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A Comparison of Pre-European Settlement and Present-Day Forests in the High Plains Region of the Huron National Forest, Northern Lower Michigan

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A COMPARISON OF PRE-EUROPEAN SETTLEMENT AND PRESENT-DAY FORESTS IN THE HIGH PLAINS REGION OF THE HURON NATIONAL FOREST, NORTHERN LOWER MICHIGAN

By

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ABSTRACT

A COMPARISON OF PRE-EUROPEAN SETTLEMENT AND PRESENT-DAY FORESTS IN THE HIGH PLAINS REGION OF THE HURON NATIONAL FOREST, NORTHERN LOWER MICHIGAN

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General Land Office survey records of 1838-1846 were used to reconstruct the composition, structure, and disturbance regime of pre-European settlement forest communities along an edaphic gradient in northern lower Michigan. These data were compared to plot data of second-growth forest communities on similar sites.

A *Pinus banksiana* cover type still dominates a third of the landscape as it did in the pre-European settlement period. *Acer saccharum*, *Populus* species, *Quercus* species, *Tilia americana*, *Acer rubrum*, and *Betula papyrifera* have supplanted *Pinus resinosa*, *Pinus strobus*, *Tsuga canadensis*, and *Fagus grandifolia* as forest dominants along most of the dry-mesic, mesic, and wet-mesic areas of the edaphic gradient. Forest communities have smaller trees and higher tree densities today than in the pre-European settlement period. Likewise, disturbance regimes have been substantially altered. Human-imposed disturbances since 1870 have interacted with physical factors to produce the forests we see today.

Dedicated to my parents.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

BACKGROUND

Ecological Theory and Land Management

Today's public land managers must focus on the conservation and restoration of biological diversity at several levels of spatial and temporal scale (Soule 1986; Jordan et al. 1987; Wilson 1988; Hansen et al. 1991; Probst and Crow 1991). In order to manage for the biological diversity of northern temperate forests we need a model of natural vegetation patterns. The pre-European settlement vegetation patterns and dynamics can provide useful information for the development of such a model or guideline. Furthermore, by comparing the patterns and processes of pre-European settlement northern temperate forests to those of the present we may gain a better informal understanding of those underlying principles useful in management.

Modern ecologists often decry those not taking a directly experimental approach to ecology. While establishing the causes of patterns in nature may lie at the core of ecology as a science (Tilman 1988) this does not restrict us from establishing the spatial and temporal validity of causal mechanisms already identified (Franklin 1989). For instance, we already know that vegetation patterns result from an array of abiotic and biotic factors, which more often than not interact (Whittaker 1975). We also know that secondary forest succession comes about through a variety of causal mechanisms, ultimately grounded in life-history and physiological traits of the participating species (Pickett et al. 1987). Yet mere knowledge of causal mechanisms established in disparate regions may not aid the land manager. The land manager needs more general and practical information on the relative importance of the various causal mechanisms in creating the vegetation patterns of the specific region in which that person works.

Land managers need to know how species' life histories, soil factors, topography, herbivory, and disturbance regimes interacted as forcing functions for the vegetation patterns in a particular climatic region (Grimm 1984; Rowe 1984; Host et al. 1987) during pre-European settlement time. Via this baseline data they may gauge the relative impact of management practices (no management also being a management practice) in mimicking the factors which brought about pre-European settlement biological diversity. The northern temperate forest landscape of today has come about rather directly as a result of historical factors, i.e., a biological legacy akin to that described by McCune and Cottam (1985) for southern Wisconsin. To judge how far we may have come from what Leopold (1948) called "land health" will require a study of the changes in vegetation dynamics between pre-European settlement time and now. By comparing today's northern temperate forest to the pre-European settlement one, land managers can gain an understanding of: the impact of widespread forest clearing on northern temperate landscapes; future potential successional trajectories; and what types of management might bring back non-anthropogenic evolutionary patterns.

Previous Studies of the Pre-European Settlement Forest

A number of studies on the pre-European settlement forest have occurred. Most have focused on the Midwest where the Federal rectangular survey system of the General Land Office (GLO) first came into use (White 1984). However, some have used pre-GLO survey records in the East. The purpose of these studies typically fall into one of several categories.

The pre-European settlement forest was first reconstructed from the GLO surveys by mapping tree species distributions according to the location of witness trees in the notes and plat maps. Kenoyer applied this method in southwestern Michigan as early as 1934. The entire state of Michigan was qualitatively mapped by Veatch (1959) using a combination of GLO survey and soil data. Other states have been qualitatively mapped including: Indiana by Lindsey et al. (1965); Ohio by Gordon (1969); Illinois by Anderson (1970); Minnesota by Marschner (1974); and Wisconsin by Finley (1976).

Bourdo's landmark studies (1955; 1956) "ground-truthed" the GLO survey records. Bourdo relocated the witness trees, the corner points, and the section lines used by the surveyors in old-growth forests of the upper peninsula of Michigan.

Bourdo concluded that with proper use the GLO survey records could allow for the quantitative reconstruction of the pre-European settlement forest's composition and structure. Curtis (1959) also validated the use of GLO survey data in vegetation history studies.

Many researchers have examined the relationship between pre-European settlement tree species distributions and their corresponding site factors. Crankshaw et al. (1965) did one of the first such studies in Indiana. Other salient research of pre-European settlement tree species - site relations include those by Grimm (1984) in Minnesota and Whitney (1982; 1986; 1990) in Michigan, Ohio, and Pennsylvania.

In recent years the importance of disturbance regimes to forest ecosystem structure and function has become apparent (Heinselman 1973). Lorimer's (1977) work on the pre-European settlement disturbance regime of Maine provided a benchmark for all further pre-European settlement disturbance histories. Lorimer's methods (1977; 1980a) have been applied to the pre-European settlement forests of north-central Michigan (Whitney 1986); the Allegheny Plateau (Whitney 1990); and two aspen (Populus grandidentata) dominated landscapes in northern Michigan (Palik and Pregitzer 1992). Canham and Loucks (1984) detailed the importance of, and developed the methodology for studying pre-European settlement stand-replacing windthrow disturbances. The interactions between landscape elements (topography, rivers, lakes, and prevailing wind corridors) and the pre-European settlement fire regime has come under recent scrutiny (Grimm 1984; Leitner et al. 1991; Palik and Pregitzer 1992). These studies seem to substantiate the claims made about forest fire behavior in old-growth landscapes (Romme and Knight 1981).

Those studies which have compared the pre-European settlement forest to the forests of today provide the most insight from both an ecological and management perspective. Stearns (1949) provided the first study of this kind on a northern hardwood forest in Wisconsin. Mustard (1983) compared the pre-European settlement and present-day forests of Oceana and Manistee Counties in Michigan. Whitney (1987) compared compositional and disturbance regime changes since settlement in Crawford and Roscommon Counties, Michigan. Fralish et al. (1991) examined changes in forest composition and structure over the past 180 years in the Shawnee Hills of southern Illinois. Palik and Pregitzer (1992) made a detailed study of compositional and disturbance regime changes since Euro-American settlement for two northern lower Michigan landscapes.

Knowledge Gaps

In Michigan we lack studies examining the changes in forest composition and structure since pre-European settlement time. Pre-European settlement forest structural data could aid land managers in old-growth restoration efforts. The importance of structural diversity to a forest's overall biological diversity has proved of significant importance (Franklin et al. 1981). We need to document the relationships between tree species, soil factors, and disturbance regimes during the pre-European settlement period within the many climate zones of Michigan (Barnes 1989).

PROBLEM STATEMENT

What were the patterns of forest vegetation in the pre-European settlement period and how have they changed within the High Plains Region of the Huron National Forest?

Hypotheses

1. Tree species were probabilistically distributed in the pre-European settlement forest of northern lower Michigan. Species' optima occur as nodes on a complex environmental gradient (Whittaker 1975). Those species with physiologies and life histories adapted to dry, disturbance prone, nutrient poor conditions occurred on such sites more often than expected by chance alone. The same could be said of other areas of the gradient.

2. The distribution of tree species in the pre-European settlement forest of northern lower Michigan was heterogeneous. Certain tree species with similar physiologies and life histories formed loose associations.

3. The pre-European settlement forest communities on different site types in northern lower Michigan differed markedly from each other in composition, structure, and disturbance regime.

4. The pre-European settlement forest communities

significantly differ from present-day forest communities on similar site types in northern lower Michigan in terms of composition, structure, and disturbance regime.

Objectives

1. Examine the physical factors (fire, soils, physiography, microclimate) controlling the pre-European settlement forest vegetation within the study area.

2. Determine if associations among various tree species occurred in the pre-European settlement forest and relate these to environmental gradients within the study area.

3. Reconstruct the composition, structure, and disturbance regime of pre-European settlement forest communities on different site types in the study area.

4. Examine the changes in composition, structure, and disturbance regime between pre-European settlement forest communities and present-day forest communities on similar site types within the study area.

METHODS AND MATERIALS

STUDY AREA

The Huron National Forest

The study area for this research had to meet three criteria: first, that recent overstory data were available; second, that glacial landform and soil survey maps were available; and third, the area fell within a relatively homogeneous macroclimate. Within northern lower Michigan the western half of the Huron National Forest (NF) met these criteria. The Huron NF lies in northeastern lower Michigan (Figure 1) and encompasses 163,386 ha. Utilizing the criteria

Figure 1: Location of the Huron National Forest.

above the study area became narrowed to the following thirteen townships: T24N, R3 and 4E; T25N, R1 through 5E; T26N, R1 through 5E; and T27N, R4E. The study area (Figure 2) occupies 121,212 ha within the Huron NF.

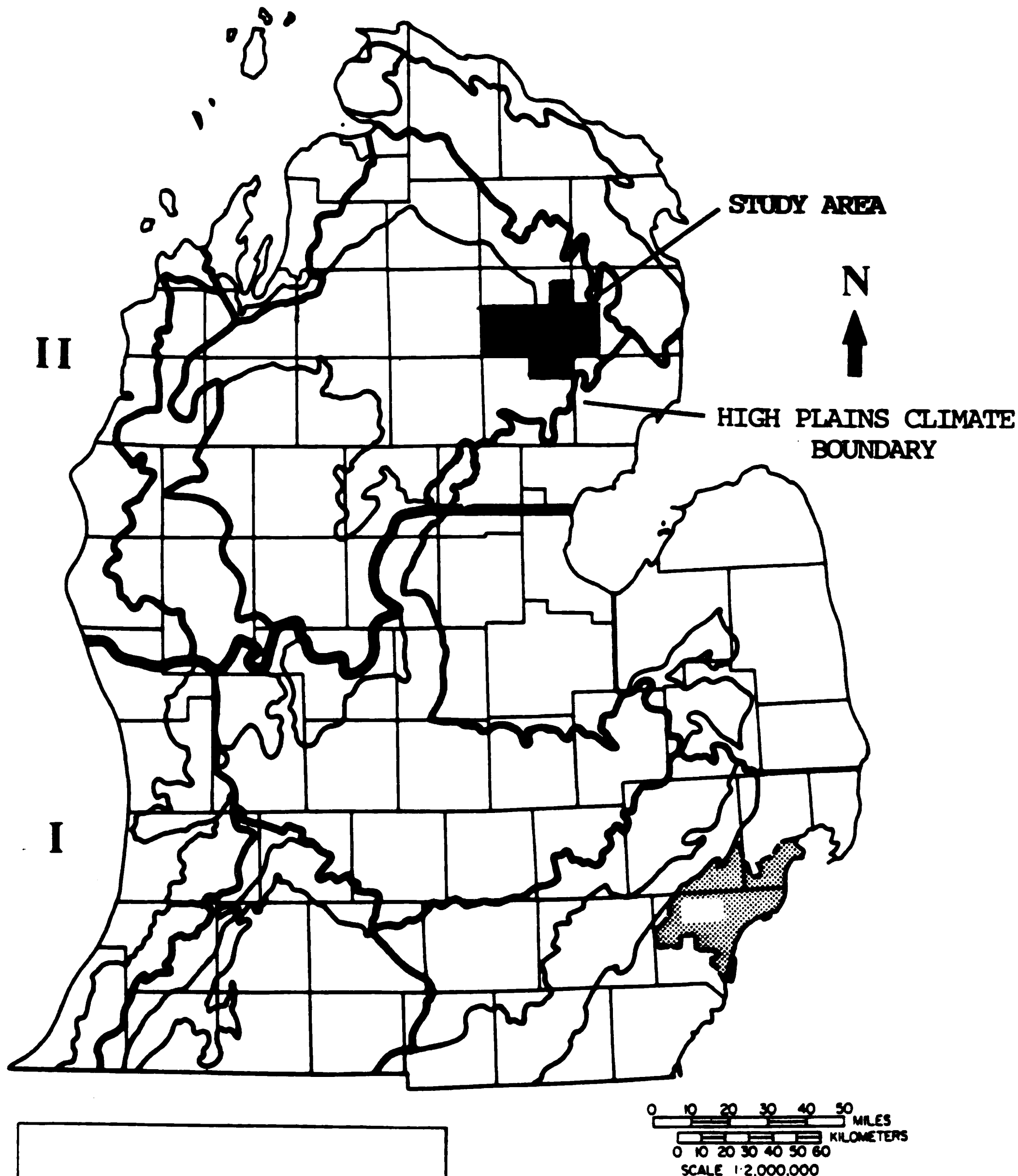
Climate

The study area lies in the 21,885 km^2 High Plains Climate District as delineated by Albert et al. (1986) (Figure 2). Because of its inland location, northern latitude, and relatively high (for Michigan) elevations, the district has the most severe climate in lower Michigan. The growing season of 115 days is the shortest and most variable yearly in lower Michigan (Albert et al. 1986). Other climatic variables include: total annual precipitation of 790 mm; annual average temperature of 6.7 °C; and an annual minimum temperature of -28 °C (Albert et al. 1986). The total growing season precipitation is similar throughout the district. Major river valleys and outwash plains form cold air drainages.

Glacial Geology

The surficial geology of the study area has come about primarily through glacial action and subsequent post-glacial erosion. The most recent glaciation being the Laurentide ice sheet of the Late Wisconsinan Period. The many readvances of first the Saginaw lobe, and then the Huron lobe between 14,800-12,500 years B.P. molded the landscape of the Huron NF (Burgis 1977). By 11,800 years B.P. most of the major drainages in the study area had been developed.

Figure 2: Location of the study area within Michigan and within a regional climate classification (after Albert et al. 1986).



STUDY AREA INSET

Most of the area is drained by the Au Sable River which discharges into Lake Huron (Burgis 1977). Glacial landformsof the study area as mapped by Burgis (1977) include: outwash plains, ice-contact topography, and moraines (Figure 3). Outwash plains occur as terraces made of well-sorted, extremely well-drained sands left by braided streams during glacial ablation (Burgis 1977). Ice-contact topography, also termed ice-disintegration topography or stagnant ice topography, forms a mosaic of kettles and kames. These mainly hilly areas have a finer soil texture than the outwash plains (Host et al. 1988). Morainal soil exhibits the greatest soil development and the finest texture (Padley 1989). Yet, Padley (1989) found that Burgis' (1977) mapping scale was too small to distinguish localized deposits of surficial material.

Soils

The major soil orders represented in the study area include Alfisols, Entisols, Histosols, and Spodosols. Upland soil families (Veatch et al. 1931; Veatch et al. 1941; U.S.D.A. Soil Conservation Service 1990) include: mixed, frigid, Alfic Udipsamments; mixed, frigid, Typic Udipsamments; fine, mixed, Typic Eutroboralfs; Euic and Dysic, Typic Borosaprists; and sandy, mixed, frigid, Entic Haplorthods.

Human History

A brief account of the study area's human history places the recent development of this landscape in perspective. The landscape before Euro-American settlement certainly did not

Figure 3: Map of the glacial landforms within the study area (after Burgis 1977).

exist in a socio-cultural vacuum. Sustainable cultures occupied the area, particularly along river basins, for centuries prior to Euro-American settlement. Between 2990-370 years B.P. the Woodland Indian culture hunted along the river basins of the study area (Lovis et al. 1978). The Ottawa tribe of Native Americans lived in the area from the beginning of the eighteenth century up until 1836 (Lovis et al. 1978). It is hard to discern what impacts these indigeneous people's had on the landscape.

After the removal of the indigeneous peoples, the land was surveyed between 1833-1846 by government surveyors. Homesteaders and lumbermen soon followed. The lumbering era was at its peak in the study area between 1850-1900 (Lovis et al. 1978). The white population of northern lower Michigan showed an explosion in numbers during this time. The study area's pines were selectively harvested between 1870 and 1890 (Veatch et al. 1931). Pines were first logged along the Au Sable River (Sargent 1884) and later in the interior uplands with the introduction of the railroad to northern Michigan in the 1880s (Maybee 1976). By the 1890s the loggers had depleted the study area's pinery and moved on to harvest hemlocks for their bark (Veatch et al. 1931). The leather industry used the tannin in hemlock's bark. Michigan led tanbark production from 1900-1920 (Fulling 1956). The exploitation of hemlock coincided with the cutting of most upland hardwood stands and even some swamp conifers (Sandberg

1983). By 1920 nearly no merchantable timber remained in the study area (Veatch et al. 1931). By the turn of the century the land had been nearly completely logged or at least high-graded. Wildfires were common due to droughts, logging equipment, and tremendous fuel loads of logging slash (Lovis et al. 1978). The lumber industries simply left the land after the big cut. With a new spirit of conservation in U.S. politics, the Huron NF was established piece-meal between 1909-1933. Wholesale fire control began in the 1930s along with widespread tree planting and erosion control measures via the Civilian Conservation Corps (Lovis et al. 1978).

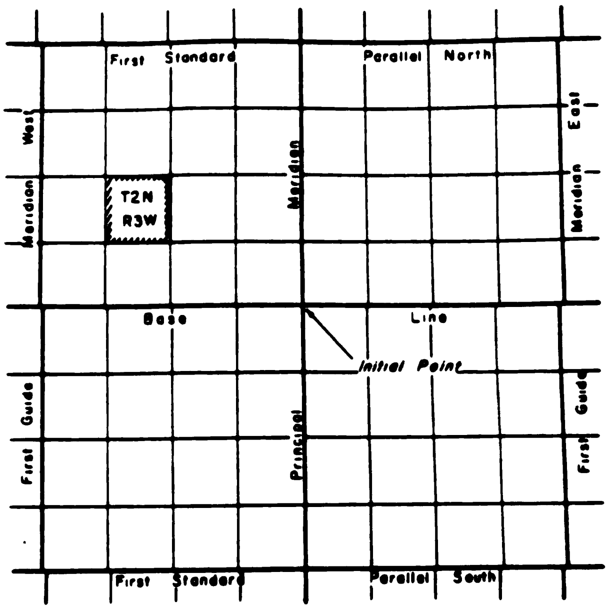
THE GENERAL LAND OFFICE (GLO) SURVEYS

The survey instructions of 1833 issued by the Surveyor General of Ohio, Indiana, and the Territory of Michigan applied to all the townships in the study area (White 1984). The plan provided for the survey of land into townships, six miles (9.66 km) square, with lines running due north and south and others crossing these at right angles (Figure 4). Initially the township lines were run, with interior section lines being subdivided later. A section was a mile (1.61 km) square; townships were surveyed in tiers of sections (Figure 4), with all excesses and shortcomings pushed to the north row and west tier (Hutchinson 1988).

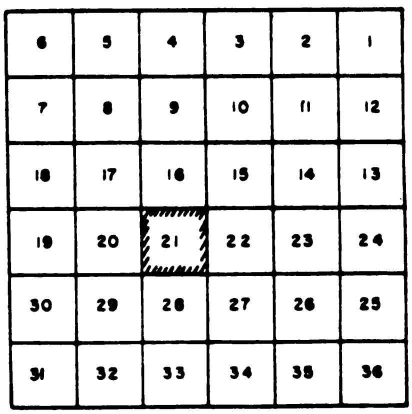
At every half mile (0.8 km) within the township grid a corner point was established by setting a wooden post into the ground at the appropriate point. At each corner point two

Figure 4: General Land Office survey land subdivision methods.

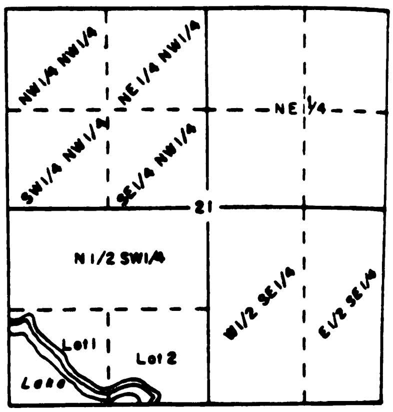
TOWNSHIP GRID



T2N R3W



SECTION 21



witness trees were marked as to their species, estimated diameter at breast height (the diameter of the tree at 1.37 m, known as d.b.h.), compass direction, and distance from the corner post. Each section line traversed included notes on the line's location; the direction of travel; the points along the line at which features were encountered, including evidence of disturbance; the names and diameters of two trees cut by the line (line trees); and a general description of the vegetation, topography, and soils along the surveyed line. At the end of surveying a township, a plat map was drawn of the township.

The exterior lines for all the townships in the study area were surveyed by Lewis Clason in 1838 and 1839. Of the thirteen townships falling within the study area bounds, five were resurveyed by John and James Mullett between 1844-1846. The eight other township interiors were surveyed by William R. Coon and Thomas Pattison in 1839 and 1840, respectively. These two men had no record of turning in fraudulent surveys (Havens 1915). Upon inspection of their work I deemed it usable for the study. The historical records for the study area indicated that no significant settlement by whites had occurred prior to the surveys.

DATA COLLECTION

Microfilm photocopies of all thirteen townships in the study area were made utilizing the GLO survey records kept at the state archives of the Library of Michigan. I used 30x60 minute (1:100,000 metric scale) U.S. Geological Survey (USGS) topographic maps in conjunction with Burgis' (1977) glacial landform map (Figure 3) to place every GLO survey corner point within a glacial landform type (outwash plains, moraines, or ice-contact features). I derived data on soil types from the soil surveys of Oscoda (Veatch et al. 1931), Alcona (Veatch et al. 1941), and Ogemaw (USDA-Soil Conservation Service 1990) Counties. The early soil types were updated to their modern soil series correlates. I scored each GLO survey corner point as to its modern soil series. This allowed me to place each corner point within a soil textural family and soil drainage class. I recorded the two witness trees by species, their d.b.h., and the distance from the corner post to the nearest witness tree for each GLO corner point within the study area. Interpretation of surveyor's handwriting followed Hutchinson (1988). I identified witness trees to the species or genus level via Bourdo's (1955) list of names used for trees by Michigan surveyors. Surveyors failed to differentiate between trembling aspen (Populus tremuloides) and big-toothed aspen (Populus grandidentata) species in northern Michigan. So, in this study I referred to both as aspen species. The surveyors also failed to differentiate between northern red oak (Quercus rubra), black oak (Quercus velutina), and Hill's oak (Quercus ellipsoidalis). I grouped all these species into a "red oak complex" category (Voss 1985). Throughout the paper I used the modern common names of species. The common names used in

Table 1: Scientific, common, and surveyor names of tree species in the study area.

Scientific Name	Common name(s) assigned by surveyors	Modern common name
Abies balsamea	Fir, balsam fir	Balsam fir
Acer rubrum	Maple	Red maple
Acer saccharum	Sugar	Sugar maple
Betula alleghaniensis	Yellow or cherry birch	Yellow birch
Betula papyrifera	White or paper birch	Paper birch
Betula species*	Birch	Birch
Fagus grandifolia	Beech	Beech
Fraxinus americana	White ash	White ash
Fraxinus nigra	Black ash	Black ash
Juniperus virginiana	Red cedar	Red cedar
Larix laricina	Tamarack	Tamarack
Ostrya virginiana	Ironwood	Ironwood
Picea species**	Spruce	Spruce
Pinus banksiana	Spruce, pitch, or scrub pine	Jack pine
Pinus resinosa	Yellow or Norway pine	Red pine
Pinus strobus	White pine, pine	White pine
Populus species***	Aspen, poplar	Aspen
Quercus alba	White oak	White oak
Quercus rubra-velutina-ellipsoidalis #	Black oak	The red oak complex, red oaks
Thuja occidentalis	Cedar	White cedar
Tilia americana	Lynn	Basswood
Tsuga canadensis	Hemlock or hem	Hemlock
Ulmus species ##	Elm	Elm

* Indicates either paper or yellow birch.

** Either Picea glauca or Picea mariana.

*** Either Populus tremuloides or Populus grandidentata.

Surveyors were unable to distinguish among Q. rubra, Q. velutina, or Q. ellipsoidalis ; therefore any of these species and hybrids between these species are indicated here (Voss 1985).

Primarily Ulmus americana, may include some Ulmus rubra.

the GLO surveys, their scientific names, and modern common names appear in Table 1.

DATA ANALYSIS

Species-Site Relations of the Pre-European Settlement Forest

To describe the complex tree species-site factor relationships in the pre-European settlement forest I first used correspondence analysis (CA) and nonmetric multidimensional scaling (NMDS). CA is a form of indirect ordination which reduces the dimensions of a matrix of count data for the occurrence of a set of species at a set of sites (James and McCulloch 1990). The object of CA is to approximate some pattern of response of the set of species to a complex environmental gradient (Digby and Kempton 1987). I made a data matrix of count data with witness tree species as column scores and landform-soil drainage types as rows and performed a CA on this matrix using a PC-SAS software program (SAS Institute Inc. 1985). Only those tree species occurring at ≥ 50 sites were included in the analysis to eliminate the skewing effect of infrequent species (Digby and Kempton 1987). The number of dimensions were reduced to two for graphical display.

NMDS is another indirect ordination method used to estimate nonlinear monotonic relationships (James and McCulloch 1990). I used witness tree presence/absence data at corners to calculate Jaccard's similarity coefficient for species pairs. I only utilized species occurring at ≥ 50 sites to avoid small sample sizes (Sokal and Rohlf 1981). To simplify the presentation of the data, I used the above similarity matrix in a nonmetric multidimensional scaling (NMDS). The nonmetric solution is given by the ordination which minimizes the "stress" function (Digby and Kempton 1987).

I directly examined pre-European settlement witness tree species-site relationships with binary discriminant analysis (BDA). The technique uses species presence/absence data to directly test species-substrate relations (Strahler 1978). I considered each GLO corner point a site on which tree species were present or absent. Only tree species occurring at ≥ 50 sites were used to avoid small sample size errors (Sokal and Rohlf 1981). The presence and absence values for each species, summed across sites, were then compared with the C categories of each site factor in a 2 x C contingency table (Strahler 1978). I used soil textural family, soil drainage, and glacial landform as site factors. Those contingency tables which had a significant G statistic were converted to standardized residuals (Haberman 1973). The standardized residuals expressed the degree of association between a species and a site factor. A high positive residual indicated a species was more common on, say, sandy loam soils than might have been expected by chance (Strahler 1978). Negative values indicated the converse of positive values.

