *Fagus-Acer* communities or the *Quercus*-dominated communities, such as *Juglans*, *Fraxinus*, *Populus*, *Tilia*, and *Ostrya,* were aligned in the center of the diagram, and may have been slighted pulled towards the community in which they were found more often. For example, *Tilia* was aligned slightly left of center on axis one and thus closer to *Acer* spp. and *Fagus*. The *Fagus g. (Acer* s.–*Tilia a.)* cluster comprised almost 15% of the forests surrounding Morrison Lake, while the *Fagus* g. community and the *Acer* s. community comprised 12% and 10% respectively.

The ordination of the pollen data from Zone M-IV (0 – 150 cal yr BP) (Figure 4.15b) corresponded most closely in time with the ordination of the PLS data (Figure 4.15a). Axis two explained less of the variance than in the ordination of the PLS data. *Quercus*, which had the highest pollen percentages in Zone M-IV, was aligned to the center of both axes. *Fagus* and *Quercus* were close together on axis one but separated significantly by axis two. *Tsuga* and *Tilia* were located close to *Fagus* while *Carya*, *Acer* spp., *Betula*, *Alnus* and *Populus* were located closer to *Quercus* in the center of ordination. *Pinus* spp., *Picea,* and *Abies* were pulled out to the upper end of axis one, apart from the rest of the species. *Fraxinus* and *Ulmus* were both isolated from the main grouping of species at the center of the graph.

The ordination of the pollen data for Zone M-III (150 – 1050 cal yr BP) (Figure 4.15c) is quite different than the ordination for Zone M-IV (Figure 4.15b). The first axis only accounted for just over 15% of the variance, while the second axis accounted for over 80% (Figure 4,16c). *Quercus* and *Fagus* were aligned closer together both low on axis one but above the center of axis two. Overall, the species were grouped much closer together in this Zone. The pollen percentages for this Zone remained relatively stable except for a slight peak in the abundance of *Ulmus* and *Tilia* in the middle of Zone M-III. Both of these species were pulled to the upper end of axis one. *Thuja*, which declined in the middle of Zone M-III, was pulled away from the other species to the outer limits of both axes.

More separation occurred in the ordination of the pollen data from Zone M-II (1050 – 2000 cal yr BP) (Figure 4.15d). *Quercus* and *Fagus* were placed relatively close together, centered on both axes. *Ulmus* was pulled closer to the center, while *Thuja, Tsuga*, and *Fraxinus* remained isolated from the group. *Populus*, *Pinus* spp., and *Picea* were all separated out from the main grouping as well. In Zone M-II, the percentages of most pollen types remained relatively stable, except for *Populus,* which increased slightly at the beginning of the Zone.

Overall, less separation between species was evident in the ordination of pollen data from Zone M-I (2100 – 2000 cal yr BP) (Figure 4.15e); although *Quercus* and *Fagus* were separated more in this diagram than in Zone M-II or

Zone M-III. *Tsuga*, *Fraxinus*, and *Thuja* remained isolated from the main grouping while *Pinus* spp., *Picea,* and *Ulmus* were drawn closer to the center of group. This pattern suggests that forests similar to the *Fagus-Acer* mesic forests were also prevalent in zone M-I.

4.4 *Interpretations*

4.4.1 *Ecotone Prevalence*

The presence of the forest tension zone was evident in the central Lower Peninsula of Michigan, just prior to Euro-American settlement and subsequent disturbance. It was also evident in reconstructions for the previous 2,000 years based on the fossil pollen record. Differences in forest types at each of the three lake sites were evident in both the cluster maps derived from the PLS data (Figure 4.3) as well as within the fossil pollen record (Figures 4.5, 4.6, 4.7). Clear differences exist in the percentages of the clusters within the pollen rain area occupying a 27 km radius circle, between each of the three lakes. For example, in the pollen rain area surrounding Morrison Lake, *Quercus* species were the most dominant taxa in almost 50% of the community types derived from the PLS data (Table 4.2). At Cowden Lake, *Quercus* species dominated only 16% of the communities within the pollen rain area, and at Hicks Lake, *Quercus* species dominated just less than 2% of the communities within the pollen rain.

More importantly, the paleoecological record generated in this research provides evidence for the existence of the ecotone during the past 2,000 years. The differences between the three lake sites are evident in the summarized pollen diagrams (Figures 4.5, 4.6, 4.7) as well in the squared-chord values (Figure 4.12) between the sites. The squared-chord distances between the study lakes demonstrate that statistical differences between the sites existed throughout the pollen records. The squared-chord values also demonstrate that the degree of difference between the data from the three study lakes was variable over time. Hence, while the three sites were always different during the last 2,000 years, and the degree of difference between them was variable. The calculated squared-chord distances for all of the comparisons were above 0.75, which indicate statistically significant differences between the pollen percentages for each time period at each site.

Thus, the pollen records of this study provide evidence for the existence of the tension zone in the central Lower Peninsula of Michigan during the last 2000 years. The detailed analysis of both the fossil pollen data and the PLS data at the meso-scale domain documented both the presence of the tension zone as well as the dynamic nature of the boundary itself. Although the ecotone has been present in the Lower Peninsula of Michigan since 11,500 cal yr BP (Webb et al. 1986), its character has changed significantly during the last 2,000 years. This research demonstrates that this ecotonal boundary was and most likely continues to be more dynamic than has previously been detected in paleoecological research.

4.4.2 Ecotone Dynamics

Several trends are evident in the plotted squared-chord distance values (Figure 4.12). At 2000 cal yr BP, all of the values start at a low point and then begin to steadily increase, indicating that the sites began to diverge thereafter (Figure 4.12). At 1700 cal yr BP, the squared-chord distance peaked slightly, indicating that the ecotone boundary, i.e. contrast between sites, was distinct. The values then steadily decrease indicating that the boundary became more diffuse from 1700 cal yr BP to 1300 cal yr BP, accompanied by a significant decrease in squared chord values just before 1500 cal yr BP. The values for Morrison Lake versus Cowden Lake did not decrease after 1500 cal yr BP but instead began to rise. After 1300 cal yr BP, the values for the comparisons between Hicks Lake versus Morrison Lake, and Hicks Lake versus Cowden Lake showed the same general trends (Figure 4.12).

At 900 cal yr BP, the squared-chord value for Hicks Lake became more similar to those of Cowden Lake and Morrison Lake. The squared-chord value for Hicks Lake and Morrison Lake were the low at this time compared. The drop in values for all sites at 900 years B.P. may have been a response to the Medieval Warm Period (MWP) which began in the region around 1200-1000 cal yr BP (Bernabo 1981). As the climate warmed during this period, the differences between the sites became less apparent as species of *Quercus* and other deciduous species would became more prevalent at Hicks Lake and Cowden Lake. After 900 cal yr BP, the values for Hicks Lake versus Morrison Lake and Morrison Lake versus Cowden Lake began to rise while the values for Hicks

Lake versus Cowden Lake began to drop. The divergence between sites may have been a response to the climatic cooling associated with the Little Ice Age (LIA), which began in the region just after 800 cal yr BP (Bernabo 1981; Soon and Baliunas 2003; Bradshaw et al. 2005b). After slight fluctuations, the values for all three sites spiked again at 500 cal yr BP. The values then decline for the most recent time grouping. The similarities here may have been the result of changes in the data due to the disturbance associated with Euro-American settlement and subsequent logging. Overall, the results from the comparison of sites based on the squared-chord values indicated that shifts in the pollen percentages occurred simultaneously at all three sites over time. The trends evident in the squared-chord values, over time demonstrate that the pollen data, and thus taxa, exhibited similar trends of divergence and convergence across space. Furthermore, these trends suggest that over time the transition between the major forests communities became more diffuse or sharp in response to variations in climate.

The synchronicity in squared chord-distance measures suggest that the ecotone was changing over time in response to fluctuations in regional climate as opposed to local disturbances. If the changes were the result of local disturbances, the changes evident in the squared-chord distance values would not generally be simultaneous or synchronous, unless the disturbance was spread over a very large geographic area. Specifically, the results support the idea that the tension zone responded not only to long-term climatic trends but also to medium-frequency changes in climate, such as the LIA and MWP. It is also important to note that several medium-frequency changes are evident over the last 2000 years, beyond these two well-recognized climatic intervals, the MWP and LIA, further supporting the notion that climate change, while episodic, is continuous at all scales and that vegetation responds to such change (Gajewski 1987).

The results from the discriminant analysis further confirm the existence of the tension zone, as well as more importantly, reconstruct shifts in the character of the tension zone during the past 2,000 years. The VZI values for Hicks Lake indicate that despite shifts in the relative percentages of pollen, the forests around Hicks Lake were of the mixed-forest type for the entire 2,000 year period (Figure 4.9). Similarly, the forests in the vicinity of Morrison Lake (Figure 4.11) were also predominately deciduous and the VZI values were constant overall. In contrast, the VZI at Cowden Lake (Figure 4.10) indicates significant transitions in forest type over the past 2,000 years. These trends are summarized below.

2000-1200 cal yr BP

From 2100 to 1950 cal yr BP, the forests within the tension zone around Cowden Lake, were predominately deciduous, while the forests around Hicks Lake were mixed, and the forests in the vicinity of Morrison Lake were deciduous. While the forests surrounding Hicks Lake continued to be of the mixed-forest type, the forests around Cowden Lake shifted dramatically just after 1700 cal yr BP to a mixed forest type. Near Morrison Lake the forests changed slightly just after 1700 cal yr BP the *Fagus-Acer* forests expanded.

Afterwards, the VZI indicated a shift towards mixed forests (Figure 4.7). The shift towards a mixed-forest type in the vicinity of Morrison Lake corresponded to increasing similarity in the squared-chord values between Morrison Lake and Cowden Lake as well as between Hicks Lake and Cowden Lake. The shift to a mixed-forest type in the vicinity of Cowden Lake at 1700 cal yr BP was characterized mainly by a greater abundance and subsequent dominance of *Fagus* and concurrent increases in the abundances of *Acer* spp., *Ulmus, Betula* and *Tsuga.* This trend suggests the expansion of mixed mesic forests similar to those of the *Fagus*-dominated community (Figure 4.3). Despite the shift to a mixed-forest type in the vicinity of Cowden Lake, the forest communities there were not similar to the mixed-forests near Hicks Lake. The forests near Hicks Lake had more *Tsuga*, *Picea*, and *Pinus* (Diploxylon) than the forests near Cowden Lake. Bernabo (1981) interpreted a cool period beginning at 1500 cal yr BP which lasted until 1200 cal yr BP north of this study area. Thus, this cooling detected by Bernabo (1981) and confirmed by this study either began earlier in the south, or the forests south of the tension zone responded faster to this climatic shift than did those in the northern Lower Peninsula.

1200-800 cal yr BP: The Medieval Warm Period

From 1200 to about 800 cal yr BP, the forests around Cowden Lake transitioned again to a deciduous forest type. At this time, the forests around Cowden Lake were more similar to those near Morrison Lake than to those near Hicks Lake. In the pollen record for Cowden Lake (Figure 4.6), *Quercus* pollen increased in abundance dramatically by 1200 cal yr BP while values for *Fagus* declined. Hence, the dynamics between *Quercus* and *Fagus* signal the shifts between mixed and deciduous forests, i.e. ecotonal movement, around Cowden Lake. These changes correspond to the MWP, a period of warmer climate, in the region most pronounced from about 1000 to 800 cal yr BP.

