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A Comparison of Presettlement and Present-day Forests in Northeastern Lower Michigan

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ABSTRACT.—General Land Office survey records of 1838–1846 were used to reconstruct the pre-European settlement vegetation along a soil moisture gradient in the Huron National Forest of northeastern lower Michigan. These data were compared to current forest data. Jack pine (*Pinus banksiana*), red pine (*P. resinosa*) and white pine (*P. strobus*) dominated fire-prone presettlement dry and dry-mesic sites on coarse-textured soils of glacial outwash plains and moraines. Hemlock (*Tsuga canadensis*), beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*) and white pine were most important on presettlement mesic sites on medium-textured soils of moraines and kame and kettle topography. Presettlement wet-mesic sites were dominated by hemlock, white pine and aspen (*Populus* spp.). White cedar (*Thuja occidentalis*) and tamarack (*Larix laricina*) dominated presettlement wet sites on organic soils of outwash plains. Important presettlement forest types included: jack pine (41%), mixed conifer-northern hardwood (22%), lowland conifer (15%) and mixed pine (14%). Tree species composition has substantially changed on dry-mesic to wet-mesic sites over the last 150 y. White pine and hemlock have significantly declined in abundance. Oak (*Quercus* spp.), sugar maple and aspen currently dominate dry-mesic to wet-mesic sites. Important current forest types include: jack pine (32%), aspen–white birch (*Betula papyrifera*; 16%), oak (16%) and northern hardwood (8%). Today's forests have smaller trees and higher tree densities than forests in the presettlement era. Widespread logging, altered fire regimes and other anthropogenic disturbances since European settlement have interacted with physical factors to produce today's forests.

INTRODUCTION

The vegetation of Michigan and the eastern United States was changed, often substantially, by European settlement (Whitney, 1994). A knowledge of forest conditions in the historic past may prove helpful to today's natural resource managers, particularly in regions without many primary forest remnants to act as baseline sites or controls (Frelich, 1995). The value of reconstructing the presettlement vegetation of a region lies in delimiting the range of vegetation types and disturbance regimes possible to a site (Sprugel, 1991). Bourdo (1956) and Curtis (1959) validated the use of General Land Office (GLO) survey data in vegetation history studies. The GLO data can be used to develop a description of natural vegetation patterns and dynamics (Grimm, 1984). Within the Great Lakes region detailed presettlement vegetation maps have been completed for Michigan (Comer *et al.*, 1995), Minnesota (Marschner, 1974) and Wisconsin (Finley, 1976).

In Michigan, several recent papers have examined the presettlement forest using GLO survey notes (Whitney, 1986, 1987; Palik and Pregitzer, 1992; Barrett *et al.*, 1995; Comer *et al.*, 1995; Van Deelen *et al.*, 1996; Zhang *et al.*, 2000). However, few studies have focused directly on a public land management area within a specific regional landscape nor have they

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included an analysis of forest structure data. This study examines the patterns of forest vegetation along a soil moisture gradient in the Huron National Forest of northeastern lower Michigan before European settlement and how these patterns subsequently changed. The objectives were to: (1) examine the physical factors controlling presettlement vegetation patterns; (2) reconstruct the composition, structure and disturbance regimes of presettlement forests; and (3) examine the changes in composition, structure and natural disturbance regimes between presettlement and present-day forests.

STUDY AREA

The study area covers 121,212 ha of the Huron National Forest in northeastern lower Michigan (Lat 44°25′ to 44°46′N, Long 83°46′ to 84°23′W) within the high plains subsection, an ecological unit with a homogeneous macroclimate and similar major physiographic features, as described by Albert (1995) within a regional landscape ecosystem classification for the upper midwest. The climate is characterized by a 115 d growing season, mean total precipitation of 79 cm/y and an annual mean temperature of 6.7 C. The surficial geology of the study area is the result primarily of glacial action and subsequent postglacial erosion. The most recent glaciation was 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 y ago molded the study area's landscape (Burgis, 1977). By 11,800 y ago most of the major drainages in the study area had been developed. The area drains primarily into the Au Sable River, which discharges into Lake Huron.

Glacial landforms of the study area (Burgis, 1977; Farrand, 1982) include outwash plains (58%), moraines (26%) and ice-contact topography (16%). Outwash plains occur as terraces made of well-sorted, extremely well-drained sands left by braided streams during glacial ablation. Ice-contact topography is a mosaic of glacial kettle depressions and kames (Farrand, 1982). This topography is the result of the disintegration of stagnant glacial ice and is characterized by the presence of closed depressions or kettles (Host *et al.*, 1988). These mainly hilly areas have medium-textured soils (Burgis, 1977; Padley, 1989). Moraines include ridgelike accumulations of glacial drift deposited at the margin of an active glacier (end moraines) and a gently rolling topography formed by glacial drift deposited under an active glacier (ground moraines; Farrand, 1982). In the study area moraines have a mix of soil textures from coarse to fine (Burgis, 1977; Padley, 1989). The major soil orders represented in the study area include Alfisols (17%), Entisols (57%), Histosols (9%) and Spodosols (17%; Veatch *et al.*, 1936, 1954; Johnson, 1990). Coarse-textured soils (sand, loamy sand, sandy loam) with rapid internal drainage dominate the study area.

Between 3000-400 y ago the Woodland Indian Culture hunted within the Au Sable River basin and the Ottawa tribe of Native Americans lived in the area at low population densities from the beginning of the 18th Century until 1836 (Lovis *et al.*, 1978). Federal land surveyors surveyed the study area between 1838–1846 according to the methods of the GLO in place at that time (White, 1984). Homesteaders and lumber companies soon followed. Heavy logging and severe wildfires occurred in the study area between 1850–1920 (Lovis *et al.*, 1978) in a pattern similar throughout northern lower Michigan (Karamanski, 1989) known as the "logging era." The Huron National Forest was established between 1909–1933 and wholesale fire control began in the 1930s along with widespread tree planting by the Civilian Conservation Corps (Lovis *et al.*, 1978).

