Introduction

Kirtland’s Warbler, a rare member of the wood warbler family (Parulidae), was discovered in 1851 near Cleveland, Ohio, and named after an eminent naturalist, Jared P. Kirtland. The warbler has its nesting grounds in northern Wisconsin, Michigan, and Michigan's Upper Peninsula. The population of Kirtland's Warbler in Wisconsin is estimated to be around 1,000 birds, compared to about 460 birds in Michigan.

Ecosystem Structure and Vegetation of the Mack Lake Burn:

A Framework for Understanding

The occurrence and behavior of Kirtland’s Warbler

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February 1, 1989
ABSTRACT

The overall objective was to establish a framework of landscape ecosystems for the Mack Lake burn as a basis for understanding warbler occurrence and behavior. Parts of two field seasons (May-August 1986 and 1987) were devoted to determining the landscape ecosystem types, sampling plots in each type, and developing both a broad (2 types) and more detailed (11 types) classification of landscape ecosystem types.

The area was subdivided into two major landscape types: a low-level outwash plain in the northern part of the burn, surrounding Mack Lake, and high-level outwash and ice-contact terrain in the southern part. Eleven landscape ecosystem types were identified, classified, and described — five in the low-level outwash plain and six in the high-level area to the south. Ecosystems were distinguished by differences in physiography, microclimate, soil, and vegetation. Ecosystems in the high-level outwash and ice-contact area typically had better soil moisture and nutrient availability than those in the low-level outwash plain.

Occupancy of the burn by the Kirtland’s warbler, both in 1986 and also in 1987, was much greater in ecosystems of the high-level outwash and ice-contact terrain than in the low-level outwash plain. Warbler sightings and nests were associated with relatively tall and dense jack pine stands of patchy (contagious pattern) occurrence in ecosystems 6, 7, 8, and 10. Depressions, in both the low- and high-level areas, were not occupied by the warbler. It is expected that the warbler will gradually colonize the low-level outwash area as the pines increase in size.

Results of a quantitative study of the pattern of occurrence of jack pine regeneration (contagious vs. random, vs. regular) indicated that pines typically exhibited a contagious pattern in areas of known warbler occurrence — especially in the high-level area. In contrast, the pattern tended to be random in plots of ecosystem types where the warbler was not observed.

Marked differences in microclimate were found between depressions and adjacent uplands in both low-level and high-level areas. Major differences in ground-cover vegetation were observed between the low-level outwash plain and the high-level area and among ecosystem types in each of these areas. Significant differences were found in jack pine density and 1985 height among ecosystem types. Variation among plots within ecosystems was great. Biologically meaningful trends were found among ecosystem types, although some ecosystem means were not significantly different.

The pattern of warbler occurrence appears closely related to the area’s physiography (landform, parent material, local topography), soil, and vegetation — which are themselves closely related. In fact, for this area the pattern of warbler occurrence could be predicted by an understanding of physiography alone at the broad level. We conclude that, based on an understanding of the structure of ecosystems of a given landscape, areas of initial warbler occurrence and subsequent colonization may be determined.
INTRODUCTION

Kirtland's Warbler, a rare member of the wood warbler family (Parulidae), was discovered in 1851 near Cleveland, Ohio, and named after an eminent naturalist, Jared P. Kirtland. The warbler has its nesting grounds in northern Lower Michigan in jack pine (Pinus banksiana Lambert) forests and winters in the Bahama Islands.

PROBLEM

Never considered an abundant bird, populations of the warbler have declined from an estimated 1,000 birds in 1961 (Mayfield 1962) to about 460 birds in 1981 (Ryel 1981). The precipitous decline of 60% from 1961 to 1971 (1,000 to 400) led to the formation of the Kirtland's Warbler Recovery Team in 1975 and the adaption of a recovery plan (Byelich 1976). The plan calls for (1) development and maintenance of 36,000-40,000 acres of suitable nesting habitat for the warbler on a sustained basis, (2) protection of the warbler on its wintering grounds and along the migration route, (3) reducing key factors adversely affecting its reproduction and survival (notably the brown-headed cowbird), (4) monitoring breeding populations to evaluate response to management practices and environmental changes, and (5) studying the possibility of introducing the warbler into areas of the Upper Peninsula of Michigan or in other states or Canadian provinces.

In the spring-summer the warbler may be found in jack pine forests on sandy outwash plains in the northern Lower Peninsula of Michigan. The primary nesting grounds are in Crawford, Oscoda, Ogemaw Counties -- in the drainage area of the Au Sable River. In 1981, 81% of the singing males were found in these three counties. In the late 1970s and early 1980s, an increasing number of birds were found in Kalkaska County. In 1981, 95% of singing males were found in these four counties.

The warbler typically nests on the ground in young (8-20 years) jack pine stands, characterized by dense patches of pines interspersed by numerous, small openings. Although considerable research has been published on the warbler itself (two books and about 200 papers; Ryel 1981), little intensive research has been conducted and published on what is termed warbler habitat -- particularly on landscape ecosystems and their components of physiography, soil, and vegetation. Although the decline of the warbler may be primarily due to conditions on wintering grounds (Ryel 1981), an understanding of the ecosystems occupied by the warbler would provide information critical to the improvement of suitable nesting and foraging conditions in the Lower Peninsula of Michigan, enable suitable habitat to be chosen and created through management at the least cost, and provide the ecosystem basis for extending the range of the warbler in the Upper Peninsula, Wisconsin, and Ontario.

The Mack Lake burn of May 5, 1980, covered 23,830 acres in Oscoda County, and according to Simard et al. (1983): "may have created what in 10 years will be 10,000 to 15,000 acres of prime habitat for the endangered Kirtland's Warbler." Now, 7 years after the burn, young jack pines, together with oaks, aspens, and other species, are reforesting the area. Thus, the Mack Lake burn provides an excellent outdoor laboratory to study in detail the physiography, soil, and vegetative interrelationships that favor colonization by the warbler.
RESEARCH OBJECTIVES

General Objective: To establish a framework of landscape ecosystems as the basis for understanding warbler occurrence and behavior. To achieve this goal a study was undertaken of the occurrence of landscape ecosystems of the Mack Lake burn, with reference to colonization by the Kirtland's Warbler.\(^1\) The specific objectives are presented below.

Specific Objectives:

1. To determine the major landscape ecosystems of the Mack Lake burn by their physiographic, soil, and vegetative components. How diverse is the area in its physical environment (physiography, soil)? How diverse in vegetative communities and species? What are the interrelationships between the physical site conditions (physiography, soil, microclimate) and vegetation (overstory, understory, ground cover)?

2. To determine the tree structure and composition of jack pine communities. What is the range of densities of jack pine regeneration? What is the size variation in jack pine regeneration? How does patch size vary over the area and in relation to different ecosystem types? How is jack pine seedling density related to previous overstory conditions and to physiographic and soil conditions? What trees besides jack pine are present?

3. To determine structure of young jack pine communities (occurrence, density, patchiness) by field sampling within one or more major ecosystem types. What is the pattern of openings and jack pine communities in selected parts of the burn?

4. To determine the composition and coverage of ground-cover vegetation. What is the non-tree composition of different ecosystems? How does vegetative composition and coverage differ in jack pine stands of different densities from that in openings?

5. To determine the difference in jack pine coverage in machine-salvaged areas vs. unsalvaged areas. Are salvaged areas unsuitable for warbler colonization due to the low coverage of jack pines?

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\(^1\)Because the term "habitat" means plants to some individuals and means site conditions or physical environmental factors (physiography, soil) to other individuals, I use the term "landscape ecosystem" or "ecosystem" because it is not only inclusive of the components of climate, physiography, soil, and vegetation (overstory, understory, ground cover) but because it includes the interactions among these components. See discussion of ecosystem concept below.

\(^2\)All plants, trees, shrubs, herbs less than 0.5 in 1.35 m above the ground (dbh).
JUSTIFICATION

The study was designed to meet the needs of biologists and managers in understanding Kirtland Warbler ecosystems. Research initiative comes directly from the Recovery Plan:

Research is recommended to identify the specific soil and vegetative structure of productive Kirtland's Warbler nesting sites. When the specific nesting requirements are known, specialized guidelines will be developed to produce the desired vegetative communities on the required soil conditions (Byelich 1976, p. 21).

The research provides the basis for satisfying the objectives proposed by James M. Engel, Chief, Division of Endangered Species, in his letter of January 24, 1986, to John Byelich. The objectives are as follows:

1. To determine what constitutes optimal habitat. Optimal habitat can be defined at various levels of refinement, with the fifth and final level being the most desirable:

   a. that habitat attracting the first immigrant Kirtland Warblers;
   b. that habitat hosting the highest density of single males over the life of the stand;
   c. that habitat hosting the highest density of paired males over the life of the stand;
   d. that habitat producing the highest number of fledglings per 100 acres over the life of the stand;
   e. that habitat producing the highest number of fall migrant immature Kirtland Warblers per 100 acres over the life of the stand.

2. To determine where such habitats should be located in relation to occupied habitats in order to provide for maximum Kirtland Warbler production.

To answer the questions inherent in these objectives we need to have detailed information about the physical environment, the vegetation, and their interactions, i.e., understand ecosystems. This information would be most efficiently obtained by studying the areas supporting warbler populations. However, such areas are restricted and cannot be studied during the growing season. The Mack Lake burn provides the opportunity to study ecosystems in detail, observe the colonization process, and relate warbler nesting, foraging, and other behavior to the ecosystem structure and processes.
STUDY AREA

The research was conducted in the Mack Lake burn of 1980. The burned area covers 23,830 acres in southeastern Oscoda County (Fig. 1). The burn is located in the Northern Lower Peninsula Region, the High Plains District, and the Grayling Subdistrict of the Ecosystem Regions of Michigan (Albert et al. 1986; Fig. 2). A description of the climate and physiography of the Region, District, and Subdistrict are given in Appendix B.

The wildfire developed from a prescribed burn that was ignited at 10:30 a.m. on May 5 by the U.S. Forest Service on Huron National Forest Lands. The purpose of the prescribed fire was to facilitate planting and ultimately create conditions favorable for the Kirtland's Warbler. By midnight of May 5, the fire had burned 23,000 acres — 97% of the total area burned. A comprehensive description of the topography of the area, fire weather, fire behavior, and fire effects was presented by Simard et al. (1983).

The Mack Lake burn is the largest fire recorded on the Huron National Forest since 1911, when record keeping began. Within the area burned, five other fires in excess of 10,000 acres have occurred since 1820 (Simard and Blank 1982). The average time between major crown fires is therefore 28 years.

Jack pine overstory was present on 10,000 acres (42% of the area), and red pine (Pinus resinosa Aiton), oaks (Quercus rubra L.; Q. ellipsoidalis E. J. Hill; Q. velutina Lamarack), and aspens (Populus grandidentata Michaux, P. tremuloides Michaux) were the major tree species present.