800-150 cal yr BP: The Little Ice Age

Near Cowden Lake the forests began to change again just after 800 cal yr BP. This shift to a mixed-forest type after 800 cal yr BP was marked by significant increases in *Pinus* spp. and slighter increases in mesic species such as *Fagus* and *Tsuga*. After 800 cal yr BP, both *Acer* spp. and *Ulmus* declined slightly in local abundance. This change was most dramatic at 400 cal yr BP and signaled yet a third shift toward a mixed-forest type around Cowden Lake. Consequently, the second transition to a mixed-forest type near Cowden Lake was characterized by the expansion of *Pinus* dominated forests which prefer more xeric sites while mesic forests dominated by *Tsuga* and *Fagus* expanded less significantly. The transition to a mixed-forest type, i.e. southward expansion of coniferous species distribution, and retreat of *Quercus*-dominated forests in the south, is the expected response from a climatic cooling. In the pollen record, this response was indicated by relatively high percentages of all species of *Pinus*, *Thuja*, *Tsuga,* and *Picea* accompanied by a decrease in *Quercus* near Cowden Lake. Forest communities similar to those in the *Pinus s.* and *Pinus s. (Fagus g.–Tsuga c.)* community expanded in response to the cool dry climate

(Figure 4.3). These responses suggest that the onset of the LIA must have been accompanied by drier conditions than in the previous cool period around 1700 cal yr BP.

The shift towards a mixed-forest after 800 cal yr BP corresponded to a reversal in the trends towards similarity between the lakes, evident in the previous few centuries (i.e. during the MWP). Just after 800 cal yr BP, Cowden Lake and Morrison Lake became less similar in terms of their pollen data while Hicks and Cowden Lake became more similar. The forests at Cowden Lake shifted again slightly at 350 cal yr BP, but remained well within the mixed-forest range for the rest of the record.

150-0 cal yr BP: Historic Disturbance:

After 150 cal yr BP, the forests near Hicks Lake retained their character as did those near Morrison Lake which remained of a deciduous type after 150 cal yr BP. In contrast, the forests at Cowden Lake shifted and became more similar to a mixed forest type (highest VZI) then previously in the record. After 150 cal yr BP, the forests at all three lakes increased in similarity.

Paleoclimatic patterns

Based on the interpretations of these results from this research as well as earlier work by Bernabo (1981), the climatic variations which occurred during the past 2,000 years include: a cool period from 1500 -1200 cal yr BP; the MWP from 1000-800 cal yr BP; and the LIA from 550 to 150 cal yr BP. These climatic changes were not significant enough to result in a shifting of the tension zone as far north as Hicks Lake (within the pollen rain area) or as far south as Morrison Lake. The variations in climate were significant enough to result in three major tension zone shifts around Cowden Lake, however. The lack of major changes, i.e. shift in vegetation type from mixed to boreal, at Hicks Lake is corroborated by Bernabo's (1981) research on four lakes located just north of Hicks Lake. In other words, the climate variations were of an insufficient nature to drive a shift in complete transformation of the forest type (Bernabo 1981). But variations in relative pollen percentages for key species, i.e. *Tsuga*, *Pinus*, and *Thuja*, were detected and attributed to climatic variations which re-ordered the competitive advantages of species, in response to climate change.

4.4.3 *Within Site Variation*

The comparison of the PLS data, both the cluster types for each lake and the species ordination, provides additional insights into the dynamics of the communities surrounding each lake site. The ordination of the pollen data for the most recent pollen samples, i.e. zone IV for each of the lakes, did not correspond as well to the ordination of the PLS data as expected. The differences between the ordination of the PLS data and the pollen data for the corresponding zone may be due mainly to the major disturbances which occurred as a result of Euro-American settlement and subsequent logging. Because all species exhibited the same general pattern of a dramatic population decrease with the onset of disturbance and then gradual increase of stands towards the end of the zone, the ordination diagram is representing theses similarities instead of the ecological associations among the pollen types at each lake.

The ordination diagrams illustrate differences in the groupings of species, or assemblages, over time for each of the three lake sites. These differences summarize both the percentages of pollen as well as the trends of variations within pollen percentages for each zone. In general, the position of species in ordination space varied significantly over time, in regard to both the alignment on each axis as well as the position in relation to other species. In this manner, the communities identified in the cluster analysis of the PLS data were not always present on the landscape in these exact configurations.

Species within the clusters identified were not always aligned together in the ordination diagrams for each pollen zone, suggesting that species responded to climatic variations and disturbance in an individualistic manner. The complexity exhibited in the ordinations of taxa over time generally supports the individualistic (Gleason 1939), and later developed, continuum models of vegetation (Curtis and McIntosh 1951; Whittaker 1956) in which species vary on a landscape as a result of the chance interaction of a variety of factors, both stochastic and deterministic, within a continuously varying environmental context, forming associations. The variations between ordination diagrams illustrate the re-organization, including expansions and declines, of several taxa on the landscape in response to medium-frequency climatic oscillations (Gajewski 1987). Thus, the forests on the landscape at the time the PLS data were collected (~200 cal yr BP) did not represent climax communities, but were an assemblage of species present on the landscape only since the onset of the LIA (~600 cal yr BP).

4.5 *Discussion*

4.5.1 *Comparisons with Other Pollen Records*

<u>2000-1600 cal yrs BP</u>

The most detailed study of examining vegetation change in Lower Michigan during the time period of focus for this study was by Bernabo (1981) who conducted fossil pollen analysis on sediments from several lakes: Marion Lake, Lake 27, Heart Lake, and Jones Lake (Figure 4.16), all approximately 100 km north of Hicks Lake. Of these, Marion Lake and Lake 27 provide the most detailed and longest record of forest change (Bernabo 1981). The patterns reconstructed from the pollen data for Hicks Lake generally correspond to those from Marion Lake and Lake 27, although slight variations are evident.

From 2000 to 1600 cal yr BP, northern mesic mixed coniferous communities dominated by *Tsuga*, with *Fagus,* and *Acer* spp. and lower abundances of *Picea,* were prevalent at all three lakes. Pockets of dry-mesic forests with *Pinus* spp. and relatively low abundances of *Quercus* were also present. *Picea* and *Abies* were slightly more abundant in the forests at Hicks Lake, as compared to Marion Lake and Lake 27 (Bernabo 1981), and were most likely abundant in lowland wet forests. These assemblages correspond to relatively mild conditions with enough moisture to maintain the dominance of

Tsuga (Bernabo 1981). Whereas the low abundance of *Thuja* at this time, indicates relatively moist conditions as opposed to wet conditions.

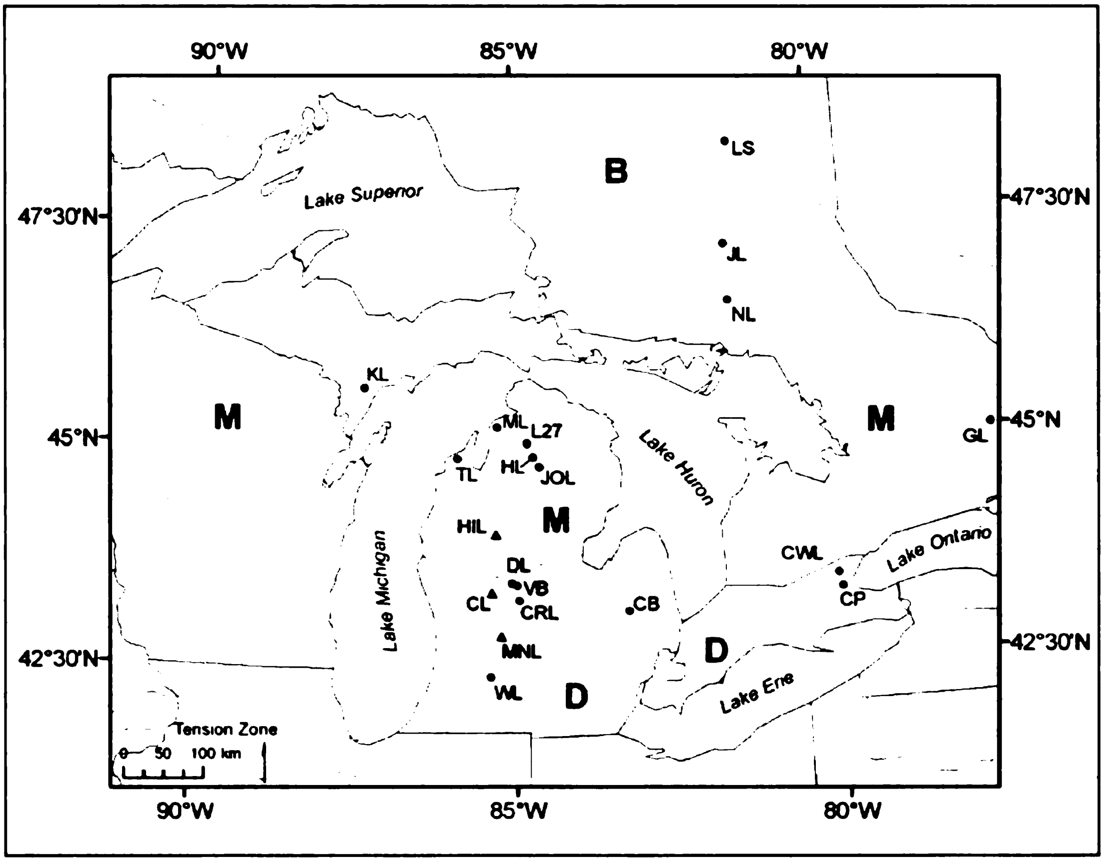

Figure 4.16 Major vegetation region within the Great Lakes Region: D = deciduous forests (eastern broadleaf forest), M = mixed forests (Laurentian forest), and B = boreal forest. Lake sites in this study (▲): HIL = Hicks Lake, CL = Cowden Lake, and MNL = Morrison Lake. Lake sites referred to in this study (●): LS = Lake Six, JL = Jack Lake, NL = Nina Lake (Lui 1990); GL = Graham Lake (Fuller 1997), CWL = Crawford Lake (Yu 2003); CP = Cootes Paradise (Finkelstein et al. 2005); ML = Marion Lake, L27 = Lake Twenty Seven, HL = Heart Lake, Jo. L = Jones Lake (Bernabo 1981); TL = Tamarack Lake (Davis 2000); DL = Demont Lake, VB = Vestaburg Bog, CRL = Crystal Lake (Kapp 1990), CB = Chippewa Bog (Bailey and Ahearn 1981); WL = Wintergreen Lake (Manny et al. 1978).

As expected for lakes positioned across an ecotonal boundary, the plant community shifts interpreted from the pollen records of Cowden Lake contrast greatly to that of Hicks Lake, as well as Marion Lake, and Lake 27 (Bernabo 1981). However, the paleoclimatic interpretations have many similarities. From 2100-1600 cal yr B, *Quercus* was the dominate taxa in the forests surrounding

Cowden Lake. These *Quercus*-dominated forests also had significant components of other deciduous taxa including *Acer* spp., *Ulmus*, *Carya*, and *Populus*. Patches of mesic forests, i.e. *Fagus-Acer* forests, were also present. Mixed coniferous-deciduous forests, such as the *Pinus-Fagus* and *Pinus-Quercus* forests also existed but in relatively low abundances as compared to later in the record for Cowden Lake. *Quercus*-dominated xeric forests were also abundant near Crystal Lake, the geographically closest pollen site to Cowden Lake, which is located approximately 33 km to the southeast (Kapp et al. 1990) (Figure 4.16). The dominance of *Quercus* and other xeric taxa, and relatively low abundances of mesophytic taxa such as *Fagus* and *Acer* spp., corroborates the interpretation of a mild and relatively dry climate evident in the records from Hicks Lake, as well as at Marion Lake, and Lake 27 (Bernabo 1981).