Pre-European Settlement Tree Species Associations

I examined the distribution of pre-European settlement tree species with respect to one another using cluster analysis on the SYSTAT software program (Wilkinson 1990). Cluster analysis is used to discover "natural groupings" in large data matrices (Digby and Kempton 1987). I took the same n x p matrix used in the CA and converted it to a matrix of Euclidean distances. I then converted this distance matrix to a dendrogram with both the average linkage and Ward's agglomerative hierarchical methods (Digby and Kempton 1987). I analyzed the strength of the relation between the distance matrices and their dendrograms with the cophenetic correlation coefficient (Sneath and Sokal 1973).

Reconstructing the Pre-European Settlement Forest

Forest Composition

Soil moisture is one of the dominant variables influencing northern temperate plant community composition and productivity (Peet and Loucks 1977; Pastor et al. 1984; Host and Pregitzer 1992). Soil drainage is a crude index of soil moisture and texture. So, I grouped the GLO corner point data by their soil drainage class. In effect, I placed GLO corner point trees along an edaphic gradient. Divisions along the edaphic gradient formed "site types" (Table 2) which aided in summarizing the data for analyses. For each site type I used the witness tree data to calculate relative density and relative dominance (Mueller-Dombois and Ellenberg 1974) of the

Table 2: Site type names.

Soil Drainage Class	Site Type
Excessive	Xeric
Somewhat excessive	Dry-Mesic
Moderately well to well	Mesic
Poor to somewhat poor	Wet-Mesic
Very poor	Hydric

overstory (trees ≥ 10 cm d.b.h.) species. All site types exceeded minimal sample sizes for composition determination (Lorimer 1977). I also calculated the relative density of species across the entire study area. To help summarize site type compositional patterns I calculated an "importance value" (i.v.) for each species by site type. The importance value equalled the average of relative density and relative dominance converted to a percentage figure for each species (Lindsey et al. 1965; Leitner et al. 1991). I compared differences in overstory composition between pre-European settlement site types with a chi-squared test of independence (Gill 1978). This procedure and all other univariate statistics in this study were calculated on the SYSTAT program (Wilkinson 1990). Tree species diversity for each site type was calculated using importance values in the Shannon-Weaver formulation (Peet 1974).

Forest Structure

I used a modification of the point-quarter method (Cottam and Curtis 1956; Fralish et al. 1991) to estimate density (trees/ha) and basal area (m^2/ha) of pre-European settlement tree species by site type. Trees were defined here as stems ≥ 10 cm d.b.h. Cottam and Curtis (1956) found that using the point-quarter method the mean distance to the nearest tree in a stand equals 0.5 times the square root of the mean area per tree. However, Kline and Cottam (1979) determined that using the median distance gave a better estimate of density when applying the point-quarter method to GLO data.

I determined the median corner-to-witness tree distance for each forest site type. Multiplying this median distance by two and squaring the product yielded the mean area (m^2) occupied by a tree. Dividing 10,000 m^2 (1 ha) by the mean area per tree gave an estimate of tree density per site type. I derived the basal area (m^2/ha) of each pre-European settlement site type by multiplying its mean basal area per witness tree by the site type's density (trees/ha). To calculate trees/ha/species and basal area/ha/species I multiplied each species' relative density by total site type density and each species' relative dominance by total site type basal area, respectively.

Calculating the mean witness tree diameter by site type gave another measure of pre-European settlement forest structure. To test for differences in mean tree density, basal area, and witness tree diameter between pre-European settlement forests on different site types I used a one-way analysis of variance with Tukey's test to compare means (Gill

1978). Surveyors infrequently described the forest's structure. However, I did record any structural descriptions and the distances the surveyors traveled in pine savannas (Curtis 1959).

To investigate the possible age structures of pre-European settlement stands I created histograms of the d.b.h. distributions for the dominant witness tree species. Lorimer (1980b) found tree diameters positively correlated with age in a southern Appalachian old-growth forest. Gates and Nichols (1930) found that diameters were approximately correlated with age of both hemlock and sugar maple in an old-growth stand of northern hardwoods in Michigan. Goff and West (1975) reported similar results in northern Wisconsin. In this study I assumed the same positive relationship between d.b.h. and tree age. Even-aged stands have a d.b.h. frequency distribution shaped like the normal curve (Smith 1986). Uneven-aged stands have a d.b.h. distribution resembling an "inverse-J" or the negative exponential distribution (Smith 1986).

Surveyor Bias

I tested surveyor bias in witness tree species selection with a one-way analysis of variance (anova) (Gill 1978). According to Delcourt and Delcourt (1974) the means of the distances from surveyed corner to witness trees will be equal among dominant species within a homogeneous environment so long as the surveyors showed no bias towards tree species. To test for surveyor bias bias in witness tree selection, forest site types formed sampling populations from which subjects (GLO corner points) were considered randomly assigned to treatments (tree species). Rejection of the anova hypothesis of equal treatment means indicated significant surveyor bias.

Bourdo (1956) stated that the mean distance from the corner post to a tree should not significantly differ between diameter classes if surveyors were not grossly biased in tree size selection. To test for surveyor bias in witness tree size selection I used a one-way anova. Ten inch (25.4 cm) diameter classes formed the grouping variables in the anova.

Surveyors were significantly ($P \leq 0.05$, Tukey's HSD) biased for red pine on xeric and dry-mesic sites. This makes sense in light of the surveyor's instructions and the structure of these dry sandy plains. Surveyors had to pick trees which were conspicuous enough for settlers to recognize and that would last until the settlers arrived. On these dry-mesic and xeric sites, red pine presented an easily recognized, long-lived, and easily marked tree for the surveyors. Surveyors failed to show any significant bias ($P \leq 0.05$, Tukey's HSD) towards any other tree species in the study area. The fact that surveyors went out of their way to blaze red pines as witness trees urges caution in the interpretation of the pre-European settlement composition of dry-mesic and xeric sites.

Results of my analysis indicated that surveyors were not significantly biased ($P \leq 0.05$, Tukey's HSD) in their selection of witness tree diameter sizes. However, Bourdo (1956) found that surveyors preferred trees ≥ 25 cm in d.b.h., and avoided using trees smaller than this. I concurred with Bourdo's work. Hence, in creating d.b.h. distributions for the dominant witness tree species I only used those trees ≥ 25 cm in d.b.h.

Forest Cover Type Map

I analyzed the spatial distribution of pre-European settlement forests in the study area with a forest cover type map. A forest cover type has a characteristic physiognomy, composition, and structure (Spurr and Barnes 1980). Forest cover types were defined by the dominant witness tree species occurring on each site type. Dominant tree species were those tree species with an importance value of ≥ 10% for a site type. A non-forested "marsh" (wetland herbaceous emergents) cover type was created from surveyor descriptions. The accuracy of cover types was checked against a correspondence analysis and a cluster analysis of the dominant forest species. The GLO survey section line descriptions were used to place every section mile in the study area within a cover type. Forested and non-forested wetlands were mapped from the surveyor's plat maps. GLO survey section line descriptions list the tree species encountered along the mile the surveyors traversed according to their order of importance. In this way, the section line descriptions were fitted to the quantitatively defined cover types. The cover type map was produced using 30 x 60 minute USGS topographic quadrangles as a base map. When boundaries needed to be inferred, topography and soils data were used to define them.

<u>Disturbance Regimes</u>

Lorimer (1977; 1980a) developed the method of determining the disturbance rotation (White and Pickett 1985) for pre-European settlement forests. The disturbance rotation is the time needed to disturb an area equal in size to the entire area of interest. In this study, only canopy replacing disturbances were included: windthrows > one hectare (Canham and Loucks 1984) and crown fires (Lorimer 1980a).

The GLO survey provided a systematic sample of the study area along a one mile (1.6 km) square grid system. I used line transect theory to determine the pre-European settlement disturbance rotations for windthrow and fire disturbances in each of the forest cover types. The following steps allowed me to elucidate the disturbance rotations: (1) I totaled the number of miles of survey lines in each cover type. Then (2) I used the section line summaries to calculate the total length of windthrown or burnt section lines in each cover type. The presence of particular vegetation types (aspen, oak, and pine "thickets") were also included as burned areas (Lorimer 1980a; Palik and Pregitzer 1992). Thirdly, the total length of disturbed section lines in each cover type was divided by the total length of survey lines in that cover type; this gave the percent of land affected by disturbance for a cover type. I divided the above figure by fifteen years to yield the average % area disturbed annually in the cover type. Lorimer (1977; 1980a) deemed fifteen years to be a conservative estimate of the number of years a prior burn or windfall would still be visible to the surveyors. Lastly, 100 was divided by the average % area disturbed annually in a cover type. This yielded the pre-European settlement disturbance rotation for either fire or windthrow for the cover type in question.

Present-Day Forests: Composition and Structure

Present-day forest stand data came from twenty nine stands sampled within the study area for the development of an ecological classification system (ECS) of the Huron NF (Michigan State University, Forestry Department data file). All stands selected were well-stocked, naturally regenerated, at least one hectare in size, and free from recent disturbance. Trees were defined as stems ≥ 10 cm d.b.h. Stand ages ranged from sixty to ninety years. The ECS sample stands failed to represent the study area's xeric and hydric sites.

I grouped stands by soil drainage class as for the pre-European settlement forest data to permit then-and-now comparisons by site type. I pooled stand data by site type and determined present-day absolute and relative density and dominance by species. As before, I also calculated an importance value for each species by site type. Tree species diversity was calculated by site type using importance values in the Shannon-Weaver formulation (Peet 1974). For each present-day forest site type I determined its mean basal area/ha, density (trees/ha), and mean d.b.h. by averaging across stands within a type.

Analyzing the Changing Forest

I compared the species composition of pre-European settlement forests to today's forests by site type with the chi-squared goodness of fit test (Gill 1978) and Bray and Curtis' (1957) index of community similarity. I could not statistically test for differences in mean basal area/ha and trees/ha between pre-European settlement and present-day forests. To test for changes in mean tree d.b.h. between pre-European settlement forests and existing forests I used paired t-tests (Gill 1978).

I assessed changes in the areal extent of forest cover types between present-day and pre-European settlement forests. To determine the areas of pre-European settlement forest cover types I used a dot grid and the forest type map. Values for the areas of present cover types were obtained for the study from the Michigan Forest Resource Inventory Program (MIRIS) and compared to pre-European settlement data.

RESULTS AND DISCUSSION

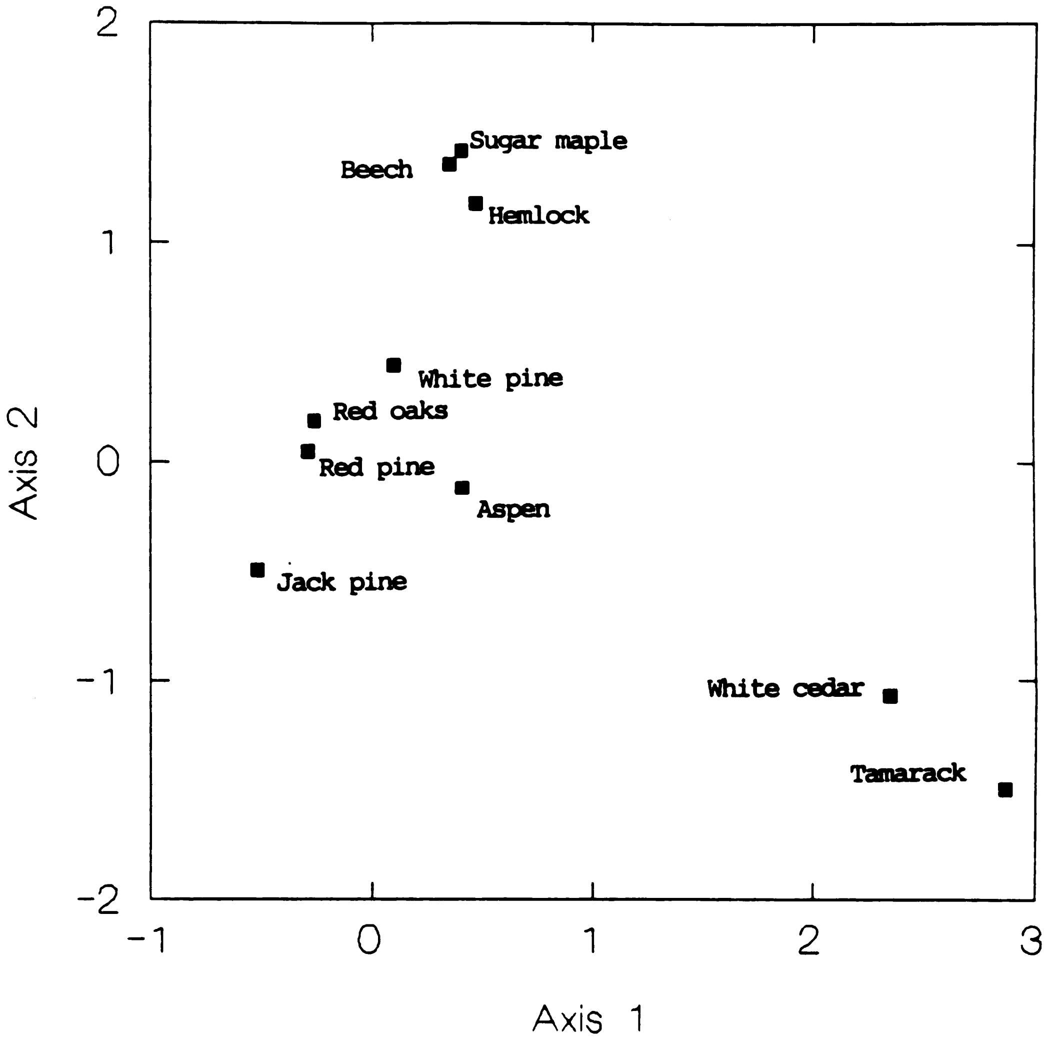
THE CHARACTER OF THE PRE-EUROPEAN SETTLEMENT FOREST

Witness Tree Species-Site Relations

In the correspondence analysis which included wetland species, 80% of the variation (total inertia) was accounted for by the first two dimensions. The correspondence analysis in which wetland species were excluded had 82% of the variation (total inertia) explained by the first two dimensions. Figures 5 and 6 are biplots of the coordinates of the species (column coordinates) for the first two dimensions of each analysis. The species' patterns in Figures 5 and 6 demonstrate the response of the witness tree species to a multidimensional environmental gradient likely comprised of soil moisture, nutrient availability, light availability, microclimate, and disturbance factors. The species probably responded individualistically in the pre-European settlement forest, creating a joint distribution of successive replacement (Austin 1985). Hence, the arch evident in both biplots represents an inherent property of the data (Wartenberg et al. 1987).

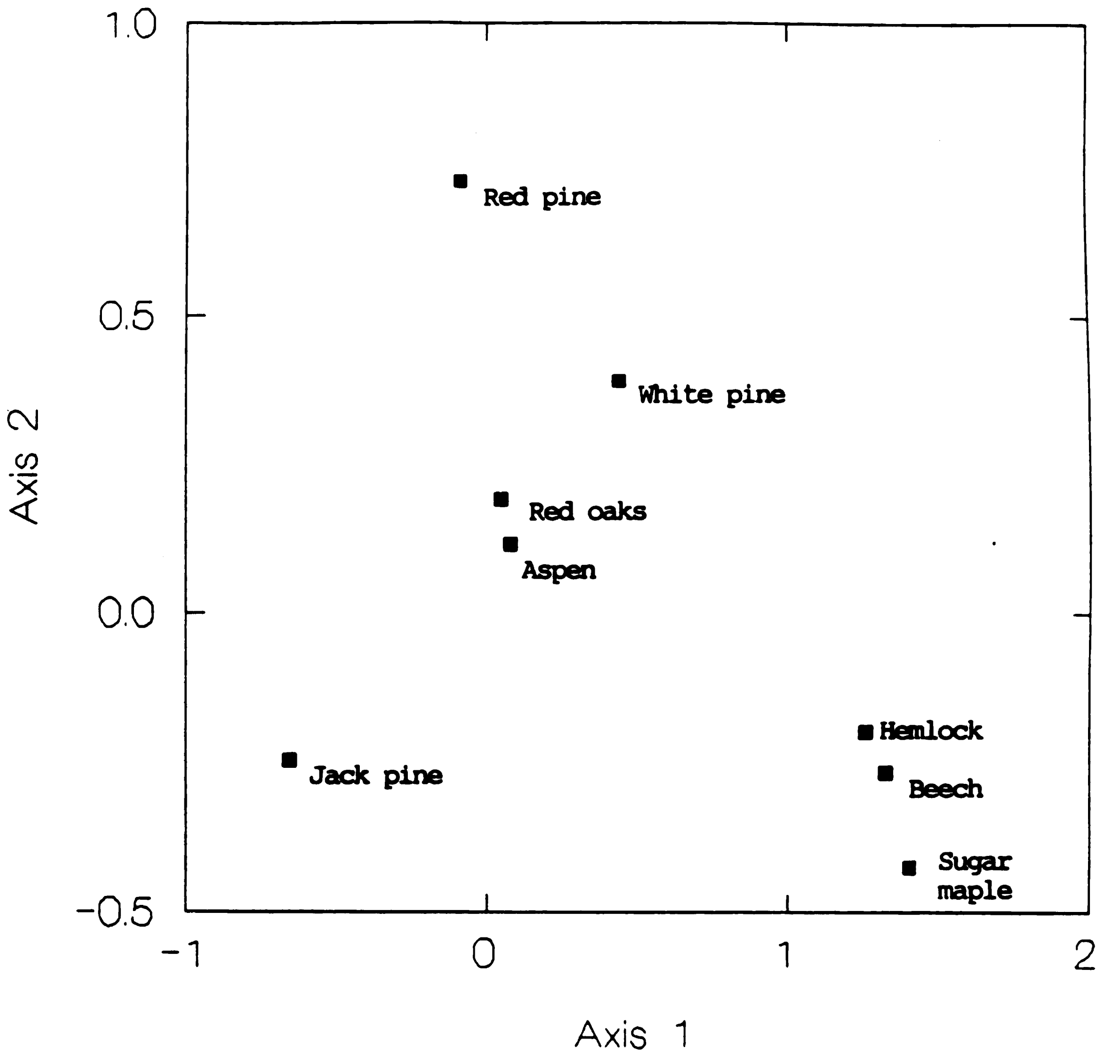
Tamarack lies on the far right side of Figure 5's biplot along with white cedar. Both species have the competitive advantage on sites with high soil moisture (Burns and Honkala 1990). Jack pine falls on the far left side of both biplots (Figures 5 and 6) probably due to its drought tolerance (Burns and Hokala 1990). A facile interpretation of the patterns in

Figure 5: Correspondence analysis of all witness tree species: axes 1 x 2 (80% of the variation).



Sugar maple
Beech
Hemlock
White pine
Red oaks
Red pine
Aspen
Jack pine
White cedar
Tamarack
Axis 2
Axis 1
2
1
0
-1
-2
-1
0
1
2
3

Figure 6: Correspondence analysis of upland witness tree species: axes 1 x 2 (82% of the variation).


1.0
0.5
0.0
-0.5
Axis 2
-1
0
1
2
Axis 1
Red pine
White pine
Red oaks
Aspen
Jack pine
Hemlock
Beech
Sugar maple

Figures 5 and 6 would state that soil moisture dominates the environmental gradient observed. However, soil moisture was highly correlated with nitrogen mineralization (Pastor et al. 1984) and fire regimes (Clark 1989) in the upper Midwest. These correspondence analyses only give a limited view of the factors which engendered the pre-European settlement forest.

In both biplots the red oak complex and red pine are grouped together (Figures 5 and 6). From this I infer that most members of the pre-European settlement red oak complex in the study area were either black oaks or northern pin oaks. Black and northern pin oak's niche dimensions are closer to red pine's than are northern red oak's (Burns and Hokala 1990).

The nonmetric multidimensional scaling (NMDS) of witness tree species produced a regular pattern among the species best described as a curvature (Figure 7). I interpret the curve as broadly defining a soil moisture gradient, as in the correspondence analyses. White cedar and tamarack lie at the lower left side of the curve and jack pine lies on the lower right side (Figure 7); indicative of a wet-dry gradient. The ordination configuration became constant after 44 iterations, with a stress of 5%, which according to Kruskal (1964) is fairly good.

The results of the binary discriminant analyses (BDA) gave direct indication of the significance of species-substrate interactions (Strahler 1978). Sugar maple and beech occupied sites with loamy sand textures on well-drained, ice-contact landforms (Table 3). Hemlock competed best on loamy sand, sandy loam, and loam textures on well-drained, morainal landforms (Table 3). These species have likely evolved in areas with moderate nutrient availability; dense shade during juvenile stages; and gap-phase disturbances. Grime (1977) would classify them as stress-tolerant competitors.

Tamarack was restricted to very poorly drained organic soils in depressional features of ice-contact and outwash landforms (Table 3). Somewhat poorly drained and very poorly drained organic soils and silty clay loam soils were dominated by white cedar predominately on outwash plains (Table 3). White cedar competes better on more basic and nutrient rich sites than does tamarack. Tamarack requires full sunlight for optimal competitive ability, while cedar needs much less sunlight (Burns and Honkala 1990). Both occupied similar sites in the pre-European settlement forest probably because of their tolerance to saturated soil conditions.

While all stress-tolerators (Grime 1977), the pines exhibited a range in their adaptation to xeric, infertile, fire-prone sites. Jack pines occurred on extremely well-drained, sandy outwash plains (Table 3). Red pines occupied somewhat excessively drained, sandy end moraines (Table 3). The nutrient, energy, and water-conserving habit of evergreen species (Monk 1966) fits well with the pre-European settlement distribution of these pine species. However, white pine

Figure 7: Ordination of witness tree species by nonmetric multidimensional scaling.

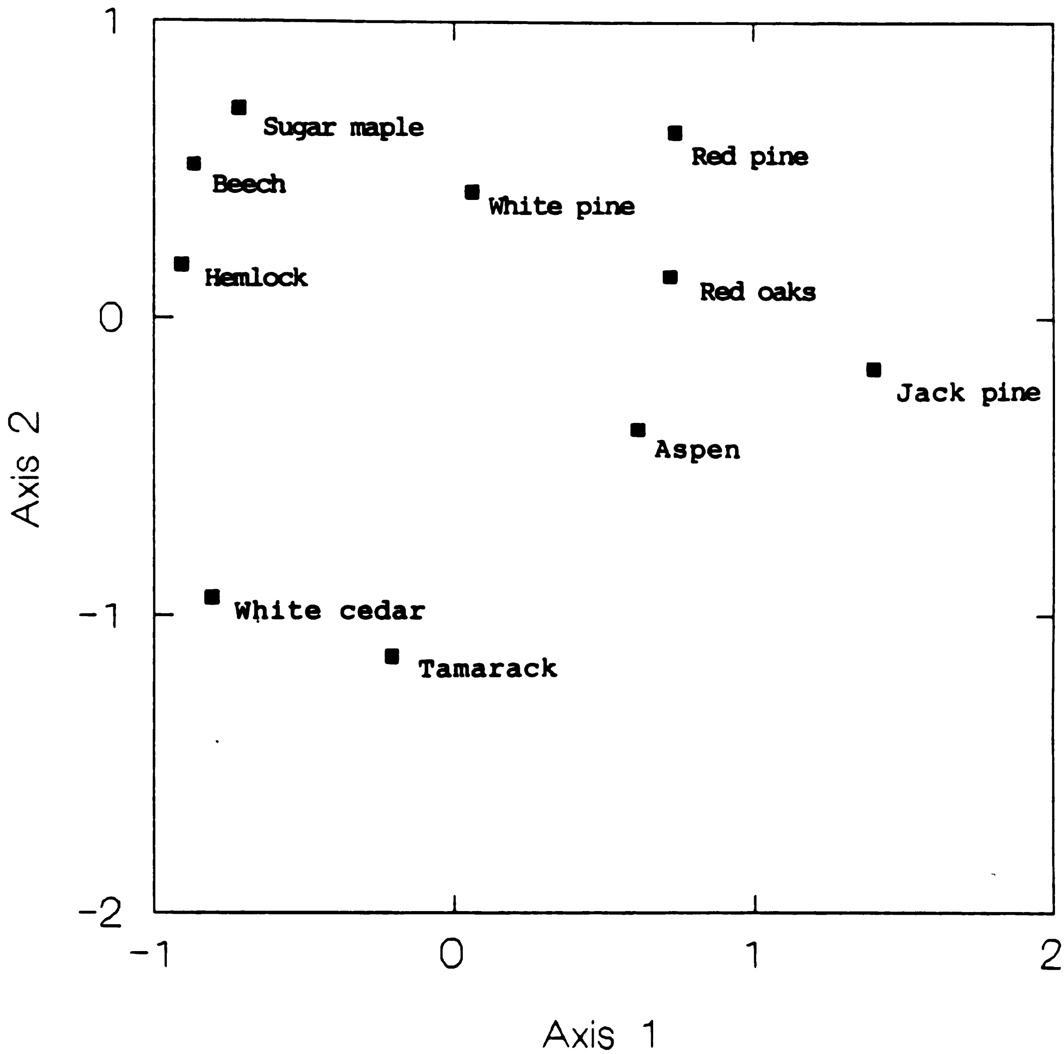

Sugar maple
Beech
Hemlock
White pine
Red pine
Red oaks
Jack pine
Aspen
White cedar
Tamarack
1
0
-1
-2
-1
0
1
2
Axis 2
Axis 1

Table 3: Standardized residuals (Haberman 1973) expressing the degree of association between witness tree species and site factors.

	Sugar Maple	Beech	Tama-rack	Jack Pine	Red Pine	White pine	Aspen	Red Oaks	White Cedar	Hemlock
Glacial landform										
Ice-contact	7.98	10.51	0.20	-9.67	0.66	2.77	-2.36	0.59	-4.05	2.36
Moraine	4.76	5.58	-3.19	-17.93	9.82	5.36	-1.64	2.40	-2.97	9.09
Outwash	- 10.20	-12.83	2.66	23.06	-9.14	-6.80	3.22	-2.56	5.67	-9.78
G value	56.61*	90.68*	6.46*	290.68*	50.37*	23.10*	5.87	3.54	20.33*	51.04*
Drainage										
Excessive	-9.20	-11.61	-15.20	27.42	0.68	-5.59	-4.71	-1.25	-9.73	-12.14
Somewhat excessive	-3.17	-2.17	-	-2.76	10.37	3.48	0.59	2.19	-4.86	-4.20
Mod. well to well	16.03	20.19	-	-20.89	-5.69	3.46	-2.18	0.21	-3.34	17.36
Poor to somewhat poor	1.29	-1.23	-0.82	-8.37	-3.05	2.39	9.23	-	4.46	7.35
Very poor	-2.87	-3.80	20.10	-8.92	-6.07	-2.16	2.91	-1.51	27.17	-3.22
G value	108.88*	170.12*	124.62*	528.51*	84.00*	23.13*	36.08*	3.42	202.69*	172.23*
Surficial Geology										
Sand	-11.79	-13.45	-23.92	17.79	10.57	-0.49	-2.73	0.98	-17.58	-12.06
Loamy sand	14.79	12.96	-	-	-4.64	-1.61	-2.55	0.40	-2.21	8.13
Sandy loam	6.14	12.50	-	-13.78	-5.76	2.81	1.10	-1.45	0.90	12.68
Loam	3.58	-0.34	-	-	-1.21	2.94	3.29	-0.34	-	4.61
Silty clay loam	-	-	-	-	-	-	6.39	-	2.10	-
Muck and peat	-2.62	-3.50	24.61	-10.55	-5.76	-2.61	1.84	-	28.57	-2.81
Mucky sand	-	-	3.00	-0.96	-2.14	0.97	3.29	-	3.89	-1.10
G value	88.75*	121.72*	140.80*	208.60*	78.86*	12.20*	21.06*	1.36	199.42*	98.15*

* G statistic significant at 5% level.

competed best on more mesic sites. These sites ranged from somewhat excessively drained to somewhat poorly drained sandy loams, loams, and mucky sands on ice-contact and morainal landforms (Table 3).