According to Simard et al. (1983), the depth of burn was shallow (1/4 to 1/2 inch), and soil micro-organisms were likely not significantly affected.

![Map of Mack Lake area with location of fire marked]
Figure 2. Map of regional ecosystems of the Lower Peninsula of Michigan. The Mack Lake burn is located in the southeastern part of Oscoda Co. in Region II (Northern Lower Michigan), District 8 (Highplains), and Subdistrict 8.2 (Grayling) (after Albert et al. 1986).
Numerous strips of unburned but scorched tree crowns (and also unscorched tree crowns) are characteristic of the burn. However, many of the strips were removed in salvage logging that occurred several years following the burn. Simard et al. (1983) attribute the unburned but scorched crown strips to downward-moving streams of air caused by horizontal roll vortices. The strips were often parallel and maintain their identity for two to four miles, and in one case, for seven miles.

Clonal, fire-dependent tree and shrub species, such as aspens, oaks, sweetfern (Comptonia peregrina), blueberries (Vaccinium spp.), and trailing arbutus (Epigaea repens), rapidly revegetated the area by sprouting from roots, rhizomes, or the root collar (oaks). Seeds of pin cherry (Prunus pensylvanica L.) germinated and seedlings developed. First-year aspens sprouts were 2 to 12 ft tall; oak sprouts were 1-4 ft tall. Observations at the end of the first growing season indicated that dense stands of jack pine seedlings were likely to become established over much of the area (Simard et al., 1983). The range of seedlings per acre on 3 plots was 2,000 to 17,000 (average 9,000).

PREVIOUS RESEARCH

Published research has centered on the biology and natural history of the warbler rather than on the specific physical site conditions and vegetation of the areas where warblers occur. The summer and winter ranges are known (Fig. 3), although relatively little is known about specific locations of the warbler in the Bahama Islands (Van Tyne 1951, Radabaugh 1974, Byelich 1976, Rye 1981, Walkinshaw 1983). The areas in Michigan where the warbler is found singing and nesting are well known, and the status of warbler nesting range as of 1975 is shown in Figure 4. Annual surveys of singing males are useful not only to determine the number of warblers but where the birds are geographically located.

The general features of warbler habitat are well known, but there are few published details on physiography, soils, and vegetation of nesting areas. The term "habitat" as used in the warbler literature has different meanings. It can mean the geographic location of the bird but also the specific environmental conditions where the bird occurs. The term habitat is often used to express where the warbler lives. In the Kirtland’s Warbler Recovery Plan (Byelich 1976, p. 45) the following definitions are given:

Critical habitat is defined to mean areas that are presently occupied by nesting pairs, and areas that can be expected to be utilized at some future time.

Potential habitat consists of those stands of jack pine that, through management, will provide acceptable habitat at some future date.

Warbler "habitat" according to the Recovery Plan

The geographic location of warblers in Michigan is relatively well known. Summarized below is information from the Recovery Plan (Byelich 1976) about the physical and vegetative components of areas supporting warblers.
Figure 3. Migration route of the Kirtland's Warbler between its wintering and breeding grounds (after Byelich 1976).
Figure 4. Status of Kirtland's Warbler nesting range in 1975 (after Byelich 1976).
First and foremost is the relationship with jack pine, and natural jack pine forest is probably the best single general descriptor of ecosystems where the warbler nests and forages.

The breeding habitat of the Kirtland's Warbler is highly distinctive. Nearly all of the nests have been found in a 8 to 20 year old jack pine stands of Christmas tree size which have resulted from forest fire. Fire also maintains the low ground cover that must be just adequate to conceal the nest which is usually imbedded in the soil. Nearly all the pines in the stand must be small, and the occurrence of deciduous trees must be limited. A tract must be at least 80 acres and preferably much larger to attract the warbler. Ideal breeding habitat consists of homogeneous thickets of small jack pine interspersed with many small openings (Byelich 1976, p. 2).

Its requirements for breeding habitat are quite specific, so exact that its numbers will probably always be limited. The essence of its habitat is the jack pine forest. For this reason it is often called the Jack Pine Warbler. However, its habitat is more than just jack pine. The bird requires certain exacting conditions for nesting. Almost without exception, it is found only in extensive, homogeneous stands of young jack pine located on some of the poorest soil in Michigan -- the Grayling sand (Byelich 1976, p. 45).

Warbler researchers emphasize that wildfires have been the most important factor in establishing natural stands of jack pine. Also, they state that under natural conditions suitable habitat was produced only by forest fires. Fire exclusion has caused a drastic decline of suitable habitat. Furthermore:

Nesting habitat generally consists of young jack pine stands between 5 and 20 feet in height. Dense stands with the pines in close juxtaposition yet interspersed with small openings are best, the pattern which often results from forest fires. Such cover is not attractive to other species of wildlife, resulting in less competition than might otherwise be expected. A breeding pair of warblers requires about 30 acres of this type for its nesting territory (Byelich 1976, p. 45).

Besides jack pine, Byelich (1976, p. 45) states that the associated vegetation is important:

The low-growing, sparse vegetation that occurs in associated with the young "Christmas tree"-size jack pine on the relatively level sandy outwash plains is an important component of the habitat necessary for the warblers. The delicate combination of conditions required exists for a relatively short period of time, lasting only 10-15 years before it is no longer acceptable.
Jack pines, openings, and ground cover

Walkinshaw (1983) states that warblers move into an area when jack pines are at least five or six years old and 0.3 to 1.8 m tall. They prefer to nest in large stands over 32.4 ha in size. In areas occupied by the warbler, tree height varies from 1.2 to 6.7 m. In a survey of pines in seven different nesting areas (12 plots around nests), the jack pines were typically less than one meter tall and had an average dbh of 4.9 cm. Further, he reported that warblers prefer stands where grassy openings and semi-openings are interspersed among dense clumps of jack pines where the trees are about equal in height. Often, the openings are scattered with trees connecting the denser stands.

Warblers utilize an area for 5-20 years following a fire (Walkinshaw 1983). Habitat utilization in naturally burned areas reaches its peak 11-17 years after fire. After this time an area is quickly abandoned. As the pines increase in height, the lower branches die and the ground cover disappears -- apparently from the increased shading of the crowns as they close with one another. The warblers appear to nest among young and small pines where there is lush ground cover and where the lower jack pine branches from each tree reach or nearly reach those of neighboring trees (Walkinshaw 1983).

Openings are important. According to Walkinshaw (1983), warblers "prefer an area containing dense stands of small trees scattered among more widely spaced stands of trees and clearings devoid of trees. The spacing of trees on a naturally burned region can vary from close proximity to 4-5 m apart. The average distance between 500 trees on natural burns used by nesting warblers was 1.0 ± 0.8 m (range, 0.25 m to 6.7 m)." In addition, based on studies in four areas, including peak and past use, Smith and Prince (undated) concluded that "the arrangement of the tree cover and openness is important and that it may predict the ability of a habitat to attract and hold more warblers."

Walkinshaw (1983) reported on the nesting habitat of the warbler, and found that all 339 nests he observed were built in or under ground cover vegetation, approximately 8-20 cm high. Most of the nests were sunken so as to be flush with the ground surface. The nests "were usually located in areas where they were shaded by small jack pines and well concealed by lush ground cover. Nests were never found on steep hills, but always on level ground or gentle slopes." The nearest tree to each nest averaged 2.7 m in height. Although jack pine is usually the nearest tree, studies on the Damon burn in Ogemaw County showed that warblers will accept an area with equal numbers of jack pine and oaks. Smith and Prince (undated) also reported that on their peak use site, the "oak and pine configuration" provided adequate tree coverage for warbler use.

Nests are typically located at the edge of a fairly dense growth of jack pines. Walkinshaw (1983) reported that "out of a group of 126 nests found in naturally burned areas, 22 nests were located exactly on the edge of an opening while 40 nests were located within the pine growth. Sixty-four nests were placed an average of 60 ± 68 cm (range, 1 cm to 366 cm) out from the edge of the trees in an opening." Thus, 65% of the nests were in openings or at the edge of openings.

Salvage operations, removing the overstory jack pine trees, were conducted in about 20% of the Mack Lake burn. The influence of overstory removal, a treatment not found in natural burns, is unknown. However, Walkinshaw (1983)
noted that the absence of large trees and snags in relatively flat terrain was significantly related to nesting success.

Ground-cover vegetation, particularly herbs, has received less attention than tree cover. Nevertheless, the composition of woody plants and herbs on natural burns has been described (Walkinshaw 1983), and a list of species found on four areas in Ogemaw and Roscommon Counties was presented by Smith and Prince (undated). The former author noted that in general one or more species of grasses mixed with the sedge, Carex pensylvanica, form the bulk of the ground cover. In other areas shrubs and other plants may dominate: blueberry, bearberry (Arctostaphylos uva-ursi), sweet fern, bracken fern (Pteridium aquilinum), wintergreen (Gaultheria procumbens), and trailing arbutus. Smith and Prince reported that on known territories, live material accounted for an average of 59% of the total ground cover. No species-specific patterns that did not relate to site differences could be identified. They concluded that "a particular plant species is not selected" but rather the overall site conditions.

Critical habitat defined

Finally, it is important to summarize the concept of habitat by listing the criteria used in the Recovery Plan to define "critical habitat" (Byelich 1976, p. 46):

1. Soil type -- Grayling sand.

2. Forest cover currently in jack pine, and where management for jack pine is feasible. Areas may contain a limited hardwood (oak) component.

3. Areas currently occupied or previously used by the species.

4. Tracts of about 320 acres or larger, preferably where five or more of them lie within two miles of each other. Tracts less than 320 acres, but not less than 80 acres, where they occur in close proximity to the larger tracts.

5. Lands preferably in public ownership (State or National Forests).

6. Limited development potential or where development could be controlled.

7. Relatively level topography.

LANDSCAPE ECOSYSTEMS

It is important to base detailed studies on communities (structure and composition) and warbler behavior on a thorough understanding of landscape ecosystems. The ecosystem concept is the basis for determining the local ecosystem types of the Mack Lake burn area. Ecosystems are the natural holistic units of the landscape that can be identified and mapped over wide areas (large regional geographic units) or at local levels (small units such as rocky knobs.
or small marsh-filled depressions). The approach is based on the ecosystem concept. Biotic communities of plants and animals and their physical environment (termed site or habitat) -- in dynamic interaction with one another -- comprise an ecological system:

\[ \text{ECOSYSTEM} = \text{Physical Environment} \quad \rightarrow \quad \text{Biotic community of plants and animals} \]

Ecosystems are layered, volumetric segments of the biosphere (Rowe 1984). Their geographic nature was stressed by Rowe (1961) who defined an ecosystem as: "...a topographic unit, a volume of land and air plus organic contents extended areally over a particular part of the earth's surface for a certain time." The biosphere itself is a giant ecosystem, and it contains a nested series of interconnecting ecosystems. The results of any scientific or management endeavor is determined by the way it is conceived and the scale at which it is conducted. Thus, the landscape is conceived as ecosystems, large and small, nested within one another in a hierarchy of spatial sizes (Rowe and Sheard 1981).