Around Morrison Lake, the forests prior to 2000 cal yr BP were dominated by *Quercus* with relatively high abundances of other taxa, such as *Carya*, *Ulmus* and *Populus*. After 2000 cal yr BP, *Fagus*, *Acer* spp., and *Ulmus* expanded and the mesic *Fagus-Acer* forests were dominant near Morrison Lake for several centuries until ~1200 cal yr BP. This assemblage contrasts greatly to the forests around Cowden Lake which were strongly dominated by *Quercus* from 2000 cal yr BP until 1600 cal yr BP. The dominance of *Quercus* prior to 2000 cal yr BP as well as an expansion of the *Fagus-Acer* mesic forests after 2000 cal yr BP is also evident in the pollen records from Wintergreen Lake (Manny et al. 1978), located approximately 60 km southeast of Morrison Lake (Figure 4.16). The Morrison Lake and Wintergreen Lake records indicate mild conditions, which does correspond to paleoclimate reconstructions from the pollen analysis of other lakes in the Lower Peninsula of Michigan (Bernabo 1981). The records from Morrison Lake and Wintergreen Lake also indicate relatively high moisture, which is not evident in the other records for the southern Lower Peninsula.

The pollen records from Cowden Lake, Hicks Lake, Morrison Lake, Crystal Lake (Figure 4.16) (Kapp 1999), as well as Marion Lake, and Lake 27 (Bernabo 1981), indicate that the forest tension zone was positioned relatively farther north in Lower Michigan from 2100-1600 cal yr BP than it is today, although it remained south of Hicks Lake. *Quercus*-dominated forests were more prevalent around Cowden Lake than at the time of the PLS survey data (Figure 4.3 and Figure 4.14). The *Quercus* band, evident in Figure 4.4, expanded northwards and was more abundant from 2100-1600 cal yr BP. The increased warmth and relative dryness allowed *Quercus* to out-compete the mesic species around Cowden Lake but not around Morrison Lake. In the vicinity of Morrison Lake the *Fagus-Acer* mesic forests were more prevalent than the xeric *Quercus* forests. This discrepancy is also evident in the VZI for Morrison Lake which rises slightly towards a mixed-forest type at 1800 cal yr BP. The squared-chord distance values for this time indicate that pollen records for Morrison Lake and Cowden Lake became increasingly different from 2000-1600 cal yr BP. This discrepancy may be explained by mild slightly moister conditions between 2000-1600 cal yr BP in southern Michigan and relatively mild temperatures and dry conditions in central and northern Lower Michigan at this time.

1600-1200 cal yr BP

At 1600 cal yr BP, major changes were evident around Hicks Lake, Marion Lake, and Lake 27, although these changes were variable between the sites. In the vicinity of Marion Lake and Lake 27, *Pinus*, *Picea*, and *Ulmus* increased in abundance while *Tsuga* and *Quercus* declined. Near Hicks Lake, *Thuja* abundance significantly increased while the abundance of *Tsuga* and *Pinus* declined (Bernabo 1981). *Picea* and *Pinus* spp., which had relatively high abundances just prior to 1600 cal yr BP, declined after 1600 cal yr BP near Hicks Lake. The differences between the timing of the decline of both *Picea* and *Pinus* spp. near the Marion Lake and Lake 27 as compared to Hicks Lake may be attributed to slight variations in chronologies, especially considering the use of the *Ambrosia* correction method in both. Bernabo (1981) does not report *Thuja* abundances at either Marion Lake or Lake 27. At Tamarack Lake, located approximately 90 km to the north of Hicks Lake and along the shores of Lake Michigan, a decline in *Pinus* spp. abundance is evident at approximately 1600 cal yr BP (Davis et al. 2000) (Figure 4.16). But because of the coarse temporal resolution in the Tamarack Lake pollen record, the record cannot be related to the specific nature and timing of the changes at Hicks Lake. At Hicks Lake, both *Fagus* and *Quercus* increased in abundance slightly just after 1600 cal yr BP, indicating an expansion of the dry-mesic and mesic northern forests. The significant increase in abundance of *Thuja* after 1600 cal yr BP indicates that the shift to a cooler climate is also accompanied by increased moisture. Overall, the forests in the vicinity of Hicks Lake remain relatively stable after 1600 cal yr BP.

Marked changes also occurred at Cowden Lake at 1600 cal yr BP, including the shift to mixed-forests dominated by *Fagus* accompanied by an increase in the abundance of *Pinus*. The *Fagus-Acer* expansion is less evident in the record for Crystal Lake (Kapp et al. 1990), probably because of the coarse temporal resolution. These changes corroborate the interpretation of shift to a cooler and moister climate after 1600 cal yr BP, evident in the records from Hicks Lake, Marion Lake, and Lake 27 (Bernabo 1981). While most coniferous taxa did not expand and remained relatively stable, *Tsuga* expanded slightly at 1350 cal yr BP concurrent with the peak in the *Fagus* expansion, suggesting the presence of *Tsuga* in the *Fagus-Acer* forests. The abundances of both *Thuja* and *Picea* decline by 1350 cal yr BP and were most likely found in very isolated instances within the mesic mixed coniferous-deciduous forests. Some small mono-specific stands of *Thuja occidentalis* may have remained in the lowlands but were less extensive. Significant shifts at Morrison Lake were not evident, although *Fagus* was at relatively abundant during this time. The decrease in *Thuja* abundance and the subsequent increase both in *Picea* and *Abies* abundances may be a delayed response to a slight climatic cooling and drying in the previous period beginning at 1500 cal yr BP lasting until 1200 cal yr BP, detected by Bernabo (1981) at Marion Lake and Lake 27.

From 1600-1200 cal yr BP the tension zone moved southward from its previous position in response to a cooler and moister climate. This shift provides evidence that other medium-frequency climatic oscillations, besides the two emphasized episodes (MWP and LIA), occurred in the Lower Peninsula of

Michigan during the past 2,000 years. Moreover, this shift was clearly apparent in the pollen records for Cowden Lake, and it was the most dramatic change which occurred in the entire record (Figure 4.10). This shift was less apparent in the pollen record for Hicks Lake. This change was characterized primarily by the southward retreat of the ecotone, evidenced by a strong decline in the areal *Quercus* forests around Cowden Lake.

1200-550 cal yr BP

Another oscillation between *Tsuga canadensis* and *Thuja occidentalis* was evident at Hicks Lake by 1200 cal yr BP (zone: H-IIb). This oscillation was marked by the decline of *Thuja* significantly from its previous expansion. The relatively high abundances of the other coniferous species and re-emergence of *Abies* as a member of the local flora, suggests that a wet-mesic to mesic coniferous forests were prevalent near Hicks Lake. Again the consistent abundances of several important deciduous taxa suggest that patches of dry-mesic and mesic northern hardwoods forests were still prevalent at 1200 cal yr BP around Hicks Lake. Overall, the forest communities evident in the previous period (~1600 cal yr BP) at Hicks Lake remained relatively stable until 1110 cal yr BP.

At Hicks Lake beginning at 1100 cal yr BP, *Quercus*-dominated communities became more abundant while *Tsuga*-dominated communities declined. Between 1000 and 800 cal yr BP significant changes were evident in the forests at Marion Lake and Lake 27 indicating a warming associated with the

MWP. These changes included: a decline in the abundances of *Picea*, *Pinus* spp., and *Tsuga* and increases in the abundances of *Quercus*, *Fagus*, and *Betula* at Lake 27; a decline in the abundances of *Picea*, *Pinus* spp., *Betula*, accompanied by increases in the abundances of *Ulmus* and *Fraxinus* spp. and only slight increases in the abundance of *Quercus* at Marion Lake. Changes associated with the MWP occur somewhat later at Hicks Lakes and are characterized by: 1) an initial increase in *Quercus* abundance at 1050 cal yr BP, 2) a dramatic increase in *Thuja* abundance beginning at 1050 cal yr BP reaching a maximum at 550 cal yr BP; and 3) declines in the abundances of *Pinus* spp., *Picea*, *Tsuga*, *Fagus*, and *Betula* also at 1050 cal yr BP. The forests surrounding Hicks Lake at this time remained dominated by wet-mesic coniferous forests with only slight expansions of both the dry-mesic and mesic-mixed northern hardwood forests towards the end of the MWP.

Around Cowden Lake, another dramatic shift occurred, characterized this time by a decline in the mesic *Fagus-Acer*-dominated forests and a shift back to the drier *Quercus*-dominated forests with sub-dominant taxa that included *Juglans nigra*, *Alnus rugosa/incana*-type, *Carya,* and *Populus.* This shift began at 1300 cal yr BP and continued until 550 cal yr BP (Zone C-III). Nonetheless, the mesophytic taxa, *Acer* spp., *Fagus, Tilia, Tsuga,* and hence the mesic *Fagus-Acer* forests, were still persistent on the landscape despite the population decline. The expansion of the *Quercus* dominated forests coincided with Bernabo's (1981) interpretation of the MWP beginning between 1200 to 1000 cal yr BP. The dramatic expansion of *Quercus* at 1150 cal yr BP and the concurrent decline in the abundance of *Acer* spp., *Ulmus*, and *Fagus* and slight increase in the abundance of *Pinus resinosa/banksiana*-type, suggests that fire may have been a factor. Later in the record, after 1100 cal yr BP (Zone: C-IIIa), the xeric *Quercus* dominated deciduous forests experienced a slight decline concurrent with a slight increase in the local abundance of *Ulmus,* which may be in response to the period of wetness at the onset of the MWP (Soon and Baliunas 2003).

The forests around Cowden Lake transitioned once again at 700 cal yr BP (Zone: C-IIIb). The abundance of both *Quercus* and *Pinus* became variable, at the same time, the abundances of several mesic taxa, *Fagus*, *Tsuga*, *Thuja*, *Acer* spp., *Betula* and *Tilia* increased. This trend once again indicates the expansion of the mesophytic *Fagus-Acer* forests, and the decline of the *Quercus* forests. These moderate fluctuations generally coincide with the onset of the LIA also detected by Bernabo (1981).

In contrast to both the Cowden Lake and Hicks Lake pollen records, the changes in species composition and dominance around Morrison Lake as interpreted from the pollen data were much more gradual. After 1200 cal yr BP, *Quercus* forests began to expand near both Morrison Lake and Wintergreen Lake (Manny et al. 1978) concurrent with the onset of the MWP. *Quercus* forests remained dominant for several centuries.

Near Morrison Lake, both *Tilia* and *Fraxinus pennsylvanica/americana*-type also expanded at 900 cal yr BP. A switch from *Fagus*-dominated forests and *Quercus* dominated forests in also evident for this general time period in the pollen record for Cootes Paradise, a coastal wetland in the western end of Lake

Ontario, located at a latitude slightly north of Morrison Lake (Figure 4.16), although a complete chronology was not established (Finkelstein et al. 2005)

From 1200 cal yr BP until approximately 700 cal yr BP, the forest tension zone moved north again, at least to Cowden Lake, as the forests around this lake were predominately dominated by *Quercus*, although to a lesser degree than from 2000-1600 cal yr BP. The forests at Cowden Lake had a greater coniferous component although the mesic *Fagus-Acer* forests were still relatively abundant. Although the tension zone shifted north, it did not reach Hicks Lake. The forest tension zone shifted south once again beginning around 700 cal yr BP, just after the onset of the LIA. Around Cowden Lake, the xeric *Quercus* forests declined slightly by 550 cal yr BP as the mixed-coniferous forests and mesic *Fagus-Acer* forests expanded.

