PATTERN OF JACK PINE OCCURRENCE IN ECOSYSTEMS OF KIRTLAND'S WARBLER SUMMER HABITAT AT MACK LAKE, NORTHERN LOWER MICHIGAN

BY

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CHAPTER I

INTRODUCTION

Background and Problem

Pattern in vegetation is the spatial arrangement of individuals of a species (Kershaw 1985). The study of pattern consists of two parts: the study of types and causes of pattern. The former is intended to reveal whether individuals of living populations have random, regular, or contagious arrangement. The latter is focused on the interrelationships between patterns of living populations and their natural environments.

The earliest accounts of the study of pattern types of plants in a community are those of Gleason (1920) and Svedberg (1922) who independently showed that several species were characterized by a non-random pattern of distribution of their individuals. Gleason employed the binomial distribution, whereas Svedberg made use of the Poisson series. Following their initial work, considerable effort has been made to detect non-randomness in vegetation. Several measures have been developed and used to test the hypothesis of random dispersion. Blackman (1935) used the -test of goodness-of-fit to test the departure from randomness of <u>Carex flacca</u> based on the Poisson series and on 200 quadrat samples. Clapham (1936), by making use of the equality of mean and variance of the Poisson distribution, developed the "variance: mean ratio" method which tests whether a population has a random, regular, or contagious pattern. Ashby (1935) suggested a method to test randomness which subdivides a random sample quadrat into a number of smaller squares and then compares the observed number of empty squares with the number of expected from the density within the quadrat. Moore (1953) further developed a method that is especially useful for very dense populations. Aberdeen (1958) pointed out that if frequency data are available from several sizes of quadrats, any departure from linearity in a graph of log percentage absence against quadrat size indicates non-random distribution. To test the significance of difference in pattern between two samples or two populations, David and Moore (1957) proposed the index of clumping (observed variance/observed mean - 1) which is zero for a random distribution. Morisita (1959) developed a measure of departure from randomness based on the measure of diversity proposed by Simpson (1949) rather than directly on the Poisson distribution. However, the data to which these measures have been applied are mostly counts of individuals or records of presence or absence in sample plots or quadrats and are generally expressed in terms of frequency. Such data are strongly influenced by the size of quadrat used in their collection (Curtis and McIntosh 1950, Pielou 1957, 1977, Kershaw 1985). Detailed discussion about these methods have been presented by Greig-Smith (1983) and Upton (1985).

To avoid the disadvantage of quadrat sampling, a number of wholly different methods have been developed. These methods are the so-called "plotless sampling" methods. What is examined is the spacing of the individuals, and there are two ways to proceed. One may locate sampling points at random and measure the distance from each random point to its nearest individual plant (point-to-plant), or, alternatively, select individual plants at random and measure the distance from each of these to its nearest neighboring individual (plant-to-plant). The distance of either point-to-plant or plant-to-plant provides a variable for the measurement of spacing that obviates the use of quadrats and therefore eliminates the effects of quadrat size. Dice (1952) seems to have been the first to use plant-to-plant distance in measuring departure from randomness. Dice's procedure consists of measuring the plant-to-plant distance in each of the six sextants of the circular area that surrounds the chosen "center of origin." However, the method is somewhat laborious. Clark and Evans (1954) later developed and simplified the method. The departure from randomness can be tested by their model based on the density of a population and the samples of plant-to-plant distances. At the same time, Hopkins (1954) generated a model to test the departure from randomness of a population by using the distances of both plant-to-plant and point-to-plant. Pielou (1959) has presented a method to determine the randomness of a population by using the combination of the density of the population and distances of point-to-plant. She described that the distance of point-to-plant is easier to obtain than that of plant-to-plant. Other methods of evaluating vegetation pattern have been summarized by Upton (1985) in detail.

Compared to the study of pattern types, the study of causes of pattern types has received less attention. It has commonly been accepted that the study of causal factors is the ultimate purpose of the study of pattern. People might conclude, through a statistical study, that trees in a forest tend to occur in clumps (contagious pattern). The conclusion might be correct and not surprising, but does not lead to any practical use. Ecology is largely concerned with the causes of pattern of distributions. The study of causal factors is especially useful in management for maintaining a contagious pattern of plant communities. Although it is much more difficult to study the causes of pattern, there has been substantial research in this area. Ashby (1948) pointed out that asexual spread and heavy seeds are the two most likely factors which cause aggregation of individuals. Goodall (1952) and Greig-Smith (1952) both suggested that cyclical regeneration in patches, as postulated by Watt (1947), could produce contagious pattern in vegetation. It has been commonly stated that the rarer species in a community, unless propagated vegetatively, are randomly distributed, whereas the more common species are less likely to be randomly distributed. This conclusion may result in part from the relationship between density and minimum quadrat size and number necessary to detect non-randomness; it should not be accepted uncritically (Greig-Smith 1983).

Kershaw (1985) has presented an excellent summary on the variation of pattern associated with morphological, environmental, and phytosociological characters of living organisms. The morphological characters include those of tussocked form, rosette basal leaves, presence of rhizomes, and age of rhizomes in plants such as those in _Vaccinium_, _Pteridium_, and _Trifolium_. The environmental factors include soil depth, soil texture, soil drainage, slope, nutrient supply, and pH. Kershaw (1958) found a close relationship between the pattern of

Agrostis tenuis and soil depth in an upland grass land. Such studies have been largely concerned with the variation of density and the occurrence of a species along environmental gradients rather than with the types of pattern. The phytosociological aspects refer to the interrelationships of species and the dynamics of these interrelationships related to changes in time and space. These relationships often take the form of a mosaic of patches of different levels of density. Additional information can be found in a summary provided by Greig-Smith (1979).

The above studies of pattern have been restricted to the population level within a species or to the community level of several species. No reports are available where the study of pattern has been carried out at the landscape ecosystem level (Rowe 1984) within a species population. Ecosystems are layered, volumetric segments of the biosphere. Plants and animals and their physical environment (termed site or habitat)--in dynamic interaction with one another--comprise an ecological system. Also, few studies have practical uses in natural resources as their goal. It has been widely accepted that different ecosystems differ in physiography, soil, and vegetation (e.g., Spies and Barnes 1985). Thus, a primary hypothesis is that the types of plant pattern in different ecosystems may also differ.

In 1986 and 1987, Dr. B. V. Barnes and teams of graduate students from the University of Michigan conducted a study of the local landscape ecosystems of the Mack Lake area, Oscoda County, northern lower Michigan. I participated briefly in this study in 1986 and was a research assistant in 1987. The Mack Lake area is the center of the summer habitat of an endangered species--the Kirtland's warbler (*Dendroica kirtlandii*). This area was burned in the summer of 1980, and jack pine (*Pinus banksiana* Lamb.) regenerated throughout much of the area. The burn provides a unique opportunity to study the local landscape ecosystems in relation to the colonization by the Kirtland's warbler. The study of pattern of jack pine occurrence in different ecosystems was also part of this overall investigation.

The Kirtland's warbler is one of the most rare and endangered songbirds in the world. Restricted to northern lower Michigan, its summer habitat comprises an area about 120 x 160 km. All nests have been found within 13 counties (Probst 1986). The first census of the warbler population was conducted in 1951; a total count of 432 males was reported (Mayfield 1953). The second census in 1961 showed a total of 502 males (Mayfield 1962). The third census in 1971, however, revealed a marked drop to 201 males (Mayfield 1972). The principal reason for this decline appears to have been nest parasitism by the brown-headed cowbird (*Molothrus ater*)(Ryel 1981). In order to monitor the population more closely, a census has been carried out each year since 1971. A strong effort has been made to control the cowbird by yearly trapping (Kelly and DeCapita 1982). The warbler population has been more or less stable from 1976 to 1986 (Personal communication from Jerry Weinrich, Table 1.1). However, the male population of the warbler declined again in 1987 to 167. This decline resulted in further concern about the future status of the warbler. Although there are many hypotheses, the reasons for the decline are not well known. Thus, it is important to review our concept of the habitat of the warbler and generate new ideas

Table 1.1 Number of male Kirtland's warblers found in censuses from 1971-1987 1/

Year	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987
Number	201	200	216	167	179	200	218	196	210	242	232	207	215	215	216	210	167

1/ Personal communication from Jerry Weinrich, Feburary, 1988.

through intensive studies of landscape ecosystems and pattern of jack pine occurrence.

Mayfield (1960) reported that the nesting sites of the warbler are generally found in an area having: 1) dense jack pines; 2) sandy porous soil; 3) repeated fire; 4) low, dense ground vegetation; and 5) generally level or gently rolling topography. Mayfield (1962) also pointed out that all but a few colonies of the warbler were located on the Grayling sand soil series. In addition, Walkinshaw (1983) stated that a preferable habitat is characterized by: 1) jack pines generally less than three meters in height; 2) openings interspersed among dense clumps of jack pines; 3) ground vegetation dominated mainly by blueberry and grasses, occurring either separately or in combination; and 4) areas preferably larger than 32.4 ha (80 acres). Smith and Prince (undated) reported that the peak use sites of the warblers were often found in areas consisting of both jack pines and oaks. Other studies about the summer habitat, especially on vegetational structure and plant composition, were conducted by Trautman (1979), Ryel (1978), Buech (1980), and Probst (1986). These studies provide very useful details. The criteria for the warbler's summer habitat were summarized in the Kirtland's Warbler Recovery Plan (Byelich 1976):

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. 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.

4. Relatively level topography.

It is widely accepted that the warbler requires numerous small openings interspersed among dense patches of jack pine. Therefore, my second working hypothesis is that there is a relationship between the pattern of jack pine occurrence in an area and the degree of occupancy of Kirtland's warbler in that area. Thus, questions defining the problem may be stated as follows:

1. Is there more than one pattern type of jack pine occurrence in the Mack Lake burn? If yes, what are they?

2. What are the relationships among the pattern of jack pine distribution to the occurrence of the local landscape ecosystem types, and to the degree of occupancy of the Kirtland's warbler?