METHODS

Research was conducted in field seasons of 1986 and 1987. Presented below is a description of the methods of both years. Plans to use remote sensing of the area to determine the structure of the vegetation were not realized. Professor Olson was unable to fly the area in 1986 and was only able to fly a small portion in 1987. The U.S. Fish and Wildlife Service flights came too late for us to use in 1987.

Determination of local ecosystem types followed the methods used in the Upper Peninsula of Michigan at the Cyrus H. McCormick Experimental Forest (Barnes et al. 1982, Pregitzer and Barnes 1984) and the Sylvania Recreation Area (Spies and Barnes 1985). An iterative approach of reconnaissance, plot sampling, and data compilation and analysis was used to develop successive approximations of the classification. Univariate and multivariate analyses have yet to be applied to the data to test the tentative classification.

1986 Field Season

Landscape ecosystems

Reconnaissance of the area was initiated May 20. The marked difference in physiography between the northern and southern parts of the burn became immediately apparent through reconnaissance coupled with study of topographic and soil maps. A relatively gradual transition separated the flat to gently sloping outwash plain of the northern part from the hilly ice-contact area of the south part. The identification of ecosystem types within each of these landform zones was accomplished by further reconnaissance and plot sampling. The soil map of the area, provided by Dave Clelland (Huron-Manistee N.F.), was particularly useful in our work. A first approximation of the ecosystem types was made in late June. Species-area curves, located away from roads, were used to help determine the size of sample plots. 200 m² was found to be an acceptable size for sampling ground-cover vegetation. 10 x 20-m plots were used to sample ecosystem types. A stratified-random system of plot location was used, i.e., the landscape was stratified into our hypothesized ecosystem types.
and sample plots established randomly within the types. A 5 x 20-m strip in the center of the plot was used to determine the coverage of ground-cover species. We attempted to determine the species and size (diameter breast height if standing and stump height at 5 cm if the tree was fallen or cut) of all pine trees. All understory species were measured at dbh in the entire plot. A soil pit was dug to about 130 cm and profile characteristics of texture, structure, depth, pH, color, rooting, and % pebbles and cobbles were determined. Soil samples of most horizons were taken for laboratory analysis. A soil auger was used in the bottom of the pit to reach a depth of approximately 4 m below the surface.

Species composition and jack pine density/coverage

Reconnaissance by foot and car revealed an enormous variation in the density of jack pine seedlings. A survey map of seedling density, provided by Bill Jarvis (Huron-Manistee N.F.), proved to be very useful in the density work. Local variation could be extremely great. Also, a marked difference in height of jack pines between the outwash and ice-contact zones, and also within each zone, was observed. To obtain some hard data on variation in jack pine density and height and size of openings, a sampling technique using 50-m² plots was developed and applied early in the study in Sections 22 and 12. The results of these data, results of further reconnaissance, and results of the Kirtland's warbler survey led to the decision to study the density and patchiness as a primary objective of the field season.

The finding of the Kirtland's warbler survey in June that 10 of the 14 male birds (71%) had colonized the ice-contact zone, with its relatively tall and dense stands of jack pine, suggested strongly that the stand structure and height of jack pines, rather than ground-cover vegetation, was a primary reason for colonization. Thus, further jack pine density/coverage reconnaissance and surveys (using 50-m² plots) were conducted. In June, four sections (in T25N, R3E) were identified as ones for the low-level photography that would help determine patchiness of jack pine over a relatively large area. However, we were unable to accomplish this objective. Using the results of the 50-m²-plot surveys and our reconnaissance, we developed a plot sampling technique to sample three broad classes of jack pine density in the outwash and ice-contact zones. The classes are: low or sparse (0-18% coverage), medium (19-32%), and high or dense (over 32%). Because of the patchy nature of jack pine regeneration, very few areas 10 x 20-m in size have a coverage over 32%. The 10 x 20-m density plots were designed so they could also serve as ecosystem plots. A soil pit was not dug, but the soil profile was described by a single auger boring. The following data was taken on the density plots:

a) number of jack pine seedlings in each of the 8, 5 x 5-m² subplots of a 10 x 20-m plot.

b) the height class (at end of 1985 growing season = 1986 whorl) of all jack pines within subplots (classes: (1) less than 50 cm, (2) 50-100 cm, (3) 100-150 cm, (4) 150-200 cm, (5) 200-250 cm).

c) salvage status.

d) openness class (sparse, medium, dense).
e) size of the largest opening adjacent to any corner of the plot.

f) notes on patchiness.

g) data on 10 sample trees in two, 5 x 5-m² subplots; one plot was randomly selected at the north end of the main plot and one plot was randomly selected at the south end of the main plot. The following information was taken on the 10 trees nearest the plot stake:

(1) age.
(2) height (cm) at 1986 whorl (through the 1985 growing season).
(3) stem diameter at 15 cm above ground line.
(4) dbh if over 1.3-m tall.
(5) height (cm) of lowest branch above ground line.
(6) crown diameter (cm) at widest point (2 readings perpendicular to each other).

h) The following data were taken on the tree tallest jack pines in each subplot: height (cm) at each yearly whorl (1986, 1985, 1984, 1983, etc.); length (cm) of 4 main branches by whorl (1986, 1985, 1984, etc.); vertical distance between proximal and distal ends of 4 branches.

i) diameter stump height or breast height of each stump or snag.

j) number of northern pin oak clones and number of ramets (sprouts) per clone.

k) number of northern pin oak seedlings.

l) height (m) of tallest oak stem.

m) percent coverage of jack pine, northern pin oak, oak plus pine, other species.

n) coverage of all ground-cover species in the two randomly selected 5 x 5-m subplots.

o) average height of all ground-cover species in 2 randomly selected 1 x 1-m plots in each subplot.

Within the outwash zone small depressions with trapped air drainage proved to have different vegetation than adjacent uplands. In particular, northern pin oak was conspicuously lacking, jack pines were small, and their current leaders were damaged (deformed or killed) by frost. Following the major frost on May 19, the northern pin oak clones surrounding depressions were severely damaged— all new foliage killed on many plants. In addition, serviceberry (Amelanchier spp.) and snowberry (Symphoricarpas albus (L.) Blake) were typically present to common in depressions but often absent or infrequent in the adjacent uplands. Serviceberry is one of the first shrubs/trees to flower and flush leaves in the spring and thus known to be highly resistant to frost.
Maximum-minimum thermometers were set up in shallow and deep depressions and on uplands adjacent to each depression. Minimums were always lower and maximums were always higher in the depressions than on the adjacent uplands. Below freezing temperatures were found in June, July, and August, even in the shallow depression (4.2 m below the upland).

Soil sampling and use of soil auger showed that the soils of the uplands and adjacent depressions were not different, except that some of the depressions were subirrigated. However, this moisture was at depths below the rooting zone of the ground-cover, and probably most of the young pines as well. Thus, widespread ecosystem types were identified in the outwash zone -- uplands and depressions with trapped air drainage. They differ primarily in physiography and microclimate and secondarily in vegetation.

1987 Field Season

The principal field research in 1986, Michael Bosio, unexpectedly dropped out of school in January 1987. An entirely new student research team of Corinna Theiss and Xiaoming Zou was recruited.

Soil analyses for most of the samples collected in 1986 were conducted in winter 1987 and proved useful in guiding the research in 1987. These analyses included standard mechanical analyses and pH determination.

During May 1987, the 1986 plots and many additional areas were visited to become familiar with the spectrum of ecosystems present. Topography, soils (augured to 1.8 m), and vegetation was described at each place during this reconnaissance.

During the reconnaissance, eight depressions and one outwash channel were identified for studying temperature differences between the low point of the depression and the general level of surrounding terrain. Four depressions were located in the low-level outwash plain and four were located in the high-level outwash/hilly ice-contact terrain. The depressions were selected to represent shallow, moderate, and deep depressions.

Maximum-minimum thermometers were placed in depression bottoms and at the edge of the depression at the general upland level. In two depressions, a NE-SW transect was instrumented with thermometers to assess the temperature gradient. Thermometers were kept at the same locations throughout the summer, and the entire set read 32 times during the summer. Vegetation surrounding all the thermometers were recorded. In addition, elevational transects between thermometer locations were made in all depressions to establish the exact elevation change.

After the reconnaissance phase, new ecosystem plots were located and sampled. Plot locations were selected using information from reconnaissance notes, soil maps, aerial photographs, and the jack pine density map. Plots were selected randomly within an ecosystem type.

Soil, vegetation, and physiographic data were recorded on all plots. A soil pit was dug to 150 cm. Horizons to 150 cm were described by texture, thickness, pH, structure, color, and percent pebbles and cobbles. Soil was augered and described to 400 cm, unless obstructed by a thick pebble-cobble
layer. Coverage of all groundcover vascular species was estimated using the same method as in 1986. All jack pines on each plot were tallied, and their heights were measured by height classes. Some additional data on jack pine height were taken on plots established in 1986.

All plots were permanently marked with 1/2-inch reinforcing rods in the NE corner of the plot.

Visits were made to other Kirtland's warbler areas to compare the physiography and soil conditions with those of the Mack Lake Burn.

Pattern of jack pine occurrence

A study of the pattern of jack pine occurrence (contagious, random, regular) was conducted using the ecosystem plots. Twenty-three plots were sampled in the following ecosystem types: 1, 3, 4, 6, 8, 9, and 10. The number of plots sampled in each ecosystem is shown below:

<table>
<thead>
<tr>
<th>Ecosystem number:</th>
<th>1</th>
<th>3</th>
<th>4</th>
<th>6</th>
<th>8</th>
<th>9</th>
<th>10</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of plots sampled:</td>
<td>4</td>
<td>2</td>
<td>3</td>
<td>3</td>
<td>5</td>
<td>3</td>
<td>3</td>
</tr>
</tbody>
</table>

Eighteen of the samples were taken in plots established in 1987, and 5 samples were taken in plots established in 1986.

Warblers were observed to occur in certain localities of ecosystem types 6, 7, 8, and 10 in the high-level outwash terraces and ice-contact terrain and in scattered parts of ecosystem 1 in the low-level outwash plain. Warblers were not observed in ecosystem 9 in the former area and ecosystems 3 and 4 in the latter area. The major objective of the study was to determine if there was any difference in the pattern of jack pine occurrence where warblers had and had not been observed — regardless of ecosystem type. Thus, the pattern of jack pine occurrence was studied in ecosystem plots near warbler sightings or nests in ecosystems 1, 6, 8, and 10. Plots were also sampled where no birds were observed in ecosystems 3, 4, and 9, and in one locality of ecosystem 6 where birds also were not noted.