METHODS

GLO survey data.—Burgis' (1977) glacial landform map was used in conjunction with 1:100,000 scale topographic maps to place every GLO survey corner within a glacial

TABLE 1.—Soil and landform characteristics of the study area

Soil moisture condition	Soil drainage class	% of study area	Soil texture	Predominant landform	Soil order
Dry	Excessive	44	Sand	Outwash plains	Entisols
Dry-mesic	Somewhat excessive	20	Sand, loamy sand	Moraines, ice-contact topography	Spodosols, Entisols
Mesic	Moderately well to well	20	Sandy loam, loam	Ice-contact topography, moraines	Alfisols
Wet-mesic	Poor to somewhat poor	7	Silty clay loam, mucky sand	Outwash plains, moraines	Alfisols, Histisols
Wet	Very poor	9	Muck and peat	Outwash plains	Histisols

landform type. Soil type data were derived from the soil surveys of Oscoda (Veatch *et al.*, 1936), Alcona (Veatch *et al.*, 1954) and Ogemaw (Johnson, 1990) counties. The early soil types were updated to their modern soil series correlates. Each GLO survey corner was scored as to its modern soil series. At each GLO survey corner surveyors recorded the two witness trees by species, diameter and the distances of the trees to the corner point. Surveyors established 1513 survey corners in the study area at which 2972 witness trees were recorded. This is an adequate sample size for reconstructing presettlement vegetation (Almendinger, 1996). Witness trees were identified to the species or genus level by Bourdo's (1954) list of names used for trees by Michigan surveyors. Surveyors did not differentiate between trembling aspen (*Populus tremuloides*) and big-toothed aspen (*P. grandidentata*) species, so both were combined in our database as aspen (*Populus* spp.). Surveyors did not separate black spruce (*Picea mariana*) from white spruce (*P. glauca*), so both were combined as spruce (*Picea* spp.). Surveyors also did not differentiate between northern red oak (*Quercus rubra*), black oak (*Q. velutina*) and Hill's oak (*Q. ellipsoidalis*), so these were combined as oak (*Quercus* spp; Voss 1985).

Binary discriminant analysis was used to examine witness tree species–physical factor patterns. Only witness tree species with a sample size ≥50 trees were used. Binary discriminant analysis directly tested species–substrate relations using presence/absence data of witness tree species grouped by various physiographic and soil factors (Strahler, 1978). Because 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), the GLO survey corners were grouped by soil drainage class. Soil drainage is a crude index of soil moisture and texture (Soil Survey Staff, 1999). In effect, GLO witness tree data were located along a soil moisture gradient. This soil moisture gradient was divided into five conditions: dry, dry-mesic, mesic, wet-mesic and wet sites (Curtis, 1959). Each soil moisture condition (site) was associated with a range of soil and landform characteristics (Table 1).

For each site, relative density, relative dominance and an importance value (IV, the sum of relative density and relative dominance divided by two; Mueller-Dombois and Ellenberg, 1974) were calculated for the witness tree species present. Dominant tree species were defined as those which singly, or combined, had an IV ≥50%. Associated species were considered as those with an IV ≥10%. Compositional similarity values (2W/a + b) using species IVs were calculated between presettlement sites; where a is the sum of the IVs in one site, b is the sum of the IVs for the other site and W is the sum of the smaller of the two IVs of the species that are common to both sites (Bray and Curtis, 1957; Fralish *et al.*, 1991).

A modification of the point-quarter method (Cottam and Curtis, 1956; Fralish *et al.*, 1991) using the median distance (Kline and Cottam, 1979) was used to estimate tree density for each site. In this formulation the median witness tree distance (m) to the corner post was determined using both the nearest tree (Q_1) and second tree (Q_2) distances for a particular site. The median witness tree distance = $0.65\sqrt{M}$, where M is the mean area per tree (m^2). Dividing 10,000 by M gave an estimate of the density (trees/ha). For each site, witness tree diameters were converted to basal area (m^2) and the average of these basal areas was determined. Multiplying the mean basal area per tree by density gave an estimate of the basal area (m^2/ha) for each site. Only witness trees >10 cm were used in these calculations. Within a site, multiplying a species' relative density and relative dominance by density (trees/ha) and basal area (m^2/ha), respectively, gave estimates of a species' actual density and basal area. Mean witness tree diameters by site were compared with ANOVA and Tukey's mean separation procedure (Zar, 1984). Surveyors apparently introduced bias against certain sizes and species of trees (Grimm, 1984), such that reconstruction of presettlement forest structure data must be viewed with caution.

Presettlement forest types (Spurr and Barnes, 1998) were identified based upon the dominant species for each site. These forest types were then mapped based upon the surveyors' section line descriptions in conjunction with maps of the distribution of witness tree species across the study area, soils and landforms. Lake and marsh cover types were also mapped based upon surveyor descriptions. The map was produced using 1:100,000 scale topographic quadrangles for a base map and a minimum polygon size of 9 ha. When boundaries needed to be inferred, topography and soils data were used to define them.

Disturbance regimes are now commonly recognized as an important factor in influencing vegetation patterns (Pickett and White, 1985). The disturbance return interval (the length of time required for a disturbance type, *e.g.*, fire, to disturb an area equal to the area of forest under consideration; Lorimer, 1977; Canham and Loucks, 1984; Whitney, 1986; Frelich, 1995; Zhang *et al.*, 1999) was used as a measure of the disturbance regime. Along each section line they traveled, the GLO surveyors recorded the evidence of moderate to severe (crown) intensity fires and large windthrows (>1 ha; Canham and Loucks, 1984). This information was used to determine the total distance of section lines by forest type with evidence of fire or windthrow. Dividing the percent of a forest type affected by a disturbance (fire or windthrow) by 15 y (the estimated number of years the burn or windthrow was still visible to the surveyors; Lorimer, 1977; Whitney, 1986) gave the average annual percent of a forest type affected by a disturbance. Lastly, the disturbance return interval was estimated for each forest type by dividing 100 by the average annual percent of a forest type affected by a disturbance. The same procedure was also applied to the study area as a whole.

The size structure of the dominant witness tree species were analyzed by calculating their mean diameters; comparing these with an ANOVA and Tukey's mean separation procedure (Zar, 1984); and graphing the species diameter frequency distributions. Dominant witness tree species were categorized by diameter size class (Leatherberry and Spencer, 1996; Tyrrell *et al.*, 1998) as being small (10–29 cm), medium (30–49 cm), large (50–69 cm) and very large (>70 cm). Only witness tree species with a sample size of >50 trees were used. However, surveyors were often biased against trees <25 cm diameter (Bourdo, 1956) and results must be interpreted with this in mind.