3. What physical site and vegetative factors are associated with the patterns, the ecosystems, and the summer habitat of the warbler? Are there interrelationshipes between characters of ecosystems and the general pattern of jack pine occurrence?

The above questions lead one to study the pattern of jack pine occurrence in several ecosystems of the Mack Lake Burn, and examine the factors associated with pattern of jack pine occurrence, including the ecosystem types and their physiography, soil, and vegetation.

Objectives

The general objective is to examine the variation of pattern of jack pine occurrence in different local landscape ecosystem types and thereby gain a better understanding of the summer habitat of Kirtland's warbler. The specific objectives are:

1. To determine the pattern of jack pine occurrence in selected landscape ecosystem types of the Mack Lake burn; and

2. To examine the relationship of the pattern of jack pine distribution to: (1) the occurrence of the local landscape ecosystem types, (2) the occurrence of the singing and nesting warblers in 1986 and 1987, and (3) the specific components (physiography, soil, and vegetation) of the local landscape ecosystem types and of the occupancy of the Kirtland's warbler.

CHAPTER II

STUDY AREA

Mack Lake is located in southeastern Oscoda county in northern lower Michigan. It is about 85 miles south to southeast of the straits of Mackinac and 40 miles west of Lake Huron, with a latitude of about 44° 38' and a longitude of about 84° 08' (Fig. 2.1). The Au Sable River, flowing eastward toward Lake Huron, passes through the town of Mio which is just north of Mack Lake. The area around Mack Lake was originally occupied by a jack pine-red pine-northern pin oak forest. On May 5, 1980, a prescribed burn initiated a wild fire which burned 23,600 acres of forest land around Mack Lake (Simard 1983). The study of patterns of jack pine occurrence was conducted in the burned area.

Climate

As a result of the influence of the Lakes Michigan and Huron, many areas in lower Michigan have a modified continental climate (Albert et al. 1986). However, the influence is minimal in Oscoda county, which is sheltered from Lake Michigan by a higher plateau to the west. It has the lowest mean minimum temperature in July in lower Michigan (Fig. 2.2). At Mio, the average maximum temperature is 1° F higher, the average minimum temperature 2° F cooler, and the average annual

Fig. 2.1, Location of the Mack Lake fire. Cross-hatched area (insert) was burned in the fire. (Simard 1983)

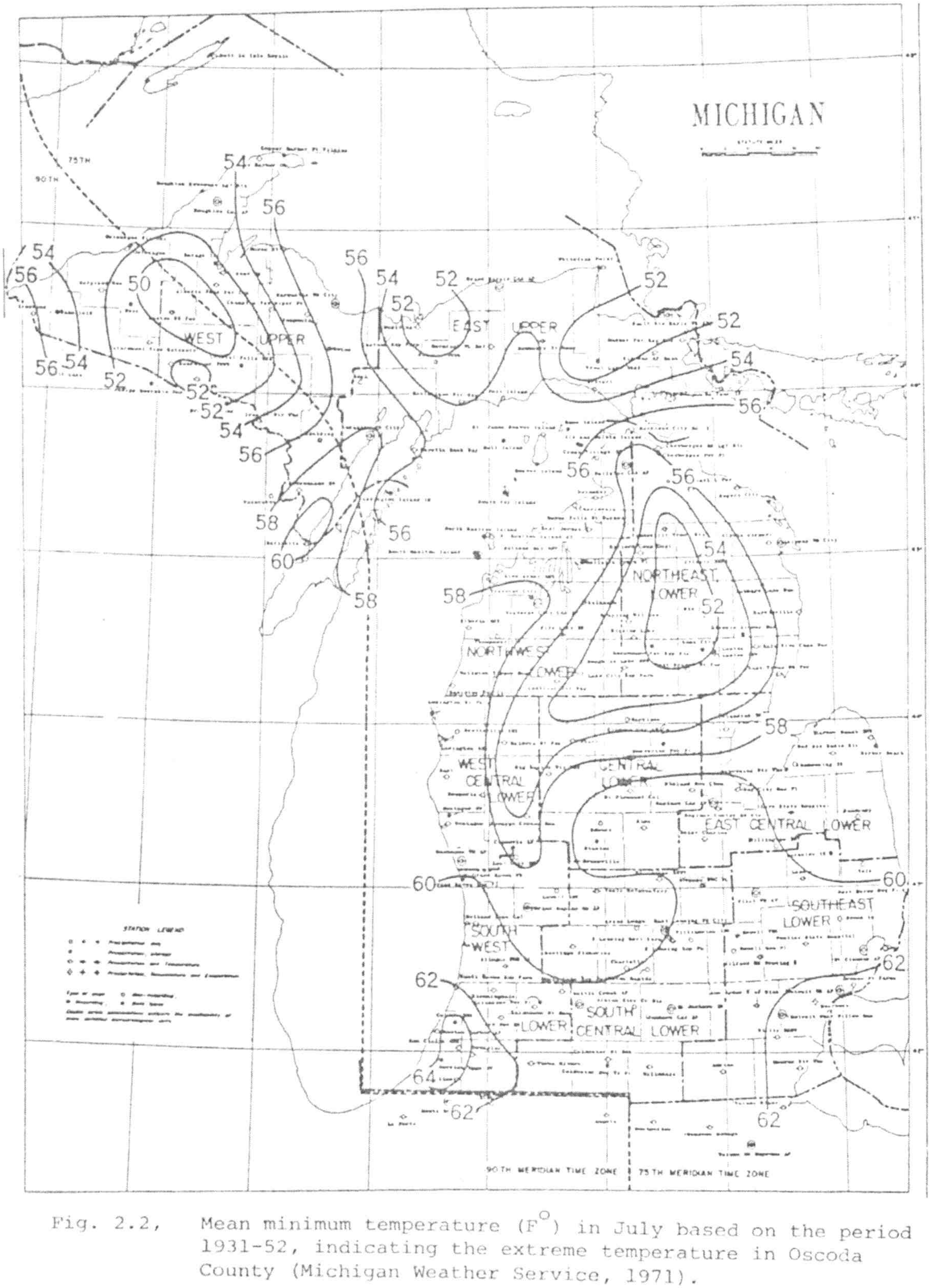


Fig. 2.2, Mean minimum temperature (F°) in July based on the period 1931-52, indicating the extreme temperature in Oscoda County (Michigan Weather Service, 1971).

precipitation 6 inches less than a weather station 30 to 40 miles to the west (Simard 1983). According to the records from 1940 to 1969, Mio has an average annual temperature of 42.9° F, an average daily maximum of 54.9° F, and an average daily minimum of 30.9° F. The average mean maximum temperatures in June, July, and August are 76.9°, 80.8°, and 78.6° F, respectively, and average minimum temperatures in the same months are 48.5°, 52.5°, and 51.5° F. The highest temperature in Michigan (112° F) was recorded at Mio on July 13, 1936 (Michigan Weather Service 1971, 1974). Although the average 26.5 inches of precipitation is well distributed throughout the year, twice as much falls in the summer (3 inches per month) as in the winter (1.4 inches per month), with spring and fall intermediate (2.3 inches per month). July, with 3.1 inches, is the wettest month, whereas February, with a 1.1-inch average, is the driest month. Summer precipitation is mainly in the form of afternoon showers and thunder showers. Evaporation during the growing season exceeds precipitation by 45 %. Prevailing winds are primarily from the west (Michigan Weather Service 1971, Officials of the National Oceanic and Atmospheric Administration 1974).

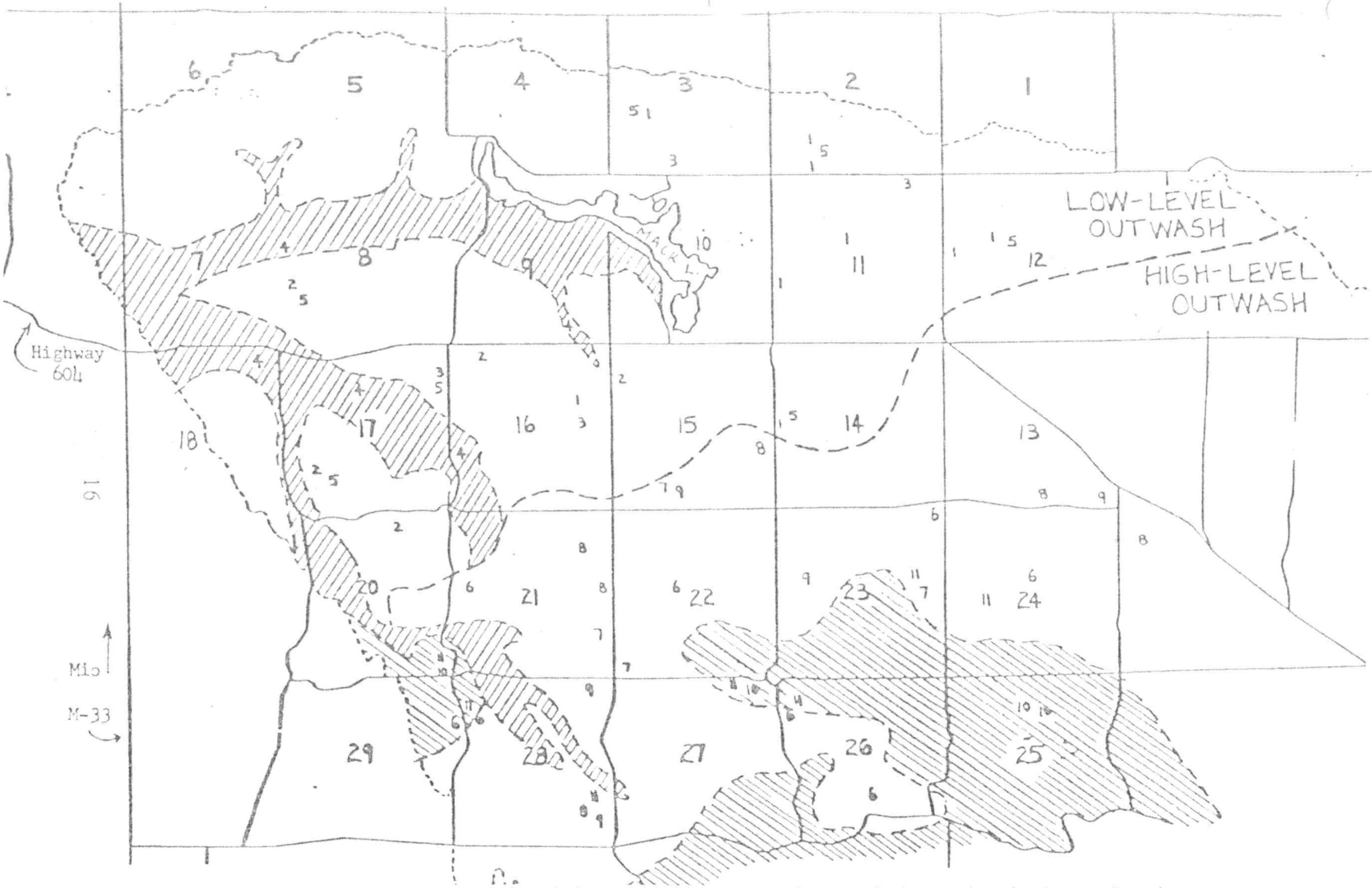
The average date of last freezing temperature in the spring is June 6, and the average date of the first freezing temperature in the Fall is September 8. The freeze-free period or growing season averages 94 days annually (Michigan Weather Service 1971). However, frost occurs on June mornings in young jack pine areas, whereas none is visible in towns, cultivated areas or mature woods. Measurements in 1987 (Barnes et al. 1987) indicated that there is no month in which the Mack Lake Burn did not have minimum temperatures below freezing.