Data was collected by two sampling procedures:

1. In each plot the distance from each of 50 randomly located points to the nearest jack pine tree was determined.

2. In each plot the distance from each of 50 randomly located jack pines to the nearest neighbor (jack pine) was determined.

Random points within each plot were determined by a system of coordinates. Random locations were determined along each side of the 10 x 20-meter plot by determining random distances in decimeters from the northeast corner of the plot. The intersection of lines from the two random locations determined a given random point. The random jack pine trees were selected from a random number table depending on the number of pines in each plot. Given a random number and starting at the northeast corner, trees were counted until the random tree was determined.
Methods of Hopkin-Skellam (1954), Clark-Evans (1954), and Pielou-Mountford (Pielou 1962) were used to test whether the pattern of pine distribution was contagious, random, or regular. Two-way analysis of variance (ANOVA) was used to test for significance of jack pine distribution among ecosystems and the three methods used. T-tests of multivariate comparisons for all ecosystems were made using a SAS program.

RESULTS AND DISCUSSION

The results of research to date are presented below in several sections. A brief summary of the major results, corresponding to these sections, are as follows:

1. Eleven local ecosystem types, based on physiography/landform, soil, vegetation, and microclimate, were distinguished. They represented two major landscapes of the burn: the low-level outwash plain that surrounds Mack Lake itself in the northern part of the area and the high-level outwash and ice-contact terrain on higher land on the southern part (see below Table 1 and Fig. 1). Differences in physiography, soil, vegetation, and climate also distinguish these two major landscapes.

The low-level outwash plain differs from the high-level outwash and ice-contact terrain by (1) lower absolute elevation and hence a somewhat colder climate (especially in the depressions and outwash channels), (2) coarse sand and relative lack of fine-textured bands, i.e., lower moisture and nutrient availability, (3) shallower depressions, (4) less diverse ground-cover flora, (5) somewhat less dense, less patchy (less contagious pattern), and somewhat shorter jack pine regeneration.

Besides the overall differences in the lower/northern and the higher/southern parts of the burn, discernible differences were found in the ecosystem structure and climate of local ecosystem types within each area. However, a high degree of variability characterizes both the northern and southern parts of the burn and many attributes of the ecosystem types. Jack pine height, density, and patchiness may be affected by pre-burn and post-burn factors (stand age, density, and hence, seed availability; interplanting of red pine; severity of burn; kind and degree of salvage) that may be independent of ecosystem type.

2. Occupancy of the burn by the Kirtland's warbler, both in 1986 and 1987, was greater in ecosystems of the high-level outwash and ice-contact terrain than in the low-level outwash plain. Warbler sightings and nests were associated with relatively tall and dense jack pine stands of patchy (contagious pattern) occurrence in ecosystems 6, 7, 8, and 10. Depressions, in both the low- and high-level areas, were not occupied by the warbler.

3. Results of a quantitative study of the pattern of occurrence of jack pine regeneration (contagious vs. random, vs. regular) indicated that pines typically exhibited a contagious (patchy) pattern in areas of known warbler occurrence in several difference ecosystem types -- especially of the high-level outwash and ice-contact terrain. In contrast, the pattern of the study plots tended to be random in ecosystem types where the warbler was not observed.
4. Marked differences in microclimate were found between depressions and adjacent uplands in both the low-level outwash plain and in the high-level outwash and ice-contact terrain.

5. Major differences in ground-cover vegetation were observed between the low-level outwash plain and the high-level outwash and ice-contact terrain and among local ecosystem types in each of these areas.

6. Significant differences were found in jack pine density and 1985 height among ecosystem types. Variation among plots within ecosystems was great. Biologically meaningful trends were found among ecosystem types, although some ecosystem means were not significantly different.

The sections below provide specific results and discussion concerning each of the above points.

1. Tentative ecosystem classification

Eleven local ecosystem types were distinguished, based on field observations and analysis of plot data (Table 1). Glacial, water-laid deposits were different in the northern and southern parts of the burn, and these two parts are identified in Table 1 and Fig. 5: the low-level outwash plain in the northern part surrounding Mack Lake and the high-level outwash and ice-contact terrain on the higher land to the south. The wetland areas around Mack Lake and scattered wet depressions in the northern part of the burn were not considered in the study.

Great local variation was found in topography, soil, and microclimate in both the northern and southern parts because of the highly variable nature of water-laid deposits. Whereas one or two ecosystems in each of these areas would be desirable from a user standpoint, we found it unavoidable to recognize more ecosystem types because of coincident differences in topography, soil, microclimate, and vegetation.

Initially only two difference ecosystem types were distinguished for the low-level outwash plain -- an upland sand type (ecosystem 1) and depressions (ecosystem 5) characterized by freezing conditions in late spring and early summer. However, two ecosystems were insufficient to encompass the variability of the entire northern area. Thus, we added a channel ecosystem type which differed in topography, soil, microclimate, and vegetation from the "depression" type. Because the Kirtland's warbler is known to avoid cold areas, we gave special attention to microclimate in distinguishing ecosystems of the burn. A rare but distinctive type (ecosystem 3) occurs where thick clay loam or clay bands are found below 1 meter. In addition, some areas were found to differ from the "standard" upland type 1 in that they were slightly elevated, had finer textured soils and often thin textural bands, and a different vegetation (ecosystem 2). The tentative recognition of five ecosystem types (Table 1) will be tested by quantitative analysis.

In the high-level outwash and ice-contact terrain, we attempted to identify the same pattern of ecosystem types as in the low-level outwash plain. The analogous ecosystem of type 1 is type 6; type 9 is analogous to to ecosystem 3 in having a clay band in the subsoil; ecosystem 11 is the comparable depression type 5 in the north; and type 8 is most closely related to ecosystem 2.
Table 1. Local ecosystem types of the Mack Lake Burn.

I. Low-level outwash plains (Elevation 1160-1220 ft).
   A. Upland topography (flat to gently sloping, depressions <5 ft); excessively to somewhat excessively drained.
      1. Medium and medium-fine sand, very infertile soils.
      2. Medium sand, infertile soils in areas of higher relative elevation between the major outwash channels.
      3. Sand to loamy sand over bands of fine texture.
   B. Channels and depressions; excessively to somewhat excessively drained.
      4. Outwash channels (usually 20-50 ft deep) with a distinct pebble/cobble layer.
      5. Depressions (5-20 ft deep) with extreme microclimate; soils as in ecosystems 1, 2, or 3.

II. High-level outwash and ice-contact terrain (Elevation 1220-1280 ft).
   A. High-level uplands (flat to moderately steep slopes); excessively to somewhat excessively drained.
      6. Outwash, gently sloping topography, infertile, medium sand.
      7. Outwash, flat topography, typically very infertile, >25% fine sand in top 50-70 cm.
      8. Outwash, slightly infertile loamy sand to sand soils; 5-10 cm (cumulative) of fine textural bands.
      9. Outwash, slightly to moderately infertile, loamy sand soil or a relatively thick textural band (>10 cm).
      10. Ice-contact terrain, infertile sandy kamic hills.
   B. Depressions.
      11. Depressions (6-50+ ft) with extreme microclimate; soils as in ecosystems 6-10.
Fig. 5. Mack Lake burn area, Oscoda, Co., Michigan showing tentative location of low-level outwash plain (north of dashed line) and the high-level outwash terraces and ice-contact terrain (south of dashed line). Small numbers indicate plot locations and ecosystem type number. Approximate areas of outwash channels and ice-contact terrain are also shown (see key).
Ecosystems 7 (fine sand) and 10 (hilly ice-contact soils) have no counterparts in the low-level outwash plain, and no channels exist in the southern part of the burn.

A concise description of the physiography and soil for each ecosystem type is presented on the following pages.

Description of Ecosystems

ECOSYSTEM 1: Low-level outwash plain -- deep, acid, medium and medium-fine sand.

PHYSIOGRAPHY

Flat to gently sloping outwash plain (0-6% slope). Elevation is from 1198-1217 ft. This is lower than all other upland ecosystems.

SOILS - Grayling series

Texture: Deep medium sand without lamellae or bands of finer-textured soils. Medium sand with 20-40% fine sand plus very fine sand.

Drainage: Excessively drained. No fine textured layers to slow drainage.

Development: A/E horizon generally from 2.5-3.5 cm thick; C horizon is found at an average depth of 101 cm.

Stone and Gravel Content: Typically no distinct pebble/cobble bands in the top 150 cm. Small amounts of pebbles may be scattered throughout the B horizon; total content typically less than 2%. Gravel or pebble bands frequently found at depths between 200-400 cm.

pH: Weighted pH of upper 150 cm is typically most acid of all ecosystems. From 10-30 cm the weighted pH averages 4.9, from 30-150 cm pH averages 5.0. Average depth to a field pH of 7 is one of the deepest of all ecosystems averaging 302 cm, and ranging from 200-400 cm.

DISCUSSION AND COMPARISON WITH OTHER ECOSYSTEMS

This ecosystem covers a major portion of the low-level outwash plain and may be considered the standard, non-depression ecosystem type for the low-level outwash plain.

Distinguished from ecosystem 2 by lower relative elevation, more acid sand to greater depths. Distinguished from ecosystem 3 by lack of significant fine textured bands.
Description of Ecosystems (continued).

ECOSYSTEM 2: Higher, isolated outwash areas between major channels in low-level outwash plain; deep medium sand.

PHYSIOGRAPHY

Flat to gently sloping (0-6% slope). Relatively higher, isolated outwash areas between major channels of the low-level outwash plain.

SOILS

Texture: Deep medium sands. Fine sand plus very fine sand may compose up to 25% of the soil. Coarser gravel layers may be found at depths from 120-400 cm.

Drainage: Excessively drained.

Development: A/E horizon is 3-4 cm thick. The C horizon is found at an average depth of 94 cm.

Stone and Gravel Content: Small amounts of pebbles may be scattered throughout the upper 150 cm. May or may not have distinct pebble/cobble layer.

pH: Weighted pH from 30-150 cm averages 5.6. Average depth to a field pH of 7 or greater occurs at 168 cm.

DISCUSSION AND COMPARISON WITH OTHER ECOSYSTEMS

The isolated, relatively higher topographic position within the low-level outwash plain indicates a slightly different history in water deposition of soil particles or erosional events.

Distinguished from the low-level outwash plains of ecosystem 1 by its relatively higher and isolated position in the outwash plain, its higher pH from 30-150 cm, its shallower depth to an average pH of 7, and its slightly thicker E horizon. Ecosystem 2 tends to have more coarse plus very coarse sand and less fine plus very fine sand than ecosystem 1.
Description of Ecosystems (continued).

ECOSYSTEM 3: Sands or loamy sands over bands of finer textured soil in low level outwash plain.

PHYSIOGRAPHY

Flat to gently sloping outwash plain (0-3% slope). Found at any elevation in outwash plain area.