550-150 cal yr BP

By 550 cal yr BP, changes associated with the LIA cooling were evident in the forests near Hicks Lake, as well as Marion Lake, and Lake 27 (Bernabo 1981). The changes included: 1) near Lake 27, *Picea* and *Pinus* spp. increased in abundance while *Tsuga*, *Quercus*, *Fagus*, and *Acer* spp. moderately declined in abundance; 2) at Marion Lake, *Picea*, *Pinus* spp., *Tsuga*, increased in abundance while *Quercus*, *Ulmus*, and *Fraxinus* spp. declined in abundance by 550 cal yr BP; 3) at Hicks Lake, *Thuja* declined in abundance dramatically, with a moderate decline in the abundances of *Fagus*, while *Picea*, *Pinus* spp., and *Tsuga* expanded after 400 cal yr BP. Thus, the *Pinus* spp. dominated northern dry forests expanded during the LIA in most of the northern Lower Peninsula while the northern mesic forests declined north of Hicks Lake. Near Hicks Lake, the initial onset of the LIA was characterized by the dominance of *Thuja occidentalis* in wet lowland and northern wet-mesic forests, indicating increased moisture from 900-500 cal yr BP. This shift is concurrent with the transition from the MWP to the LIA.

Soon after, *Thuja* declined in abundance as *Tsuga* expanded and the northern mesic forests became more abundant in the area near Hicks Lake. The decline in *Fagus* and increase in abundance of *Pinus* spp. and *Picea* after the onset of the LIA is also evident in other records of the Great Lakes region, specifically within the mixed Laurentian forests in Ontario, Canada (Fuller 1997). Cluster analysis of 33 sites in Ontario detected widespread change associated with the LIA. These changes included the expansion of *Pinus strobus* in the central and southern portions of its range limit and a population decline of *Fagus* at its northern limit. This study indicates an overall increase in the abundance of *Pinus strobus* in most of the Laurentain forests (Campbell and McAndrews 1991). Alternatively, the pollen record for Graham Lake (Figure 4.16), located at approximately the same latitude as Hicks Lake in southern Ontario, shows a decline in the abundance of *Tsuga* during the onset of the LIA (Fuller 1997).

A significant increase in *Tsuga* around 300 cal yr BP is evident in the pollen records for Hicks Lake, Marion Lake, and Lake 27, indicating increased presence of *Tsuga* in the northern mesic forests as well as an increase in the spatial extent of the northern wet-mesic forests. This trend continues until Euro-

American settlement and disturbance at 150 cal yr BP, but continues again afterward, as the *Tsuga* population recovered from logging.

Around Cowden Lake, significant changes are also evident at the onset of LIA just after 550 cal yr BP including significant increases in the abundances of *Pinus* spp. and *Fagus* concurrent with decreases in the abundances of *Quercus*, *Acer* spp., *Ulmus*, and *Carya*. *Thuja* was a relatively significant component of the forest near Cowden Lake, prior to 600 cal yr BP, but at 550 cal yr BP, it declined concurrent with its decline near Hicks Lakes. This population decline indicates a drier climate at the time associated with the onset of the LIA. While the *Quercus*-dominated forests at Cowden Lake declined significantly in areal extent, they did persist. During most of the LIA, a dry-mesic northern hardwoods forest dominated by *Pinus strobus* and *Fagus* were dominant near Cowden Lake. A *Tsuga* expansion was also evident in the Cowden Lake pollen record corresponding to the *Tsuga* expansion at 300 cal yr BP reconstructed for the areas around Hicks Lake, Marion Lake, and Lake 27 (Bernabo 1981). The *Tsuga* expansion was concurrent with an expansion in *Acer* spp. and *Ulmus*, suggesting the increase of mesophytic taxa in the *Pinus-Fagus* forests.

In contrast to both Hicks Lake and Cowden Lake, major changes in the forests near Morrison Lake are not evident at the onset of the LIA. *Quercus* abundance declined slightly at 550 cal yr BP accompanied by increased abundance of *Fagus*, *Acer* spp., and *Carya* around Morrison Lake. Consequently, the *Fagus-Acer* mesic forests expanded slightly. The *Fagus-Acer* forests may have been limited by the relatively drier conditions associated with the onset of the LIA, as indicated in the pollen records for Hicks Lake and Cowden Lake by decreases in the abundance of *Thuja* in local floras. Near Wintergreen Lake, a more significant decline in *Quercus* abundance was evident, although this decline was not accompanied by an increase in the abundance of *Fagus* or *Acer* spp. (Manny et al. 1978).

Beginning with the onset of the LIA before 550 cal yr BP, the forest tension zone shifted south in response the climatic cooling. This shift differed from the previous southerly shift prior to 1600 cal yr, because it was characterized by a greater presence of coniferous species in the vicinity of Cowden Lake, particularly the increased abundance of *Pinus* spp., *Thuja*, as well as *Tsuga*.

150-0 cal yr BP

At the onset of Euro-American settlement and subsequent disturbance, pollen values for a majority of taxa decreased concurrently with a rise in *Ambrosia*-type in the pollen records for Hicks Lake, Cowden Lake and Morrison Lake. Around Hicks Lake, the post-logging forests were very similar in species composition to those before this disturbance, with less *Pinus strobus* and *Fagus*. The post-logging forests near both Marion Lake and Lake 27 also resemble the pre-logging forests in terms of the taxa identified but with significantly less *Pinus* spp., *Fagus*, and *Acer* spp. (Bernabo 1981). The pollen records for Hicks Lake, Marion Lake, and Lake 27 document a post-logging expansion of *Tsuga*. The post-logging forests at Cowden Lake were similar to those before, with the exception of slight decline in the abundance of *Pinus* spp.. Overall, most pollen types were less abundant, smaller populations, than before logging. A decline in all pollen types was also evident in the study of Crystal Lake but the record does not document post-logging recovery (Kapp et al. 1990). Near Morrison Lake, the post-logging forests were also similar in species composition to those before.

After the disturbance associated with Euro-American settlement and subsequent disturbance, the tension zone reformed. The pollen data indicate (Figure 4.10) that the ecotone re-formed in its relative position but the forests near Cowden Lake were more similar to the mixed Laurentian forests, with higher percentages of coniferous species than in the past.

The three shifts in the location of the forest tension zone of the central Lower Peninsula of Michigan detected in this study occurred at 1600 cal yr BP, 1200 cal yr BP, and 550 cal yr BP, in response to medium frequency climatic oscillations. These vegetation shifts were not detected in a study of ecotonal movements between the boreal forest and the St. Lawrence forest in Northern Ontario (Liu 1990). This macro-scale research detected several shifts in the boreal-St. Lawrence ecotone throughout the Holocene, at 7000 cal yr BP in association with the Hypsithermal; and later during the onset of climatic cooling at 3300 cal yr BP. Lui (1990) indicated that the ecotone reached its current position around 2600 cal yr BP at which time it became stabilized. The pollen records for Nina Lake (Figure 4.16), located 60-80 km south of ecotonal boundary well within the St. Lawrence forests, and Jack Lake, located directly on the ecotonal boundary between the St. Lawrence and boreal forests, both document fluctuations during the last few millennia in the abundances of several important taxa. These taxa included *Thuja*, *Pinus* spp., *Picea*, *Betula*, and *Ostrya/Carpinus*. The VZI values for both of these lakes also fluctuate slightly during the last few millennia. Because the latest ^{14}C dates obtained was 3450 ^{14}C BP for Jack Lake and 3960 ^{14}C BP for Nina Lake, a detailed chronology was not established for the last few millennia and so direct comparisons with this study cannot be made. Finer scale pollen research, i.e. meso-scale, may detect fluctuations in the boreal-St. Lawrence ecotone in northern Ontario in association with medium-frequency climatic oscillations, particularly in response to the MWP and LIA. These climatic perturbations have been detected in this study as well as other studies in the Great Lakes Region (Gajewski 1987; Campbell and McAndrews 1991). The discrepancies between the results from this study of late Holocene change in the forest tension in the central Lower Peninsula and the study of the boreal-St. Lawrence ecotone in northern Ontario may be primarily due to differences in the scale at which these pollen studies were conducted.

4.5.2 *Influence of Soils on Vegetation*

As discussed earlier, previous research has suggested that soil geography, particularly, soil texture, exerts influence on the distribution of tree species, especially within the tension zone itself (Medley and Harman 1987). Changes in vegetation, similar to those detected in this research, can be greatly impacted by soil geography in addition to climate change and other types of disturbance. This was demonstrated by Brubaker's (1975) pollen studies which detected the influence of till and outwash soils on plant distributions in the Upper Peninsula of Michigan during the entire Holocene period. Bernabo's (1981) research in the northern Lower Peninsula also provides evidence, although to a lesser degree, for the influence of soils in vegetation change. The most pronounced changes in vegetation, evident in Bernabo's (1981) research on four lakes in northern Lower Michigan, occurred at Marion Lake and Lake 27. Both of these lakes have the finest textured soils, whereas coarse textured soils surrounding Heart Lake and Jones Lakes, constrained vegetation change. Although Bernabo (1981) recognized the importance of soil texture in determining vegetation patterns he still considered climate to be the driving factor and edaphic factors to be secondary.

In this study of late Holocene changes in the forest tension zone in the central Lower Peninsula, lake sites were selected which had texturally similar soils, within the area of pollen rain (~27 km radius), in order to minimize the influence of edaphic factors on vegetation change at fine scales. While soil texture may influence vegetation change, that influence was not evident in this study. Davis and Botkin (1985) suggested that only paleoecological sites on fine-textured soils would carry a detectable signal from LIA, but subsequent research has detected LIA signals in records from sites with a wide variety of soil textures in Ontario, Canada (Campbell and McAndrews 1991).

Factors, such as medium frequency climatic oscillations and higher frequency disturbance events, such as fire, evidently play a large role in the dynamics of forest ecosystems within the forest tension zone. Overall, the largest amount of vegetation change, as indicated by changes in pollen percentages as well as the in the discriminant analysis, occurred at Cowden Lake, located within the tension zone. The least amount of change occurred near Morrison Lake, south of the ecotone. The soils surrounding Cowden Lake were formed in approximately 68% till and 30% outwash, while the soils at Morrison Lake were formed on 79% till and 21% outwash. The differences in the magnitude and degree of vegetation change at these two sites is more than likely due to their position relative to the tension zone as opposed to soil texture. In order to evaluate soil texture directly, sites must be chosen with similar positions in regard to the tension zone but with different soil textures in the pollen rain area. If soil texture strongly limited the dynamics of tree species during climatic variations; we would expect to see the most change on soils which are fine textured. I do not discount the role of soil in vegetation dynamics, especially within the tension zone itself, but evidence demonstrating the role of soil texture was not apparent nor was this study designed to examine it.

4.5.3 *Disturbance*

The results of this study indicate that changes in the forest ecotone detected in the fossil pollen records for Hicks Lake, Cowden Lake, and Morrison Lake are related to variations in climate over the past 2,000 years. The general climatic variations detected over this time period were initially identified and discussed by other researchers for this region (Bernabo 1981) and elsewhere in North America (Crowley 2000; Soon and Baliunas 2003). It is well known that climate is the main driver of species' distributions and major forest change at regional scales in the Lower Peninsula of Michigan (Denton and Barnes 1987). The similarity of the overall trends for indicator taxa (*Tsuga*, *Thuja*, *Pinus* spp., *Fagus*, *Acer* spp., *Quercus,* and *Ulmus*) and the synchronous nature of the changes across the three sites suggests that overall the documented changes were the result of medium-frequency oscillations in climate as opposed to specific higher frequency disturbance events (Gajewski 1987). A similar conclusion regarding climatic variations as the dominant driver of forest dynamics in the northern Lower Peninsula was reached by Bernabo (1981) for this same time period of the Holocene.