Present-day forest data.—Present-day forest stand data came from 29 stands sampled within the study area for the development of an ecological classification system (ECS) of the Huron National Forest (Michigan State University, Forestry Department data file). All stands selected were well-stocked, naturally regenerated, >1 ha and free from recent disturbance. Trees were defined as stems >10 cm diameter. Stand ages ranged from 60–90 y. The ECS

TABLE 2.—Presettlement tree composition of the study area. Relative density, relative dominance and importance values (rel. dens. + rel. dom. ÷ 2) derived from witness tree data

Common name	Scientific name	No. trees	Rel. dens.	Rel. dom.	I.V.
Jack pine	*Pinus banksiana*	1165	39.2	13.8	26.5
Red pine	*Pinus resinosa*	443	14.9	32.2	23.6
White pine	*Pinus strobus*	199	6.7	17.8	12.2
Hemlock	*Tsuga canadensis*	217	7.3	11.0	9.2
Beech	*Fagus grandifolia*	226	7.6	4.7	6.1
Sugar maple	*Acer saccharum*	158	5.3	4.6	5.0
White cedar	*Thuja occidentalis*	116	3.9	4.0	3.9
Oak	*Quercus rubra*, *Quercus velutina* or *Quercus ellipsoidalis*	101	3.4	1.9	2.6
Tamarack	*Larix laricina*	68	2.3	2.4	2.3
Aspen	*Populus grandidentata* or *Populus tremuloides*	59	2.0	2.4	2.2
White birch	*Betula papyrifera*	33	1.1	0.9	1.0
Birch	*Betula* spp.	27	0.9	0.7	0.8
Spruce	Mainly *Picea mariana*, some *Picea glauca*	24	0.8	0.7	0.7
Black ash	*Fraxinus nigra*	21	0.7	0.8	0.7
Balsam fir	*Abies balsamea*	27	0.9	0.4	0.7
Red maple	*Acer rubrum*	21	0.7	0.4	0.6
Yellow birch	*Betula alleghaniensis*	21	0.7	0.2	0.5
Basswood	*Tilia americana*	12	0.4	0.5	0.5
White oak	*Quercus alba*	18	0.6	0.2	0.4
Elm	*Ulmus* spp.	9	0.3	0.2	0.3
White ash	*Fraxinus americana*	3	0.1	0.1	0.1
Other species[a]		6	0.2	0.1	0.1
Totals		2972	100.0	100.0	100.0

[a] Includes: *Carya* spp., *Ostrya virginiana* and *Prunus serotina*

sample stands failed to represent the study area's dry and wet sites, precluding site-specific then-and-now comparisons for these soil moisture conditions. However, broad comparisons of forest changes on dry and wet sites were made based upon forest inventory reports in the literature (Veatch *et al.*, 1936; Simard *et al.*, 1983; Leatherberry and Spencer, 1996) that covered portions of the study area.

ECS stand data were pooled by soil drainage class to permit site-specific comparisons between current and presettlement forests. Tree species composition of presettlement forests were compared to today's with a similarity index (Bray and Curtis, 1957; Fralish *et al.*, 1991). Changes in land cover types on 85% of the study area were assessed using the presettlement forest type map and data from the Michigan Resource Information System (MIRIS) database (Michigan Department of Natural Resources, 1990a, b). MIRIS land cover data are derived from photo-interpretation and field checking of 1:24,000 scale color-infrared and black-and-white aerial photographs. These data were not available for that part of the study area in Alcona County.

RESULTS AND DISCUSSION

Composition and structure across the presettlement forest.—Jack and red pines (*Pinus banksiana* and *P. resinosa*) dominated the presettlement study area with a combined IV of 50.1 (Table 2).

TABLE 3.—Matrix of percent compositional similarity values between presettlement forests by soil moisture condition. Similarity values calculated based upon tree species IVs

	Dry	Dry-mesic	Mesic	Wet-mesic
Dry	—			
Dry-mesic	71.5	—		
Mesic	29.5	42.0	—	
Wet-mesic	34.9	46.7	64.5	—
Wet	15.8	17.2	28.8	38.3

Sandy soil textures and rapidly drained soils account for 75% and 64%, respectively, of the study area's soils (Table 1). GLO surveyors' section line descriptions indicated that about 6% of the study area was burned-over. This combination of droughty infertile soils and a frequent fire regime resulted in a preponderance of jack and red pines in the presettlement forest. Mesophytic species, beech (*Fagus grandifolia*), hemlock (*Tsuga canadensis*), white pine (*Pinus strobus*) and sugar maple (*Acer saccharum*) had a combined IV of 32.5 (Table 2), in accordance with the extent of loamy (16%) and moderately drained (20%) soils (Table 1). Wetland adapted tamarack (*Larix laricina*) and white cedar (*Thuja occidentalis*) had a combined IV of 6.2, corresponding with the extent of poorly drained muck and peat soils (9%; Table 1).

Separating witness tree data by sites based upon soil drainage classes produced readily identifiable compositional differences. The percent compositional similarity between sites ranged from 15.8–71.5% (Table 3). Stands with an index of similarity > 75% are typically considered to be compositionally equivalent (Mueller-Dombois and Ellenberg, 1974). The mean percent compositional similarity between sites was 38.9%. However, dry and dry-mesic and mesic and wet-mesic sites had a moderately high degree of compositional similarity, 71.5% and 64.5%, respectively (Table 3).

Across the presettlement study area, jack pine, tamarack, beech and white cedar stems were concentrated in small diameter size classes (Fig. 1), with mean tree diameters of 18, 21, 26 and 27 cm, respectively (Table 4). Sugar maple, hemlock, red and white pine stems mainly occurred in medium diameter size classes (Fig. 1), with mean tree diameters of 31, 36, 44 and 46 cm, respectively (Table 4). White and red pine, hemlock and sugar maple all had over 10% of their stem densities in large to very large diameter size classes (Fig. 1).