SOILS

Texture: Medium and fine sands or loamy sands over bands (total thickness greater than 10 cm) of finer textured soils (loam, clay loam, and clay). Bands at depths up to 3 meters.

Drainage: Somewhat excessively drained to well drained. Drainage impeded by bands of finer textured soils at various levels, usually below 50 cm.

Development: Oe/Oa horizon relatively thick (typically 2.5-4.5 cm thick); A/E horizon typically 3-4 cm thick; C horizon found at an average depth of 115 cm.

Stone and Gravel Content: Small amount of pebbles may occur in top 150 cm.

pH: Weighted pH from 30-150 cm is relatively high, averaging 6.1. Average depth to field pH of 7 or greater occurs at 157 cm, and at least by the depth of the finer textured band.

DISCUSSION AND COMPARISON WITH OTHER ECOSYSTEMS

Distinct from all other low-level outwash ecosystems due to its band(s) of finer textured soils, it sometimes loamy sand horizons in the top 150 cm, and its higher pH at depths from 30-150 cm. The fine textured bands significantly increase moisture and nutrient availability.
Description of Ecosystems (continued).

ECOSYSTEM 4: Outwash channel-frost pocket; deep, somewhat excessively drained sands with distinct pebble/cobble layer in top 50 cm.

PHYSIOGRAPHY

Major outwash channels formed at the time of ice melting. Channels are typically 30-50 feet below the general land level, and act as cold air sinks, especially on days with little wind. The channel area is flat with slopes ranging from 0-2%, and has a 1-7 mi. distance between channel walls.

SOILS

Texture: Deep medium sands with variable amounts of fine plus very fine sand. Within the top 50 cm is a distinct pebble/cobble layer. Some areas in the channel may have horizons with a greater percent of fine and very fine sands or layers of finer textured soil.

Drainage: Somewhat excessively drained. Cobble/pebble band slows drainage somewhat.

Development: Thickness of the A/E horizon varies considerably. The C horizon begins at an average depth of 97 cm.

Stone and Gravel Content: Mainly limited to a pebble/cobble band within the top 50 cm. The pebbles and cobbles occupy greater than 30% of the volume of the band. Stones and gravel generally are not scattered throughout horizons.

pH: Weighted pH from 30-150 cm averages 5.9. Average depth to field pH of 7 or greater occurs at 170 cm.

DISCUSSION AND COMPARISON WITH OTHER ECOSYSTEMS

Distinguished from other outwash ecosystems by lower relative elevation, colder lower minimum temperatures, and slightly better moisture conditions (due to the pebble/cobble layer in the top 50 cm).

Distinguished from depressions in low-level outwash by not trapping cold air as well, and by its distinct pebble/cobble layer.
Description of Ecosystems (continued).

ECOSYSTEM 5: Low-level outwash plain depressions with sand to sandy loam soils.

PHYSIOGRAPHY

Depressions in outwash plain, typically 5-20 ft lower than surrounding land level.

SOILS

Texture: Soils variable since the more extreme microclimate (lower minimum temperatures and higher maximum temperatures) is the overriding factor. Medium sands (with 25-40% fine sand) to loamy medium sands. May include bands of finer textured soils.

Drainage: Somewhat excessively to excessively drained; drainage may be slowed by loamy soil, topsoil and textural bands.

Development: A/E horizon moderately to well developed (4 cm thick on average) probably due to the more dense grass roots. Upper B horizon typically less yellow or darker and grayer in color than those in outwash uplands. Depth to C horizon varies greatly.

Stone and Gravel Content: Typically with 0-1% pebbles and cobbles in top 150 cm, though a pebble/cobble band may be present.

pH: Weighted pH from 30-150 cm is relatively low, averaging 5.1. pH from 10-30 cm also averages 5.1. Depth to field pH of 7 or greater is relatively deep, being 248 cm on average.

DISCUSSION AND COMPARISON WITH OTHER ECOSYSTEMS

Distinguished from upland outwash ecosystems by its locally lower topographic position, resulting extreme microclimate, relatively thick A/E horizon, less yellow or darker and grayer upper B horizon. Distinct from the outwash channel by a typical lack of definite pebble/cobble layer, and a less yellow or darker and grayer darker upper B horizon.

The lower relative elevation of the depressions results in lower minimum temperatures due to the trapping of cold air. Minimum temperatures for depressions of all depths (from 5-16 ft) varied similarly with respect to their associated uplands -- depression minimum temperatures were 4-7°F lower than the upland minimum temperatures. Differences in maximum temperature did not show such a clear trend in temperature differences.
Description of Ecosystems (continued).

ECOSYSTEM 6: High-level outwash with deep medium sands.

PHYSIOGRAPHY

Flat to gently sloping terrain (0-5% slope); elevation 1210-1250 ft -- 20-40 ft higher than ecosystems in the low-level outwash plain.

SOILS

Texture: Deep medium sand; up to 25% fine sand plus very fine sand.

Drainage: Excessively drained.

Development: A/E horizon moderately well-developed 4 cm thick on average; C horizon found at an average depth of 95 cm.

Stone and Gravel Content: Pebbles/cobbles scattered in top 150 cm, pebble/cobble bands sometimes present. Gravel bands found at depths of 150-350 cm.

pH: Weighted pH from 10-30 cm averages 5.1. pH from 30-150 cm averages 5.5. Average depth to field pH of 7 extremely variable, ranging from 73-370 cm.

DISCUSSION AND COMPARISON WITH OTHER ECOSYSTEMS

Distinct from other high-level outwash ecosystems 8 and 9 by lack of finer textured layers or bands. Distinguished from ecosystem 7 by having less than 25% fine plus very fine sand from 10-30 cm, or by lacking very thin bands of finer textures. Distinguished from ecosystem 10 by flatter topography.

Distinguished from low-level outwash plain ecosystems 1 and 2 by higher absolute elevation, hence warmer microclimate.
Description of Ecosystems (continued).

ECOSYSTEM 7: High-level outwash; relatively high content fine sand and/or thin bands of finer textured soils totalling less than 5 cm in thickness.

PHYSIOGRAPHY

Flat with 0-2% slopes; elevation 1210-1250 ft.

SOILS

Texture: Deep sands with 25% or greater of fine sand plus very fine sand from 10-30 cm. May have lamellae of fine textured soil totalling less than 5 cm in thickness.

Drainage: Somewhat excessively drained to excessively drained. Drainage slowed slightly by the fine sand and/or bands of finer textured soil.

Development: The A/E horizon averages 3.7 cm. The depth of the C horizon is one of the shallowest of the ecosystems, occurring at an average depth of 64 cm.

Stone and Gravel Content: Pebbles or cobbles may be absent or present.

pH: Weighted pH from 30-150 cm averages 5.2. Average depth to a field pH of 7 or greater is moderately deep at 223 cm.

DISCUSSION AND COMPARISON WITH OTHER ECOSYSTEMS

Distinct from ecosystem 6 by having greater than 25% fine plus very fine sand from 10-30 cm, or by having very thin bands of finer texture. Distinct from ecosystems 8 and 9 by lacking bands of finer texture, or if present these bands have a total thickness less than 5 cm. Distinct from ecosystem 10 by flatter topography, and usually having a slightly thinner E horizon. Ecosystem 7 also has a typically thin Oe/0a horizon (averaging 1 cm thick), and a relatively shallow B horizon.

Distinguished from low-level outwash ecosystems by its greater absolute elevation and is typically flatter topography.
Description of Ecosystems (continued).

ECOSYSTEM 8: High-level outwash; loamy sand and medium to fine sand in upper B horizon over bands of loam totaling 5-10 cm in thickness.

PHYSIOGRAPHY

Nearly flat to gently sloping (1-5% slope); elevation 1210-1250 ft.

SOILS

Texture: Loamy sand from 10-30 cm. From 30-150 cm medium sand with 30-40% fine plus very fine sand and with bands of finer texture (usually sandy loam) with a total thickness of 5-10 cm found at depths of 70-170 cm.

Drainage: Somewhat excessively drained. Drainage is slowed by loamy sands in the upper B horizon and by bands, totaling 5-10 cm in thickness, of finer textured soils.

Development: C horizon is found at an average depth of 105 cm.

Stone and Gravel Content: Some pebbles and cobbles either scattered throughout B horizon or found in a layer within the top 150 cm.

pH: Weighted pH from 30-150 cm is relatively high averaging 5.8, typically greater than 5.4. Average depth to field pH of 7 or greater is relatively moderate, occurring at 200 cm.

DISCUSSION AND COMPARISON WITH OTHER ECOSYSTEMS

Distinct from other high-level outwash terraces by having loamy sand and sand on bands of loam totaling 5-10 cm in thickness. pH from 30-150 cm is greater than 5.4 while those of ecosystem 7 and 10 are typically less than 5.4. Distinct from ecosystem 10 by having flatter topography.

Distinguished from low-level outwash ecosystems by its greater absolute elevation.
Description of Ecosystems (continued).

ECOSYSTEM 9: High-level outwash; loamy sand throughout upper 80 cm or sands and
loamy sand over a layer of finer-textured soil (sandy loam to
clay) greater than 10 cm thick.

PHYSIOGRAPHY

Flat to gentle slopes (0-2% slope); elevation 1215-1250 ft.

SOILS

**Texture:** Loamy sand throughout upper 80 cm, or loamy sand and sands (medium
or fine) in upper horizons underlain by a single layer greater than 10 cm
of finer textured soils (loam, clay loam, or clay), at depths from
60-120 cm.

**Drainage:** Somewhat excessively drained. Drainage slowed by loamy sand
horizons in top 150 cm and bands (greater than 10 cm thick) of finer
textured soils.

**Development:** A/E horizon relatively thick, ranging from 3-5 cm. C horizon
found at a moderate depth of .93 cm on the average.

**Stone and Gravel Content:** Pebble and cobbles found scattered throughout some
horizons or in definite layers in a horizon. Pebbles and cobbles occupy
1-13% of top 150 cm.

**pH:** Weighted pH from 30-150 cm averages 5.6. Average depth to pH of 7 or
greater occurs at a depth of 167 cm.

DISCUSSION AND COMPARISON WITH OTHER ECOSYSTEMS

Distinguished from ecosystem 7 and 8 by loamy sand throughout upper 80 cm
or a single band (greater than 10 cm thick) of finer textured soil, and
resulting improved moisture and nutrient availability.

Distinct from low-level outwash plains ecosystems by its higher absolute
elevation.
Description of Ecosystems (continued).

ECOSYSTEM 10: Ice-contact terrain.

PHYSIOGRAPHY

Hilly land with slopes varying from 3-30°; elevation 1240-1280 ft.

SOILS - Roselawn series

Texture: Deep medium sand with up to 40% fine plus very fine sand. Coarse sand and gravel often found at depths of 200-400 cm.

Drainage: Excessively drained.

Development: A/E horizon is moderately well developed ranging from 4-6 cm and averaging 4.5 cm. Depth to C horizon is moderate, average 95 cm.