Topography and Soil

Oscoda county is on the eastern edge of the lower Michigan highlands. Average elevation is 381 meters. The area is generally level. Mack Lake is situated in the north central part of the burn and has the lowest elevation (357 m) in the burned area. The land rises slightly both south and north of the Lake. The northern part of the burn is characterized by rolling terrain of low ridges and shallow depressions. Ridges are typically 30-100 m in width with slopes ranging from 1-10 %. The southern part of the burn is characterized by nearly level terraces and hilly ice-contact terrain. The average elevation is about 375 meters in the terraces. Kettles are frequently found throughout the entire area. They become denser, larger, and deeper towards the south. Average depth of the kettles is 9.5 meters, ranging from 1.6 to 17.6 meters. Hilly areas are adjacent to the southern edge of the level terraces. Depressions become further larger and deeper. Here, slopes average about 10 % and range from 5-30 %.

There are two post-glacial drainage channels (Fig. 2.3) extending from east to west in the central portion of the burn. The northern one is connected to Mack Lake. The southern one gradually rises in elevation to the east and finally emerges to the terraces.

The soils in the area are dominated by sand. Although several other soil series occur, the Grayling and Rubicon series cover most parts of the northern area. In the terraces, Montcalm and Graycalm series appear frequently along with the Grayling series. In addition to



Key:

Ice-cantact

Outwash channel

Fig. 2.3. Major landscape forms of the Mack Lake burn, Oscoda Co., Michigan, showing low-level outwash plain (north of dashed line) and high-level outwash terraces and ice-contact terrain (south of dashed line). Small number indicate plot locations and ecosystem type numbers (Table 2.1). Approximate areasof outwash channels and ice-contact terrain are also shown (see key)(Modified from Barnes et al. 1987).

Mack Lake, there are two other very small ponds in the burn. Soils in the majority of the area are excessively drained.

Vegetation

Prefire vegetation was mainly dominated by jack pine and northern pin oak (*Quercus ellipsoidalis* E. J. Hill). There were also red pine (*Pinus resinosa* Aiton) plantations, with some of them interplanted with jack pine. The jack pine stands accounted for 42 % of the burned area. Hardwoods and red pine plantations contributed 25 and 24 %, respectively.

Sixty-two percent of the jack pine stands before the burn was in the pole-size class and 38 % in the seedling and sapling class (Simard 1983). Stand density ranged from less than 100 stems per acre in open areas to over 5,000 stems per acre in dense areas. Pole timber density generally ranged from 400 to 1,200 stems per acre. Tree height varied from 6 to 20 meters. Diameter at breast height (DBH) ranged from 10-25 cm. Red pine plantations were scattered throughout the jack pine distribution area.

Hardwoods were mostly concentrated along the eastern and southeastern boundaries and were occasionally found in the burned area. Principal species were northern pin oak, red oak (*Quercus rubra* L.), black oak (*Q. velutina* Lamarack), trembling aspen (*Populus tremuloides* Michaux), red maple (*Acer rubrum* Linnaeus), sugar maple (*A. saccharum*

Marshall), and, to a less extent, red pine and white pine (P. Strobus L.)(Simard 1983).

According to Simard (1983), the understory vegetation in jack pine stands and red pine plantations consisted of sedge (Carex pennsylvanica), trailing arbutus (Epigaea repens), bracken fern (Pteridium aquilinum), blue berries (Vaccinium Angustifolium and V. myrtilloides), sweetfern (Comptonia peregrina), Mosses (Dicranum, Polysetum) and Lichens (Cladonia Spp.) (Simard 1983). Information about the abundance and height of ground-cover species was not available. There was also lack of prefire information about the understory vegetation in hardwoods.

Fire History

The area was burned during the period from 1910 to 1913 (Simard 1983). Much of the pole-sized jack pine stands were originated following the burning. In 1946, part of the northern area was burned again, and parts of it had seeded in naturally. In 1964, a prescribed burn was conducted in the northern part of the area. Jack pine regeneration varied from 1.5-3.0 m in height at the time of the Mack Lake fire.

Local Landscape Ecosystem Types

Eleven landscape ecosystem types were distinguished on the basis of field reconnaissance, plot taking, and the analysis of sample data (Barnes et al. 1987)(Table 2.1). The ecosystems were named and characterized by features in physiography, soil, vegetation, and microclimate. Two major landforms were recognized and subsequently termed "low-level outwash area vs. high-level outwash terraces and ice-contact terrain" (Fig. 2.3). They differ in elevation, soil texture, soil moisture and nutrients, microclimate, vegetation, and topography. The low-level outwash area is located in the northern part of the burn. It is characterized by rolling topography. The high-level outwash terraces and ice-contact terrain are located in the southern part of the burn. This landform can be further divided into two parts: outwash terraces and ice-contact terrain. The terraces were frequently found having fine soil texture below the surface soil. The ice-contact terrain is situated in the southern edge of the burn with and readily distinguished by steep, hilly topography. Compared with the low-level outwash, the high-level outwash and ice-contact terrain is higher in elevation, finer in soil texture, richer in soil nutrients, better in soil moisture condition, warmer in microclimate, and more diverse in plant species.

Five ecosystem types (types 1, 2, 3, 4, and 5; Table 2.1) were characteristic of the low-level outwash area. Ecosystem types 1, 2, and 3 occur on slightly higher terrain than types 4 and 5. Ecosystem types 1, and 2 are characterized by a high proportion of sand in the top 150

(Barnes et al. 1987)

I. Low-level outwash plains (Elevation 1190-1220 ft).

A. Upland topography (flat to gently sloping, depressions <5 ft); excessively to somewhat excessively drained.

1. Medium sand, very infertile soils.

2. Medium sand; isolated areas surrounded by outwash channels; soils occasionally with thin fine textural bands.

3. Sand to loamy sand over bands of sandy loam to clay.

B. Channels and depressions; excessively to somewhat excessively drained; cooler microclimate than ecosystems 1, 2, and 3.

4. Outwash channels (usually 20-50 ft deep) with a distinct pebble/cobble layer; moister soil.

5. Depressions (5-20 ft deep); with extreme microclimate; soils as in ecosystems 1, 2, or 3.

II. High-level outwash terraces and ice-contact terrain (elevation 1220-1280 ft).

A. High-level uplands (flat to moderately steep slopes); Excessively to somewhat excessively drained.

6. Outwash terrace; very infertile; medium sand.

7. Outwash terrace; very infertile; fine sand throughout the B horizon.

8. Outwash terrace; infertile loamy sand/sand soils; 5-10 cm (cumulative) of fine textural bands.

9. Outwash terrace; infertile; loamy sand soil or a relatively thick textural band (>10 cm).

10. Ice-contact terrain; sandy kamic hills; soils often have fine texture bands.

B. Depressions; cooler microclimate than ecosystems 6, 7, 8, and 9.

11. Depressions (6-50+ ft) with extreme microclimate; soils as in exosystems 6-10.

cm of soil (Table 2.2). An average of more than 60% of medium sand was typically found in soil at a depth ranging from 10-150 cm. These two ecosystem types both have very acid surface soil (an average pH = 5.0 for soils of 10-30 cm in depth). Ecosystem type 1 is often found in the eastern parts of the low-level outwash, whereas ecosystem type 2 is found more commonly in the western part of the area. It is isolated and surrounded by the outwash channels (see ecosystem type 4 below). The soil of ecosystem 2 is generally better in moisture and nutrient status than that of ecosystem 1. Occasionally, it has very thin layers of fine textural bands or layers of pebbles/cobbles. Therefore, the coverage of vegetation is higher here than that in the ecosystem type 1. The number of northern pin oak clumps and the number of oak seedlings in ecosystem type 2 are much higher than that in ecosystem type 1 (Table 4.2). The average height of dominant oak sprouts in ecosystem 2 is 97 cm compared to 17 cm in ecosystem type 1. Ecosystem 3 is typically characterized by a layer of heavy textured soil (sandy loam to clay) existing in the top 250 cm of soil. It is frequently associated with several ground-cover species such as *Oryzopsis asperifolia* and *Salix humilis*. In general, the coverage of ground vegetation is much greater than that of the other more elevated ecosystem types. As a juvenile, jack pine grows slowly in ecosystem 3 probably because of the severe competition from ground-cover species.