Dry sites.—Jack pine dominated presettlement dry sites with red and white pine associates (Table 5). Jack pine was significantly ($P < 0.05$) associated with sandy, excessively drained soils on outwash plains (Table 6). Presettlement dry sites had low mean tree density, basal area and diameter (Table 7). Jack pine had the greatest density and red pine the largest basal area (Table 8). The low density and basal area of presettlement dry sites matches current descriptions of jack pine barrens or open woodlands (Pregitzer and Saunders, 1999). The jack pine forest type covered 41% (Table 9) of the presettlement study area primarily around Mack Lake and westward and north of the Au Sable River (Fig. 2). The composition of this and the other forest types corresponds well with a natural community classification for Michigan (Michigan Natural Features Inventory, 1990). Surveyors described jack pine barrens or open woodlands (Pregitzer and Saunders, 1999) as "barrens," "a thin growth of spruce [jack] and yellow [red] pine," "scattering timber" or "burned plain covered with grasses." Blueberries (*Vaccinium* spp.) were frequently mentioned in the surveyors' line descriptions for the undergrowth on these sites. Surveyors' line descriptions indicated that jack pine barrens covered about 3% of the study area.

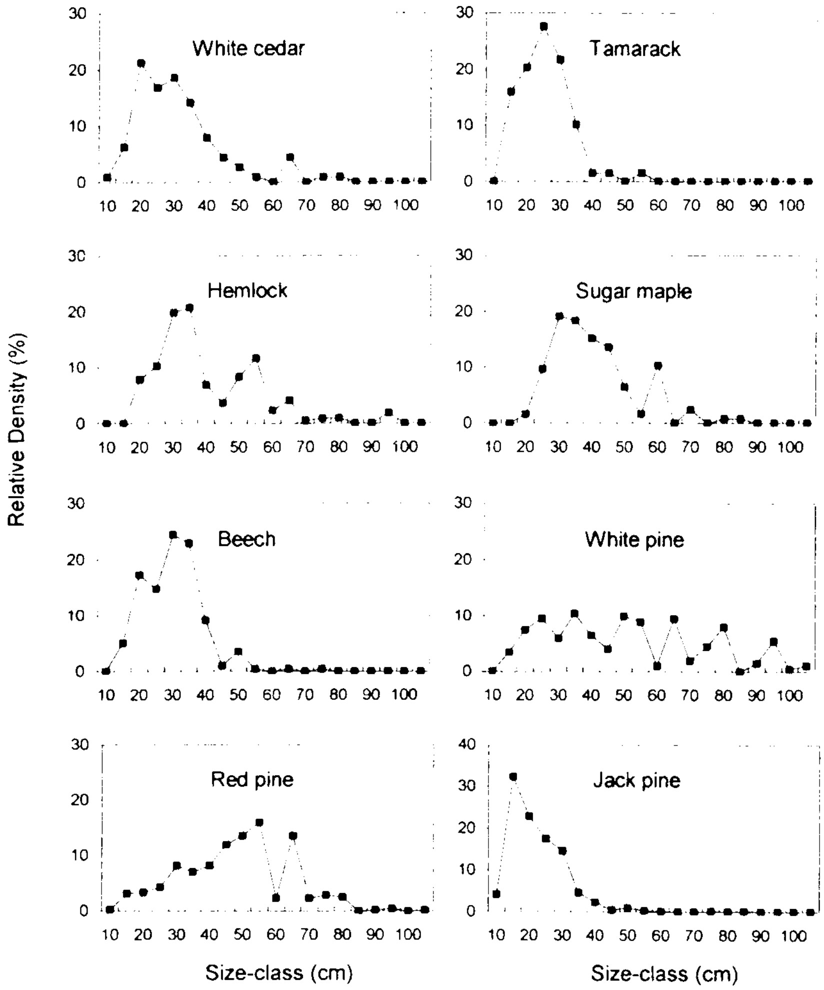

FIG. 1.—Witness tree species diameter distributions by 5 cm diameter classes for trees >10 cm diameter for the entire study area

Although stand data were unavailable from the ECS study for today's dry sites, Simard *et al.* (1983) reported on the forest composition of the Mack Lake outwash plain (the 9000 ha dominant outwash plain landform with coarse-textured, rapidly drained soils in the study area; Fig. 2). In 1980 the Mack Lake outwash plain was dominated by jack and red pines (42% and 16% of timber volume, respectively) with aspen (14%) and oak (12%) associates. These data were taken as a representative sample of current forest composition on the study area's dry sites. As in the presettlement period (Table 5), jack and red pines dominate on the dry sites. However, the importance of white pine has declined and aspen and oak have greatly increased on present-day dry sites.

Currently dry sites dominated by jack pine on the Mack Lake outwash plain average 1975 trees/ha with a mean basal area of 29 m^2/ha (Simard *et al.*, 1983). These figures indicate

TABLE 4.—Mean (SE) witness tree diameters by dominant species for the presettlement study area

Species	Mean diameter (SE)[a]
Pinus banksiana	18 (0.3) a
Larix laricina	21 (0.9) a
Fagus grandifolia	26 (0.6) a
Thuja occidentalis	27 (1.3) a, b
Acer saccharum	31 (1.1) b
Tsuga canadensis	36 (1.1) b
Pinus resinosa	44 (0.8) c
Pinus strobus	46 (1.7) c

[a] Column means with different letters are significantly different, ANOVA, $P < 0.05$, Tukey's HSD

a ninefold increase in mean tree density and a doubling of mean basal area in comparison to presettlement conditions (Table 7). The jack pine forest type has declined in extent (−9%; Table 9) since the presettlement period.

Dry mesic sites.—Red and jack pine dominated presettlement dry-mesic sites with white pine as an associated species (Table 5). Red pine was significantly ($P < 0.05$) associated with sandy, somewhat excessively drained soils on moraines (Table 6). Presettlement dry-mesic sites had an intermediate mean tree density, basal area and diameter in comparison to the other sites (Table 7). Jack pine had the greatest density and red pine the largest basal area (Table 8). This mixed pine forest type occurred primarily to the east and northeast of large, dry outwash plains (Fig. 2). The mixed pine forest covered 14% of the presettlement study area (Table 9). Surveyors described these forests as a "handsome pinery" with "mostly yellow [red] pine, some white pine." When surveyors recorded the undergrowth condition here they described it as "free from undergrowth" or dominated by "hazel" (*Corylus* spp.) and "dwarf oaks."