Other disturbances, particularly fire, as well as wind storms (tornadoes), ice storms, disease, and insect outbreaks also significantly affect the forests in this region, but most of these are difficult to discern with fossil pollen data. Many researchers have suggested that fire was a significant component of these forest systems before Euro-American arrival and subsequent disturbances (Kapp et al. 1975; Cleland et al. 2004). The importance of fire in the historic (i.e. presettlement) landscape of the northern Lower Peninsula has been demonstrated in recent work (Cleland et al. 2004), in which the fire return interval for dry-mesic forest associations (*Pinus strobus-Tsuga canadensis)* was estimated to be as high as 47 years and 59 years for the extremely xeric associations dominated by *Pinus banksiana.* The changes in the forest tension zone detected in this research were not directly attributed to disturbances other than climatic variations.

At 1250 cal yr BP, *Quercus* increased in abundance dramatically along with the concurrent decrease in the abundance of fire-sensitive species such as *Fagus*, *Acer* spp., and *Ulmus*, and slight increase in the abundance of *Pinus* (Diploxylon) at Cowden Lake. These trends suggest that fires may have occurred and explain at least some of the dramatic changes in the vegetation of the forest tension zone. Several charcoal peaks were detected in sediments collected from various sites, Demont Lake and Crystal Lake (Figure 4.16) in the Pine River watershed, located in the central Lower Peninsula (Kapp 1975). An expansion of *Pinus* spp. and declines in the abundance of the mesic taxa, *Fagus* and *Acer* spp. was evident after the charcoal peaks (Kapp 1975). This research suggests that forest fires occurred periodically in the Pine River watershed and impacted the forest tension zone (Kapp et al. 1975).

Although sediments from all three lakes in this study were thoroughly sieved with 212 µm to 450 µm mesh sieves, to detect macroscopic charcoal particles, only a minuscule amount of charcoal was recovered. Pollen slides were also examined for microscopic charcoal. A miniscule amount of charcoal was detected, indicating that regional fires did occur (Whitlock et al. 2003). Without adequate amounts of charcoal, linking the dynamics of these forests systems directly to fire or other disturbance would be speculative. Conclusive signals in the pollen records suggesting fire events were not detected. This analysis does not intend to discount the role of disturbance in these systems. Future research should be conducted to detect fire events and better assess the role of disturbance in the dynamics of the forest tension zone.

4.6 *Conclusions*

4.6.1 *Summary of Ecotone and Climate Changes*

2100 – 1800 cal yr BP: Mild Climate

This period was climatically mild in that the forests around both Morrison Lake and Cowden Lake were predominately deciduous. Both the xeric *Quercus*-dominated forests and mesic *Fagus-Acer* forests were relatively abundant in the vicinity of Morrison Lake while the forests near Cowden Lake were dominated by *Quercus* with relatively low abundances of coniferous species. Mixed forests, predominately dry-mesic and mesic northern forests dominated by *Pinus* spp., *Tsuga*, and *Picea*, with relatively high percentages of both *Quercus* and *Fagus,* prevailed near Hicks Lake. The forests around Cowden Lake were quite different from those near Hicks Lake and much more similar to those near Morrison Lake. The climate in most of the study area was relatively mild and dry; although it appears that in the southern Lower Peninsula near Morrison Lake, the climate may have been slightly moister. At this time the tension zone was as least as far north as Cowden Lake but south of Hicks Lake. The *Quercus* band evident in the forest communities identified near Cowden Lake from the PLS data, migrated northward and expanded at Cowden Lake. These interpretations generally correspond to those of Bernabo (1981) for his lakes north of the study area.

1800 -1300 cal yr BP: Cool Climate

This period is markedly different than the previous period. The differences were characterized mainly by the migration of the tension zone south back towards Cowden Lake and remained north of Morrison Lake. The forests near Cowden Lake transitioned from xeric *Quercus* forests to a mesic *Fagus-Acer* community which contained significant components of *Pinus* and *Tsuga*. *Fagus-Acer* mesic forests expanded and became dominant near Morrison Lake as well. *Thuja*, predominately *Thuja occidentalis*, increased in abundance signaling the expansion of wet-mesic and wet-lowland coniferous forests, around Hicks Lake. These changes indicate a shift to a cooler climate with significant increases in moisture. Similar changes are evident and interpreted as cooling in the northern Lower Peninsula based on the pollen analysis of Marion Lake and Lake 27 (Bernabo 1981).

1300 – 700 cal yr BP: Warm Climate

During the period from 1300 to 700 cal yr BP, the ecotone once again shifted north of Cowden Lake, as the xeric *Quercus* forests, now with significant components of *Carya* and *Juglans* expanded. Correspondingly, the mesic *Fagus-Acer* dominated forests with sub-dominants *Ulmus*, and *Betula*, declined. This transition was also marked by a slight decrease in *Pinus*, *Thuja*, *Tsuga* and *Picea* near Cowden Lake. The forests surrounding Hicks Lake remained relatively stable with a slight expansion of *Quercus* around 1300 cal yr BP. By 900 cal yr BP, *Thuja* expanded dramatically again signaling increased moisture and the expansion of wet-mesic forests. *Quercus*-dominated forests expanded near Morrison Lake with a concurrent decline in the *Fagus-Acer* mesic forests. These shifts coincide with other studies which documented increased warmth, most likely and increase of less than 1°C and greater moisture during the MWP in the Midwest (Bernabo 1981; Stine 1998).

700 – 150 cal yr BP: Cold Climate

The tension zone shifted south once again between 700 to 150 cal yr BP. In contrast to the previous transitions of the tension zone, populations of *Quercus* declined only slightly near Cowden Lake but the *Pinus* spp. dominated forests expanded. Near Hicks Lake after 500 cal yr BP, *Thuja* populations declined dramatically, most likely in response to a decrease in moisture while *Tsuga*, *Pinus* spp. and *Picea* also expanded shortly thereafter. The forests near Morrison Lake remained relatively stable with only a slight increase of *Fagus-Acer* mesic forests. Early in this period, the forests surrounding Cowden were more similar to those near Morrison but by the end of the period a reversal occurred as the forests near Cowden became mixed and thus more similar to those surrounding Hicks Lake. The transitions which occurred during this time, i.e. movement of the tension zone south, were in response to the climatic cooling associated with the LIA which has been documented in elsewhere northern Lower Michigan and elsewhere in the Great Lakes region (Bernabo 1981).

150 – 0 cal yr BP: Disturbance

The period from 150 cal yr BP to present was marked by the typical decrease in all pollen types and rise in *Ambrosia*-type as a result of the disturbances association with Euro-American settlement and subsequent disturbance.

Ecotone Transitions

Transitions in the forest ecotone in the central Lower Peninsula over the past 2,000 years have been reconstructed and examined with the analysis of fossil pollen and historical survey data (PLS). The results of this study demonstrate the existence of the forest ecotone in the central Lower Peninsula of Michigan during the past 2,000 years. The results show three major movements or transitions of the tension zone over this time period. These transitions are associated with variations in climate detected in this region by previous researchers (Bernabo 1981; Soon and Baliunas 2003). These transitions included a southward expansion of mixed-forests, coniferous-deciduous, during a cool period from 1700 cal yr BP to 1500 cal yr BP, a subsequent movement of the tension zone northward from 1300 to 700 cal yr BP, and a final shift southward, associated with the LIA from 700 to 250 cal yr BP. Shifts in the tension zone are primarily signaled by the dynamics of *Quercus* and *Fagus* near Cowden Lake. The vegetation responses to medium frequency climatic oscillations were variable at the three lakes and are characterized by: the dynamics between *Thuja*, mainly *Thuja occidentalis*, *Tsuga* and *Pinus* spp. near Hicks Lake and the expansion and contractions of the xeric *Quercus* dominated forests and the mesic *Fagus-Acer* forests near Cowden Lake and Morrison Lake.

The forest communities, specifically species assemblages, identified using the historical survey data (PLS) collected just prior to the onset of Euro-American settlement and subsequent disturbance, were not static in time but changed significantly over the past 2,000 years. The evidence from the pollen records suggests that the species assemblages identified with the historical survey notes were only in existence in such configurations for at most the last 700 years. This research indicates that the composition of the forest communities within the study area changed dramatically, both in terms of species groupings, community composition, as well as the dominance of species within communities over space. The complexity exhibited in the pollen diagrams, as compared to the PLS data, support the continuum models of vegetation (Curtis and McIntosh 1951; Whittaker 1956). In this model species vary on a landscape as a result of the chance interaction of a variety of factors, both stochastic and deterministic, within a continuously varying environmental context, forming associations.

During the past 2,000 years, the character of the ecotone itself also changed in response to variations in climate. Changes in the character of the tension zone were detected by the degree of difference in the pollen records between each of the three sites. At 1800 cal yr BP, the tension zone was distinct, i.e. there were sharp differences between the three sites in terms of the vegetation reconstructions. Thereafter, the tension zone became more diffuse as indicated by the greater similarity between the forest associations of the three sites. By 700 cal yr BP, the forest communities of the three sites diverged once again and the ecotonal boundary became more defined.

This research demonstrated the usefulness of examining meso-scale forest dynamics using both the fossil pollen and PLS data. The analysis of these two different data sources, each representing a different level of detail, time period, and spatial scale, provided new insights into the dynamics of forest ecosystems in the Great Lakes region. This research showed that the forests of this region are dynamic, changing frequently over space and time. These forests are not only dynamic in nature at an ecotonal boundary, such as the tension zone, but also within regional forests associations, as demonstrated in the dramatic changes in the forest composition around Hicks Lake, north of the tension zone through time. Furthermore, the forests present on the landscape at the time of Euro-American settlement were only present in that configuration for less than 700 years, yet often the goal of managers is to emulate these natural systems. This research also demonstrates that the forests in the Great Lakes region are likely to change quickly, in terms of shifts in species associations, species abundance and the geographic distribution of species on the landscape, in response to short-term, and potentially long-term, climatic change associated with global warming. The dynamic nature of these forests must be considered when management decisions are made with regard to the future of these forests in the Great Lakes region.

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Chapter 5

Conclusions

5.1 Summary of Research and Results

The goal of this dissertation research was to examine the dynamics of a mid-latitude forest ecotone at the meso-scale domain, i.e. intermediate spatial (<500 km^2) and temporal scales (over several thousand years at 10 to 100-yr intervals). This research focused on the tension zone in the central Lower Peninsula of Michigan, an ecotone between mixed coniferous-deciduous forests to the north and deciduous forests to the south. Because many tree species reach their distribution limits within the tension zone in the Lower Peninsula of Michigan, these forests are particularly sensitive to changes in climate and other disturbances.

Historical data, the Public Land Survey (PLS) bearing tree data collected by the General Land Office Survey from 1816-1836, as well as fossil pollen data were analyzed to reconstruct forest changes and in relation to the tension zone during the past 2,000 years. The PLS data were used to generate a comprehensive spatial database of forest community composition before the onset of Euro-American settlement and subsequent disturbance. Fossil pollen data from three lakes, situated in a north-to-south transect crossing the tension zone, Hicks Lake (north), Cowden Lake (within), and Morrison Lake (south), were used to reconstruct the vegetation history of the forest tension zone. Both data-sets were then used in concert to investigate the dynamics of the tension zone over time.

A quantitative spatial database was developed from the statistical analysis of PLS bearing tree data. The bearing tree data were gathered from mylar-maps prepared by Michigan Natural Features Inventory. A total of 20 different forest community types were identified. *Fagus grandifolia*, clearly the most dominant species on the landscape, was the most important species on 33% of the landscape. Communities dominated by *Fagus grandifolia* were found in all portions of the study area. Communities dominated by *Quercus alba*, the second most common community type occupying just over 15% of the landscape, were distributed predominately in the southern portion of the study area. Communities dominated by *Pinus strobus*, were the third most dominant type, inhabiting 14% of the landscape, located mainly in the center and northern portion of the study area. Several transitional communities, those found primarily within the tension zone itself, were identified. These communities were characteristic of the ecotone and demonstrated the diffuse nature of the boundary between forest types. The distribution and compositional nature of these transitional communities suggested that the tension zone, at least in the presettlement forests, was defined mainly by the competition between *Pinus strobus* and *Quercus alba*.