The more low-lying ecosystem types of the low-level outwash consist of outwash channels and depressions. They have cooler night temperatures than adjacent higher-lying lands. Freezing temperatures occur earlier in September and disappear later in June than the more

Table 2.2 Mean and standard deviation of selected variables of physiography, soil, and ground-cover species in ecosystem types of the Mack Lake burn 1/

Variable	Ecosystem type										
	1	2	3	4	5	6	7	8	9	10	11
Percent of sand (10-30 cm)	92.1 (3.2)	91.2 (3.5	88.0 (3.9)	88.0 (2.2)	90.0 (6.5)	90.8 (1.5)	91.6 (2.8)	86.3 (2.3)	84.6 (7.4)	92.5 (2.0)	79.2 (26.4)
Percent of very coarse sand (10-30 cm)	1.1 (2.0)	2.2 (1.9)	2.3 (1.1)	0.9 (0.5)	1.4 (1.0)	1.1 (0.6)	1.0 (1.0)	0.9 (0.6)	1.0 (0.4)	1.0 (1.1)	1.2 (0.7)
Percent of medium sand (10-150 cm)	60.5 (8.5)	65.8 (2.0)	53.0 (16.7)	57.5 (19.4)	56.7 (12.4)	69.7 (5.4)	64.7 (8.1)	55.5 (9.5)	54.9 (11.1)	59.9 (6.9)	58.1 (8.6)
Depth to loam or clay band	>400	>400	137.0 (71.5)	>400	>400	>400	>400	>400	84.8 (23.0)	>400	>400
Total thickness of clay and loam (0-150 cm)(cm)	0	0	16.5 (17.1)	0	0	0	0	0	41.8 (15.4)	0	4.6 (12.1)
Percent of pebble and cobble (0-150 cm)	3.4 (7.5)	3.1 (5.5)	1.4 (1.4)	15.1 (9.3)	1.2 (2.6)	2.7 (3.2)	4.3 (6.5)	4.1 (4.7)	3.3 (2.9)	0.9 (0.8)	4.2 (8.9)
Elevation (m)	368.0 (2.2)	368.4 (0.5)	369.2 (2.1)	358.2 (3.6)	367.6 (2.1)	376.6 (3.7)	376.4 (6.0)	375.2 (4.1)	375.6 (3.4)	384.2 (4.8)	371.2 (8.4)
Percent of maximum slope	2.3 (1.6)	2.9 (2.1)	1.9 (0.9)	1.0 (0.8)	4.5 (3.2)	1.4 (2.1)	1.2 (1.1)	2.9 (1.6)	0.9 (0.7)	8.4 (7.2)	10.0 (5.3)
Depth of channel and depression (m)	0	0	0	7.6 (3.6)	3.3 (1.7)	0	0	0	0	0	9.5 (5.6)
Average pH (10-30 cm)	5.0 (0.3)	5.0 (0.4)	5.2 (0.2)	5.3 (0.1)	5.1 (0.2)	5.1 (0.3)	5.0 (0.1)	5.4 (0.3)	5.1 (0.2)	5.1 (0.4)	5.2 (0.2)
Height of 1st living JP branch (cm)	14.7 (5.4)	12.3 (6.1)	14.3 (2.9)	22.8 (7.1)	11.6 (9.7)	21.2 (8.6)	25.2 (6.9)	23.0 (5.0)	22.2 (6.7)	22.3 (7.9)	21.1 (5.3)
Number of oak clumps	0.9 (1.5)	6.3 (7.4)	5.0 (8.0)	1.2 (1.6)	1.1 (1.6)	8.6 (6.4)	5.8 (3.4)	7.0 (3.4)	3.8 (2.5)	11.5 (12.3)	10.0 (6.1)
Number of oak seedlings	0.6 (0.8)	3.3 (3.6)	2.8 (1.9)	1.2 (1.8)	1.1 (1.5)	6.2 (4.0)	9.2 (6.9)	6.6 (3.3)	11.0 (6.5)	15.5 (14.0)	3.0 (2.2)
Height of dominant oaks (cm)	17 (23)	97 (78)	131 (150)	20 (31)	33 (43)	82 (49)	247 (106)	190 (153)	134 (80)	139 (165)	71 (68)
Percent of coverage of oaks	2.2 (6.8)	3.3 (3.4)	10.5 (20.3)	0.7 (1.0)	0.1 (0.2)	3.4 (2.5)	18.0 (14.9)	5.9 (5.3)	3.4 (2.7)	14.4 (8.0)	1.9 (2.3)
Number of understory jack pines	1.9 (3.4)	1.5 (2.4)	0	4.6 (8.2)	0	3.4 (7.6)	14.2 (18.7)	28.4 (40.8)	4.0 (7.3)	18.8 (22.0)	0
Number of understory oaks	0.6 (1.9)	1.0 (2.0)	8.8 (15.0)	0.4 (0.9)	0	2.6 (5.3)	10.8 (9.0)	10.3 (13.3)	1.2 (2.9)	14.3 (8.0)	0.9 (2.3)

1/ Values are means and standard deviation (in parentheses).

highly-elevated ecosystems. Even in July and August, the low-lying ecosystems may still have freezing temperatures in early morning. The low temperatures in the early growing season often cause damage to the new shoots of jack pines. The young shoots of northern pin oaks are mostly killed by the freezing temperatures at this time. As a result, the average height and coverage of jack pine and northern pin oak in low-lying ecosystems are much lower than these in higher-elevated types. The northern pin oak is often absent in such frost pockets.

Ecosystem type 4 is characteristic of outwash channels. Its soil commonly has a thick pebble/cobble layer within 100 cm below ground surface. Moisture conditions are better than that in the adjacent higher-elevated ecosystems and most of the depressions (ecosystem type 5). The average height of the first living jack pine branch is greater than that within any of the other ecosystem types in the low-level outwash.

Depressions in the low-level outwash are identified as ecosystem type 5. Due to frost early in the growing season, jack pine, northern pin oak, and bracken fern are often damaged. Although jack pine can survive in the depression, its juvenile growth rate is very low. In addition the average density observed was typically about one fourth of that in upland ecosystem types. Northern pin oak and bracken fern, on the other hand, are mostly killed back by freezing temperatures. Oaks are typically absent from the depressions. The data in Table 2.2 show that there were no jack pines reaching understory size in 1986 and 1987, and the coverage of northern pin oak averaged only 0.1%. Living oaks form a distinct line on slopes surrounding the depressions. This line, together with the concave landform, may serve to distinguish ecosystem type 5 from other ecosystems of the same area.

Six ecosystem types (6, 7, 8, 9, 10, and 11; Table 2.1) were distinguished in the high-level terraces and ice-contact terrain. Ecosystem types 6, 7, 8, and 9 are distributed in the outwash terraces, ecosystem type 10 in the ice-contact terrain, and ecosystem type 11 includes depressions in both areas.

Similar to ecosystem type 1 in the low-level outwash, the soil of ecosystem type 6 is characterized by a high proportion of sand--69.7 % medium sand alone at 10-150 cm depth was observed (table 2.2). It is the poorest ecosystem type in moisture and nutrients in the high-level outwash terraces. However, it is slightly richer in surface soil than ecosystem 1. The average proportion of total sand at 10-30 cm depth in the surface soil of ecosystem type 6 is 90.8 % compared with 92.1 % in ecosystem type 1. Ecosystem 6 also has a higher coverage of vegetation and is more diverse in plant species than ecosystem 1.

Ecosystem type 7 is typically characterized by a high proportion of fine sand in the B horizon. The surface soil is nutrient poor, having 91.6 % sand at 10-30 cm depth in the horizon. Compared with other ecosystems, jack pine reaches its highest density and height in this ecosystem. The first living branch of jack pine is found at 25.2 cm above the ground which was the highest of all other ecosystems. The ground vegetation is dominated by low sweet blueberry (Vaccinium angustifolium), bearberry (Arctostaphylos uva-ursi), sweet fern

(Comptonia peregrina), and the blue stem grasses (Andropogon gerardii, A. scoparius).

Ecosystem type 8 is characterized by having a cumulative thickness of 5-10 cm fine textural bands of sandy loam to silt loam within the top 150 cm of soil. It has much higher coverage of ground vegetation than ecosystem types 6 and 7. The low sweet blueberry reaches its peak abundance in this ecosystem. This ecosystem also has a high coverage of oaks. The average height of the dominant oaks reaches 190 cm. The average number of oak individuals of understory size is 10.3 per plot. Jack pine also has a fast growth rate and a high density here. The average number of understory jack pines is 10.3 per plot.

Similar to ecosystem type 3, ecosystem type 9 is distinguished by a layer of sandy loam to clay thicker than 10 cm. The average thickness of this layer is 41.8 cm, and the average depth of this layer is 84.8 cm. The soil is the richest compared with those of all other ecosystem types. It has the most diverse plant community. The dominant species include Oryzopsis asperifolia, bracken fern (Pteridium aquilinum), and willow (Salix humilis). Other species appearing frequently include Populus tremuloides, Prunus serotina, and Acer rubrum.

Ecosystem type 10, in the ice-contact terrain, is defined to encompass the upper slopes of depressions and tops of hills, but not the depressions themselves. Soils are mostly sandy, but they often have several layers of thin textural bands at a depth less than 200 cm. Gaylussacia baccata is a reliable indicator of this ecosystem type. Other species such as Populus grandidentata, and Hamamelis virginiana appear frequently in the area. Oaks are vigorous. The average number of oaks of understory size reaches 14.3 stems per plot. The average number of oak seedlings, 15.5 per plot, is the highest among all ecosystem types. Jack pine grows well here and its density is high.

Depressions in both high-level outwash terraces and the ice-contact terrain are categorized as ecosystem type 11. This type is cooler in temperature than surrounding ecosystem types. Northern pin oak often grows poorly or may even be absent. The soils in the depressions are generally richer in moisture and nutrients than those of more highly-elevated ecosystem types. Grass species such as Schizachne purpurascens, and Poa pratensis often dominate the area. The low sweet blueberry has a very low coverage apparently because of both the cooler temperature and the competition from sedge and grasses.