Present-day forests on dry-mesic sites have an index of compositional similarity of only 13% with their presettlement condition (Table 5). Pines have been nearly eliminated on dry-mesic sites, a result reported in other historical studies of Lake States forests (Whitney, 1987; Palik and Pregitzer, 1992; Frelich, 1995). Oak and aspen dominate today's dry-mesic sites with white oak (*Quercus alba*) and red maple (*Acer rubrum*) associates (Table 5). Mean tree density has tripled between the presettlement period and today. Mean basal area and mean tree diameter have declined between the two time periods (Table 7). The mixed pine forest type has declined in extent since the presettlement era (−10%) such that it only covers 25% of its former extent (Table 9).

Mesic sites.—Hemlock, beech and sugar maple dominated presettlement mesic sites and white pine was an associated species (Table 5). Hemlock was significantly associated ($P < 0.05$) with moderately well to well drained sandy loam soils on moraines (Table 6). Beech and sugar maple were both significantly associated ($P < 0.05$) with moderately well to well drained loamy sand soils on ice-contact topography. White pine was associated with a variety of intermediate soil drainage and textural conditions on moraines and ice-contact topography. Presettlement mesic sites had an intermediate mean tree density and basal area, but the largest mean tree diameter (Table 7). Beech had the greatest density and hemlock the largest basal area (Table 8). This mixed conifer–northern hardwood forest type covered 22% of the study area (Table 9) on topographically diverse areas of short, steep hills, swell and swale features and small hollows mainly south and east of the Mack Lake outwash plain (Fig. 2). Surveyors described such areas as "land rolling" and "good second

TABLE 5.—Tree species importance values by soil moisture condition for presettlement (PS) and present-day (PD) forests and the study area. Tree species ranked by IV for the entire study area. Species with an IV >10% printed in boldface. Present-day values for dry and wet soil moisture conditions unavailable from the FCS data set

Species	Study area	Dry	Dry-mesic		Mesic		Wet-mesic		Wet
	PS	PS	PS	PD	PS	PD	PS	PD	PS
Pinus banksiana	**26.5**	**51.6**	**23.8**	—	1.1	—	5.2	—	7.4
Pinus resinosa	**23.6**	**29.1**	**41.5**	0.2	9.7	—	**11.1**	—	0.8
Pinus strobus	**12.2**	**10.5**	**15.3**	1.0	**14.8**	—	**14.5**	1.0	2.1
Tsuga canadensis	9.2	1.2	3.6	—	**25.4**	—	**22.0**	—	1.1
Fagus grandifolia	6.1	0.9	3.5	0.2	**20.0**	3.4	3.2	0.5	0.3
Acer saccharum	5.0	0.6	1.9	5.1	**15.1**	**41.3**	4.4	**25.6**	0.3
Thuja occidentalis	3.9	0.2	0.4	—	1.3	—	8.3	—	**32.2**
Quercus spp.	2.6	2.1	3.7	**39.7**	3.7	9.4	1.5	**18.0**	—
Larix laricina	2.3	0.2	—	—	—	—	1.6	—	**26.2**
Populus spp.	2.2	2.1	3.6	**22.7**	1.9	**12.9**	**11.0**	1.6	7.1
Betula papyrifera	1.0	0.3	0.3	1.1	0.8	1.2	4.8	**20.2**	2.3
Abies balsamea	0.7	0.1	0.1	—	—	—	2.4	—	4.6
Picea spp.	0.7	0.1	0.3	—	—	—	0.4		7.3
Acer rubrum	0.6	0.2	0.5	**10.1**	0.8	4.4	1.0	9.7	1.6
Tilia americana	0.5	0.1	—	1.1	2.1	**18.7**	—	**15.2**	—
Quercus alba	0.4	0.3	1.1	**16.6**	0.4	—	0.3	1.3	—
Other species[a]	2.5	0.4	0.2	2.2	3.1	8.9	8.7	7.0	6.7
Totals	100	100	100	100	100	100	100	100	100
% Similarity			13		28		17		

[a] Includes: *Betula alleghaniensis*, *Betula* spp., *Carya* spp., *Fraxinus americana*, *F. nigra*, *Ostrya virginiana*, *Prunus serotina* and *Ulmus* spp.

rate soil, clay and sand," with commonly encountered undergrowth species of beech, red maple, sugar maple and hemlock.

Present-day mesic sites are dominated by sugar maple and basswood (*Tilia americana*) with aspen as an associate (Table 5). Compositional similarity between presettlement and current mesic sites is 28% (Table 5). Hemlock, white pine and beech have been nearly eliminated. Mean tree density has nearly quadrupled in comparison to presettlement conditions (Table 7). Mean basal area has increased while the mean stem diameter has decreased. The mixed conifer-northern hardwood forest type is today predominantly northern hardwoods and has declined in area (−14%) compared to its presettlement distribution (Table 9).

Wet-mesic sites.—Hemlock, white pine and aspen dominated presettlement wet-mesic sites (Table 5). Red pine had an abnormally high IV of 11.1 for wet-mesic sites (Table 5). While hemlock and white pine were significantly associated ($P < 0.05$) with poor to somewhat poorly drained soils, red pine did not show a significant positive association with these soils (Table 6). The physiology of red pine (Rudolf, 1990) would preclude its importance on wet-mesic sites. Inclusions within soil mapping units are not uncommon (Soil Survey Staff, 1999), and the unusual importance of red pine on wet-mesic sites is due to inclusions of somewhat excessively drained soils as small islands within the soil mapping units identified as wet-mesic. White cedar had a significant association ($P < 0.05$) with poor to somewhat poorly drained soils (Table 6) and its physiology is adapted to wet-mesic sites (Johnston, 1990a). White cedar was considered an associate on wet-mesic sites, although its IV of 8.3 was

TABLE 6.—Standardized residuals (Strahler, 1978) expressing significant (P < 0.05) associations between witness tree species and physical factors