Pollen analysis in this study provided a meso-scale reconstruction of the vegetation history of the forest tension zone during the past 2,000 years. This research indicated that the forests in the central Lower Peninsula of Michigan changed significantly during the past 2,000 years in response to climatic variations. Although no direct evidence was found within this study, the data suggest that other disturbance events such as fire and windthrow also play a role in the dynamics of the tension zone. Pollen records provided evidence of significant vegetation changes at all three sites, which were most pronounced for the Cowden Lake area. These records documented significant vegetation changes which corresponded to two known climatic anomalies over this time period, the Medieval Warm Period beginning from around 1200 to 1000 cal yr BP and lasting until about 800 cal yr BP, and the Little Ice Age from 800 to 250 cal yr BP. The pollen records illustrate the intense competition between species which exists at an ecotonal boundary. The pollen records for Hicks Lake documented intense competition between Cupressaceae, mainly *Thuja occidentalis*, and *Tsuga*. While the record at Cowden Lake documented strong competition between *Quercus*-dominated forests and *Fagus-Acer-* dominated forests. Competition between *Quercus* and *Fagus* was also evident, although to significantly lesser degree in the records for Morrison Lake. The fossil pollen records provided here generally corresponded to records for other lakes in the Lower Peninsula of Michigan. To date, this research provided the most detailed reconstruction of forest change and dynamics within the forest tension zone over the past 2,000 years.

The fossil pollen data from the three lakes (Hicks Lake, Cowden Lake, and Morrison Lake) were further analyzed using discriminant analysis to detect ecotone shifts. Each pollen sample from the three lakes was statistically compared to modern pollen data from 196 sites in the Great Lakes region, each with a known modern vegetation assemblage. The statistical comparison assigned a probability of modern analog to each fossil pollen sample as well as determined which modern vegetation assemblage the sample shared the most similarity. This analysis detected three separate shifts in the location of the tension zone around Cowden Lake, while the vegetation around Hicks Lake and Morrison Lake were most similar to their respective vegetation assemblages, mixed and deciduous, for the last 2,000 years.

These transitions included a southward expansion of mixed coniferous-deciduous forests during a cool period from 1700 to 1500 cal yr BP, a subsequent movement of the ecotone northward from 1300 to 700 cal yr BP, as indicated by expansion of *Quercus*-dominated forests towards Cowden Lake. And a final shift southward, marked by the expansion of mixed-forests near Cowden Lake, which was interpreted as a response to the LIA from 700 to 250 cal yr BP. Shifts in the ecotone were primarily signaled by the competitive dynamics of *Quercus* versus *Fagus* around Cowden Lake. The vegetation responses to the medium-frequency climatic oscillations detected in the pollen record were variable between the three lakes and characterized by: the dynamics between Cupressaceae, mainly *Thuja occidentalis*, *Tsuga* and *Pinus* spp. around Hicks Lake and the increases and decreases in the abundance of the xeric *Quercus*-dominated forests and the mesic *Fagus-Acer* forests surrounding Cowden Lake and Morrison Lake. Although the ecotone did experience three major transitions, these transitions were not significant enough to impact the overall species assemblages surrounding Hicks Lake or Morrison Lake. Thus, the forests near Hicks Lake remained mixed coniferous-deciduous while forests near Morrison Lake remained deciduous.

During the past 2,000 years, the character of the ecotone itself also changed in response to variations in climate. Shifts in the character of the ecotone were detected by the degree of differences between the pollen records of each of the three sites. The ecotone was distinct, i.e. sharp differences between the pollen data of the three sites, at 1800 cal yr BP. Thereafter, the ecotone became more diffuse as indicated by the greater similarity in the pollen records between the three sites. By 700 cal yr BP, the pollen records diverged once again and the ecotonal boundary became more defined.

The forest communities identified by the historical survey data (PLS) collected just prior to the onset of Euro-American settlement and subsequent disturbance were not static in time, but changed significantly over the past 2,000 years. The evidence from the pollen records suggested that the communities identified using the historical survey notes were only in existence for at most the last 700 years. This research indicated that the composition of the forest communities within the study area changed dramatically, both in terms of species abundance over space, community composition, as well as the dominance of species within communities. The results from both the pollen analysis and the PLS data supported the continuum model of vegetation (Curtis and McIntosh 1951; Whittaker 1956). In this model a species distribution on landscape varies as a result of the chance interaction of a variety of factors, both stochastic and deterministic, within a continuously varying environmental context, forming associations.

The communities identified in the cluster analysis of the PLS data were not always present on the landscape in those exact configurations. Species within the clusters identified were not always aligned together in the ordination diagrams for each pollen zone, suggesting that species responded to climatic variations and disturbance in an individualistic manner. Moreover, the results also indicated that the communities identified at the time of Euro-American settlement in the region were not in existence for more than the previous 700 years and during this time variations occurred in the composition of these communities. Forest communities present before 700 cal yr BP were significantly different than those identified for circa 250 cal yr BP. This difference is characterized primarily by the increase presence of *Pinus strobus* since 550 cal yr BP, just after the onset of the Little Ice Age (LIA), in the vicinity of both Cowden Lake and Hicks Lake. Prior to the LIA, *Pinus strobus* was a sub-dominant species in the forests surrounding these lakes.

This research demonstrated the dynamic nature of temperate forest systems. The composition of forest communities within the study area changed significantly over the past 2,000 years as evidenced by three major transition of the forest ecotone during this time. Thus, variations in climate as small as 1 to 2°C, a temperature change which has been estimated by temperature reconstructions and historical documents in other studies, can trigger major shifts in temperate forest systems. The forests on the landscape today and in the recent past have only existed in similar species composition for the last 700 years and are a result of cooling associated with the Little Ice Age from 700 to 150 cal yr BP. Thus we must consider the dynamic nature of such systems when attempting to successfully manage these systems. From this research, it is evident that any management strategy must take into account the fact that species abundances and community composition are in constant fluctuation on the landscape. Management strategies that seek to emulate a "climax" community based on the presettlement forests data would not be factoring in the dynamic nature of these systems. This research demonstrated that the species assemblages and abundances of presettlement forests were relatively new on the landscape and were a result of the climatic cooling associated with LIA.

This research also has implications for the prediction of future forest change. Particularly, this research demonstrated that forests in the Great Lakes region respond quickly, in less than 200 years, to temperature fluctuations reconstructed by paleoclimatologists of less than 1°C. Climate models of the Great Lakes region predict that the climate will be 2 °C warmer and wetter, 15-20% more precipitation, by the end of the 21st century as a result of global warming. This research documented significant changes in forests communities with the forest tension zone in response to climate change of less magnitude (1-2°C). Vegetation changes were most evident within the forest tension zone, but shifts in species dominance also occurred both north and south of the tension zone. Therefore, focusing future efforts on the tension zone for monitoring the response of forests in the Great Lakes region would be useful since this research has shown that this ecotone is sensitive to small fluctuations in climate.

5.2 Assessment of Methodology

The Public Land Survey data proved to be an invaluable resource in reconstructing the character of the forest tension zone in the Lower Peninsula of Michigan before Euro-American settlement and subsequent disturbance. The scale at which the PLS data were collected and analyzed allowed local details to emerge, which were not evident in previous qualitative studies. Surveyor bias was evident in the data, especially in the case of the underestimated importance of *Carya* spp. and other taxa known to be important components of the *Quercus* forests in Region VI, south of the tension zone. Also, the importance of long-lived, easily identifiable species were most likely overestimated due to a well known surveyor bias, especially for species such as *Fagus grandifolia* and *Pinus strobus*. The lack of a species designator in 10% of the data set did affect the cluster analysis in that several clusters had dominant taxa without a species designation. Despite this fact, none of the non-species specific clusters emulated the same importance values for the top ten dominants (Appendix I) of the other clusters with the same genus as dominant. Therefore these communities were evidently different. Overall, the lack of species designations was not a major problem in this analysis. The use of historical data to examine the presettlement characteristics of the forest ecotone has been extremely useful, especially in light of the highly disturbed state of these systems today.

The utility of meso-scale paleoecological research was demonstrated in this study. Fine-scale changes in species dominance in the forests of the central Lower Peninsula of Michigan during the past 2,000 years were detected that are typically not evident in paleoecological studies conducted at the macro-scale domain. These changes include shifts in the location of the tension zone. This meso-scale study provided a higher level reconstruction of the history of the forest tension zone than has been available from previous research. This research also detected responses to medium frequency climatic oscillations, the LIA and MWP, not previously detected within the tension zone. This research also demonstrated that the changes associated with medium-frequency climatic oscillations were synchronous across the three sites.

The site selection strategy employed in this research was successful. The use of a Geographic Information System to manage and analyze multiple spatial parameters for the selection of paleoecological sites was unique in this study. The use of a GIS allowed several parameters to be considered. For example the GIS permitted the calculation of the pollen rain source area around each lake. Furthermore, the percentages of glacial substrate and presettlement forests types within the pollen rain area of each lake could be calculated. This analysis provided a high degree of detail regarding the pollen rain area for each lake. The GIS allowed several lakes to be evaluated as candidates for study at once which permitted for further inspection including onsite field visits and discussion with local lake managers and the Department of Environmental Quality. The addition of a state-wide network of Lake Bathymetry would be extremely useful in this process.

The location of the three lakes with regard to the tension zone itself and their respective representation of different forest communities were successful in this study. The location of Cowden Lake, directly within the center of the ecotone was crucial for detection of compositional change. The edge of estimated pollen rain area for Hicks Lake was approximately 20 km north of the northern edge of the estimated pollen rain for Cowden Lake. The tension zone fluctuated significantly at Cowden Lake but the tension zone did not move as far north as to impact the pollen rain source area around Hicks Lake. If a northern lake was chosen that was closer to the pollen rain area of Cowden Lake, movement of the tension zone northward of the Cowden Lake area may have been detected. Regardless, significant changes in the forests around Hicks Lake were detected and were synchronous with movements of the ecotone in the vicinity of Cowden Lake.

Chronological control was a problem in this study. The sediments in each in the three lakes did not contain enough upland plant macrofossils or charcoal to provide AMS radiocarbon dates. As discussed earlier, high resolution and reliable chronologies are lacking for the majority of existing paleoecological studies in the Lower Peninsula of Michigan. A more precise chronology would have provided the exact timing of the vegetation responses to the LIA and MWP in the Lower Peninsula of Michigan. The data presented in this dissertation would have wider utility if a more precise chronology was constructed.

Unfortunately some combination of individual basin characteristics and physical geography, i.e. topography, hydrology, soils, prohibited the deposition of plant macrofossils and charcoal at the coring locations as well as the formation of varves, which are rare in many of the lakes in the Lower Peninsula, preventing the use of this chronological method. In order to ensure that a precise chronology can be constructed from the sediments of lakes in the Lower Peninsula, future researchers should examine the sediments prior to site selection and study.

In this research, there was a tradeoff between lakes that would be more likely to contain datable materials, and the lakes that fit the other suite of spatial criteria designed to detect ecotone change. Lakes with preferred bathymetry and topographic surroundings, i.e. a steep-sided lake basin with significant topographic change in the immediate watershed, were not present within areas which fit the suite of spatial criteria, especially within the central and southern portions of the study area. Although the landscapes of the Lower Peninsula of Michigan contain abundant lakes, the central portion of the Lower Peninsula is rather devoid lakes and therefore site selection was further limited in this area.