The red oak complex failed to show a significant association with any of the site factors ($P \leq 0.05$, G-statistic, Table 3). Curiously, aspen species mainly occupied wet sites in the pre-European settlement forest. Aspen species were found on somewhat poorly drained, silty clay loam, loam, and mucky sand soils (Table 3). The surveyors often described aspen's lowland position: "...dense aspen swamp...aspen and alder swale...wet aspen flat...swampy aspen thicket..."

Witness Tree Associations of the Pre-European Settlement Forest

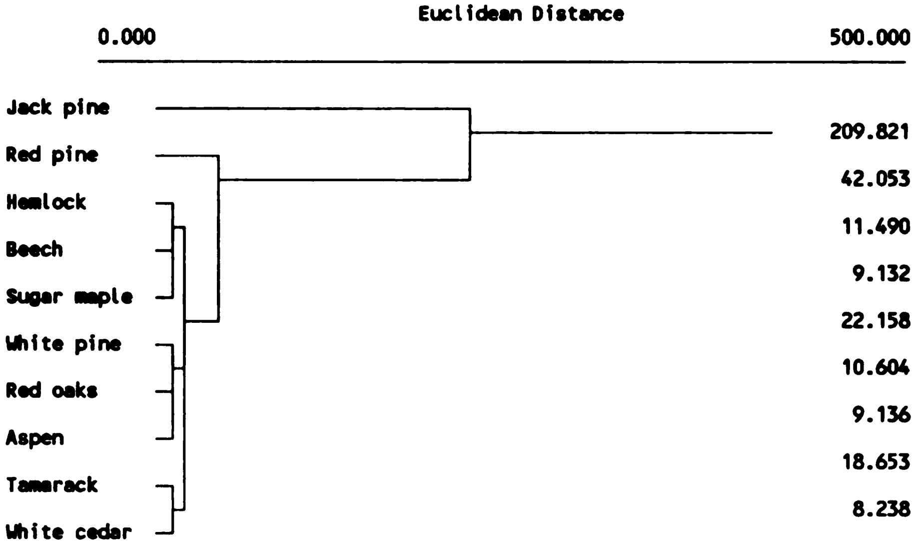
In the NMDS biplot, white cedar and tamarack form a loose, but discernable group (Figure 7). Beech, hemlock, and sugar maple cluster closely together (Figure 7). Jack pine forms a distinct group unto itself as does white pine (Figure 7). Red pine, the red oak complex, and the aspen species form a loosely joined group (Figure 7). These five groups represent hypotheses of pre-European settlement forest associations. Associations here indicate tree species with similar ecological amplitudes.

Cluster analysis finds the "natural grouping" in a data matrix, but will produce clusters from random data (James and McCulloch 1990). Using the Euclidean distance metric, both the average linkage method and Ward's minimum variance method produced five similar clusters of pre-European settlement witness tree species (Figures 8 and 9). For the average linkage dendrogram (Figure 8), the cophenetic correlation coefficient (Sneath and Sokal 1973) was 0.997. The cophenetic correlation coefficient of Ward's dendrogram (Figure 9) was 0.996. Both dendrograms were in good agreement with the original distance matrix.

As in the correspondence analysis (Figure 5) and the nonmetric multidimensional scaling (Figure 7); beech, sugar maple, and hemlock form a distinct group in both dendrograms (Figures 8 and 9). The dendrograms show a distinct tamarack-white cedar group. From these numerical procedures I surmise that at least three forest associations occurred in the pre-European settlement forest: jack pine, beech-sugar maple-hemlock, and tamarack-white cedar. Not surprisingly, these three associations form the xeric, mesic, and hydric nodes of the soil moisture gradient.

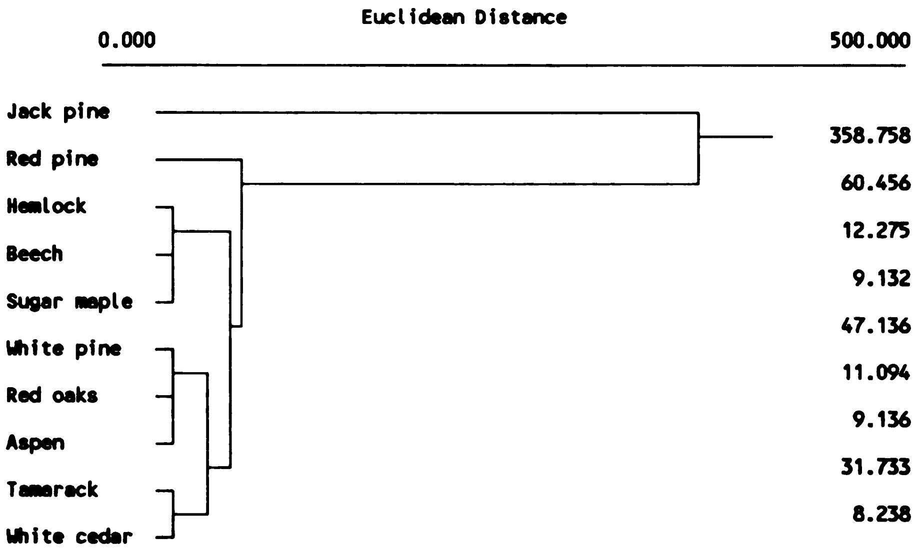
Pre-European Settlement Forest Communities Across the Edaphic Gradient

The site types (Table 2) chosen to group GLO corner points represent diffuse, but definable forest communities of the pre-European settlement forest. Hereon I consider forest site types and communities synonymous. In describing the composition of these forest communities I defined dominant tree species as those with an importance value ≥ 10%, and



r (cophenetic correlation) = 0.997

Figure 8: Dendrogram showing possible associations of witness tree species. Clusters were formed using the average linkage method (Sneath and Sokal 1973).



r (cophenetic correlation) = 0.996

Figure 9: Dendrogram showing possible associations of witness tree species. Clusters were formed using the Ward linkage method (Ward 1963).

associate (subdominant) species as those with an importance value of 1-9%. Current ecosystem studies in northwestern lower Michigan have determined that soil moisture availability and related nutrient dynamics constrain forest production and composition in a probabilistic manner (Host et al. 1988; Zak et al. 1989; Host and Pregitzer 1992). Hence, the forest communities I have defined for the pre-European settlement forest, while artificial, do have a functional basis. Below I describe the structure and composition of the pre-European settlement forest communities in relation to interacting site and disturbance factors.

The Xeric Forest Community

The dominant tree species of this community were jack pine, red pine, and white pine (Table 4, Appendix A: Figure 21). Associates included the aspen species, the red oak complex, and hemlock (Table 4, Appendix A: Figure 21). Jack pines were small and numerous (146 trees/ha, 5 m^2/ha, Table 4). Red pines were scattered and large (35 trees/ha, 6 m^2/ha, Table 4). White pines were infrequent and very large (9 trees/ha, 2 m^2/ha, Table 4). I defined this community as the jack pine-red pine-white pine forest type for the cover type map (see maps). The numerical procedures consistently separated jack pine (Figures 5-9) from the other species along multidimensional environmental gradients. This community occupied droughty, sandy outwash plains and drainageways (Table 3, see maps). Surveyors described this community as:

> ...land...very slightly rolling. Thinly timbered with a little yellow and spruce pine and stunted oaks; spruce pine plains; very handsome, high [and] nearly level...have a good view of Au Sable [river] for a long distance.

Community-level overstory basal area (trees ≥ 10 cm d.b.h.) was 13 m^2/ha (Table 4). Similar sites in northern lower Michigan had low potential net N mineralization rates (Zak et al. 1989). The surveyors often mentioned the presence of Vaccinium species in the understory of this community. Vaccinium species were indicative of low N availability and low soil moisture in northern lower Michigan (Host and Pregitzer 1991).

Jack pine's pre-European settlement size structure (Figure 10) shows a large, likely even-aged cohort of very small trees. This even-aged structure fits well with jack pine's autecology. Jack pines are extremely shade intolerant (Burns and Honkala 1990). For jack pines to establish themselves as a canopy dominant, they need to regenerate under conditions of full sunlight on a mineral soil seedbed. Jack pines cannot survive for long under canopies of any tree species and therefore typically do not develop an uneven-aged structure.

Crown fires were a frequent occurence in this community. The fire rotation (White and Pickett 1985) was ≈ 100 years. Stand-replacing windthrows were infrequent, their rotation period (Canham and Loucks 1984) was ≈ 2000 years. Whitney

Table 4: Composition and tree species diversity of pre-European settlement forests (trees ≥ 10 cm d.b.h.) on xeric sites.

Tree species	Percent Relative Density	Percent Relative Dominance	IV	Density	Dominance
Pinus banksiana	68.38	34.73	51.55[1]	146.20[2]	4.58[3]
Pinus resinosa	16.23	41.99	29.11	34.70	5.54
Pinus strobus	4.19	16.76	10.48	8.96	2.21
Populus species	2.90	1.35	2.13	6.20	0.18
Quercus rubra-velutina-ellipsoidalis	3.43	0.78	2.11	7.33	0.10
Tsuga canadensis	1.14	1.29	1.22	2.44	0.17
Fagus grandifolia	0.99	0.83	0.91	2.12	0.11
Acer saccharum	0.61	0.67	0.64	1.30	0.09
Betula species	0.46	0.36	0.41	0.98	0.05
Betula papyrifera	0.38	0.27	0.33	0.81	0.04
Quercus alba	0.30	0.23	0.27	0.64	0.03
Acer rubrum	0.23	0.12	0.18	0.49	0.02
Thuja occidentalis	0.15	0.15	0.15	0.32	0.02
Larix laricina	0.15	0.15	0.15	0.32	0.02
Picea species	0.15	0.08	0.12	0.32	0.01
Tilia americana	0.08	0.12	0.10	0.17	0.02
Abies balsamea	0.15	0.03	0.09	0.32	0.00
Juniperus virginiana	0.08	0.09	0.09	0.17	0.01
Totals	100.00	100.00	100.00	213.80	13.20

Diversity (H') = 0.6

[1] Importance Value = (relative density + relative dominance)/2 * 100

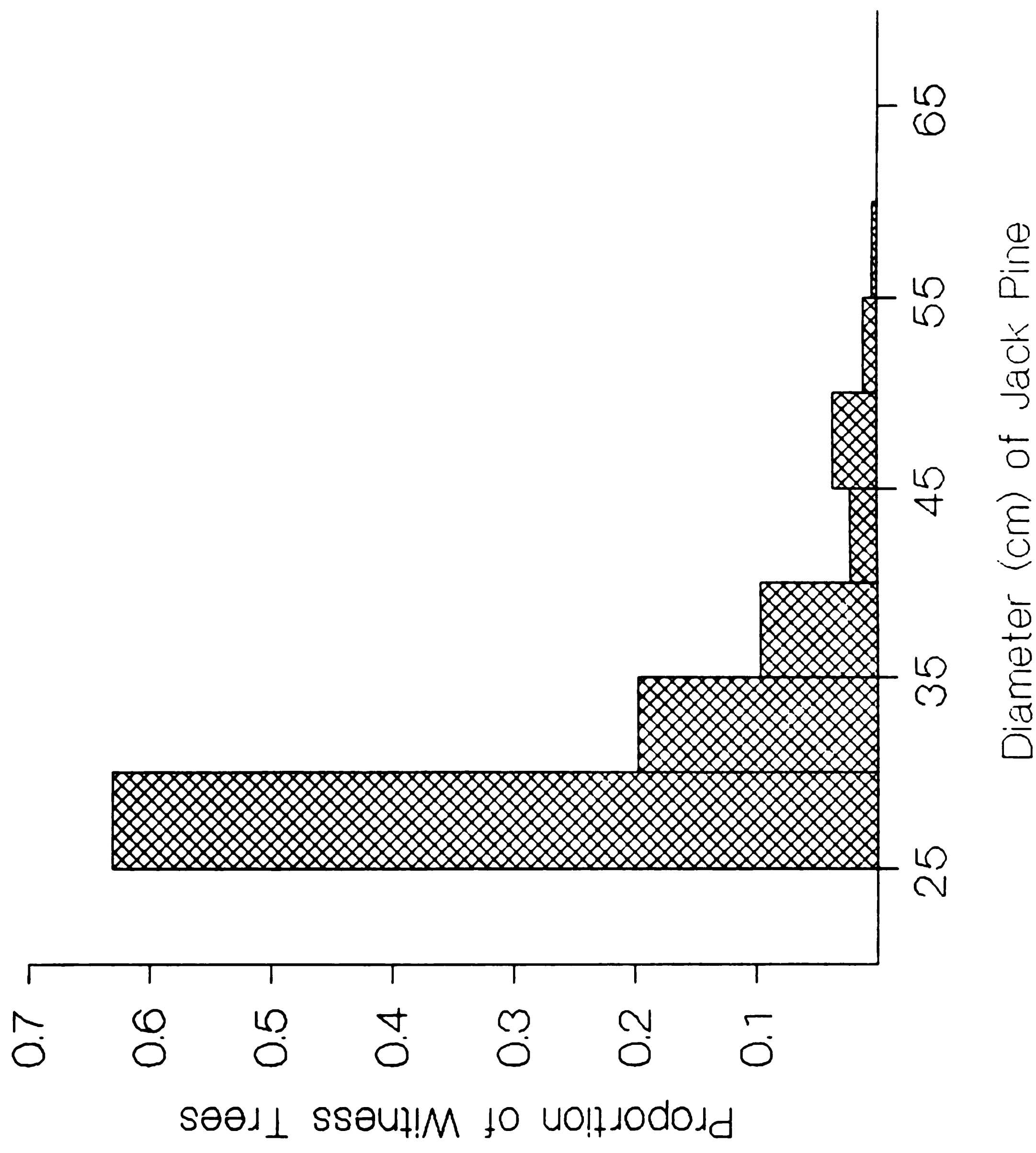
[2] trees/ha

[3] basal area (m^2/ha)

(1987) found the pre-European settlement fire rotation period for jack pine stands in nearby Roscommon and Crawford Counties was ≈ 83 years. Simard and Blank (1982) determined that the pre-European settlement fire-return time (average time between successive disturbances at a particular site) for "major" fires (fires burning 4047+ ha) was ≈ 35 years on the Mack Lake outwash plain (the dominant outwash plain in the study area). With a crown fire burning over this community at the minimum of every 100 years, it is safe to say that new forest stands in this community were established after major fire events. Jack pine's longevity is from 80-100 years and its cones are predominantly serotinous (Burns and Honkala 1990). Jack pine depended on fire to reproduce and maintain itself in this community. The presence of large red and white pines in this community indicates that fires probably burned in a stochastic pattern across the outwash plains; allowing certain juvenile red and white pines to mature.

I conceptualize this community in pre-European settlement time as a slightly undulating "sea" of jack pine. Small "islands" of white pine, red pine, and hemlock occupied areas protected from fire (the lee side of lakes and wetlands) or lucky enough to miss several fires in a row. Small aspen clones and pygmy forests of oak grubs occurred as patches in the jack pine matrix in areas that had experienced repeated intense fires.

Figure 10: Histogram showing distribution of jack pine witness trees by 5 cm d.b.h. classes.


Proportion of Witness Trees
0.7
0.6
0.5
0.4
0.3
0.2
0.1
Diameter (cm) of Jack Pine
25
35
45
55
65

The Dry-Mesic Forest Community

Red pine, jack pine, and white pine were the dominants of this community (Table 5, Appendix A: Figure 22). Associates of this community included: species of the red oak complex, hemlock, aspen species, beech, sugar maple, and white oak (Table 5, Appendix A: Figure 22). Red pine was classified as a separate group in both cluster analyses (Figures 8 and 9). I defined the red pine-jack pine-white pine cover type of the forest type map (see maps) from this community. This community had many, large red pines (91 trees/ha, 17 m^2/ha, Table 5) and many, small jack pines (112 trees/ha, 4 m^2/ha, Table 5). White pines were sparsely distributed, but just as large as the red pines (32 trees/ha, 6 m^2/ha, Table 5). When surveyors mentioned the understory in this community they described it as either "free from undergrowth" or dominated by "hazel" (Corylus species) and "dwarf oaks." Surveyors described this community as:

> Handsome pinery...mostly yellow pine, some white pine; yellow and white pine not large but thrifty and tall; timber a few large pines and dense thicket of aspen.

This community was found on sandy end moraines and coarse-textured ice-contact features (Table 3) typically directly east or northeast of the xeric forest community (see maps). Community-level overstory basal area (trees ≥ 10 cm d.b.h.) was 31 m^2/ha. From red pine's size structure (Figure

Table 5: Composition and tree species diversity of pre-European settlement forests (trees ≥ 10 cm d.b.h.) on dry-mesic sites.

Tree species	Percent Relative Density	Percent Relative Dominance	IV	Density	Dominance
Pinus resinosa	29.00	53.97	41.49[1]	91.41[2]	16.68[3]
Pinus banksiana	35.67	11.98	23.83	112.43	3.70
Pinus strobus	10.17	20.51	15.34	32.06	6.34
Quercus rubra-velutina-ellipsoidalis	5.33	2.12	3.73	16.80	0.66
Tsuga canadensis	3.50	3.71	3.61	11.03	1.15
Populus species	5.33	1.88	3.61	16.80	0.58
Fagus grandifolia	4.83	2.20	3.52	15.22	0.68
Acer saccharum	2.00	1.72	1.86	6.30	0.53
Quercus alba	1.67	0.59	1.13	5.26	0.18
Acer rubrum	0.83	0.19	0.51	2.62	0.06
Thuja occidentalis	0.50	0.37	0.44	1.58	0.11
Picea species	0.33	0.31	0.32	1.04	0.10
Betula papyrifera	0.33	0.24	0.29	1.04	0.07
Fraxinus americana	0.17	0.09	0.13	0.54	0.03
Betula alleghaniensis	0.17	0.06	0.12	0.54	0.02
Abies balsamea	0.17	0.06	0.12	0.54	0.02
Totals	100.00	100.00	100.00	315.20	30.90

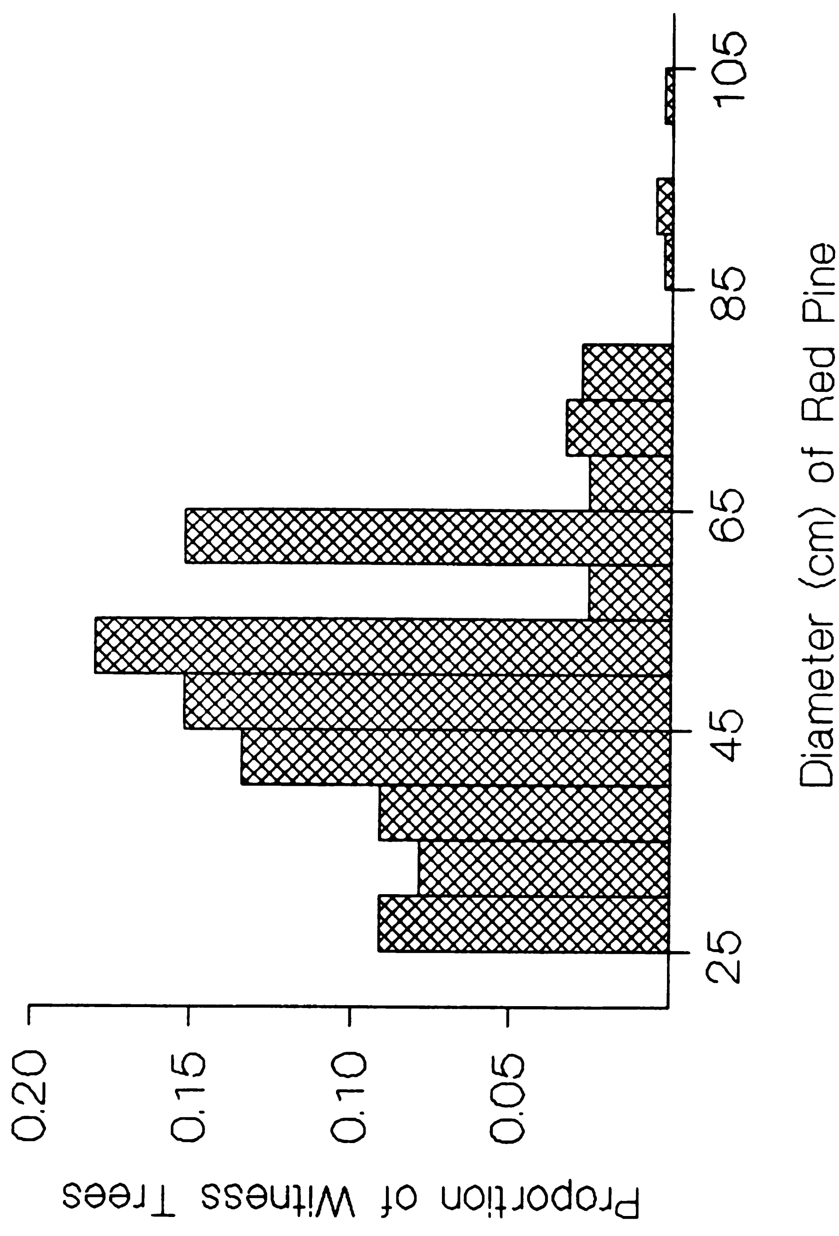
Diversity (H') = 0.7

[1] Importance Value = (relative density + relative dominance)/2 * 100

[2] trees/ha

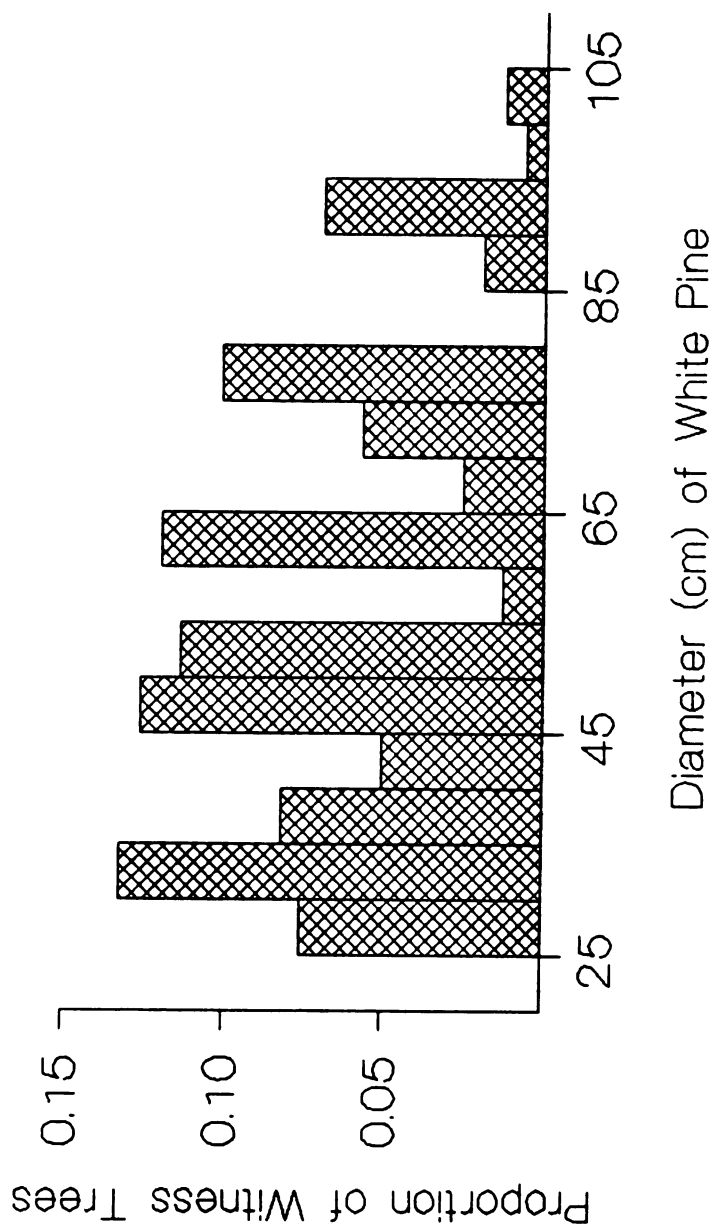
[3] basal area (m^2/ha)

Figure 11: Histogram showing distribution of red pine witness trees by 5 cm d.b.h. classes.



Proportion of Witness Trees
0.20
0.15
0.10
0.05
25
45
65
85
105
Diameter (cm) of Red Pine

Figure 12: Histogram showing distribution of white pine witness trees by 5 cm d.b.h. classes.


Proportion of Witness Trees
0.15
0.10
0.05
25
45
65
85
105
Diameter (cm) of White Pine

11) I infer that its age structure was composed of two even-aged cohorts. White pine's size structure (Figure 12) indicates a possible multi-age class structure. Up to five different cohorts of white pine may have existed in the pre-European settlement forest (Figure 12).

The fire rotation period for this community was ≈ 100 years. The rotation period for catastrophic windthrow was ≈ 900 years. The structure and composition of this community resulted from an interaction between edaphic factors and the fire regime. Red pines need a mineral seedbed and the absence of competing plants to reproduce themselves (Burns and Honkala 1990). Red pines therefore depend on fire to maintain themselves as canopy dominants and did so in this pre-European settlement community. Both white and red pine's longevities (200-450 years and 200-300 years, respectively) exceed the fire rotation period. This provides further evidence of the importance of fire in this community. The hypothesized even-aged cohorts of red and white pine described above (Figures 11 and 12) probably originated after major fire events.

I visualize this community as the classic Great Lakes pine forest as described by Curtis (1959). Park-like stands of large white and red pines towered over a permanent understory of red oak species. Where intense lightning fires occurred frequently enough to eliminate the red and white pines, jack pines and aspen maintained themselves. In protected microsites hemlock managed to reproduce and persist along with beech and sugar maple.