Stone and Gravel Content: Pebbles and cobbles may be scattered throughout soil horizons in the top 150 cm.

pH: Weighted pH from 30-150 cm averages 5.2. Depth to pH of 7 or greater is relatively deep averaging at about 264 cm.

DISCUSSION AND COMPARISON WITH OTHER ECOSYSTEMS

Very hilly topography distinguishes this ecosystem from all others. Distinct from depressions due to higher relative elevation and resulting milder microclimate.
Description of Ecosystems (continued).

ECOSYSTEM 11: Depressions in high-level outwash or in ice-contact terrain.

PHYSIOGRAPHY

Depressions located at general land level of 1210-1260 ft. Depressions depths vary from 9-50 ft below the surrounding general land level.

SOILS

Texture: Variable since more extreme microclimate (higher maximum temperatures and lower minimum temperatures) is the overriding factor. Often with medium to medium/fine sand and loamy sand horizons, though top horizons can vary from sandy loam to sand. Sandy loam bands may be present up to depths of 300 cm.

Drainage: Varies from excessively to well drained.

Development: A/E horizon typically thickest of all ecosystems, averaging 8.4 cm. The B horizon is typically darker and grayier than that of upland ecosystems (often with a Munsell color notation of 10 YR 3/4). Average depth to C horizon is relatively shallow -- 76 cm.

Stone and Gravel Content: Variable; pebbles and cobbles absent or found concentrated in some soil horizons.

pH: Weighted pH from 30-150 cm averages 5.2. Depth to pH of 7 or greater is moderately deep, ranging from 200-400 cm.

DISCUSSION AND COMPARISON WITH OTHER ECOSYSTEMS

The depressions' lower relative elevation results in lower minimum temperatures due to the trapping of cold air. The difference between the depressions and its associated upland minimum temperatures increases with increasing depth in the high-level ecosystems.

Deeper depressions (those greater than 20 ft) have slightly higher (2-4°F) maximum temperatures than their associated uplands, whereas shallower depressions have slightly lower (2-4°F) maximum temperatures than their associated uplands.

Distinguished from ice-contact terrain and all high-level outwash ecosystems by lower relative topographic position and more extreme microclimate. Distinct from low-level outwash depressions by the higher absolute elevation of the general land level, the greater depression depths, and the greater occurrence of finer textured soil horizons. Distinguished from all other ecosystems by a thicker A/E horizon and a darker color in the upper B horizon.
2. Colonization and occupancy of the burn by Kirtland's warblers in relation to ecosystem types.

1986 was the first year of significant occurrence of the Kirtland's warbler on the burn: 14 singing males were noted by the census in June. Most of the males (71%) were heard or observed in the high-level outwash and ice-contact terrain of the southern part of the burn — probably in ecosystem types 7, 8, and 10 (Fig. 6).

In 1987, 58% of single males also were found in the southern area (Fig. 7), and 65% of the female observations/nesting sites (determined by John Probst, USFS, North Central Forest Experiment Station, St. Paul, MN) were in this high-level terrain (Fig. 8). Because of concern for disturbing the warblers, we were unable to determine exactly the ecosystems where each bird was singing or nesting. The study would be much more definitive if this could have been done. Such detail work is a high priority for future research as long as the birds are not significantly disturbed by observing their specific territories. However, because we could not exactly determine the conditions where each bird was observed (or was nesting) it is not possible to say the extent to which ecosystem factors of physiography, microclimate, soil, and vegetation or other factors, such as stand age and density, overstory composition, or burn intensity may account for the warbler's presence.

As a working hypothesis, we attribute the greater occupancy of the warbler in the high-level outwash terraces and ice-contact terrain (ecosystems 7, 8, 10), as compared to many parts of the low-level outwash plain, to (1) greater height of jack pine (see point 3 below), (2) greater density of pine regeneration, (3) greater patchiness of pine reproduction, and (4) greater ground-cover species diversity. We have not had time to examine other possible vegetative differences that might also in part explain this finding. These attributes are, in turn, related (but not exclusively) to the specific landform and soil features of the high-level terraces and ice-contact terrain.

However, other factors such as (1) pre-burn species composition, density, and age, (2) severity of burn, and (3) kind and degree of salvage may also explain in part the height, density, and patchiness of jack pine regeneration. For example, red pine had been planted in the jack pine stands in many places. As a result, the amount of jack pine seeds available is probably less (because of fewer jack pine trees) than in a pure jack pine stand. Also, we observed that where the burn was very intense — baring mineral soil and reducing the ground cover competition — the jack pines tended to be quite tall. In one area of ecosystem 1 in the low-level outwash, an upper slope that had been severely burned had much taller pines than adjacent less severely burned areas of the same ecosystem. The best example, however, of the effect of mineral soil seeded on jack pine height is the remarkable pine regeneration in fire breaks. Pines in the bottom of the freshly plowed strips were very dense and much taller than adjacent pines on burned surface that had not been plowed.

Although the majority of the warblers in 1986 and 1987 appeared to favor the high-level outwash terraces and ice-contact terrain, there were local areas of relatively dense, tall, and patchy jack pine regeneration in the low-level outwash on areas of better soil (ecosystems 1 and 2) and where a severe burn and abundant seed rain favored excellent regeneration. As pines in the low-level outwash become taller, more and more birds are expected to colonize this area.
Fig. 6. Mack Lake burn area, Oscoda, Co., Michigan. Location of landscape ecosystem types (small numbers) and location of singing, male (♂) Kirtland's warblers, June, 1986.
Fig. 7. Mack Lake burn area, Oscoda, Co., Michigan. Location of landscape ecosystem types (small numbers) and location of singing, male (♂) Kirtland's warblers, June, 1987.
In conclusion, the landscape ecosystem approach appears to provide a useful framework for understanding in large part the progression of occupancy by the warbler. It also provides a basis for understanding the abiotic factors (physiography, soil, microclimate) that are closely related to relative growth rate and density of the jack pines and oaks. Detailed examination of the ground-cover relationships by ecosystem type may reveal additional insights to the favorableness of certain ecosystems for early colonization by the warbler.

3. Pattern of jack pine occurrence

The results of the study of jack pine occurrence for individual plots, ecosystems, and type of method are shown in Table 2. A contagious (patchy) pattern of jack pine occurrence was typical of most plots studied that were near a warbler sighting or nest in ecosystem types 1, 6, 8, and 10 (Table 2). Either a low degree of contagion or a random pattern was observed for the plots studied in ecosystems 3, 4, and 9 where no warblers had been observed. All three methods (Clark-Evans, Hopkin-Skelan, and Pielou-Mountford) gave similar results -- as determined by the two-way ANOVA (Table 3). A significant difference (5% level) in the pine distribution patterns was found among different ecosystems (Tables 3 and 4).

Based on the criterion of a contagious jack pine pattern, areas suitable for warbler occupancy were found in ecosystems 1, 6, 8, and 10. These ecosystems appear to be more favorable for early warbler occupancy than areas in ecosystems 3, 4, and 9. We are examining the reasons for this relationship. Ecosystem 1 occupies large areas of the low-level outwash plain. Parts of it are suitable for warbler occupancy, but it has not yet been so widely occupied as ecosystems in the high-level outwash terraces and ice-contact terrain -- possibly due to less dense stands of jack pine and somewhat smaller trees. Nevertheless, the areas of ecosystem 1 that were occupied in 1987 exhibited a contagious pattern of pine occurrence.

To compare the more favorable and less favorable ecosystems for warbler occupancy, an additional two-way ANOVA was run again using the three methods. A significant difference (5% level) in jack pine pattern was found between the favorable and unfavorable ecosystem types (Table 5).

We recognize that the pattern of pine occurrence is only one factor favoring warbler occupancy of an area, and that the contagious pattern might be due to factors (pre-burn history, fire intensity) other than those determining ecosystem types such as physiography, soil, and microclimate. A given ecosystem does not necessarily have one pattern of pine occurrence.
Table 2. Pattern of jack pine occurrence (random vs. contagious) on selected ecosystems of the Mack Lake Burn.

<table>
<thead>
<tr>
<th>Eco-system</th>
<th>Warbler observed/ near plot?</th>
<th>Trees Sampled</th>
<th>Clark-Evans Statistic</th>
<th>Hopkins-Skellon Pattern Statistic</th>
<th>Pielou-Mountford Pattern Statistic</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Yes</td>
<td>50</td>
<td>4.17</td>
<td>C</td>
<td>6.75</td>
</tr>
<tr>
<td>1</td>
<td>Yes</td>
<td>49</td>
<td>1.90</td>
<td>R</td>
<td>4.58</td>
</tr>
<tr>
<td>1</td>
<td>Yes</td>
<td>50</td>
<td>2.19</td>
<td>C</td>
<td>4.53</td>
</tr>
<tr>
<td>1</td>
<td>Yes</td>
<td>50</td>
<td>4.76</td>
<td>C</td>
<td>3.78</td>
</tr>
<tr>
<td>3</td>
<td>No</td>
<td>50</td>
<td>1.15</td>
<td>R</td>
<td>1.77</td>
</tr>
<tr>
<td>3</td>
<td>No</td>
<td>50</td>
<td>1.80</td>
<td>R</td>
<td>5.73</td>
</tr>
<tr>
<td>4</td>
<td>No</td>
<td>50</td>
<td>4.11</td>
<td>C</td>
<td>0.23</td>
</tr>
<tr>
<td>4</td>
<td>No</td>
<td>50</td>
<td>1.15</td>
<td>R</td>
<td>2.39</td>
</tr>
<tr>
<td>4</td>
<td>No</td>
<td>50</td>
<td>1.89</td>
<td>R</td>
<td>1.19</td>
</tr>
<tr>
<td>6</td>
<td>No</td>
<td>50</td>
<td>4.02</td>
<td>C</td>
<td>5.61</td>
</tr>
<tr>
<td>6</td>
<td>Yes</td>
<td>50</td>
<td>2.09</td>
<td>C</td>
<td>4.03</td>
</tr>
<tr>
<td>6</td>
<td>Yes</td>
<td>50</td>
<td>3.37</td>
<td>C</td>
<td>15.05</td>
</tr>
<tr>
<td>8</td>
<td>Yes</td>
<td>50</td>
<td>3.77</td>
<td>C</td>
<td>3.42</td>
</tr>
<tr>
<td>8</td>
<td>Yes</td>
<td>50</td>
<td>4.29</td>
<td>C</td>
<td>5.79</td>
</tr>
<tr>
<td>8</td>
<td>Yes</td>
<td>50</td>
<td>2.22</td>
<td>C</td>
<td>3.65</td>
</tr>
<tr>
<td>8</td>
<td>Yes</td>
<td>50</td>
<td>2.82</td>
<td>C</td>
<td>2.85</td>
</tr>
<tr>
<td>8</td>
<td>Yes</td>
<td>50</td>
<td>6.35</td>
<td>C</td>
<td>19.68</td>
</tr>
<tr>
<td>9</td>
<td>No</td>
<td>50</td>
<td>3.13</td>
<td>C</td>
<td>2.57</td>
</tr>
<tr>
<td>9</td>
<td>No</td>
<td>50</td>
<td>1.36</td>
<td>R</td>
<td>2.73</td>
</tr>
<tr>
<td>9</td>
<td>No</td>
<td>50</td>
<td>0.42</td>
<td>R</td>
<td>1.21</td>
</tr>
<tr>
<td>10</td>
<td>Yes</td>
<td>50</td>
<td>3.24</td>
<td>C</td>
<td>6.49</td>
</tr>
<tr>
<td>10</td>
<td>Yes</td>
<td>50</td>
<td>4.30</td>
<td>C</td>
<td>6.97</td>
</tr>
<tr>
<td>10</td>
<td>Yes</td>
<td>50</td>
<td>2.10</td>
<td>C</td>
<td>2.85</td>
</tr>
</tbody>
</table>

1/ Yes = if a warbler, or warbler's nest was known to be near the plot; No = if a warbler, or warbler's nest was not near the plot.