CHAPTER III

METHODS

The classification of local landscape ecosystem types was initiated in 1986 and was essentially accomplished by the end of July 1987 (Barnes et al. 1987). Information on the occurrence of the warbler was obtained from the United States Forest Service and Fish & Wildlife Service in 1986 and 1987. The samples for the study of the pattern of jack pine occurrence in selected ecosystem types was carried out in August, 1987.

Field Sampling

Sampling of Variables in Landscape Ecosystem Plots

The study of pattern of jack pine occurrence was based on an understanding of the landscape ecosystems in the burn. A modification of a landscape ecosystem classification used in southwestern Germany (Baden-Wurttemberg)(Barnes 1984) and adopted to Michigan conditions (Barnes et al. 1982; Pregitzer and Barnes 1984; Spies and Barnes 1985; and Archambault 1987) was undertaken to identify and describe ecosystem types in the Mack Lake burn. A total of 64 plots (10 x 20 m) were sampled. Although only one plot was established in the areas where singing male warblers were observed or heard in 1986 season, 13 ecosystem plots were established in the areas where warblers were observed or heard in 1987 season. In addition, four of the 1986 plots were located in ecosystem types having warblers in 1987.

The plots were designed to sample representative areas of each ecosystem type. They were located by detailed reconnaissance and study of the area using aerial photographs. The exact location of the northeast corner of a plot was determined by a random spin of the compass and by a number chosen from a random number table within a distance representative of the same area (Spies and Barnes 1985). The northeast corner of the plot was located using the random direction and distance from the starting point. In general, the starting point was at the center of a representative and relatively homogeneous area of the ecosystem type. Plots were laid out 20 m along the north-south direction and 10 m along the east-west direction. Each plot was subdivided into eight equal size subplots (5 x 5 m each)(Fig. 3.1). A metal reinforcing rod was set at the northeast corner of each plot as a permanent marker.

The physiographic variables recorded at each plot were elevation, glacial origin, land form, aspect, slope (average, maximum, minimum), length of slope, and position (ridge, upper slope, midslope, lowslope, foootslope, and depression) (Appendix I). One soil pit was located adjacent to each plot. Each soil pit was dig to 150 cm, and then an auger was used to sample, whereas possible, to a depth of 400 cm. The soil profile was described in detail for the top 150 cm; careful notes were taken for the auger boring. The variables described included

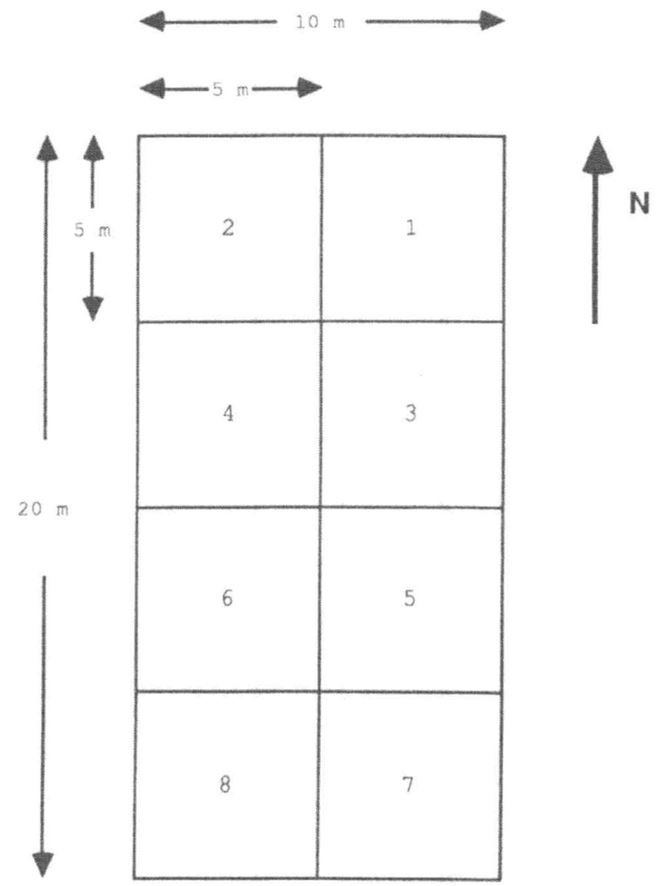


Fig. 3.1 Plot outline used to sample vegetation and patterns of jack pine occurrence in the Mack Lake Burn.

horizon, depth (both range and average), field PH, texture, structure, color, pebble (2-75 mm diameter) and cobble (75-250 mm diameter) content, rooting depth, earthworm activity, and drainage class. A soil sample for each B and C horizon was collected. Soil texture was determined by the field methods of texture analysis (Thien 1979). Soil color was determined using a Munsell soil color charts manual. Soil particle size data was determined using modifications (Grigal 1973) of the hydrometer method of Day (1965). Soil pH value of a 10 ml sample was determined in a 1:1 soil to water solution using a glass electrode organic.

No "overstory" stem (>3.5 inches in diameter breast height-DBH) was measured. The number of individuals of each species in the "understory" (0.5-3.5 inches in DBH) was recorded in each plot. Three understory classes were recognized: 1 = 1.5-4.0 cm, 2 = 4.1-6.6 cm, and 3 = 6.7-9.2 cm (Appendix I). Coverage estimates were made for four groups of plants: moss-creeper, herbaceous, shrub-sapling, and small tree. The number of jack pine in each of the eight subplots of a 10 x 20 m plot was counted according to the following height classes (1 = 0-50 cm, 2 = 51-100 cm, 3 = 101-150 cm, 4 = 151-200 cm, 5 = 201-250 cm, and 6 = 251-300 cm). Other variables for the whole plot or general area included the status of salvage (yes or no), openness class (sparse = 0-18%, medium = 19-32%, dense > 32% in jack pine coverage), largest opening dimension and patchiness classes in both plot and the general area surrounding the plot.

Ground-cover species were recorded in a randomly determined half of a plot (5 x 20 m). Percentage of coverage of each species was described by 12 coverage classes (Table 3.1) and determined using a 1000 cm^2 frame. In addition, the coverages of woody debris and bare ground were also estimated (Appendix I).

Two 5 x 5 subplots were randomly chosen separately from subplots 1 and 2, and from subplots 7 and 8. Three dominant jack pines were selected in each of the two subplots according to the criteria: (1) dominant in height, and (2) free from insect and frost damage. Where two dominants occurred side by side only one was measured. The variables measured for the dominants include age, height of each yearly node, diameter at 15 cm above ground, height of first branch above ground, largest crown diameter, yearly growth of four dominant branches and their perpendicular distances from the stems to the 1985 whorl. The number of standing snags and stumps of jack pine, red pine, and northern pin oak were measured. Their stem diameter at 20 cm above ground and their height classes (class 1 = 0-1.52 m, class 2 = 1.53-3.05 m, class 3 = 3.06-4.57 m, etc.) were recorded. The number of oak clumps and oak seedlings were counted. Heights of dominant oaks were measured. The coverages of jack pine, oak, and jack pine and oak together were estimated (Appendix I).

Two 1 x 1 m plots were established at two randomly selected corners of the 5 x 5 subplots. The height of each ground-cover species within the 1 x 1 m plots was measured using 10-cm height classes: 1 = 0-10 cm, 2 = 11-20 cm, 3 = 21-30 cm, etc.

Table 3.1 Coverage classes used in determining areal coverage of species in sample plots

Coverage class	Range of coverage (%)	Median of class	Number of frames	Area in plot 250 cm^2 frame	Area in plot 1000 cm^2 frame
0.25	tr-.005	.0025	0-.05	0-12.5 cm^2	0-50 cm^2
0.5	.005-.01	.0075	.05-.1	12.5-25 cm^2	50-100 cm^2
1	.01-.1	.055	.1-1.0	25-250 cm^2	100-1000 cm^2
2	.1-.5	0.3	1-5	250-1250 cm^2	1000-5000 cm^2
3	.5-1	0.75	5-10	1250-2500 cm^2	.5-1.0 m^2
4	1-2	1.5	10-20	.25-.5 m^2	1-2 m^2
5	2-4	3	20-40	.5-1.0 m^2	2-4 m^2
6	4-8	6	40-80	1-2 m^2	4-8 m^2
7	8-16	12	80-160	2-4 m^2	8-16 m^2
8	16-32	24	160-320	4-8 m^2	16-32 m^2
9	32-64	48	320-640	8-16 m^2	32-64 m^2
10	64-100	82	640-1000	16-25 m^2	64-100 m^2

Notes were also taken to describe ecological features of plots and the area around the plots. A physiographic sketch was drawn of the area around each plot. The location of the plots was marked on a topographic map, and the directions and distances from the nearest road were written for relocation of the plots.

Sampling of Pattern of Jack Pine Occurrence

The study was designed so that jack pine pattern was examined in ecosystem types where warblers singing or nesting were and were not found. Of 25 plots sampled, 15 were located in ecosystem types (1, 6, 8, and 10) where warblers were singing or nesting, and 10 were located in ecosystem types (3, 4, and 9) without warblers. The locations of singing males were identified according to the maps provided by Dr. John Probst (USFS, North Central Forest Experiment Station, St. Paul, MN). Additional information was supported by Dr. Cameron B. Kepler and Dr. Paul W. Sykes Jr. (USF&WS, Patuxent Wildlife Research Center, Endangered Species Branch). Twenty-two plots were ecosystem plots. Three other plots were also established, all in ecosystem type 1. One plot was located in jack pine plantation with created openings (Sec. 5), and the other two were sampled outside the burn. One was in a red pine plantation (Sec. 34, R. 3 E., T. 26 N.)(North to Sec. 3, Fig. 2.3). Another was sampled in the NE 1/4 of Section 2 which was burned in 1964. The plot size in the jack pine plantation was 100 x 100 m; all other plots were 10 x 20 m. Three male warblers were found in the jack pine plantation in 1987; and three were found in the red pine plantation.

Warblers had been found before 1985 in the NE 1/4 of Sec.2 of the 1964 burn but have not been found in the area since.