The Mesic Forest Community

Forest dominants here included: hemlock, beech, sugar maple, and white pine (Table 6, Appendix A: Figure 23). Associates of these dominant trees were red pine, the red oak complex, basswood, aspen, white cedar, black ash, and jack pine. Medium sized hemlock (57 trees/ha, 7 m^2/ha, Table 6), beech (60 trees/ha, 4 m^2/ha, Table 6), and sugar maple 39 trees/ha, 4 m^2/ha, Table 6) made up the bulk of this community. However, white pines occurred throughout this community and attained their largest sizes here (24 trees/ha, 5 m^2/ha, Table 6). From this community I defined the hemlock-beech-sugar maple-white pine cover type for the forest type map (see maps). Surveyors mentioned pine, beech, hazel, red maple, aspen, sugar maple, and hemlock as common understory species. One surveyor described this community as:

> ...land rolling, good 2nd rate soil, clay and sand...Sugar, Beech, Elm, Maple, Lynn, Ironwood, and some first rate white pines.

Hemlock, beech, and sugar maple were grouped together in all of the ordinations and classifications (Figures 5-9). I surmise this reflects their similar environmental tolerances. Physiographically this community occupied end moraines, ground moraines, and ice-disintegration features (Table 3, see maps). Topographically these areas have short, steep hills, swell and

Table 6: Composition and tree species diversity of pre-European settlement forests (trees ≥ 10 cm d.b.h.) on mesic sites.

Tree species	Percent Relative Density	Percent Relative Dominance	IV	Density	Dominance
Tsuga canadensis	23.79	27.00	25.40[1]	57.41[2]	6.86[3]
Fagus grandifolia	25.02	14.88	19.95	60.37	3.78
Acer saccharum	16.03	14.16	15.10	38.68	3.60
Pinus strobus	9.83	19.81	14.82	23.72	5.03
Pinus resinosa	7.24	12.06	9.65	17.47	3.06
Quercus rubra-velutina-ellipsoidalis	3.79	3.68	3.74	9.15	0.93
Tilia americana	2.07	2.09	2.08	4.99	0.53
Populus species	2.93	0.87	1.90	7.07	0.22
Thuja occidentalis	1.38	1.14	1.26	3.33	0.29
Fraxinus nigra	1.38	1.02	1.20	3.33	0.26
Pinus banksiana	1.72	0.55	1.14	4.15	0.14
Betula papyrifera	1.21	0.45	0.83	2.92	0.11
Acer rubrum	1.03	0.55	0.79	2.49	0.14
Ulmus species	0.86	0.53	0.70	2.08	0.13
Betula species	0.52	0.40	0.46	1.25	0.10
Quercus alba	0.69	0.04	0.37	1.66	0.01
Betula alleghaniensis	0.17	0.40	0.29	0.41	0.10
Fraxinus americana	0.17	0.33	0.25	0.41	0.08
Ostrya virginiana	0.17	0.04	0.11	0.41	0.01
Totals	100.00	100.00	100.00	241.30	25.40

Diversity (H') = 0.9

[1] Importance Value = (relative density + relative dominance)/2 * 100

[2] trees/ha

[3] basal area (m^2/ha)

swale features, and small hollows. This community occurred on loamy sand, sandy loam, and loam textures (Table 3). Present-day communities on similar sites in northwestern lower Michigan had relatively high potential rates of N availability (Zak et al. 1989). Community-level overstory basal area (trees ≥ 10 cm d.b.h.) here was 25 m^2/ha (Table 6).

I surmise that hemlock's pre-European settlement size structure (Figure 13) indicates a multi-age class structure of about four cohorts. Sugar maple's size structure (Figure 14) also appears indicative of a four cohort, multi-age class structure. I infer that beech's size structure reflects a multi-age class structure of three to four cohorts (Figure 15).

The fire rotation period for this community was ≈ 5600 years. The catastrophic windthrow rotation period was ≈ 1200 years. Longevities of hemlock, sugar maple, and beech are 250-800 years, 300-400 years, and 300 years, respectively (Burns and Honkala 1990). Catastrophic windthrows occurred far too infrequently in this community to greatly affect stand structure and composition. Hemlock, beech, and sugar maple are all very shade tolerant and respond rapidly to release (Burns and Honkala 1990). I assume that single-stem treefalls and gap-sized windfalls (Runkle 1982) provided the mechanisms whereby the shade-tolerant members of this community established themselves in the canopy. White pine may have established itself in infrequent community-wide patch

Figure 13: Histogram showing the distribution of hemlock witness trees by 5 cm d.b.h. classes.

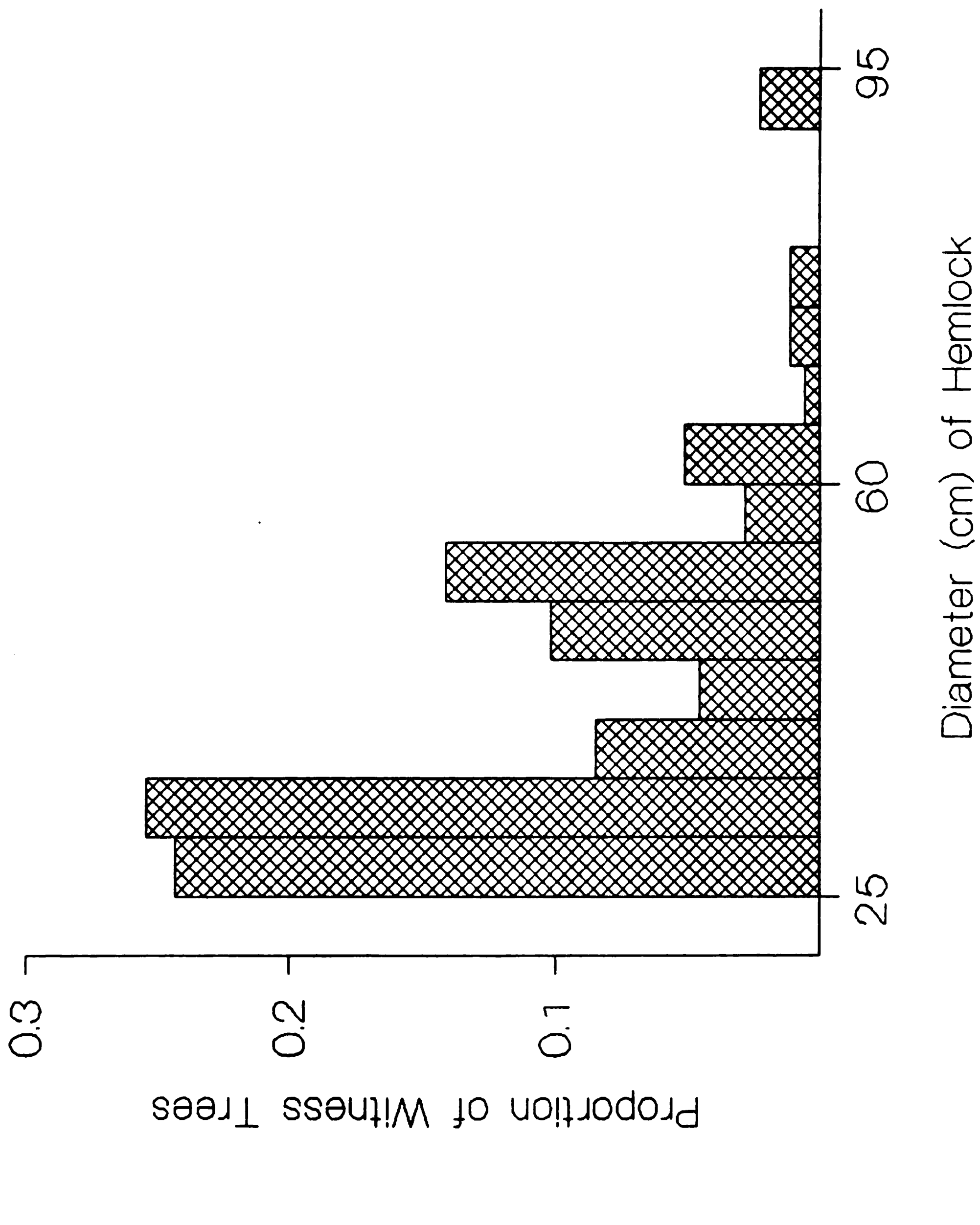

Proportion of Witness Trees
0.3
0.2
0.1
25
60
95
Diameter (cm) of Hemlock

Figure 14: Histogram showing the distribution of sugar maple witness trees by 5 cm d.b.h. classes.

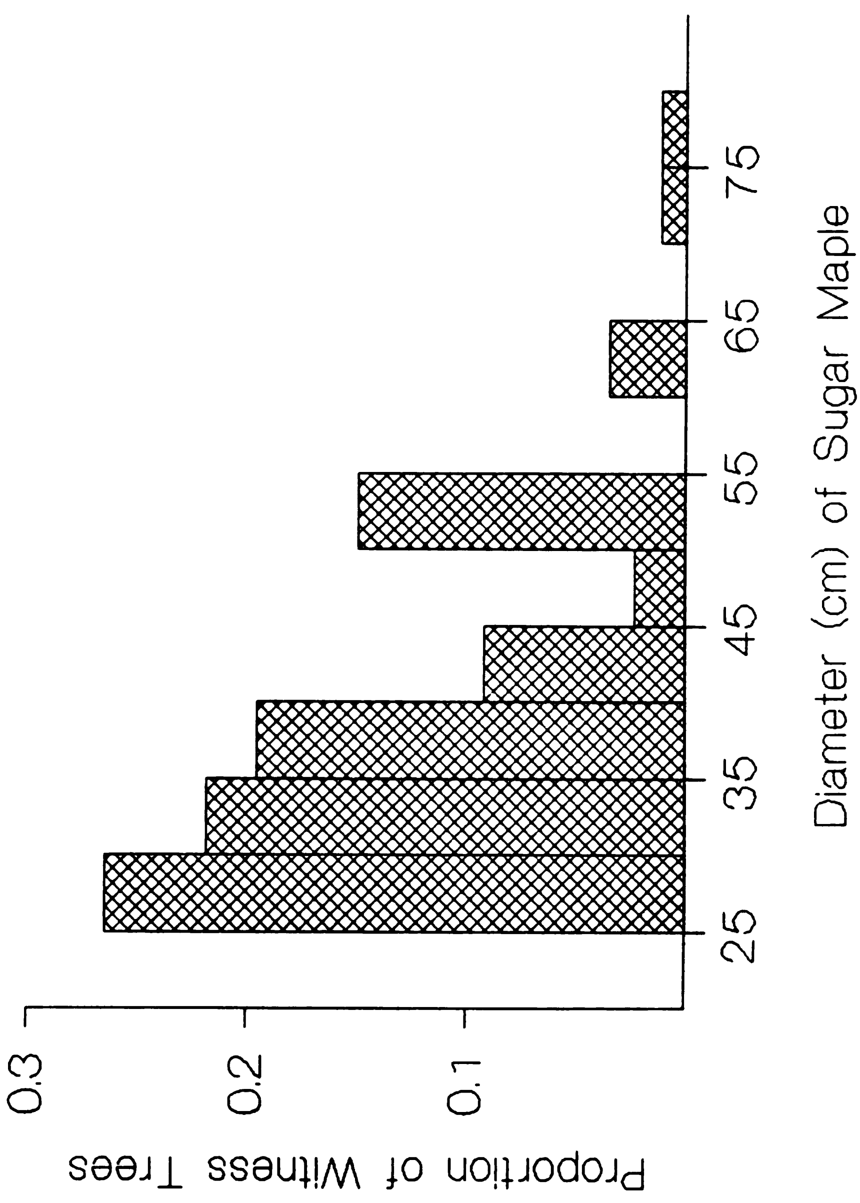
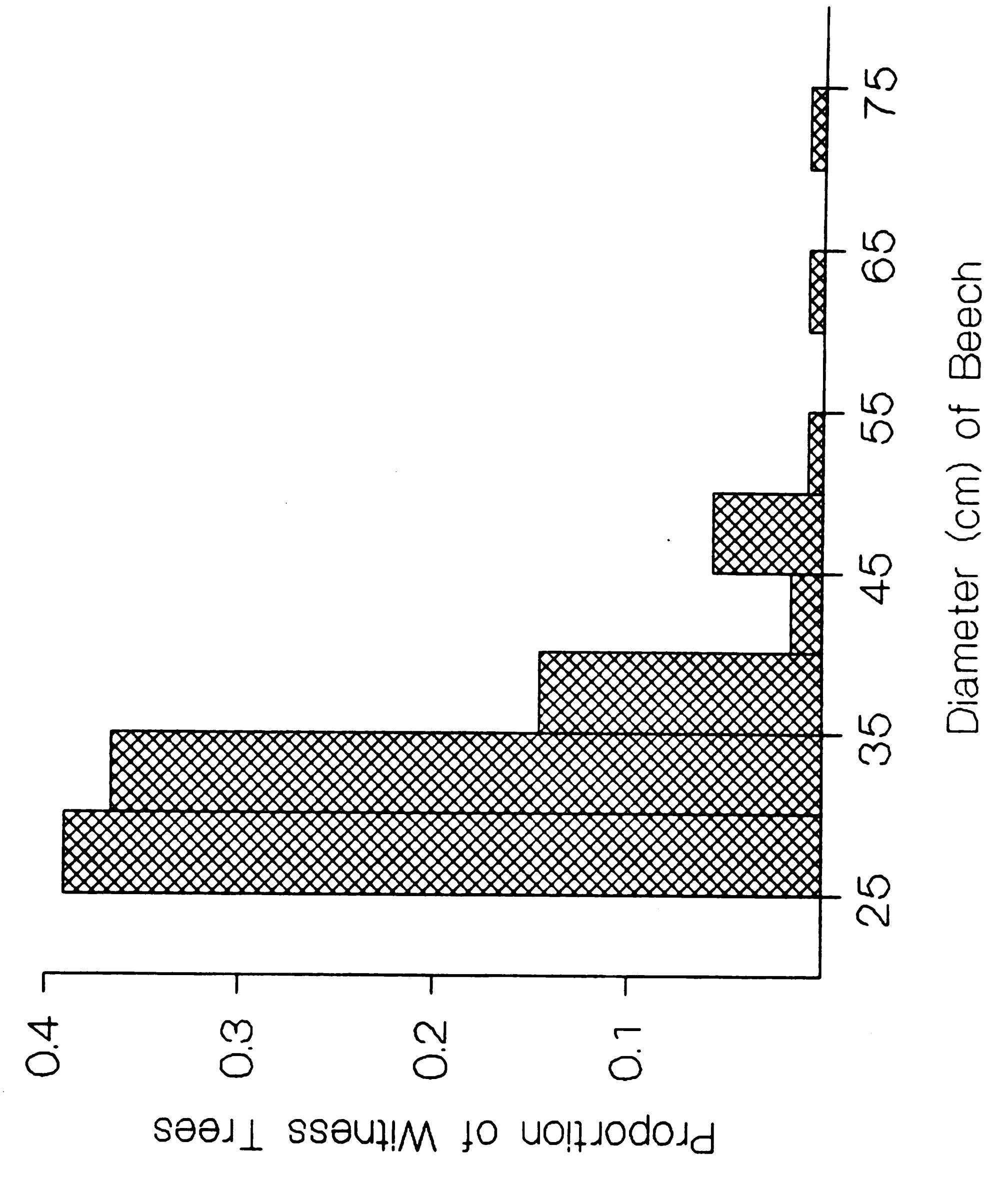

Proportion of Witness Trees
0.3
0.2
0.1
25
35
45
55
65
75
Diameter (cm) of Sugar Maple

Figure 15: Histogram showing the distribution of beech witness trees by 5 cm d.b.h. classes.


Proportion of Witness Trees
0.4
0.3
0.2
0.1
25
35
45
55
65
75
Diameter (cm) of Beech

blowdowns.

I associate this pre-European settlement community with the misguided idea of the "climax community" so prevalent in early ecological work (McIntosh 1985). I surmise that community dynamics here resulted mainly from competition for light and space (above and below-ground) resources. This community was a thorough mix of medium-sized hemlock, beech, and sugar maple in the canopy. Large white pines probably formed a "super-canopy" in some places. Hemlock germinates best on rotting logs (Burns and Honkala 1990). Because of hemlock's predominance in this community I hypothesize that coarse-woody debris loads (Harmon et al. 1986) were substantial here.

The Wet-Mesic Forest Community

Hemlock, white pine, red pine, and aspen species were the dominants of this community (Table 7, Appendix A: Figure 24). The many associates included: white cedar, jack pine, paper birch, sugar maple, birch species, beech, balsam fir, black ash, tamarack, red oaks, yellow birch, elms, and red maple (Table 7, Appendix A: Figure 24). This community was highly heterogeneous in composition. The most apparent pattern was the dominance of many large hemlock trees (64 trees/ha, 9 m^2/ha, Table 7). Scattered large red and white pines were also present (Table 7). However, after hemlock the most frequently encountered tree would have been small aspens (58 trees/ha, 2 m^2/ha, Table 7). The numerical procedures

Table 7: Composition and tree species diversity of pre-European settlement forests (trees ≥ 10 cm d.b.h.) on wet-mesic sites.

Tree species	Percent Relative Density	Percent Relative Dominance	IV	Density	Dominance
Tsuga canadensis	17.61	26.47	22.04[1]	64.36[2]	9.48[3]
Pinus strobus	9.26	19.64	14.45	33.85	7.03
Pinus resinosa	6.02	16.14	11.08	22.00	5.78
Populus species	15.74	6.15	10.95	57.53	2.20
Thuja occidentalis	8.33	8.16	8.25	30.45	2.92
Pinus banksiana	8.80	1.60	5.20	32.16	0.57
Betula papyrifera	5.09	4.47	4.78	18.60	1.60
Acer saccharum	5.09	3.74	4.42	18.60	1.34
Betula species	4.63	2.43	3.53	16.92	0.87
Fagus grandifolia	3.70	2.65	3.18	13.52	0.95
Abies balsamea	3.70	1.09	2.40	13.52	0.39
Fraxinus nigra	1.39	2.31	1.85	5.08	0.83
Larix laricina	2.31	0.78	1.55	8.44	0.28
Quercus rubra-velutina-ellipsoidalis	1.39	1.69	1.54	5.08	0.61
Betula alleghaniensis	1.85	0.85	1.35	6.76	0.30
Ulmus species	1.85	0.49	1.17	6.76	0.18
Acer rubrum	1.39	0.67	1.03	5.08	0.24
Fraxinus americana	0.93	0.39	0.66	3.40	0.14
Picea species	0.46	0.24	0.35	1.68	0.09
Quercus alba	0.46	0.04	0.25	1.68	0.01
Totals	100.00	100.00	100.00	365.50	35.80

Diversity (H') = 1.1

[1] Importance Value = (relative density + relative dominance)/2 * 100

[2] trees/ha

[3] basal area (m^2/ha)

(Figures 5-9) failed to produce any clear grouping among the dominants of this community. Thus, the hemlock-white pine-red pine-aspen cover type (see maps) defined by this community must be viewed with caution.

Site factors were also heterogeneous in this community. Physiographically this community was usually on the interfacebetween morainal complexes and outwash plains (Table 3, see maps); probable seepage areas. The wet, sandy flats of this community also exhibited intermittent, dry, sandy ridges (surveyor descriptions). So, while the majority of this community occupied wet-mesic sites (hemlock, white pine, aspen species, and white cedar; Table 3), some small, dry-mesic sandy ridges supported red pine, jack pine, and paper birch (Table 3). Interestingly, aspen was associated with somewhat poorly drained sites having loam, silty clay loam, muck and peat, and mucky sand surficial materials (Table 3). Surveyors decribed these aspen stands as: "Swampy aspen thicket[s]; wet aspen flats; [and] dense aspen swamps."

Community-level overstory basal area (trees $\geq$ 10 cm d.b.h.) was 36 m^2/ha (Table 7). Nutrient availability was probably moderate in this community being limited by low soil pH and seasonal wetness. Hemlock's pre-European settlement size structure (Figure 13) suggests multi-age class stands. Red and white pine's size structures (Figures 11 and 12, respectively) indicate even-aged stands. Aspen's size structure (Figure 16) shows a likely even-aged clonal cohort.

Figure 16: Histogram showing the distribution of aspen witness trees by 5 cm d.b.h. classes.

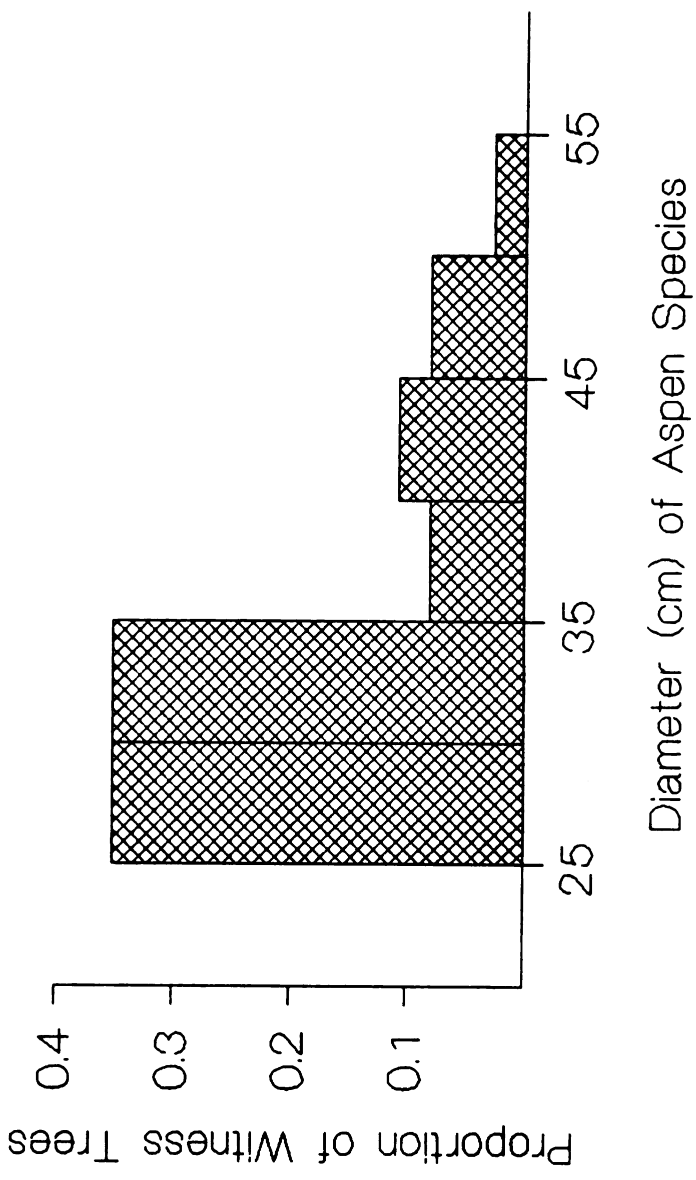
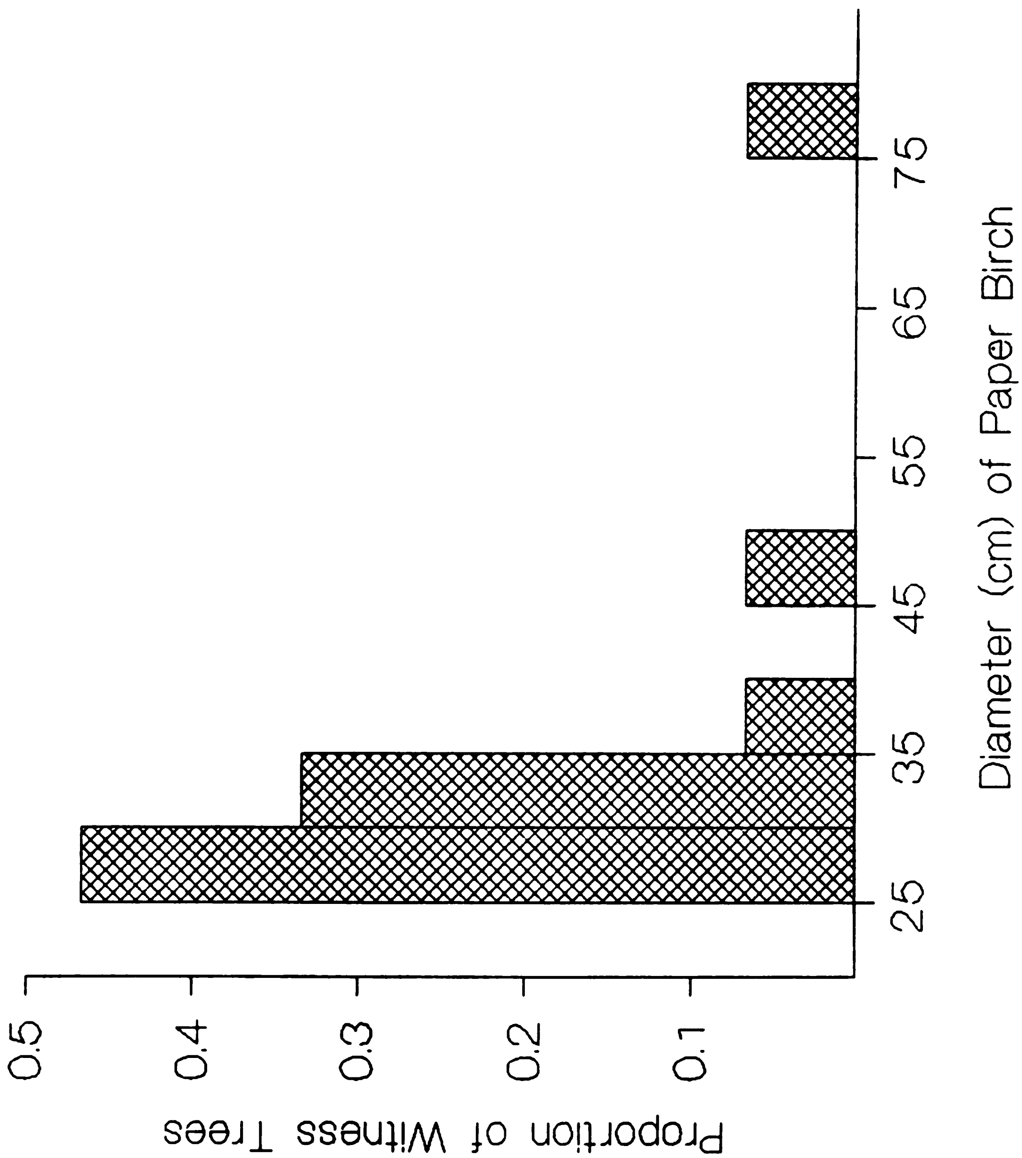

Proportion of Witness Trees
0.4
0.3
0.2
0.1
25
35
45
55
Diameter (cm) of Aspen Species

Figure 17: Histogram showing the distribution of paper birch witness trees by 5 cm d.b.h. classes.