2/ C = contagious distribution; R = random distribution.
Table 3. Comparison of pattern of jack pine occurrence on the Mack Lake Burn by ecosystem type and method of analysis.

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>Type ISS</th>
<th>F value</th>
<th>PR&gt;F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ecosystem</td>
<td>6</td>
<td>17.37</td>
<td>3.11</td>
<td>0.01</td>
</tr>
<tr>
<td>Methods^1/</td>
<td>2</td>
<td>0.28</td>
<td>0.15</td>
<td>0.86</td>
</tr>
<tr>
<td>Ecosystem x method</td>
<td>12</td>
<td>4.40</td>
<td>0.39</td>
<td>0.96</td>
</tr>
</tbody>
</table>

^1/Methods: Clark-Evans, Hopkin-Skellan, Pielou-Mountford.

Table 4. Comparison of pattern of jack pine occurrence by ecosystem type using T-test multivariate comparison.

<table>
<thead>
<tr>
<th>Ecosystem type</th>
<th>Mean</th>
<th>Significance^1/</th>
</tr>
</thead>
<tbody>
<tr>
<td>8</td>
<td>0.486</td>
<td>A</td>
</tr>
<tr>
<td>1</td>
<td>0.360</td>
<td>A</td>
</tr>
<tr>
<td>6</td>
<td>0.332</td>
<td>A</td>
</tr>
<tr>
<td>10</td>
<td>0.369</td>
<td>A C</td>
</tr>
<tr>
<td>4</td>
<td>-0.636</td>
<td>B C</td>
</tr>
<tr>
<td>9</td>
<td>-0.647</td>
<td>B</td>
</tr>
<tr>
<td>3</td>
<td>-0.735</td>
<td>B</td>
</tr>
</tbody>
</table>

^1/The same letter means no significant different among ecosystems (5% level).

Table 5. Comparison of favorable (1, 6, 8, 10) and unfavorable (3, 4, 9) ecosystem types and Kirtland’s warbler occupancy in the Mack Lake Burn.

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>Type ISS</th>
<th>F value</th>
<th>PR&gt;F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ecosystem Groups</td>
<td>1</td>
<td>17.02</td>
<td>21.71</td>
<td>0.0001</td>
</tr>
<tr>
<td>Method</td>
<td>2</td>
<td>0.24</td>
<td>0.15</td>
<td>0.86</td>
</tr>
<tr>
<td>Groups x method</td>
<td>2</td>
<td>0.04</td>
<td>0.02</td>
<td>0.98</td>
</tr>
</tbody>
</table>
4. Temperature differences in depressions vs. adjacent uplands

Below freezing minimum temperatures were recorded in the uplands and depressions bottoms in June (4, 6, 10), on July 15, and on August 24. Low-level temperatures, as a group, were significantly (p<.05) less than those of the high-level area. However, the average minimum temperature for the relatively shallow low-level depressions was similar to that of the deep high-level depressions (43.7°F vs. 43.8°F) (Table 6). The average maximum temperature in the high-level upland areas was 2.7°F warmer than those of the low-level uplands.

Table 6. Average daily minimum temperatures and average daily maximum temperatures in low-level and high-level outwash depressions and uplands.

<table>
<thead>
<tr>
<th></th>
<th>Low-Level Area</th>
<th>High-Level Area</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Depression Bottom</td>
<td>Upland</td>
</tr>
<tr>
<td>Minimum temperature (°F)</td>
<td>39.5</td>
<td>43.7</td>
</tr>
<tr>
<td>Maximum temperature (°F)</td>
<td>85.3</td>
<td>84.2</td>
</tr>
</tbody>
</table>

The minimum temperatures for all depression bottoms were significantly different (p<.05) from their associated upland minimum temperatures. In the low-level outwash region, the average depression bottom minimum temperature was 4°F lower than the associated average upland minimum temperature (Table 6). This same temperature difference was also recorded in the high-level outwash region (Table 6).

Differences in minimum temperatures from depression bottom to associated upland showed an increase with increasing depth of depression. The deepest (40 ft) depression had minimum temperatures 7-11°F lower than its associated upland. In contrast, the shallowest (6 ft) depression had minimum temperatures 2-4°F lower than the upland. Moderate depressions showed an intermediate difference.

The maximum temperatures for all depression bottoms were not significantly different (at the .05 error level) from their associated upland maximum temperatures. However, the deeper (greater than 20 ft) high-level depressions had maximum temperatures 2-4°F higher than their associated uplands. In contrast, the shallower (less than 20 ft) had maximum temperatures 2-4°F lower than their associated uplands. This indicated that the deeper depressions receive significant reradiation of heat from the depression walls compared to reradiation in shallower depressions.

Depressions in the high-level outwash and ice-contact area (ecosystem 11) are similar to those in the low-level outwash plain in that they have oak seedlings in the ground cover (often dying back due to frost), but they lack oak seedlings greater than 1 cm dbh. The vegetation of ecosystem 11 is different from the low-level outwash depressions by the presence of many Prunus serotina seedlings, saplings, and sprouts (often 3-4 m tall). Also, there is a greater frequency and coverage of the wide-leaved grasses, Oryzopsis asperifolia and
Schizachne purpurascens. These vegetative differences reflect the better nutrient and moisture conditions in ecosystem II.

New shoot growth and emerging leaves on oak sprouts were especially susceptible to freezing damage by the low minimum temperatures of depressions. Oaks in depressions tended to flush later. Hence, their leaves were more susceptible to freezing temperatures than the relatively older, more hardened leaves on the associated uplands. Thus, depressions typically lack vigorous oak seedlings or sprouts. If oaks are present at all, they are stunted.

Oak seedlings may become established in depressions under the canopies of pre-fire jack and red pines. The crown cover of the pines acts to moderate the marked temperature difference between the bottom of a depression and the adjacent upland. Temperature readings from thermometers placed under a jack pine-northern pin oak overstory in both depression and adjacent upland showed no differences in minimum temperatures between the two locations. Once the overstory trees are killed by fire, however, the young seedling oaks are highly susceptible to freezing damage. Most have been killed in the 6-7 years since the fire and the onset of freezing temperatures in the depressions.

New shoot growth of jack pine was also visibly affected by freezing temperatures in June. New shoots of pines in depressions were affected more than in uplands due to the lower minimum temperatures in the depressions. Thus, the growth of jack pine in depressions was typically less vigorous than that of pines in non-depression areas (see Table 7).

Colder microclimate of the outwash channels and low-level outwash uplands (ecosystems 1 and 4) probably plays a role in slowing the growth of jack pines in these areas compared to the growth of jack pine in the high-level outwash and ice-contact terrain (ecosystems 6-10) where the climate may be slightly warmer. However, because soil moisture and nutrient status is confounded with elevation (soils tend to have more moisture and nutrients in the higher lands) the effect of temperature alone may be difficult to prove conclusively.

5. Vegetation differences among ecosystem types

Six ecological species groups, groups of plants exhibiting similar environmental requirements and named for a characteristic species, were determined. The species of each groups are given below followed by the characteristics of each group.

List of Groundcover Species in Ecological Species Groups

<table>
<thead>
<tr>
<th>Arctostaphylos uva-ursii Group</th>
<th>Vaccinium angustifolium Group</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arctostaphylos uva-ursii</td>
<td>Amelanchier sanguinea</td>
</tr>
<tr>
<td>Comptonia peregrina</td>
<td>Prunus pumila</td>
</tr>
<tr>
<td>Epigaea repens</td>
<td>Prunus virginiana</td>
</tr>
<tr>
<td>Antennaria neglecta</td>
<td>Vaccinium angustifolium</td>
</tr>
<tr>
<td>Polygala polygama</td>
<td>Helianthus canadensis</td>
</tr>
<tr>
<td>Potentilla tridentata</td>
<td>Houstonia longifolia</td>
</tr>
<tr>
<td>Andropogon gerardii</td>
<td>Solidago hispida</td>
</tr>
<tr>
<td>Andropogon scoparius</td>
<td>Solidago spathulata</td>
</tr>
<tr>
<td>Carex pensylvanica</td>
<td></td>
</tr>
<tr>
<td>Danthonia spicata</td>
<td></td>
</tr>
<tr>
<td>Panicum linearifolium</td>
<td></td>
</tr>
<tr>
<td>Oryzopsis pungens</td>
<td></td>
</tr>
<tr>
<td>Prunus pensylvanica Group</td>
<td>Ceanothus ovatus Group</td>
</tr>
<tr>
<td>-----------------------------------------------</td>
<td>----------------------------------------</td>
</tr>
<tr>
<td>Prunus pensylvanica</td>
<td>Ceanothus ovatus</td>
</tr>
<tr>
<td>Melampyrum lineare</td>
<td>Gaylussacia baccata</td>
</tr>
<tr>
<td>Physalis virginiana</td>
<td>Hamamelis virginiana*</td>
</tr>
<tr>
<td>Deschampsia flexuosa</td>
<td>Anemone cylindrica</td>
</tr>
<tr>
<td></td>
<td>Aster ptarmicoides</td>
</tr>
<tr>
<td></td>
<td>Convolvulus spithamaeus</td>
</tr>
<tr>
<td></td>
<td>Senecio pauperculus</td>
</tr>
<tr>
<td></td>
<td>Bromus kalmii</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Gaultheria procumbens Group</th>
<th>Rosa blanda Group</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amelanchier spicata</td>
<td>Acer rubrum</td>
</tr>
<tr>
<td>Crataegus Spp.</td>
<td>Populus grandidentata</td>
</tr>
<tr>
<td>Diervilla lonicera</td>
<td>Populus tremuloides</td>
</tr>
<tr>
<td>Gaultheria procumbens</td>
<td>Prunus serotina</td>
</tr>
<tr>
<td>Lonicera dioica</td>
<td>Rosa blanda</td>
</tr>
<tr>
<td>Fragaria virginiana</td>
<td>Rubus flagellaris</td>
</tr>
<tr>
<td>Pyrola elliptica</td>
<td>Salix humilis</td>
</tr>
<tr>
<td>Taenidia integerrima</td>
<td>Maianthemum canadense</td>
</tr>
<tr>
<td></td>
<td>Pteridium aquilinum</td>
</tr>
<tr>
<td></td>
<td>Oryzopsis asperifolia</td>
</tr>
<tr>
<td></td>
<td>Schizachne purpurascens</td>
</tr>
</tbody>
</table>

* = Did not occur in sample plots but was often associated with these species.