The data collected in each plot for the study of patterns of jack pine occurrence include:

1. density of jack pine in each plot,
2. distance from each of 50 randomly located points to the nearest jack pine tree, and
3. distance from each of 50 randomly selected jack pines to the nearest neighbor jack pine.

The total number of jack pine in each plot was counted to determined the density per plot. Random points within each plot were determine by a system of coordinates. Random locations were determined along north and east sides of the sampling plot by determining random distances in decimeters from the northeast corner of a plot. The intersection of lines from the two random locations determined a given random point. The random jack pines were selected from a random number table after the density of each plot was counted. Given the selected random jack pine numbers and starting at the northeast corner, jack pines were counted until the random jack pines were located.

Statistical Analysis

Data on soil texture, collected and analyzed by horizons, were transformed to a weighted average for depth of 10-30 cm and 10-150 cm. The same method was used to transform data on soil reaction values for the upper 10 cm, 10-30 cm, and 30-150 cm, and for the percentage of pebbles and cobbles in the top 150 cm. These transformations were necessary to standardize the different horizon sequences presented in individual plots (Spies 1983). The coverage classes of each species was transformed back to the actual percent coverage by using the median of each class. Average height of jack pine was the average median of height classes weighted by the number of jack pine trees in each class.

Pattern Analysis

The methods of Hopkins-Skellam (1954), Clark-Evans (1954), and Pielou-Mountford (Pielou 1959, Mountford 1961) were used to test patterns of jack pine occurrence. Each sample was tested for a random, regular, or contagious distribution. The statistic of each of the three methods was standardized separately for all the sample plots. Two-way analysis of variance (ANOVA) (Scheffe, 1959) was used to test for significances of differences in the patterns of jack pine occurrence among the three methods and between ecosystems where the warbler was presented in 1987 and ecosystems where the warbler was absent. Shapiro-Wilk test (Fisher, 1973; Stephens 1974) was used to examine the normality assumption of the standardized data. The coefficient of the test indicated that the assumption was met at a significance level of 0.05. The plot of the residuals vs. the predicted values of the standardized data showed no serious departure from the homogeneity assumption.

The test of Hopkins and Skellam hinges on the fact that if, and only if, a pattern is random, the distribution of the distance from a random point to its nearest plant is identical with the distribution of the distance from a random plant to its nearest neighbor. Denote by w_1 the square of a point-to-plant distance and by w_2 the square of a plant-to-plant distance, and suppose a sample is obtained of n distances of each kind. The statistic $A = \sum w_1/\sum w_2$ then has an expected value of 1 if the pattern is random and A may be used as a measure of nonrandomness. Clearly, if the plants are contagiously distributed, we shall have $A > 1$; conversely, if they are more evenly spaced than in a randomly dispersed population, $A < 1$. The formula to determine whether A departs significantly from its expected value of 1 is:

$$x = \sum w_1 \;/\; (\sum w_1 + \sum w_2)$$

The variance for x is $var(x) = [4(2n + 1)]^{-1}$. The distribution of x tends to be normal when $n \geq 50$. The testing hypothesis is: H_0: $X = 0.5$.

The test proposed by Clark and Evans requires a knowledge of population density and a sample of n plant-to-plant distances (r). Let d be the density of plants per unit area. Then, for a randomly distributed population, one can have

$$E(r) = (2\sqrt{d})^{-1} \quad \text{and} \quad var(r) = (4-\pi)/4\pi d.$$

If the sample size n is large enough, say ≥ 50, one may assume the average value of r is normally distributed.

To determine the pattern types of a given population, the ratio of the observed to the expected mean distance is computed

$$R = \sum r / [n\ E(r)].$$

In a random population $E(R) = 1$; for contagious populations $R < 1$; and for a more regular population $R > 1$.

The test described by Pielou and Mountford requires measurements of population density and point-to-plant distances (r). Let the population density per unit area be d and per plot be m. Square the distance, $w = r^2$. Taking as an index of nonrandomness $\beta = (\pi d \sum w)/n$, one sees that $E(\beta) = 1$ and $var(\beta) = [1 + (n + 1)/m]/n$. In a random population, $2n\beta$ is distributed like a with 2n degrees of freedom. If β does not differ significantly from $(n-1)/n$ the population may be assumed to be random. In a contagious population one would expect a preponderance of large values of w, giving a higher value of β; conversely in a regularly dispersed population there would be few large values of w and β would be less than $(n-1)/n$.

Multivariate Analysis

A total of 190 original variables was collected (Appendix `. Among them 120 are variables of ground-cover vegetation, 38 are physiography-soil attributes, and 32 are tree species.

Stepwise discriminant analysis (Jennrich 1977) was used to select variables of ground-cover vegetation that differ significantly among ecosystems. Same method was used to selecte variables of physiography-soil and those of tree species. A stopping rule of alpha = 0.15 was used to include or exclude a variable. All the selected variables were tested for their significance among ecosystem types by one-way ANOVA. Duncan's method of multiple range test (Neter 1985, Steel and Torrie 1980) was conducted for variables that differed significantly among ecosystem types. The significance level for both tests was set at 0.05.

Differences among ecosystem types were also examined using canonical variate analysis (Lawley 1959, Williams 1981). Variables computed in the analysis were the first 20 principal components that were generated from the above selected variables by Principal component analysis (Mardia et al. 1979).

CHAPTER IV

RESULTS AND DISCUSSION

Patterns of Jack Pine Occurrence in Selected Local Landscape Ecosystem Types

Both random and contagious patterns of jack pine occurrence were found in different local landscape ecosystem types using the Clark-Evans, Hopkins-Skellam, and Pielou-Mountford methods. A contagious pattern of jack pine occurrence was typically found in ecosystem types 1, 6, 8, and 10, whereas a random pattern was frequently associated with ecosystem types 3, 4, and 9 (Table 4.1).

In most cases, samples from ecosystem types 1, 6, 8, and 10 showed a contagious pattern of jack pine occurrence as determined by all the three methods. However, exceptions were also noticed. The exceptions were often associated with prefire history and management activities. Three plots in ecosystems 1, 8, and 10 showed a random pattern, as determined by either Clark-Evans or Pielou-Mountford method (Table 4.1). Plots 107 and 109 (ecosystems 8 and 1) were salvaged for oaks. Such operations usually kill some jack pines and thus change the original distribution pattern. In addition, random sampling error might also contribute to the causes in that the statistics from the other two methods indicate a contagious pattern for the three plots.

Table 4.1 Pattern of jack pine occurrence for selected ecosystem types of the Mack Lake burn

Ecosystem type	Plot	Presence 1/ of warbler	Sample size	Clark-Evans Statistic	Pattern 2/	Hopkins-Skellam Statistic	Pattern	Pielou-Mountford Statistic	Pattern
1	3	Yes	50	4.17	C	6.75	C	3.54	C
1	109	Yes	49	1.90	R	4.58	C	2.60	C
1	114	Yes	50	2.19	C	4.53	C	2.36	C
1	121	Yes	50	4.76	C	3.78	C	1.34	C
3	108	No	50	1.15	R	1.77	R	1.25	R
3	111	No	50	1.80	R	5.73	C	1.18	R
4	106	No	50	4.11	C	0.23	R	1.61	C
4	116	No	50	1.15	R	0.39	R	1.41	C
4	120	No	50	1.89	R	1.19	R	1.15	R
6	37	No	50	4.02	C	5.61	C	1.43	C
6	115	Yes	50	2.09	C	4.03	C	1.93	C
8	107	Yes	50	3.77	C	3.42	C	1.21	R
8	110	Yes	50	4.29	C	5.79	C	2.27	C
8	117	Yes	50	2.22	C	3.65	C	1.98	C
8	118	Yes	50	2.82	C	2.85	C	1.63	C
8	122	Yes	50	6.35	C	19.68	C	3.18	C
9	36	No	50	3.13	C	2.57	C	1.99	C
9	40	No	50	1.36	R	2.73	C	1.51	C
9	113	No	50	0.42	R	1.21	R	1.26	R
10	35	Yes	50	3.24	C	6.49	C	2.44	C
10	112	Yes	50	4.30	C	6.97	C	2.88	C
10	119	Yes	50	2.10	C	2.85	C	1.29	R
Jack pine plantation		Yes	100	3.63	C	16.21	C	1.36	C
Red pine plantation		Yes	50	0.74	R	8.04	C	1.20	R
1966 burn		No	50	0.82	R	1.48	R	1.45	C

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 pattern; R = random pattern.

Although a random pattern of jack pine occurrence was frequently found in ecosystem types 3, 4, and 9, there were several cases where all three methods showed a contagious pattern for individual plots. Again, exceptions may be due to management activities. Plot 36 (ecosystem type 9) and plots 106 and 116 (ecosystem type 4) are situated in old red pine plantations that were furrowed for planting. The furrowing could change the micro-site conditions by exposing the mineral soil and by reducing the competition from ground-cover plants. Also, the presence of oak or willow clumps may cause a contagious pattern in jack pine occurrence. For example, plot 40 (ecosystem type 9) has a very high coverage of clumps of northern pin oak. Jack pines are unable to establish in such clumps. Plot 111 (ecosystem 3) was located in an area which has abundant willow clones, and no pines were observed in such dense clones. In addition, random sampling errors also could contribute to the causes of the exceptions. Obviously, more and larger sample plots are desirable in areas of high disturbances and low density of jack pine, e.g., in ecosystem types such as 3 and 9.

Based on the overall difference in the pattern of jack pine occurrence, the ecosystem types were divided into two groups: the contagious group (types 1, 6, 8, and 10) and the random group (types 3, 4, and 9). The differences between the groups in pattern of jack pine occurrence were then tested using analysis of variance (ANOVA). Differences among the three methods (Clark-Evans, Hopkins-Skellam, and Pielou-Mountford) were also tested (Table 4.2). A significant difference ($P = 0.0001$) was found between the two groups. Although there were differences among individual plots (Table 4.1), the three

methods are identical ($P = 1$) in determining of the overall pattern of jack pine occurrence. The results also indicate that there is no interaction ($P = 0.96$) between the methods and the ecosystem groups.