Proportion of Witness Trees
0.1
0.2
0.3
0.4
0.5
25
35
45
55
65
75
Diameter (cm) of Paper Birch

Paper birch appears to have had two even-aged cohorts in this community (Figure 17).

The fire rotation period for this community was ≈ 900 years. The catastrophic windthrow rotation period was ≈ 200 years. On the wettest portions of this community I propose that the catastrophic windthrow rotation was even shorter than 200 years. Trees grown on soils with high seasonal water tables have shallow, spreading root systems (Kozlowski et al. 1991). Such trees are prone to windthrow. Large, frequent windthrows in this community could explain the significant presence of aspen. The white and red pine which occupied the dry sandy ridges and lower morainal slopes of this community would have had a difficult time establishing without fire. These species probably were established here after major fires (fires during subcontinental drought episodes).

The Hydric Forest Community

This community was dominated by white cedar and tamarack (Table 8, Appendix A: Figure 25). Associate tree species included: jack pine, spruce species, aspen species, balsam fir, black ash, birch species, paper birch, white pine, and red maple (Table 8). The multivariate analyses consistently showed white cedar and tamarack as a natural group (Figures 5, 7, 8, and 9). The white cedar-tamarack forest cover type was created from this community (see maps). White cedar (113 trees/ha, 6 m^2/ha, Table 8) and tamarack (85 trees/ha, 5 m^2/ha, Table 8) were fairly numerous and of small-medium size.

Table 8: Composition and tree species diversity of pre-European settlement forests (trees ≥ 10 cm d.b.h.) on hydric sites.

Tree species	Percent Relative Density	Percent Relative Dominance	IV	Density	Dominance
Thuja occidentalis	30.83	33.54	32.19[1]	112.68[2]	6.14[3]
Larix laricina	23.31	29.07	26.19	85.20	5.32
Pinus banksiana	9.39	5.34	7.37	34.32	0.98
Picea species	7.52	7.17	7.35	27.49	1.31
Populus species	7.14	7.07	7.11	26.10	1.29
Abies balsamea	5.64	3.64	4.64	20.61	0.67
Fraxinus nigra	3.01	3.60	3.31	11.00	0.66
Betula species	3.01	2.82	2.92	11.00	0.52
Betula papyrifera	2.63	1.87	2.25	9.61	0.34
Pinus strobus	2.63	1.58	2.11	9.61	0.29
Acer rubrum	1.50	1.59	1.55	5.48	0.29
Tsuga canadensis	1.50	0.78	1.14	5.48	0.14
Pinus resinosa	0.75	0.93	0.84	2.74	0.17
Ulmus species	0.38	0.55	0.47	1.39	0.10
Acer saccharum	0.38	0.31	0.35	1.39	0.06
Fagus grandifolia	0.38	0.14	0.26	1.39	0.03
Totals	100.00	100.00	100.00	365.50	18.30

Diversity (H') = 1.1

[1] Importance Value = (relative density + relative dominance)/2 * 100

[2] trees/ha

[3] basal area (m^2/ha)

Surveyors mentioned cedar, hemlock, ground hemlock (<u>Taxus canadensis</u>), mosses, and wintergreen (<u>Gaultheria procumbens</u>) as common understory plants in this community.

The pitted outwash plain of the study area was thiscommunity's most common landscape position (Table 3, see maps). Here, this forested wetland community occurred along river and stream drainages; in kettle features; and in larger areas of the outwash plain with a lack of integration in the drainage system. This community occupied muck and peat, and mucky sand soils (Table 3); where soil drainage was very poor. Community-level overstory basal area (trees $\geq$ 10 cm d.b.h.) was 18 m^2/ha (Table 8). Nutrient conditions vary with soil acidity. More neutral, nutrient-rich sites with flowing water probably had a larger component of white cedar than tamarack. Tamarack probably dominated sites with acidic, stagnant water, and low nutrient availability (Burns and Honkala 1990).

Structurally this community seems to have had both even and uneven aged stands. White cedar's size structure (Figure 18) appears to resemble an "inverse-J" indicative of an uneven-aged stand (Smith 1986). Tamarack and the spruce species (mainly black spruce) both exhibited size structures reminiscent of even or two-aged stands (Figures 21 and 22).

The fire rotation period for the hydric forest community was $\approx$ 1100 years. The catastrophic windthrow rotation period was $\approx$ 700 years. Longevities of white cedar, black spruce, and tamarack are: 400, 150-200, and 150-180 years,

Figure 18: Histogram showing distribution of white cedar witness trees by 5 cm d.b.h. classes.

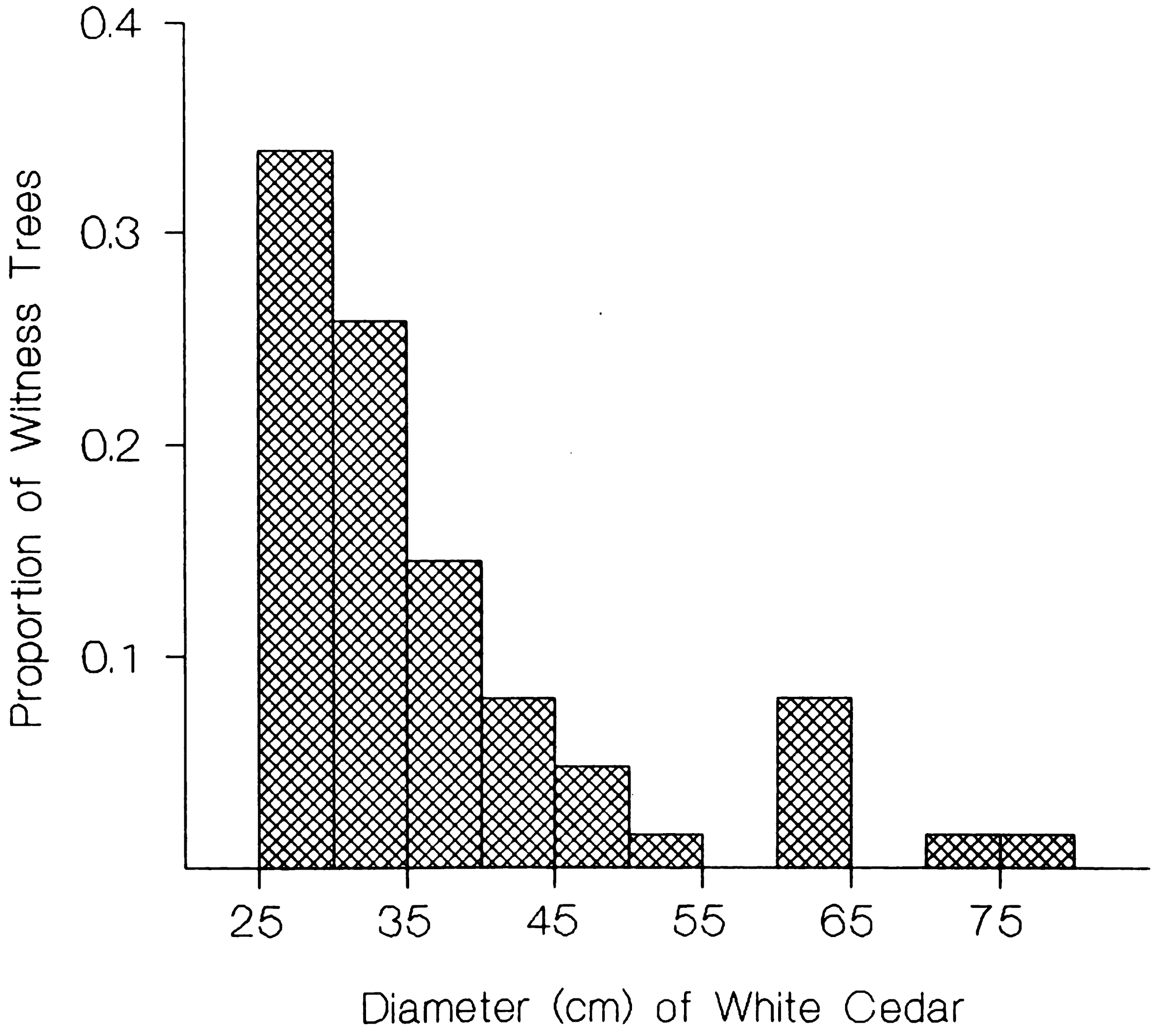

0.4
0.3
0.2
0.1
Proportion of Witness Trees
25
35
45
55
65
75
Diameter (cm) of White Cedar

Figure 19: Histogram showing distribution of tamarack witness trees by 5 cm d.b.h. classes.

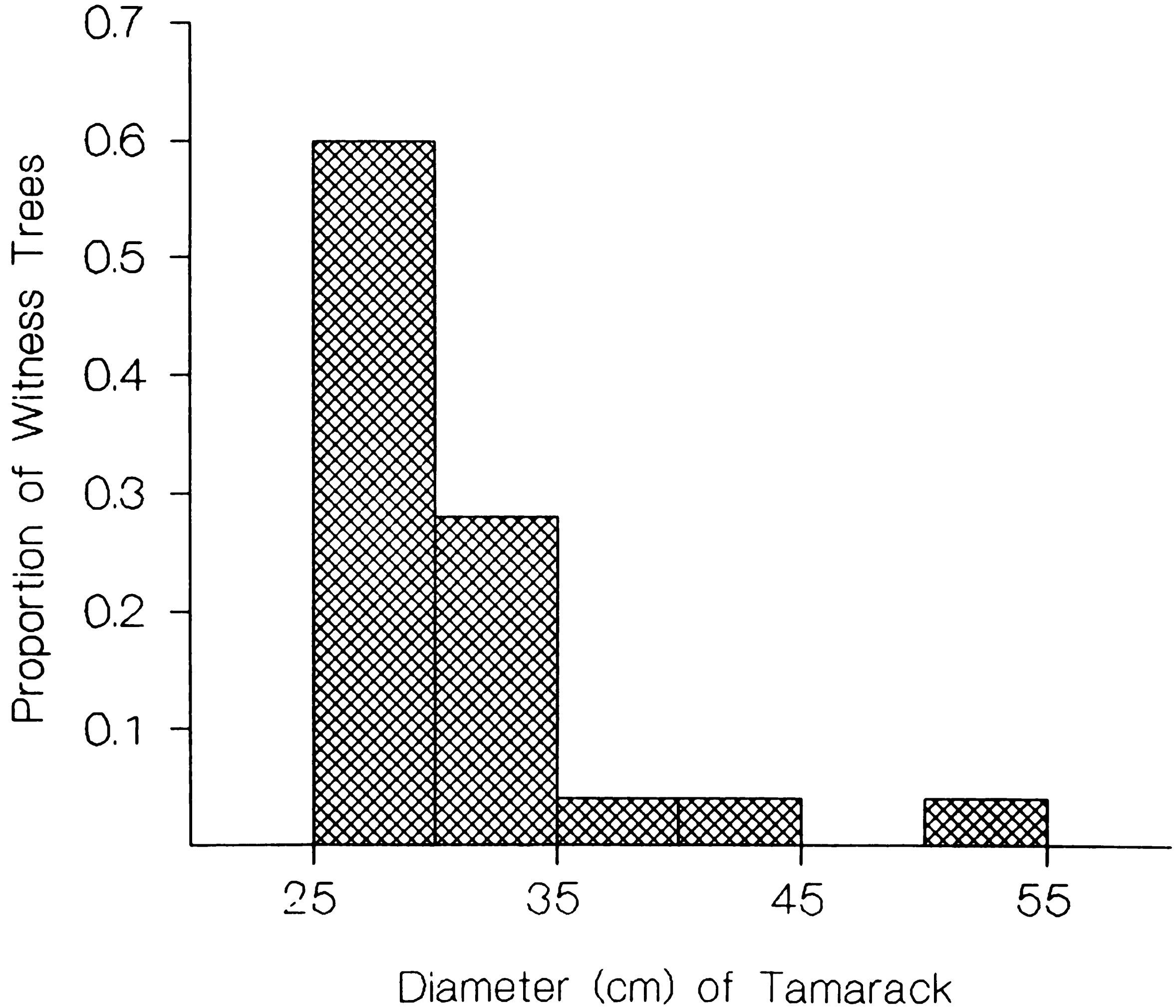
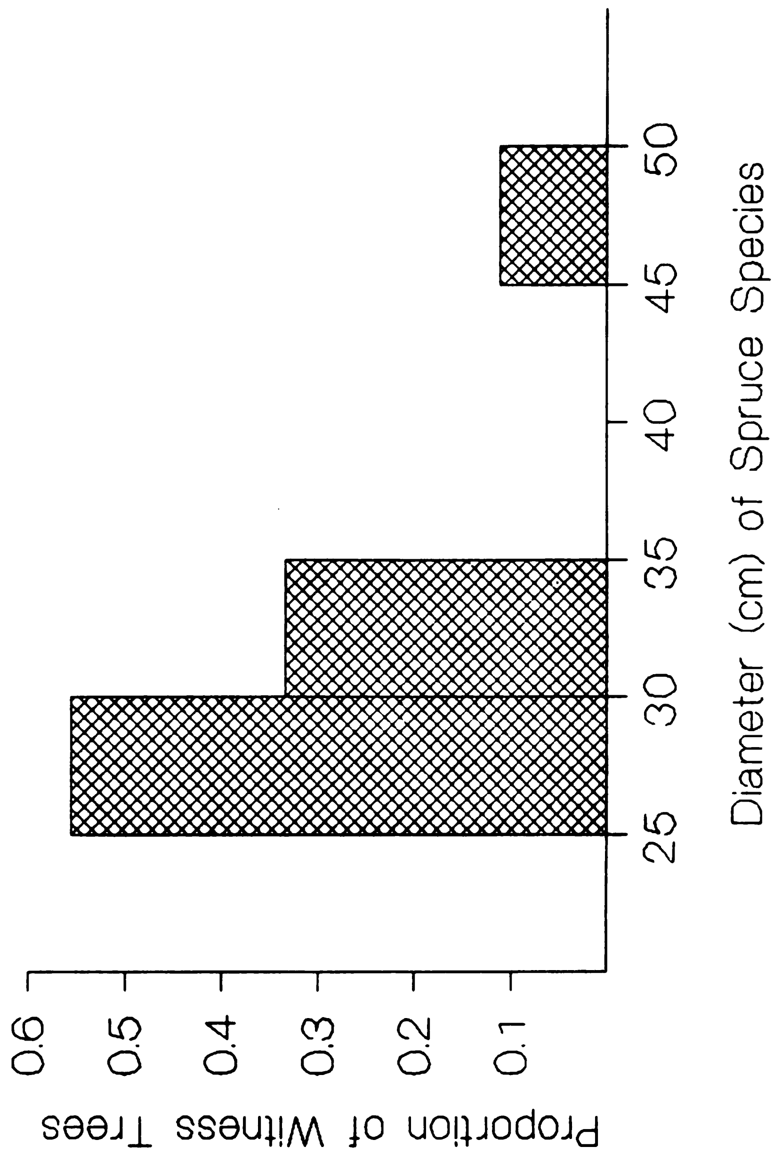

0.7
0.6
0.5
0.4
0.3
0.2
0.1
Proportion of Witness Trees
25
35
45
55
Diameter (cm) of Tamarack

Figure 20: Histogram showing distribution of spruce (primarily black spruce) witness trees by 5 cm d.b.h. classes.


Proportion of Witness Trees
0.6
0.5
0.4
0.3
0.2
0.1
25
30
35
40
45
50
Diameter (cm) of Spruce Species

respectively (Burns and Honkala 1990). The disturbance rotation periods above appear correct for stands dominated by white cedar. White cedar was likely uneven-aged in this community and rotation periods longer than its longevity would have fostered this age structure. However, tamarack and black spruce most likely had even-aged stands. Such long rotation periods as above could not have created such age structures. Tamarack requires full sunlight for germination and establishment (Burns and Honkala 1990). In the case of tamarack and black spruce, either of two conditions may have favored their development in this community. One, they could have been bog succession pioneers; or two, their establishment was related to large fires during severe drought episodes.

I picture this forest community as composed of two sub-types in the pre-European settlement forest. The first sub-type was dominated by white cedar stands. Stand replacing disturbances here had rotation periods greater than species' longevities. Gap-phase disturbances (Runkle 1982) and the shade tolerance of white cedar (Burns and Honkala 1990) allowed for an uneven-aged structure. Given white cedar's nutrient demands and the surveyor descriptions, this subtype was likely located on near neutral stream-side swamps. The second sub-type was dominated by even-aged tamarack-black spruce stands. These sites were likely highly acidic and nutrient-efficient species such as tamarack and black spruce were most competitive here. These species were able to establish here due to the lack of competition and infrequent fires which prepared the seedbed.

<u>The Pre-European Settlement Landscape Patterns</u>

Witness Tree Compositional Trends

All but one of the ten pair-wise comparisons of pre-European settlement communities showed significant compositional differences between communities ($P \leq 0.05$, chi-squared test of independence, Table 9). The dry-mesic and xeric communities did not significantly differ in tree species composition (Table 9). In general, the pre-European settlement landscape was compositionally heterogeneous. Tree species diversity (H′) increased along the environmental gradient from a low H′ value in the xeric community (Table 4) to the largest H′ in the wet-mesic and hydric communities (Table 8). Table 10 shows that the pre-European settlement landscape was dominated by conifers, particularly the pines (61% of the study area's relative density, Table 10). Angiosperms made up only 21% of the study area's relative density (Table 10); in fairly close accordance with the fact that 17% of the study area's soils are Alfisols. Jack pine alone accounted for 39% of the study area's relative witness tree density (Table 10). Pine dominated forest types covered 57% of the study area (Table 11). The best evidence for pine's pre-European settlement dominance lies in the physical site factors of the study area.

58% of the study area is covered by outwash plains (Table

12). 64% of the study area has either excessively or somewhat excessively drained soils (Table 13). 80% of the study area's surficial geology consists of coarse-textured materials

Table 9: Pair-wise comparisons of compositional differences between pre-European settlement communities using the chi-squared test of independence.

	Community				
	Xeric	Dry-Mesic	Mesic	Wet-Mesic	Hydric
Community					
Xeric	-				
Dry-Mesic	19.4#	-			
Mesic	116.1*	83.4*	-		
Wet-Mesic	95.7*	71.8*	46.2*	-	
Hydric	148.1*	145.7*	157.3*	92.7*	-

q-value (test statistic)
* Significant difference between communities at $P \leq 0.05$.

(Table 12). Entisols and spodosols make up ≈ 57% and 17% of the study area, respectively. These droughty, infertile soils created conditions in the pre-European settlement forest that gave pines the competitive advantage (Aber and Melillo 1991). In turn, the pines evolved in tandem with a regime of frequent surface fires and less frequent crown fires (White 1979). Fires maintained the dominance of pines which in turn maintained the poor litter quality and nutrient status of these sites. The soil, conifer overstory, and fire regime created a complex nexus of feedback mechanisms which created and maintained the pre-European settlement pine forests.

Pine barrens (Curtis 1959) occupied 3% of the study area

(Table 11). These areas demonstrate pine's xeromorphy and fire-adaptiveness. Surveyors described the pine barrens as such:

> Yellow pine rather scattering and some spruce pine...A thin growth of spruce and yellow pine...burned plain covered with grasses...

From surveyor descriptions these areas contained small jack pines and black oak grubs and widely scattered large red pines. A graminoid ground layer was frequently mentioned.

Witness Tree Structural Trends

Overstory basal area (trees ≥ 10 cm d.b.h.) of the pre-European settlement forest followed a predictable pattern. Xeric and hydric forest communities had the lowest basal areas: 13 m^2/ha and 18 m^2/ha, respectively (Table 15). The mean witness tree diameters of these two communities while not significantly different from each other, were significantly ($P \leq 0.05$) smaller than in the other communities (Table 15). Jack pine had the smallest mean d.b.h. of all witness trees (Table 16). Its presence as the dominant species of the xeric community helps to explain this community's low basal area and mean d.b.h. White cedar and tamarack dominated the hydric sites and their small-medium mean d.b.h.'s (Table 16) created this community's low basal area and mean d.b.h. In both of these communities the presence of very low or high soil moisture and/or nutrient

Table 10: Species composition by percentage of the study area.

Species	%
Abies balsamea	0.87
Acer rubrum	0.71
Acer saccharum	4.20
Betula alleghaniensis	0.20
Betula papyrifera	1.08
Betula species	0.91
Fagus grandifolia	6.59
Fraxinus americana	0.13
Fraxinus nigra	0.64
Juniperus virginiana	0.03
Larix laricina	2.32
Ostrya virginiana	0.03
Picea species	0.84
Pinus banksiana	39.17
Pinus resinosa	14.93
Pinus strobus	6.73
Populus species	1.95
Quercus alba	0.64
Quercus rubra-velutina-ellipsoidalis	3.43
Thuja occidentalis	3.80
Tilia americana	0.44
Tsuga canadensis	7.26
Ulmus species	0.34
Total	100.00

availability influenced species composition and restricted tree growth. These factors in turn may explain the low pre-European settlement overstory basal area of these sites.

Those communities along the middle of the edaphic gradient all had basal areas within the range found for old-growth upland hardwood stands in northern Michigan (McIntire 1931). Trees were indeed large in all three communities (dry-mesic, mesic, and wet-mesic). Red pine achieved large sizes in the pre-European settlement forest (Table 16). Its preponderance in dry-mesic communities may explain the substantial pre-European settlement basal area and mean d.b.h. there. Species competitive in these communities were often not restrained from achieving their genotypic maximum sizes.

Density trends in conjunction with basal area trends allow for a conceptualization of the pre-European settlement forest's structure. Xeric communities were open, with small trees. Enough light probably made it to the forest floor here to support a rich herbaceous community. Dry-mesic communities had small groves of large trees interspersed with dense patches of small trees. The mesic community was nearly a uniform matrix of medium sized trees with occasional patches of densely spaced small trees and occasional large super-canopy trees. The wet-mesic community consisted of small ridges of large trees within a dense matrix of small trees. Dense patches of small trees, small groves of medium- sized trees, and small open patches comprised the hydric sites.

Table 11: Pre-European settlement extent of vegetation cover types for the study area.

Type	Area (ha)	% of study area
Jack pine-red pine-white pine	46,583	38.43
Jack pine barrens	3,442	2.84
Red pine-jack pine-white pine	18,461	15.23
Hemlock-beech-sugar maple-white pine	26,000	21.45
Hemlock-white pine-red pine-aspen	5,248	4.33
Swamp conifers	18,436	15.21
Marsh	1,248	1.03
Lakes	1,794	1.48
Totals	121,212	100.00

Table 12: Soil and landform composition of the study area.

Soil Type	% of study area
Sand	74.85
Loamy sand	5.45
Sandy loam	8.81
Loam	1.48
Silty clay loam	0.20
Muck and peat	7.73
Mucky sand	1.48
Total	100.00

Landform Type	% of study area
Ice-contact	16.34
Morainal	25.82
Outwash	57.83
Total	100.00

Table 13: Extent of the different soil drainage types in the study area.

Drainage Class	% of study area
Excessive	44.16
Somewhat excessive	20.17
Well and moderately well	19.50
Poor to somewhat poor	7.26
Very poor	8.94
Total	100.00

Disturbance Regime Patterns

Annually, ≈ 6% of the study area was in a burned-over condition in the pre-European settlement period (Table 14). Whitney (1986) obtained a similar value of 7% for nearby Crawford and Roscommon Counties. In northeastern Maine Lorimer (1977) found 9% of the pre-European settlement landscape in burned land. Only ≈ 2% of the study area was in windfall in the pre-European settlement period (Table 14). For the study area as a whole, fire likely played an important role in structuring ecosystems. Large windfalls seemed infrequent enough to have a minimal impact on species adaptations.

The intensity, frequency, and extent of fires in the pre-European settlement forest seems to be directly related to vegetation types, soil types, and landscape configuration. As described earlier, pine dominated ecosystems on dry, flat, infertile sites burned most frequently and with the greatest

Table 14: Disturbance regimes of the pre-European settlement forest.

	Forest Type					
	Jack pine-red pine-white pine	Red pine-jack pine-white pine	Hemlock-beech-sugar maple-white pine	Hemlock-white pine-red pine-aspen	Swamp conifers	Study area
% area affected by windthrow	1	2	1	7	2	2
est. rotation period (yr) for windthrow	2000	900	1200	200	700	900
% area affected by fire	12	11	0	2	1	6
est. rotation period (yr) for fire	100	100	5600	900	1100	200

Table 15: A comparison of pre-European settlement forest structural attributes (trees ≥ 10 cm d.b.h.) by forest community or site type.

Site Type	Mean d.b.h. (cm) ± SEM	Basal area m^2/ha ± SEM	Trees/ha ± SEM
Xeric	23 ± 0.4 a[1]	13 ± 0.7	214 ± 11.2 a
Dry-Mesic	30 ± 0.8 b	31 ± 1.5	315 ± 15.0 a,b
Mesic	33 ± 0.7 c	25 ± 1.4	241 ± 13.3 a,b
Wet-Mesic	30 ± 1.2 b,c	36 ± 11.8	366 ± 120.4 a,b
Hydric	23 ± 0.7 a	18 ± 3.1	366 ± 62.1 b

[1] Column means with different letters (a,b,c) significantly different at P≤0.05, Tukey's HSD.

* SEM = Standard Error of the Mean

Table 16: Mean witness tree diameters (trees ≥ 10 cm d.b.h.) by species.

Species	Mean d.b.h. (cm) ± SEM
Jack pine	18 ± 0.3 a*
Aspen	19 ± 0.8 a
Red oaks	19 ± 1.4 a
Tamarack	21 ± 0.9 a
Beech	26 ± 0.6 a
White cedar	27 ± 1.3 a,b
Sugar maple	31 ± 1.1 b
Hemlock	36 ± 1.1 b
Red pine	44 ± 0.8 c
White pine	46 ± 1.7 c

* Means followed by different letters (a,b,c) significantly different at P≤0.05, Tukey's HSD.

intensity. In some instances the fires started in the pine dominated ecosystems went beyond the limits of the droughty, infertile outwash soils and created pine communities on fairly mesic morainal and ice-contact features (see maps). In such cases the position of these pine dominated morainal and ice-contact features was just east of extensive outwash plains (see maps). Strong westerly and northwesterly winds associated with fire spotting in the study area (Simard et al. 1983) could have spread fires to specially situated moraines and ice-contact landforms.

150 YEARS OF FOREST CHANGE

Changes in Forest Communities Across the Edaphic Gradient

Changes in the Xeric Forest Community

Although stand data were unavailable for today's xeric sites, the literature indicated that compositional changes have been minimal since the pre-European settlement period. The Mack Lake outwash plain (Figure 3) was composed of the following timber types in 1980 (Simard et al. 1983): jack pine (42%), red pine (16%), oak/pine (8%), oak/hardwood (12%), and aspen (14%). In the pre-European settlement period jack pine (52% i.v., Table 4), red pine (29% i.v.), and white pine (10% i.v.) were forest dominants with aspen (2% i.v.) and red oak (2% i.v.) associates. Hence, today's xeric forests are nearly a compositional facsimile of pre-European settlement conditions.