This research also demonstrated the value of using both fossil pollen and historical tree data to better understand forest systems at different temporal and spatial scales. By using such an approach new insights were gained into the dynamics of these forests that would not be evident with the use of only one of these data sources. These insights include the dynamic nature of the forests communities identified with the PLS data and the idea that the presettlement forests were relatively new on the landscape and had formed in response to the LIA.

5.3 Future Research Directions

Throughout this research, many new questions arose. While it was apparent that the major vegetation changes which occurred during the past 2,000 years were associated with known medium-frequency climatic oscillations, the role disturbance played in causing these changes remains unclear. The dramatic increase of *Quercus* at 1250 cal yr BP along with the concurrent decrease in the abundance of fire-sensitive species, such as *Fagus*, *Acer* spp., and *Ulmus*, and slight increase in the abundance of *Pinus* (Diploxylon) at Cowden Lake, suggest that fires may have occurred. While the occurrence of fire may explain at least some of the dramatic changes in the vegetation of the forest tension zone, charcoal data, or lack thereof, were inconclusive. This analysis does not intend to discount the role of disturbance in these systems. Future research will be conducted to detect fire events and better assess the role of disturbance and historic legacies in the dynamics of the forest tension zone. This may include charcoal analysis, fire scar analysis, or further examination of the PLS data.

The forest communities, specifically species assemblages, identified with the historical survey data (PLS) collected just prior to the onset of Euro-American settlement and subsequent disturbance, were not static in time but changed significantly over the past 2,000 years. Evidence from the pollen records suggests that the species assemblages identified with the historical survey notes were only in existence in such configurations at most for the last 700 years. Of particular note is the increased abundance of *Pinus strobus* in the pollen records for Hicks Lake and Cowden Lake after the onset of the LIA around 550 cal yr BP. It appears that *Pinus strobus* was a relatively minor component of the forests in the Lower Peninsula prior to the onset of the LIA. Therefore, the abundance of the large and commercial valuable *Pinus strobus* trees in the presettlement forests may have been a relatively recent phenomenon. Further research is needed to investigate these observations in order to make further conclusions about the nature of presettlement forests.

The results from the analysis of the PLS data emphasized the complexity of forest systems in the Great Lakes region, especially within the forest tension zone. The results from this research can be used to further explore the nature of the tension zone with regard to its driving factors, i.e. physical geography, biotic interactions, and historic legacies. The data gathered in this research will also be used to further analyze the distribution of species assemblages as well as the distributions of individual species abundances on the landscape. Specifically, individual species gradients could in future research to investigate underlying causal factors.

As noted earlier, this research documented significant changes of forests communities with the forest tension zone in response to climate change of less magnitude (1-2°C). The climatic changes which occurred in the Lower Peninsula of Michigan during the last 2,000 years were less dramatic than those expected as a result of global warming, yet the forests responded significantly in the past and will likely do so in the future. During the last 2,000 years, the landscapes of the Lower Peninsula were primarily a result of the interaction of physical, biological and historical factors, with relatively little evidence for prehistoric anthropogenic activity. The landscapes in the Lower Peninsula today are quite different in historic times in that anthropogenic factors are now the determining agent of landscape change. The forests of the Lower Peninsula today occupy a relatively small percentage of the landscape and exist in a mosaic of many other land uses. The results of this study in light of the current state of forests today brings forth many questions regarding changes in the future including: *How will the anthropogenic factor play a role in the dynamics of the forests of the Lower Peninsula today and in the future? How will the tension zone respond to global warming? Does the tension zone still exit today in the mosaic of forests and other land uses in the Lower Peninsula of Michigan today? If there are remnants of the tension zone, how will the surrounding land uses affect the dynamic nature of this discontinuous tension zone?* Further research into the dynamics of the existing forest tension zone must be undertaken to address these questions.

Appendix 1: List of species, common and Latin names, and relative importance values of each species within each of the 20 clusters.

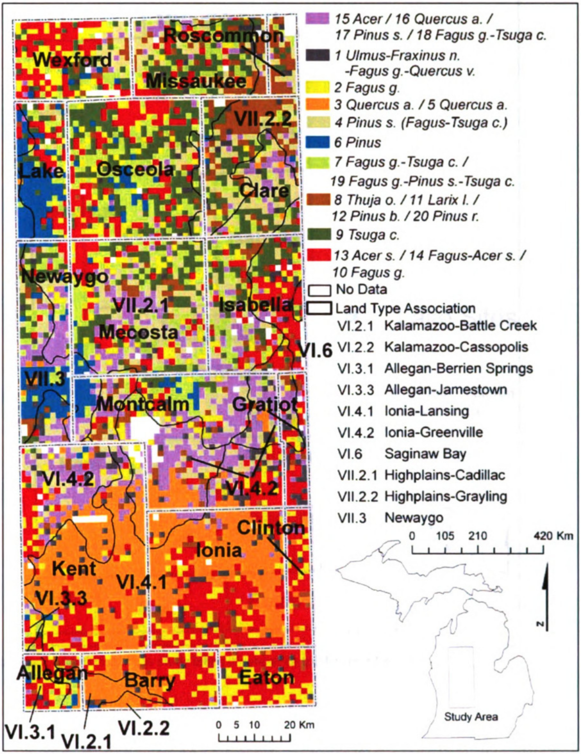
	Clusters	1	2	3	4	5	6
Common Name	**Scientific Name**	4.8	9.3	9.2	9.9	4.4	4.8
Ash (white, black or red)	*Fraxinus* spp.	0.6	0.6	0.9	0.2	0.0	0.0
Aspen (Quaking or Bigtooth)	*Populus* spp.	3.4	0.1	2.0	0.7	0.6	2.3
Balsam Fir	*Abies balsamea*	0.4	0.0	0.0	0.1	0.0	0.0
Basswood	*Tilia americana*	4.7	2.3	2.6	0.9	0.3	0.4
Beech	*Fagus grandifolia*	9.0	66.2	5.3	14.2	0.0	7.0
Birch	*Betula* spp.	2.7	0.6	0.1	0.8	0.0	0.4
Black Ash	*Fraxinus nigra*	15.4	1.6	1.8	2.3	0.2	0.7
Black Cherry	*Prunus serotina*	0.3	0.2	0.5	0.1	0.1	0.1
Black Gum	*Nyssa sylvatica*	0.1	0.0	0.1	0.0	0.0	0.0
Black Oak (Pin & N. Pin)	*Quercus velutina*	7.5	0.4	7.8	1.9	2.1	4.6
Black Walnut	*Juglans nigra*	0.3	0.0	0.1	0.0	0.1	0.0
Bur Oak	*Quercus macrocarpa*	1.9	0.0	1.7	0.0	0.8	0.0
Butternut	*Juglans cinera*	0.2	0.1	0.1	0.0	0.0	0.0
Chinkapin Oak	*Quercus muehlenbergii*	0.5	0.1	4.0	0.1	1.5	0.1
Cottonwood	*Populus deltoides*	0.1	0.0	0.0	0.0	0.0	0.1
Eastern Hemlock	*Tsuga canadensis*	2.7	3.3	0.1	9.4	0.0	4.3
Elm (American or Slippery)	*Ulmus* spp.	16.7	4.0	4.7	1.6	0.7	0.9
Hackberry	*Celtis occidentalis*	0.1	0.0	0.3	0.0	0.1	0.0
Hawthorn (Thornapple)	*Crataegus*	0.0	0.0	0.0	0.0	0.0	0.0
Hickory	*Carya* spp.	0.4	0.6	2.3	0.1	0.5	0.0
Ironwood (Hornbeam)	*Ostrya virginiana*	0.6	1.1	0.7	0.4	0.0	0.2
Jack Pine	*Pinus banksiana*	0.2	0.0	0.1	0.5	0.0	0.1
Maple	*Acer* spp.	5.6	2.3	2.5	6.6	0.5	4.0
Northern White Cedar	*Thuja occidentalis*	1.2	0.2	0.1	2.8	0.1	1.7
Oak	*Quercus* spp.	0.0	0.0	0.1	0.1	0.0	0.5
Pine	*Pinus* spp.	1.1	0.3	0.1	0.4	0.0	57.8
Quaking Aspen	*Populus grandidentata*	0.0	0.0	0.2	0.1	0.0	0.0
Red Oak	*Quercus rubra*	0.5	0.3	3.0	0.3	0.3	0.2
Red Pine	*Pinus resinosa*	0.4	0.1	0.3	5.8	0.0	0.4
Silver Maple	*Acer saccharinium*	0.5	0.1	0.1	0.0	0.0	0.0
Speckled Alder	*Alnus rugosa*	0.9	0.0	0.0	0.0	0.0	0.0
Spruce	*Picea* spp.	0.1	0.0	0.0	0.6	0.1	0.0
Sugar Maple	*Acer saccharum*	3.9	9.5	2.7	1.7	0.3	1.6
Swamp White Oak	*Quercus bicolor*	0.4	0.1	0.2	0.0	0.0	0.0
Sycamore	*Plantus occidentalis*	0.3	0.0	0.1	0.1	0.0	0.0
Tamarack	*Larix laricina*	3.9	0.8	1.8	1.9	0.9	0.6
Tulip Tree	*Liriodendron tulipifera*	0.4	0.1	0.1	0.0	0.0	0.0
White Ash	*Fraxinus americana*	0.9	1.4	0.9	0.5	0.1	0.3
White Birch	*Betula papyrifera*	0.3	0.1	0.0	0.3	0.0	0.1
White Oak	*Quercus alba*	4.1	1.8	51.5	2.3	90.5	8.9
White Pine	*Pinus strobus*	6.4	1.6	0.5	42.8	0.3	2.8
Willow	*Salix* spp.	0.5	0.0	0.2	0.0	0.1	0.0
Yellow Birch	*Betula alleghaniensis*	0.4	0.1	0.0	0.1	0.0	0.1