Theoretically, the sample taken from the jack pine plantation (with human-created openings)(Table 4.1) should indicate a contagious pattern. In fact, the statistics of the three methods bear this out. The reasons for the contagious pattern may be due not only to the created openings, but also to the natural regeneration and the natural dying of jack pines in the plantation. Plantations commonly receive seeds from the adjacent jack pine stands, and seedlings become established. Also, some young jack pine seedlings die soon after being planted. In addition, planting machines sometimes plant more than one seedling at a single spot. In these ways a contagious pattern may arise.

One might expect that the sample from the red pine plantation (without human-created openings) should indicate a regular pattern of jack pine occurrence. However, the statistic from the Hopkins-Skellam method indicates a contagious pattern for this plantation. Such a finding may be also due to the natural regeneration of jack pine in the red pine plantation as well as death of some planted red pines. This possible disruption of plantation regularity is supported by the fact that a random pattern, rather than the expected regular pattern, for this plantation was found using the other two methods (Table 4.1).

Pattern in the naturally regenerated stands of the 1966 burn is random according to the statistics of the Clark-Evans and the Hopkins-

Skellam methods (Table 4.1). This finding is based on data collected only for living jack pines. Because many young jack pine had died in the past several years, a more contagious pattern was probably present at an earlier date. Currently the 10 x 20 m plot has 423 stems of jack pines. Density was greater and jack pines were probably patchier when the stand was younger. As the stands developed, a more random pattern developed with the death of jack pines in the dense patches. Thus, a general developmental trend might be predicted with increasing age of jack pine stands from a contagious pattern to a more random one and possibly even to a regular pattern. The statistics of the Pielou-Mountford method still indicate a contagious pattern for the 1966 burn.

Patterns of Kirtland's Warbler Occupancy in Local Landscape Ecosystem Types

In 1987, Kirtland's warblers were limited to the areas dominated by the local landscape ecosystem types 1, 6, 7, 8, or 10 which are termed the "favorable ecosystem group." None of the warblers in 1987 was found in areas dominated by ecosystem types 2, 3, 4, 5, 9, or 11, the "unfavorable ecosystem group." This difference in ecosystem types also corresponds with that between the two pattern types of jack pine occurrence (the contagious pattern vs. the random pattern).

Forty-one singing males and 22 female warblers were found in the Mack Lake burn in 1987. The distribution of the singing males in the local landscape ecosystem types is listed in Table 4.3. We examined 28 of the male locations (68 % of the male population in the burn) and 16

Table 4.3 Distribution in 1987 of 28 male Kirtland's warblers by ecosystem types at the Mack Lake burn

Ecosystem type	1	6	7	8	10
Number of warblers	12	3	3	8	2

of the female locations (73 % of the female population in the burn) during the field season. All the warbler sightings and nests were found in the area dominated by ecosystem types of the favorable group--with generally a contagious pattern of jack pine distribution.

Ecosystem type 1, covering the largest area of all ecosystems, had the largest population of the male warblers in 1987. Most of the locations occupied by the warbler had denser and taller jack pines than the rest of the areas in the same ecosystem. Ecosystem type 6 had only three male warblers. This is the poorest ecosystem type (in moisture and nutrients) in the terraces, and the jack pine is the shortest and its density is one of the lowest. These two ecosystem types are expected to host more warblers as the jack pine increases in height.

Ecosystem type 7 has one of the smallest areas of all ecosystem types. The warblers were first found in this ecosystem type in 1986. In 1987, it only hosted 3 male warblers. Ecosystem type 8 had eight warblers--the second highest number of males. Compared with ecosystem 1, it occupies a much smaller area. However, jack pines in this ecosystem are dense and tall, and oaks are vigorous and abundant. Ecosystem type 10 had only 2 male warblers. It is also a minor ecosystem in the ice-contact terrain. Jack pine and oaks are both dense and tall.

The occurrence of Kirtland's warbler occupancy in the Mack Lake burn is apparently associated to the physiography of the landscape (Barnes et al., 1987). A higher proportion of singing male warblers were in the high-level outwash terraces than in the low-level outwash in both 1986 and 1987, despite the fact that these two areas are similar in size. However, this difference was smaller in 1987 than in 1986. It is expected the difference will by even smaller as the jack pines become taller.

Analysis of Relationships of physical and vegetative Factors to Selected Ecosystem Types, Pattern of Jack Pine Occurrence, and Occupancy of the Kirtland's Warbler

A total of 56 variables of physiography-soil, tree species, and ground vegetation were selected by stepwise discriminant analysis. Twenty-three variables which differ significantly among the selected ecosystem types were further selected from the variables by one-way ANOVA. These variables, together with those determined by canonical variate analysis, facilitated comparison of the ecosystem types in relation to the pattern of jack pine occurrence and the occupancy by the warbler in 1987.

Analysis of Variables of Physiograhpy-soil, Tree Species, and Ground-cover Vegetation Selected by Stepwise Discriminant Analysis

Eleven variables of physiography-soil (Table 4.4) were selected from 38 original ones. They comprise major features of the local landscape ecosystem types, including physiography, soil texture, and soil reaction.

Table 4.4 Mean and standard deviation of physiographic-soil variables selected by stepwise discriminant analysis 1/

Variable 2/	Ecosystem type						
	1	6	8	10	4	3	9
Depth to layer of clay or loam (cm)	>400	>400	>400	>400	>400	137.0 (71.5)	84.83 (23.03)
Depth of depressions or channels (m)	0	0	0	0	7.57 (3.57)	0	0
Elevation (m)	368.0 (2.2)	376.6 (3.7)	375.2 (4.1)	384.2 (4.8)	358.2 (3.6)	369.2 (2.1)	375.6 (3.4)
Thickness of clay & loam (cm) (0-150 cm)	0	0	0	0	0	16.50 (17.14)	41.83 (15.41)
Depth to lamellae (cm)	>400	>400	224.0 (339.5)	>400	>400	>400	>400
Average pH (30-150 cm)	5.04 (.32)	5.45 (0.29)	5.76 (0.29)	5.15 (0.39)	5.87 (0.51)	6.10 (1.06)	5.65 (0.64)
Thickness of A1 horizon (cm)	3.12 (1.64)	4.46 (1.72)	2.36 (1.55)	4.50 (1.00)	4.64 (3.53)	3.13 (1.18)	4.30 (0.79)
Percent of pebbles & cobbles (0-150 cm)	3.37 (7.47)	2.73 (3.17)	4.09 (4.68)	0.94 (0.82)	15.08 (9.34)	1.36 (1.42)	3.31 (2.87)
Percent of medium sand (10-150 cm)	60.5 (8.45)	69.66 (5.35)	55.50 (9.52)	59.9 (6.88)	57.54 (19.39)	53.02 (16.71)	54.93 (11.14)
Percent of very fine sand (10-150 cm)	1.70 (0.94)	2.06 (1.69)	3.50 (2.34)	2.10 (1.01)	4.70 (6.70)	5.05 (6.55)	3.77 (2.77)
Slop aspect of plot	218.4 (94.3)	153.2 (148.9)	180.14 (106.3)	253.3 (144.0)	139.6 (142.8)	107.0 (50.1)	165.0 (101.3)

1/ Values are means and standard deviation (in parentheses).

2/ Variables are presented in order determined by the analysis

Eight variables of tree species (Table 4.5) were selected from an original set of 32 variables. All of these variables are those related to density of jack pine and the northern pin oak, the growth rate of oaks, or the openness class in the study area. None of these included variables of red pine snags or jack pine growth.

From the original set of 120 variables of ground-cover vegetation, 37 variables (primarily coverage of individual species) were selected (Table 4.6). Among them, two are the number of shrub and lichen species and two are the percentage of bare ground and the coverage of large woody debris. All others are the coverages of individual ground-cover species or groups of plants, such as mosses and lichens. In general, the low-level outwash, especially ecosystem type 1, has fewer shrub species than the high-level outwash and ice-contact terrain (Table 4.6). The average number of shrub species in ecosystem types 1 and 4 is 5.2 and 7.8, respectively, which is less than that observed in other ecosystem types in the terraces and ice-contact terrain. The ground-cover species differ considerably in both the percent of coverage and their frequency of presence in different ecosystem types. Three groups of ground-cover species can be recognized according to their coverage and frequency of presence in different ecosystem types. The first group consists of those which are abundant in certain ecosystem types but also common in other types. Such species include Quercus ellipsoidalis, Prunus pumila, Vaccinium angustifolium, Pinus banksiana, and Arctostaphylos uva-ursii. Species in the second group are those which are common only in certain ecosystem types but rare in other types. Examples are Amelanchier sanguinea, Cretaegus spp., Fragaria virginiana,

Table 4.5 Mean and standard deviation of tree species variables selected by stepwise discriminant analysis [1/]

Variable [2/]	Ecosystem type						
	1	6	8	10	4	3	9
Number of oak seedlings	0.60 (0.84)	6.20 (3.96)	6.57 (3.31)	15.50 (14.01)	1.20 (1.79)	2.75 (1.89)	11.00 (6.51)
Basal diameter of oak snags (in)	0.37 (1.17)	0	1.11 (1.90)	3.80 (2.59)	0	0.72 (1.45)	0
Average height of dominant oaks (cm)	17.30 (23.74)	82.20 (49.09)	190.14 (153.1)	138.50 (165.05)	19.60 (30.67)	130.50 (149.7)	133.83 (79.47)
Openess class in general area	2.10 (0.74)	1.60 (0.55)	2.43 (0.79)	2.00 (0.82)	1.20 (0.45)	1.25 (0.50)	1.83 (0.41)
Average height of 1st living JP branch (cm)	14.70 (5.36)	21.20 (8.61)	23.00 (5.03)	22.25 (7.93)	22.80 (7.12)	14.25 (2.87)	22.17 (6.71)
Openess class in plot	1.90 (0.88)	1.40 (0.55)	2.43 (0.79)	1.75 (0.96)	1.40 (0.55)	1.25 (0.50)	1.33 (0.52)
Number of JP in selected two subplot	82.50 (62.02)	88.20 (81.37)	107.43 (51.74)	108.25 (103.36)	43.40 (38.06)	27.75 (22.79)	66.17 (34.68)
Number of oak clumps	0.90 (1.52)	8.60 (6.43)	7.11 (3.37)	11.50 (12.34)	1.20 (1.64)	5.00 (8.04)	3.83 (2.48)

1/ Values are means and standard deviation (in parentheses).