Present-day jack pine stands on the Mack Lake outwash plain range from 246-2962 trees/ha; mean density is 1975 trees/ha (Simard et al. 1983). It seems that most present-day jack pine stands are far denser than pre-European settlement stands. On the Mack Lake outwash plain present-day mean d.b.h. ranges from 13 cm in jack pine stands to 20 cm in red pine stands. Basal areas likewise range from 25 m^2/ha to 33 m^2/ha (Simard et al. 1983). Present-day basal areas are larger than in pre-European settlement time perhaps due to a decline in jack pine barrens. Jack pine's age-structure on xeric sites in Roscommon County, Michigan, is even-aged today (Larsen 1982) as it likely was 150 years ago. Structurally, these xeric sites seem to have changed. Such changes undoubtedly have impacted populations of the endangered Kirtland's Warbler (Dendroica kirtlandii) (Probst 1988).

Whitney (1986) determined that the fire rotation period for the jack pine cover type in nearby Roscommon and Crawford Counties was ≈ 392 years during the fire protection era (1965-1985). The fire rotation period for the Huron National Forest from 1950-1981 was ≈ 398 years (Simard and Blank 1982). The average annual area burned in the Huron NF decreased from 5261 ha during the 1910s to 155 ha during the 1970s (USDA Forest Service 1980). Organized fire control beginning around 1930 diminished the frequency, severity, and extent of fires in the study area (Simard and Blank 1982). However, on May 5, 1980, a forest fire burned nearly 9713 ha on the Mack Lake outwash plain, crowning in several areas (Simard et al. 1983). This was the sixth major fire (4047+ ha) on the Mack Lake plain since 1820 (Simard and Blank 1982). Even today the study area's xeric sites retain a pyric nature. This may have allowed the fire-dependent Kirtland's Warbler to survive 20th century fire management practices.

Changes in the Dry-Mesic Forest Community

This forest community has changed from a pre-European settlement red pine (41% i.v., Table 17, Appendix D: Figure 26), jack pine (24% i.v.), and white pine (15% i.v.) type to today's red oak complex (40% i.v., Table 17, Appendix C: Table 24), big-toothed aspen (23% i.v.), white oak (17% i.v.), and red maple (10% i.v.) type. Pre-European settlement forest associates included beech, sugar maple, and white oak (Table 5). Associates of the present-day forest are sugar maple, white ash, paper birch, basswood, and white pine (Table 17, Appendix C: Table 24). The tree species composition of this community has significantly changed (Table 18).

Table 17: Importance values and other attributes of tree species by community type in the pre-European settlement and present-day forest.

Tree Species	Dry-Mesic PS[1]	Dry-Mesic PD	Mesic PS	Mesic PD	Wet-Mesic PS	Wet-Mesic PD
Abies balsamea	0.12[2]	0.00	0.00	0.00	2.40	0.00
Acer rubrum	0.51	10.11	0.79	4.39	1.03	9.70
Acer saccharum	1.86	5.10	15.10	41.31	4.42	25.56
Betula alleghaniensis	0.12	0.00	0.29	0.00	1.35	0.00
Betula papyrifera	0.29	1.12	0.83	1.21	4.78	20.18
Betula species	0.00	0.00	0.46	0.00	3.53	0.00
Carya species	0.00	0.00	0.00	0.45	0.00	0.00
Fagus grandifolia	3.52	0.21	19.95	3.39	3.18	0.45
Fraxinus americana	0.13	1.37	0.25	6.98	0.66	3.93
Fraxinus nigra	0.00	0.00	1.20	0.00	1.85	0.00
Juniperus virginiana	0.00	0.00	0.00	0.00	0.00	0.00
Larix laricina	0.00	0.00	0.00	0.00	1.55	0.00
Ostrya virginiana	0.00	0.38	0.11	1.25	0.00	0.00
Picea species	0.32	0.00	0.00	0.00	0.35	0.00
Pinus banksiana	23.83	0.00	1.14	0.00	5.20	0.00
Pinus resinosa	41.49	0.16	9.65	0.00	11.08	0.00
Pinus strobus	15.34	1.04	14.82	0.00	14.45	1.02
Populus species	3.61	22.70	1.90	12.87	10.95	1.60
Prunus serotina	0.00	0.43	0.00	0.11	0.00	0.00
Quercus alba	1.13	16.60	0.37	0.00	0.25	1.26
Quercus rubra-velutina-ellipsoidalis	3.73	39.72	3.74	9.39	1.54	18.01
Thuja occidentalis	0.44	0.00	1.26	0.00	8.25	0.00
Tilia americana	0.00	1.10	2.08	18.68	0.00	15.23
Tsuga canadensis	3.61	0.00	25.40	0.00	22.04	0.00
Ulmus species	0.00	0.00	0.70	0.00	1.17	3.08
Totals	100.00	100.00	100.00	100.00	100.00	100.00
Diversity (H')	0.7	0.7	0.9	0.8	1.1	0.8
Similarity Index	13		28		17	

[1] Where PS and PD indicate presettlement and present-day, respectively.
[2] Importance value = (relative density + relative dominance)/2 * 100

Table 18: Pair-wise comparisons of compositional differences between pre-European settlement and present-day forest communities on similar site types using the chi-squared goodness of fit test.

	Site Types		
Site Types	Dry-mesic	Mesic	Wet-mesic
Dry-mesic	946.6#*		
Mesic		528.4*	
Wet-mesic			503.7*

q-value (test statistic)
* Present-day and pre-European settlement communities significantly different in composition, $P \leq 0.05$.

The probable causes of these changes lie in the interaction between historical events of the past 150 years;available tree species pools; the adaptive strategies of the new dominants; and chance factors. Red and white pine have been nearly eliminated (Table 17) from this community. This occurred because of the destruction of their reproductive potential. Red and white pine were selectively logged from this community, removing most of the available seed trees. Kittredge and Chittenden (1929) determined that the fire rotation period was ≈ nine years in cut-over mixed pine stands of northern lower Michigan in the logging era. The red and white pine advance regeneration provided by the few remaining seed trees was eliminated by these frequent and intense slash fires (Ahlgren and Ahlgren 1983). Red and white pine become reproductively mature between twenty and thirty years of age

(Burns and Honkala 1990). So, those juveniles which did escape one or two fires were most likely destroyed by a third before they could reproduce. The failure of the pines to reproduce in the logging era helps to explains the changes in this community. The introduction of white pine blister rust (Cronartium ribicola) further hindered the regeneration of white pines.

The present-day dominants in this community were either associates in the pre-European settlement forest (the red oaks, aspen, and white oak; Table 5) or at least present (red maple, Table 5). The red oaks are vigorous sprouters and drought tolerant (Burns and Honkala 1990). Logging created drier soil conditions and frequent slash fires which gave the oaks a greater reproductive ability than the pines. The logging and repeated fires would have stimulated the suckering of aspen (Burns and Honkala 1991). New areas of mineral seedbed allowed for aspen's copious wind-dispersed seed to colonize large areas of this community. Red maple sprouts fairly well and produces a large seed rain (Burns and Honkala 1990). This may explain red maple's present success in this community.

The community-level overstory basal area (trees $\geq$ 10 cm d.b.h.) has decreased from 31 m^2/ha to 27 m^2/ha over the past 150 years (Table 19). The mean d.b.h. of this community has significantly decreased ($P \leq 0.05$, paired t-test) from 30 cm to 20 cm (Table 19). This is not surprising, as the former dominants of this community, white and red pine, were the largest in girth (Table 16) in the pre-European settlement forest. Commensurate with this decrease in tree size has been a three-fold increase in tree density in this community from 315 trees/ha to today's 904 trees/ha (Table 19).

The structural nature of this community has changed. Horizontally, the forest is less open and park-like. The canopy configuration has surely changed as the canopy is now composed of different tree species with different canopy architectures. The age-class diversity has likely decreased. Present-day stands do not exceed 100 years of age. In the pre-European settlement forest, judging by their size, some white and red pines may have been between 200 and 450 years old (Burns and Honkala 1990).

Whitney (1987) determined that the fire rotation period for similar sites in nearby Roscommon and Crawford Counties was ≈ 313 years for the fire protection era (1965-1985). The pre-European settlement fire rotation was ≈ 100 years (Table 14). The advent of fire suppression in the study area may explain the presence of such mesic species as sugar maple, basswood, and white ash as associates in today's overstory (Table 17) and maple's (red and sugar) ubiquitous presence in the seedling and sapling stages (Padley 1989; Palik and Pregitzer 1992).

Angiosperms have replaced gymnosperms as the dominants of this community. Such a change has likely had functional

Table 19: A comparison of pre-European settlement and present-day forest structural attributes (10 cm minimum d.b.h.)

Site Type	Mean trees/ha ± SEM		Mean ba/ha (m^2/ha) ± SEM		Mean d.b.h. (cm) ± SEM	
	PS*	PD	PS	PD	PS	PD
dry-mesic	315±15.0	904±56.8	31±1.5	27±2.5	30±0.8a[1]	20±0.2b
mesic	241±13.3	915±79.1	25±1.4	31±7.1	33±0.7as	20±0.4b
wet-mesic	366±120.4	1203±230.2	36±11.8	36±1.2	30±1.2a	18±0.3b

* Where PS and PD indicate pre-European settlement and present-day, respectively.

1 Row means with different letters (a,b) significantly different at P=0.05, paired t-test.

Table 20: Changes in d.b.h. by tree species since Euro-American settlement (10 cm minimum d.b.h.)

Tree Species	Pre-European Settlement Mean d.b.h. (cm)	Present-day Mean d.b.h. (cm)
Red maple	22a	16b*
Sugar maple	31a	18b
Paper birch	23a	16b
Aspen	19a	21b
White oak	17a	17a
Red oaks	19a	22b
Basswood	35a	20b

* Row means followed by a different letter (a,b) are significantly different at P=0.05, paired t-test.

repercussions in this ecosystem. Seral wildlife species haveundoubtedly benefited from the increase in palatable browse species here (Heinen and Sharik 1990). The C:N ratio of this community's litter has likely decreased, increasing N-mineralization rates (Pastor et al. 1984) and decreasing the residence time of litter on the forest floor. The presence of less pyric deciduous tree species has likely reinforced the human-imposed fire suppression program.

Changes in the Mesic Forest Community

This forest community was dominated by hemlock (25% i.v., Table 6, Appendix D: Figure 27), beech (20% i.v.), sugar maple (15% i.v.), and white pine (15% i.v.) in the pre-European settlement period. Present-day stand dominants are sugar maple (41% i.v., Table 17, Appendix D: Figure 27), basswood (19% i.v.), and big-toothed aspen (13% i.v.). Pre-European settlement associates included: red pine, red oaks, basswood, aspen, white cedar, black ash, and jack pine (Table 6). Red oaks, white ash, red maple, beech, ironwood, and paper birch are the present-day forest associates (Table 17, Appendix C: Table 25). The overstory composition of this community has changed significantly (Table 18). The tree species diversity (H') of this community has declined (Table 17).

Hemlock , white pine, and beech were eliminated from this community. Hemlock's demise was linked to its selective cutting for the leather industry as a source of tannin. This eliminated a great many seed trees. The increased exposure and drying of the soil after logging prevented the establishment of hemlocks from the few seed trees left (Buttrick 1923). In recent times deer (*Odocoileus virginianus*) browsing and the lack of coarse woody debris may have prevented regeneration of hemlock from the rare seed trees remaining (Frelich and Lorimer 1985). While beech frequently root sprouts, it cannot regenerate under a regime of repeated cuttings; nor can it disperse its seeds by wind (Burns and Honkala 1990). Furthermore, beech is slow-growing and ineffectively responds to release (Burns and Honkala 1990). Beech's life history traits help explain its failure to reproduce after extensive logging. White pine's elimination here probably hinged on its subjection to exhaustive selective logging.

Sugar maple had an extensive development of advance regeneration in old-growth northern hardwoods of northern Michigan (Frelich and Lorimer 1991). Sugar maple strongly responds to release (Burns and Honkala 1990). When the mesic community was logged, sugar maple seedlings and saplings probably rapidly established themselves as new canopy dominants. Sugar maple can also stump sprout and has a prolific seed rain (Burns and Honkala 1990). Taken together these factors may explain sugar maple's present-day dominance (41% i.v.) in this community. Basswood was an associate species in the pre-European settlement forest (Table 6). It achieved its present dominant status probably via sprouting;

wind dispersal of seeds; its rapid growth rate; and its ability to remain in the seed bank for up to three years (Burns and Honkala 1990). Big-toothed aspen's present status depended on the logging and surface fires at the turn of the century. Aspen in pre-European settlement windfall gaps suckered into the newly opened spaces of this forest. Where surface fires exposed mineral soil on logged sites, aspen seeded in (Davis 1935).

Overstory basal area increased from 25 m^2/ha to 31 m^2/ha (Table 19) over the past 150 years. This may reflect a large ingrowth of pole-sized trees (Table 19) in recent time. As in the other forest communities, the mesic forest had less trees (241 trees/ha, Table 19) in pre-European settlement time than today (915 trees/ha, Table 19). Along with this increase in tree density, the mean d.b.h. has significantly ($P \leq 0.05$, paired t-test) decreased from 33 cm to 20 cm (Table 19) in this community. The significant ($P \leq 0.05$, paired t-test) post-European settlement reduction in sugar maple's mean d.b.h. (Table 20) may account for the decline in this community's mean d.b.h.

During the logging era (1870-1920) fires were less common here than in the previous communities (Roth 1905). Whitney (1987) calculated a fire rotation period of 276 years for the hemlock-white pine-northern hardwoods type of Roscommon and Crawford Counties during the fire suppression era (1965-1985). I calculated a pre-European settlement fire rotation period of

5600 years. This indicates that fires may have been more frequent in this community since Euro-American settlement.

This community has changed in composition and structure. Sugar maple has assumed dominance via release of advance regeneration and seeding in. Interestingly, basswood has also assumed a co-dominant position in this community. If gap-phase type disturbances are maintained in this community, sugar maple and basswood could likely perpetuate themselves here.

Beech has low quality litter (Melillo et al. 1982). Sugar maple and basswood have high quality litter (Melillo et al. 1982; Pastor et al. 1984). The loss of beech and subsequent increase in sugar maple and basswood in this community has likely changed nutrient cycling. Present-day litter decomposition rates and N-mineralization rates may exceed pre-European settlement rates.

Changes in the Wet-Mesic Forest Community

This community has gone from a pre-European settlement conifer dominated system (65% i.v., Table 7) to today's angiosperm dominated forest (99% i.v., Table 17, Appendix D: Figure 28). Pre-European settlement dominants included hemlock, white pine, red pine, and aspen (Table 7). Today's dominants are sugar maple, paper birch, the red oaks, and basswood (Table 17). Pre-European settlement associate tree species included: white cedar, jack pine, sugar maple, birch species, beech, balsam fir, black ash, tamarack, red oaks, yellow birch, elms, and red maple (Table 7). Today's associates are: red maple, white ash, elms, big-toothed aspen, white oak, and white pine (Table 17, Appendix C: Table 26). This community's tree species composition has significantly changed (Table 18). Tree species diversity (H') has declined in this community (Table 17).

The history of logging in this area resulted in today's lack of hemlock, red pine, and white pine. But aspen's move from a dominant to an associate appears counter-intuitive given the amount of disturbance during the logging era. Turn of the century slash fires likely fostered paper birch and red oaks; species present as associates in the pre-European settlement forest. Sugar maple and basswood may have attained their present status here by sprouting; seed dispersal; and recruitment from the understory. While sugar maple was a pre-European settlement associate in this community, basswood was not recorded as a witness tree here (Table 7).

Community-level overstory basal area (trees ≥ 10 cm d.b.h.) has remained nearly the same since Euro-American settlement (Table 19). Yet, the mean d.b.h. has significantly declined from 30 cm to today's 18 cm ($P \leq 0.05$, paired t-test, Table 19). Conversely, the mean tree density has tripled (Table 19) from 366 trees/ha to 1203 trees/ha. Such changes indicate the transition of this forest from one with a diversity of size classes to today's more uniform structure.

Like the dry-mesic forest community, this community has changed in composition. All of the pre-European settlement dominants have been supplanted today by what were pre-European settlement associates. This change followed a pulse of disturbance at the turn of the century. This community is physiographically heterogeneous and actually consists of broad, wet, sandy flats interspersed with well-drained, narrow, linear ridges. Sugar maple and the red oaks do not tolerate soil wetness very well. Hence, they likely occupy today's ridge sites. Paper birch and basswood can tolerate more poorly drained areas (Burns and Honkala 1990) and may predominate on the wet flats. I propose that fires are much less frequent on this community's dry, sandy ridges than in pre-European settlement time. On the wet, sandy flats, the occurrence of windthrow probably exists as it did 150 years ago.

Changes in the Hydric Forest Community

I lacked site specific present-day stand data for this community. However, some broad comparisons to observations in the literature were made. Veatch et al. (1931) reported that in Oscoda County the only major change within unlogged swamp conifer stands was the great decrease in tamarack due to larch sawfly (Lygaeonematus erichsonii) outbreaks. Where the swamp conifer type was logged and/or severly burned in the logging era, four new cover types came to dominate this community in different parts of Oscoda County: paper birch, alder (Alnus rugosa) thicket, red maple, or aspen (Veatch et al. 1931).

Surveyor accounts of abundant yew (Taxus canadensis) populations on these sites constrast sharply with the lack of yews in today's swamps (Frelich and Lorimer 1985). The modern irruption of deer populations in Michigan may account for this lack of yew regeneration.

Changes in the Landscape Patterns Since Euro-American Settlement

The study area's landscape patterns have definitely changed since 1840, albeit not nearly as drastically as in southern lower Michigan. Non-forested cover types have increased by 14% in the study area (excluding Alcona County, Table 21). Angiosperm cover types have increased by 22% in area while conifer cover types have declined by 35% in area (Table 21). These changes resulted from human imposed disturbances.

Pine cover types still cover the greatest area, but they have declined by 17% since the pre-European settlement period (Table 21). This loss approximates the pre-European settlement areal extent of the red pine-jack pine-white pine type (dry-mesic community, Table 11). Today's pine cover type is nearly all jack pine. Therefore, the pre-European settlement jack pine-dominated xeric community has not changed in area. The red pine-jack pine-white pine type has seemingly been replaced by the new aspen-birch cover type (Table 21).

The northern hardwoods cover type has declined by 14% in areal extent (Table 21). In addition, it has lost hemlock,

Table 21: Pre-European settlement and present-day extent of various cover types in the study area (excluding Alcona County).

MIRIS cover type (code)	Pre-European Settlement Area (ha)	Pre-European Settlement % of Area	Present-day Area (ha)	Present-day % of Area
Pine (421)	54,050	52.70	36,464	35.55
Northern Hardwoods (411)	22,542	21.98	7,851	7.67
Other upland conifers (422)	5,171	5.04	228	0.22
Lowland conifers (423)	15,649	15.26	3,998	3.89
Emergent marsh (622)	1,196	1.17	179	0.17
Lakes (52)	1,794	1.75	614	0.60
Pine barrens (333)	2,162	2.10	0	0.00
Central hardwoods (412)	0	0.00	16,466	16.05
Aspen-birch (413)	0	0.00	17,634	17.19
Lowland hardwoods (414)	0	0.00	2,944	2.87
X-mas trees (429)	0	0.00	5	0.00
Agriculture	0	0.00	2,586	2.52
Other wetlands	0	0.00	2,777	2.71
Other non-forested	0	0.00	6,255	6.10
Urban	0	0.00	4,573	4.46
Totals	102,564	100.00	102,564	100.00

beech, and white pine as integral components (Table 17).The 16% areal gain in the new central hardwoods cover type (sugar maple, basswood, red oak) has likely replaced the above loss in the northern hardwoods cover type.

Wetland cover types (forested and non-forested) show a net loss of 41% in coverage (Table 21). The swamp conifer cover type shows a net area loss of 74% since the pre-European settlement period (Table 21). The area lost by the swamp conifer type has likely been replaced by reservoirs (Alcona and Mio Dam Ponds) and three of the new cover types: lowland hardwoods (black ash, elm, red maple, aspen, and white birch), the aspen-birch type, and the "other"wetlands type (mainly shrub dominated wetlands).

The areal decline in wetland cover types and conifer cover types (particularly swamp conifers and hemlock) since the pre-European settlement period must have had and continue to have functional effects on the study area's landscape ecosystems. The increase in non-pyric hardwoods on all but the xeric sites has certainly augmented modern fire control efforts. A decrease in wetland area has certainly changed landscape-level hyrologic processes.

Surveyor accounts of Native American land-use in the study area only mention a major trading trail along the Au Sable River. Today, humans have fragmented the study area's landscape to a much greater degree. 13% of the study area exists as direct human artifacts (i.e., agriculture, right-ofways, roads, and urban areas; Table 21). These human artifacts increase the amount of forest edge area relative to interior forest conditions (Noss 1983). Thus, I suspect that edge species (e.g. deer, ruffed grouse [Bonasa umbellus], and cowbird [Molothrus ater]) populations have increased in the study area as a result of such habitat modifications. The introduction of road systems, agriculture, and housing must have definite impacts on species dispersal patterns and forest fire behavior.

CONCLUSIONS

EVIDENCE FOR/AGAINST HYPOTHESES

Tree species were not randomly distributed across the pre-European settlement landscape. The correspondence analyses and nonmetric multidimensional analysis show that witness tree species were responding to an underlying gradient. The primary axis of this gradient was soil moisture, but several other axes undoubtedly affected species distributions (i.e., fire regime, soil nutrients, light availability, and herbivory). These numerical analyses seem to substantiate the Gaussian model of community structure in the pre-European settlement forest. The binary discriminant analyses show that certain witness tree species occurred on certain landforms, soil types, and soil drainage conditions with statistically significant probabilities. An overlay of the two maps (see maps) shows that certain pre-European settlement forest cover types had definite affinities for certain landform positions. The fact that the grouping of the witness trees by site types explains much of the variance in the pre-European settlement forest demonstrates that tree species were probabilistically distributed.

The cluster analyses interpreted against the composition of the site types and the indirect ordinations seem to indicate that loose associations did occur between tree species in the pre-European settlement forest. However, each of the possible associations (beech-sugar maple-hemlock, white cedar-tamarack, red pine-jack pine) were composed of species with similar responses to parts of the environmental gradient. Hence, these associations were not tightly linked and may merely indicate the response of physiologically similar species to their environment.

The pre-European settlement forest communities all significantly differed from each other in composition save for the compositional similarity between the xeric and dry-mesic communities. These two communities compositionally converged due to the overriding influence of the fire regime. Forest structure changed along the edaphic gradient. Disturbance regimes were correlated with the soil moisture gradient; fire being most common on the xeric sites and catastrophic windthrow most common on the hydric sites.

Over the last 150 years, the composition and structure of the study area's forests have changed. However, the magnitude of such changes are specific to site types. Present-day xeric and hydric sites are compositionally similar to pre-European settlement conditions. Dry-mesic, mesic, and wet-mesic sites have changed in both composition and structure since Euro-American settlement.

A VERBAL MODEL OF THE STUDY AREA'S VEGETATION

A complex interplay among substrate, disturbance, and biotic factors created the pre-European settlement forest patterns. Viewed as a whole, the study area in the pre-European settlement period was a non-equilibrium landscape as defined by Shugart (1984). Present-day forest communities show historic chance events often overriding competition-mediated environmental determinism in their composition. Today's communities are rapidly succeeding to other types (Palik and Pregitzer 1992). I suggest that the present-day landscape is still re-equilibrating to the turn of the century disturbance pulse.

MANAGEMENT IMPLICATIONS

Because forest communities can have multiple stable states (Shugart et al. 1981) and climate constantly changes (Brubaker 1988) defining the 'natural' vegetation for the study area is fraught with problems. Managers and the public must realize that we cannot return the landscape to 1840 for both practical and evolutionary-ecological reasons. The value of vegetation history lies in delimiting the range of vegetation types and disturbance regimes in which species have evolved (Sprugel 1991). The National Forest Management Act specifies that biological diversity be considered in national forest planning. What management practices might be considered in light of pre-European settlement biodiversity patterns?

Today's forests lack: a mosaic of tree age-classes; coarse-woody debris; within-community tree species diversity; natural fire regimes; very old trees; and low forest edge:interior ratios. The following management proposals may help to restore the dynamics of pre-European settlement forests to the study area:

1. Stands should be managed with longer rotations.

2. Tree species such as red pine, white pine, beech, and hemlock might be artificially regenerated on the same sites they occupied in pre-European settlement time.

3. Dead trees should be left on the forest floor.

4. Some large "wolf" trees and dead and dying trees should be left in stands.

5. Some stands should be allowed to pass through several natural rotations.

6. Prescribed burning should be used more often in forest regeneration.

7. Clearcuts should be reduced in number and increased in mean size.

APPENDICES

APPENDIX A

Bar graphs of witness tree species importance values by site type

Figure 21: Importance values of witness tree species on xeric sites.