Appendix 1 continued

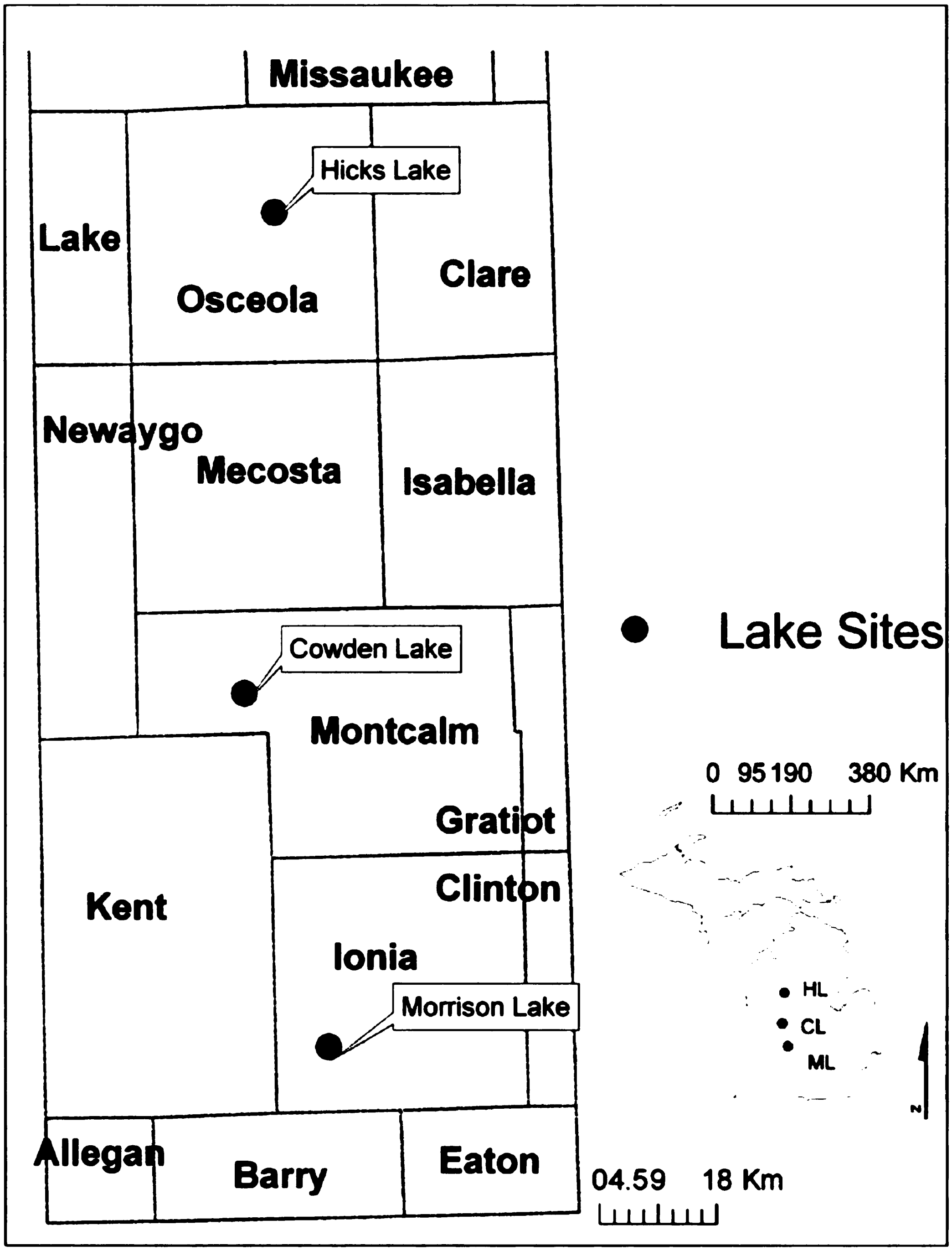
	Clusters	7	8	9	10	11	12
Common Name	**Scientific Name**	6.4	1.3	11.6	6.9	3.3	1
Ash (white, black or red)	*Fraxinus* spp.	0.1	0.0	0.0	3.4	0.9	0.0
Aspen (Quaking or Bigtooth)	*Populus* spp.	0.2	1.0	0.6	0.4	0.7	2.6
Balsam Fir	*Abies balsamea*	0.4	2.1	0.4	0.0	0.1	0.3
Basswood	*Tilia americana*	1.4	0.5	1.4	11.9	0.9	0.3
Beech	*Fagus grandifolia*	35.8	3.1	14.8	30.1	15.7	0.7
Birch	*Betula* spp.	1.0	2.4	1.8	0.4	1.1	0.4
Black Ash	*Fraxinus nigra*	2.0	2.6	3.1	3.2	1.2	1.1
Black Cherry	*Prunus serotina*	0.3	0.2	0.1	0.6	0.1	0.0
Black Gum	*Nyssa sylvatica*	0.0	0.1	0.0	0.1	0.0	0.0
Black Oak (Pin & N. Pin)	*Quercus velutina*	0.5	0.3	0.4	3.0	0.5	0.1
Black Walnut	*Juglans nigra*	0.0	0.0	0.0	0.1	0.0	0.0
Bur Oak	*Quercus macrocarpa*	0.0	0.0	0.0	0.1	0.1	0.0
Butternut	*Juglans cinera*	0.0	0.0	0.0	0.2	0.0	0.0
Chinkapin Oak	*Quercus muehlenbergii*	0.0	0.0	0.0	0.0	0.3	0.0
Cottonwood	*Populus deltoides*	0.0	0.0	0.0	0.0	0.0	0.0
Eastern Hemlock	*Tsuga canadensis*	25.1	13.5	47.7	0.6	3.4	3.0
Elm (American or Slippery)	*Ulmus* spp.	1.7	1.9	1.5	10.6	3.2	1.4
Hackberry	*Celtis occidentalis*	0.0	0.2	0.0	0.1	0.0	0.0
Hawthorn (Thornapple)	*Crataegus*	0.0	0.0	0.0	0.1	0.0	0.0
Hickory	*Carya* spp.	0.0	0.2	0.0	0.9	0.1	0.0
Ironwood (Hornbeam)	*Ostrya virginiana*	0.5	0.0	0.5	1.3	0.3	0.0
Jack Pine	*Pinus banksiana*	0.0	0.0	0.0	0.0	0.6	56.9
Maple	*Acer* spp.	4.1	1.7	3.1	4.1	5.0	2.7
Northern White Cedar	*Thuja occidentalis*	2.6	53.0	4.4	0.1	0.8	1.9
Oak	*Quercus* spp.	0.1	0.0	0.0	0.0	0.0	0.1
Pine	*Pinus* spp.	0.5	0.2	2.7	0.3	0.3	0.0
Quaking Aspen	*Populus grandidentata*	0.0	0.0	0.0	0.0	0.0	0.0
Red Oak	*Quercus rubra*	0.1	0.0	0.1	1.6	0.9	0.0
Red Pine	*Pinus resinosa*	0.8	1.3	1.2	0.0	2.7	11.7
Silver Maple	*Acer saccharinium*	0.0	0.2	0.0	0.5	0.0	0.0
Speckled Alder	*Alnus rugosa*	0.0	0.1	0.1	0.0	0.1	0.1
Spruce	*Picea* spp.	0.3	1.6	0.3	0.0	1.5	0.6
Sugar Maple	*Acer saccharum*	8.1	0.7	5.0	12.6	4.3	0.3
Swamp White Oak	*Quercus bicolor*	0.0	0.0	0.0	0.2	0.0	0.0
Sycamore	*Plantus occidentalis*	0.0	0.0	0.0	0.6	0.0	0.0
Tamarack	*Larix laricina*	1.3	6.4	2.1	1.1	38.3	1.8
Tulip Tree	*Liriodendron tulipifera*	0.0	0.0	0.0	0.1	0.0	0.0
White Ash	*Fraxinus americana*	0.3	0.1	0.4	3.6	0.9	0.4
White Birch	*Betula papyrifera*	0.4	0.2	0.2	0.2	0.2	0.0
White Oak	*Quercus alba*	1.2	0.2	0.5	6.2	4.1	0.6
White Pine	*Pinus strobus*	10.6	5.6	6.3	0.7	11.6	12.6
Willow	*Salix* spp.	0.0	0.0	0.0	0.2	0.3	0.0
Yellow Birch	*Betula alleghaniensis*	0.5	0.7	0.7	0.1	0.0	0.1

Appendix 1 continued

	Clusters	13	14	15	16	17	18	19	20
Common Name	**Scientific Name**	8.2	3.6	1.4	1.6	4	3.9	2.7	1
Ash (white, black or red)	*Fraxinus* spp.	1.0	0.2	0.3	0.1	0.1	0.4	0.1	0.0
Aspen (Quaking or Bigtooth)	*Populus* spp.	0.1	0.1	1.1	1.0	0.5	1.1	0.2	2.3
Balsam Fir	*Abies balsamea*	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.3
Basswood	*Tilia americana*	3.4	1.9	1.9	0.6	0.3	1.7	1.1	0.2
Beech	*Fagus grandifolia*	18.9	46.0	22.5	6.8	7.8	40.9	40.9	4.8
Birch	*Betula* spp.	0.9	0.7	0.2	0.5	0.3	0.5	1.2	0.2
Black Ash	*Fraxinus nigra*	2.6	1.0	1.0	0.5	0.7	1.7	1.3	0.6
Black Cherry	*Prunus serotina*	0.2	0.3	0.2	0.3	0.1	0.2	0.0	0.1
Black Gum	*Nyssa sylvatica*	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0
Black Oak (Pin & N. Pin)	*Quercus velutina*	0.6	0.3	1.5	1.6	1.8	1.1	2.1	1.4
Black Walnut	*Juglans nigra*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Bur Oak	*Quercus macrocarpa*	0.1	0.0	0.1	0.0	0.0	0.0	0.1	0.0
Butternut	*Juglans cinera*	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Chinkapin Oak	*Quercus muehlenbergii*	0.0	0.0	0.0	0.6	0.7	0.0	0.1	0.0
Cottonwood	*Populus deltoides*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Eastern Hemlock	*Tsuga canadensis*	7.3	5.1	1.4	0.6	0.9	1.0	5.4	4.1
Elm (American or Slippery)	*Ulmus* spp.	9.3	3.4	2.1	0.5	0.8	1.0	1.3	0.6
Hackberry	*Celtis occidentalis*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hawthorn (Thornapple)	*Crataegus*	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hickory	*Carya* spp.	0.6	0.2	0.0	0.4	0.1	0.1	0.0	0.0
Ironwood (Hornbeam)	*Ostrya virginiana*	1.3	1.1	0.6	0.4	0.4	0.7	0.8	0.2
Jack Pine	*Pinus banksiana*	0.0	0.0	0.1	0.0	0.3	0.1	0.0	3.8
Maple	*Acer* spp.	2.1	0.5	40.1	6.1	3.9	3.0	4.2	3.4
Northern White Cedar	*Thuja occidentalis*	1.1	0.2	0.4	0.1	0.4	0.3	0.5	1.3
Oak	*Quercus* spp.	0.0	0.0	0.0	0.0	0.1	0.1	0.1	0.1
Pine	*Pinus* spp.	0.3	2.2	1.6	0.1	0.3	0.5	30.9	2.8
Quaking Aspen	*Populus grandidentata*	0.0	0.0	0.0	0.1	0.0	0.1	0.0	0.0
Red Oak	*Quercus rubra*	0.6	0.3	0.7	0.8	0.3	1.6	0.5	0.0
Red Pine	*Pinus resinosa*	0.2	0.0	1.0	0.2	0.7	0.1	0.1	54.3
Silver Maple	*Acer saccharinium*	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0
Speckled Alder	*Alnus rugosa*	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Spruce	*Picea* spp.	0.0	0.0	0.0	0.1	0.1	0.0	0.1	0.6
Sugar Maple	*Acer saccharum*	43.6	35.1	2.9	1.2	0.8	5.2	2.4	0.8
Swamp White Oak	*Quercus bicolor*	0.1	0.0	0.1	0.3	0.0	0.1	0.0	0.0
Sycamore	*Plantus occidentalis*	0.1	0.0	0.3	0.3	0.0	0.0	0.0	0.0
Tamarack	*Larix laricina*	1.2	0.1	1.6	1.0	1.1	1.1	1.9	1.1
Tulip Tree	*Liriodendron tulipifera*	0.1	0.1	0.1	0.0	0.0	0.0	0.2	0.0
White Ash	*Fraxinus americana*	1.0	0.4	0.9	0.3	0.2	0.3	0.7	0.2
White Birch	*Betula papyrifera*	0.4	0.0	0.5	0.2	0.1	0.2	0.1	0.1
White Oak	*Quercus alba*	0.9	0.1	2.3	39.9	6.2	3.5	2.8	0.8
White Pine	*Pinus strobus*	1.2	0.1	13.7	35.4	70.9	33.1	0.8	14.8
Willow	*Salix* spp.	0.0	0.1	0.0	0.1	0.0	0.0	0.0	0.0
Yellow Birch	*Betula alleghaniensis*	0.5	0.1	0.0	0.0	0.0	0.0	0.0	0.1



Appendix 2 Map of identified clusters for the study area. Map shows the assignment of each individual Public Land Survey section (2.65 km^2) to its assigned clusters based on the cluster analysis. Clusters are grouped based on the dominant species and position on the dendrogram. This map is a version of Figure 2.11. County boundaries and county names are added for reference purposes.



Appendix 3 Location of three study lakes in reference to Michigan Counties.