**Arctastaphylos uva-ursii**
Very wide range of occurrence: from very dry and very infertile to moderately moist and moderately fertile; species do not have greater coverage in sites with better moisture and nutrient conditions.

**Vaccinium angustifolium**
Very wide range of occurrence: from very dry and very infertile to moderately moist and moderately fertile; these species do take advantage of slightly better moisture and nutrient conditions by having greater coverage in dry, infertile areas.

**Prunus pensylvanica**
Ranges from very dry to very slightly moist, and very infertile to slightly infertile; species have greatest coverage in dry and very infertile sites.

**Ceanothus ovatus**
Ranges from very dry to dry and from infertile to slightly infertile; species have greatest coverage in very dry, slightly infertile sites.

**Gaultheria procumbens**
Ranges from very dry to moderately moist and from infertile to moderately fertile; not typically found in very infertile sites; species appear most often in very slightly moist, slightly fertile sites.

**Rosa blanda**
Ranges from dry to moderately moist and from infertile to moderately fertile; species do take advantage of the most fertile and moist sites by having greatest coverage in the moderately fertile and moderately moist sites.
The vegetation of the low-level outwash plain differs markedly from that of the high-level outwash and ice-contact terrain. Low-level outwash plain ecosystems (1-5) typically have the lowest species diversity and the greatest amount of bare ground. Ground-cover species that are commonly found include: Pinus banksiana, Vaccinium angustifolium, Carex pensylvanica, Prunus pumila, Quercus ellipsoidalis, Comptonia peregrina, Arctostaphylos uva-ursi, Hieracium venosum, Cladonia cristatella, Oryzopsis pungens, Panicum linearifolium, Viola adunca, Polytrichum juniperinum, and Polytrichum piliferum.

Species occurring in the high-level outwash terraces and ice-contact terrain, and not typically found in the low-level outwash plain are: Populus grandidentata, Populus tremuloides, Acer rubrum, Prunus pensylvanica, Prunus serotina, Vaccinium myrtilloides, Anemone cylindrica, Pyrola elliptica, Gaylussacia baccata, and Lonicera dioica.

Species in the Prunus pensylvanica group, the Ceanothus ovatus group, the Gaultheria procumbens group, and the Rosa blanda group are found mainly in the uplands of the high-level area. Whereas species of these three groups may be found occasionally in the uplands of the low-level outwash plains, their occurrence is infrequent, their coverage is low, and their presence would usually be in the less acid and higher elevated ecosystem 2, or in a relatively rich ecosystem 3.

Vegetational differences also occur among the low-level outwash plain ecosystems. Ecosystem 2 (less acid soils than ecosystem 1 and slightly higher relative elevation) supports some species that tend to occur more frequently on the high-level outwash terraces and ice-contact terrain. For example, Convolvulus spithamaeus, Rubus flagellaris, Ceanothus ovatus, Gaultheria procumbens, Rosa blanda, and Maianthemum canadense may be found as ground-cover in ecosystem 2 but typically do not occur in ecosystem 1. These species (except Gaultheria procumbens) belong to the Ceanothus ovatus species group and the Rosa blanda species group.

The better soil conditions of ecosystem 3, relative to ecosystems 1 and 2, are reflected in the increased shrubiness of the ground-cover. Ecosystem 3 has increased frequency, greater coverage, and greater height of the following shrubs: Rubus flagellaris, Salix humilis, and Rosa blanda. In addition, Oryzopsis asperifolia, Pteridium aquilinum, Fragaria virginiana, Maianthemum canadense, and Schizachne purpurascens occur at greater frequency and coverage than they do in ecosystems 1 and 2. Pteridium aquilinum and Oryzopsis asperifolia are particularly good indicators of ecosystem 3.

Outwash channels (ecosystem 4) and depressions (ecosystem 5) in the low-level outwash plain typically lack northern pin oaks greater than 1 cm dbh (diameter at breast height). The lack of large oaks is a significant indicator of the colder microclimates of outwash channels and depressions. On the slopes of the channel and walls of depressions, an elevational line occurs where oaks are no longer markedly stunted. These elevational oak lines indicate the point at which the microclimate is no longer substantially affected by the trapped cold air.

Although outwash channels and depressions both lack vigorous oaks, they differ from one another in their shrub and grass coverage. Specifically, Deschampsia flexuosa, Koeleria macrantha, and Schizachne purpurascens tend to be
more common and have greater coverage in depressions than in channel areas or in the low-level outwash plain uplands. In contrast, channel areas have greater shrub coverage than low-level outwash plain uplands and depressions. Specifically, channels have greater coverage of Prunus pumila, Diervilla lonicera, Vaccinium angustifolium, and Amelanchier sanguinea.

The high-level outwash/ice-contact ecosystem types typically have greater species diversity than those of the low-level outwash plain. For example, ecosystems 1 and 6 are similar in physiography and soil and differ only in their elevational position in the landscape. Plots in ecosystem 6 have 30-47 species (with 9-16 species of shrubs), while plots in ecosystem 1 have 15-31 species (with 3-8 species of shrubs). Most of the species found in ecosystem 6 not in ecosystem 1 belong to the Ceanothus ovatus species group and the Rosa blanda species group. Crataegus spp., Lonicera dioica, and Fragaria virginiana from the Gaultheria procumbens species group, as well as Prunus pensylvanica from the Prunus pensylvanica species group may also be found in ecosystem 6 but not in ecosystem 1.

Ecosystem 7, like ecosystem 1, has a low number of ground-cover species—due mainly to the very dense coverage of jack pine. Species in the Rosa blanda species group, the Gaultheria procumbens species group and the Ceanothus ovatus species group are not frequently found (nor do they have high coverage if found) in ecosystem 7. In contrast, species in the Prunus pensylvanica group are frequently found in ecosystem 7.

Ecosystems 8 and 9 have the richest soils and best moisture conditions of the high-level outwash/ice-contact area. Ecosystem 9, with its loamy sand upper horizon and/or thick fine textured band, has better nutrient and moisture relations than ecosystem 8. These better site conditions are indicated by its ground-cover—the densest and tallest of all ecosystems. A species most consistently associated with the more fertile, clay-banded soils is Dryopteris asperifolia. Other species more frequently found, and having higher coverage than in other ecosystems are: Maianthemum canadense, Rosa blanda, Rubus flagellaris, Lactuca canadensis, and Crataegus spp. With the exception of Crataegus spp., these species belong to the Rosa blanda species group.

Ecosystem types 6 and 10 both have predominantly medium sand soils. However, differences in vegetation, together with differences in topography (ecosystem 10 is found in very hilly terrain) help distinguish these ecosystems. Species such as Diervilla lonicera, Gaylussacia baccata, Prunus pensylvanica, and Melampyrum lineare are typically present in ecosystem 10 but not in ecosystem 6.

Northern pin oak, a major component of the overstory of mature forests of the Mack Lake area, is typically absent in depressions and outwash channels. Sprouting oak clumps were observed to increase markedly in abundance where clay loam or clay bands were within 1-3 m of the surface. Their deep tap root system are able to tap the moisture and nutrients of the heavy bands and thus respond vigorously in such situations. Oak is found throughout the burn area, except in depressions and outwash channels, but is particularly evident in ecosystem 3 in the outwash plain and ecosystems 8 and 9 in the high-level outwash/ice-contact area.
In conclusion, vegetative differences are found not only between the two major landform areas (low-level outwash plain vs. high-level outwash terraces and ice-contact terrain) but also occur among different ecosystems within each of these areas.

6. Density and height of jack pine

Significant differences in jack pine density and height were found among ecosystems (Table 7). Trends of average density appeared to be biologically meaningful based on field observations. The density of ecosystem 7 was significantly different from the densities of the other ecosystems. Also, average density of the depression ecosystems 5 and 11 was significantly different from the other ecosystems. Although some means were significantly different, many were not. The lack of significance is due to low number of sample plots per ecosystem type and the extremely high variation in plot density within the ecosystems.

Height of pines in ecosystems of the high-level outwash terraces and ice-contact terrain are generally greater than those of the low-level outwash plain, although most means are not significant from one another. In the high-level outwash area the tallest pines were in ecosystem 7 with fine sand soil. The fine sand, by providing greater moisture availability without significantly improved nutrient content, affords jack pine greater growth with less competition from other species. The shortest jack pines in the high-level outwash area are those in depressions -- jack pine growth is probably limited by the colder minimum temperatures as well as denser grass rooting. The growth of jack pine in the low-level outwash depressions is limited by these same factors.

In the low-level outwash area, jack pines in ecosystem 2 are often taller than those in ecosystem 1. Jack pines in ecosystem 3 are shorter than the jack pine in both ecosystems 1 and 2. The jack pine growth in ecosystem 3 is probably limited by the competition of the more abundant shrubs found in ecosystem 3. The jack pine in the depressions are also among the shortest in the low level.
LITERATURE CITED


ACKNOWLEDGMENTS

We wish to thank many individuals for their assistance and encouragement in the field work and other phases of the project. Dr. Sylvia Taylor has provided enthusiastic support and logistical assistance in both 1986 and 1987. Her encouragement has been invaluable. Jerry Weinrich has been extremely helpful in both years -- particularly because of his knowledge of the behavior of the Kirtland's warbler and the Mack Lake area. David Kline and the staff of the Mio Ranger Station of the Huron-Manistee National Forest, including Roger Moore, Randy Marzolo, and Phil Huber, were very helpful with maps, aerial photographs, and records. Rose Moore gave us a detailed settlement map which was quite useful. Dave Cleland provided us a soils map of the area, and Bill Jarvis gave us a copy of the pine diversity map of the area.

In 1987, Cameron Kepler and John Probst were particularly helpful to provide information about the location of warblers and assistance in field work. Cameron also helped us with information about aerial photos of the burn. Dr. Charles E. Olson, Jr. took aerial photographs for us of part of the burn in 1987.

We acknowledge the fine work of our field research assistants: Mike Bosio, Philip Stuart, Tom Simpson, and Jim Prine in 1986 and Kirk Radford in 1987.

We also wish to thank John Byelick and Harold Mayfield for their encouragement of our work.

Finally, Carole Shadley has done a superb job with proposals, reports, and correspondence throughout the project.