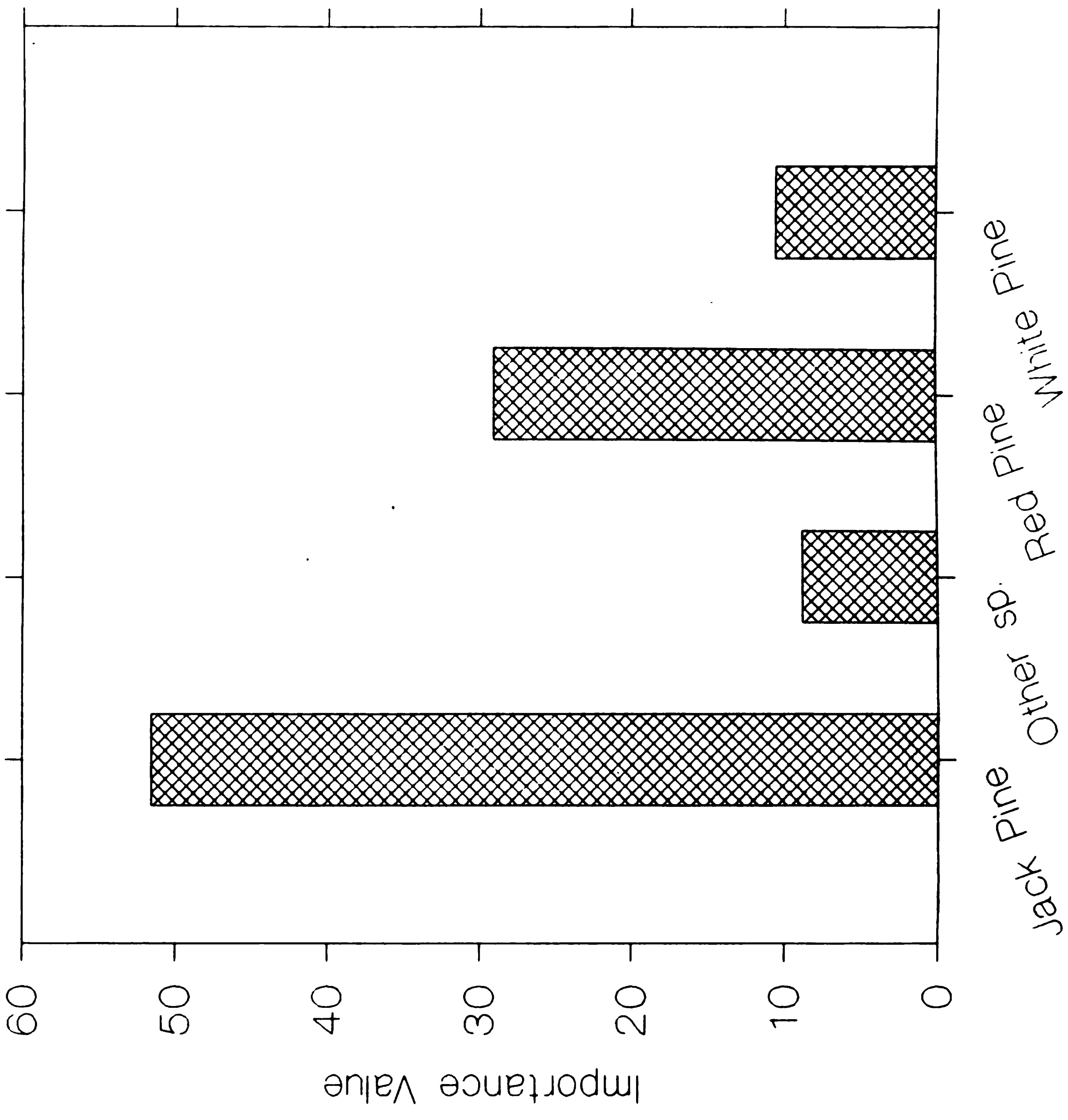

Importance Value
0
10
20
30
40
50
60
Jack Pine
Other sp.
Red Pine
White Pine

Figure 22: Importance values of witness tree species on dry-mesic sites.

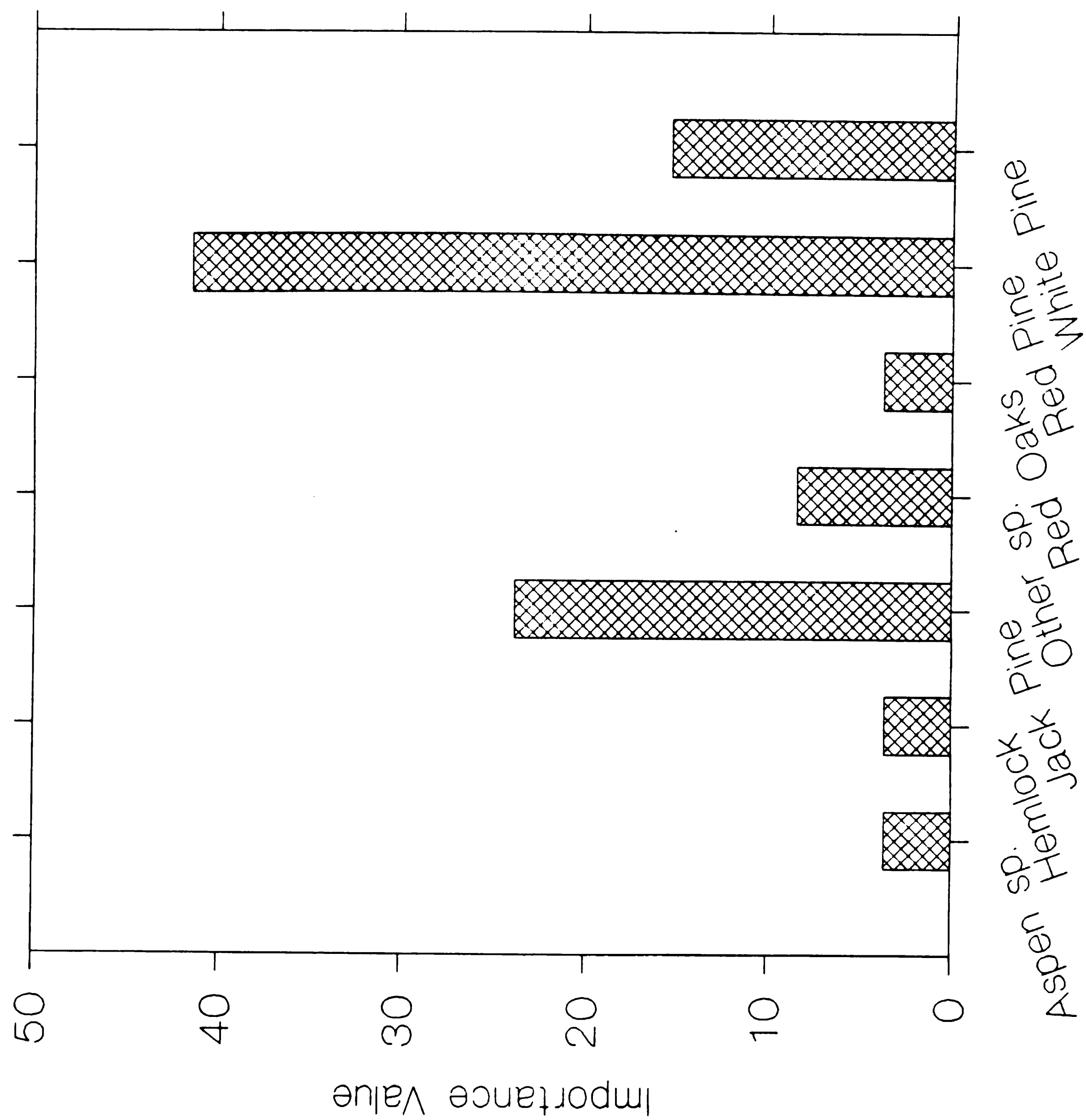

Importance Value
0
10
20
30
40
50
Aspen sp.
Hemlock
Jack Pine
Other Pine sp.
Red Oaks
Red Pine
White Pine

Figure 23: Importance values of witness tree species on mesic sites.

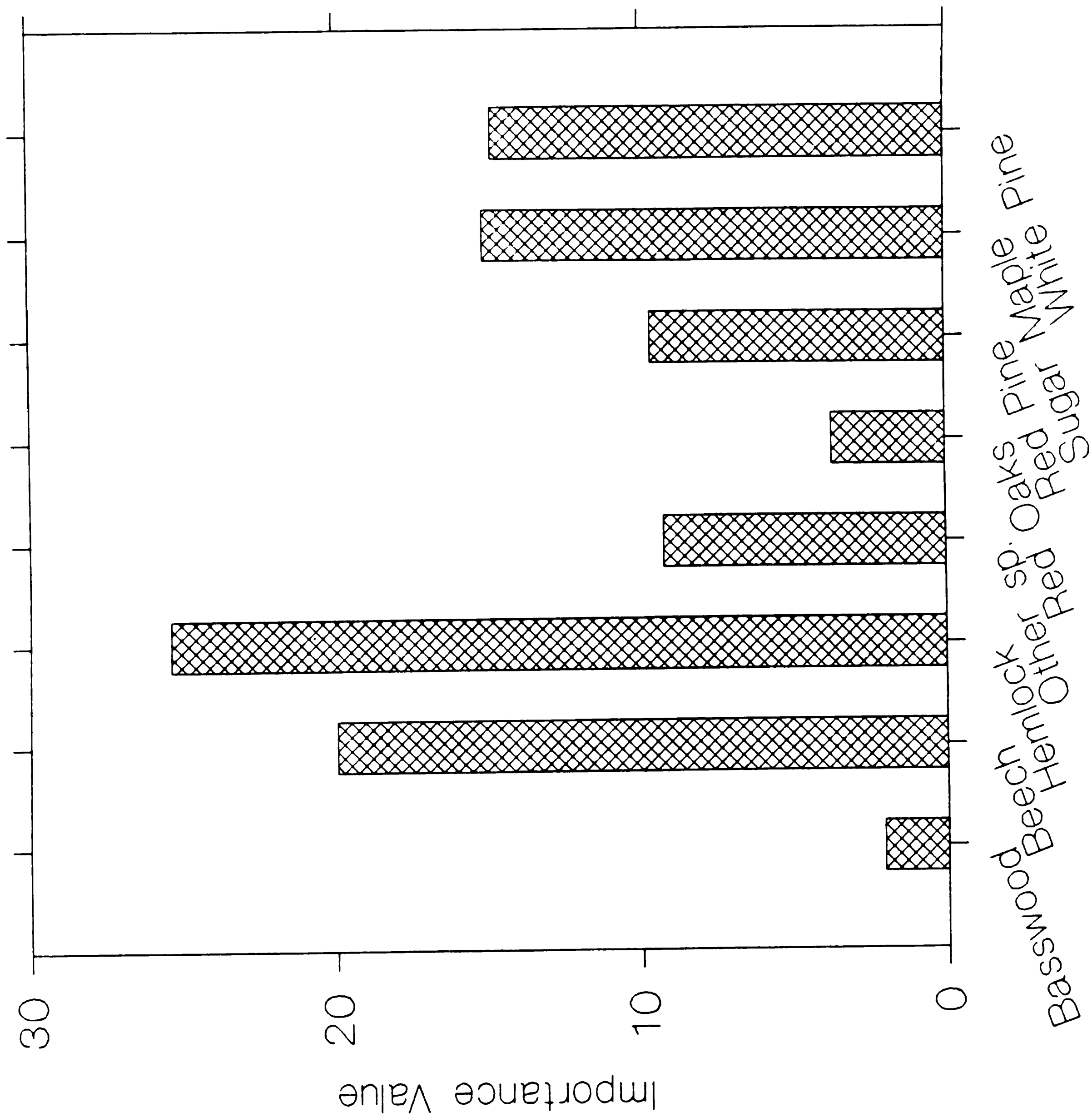

Importance Value
0
10
20
30
Basswood
Beech
Hemlock
Other Red sp. Oaks
Red Pine
Sugar Maple
White Pine

Figure 24: Importance values of witness tree species on wet-mesic sites.

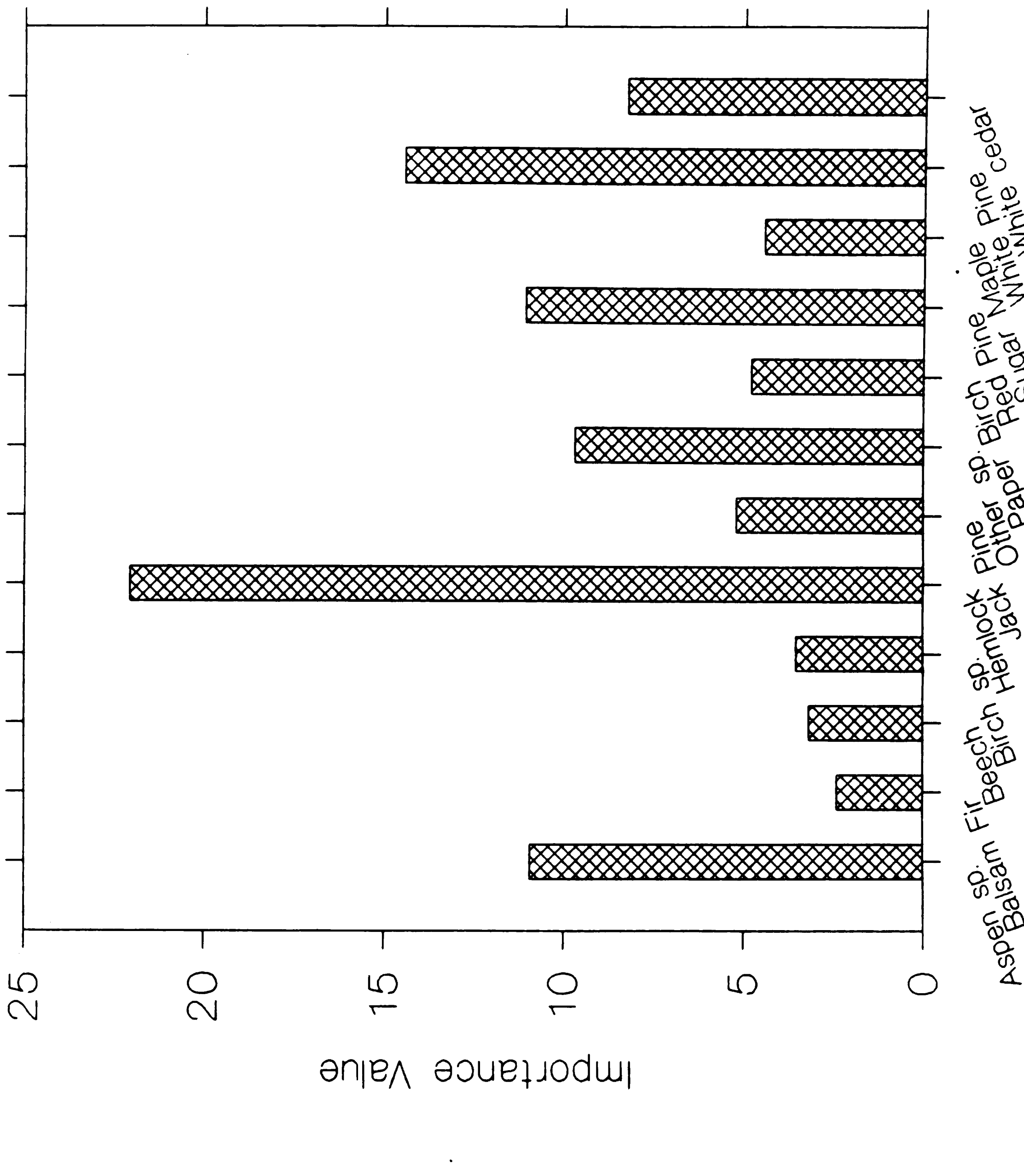
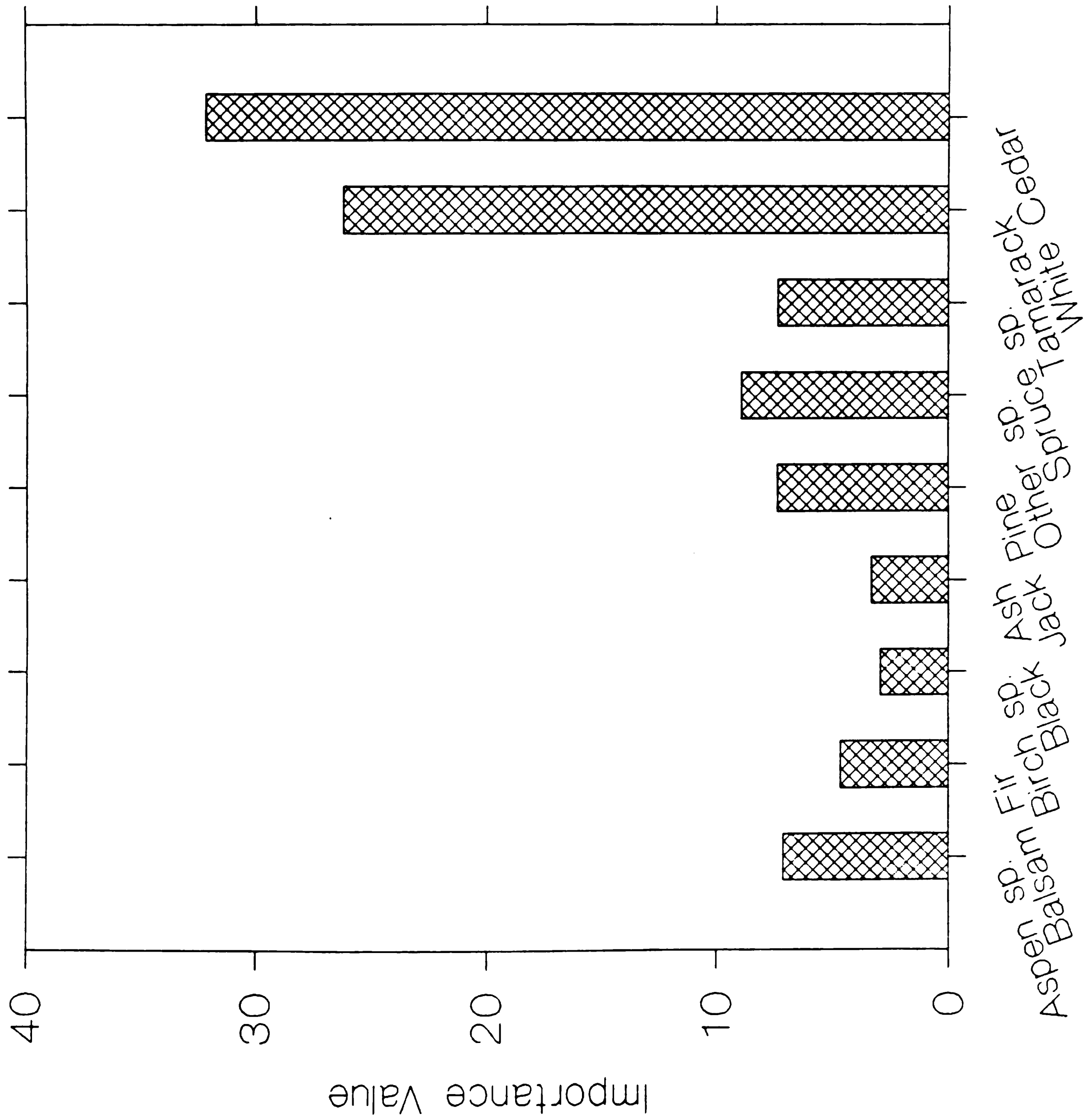

Importance Value
0
5
10
15
20
25
Aspen sp.
Balsam Fir
Beech
Birch sp.
Hemlock
Jack Pine
Other sp.
Paper Birch
Red Pine
Sugar Maple
White Pine
White cedar

Figure 25: Importance values of witness tree species on hydric sites.


Aspen sp.
Balsam Fir
Birch sp.
Black Ash
Jack Pine
Other sp.
Spruce sp.
Tamarack
White Cedar
0
10
20
30
40
Importance Value

APPENDIX B

Structural data summaries for pre-European settlement and present-day communities

Table 22: Density of tree species (trees ≥ 10 cm d.b.h.) by community type in the pre-European settlement and present-day forest.

	Dry-Mesic		Mesic		Wet-Mesic	
Tree Species	PS[1]	PD	PS	PD	PS	PD
Abies balsamea	0.54[2]	0.00	0.00	0.00	13.52	0.00
Acer rubrum	2.62	113.40	2.49	46.11	5.08	127.92
Acer saccharum	6.30	57.11	38.68	452.00	18.60	317.58
Betula alleghaniensis	0.54	0.00	0.41	0.00	6.76	0.00
Betula papyrifera	1.04	12.38	2.92	11.44	18.60	284.12
Betula species	0.00	0.00	1.25	0.00	16.92	0.00
Carya species	0.00	0.00	0.00	4.39	0.00	0.00
Fagus grandifolia	15.22	1.45	60.37	29.64	13.52	4.93
Fraxinus americana	0.54	10.66	0.41	57.72	3.40	37.06
Fraxinus nigra	0.00	0.00	3.33	0.00	5.08	0.00
Juniperus virginiana	0.00	0.00	0.00	0.00	0.00	0.00
Larix laricina	0.00	0.00	0.00	0.00	8.44	0.00
Ostrya virginiana	0.00	2.98	0.41	16.56	0.00	0.00
Picea species	1.04	0.00	0.00	0.00	1.68	0.00
Pinus banksiana	112.43	0.00	4.15	0.00	32.16	0.00
Pinus resinosa	91.41	0.45	17.47	0.00	22.00	0.00
Pinus strobus	32.06	13.37	23.72	0.00	33.85	14.80
Populus species	16.80	184.61	7.07	93.58	57.53	13.60
Prunus serotina	0.00	5.42	0.00	0.55	0.00	0.00
Quercus alba	5.26	147.47	1.66	0.00	1.68	11.07
Quercus rubra-velutina-ellipsoidalis	16.80	344.45	9.15	59.83	5.08	193.39
Thuja occidentalis	1.58	0.00	3.33	0.00	30.45	0.00
Tilia americana	0.00	9.85	4.99	142.98	0.00	143.93
Tsuga canadensis	11.03	0.00	57.41	0.00	64.36	0.00
Ulmus species	0.00	0.00	2.08	0.00	6.76	55.00
Totals	315.20	903.60	241.30	914.80	365.50	1203.40

[1] Where PS and PD indicate presettlement and present-day, respectively.
[2] trees/ha

Table 23: Basal area of tree species (trees ≥ 10 cm d.b.h.) by community type in the pre-European settlement and present-day forest.

Tree Species	Dry-Mesic PS[1]	Dry-Mesic PD	Mesic PS	Mesic PD	Wet-Mesic PS	Wet-Mesic PD
Abies balsamea	0.02[2]	0.00	0.00	0.00	0.39	0.00
Acer rubrum	0.06	2.05	0.14	1.16	0.24	3.83
Acer saccharum	0.53	1.03	3.60	10.33	1.34	9.50
Betula alleghaniensis	0.02	0.00	0.10	0.00	0.30	0.00
Betula papyrifera	0.07	0.23	0.11	0.36	1.60	8.50
Betula species	0.00	0.00	0.10	0.00	0.87	0.00
Carya species	0.00	0.00	0.00	0.13	0.00	0.00
Fagus grandifolia	0.68	0.07	3.78	1.10	0.95	0.15
Fraxinus americana	0.03	0.41	0.08	2.38	0.14	1.11
Fraxinus nigra	0.00	0.00	0.26	0.00	0.83	0.00
Juniperus virginiana	0.00	0.00	0.00	0.00	0.00	0.00
Larix laricina	0.00	0.00	0.00	0.00	0.28	0.00
Ostrya virginiana	0.00	0.11	0.01	0.21	0.00	0.00
Picea species	0.10	0.00	0.00	0.00	0.09	0.00
Pinus banksiana	3.70	0.00	0.14	0.00	0.57	0.00
Pinus resinosa	16.68	0.07	3.06	0.00	5.78	0.00
Pinus strobus	6.34	0.16	5.03	0.00	7.03	0.44
Populus species	0.58	6.66	0.22	4.82	2.20	0.41
Prunus serotina	0.00	0.07	0.00	0.05	0.00	0.00
Quercus alba	0.18	4.50	0.01	0.00	0.01	0.33
Quercus rubra-velutina-ellipsoidalis	0.66	11.03	0.93	3.80	0.61	5.79
Thuja occidentalis	0.11	0.00	0.29	0.00	2.92	0.00
Tilia americana	0.00	0.30	0.53	6.75	0.00	4.31
Tsuga canadensis	1.15	0.00	6.86	0.00	9.48	0.00
Ulmus species	0.00	0.00	0.13	0.00	0.18	1.65
Totals	30.90	26.70	25.40	31.10	35.80	36.00

[1] Where PS and PD indicate presettlement and present-day, respectively.

[2] basal area (m^2/ha)

APPENDIX C

Present-day communities: structure and composition

Table 24: Composition of present-day forests (trees ≥ 10 cm d.b.h.) on dry-mesic sites.

Tree species	Percent Relative Density	Percent Relative Dominance	IV	Density	Dominance
Quercus rubra-velutina-ellipsoidalis	38.12	41.31	39.72[1]	344.45[2]	11.03[3]
Populus grandidentata	20.43	24.96	22.70	184.61	6.66
Quercus alba	16.32	16.87	16.60	147.47	4.50
Acer rubrum	12.55	7.66	10.11	113.40	2.05
Acer saccharum	6.32	3.87	5.10	57.11	1.03
Fraxinus americana	1.18	1.55	1.37	10.66	0.41
Betula papyrifera	1.37	0.86	1.12	12.38	0.23
Tilia americana	1.09	1.11	1.10	9.85	0.30
Pinus strobus	1.48	0.60	1.04	13.37	0.16
Prunus serotina	0.60	0.26	0.43	5.42	0.07
Ostrya virginiana	0.33	0.43	0.38	2.98	0.11
Fagus grandifolia	0.16	0.26	0.21	1.45	0.07
Pinus resinosa	0.05	0.26	0.16	0.45	0.07
Totals	100.00	100.00	100.00	903.60	26.70

[1] Importance Value = (relative density + relative dominance)/2 * 100

[2] trees/ha

[3] basal area (m^2/ha)

Table 25: Composition of present-day forests (trees ≥ 10 cm d.b.h.) on mesic sites.

Tree species	Percent Relative Density	Percent Relative Dominance	IV	Density	Dominance
Acer saccharum	49.41	33.21	41.31	452.00	10.33
Tilia americana	15.63	21.72	18.68	142.98	6.75
Populus grandidentata	10.23	15.50	12.87	93.58	4.82
Quercus rubra-velutina-ellipsoidalis	6.54	12.23	9.39	59.83	3.80
Fraxinus americana	6.31	7.64	6.98	57.72	2.38
Acer rubrum	5.04	3.74	4.39	46.11	1.16
Fagus grandifolia	3.24	3.53	3.39	29.64	1.10
Ostrya virginiana	1.81	0.69	1.25	16.56	0.21
Betula papyrifera	1.25	1.16	1.21	11.44	0.36
Carya species	0.48	0.42	0.45	4.39	0.13
Prunus serotina	0.06	0.16	0.11	0.55	0.05
Totals	100.00	100.00	100.00	914.80	31.10

[1] Importance Value = (relative density + relative dominance)/2 * 100

[2] trees/ha

[3] basal area (m^2/ha)

Table 26: Composition of present-day forests (trees ≥ 10 cm d.b.h.) on wet-mesic sites.