Physical factor	*Acer saccharum*	*Fagus grandifolia*	*Larix laricina*	*Pinus banksiana*	*Pinus resinosa*	*Pinus strobus*	*Thuja occidentalis*	*Tsuga canadensis*
Glacial landform								
Ice-contact	8.0	10.5	0.2	-9.7	0.7	2.8	-4.1	2.4
Moraine	4.8	5.6	-3.2	-17.9	9.8	5.4	-3.0	9.1
Outwash	-10.2	-12.8	2.7	23.1	-9.4	-6.8	5.7	9.8
Soil drainage								
Excessive	9.2	11.6	15.2	27.4	0.7	-5.6	-9.7	-12.1
Somewhat excessive	-3.2	-2.2	—	-2.8	10.4	3.5	-4.9	-4.2
Moderately well to well	16.0	20.2	—	-20.9	-5.7	3.5	-3.3	17.4
Poor to somewhat poor	1.3	-1.2	-0.8	-8.4	-3.1	2.4	4.5	7.4
Very poor	-2.9	-3.8	20.1	-8.9	6.4	-2.2	27.2	-3.2
Surficial geology								
Sand	11.8	-13.5	-23.9	17.8	10.6	-0.5	-17.6	-12.1
Loamy sand	14.8	13.0	—	—	-4.6	-1.6	-2.2	8.1
Sandy loam	6.1	12.5	—	-13.8	5.8	2.8	0.9	12.7
Loam	3.6	-0.3	—	—	-1.2	2.9	—	4.6
Silty clay loam	—	—	—	—	—	—	2.1	—
Muck and peat	-2.6	-3.5	24.6	-10.6	-5.8	-2.6	28.6	-2.8
Mucky sand	—	—	3.0	-1.0	-2.1	1.0	3.9	-1.1

TABLE 7.—Means (SE) of presettlement (PS) and present-day (PD) forest structure by soil moisture condition. Present-day values for dry and wet sites unavailable

Soil moisture condition	Density (trees/ha)		Basal area (m^2/ha)		Stem diameter (cm)[a]	
	PS	PD	PS	PD	PS	PD
Dry	214 (11.2)	—	13 (0.7)	—	23 (0.4) a	—
Dry-mesic	315 (15.0)	904 (56.8)	31 (1.5)	27 (2.5)	30 (0.8) b	20 (0.2)
Mesic	241 (13.3)	915 (79.1)	25 (1.4)	31 (7.1)	33 (0.7) c	20 (0.4)
Wet-mesic	366 (120.4)	1230 (230.2)	36 (11.8)	36 (1.2)	30 (1.2) b, c	18 (0.3)
Wet	366 (62.1)	—	18 (3.1)	—	23 (0.7) a	—

[a] Column means with different letters are significantly different, ANOVA, $P < 0.05$, Tukey's HSD. Test for PS stem diameters only

lower than the arbitrary IV = 10 cut-off for associated species. Aspen did not have any significant physiographic or soil factor associations.

Presettlement wet-mesic sites had a high mean tree density and basal area and an intermediate mean tree diameter (Table 7). Hemlock had the highest density and basal area (Table 8). This mixed conifer–aspen forest type covered only 5% of the study area (Table 9) and was found on fine-textured and organic soils of outwash plains, gently rolling moraines and kettle holes in ice-contact topography (Fig. 2).

Sugar maple, white birch (*Betula papyrifera*) and oak dominate current wet-mesic sites with basswood and red maple associates (Table 5). Conifers have declined sharply on wet-mesic sites since the presettlement era. Present-day forests on wet-mesic sites have an index of compositional similarity of only 17% with their presettlement condition (Table 5). Mean tree density has tripled between the presettlement period and today (Table 7). Mean basal area has remained constant while mean tree diameter has declined between the two time periods. The mixed conifer–aspen forest type is no longer recognizable; having been supplanted by the northern hardwood, oak and aspen-white birch forest types (Table 9).

Wet sites.—White cedar and tamarack dominated presettlement wet sites (Table 5). Both of these species were significantly associated ($P < 0.05$) with very poorly drained muck and peat (130+ cm of organic soil) and mucky sand (40–130 cm of organic soil over sand) soils on outwash plains (Table 6). Presettlement wet sites had a high mean tree density and a low mean basal area and tree diameter (Table 7). White cedar had the greatest density and basal area (Table 8). Because only trees with a diameter >10 cm were used in the calculations of forest structure, some bogs dominated by black spruce (*Picea mariana*) and tamarack with very low densities of small trees (<10 cm diam) were eliminated from the presettlement data set. This created an artifact in the data whereby presettlement wet sites likely have an elevated mean tree density value (Table 7). This lowland conifer forest type covered 15% of the study area (Table 9). It occurred mainly on outwash plains, but also on gently rolling moraines, and in kettle depressions and around kettle lakes in ice-contact topography (Fig. 2). Surveyors frequently mentioned white cedar, hemlock, mosses and Canadian yew (*Taxus canadensis*) in the understory of those lowland conifer forests with an overstory of primarily white cedar. Glacial lakes and open, herbaceous marshes accounted for the remaining land cover (3%) of the study area (Table 9).

Site specific present-day stand data were lacking for wet sites. However, some broad comparisons to observations in the literature were made. Veatch *et al.* (1936) reported that in the study area the only major change since settlement within unlogged wet sites was the great decrease in tamarack due to larch sawfly (*Pristiphora erichsonii*) outbreaks. Where wet

TABLE 8.—Tree density and basal area of the dominant presettlement tree species by soil moisture condition. Tree species arranged along the soil moisture gradient

Species	Dry		Dry-mesic		Mesic		Wet-mesic		Wet	
	Density (trees/ha)	Basal Area (m^2/ha)	Density (trees/ha)	Basal Area (m^2/ha)	Density (trees/ha)	Basal Area (m^2/ha)	Density (trees/ha)	Basal Area (m^2/ha)	Density (trees/ha)	Basal Area (m^2/ha)
Pinus banksiana	146.2	4.6	112.4	3.7	4.2	0.4	32.2	0.6	34.3	1.0
Pinus resinosa	34.7	5.5	91.4	16.7	17.5	3.1	22.0	5.8	2.7	0.2
Pinus strobus	9.0	2.2	32.1	6.3	23.7	5.0	33.8	7.0	9.6	0.3
Tsuga canadensis	2.4	0.2	11.0	1.2	57.4	6.9	64.4	9.5	5.5	0.1
Fagus grandifolia	2.1	0.1	15.2	0.7	60.4	3.8	13.5	1.0	1.4	0.0
Acer saccharum	1.3	0.1	6.3	0.5	38.7	3.6	18.6	1.3	1.4	0.1
Populus spp.	6.2	0.2	16.8	0.6	7.1	0.2	57.5	2.2	26.1	1.3
Thuja occidentalis	0.3	0.0	1.6	0.1	3.3	0.3	30.5	2.9	112.7	6.1
Larix laricina	0.3	0.0	0.0	0.0	0.0	0.0	8.4	0.3	85.2	5.3