Tree species	Percent Relative Density	Percent Relative Dominance	IV	Density	Dominance
Acer saccharum	26.39	24.72	25.56[1]	317.58[2]	9.50[3]
Betula papyrifera	23.61	16.75	20.18	284.12	8.50
Quercus rubra-velutina-ellipsoidalis	16.07	19.94	18.01	193.39	5.79
Tilia americana	11.96	18.50	15.23	143.93	4.31
Acer rubrum	10.63	8.77	9.70	127.92	3.83
Fraxinus americana	3.08	4.78	3.93	37.06	1.11
Ulmus species	4.57	1.59	3.08	55.00	1.65
Populus grandidentata	1.13	2.07	1.60	13.60	0.41
Quercus alba	0.92	1.59	1.26	11.07	0.33
Pinus strobus	1.23	0.80	1.02	14.80	0.44
Fagus grandifolia	0.41	0.49	0.45	4.93	0.15
Totals	100.00	100.00	100.00	1203.40	36.00

[1] Importance Value = (relative density + relative dominance)/2 * 100

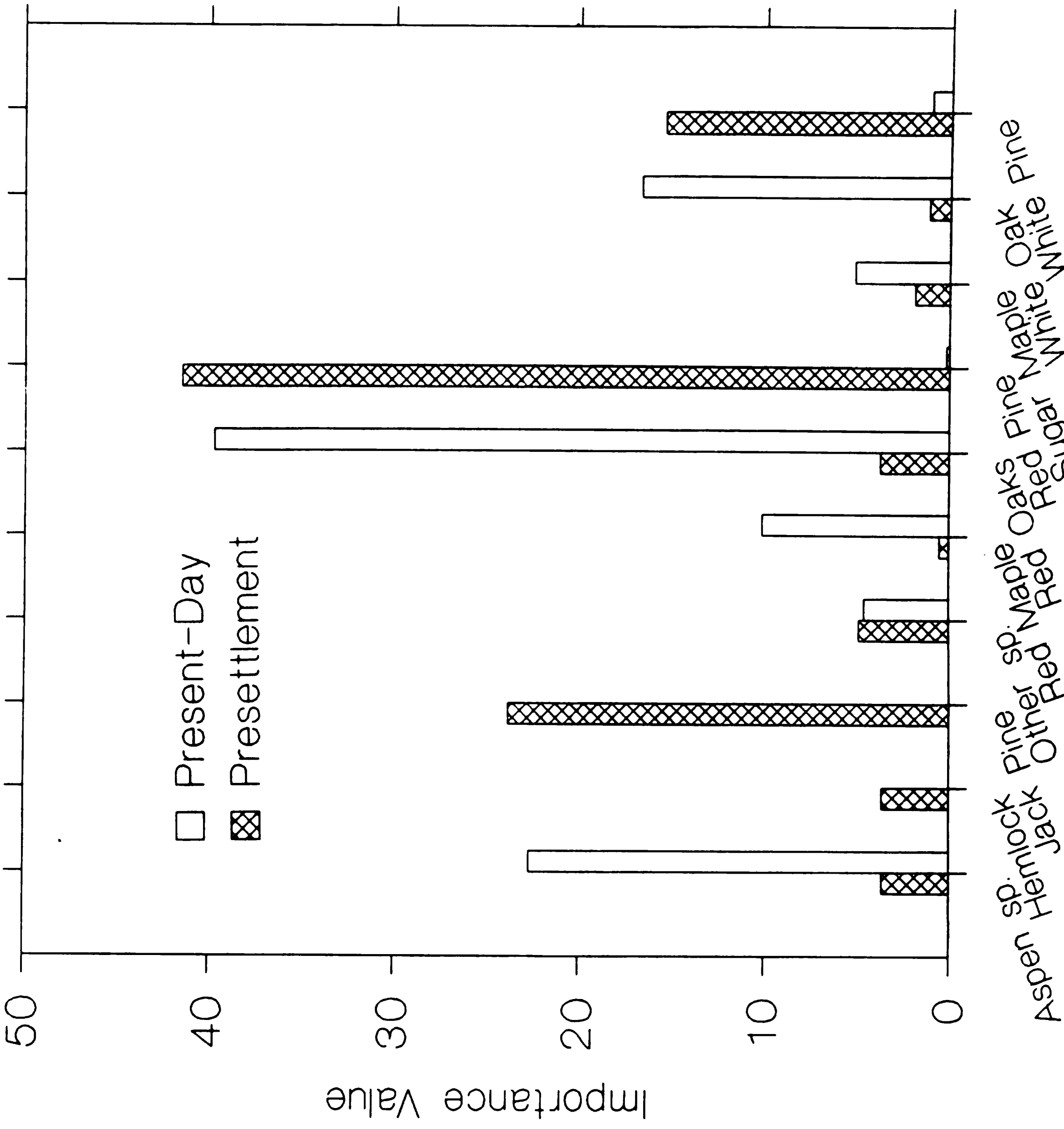
[2] trees/ha

[3] basal area (m^2/ha)

APPENDIX D

Bar Graphs of Compositional Changes Since Euro-American Settlement

Figure 26: Importance values of pre-European settlement and present-day tree species on dry-mesic sites.



Present-Day
Presettlement
Importance Value
0
10
20
30
40
50
Aspen sp.
Hemlock
Jack Pine
Other Pine sp.
Red Maple
Red Oaks
Red Pine
Sugar Maple
White Oak
White Pine

Figure 27: Importance values of pre-European settlement and present-day tree species on mesic sites.

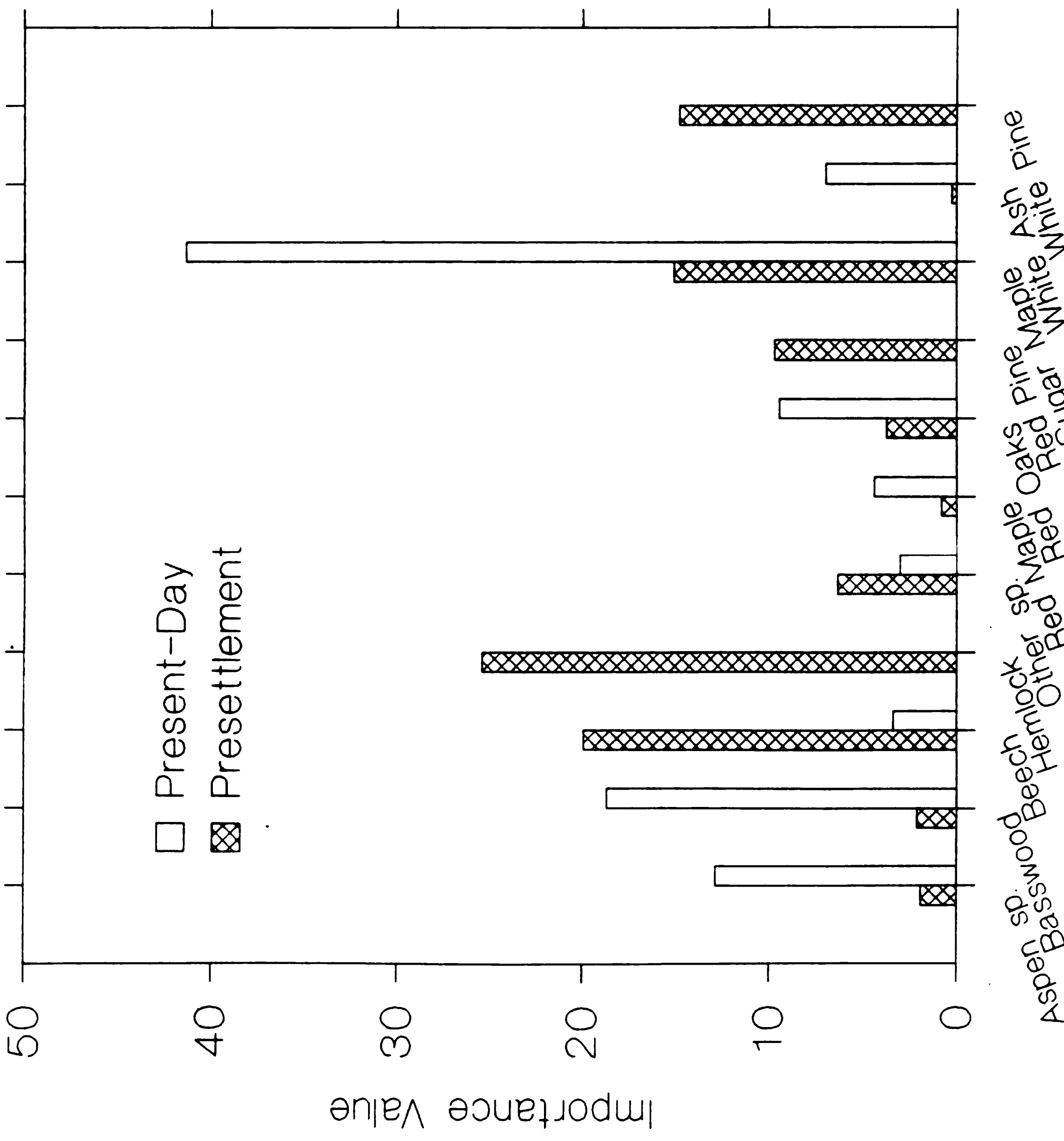
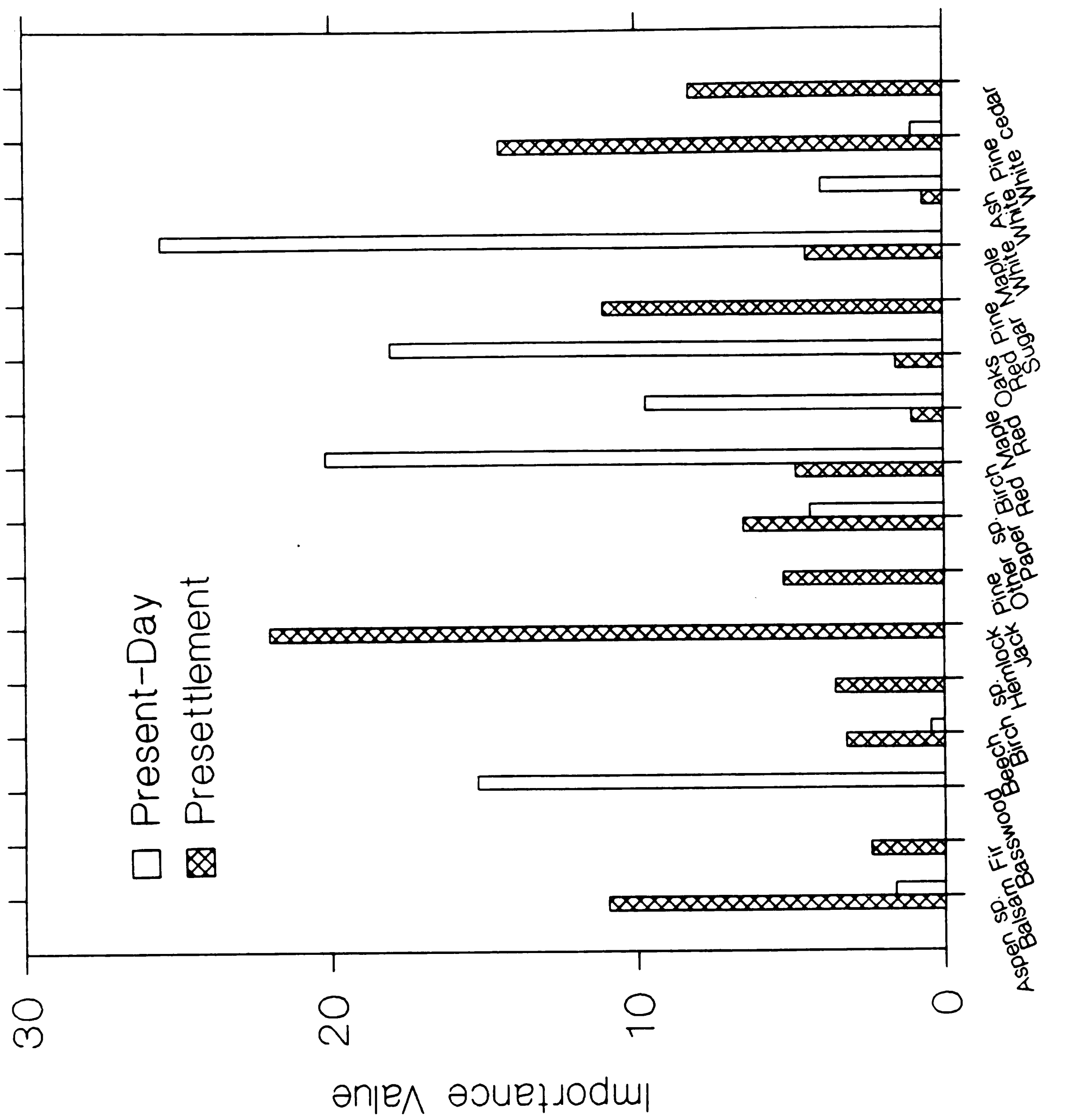

Present-Day
Presettlement
Importance Value
0
10
20
30
40
50
Aspen sp.
Basswood
Beech
Hemlock
Other sp.
Red Maple
Red Oaks
Red Pine
Sugar Maple
White Ash
White Pine

Figure 28: Importance values of pre-European settlement and present-day tree species on wet-mesic sites.


Present-Day
Presettlement
Importance Value
0
10
20
30
Aspen sp.
Balsam Fir
Basswood
Beech
Birch sp.
Hemlock
Jack Pine
Other Pine sp.
Paper Birch
Red Maple
Red Oaks
Red Pine
Sugar Maple
White Ash
White Pine
White cedar

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Pocket has: 2 maps

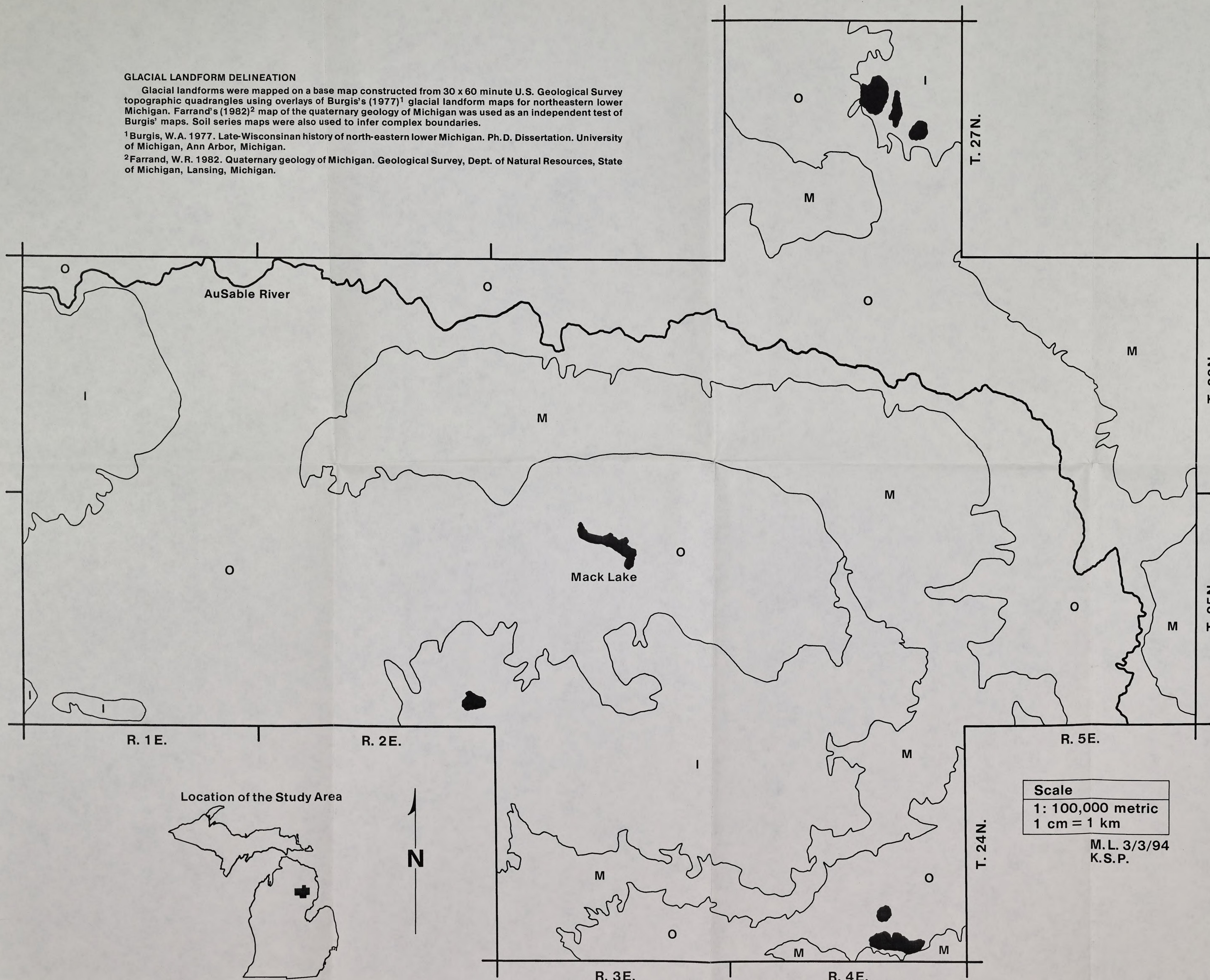
Glacial Landforms of the High Plains Region of the Huron National Forest (After Burgis 1977)

GLACIAL LANDFORM DELINEATION

Glacial landforms were mapped on a base map constructed from 30 x 60 minute U.S. Geological Survey topographic quadrangles using overlays of Burgis's (1977)[1] glacial landform maps for northeastern lower Michigan. Farrand's (1982)[2] map of the quaternary geology of Michigan was used as an independent test of Burgis' maps. Soil series maps were also used to infer complex boundaries.

[1] Burgis, W.A. 1977. Late-Wisconsinan history of north-eastern lower Michigan. Ph.D. Dissertation. University of Michigan, Ann Arbor, Michigan.

[2] Farrand, W.R. 1982. Quaternary geology of Michigan. Geological Survey, Dept. of Natural Resources, State of Michigan, Lansing, Michigan.



GLACIAL LANDFORM TYPES

Type O: Glacial outwash sand and gravel and postglacial alluvium comprise this type. This type occurs as fluvial terraces along current and abandoned drainage-ways, as fans and sheets flanking end moraines, and as deltas along glacial lake margins. Glacial debris here is usually well sorted and well-stratified. Textures are predominantly sand, but significant areas of muck and peat and shallow organic soils occur. Topographically these areas are nearly level with only small kettle depressions interrupting the planar topography of this landscape. Soil drainage classes here tend to fall into either of the two extremes: excessively drained or poorly drained.

Type M: End and ground moraines comprise this type. The bulk of these areas are end moraines which topographically occur as linear belts of hummocky relief marking former stillstands of the ice-sheet margin. Texturally these areas are heterogeneous with loamy sands, sandy loams, and loams predominating. Small areas of muck and peat occur in kettle features embedded in the morainal complex. Glacial debris here is usually non-sorted, but small areas of well-sorted fluvial deposits occur. Soils are mainly well drained to moderately well-drained.

Type I: Ice-contact outwash sand and gravel comprise this type. Topographically this type is usually rugged, with short, steep hills, and abrupt depressions. The type can be subdivided into component landforms: kames, eskers, interlobate tracts, proglacial outwash, sandy till, and kettle holes. Textures here are predominantly sand and loamy sand with considerable cobbles and gravel. Glacial debris is often poorly sorted, non-stratified, and has slump and deformational features. Soil texture can be quite heterogeneous over short distances. Soils are somewhat excessively drained and well drained.

Pre-European Settlement Forest Cover Types of the High Plains Region of the Huron National Forest

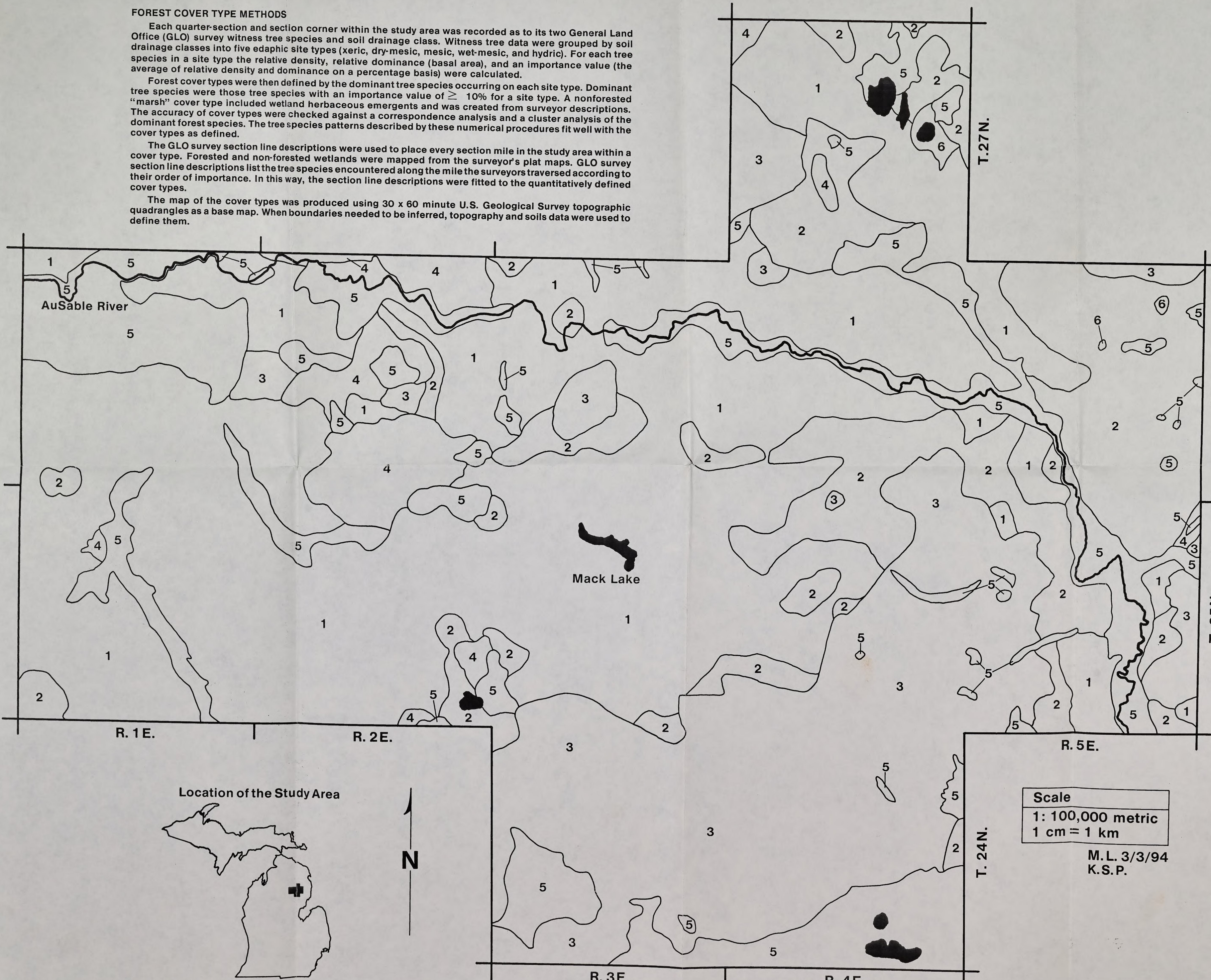
FOREST COVER TYPE METHODS

Each quarter-section and section corner within the study area was recorded as to its two General Land Office (GLO) survey witness tree species and soil drainage class. Witness tree data were grouped by soil drainage classes into five edaphic site types (xeric, dry-mesic, mesic, wet-mesic, and hydric). For each tree species in a site type the relative density, relative dominance (basal area), and an importance value (the average of relative density and dominance on a percentage basis) were calculated.

Forest cover types were then defined by the dominant tree species occurring on each site type. Dominant tree species were those tree species with an importance value of $\geq$ 10% for a site type. A nonforested "marsh" cover type included wetland herbaceous emergents and was created from surveyor descriptions. The accuracy of cover types were checked against a correspondence analysis and a cluster analysis of the dominant forest species. The tree species patterns described by these numerical procedures fit well with the cover types as defined.

The GLO survey section line descriptions were used to place every section mile in the study area within a cover type. Forested and non-forested wetlands were mapped from the surveyor's plat maps. GLO survey section line descriptions list the tree species encountered along the mile the surveyors traversed according to their order of importance. In this way, the section line descriptions were fitted to the quantitatively defined cover types.

The map of the cover types was produced using 30 x 60 minute U.S. Geological Survey topographic quadrangles as a base map. When boundaries needed to be inferred, topography and soils data were used to define them.



FOREST COVER TYPE DESCRIPTIONS

Type 1: Jack Pine-Red Pine-White Pine

Jack pine, red pine, and white pine together accounted for $\geq$ 91% of the importance value on these sites. However, jack pine truly dominated this type with an importance value of 52%. Associates (those species which had an importance value between 1 and 9%) of this type included: species of the red oak complex, aspen species, and hemlock. This type occurred on xeric sites with low soil moisture and nutrient availability. These areas were dominated by sandy soils on topographically level glacial outwash plains and drainageways. Witness tree density and basal area were low on these sites, being approximately 214 trees/ha and 13.2 m^2/ha, respectively. Average witness tree size was about 23.0-23.8 cm.

Type 2: Red Pine-Jack Pine-White Pine

Red pine, jack pine, and white pine together accounted for $\geq$ 80% of the importance value on these sites. Associates of this type included: species of the red oak complex, hemlock, aspen species, beech, sugar maple, and white oak. This type occurred on dry-mesic sites with moderately low soil moisture and nutrient availability. Physiographically this type occurred on coarse-textured end-moraines; areas of broad rolling hills. Witness tree density and basal area were approximately 315 trees/ha and 30.9 m^2/ha, respectively. Average witness tree size was about 29.0-30.6 cm.

Type 3: Hemlock-Beech-Sugar Maple-White Pine

Hemlock, beech, sugar maple, and white pine together accounted for $\geq$ 75% of the importance value on these sites. Associates of this type included: red pine, species of the red oak complex, basswood, aspen species, white cedar, black ash, and jack pine. This type occurred on mesic sites with moderate levels of soil moisture and nutrient availability. These sites were found on end moraines, ground moraines, and ice-disintegration features. Topographically this type occupied areas of short, steep hills and small hollows. Soil textures included loamy sandy, sandy loams, and loams. Witness tree density and basal area were approximately 241 trees/ha and 25.4 m^2/ha, respectively. Average witness tree size was about 32.1-33.5 cm.

Type 4: Hemlock-White Pine-Red Pine-Aspen Species

Hemlock, white pine, red pine, and aspen species together accounted for $\geq$ 59% of the importance value on these sites. Associates of this type included: white cedar, jack pine, paper birch, sugar maple, birch species, beech, balsam fir, black ash, tamarack, species of the red oak complex, yellow birch, elm species, and red maple. These sites were wet-mesic. Physiographically this type occurred on small, wet, sandy flats where morainal complexes and ice-contact features of substantial relief abutted outwash plains. Witness tree density and basal area were approximately 366 trees/ha and 35.8 m^2/ha, respectively. Average witness tree size was about 29.1-31.5 cm.

Type 5: White Cedar-Tamarack

White cedar and tamarack together accounted for $\geq$ 58% of the importance value on these sites. Associates of this type included: jack pine, spruce species, aspen species, balsam fir, black ash, birch species, paper birch, white pine, red maple, and hemlock. These sites were hydric. Topographically they occurred predominantly as poorly drained flats on outwash plains and as kettle features in all landforms. Muck and peat and thin organic deposits over sands dominated the soils of these sites. Nutrient availability varied. Witness tree density and basal area were approximately 366 trees/ha and 18.3 m^2/ha, respectively. Average witness tree size was about 22.14-23.46 cm.

Type 6: Marsh

This cover type was derived from surveyor descriptions of non-forested wetlands dominated by herbaceous emergents. The type occurred sporadically in small kettle features and surrounding small lakes in all landform types.