TABLE 9.—Presettlement and present day extent of land cover types in the study area (exclusive of Alcona County)[a]

Land cover type	Presettlement		Present day	
	Area (ha)	Area (%)	Area (ha)	Area (%)
Jack pine	42,256	41.2	32,818	32.0
Mixed conifer-northern hardwood[b]	22,542	22.0	8079	7.9
Lowland conifer	15,649	15.3	3998	3.9
Mixed pine	13,949	13.6	3646	3.5
Mixed conifer–aspen	5178	5.0	0	0.0
Lakes[c]	1794	1.7	9646	9.4
Emergent marsh[d]	1196	1.2	179	0.2
Agriculture	0	0.0	2591	2.5
Aspen–white birch	0	0.0	17,634	17.2
Lowland hardwood[e]	0	0.0	2944	2.9
Oak[f]	0	0.0	16,456	16.0
Urban	0	0.0	4573	4.5
Totals	102,564	100	102,564	100

[a] Present-day land cover types of the Michigan Resource Inventory System (MIRIS) matched to their presettlement correlates. Available MIRIS data covered 85% of the study area
[b] Current forests are nearly all northern hardwood
[c] Current acreage includes reservoirs
[d] Wetland areas dominated by erect rooted herbaceous hydrophytic plants
[e] Forests dominated by ash, elm, maple and aspen
[f] Mainly black, red and Hill's oaks

sites were logged and or severely burned in the late 1800s, these sites were then dominated by a mix of paper birch, tag alder (*Alnus rugosa*), red maple and aspen (Veatch *et al.*, 1936). Surveyor accounts of abundant Canadian yew populations on wet sites contrasts sharply with the lack of yew today (Frelich and Lorimer, 1985; Van Deelen *et al.*, 1996) in part due to the modern irruption of deer populations in Michigan. The basal area of presettlement forests on wet sites lies within the range of basal areas reported for current mature forests dominated by tamarack (Johnston, 1990b), but is much lower than current mature forests dominated by white cedar (Zogg and Barnes, 1995). The density of presettlement forests on wet sites is half that reported for current mature wet site forests. Because of intensive logging, drainage and reservoir development, lowland conifers have declined since settlement to just 26% of their former extent (Table 9).

Forest change across the study area.—The demise of conifers and beech on dry-mesic to wet-mesic sites since European settlement reported in this study and others across the Lake States has been attributed to the intensive logging and repeated wildfires of the late 1800s (Ahlgren and Ahlgren, 1983; Whitney, 1987; Karamanski, 1989). The current abundance of aspen, oak and maple on dry-mesic to wet-mesic sites is a result of the ability of these species to survive repeated logging and slash fires by sprouting (Kozlowski *et al.*, 1991). In addition, aspen and maple produce a large amount of wind dispersed seed which allowed them to readily colonize the abundant mineral seedbeds in the postlogging era (Whitney, 1987). Lastly, forestry operations in the upper midwest have favored aspen on large acreages over the last 50 y (Karamanski, 1989).

Mean tree density has tripled between the presettlement period and today across dry-mesic to wet-mesic sites (Table 7). Mean basal area has remained relatively constant across

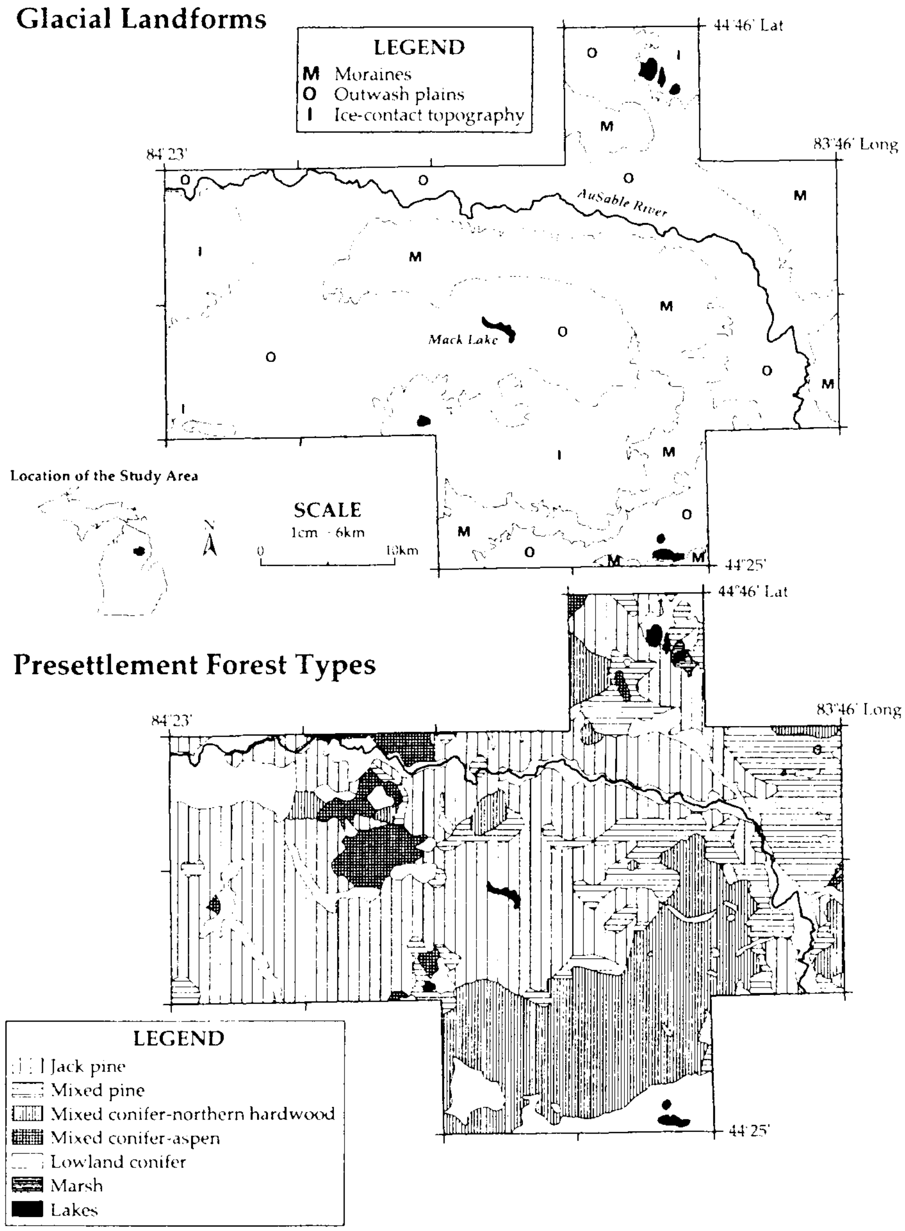

FIG. 2.—Glacial landforms and presettlement forest types of the study area

these sites while mean tree diameter has declined between the two time periods. Across the uplands of the study area, trees are smaller and more numerous today than 150 y ago. Similar results are reported in other historical studies of midwestern forests (Fralish *et al.*, 1991; Zhang *et al.*, 2000).

TABLE 10.—Estimated presettlement disturbance return intervals[a] by forest type based upon surveyors' section line descriptions

Forest type	% study area affected by disturbance		Return interval (years)	
	Fire	Windthrow	Fire	Windthrow
Jack pine	12	1	100	2000
Mixed pine	11	2	100	900
Mixed conifer–northern hardwood	< 1	1	5600	1200
Mixed conifer–aspen	2	7	900	200
Lowland conifer	1	2	1100	700
Total study area	6	2	200	900

[a] Return interval is the length of time required for a disturbance to occur over an area equal to the area of the forest type in question

The study area's landscape pattern has changed since 1840, albeit not nearly as drastically as in southern lower Michigan (Klopatek *et al.*, 1979). About 15% of the landscape is in human use today (*i.e.*, agriculture, roads, developments and reservoirs), but the study area is still primarily a forested landscape (83%; Table 9). Approximately 350 km of primary and secondary roads cross the study area. Human developments have undoubtedly increased the amount of edge habitat (Saunders *et al.*, 1991; Trombulak and Frissell, 2000) since the presettlement period. The introduction of roads, agriculture and developments must have impacts on species dispersal patterns and enhance modern forest fire suppression efforts. Whereas the presettlement landscape was conifer dominated (75%; Table 9), today's landscape is more evenly split between conifers (39%) and hardwoods (44%). Pines still cover a large area (36%), but have declined (−19%) since the presettlement period. Most current pine forests are dominated by jack pine. The decline of northern hardwoods (−14%), lowland conifers (−11%) and mixed pine forests (−10%) coincides with an increase in the aspen–white birch (+17%) and oak (+16%) forest types (Table 9).

Disturbance regimes.—The presettlement return intervals for both fire and windthrow natural disturbances varied by forest type (Table 10). It is unclear from the GLO survey notes what the sources of ignition were for the burned areas the surveyors encountered. The ratio of Native American set fires to lightning strike fires in the upper midwest before settlement is still a subject of debate (Whitney, 1994). For jack pine and mixed pine forests, fire was an important natural disturbance regime with a return interval of about 100 y. Red and jack pines require full sunlight and a mineral soil seedbed for regeneration (Rudolf, 1990; Rudolph and Laidly, 1990), a condition created by intense fires. In addition, jack pines typically have serotinous cones. Both red and jack pines have longevities (250 and 150 y, respectively) exceeding the 100 y fire return interval for the jack pine and mixed pine forest types. Presettlement jack pine and mixed pine forests depended on fire for stand initiation. Windthrow was not an important disturbance regime in these pine forests.

Both fire and windthrow return intervals (Table 10) for the presettlement mixed conifer–northern hardwood forest exceed the maximum longevities of hemlock (250–800 y; Godman and Lancaster, 1990), beech (300 y; Tubbs and Houston, 1990), sugar maple (300–400 y; Godman *et al.*, 1990) and white pine (200+ y; Wendel and Smith, 1990). Fire and windthrow were not important natural disturbance regimes in these presettlement forests. Single-stem and gap-sized treefalls (Runkle, 1982) provided the mechanisms for overstory recruitment in this forest type.

The presettlement windthrow return intervals were shortest in the mixed conifer–aspen and lowland conifer forests (200 and 700 y, respectively; Table 10) compared to the other forest types. Trees grown on soils with high seasonal water tables such as those in these forest types have shallow spreading root systems and are prone to windthrow (Kozlowski *et al.*, 1991). Windthrow was an important presettlement disturbance regime in the mixed conifer–aspen and lowland conifer forests. However, in the presettlement mixed conifer–aspen forest type, the significant component of aspen, a fire-tolerant species (Perala, 1990), indicates that fire influenced this forest type despite the long fire return interval based upon surveyor section line descriptions.

Organized fire control beginning around 1930 diminished the frequency, severity and extent of fires in the study area (Lovis *et al.*, 1978). The fire return interval for the Huron National Forest from 1950–1981 was 400 y (Simard and Blank, 1982), twice as long as during the presettlement era for the study area (Table 10). Fire suppression has encouraged the development of more dense forests on dry and dry-mesic sites over the last 150 y and has reduced the extent of jack pine barrens (Pregitzer and Saunders, 1999). It is unknown whether windthrow disturbances have significantly changed over the last 150 y.

Witness tree species were probably distributed across the presettlement forest based on a soil moisture gradient. Over the last 150 y the composition and structure of the forests have changed. Compositionally, dry sites are similar to their presettlement condition whereas dry-mesic to wet-mesic sites have changed substantially. Present-day forests show the importance of historic events, *i.e.*, the logging era, fire suppression and modern forest industries, in shaping forest composition and structure.

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