2/ Variables are presented in order determined by the analysis.

Table 4.6 Mean and standard deviation of variables of ground-cover vegetation selected by stepwise discriminant analysis[1]

Variable[2]	Ecosystem type						
	1	6	8	10	4	3	9
Quercus ellipsoidalis	1.3 (1.9)	4.0 (4.6)	6.2 (4.3)	16.5 (9.0)	.43 (.61)	3.0 (4.1)	3.5 (2.1)
Number of shrub species	5.2 (1.7)	11.2 (2.8)	8.7 (3.4)	9.0 (4.1)	7.8 (1.9)	9.25 (.50)	10.5 (2.1)
Prunus pumila	3.3 (4.6)	1.3 (1.2)	.30 (.34)	.39 (.74)	13.5 (10.3)	.71 (.57)	.44 (.59)
Solidago speciosa	.04 (.09)	.01 (.02)	.01 (.02)	.00 (.00)	.15 (.34)	.00 (.00)	.00 (.00)
Number of lichen species	1.6 (1.0)	1.6 (0.9)	3.0 (1.0)	1.75 (.96)	2.0 (1.0)	2.00 (.82)	1.2 (.41)
Krigia virginica	.01 (.02)	.00 (.00)	.00 (.00)	.00 (.00)	.00 (.00)	.00 (.00)	.00 (.00)
Cirsium hillii	.00 (.00)	.00 (.00)	.01 (.02)	.00 (.00)	.06 (.13)	.00 (.00)	.00 (.00)
Viola pedata	.01 (.02)	.00 (.00)	.00 (.00)	.00 (.00)	.00 (.00)	.00 (.00)	.00 (.00)
Maianthemum canadense	.00 (.00)	.06 (.13)	.04 (.11)	.00 (.00)	.01 (.02)	.15 (.17)	.36 (.33)
Prunus alleghaniensis	.00 (.00)	.00 (.00)	.00 (.00)	.07 (.15)	.00 (.00)	.00 (.00)	.00 (.00)
Gaylussacia baccata	.00 (.00)	.00 (.00)	.00 (.00)	3.8 (5.7)	.00 (.00)	.00 (.00)	.00 (.00)
Streptopus roseus	.01 (.02)	.00 (.00)	.00 (.00)	.07 (.15)	.00 (.00)	.00 (.00)	.00 (.00)
Rhus aromatica	.00 (.00)	.00 (.00)	.00 (.00)	.00 (.00)	.06 (.13)	.00 (.00)	.00 (.00)
Cretaegus spp.	.00 (.00)	.21 (.33)	.26 (.56)	.19 (.37)	.01 (.02)	.07 (.15)	.51 (.60)
Populus grandidentata	.00 (.00)	.00 (.00)	.43 (1.1)	.75 (1.50)	.00 (.00)	.00 (.00)	.00 (.00)
Smilacina racemosa	.00 (.00)	.00 (.00)	.00 (.00)	.01 (.03)	.00 (.00)	.00 (.00)	.00 (.00)
Aster macrophyllus	.00 (.00)	.00 (.00)	.00 (.00)	.00 (.00)	.00 (.00)	.00 (.00)	.05 (.12)

1/ Values are means of coverage or number of species and standard deviation (in parentheses).

2/ Variables are presented in order determined by the analysis.

Table 4.6 (continued)

Lichens	1.6 (1.8)	.34 (.25)	1.01 (.98)	3.3 (5.8)	1.4 (2.6)	.91 (1.4)	.13 (013)
Vaccinium angustifolium	26.4 (19.4)	30.0 (18.0)	30.0 (18.0)	42.0 (12.0)	29.4 (19.0)	50.5 (23.9)	35.7 (29.5)
Taraxacum officinale	.00 (.00)	.00 (.00)	.01 (.02)	.00 (.00)	.00 (.00)	.01 (.03)	.00 (.00)
Amelanchier sanguinea	.03 (.09)	.06 (.13)	.04 (.11)	.00 (.00)	1.4 (.55)	1.88 (2.8)	.06 (.12)
Solidago spathulata	.16 (.15)	.06 (.13)	.16 (.28)	.00 (.00)	1.3 (1.2)	1.51 (3.0)	.01 (.02)
Fragaria virginiana	.00 (.00)	.17 (.32)	.05 (.11)	.07 (.15)	.12 (.16)	.53 (.98)	.12 (.14)
Bare ground	1.1 (1.2)	0.8 (1.2)	.29 (.23)	.58 (.35)	1.3 (1.5)	.04 (.03)	.40 (.61)
Large woody debris	5.3 (2.9)	9.7 (5.2)	4.1 (2.4)	4.1 (2.5)	6.4 (5.6)	7.2 (5.7)	8.0 (3.1)
Pinus banksiana	21.2 (19.6)	10.2 (8.4)	32.7 (28.0)	15.4 (10.8)	13.5 (10.3)	5.4 (4.9)	10.0 (3.1)
Helianthus canadensis	.08 (.24)	.00 (.00)	.01 (.02)	.00 (.00)	.19 (.15)	.00 (.00)	.00 (.00)
Aster ptarmicoides	.00 (.00)	.02 (.03)	.00 (.00)	.00 (.00)	.00 (.00)	.00 (.00)	.00 (.00)
Solidago spp.	.06 (.03)	.06 (.13)	.00 (.00)	.00 (.00)	.00 (.00)	.00 (.00)	.00 (.00)
Erigeron strigosus	.00 (.00)	.00 (.00)	.00 (.00)	.00 (.00)	.01 (.02)	.00 (.00)	.00 (.00)
Senecio pauperculus	.00 (.00)	.02 (.03)	.00 (.00)	.00 (.00)	.12 (.16)	.00 (.00)	.00 (.00)
Symphoricarpus albus	.00 (.00)	.06 (.13)	.00 (.00)	.19 (.37)	2.4 (5.4)	6.01 (12.0)	.13 (.31)
Melampyrum lineare	.02 (.03)	.15 (.34)	.10 (.14)	.28 (.34)	.00 (.00)	.01 (.03)	.02 (.03)
Rosa blanda	.01 (.02)	.01 (.02)	.04 (.11)	.01 (.03)	.06 (.13)	.09 (.14)	.28 (.26)
Arctostaphylos uva-ursii	.12 (1.9)	1.3 (1.1)	1.0 (1.1)	2.4 (2.7)	.90 (1.3)	.03 (.03)	.30 (.60)
Grasses and sedges	47.4 (28.6)	43.2 (10.7)	44.0 (29.9)	21.0 (6.0)	50.0 (20.7)	34.0 (33.1)	42.7 (25.8)
Antennaria plantaginifolia	.00 (.00)	.01 (.02)	.01 (.02)	.00 (.00)	.00 (.00)	.00 (.00)	.00 (.00)

1/ Values are means of coverage or number of species and standard deviation (in parentheses).

2/ Variables are presented in order determined by the analysis.

Rosa blanda, Symphoricarpus albus, and Melampyrum lineare. The third group consists of species which only occur in certain ecosystem types and are absent in others. The representatives are Krigia virginica, Cirsium hillii, Viola pedata, Prunus alleghaniensis, Gaylussacia baccata, Streptopus roseus, Rhus aromatica, Populus grandidentata, Smilacina racemosa, Aster macrophyllus, Aster. ptarmicoides, Taraxacum officinale, Helianthus canadensis, Helianthus canadensis, Erigeron strigosus, Senecio pauperculus, and Antennaria plantaginifolia.

Relationships of Physical and Vegetative Factors to Local Landscape Ecosystem Types

Twenty-three variables of physiography-soil, tree species, and ground-cover species were found significantly associated to local landscape ecosystem types determined by one-way ANOVA and Duncan's multiple range test (Table 4.7). Among them, 7 are of physiography-soil, 6 are of tree species, and 10 are the variables of ground-cover vegetation.

Ecosystem types 3 and 9 are characterized by the presence of a heavy-textured layer. The layer in type 9 is much thicker than that in type 3. Type 4 may occasionally have this layer. Several bands of lamellae are typically present in type 8. A thick layer of pebbles and cobbles were consistently found in type 4 (outwash channels). Type 1 has the most acid soil in the 30-150 cm horizon on the average.

Table 4.7 Variables associated with ecosystem type, jack pine pattern, and the occurrence of the warbler in 1987 determined by one-way ANOVA and Duncan's multiple range test 1/

Pattern	Contagious				Random			Significance level
Occurrence of warbler 2/	Present				Absent			
Ecosystem type	1	6	8	10	4	3	9	
Variable								
Quercus ellipsoidalis	ab	ab	b	c	a	ab	ab	0.0001
Amelanchier sanguinea	b	b	b	b	a	a	b	0.009
Gaylussacia baccata	a	a	a	b	a	a	a	0.023
Prunus pumila	a	a	a	a	b	a	a	0.0001
Rosa blanda	a	a	a	a	a	a	b	0.011
Aster ptarmicoides	a	b	a	a	a	a	a	0.015
Maianthemum canadense	a	a	a	a	a	a	b	0.003
Senecio pauperculus	a	a	a	a	b	a	a	0.018
Number of shrub species	b	a	a	a	b	a	a	0.002
Number of lichen species	b	b	a	b	a	a	b	0.034
Depth to clay or loam (0- 400 cm)	c	c	c	c	b	a	a	0.0001
Thickness of clay and loam (0-150 cm)	c	c	c	c	c	a	b	0.0001
Depth to lamellae (0-400 cm)	b	b	a	ab	b	ab	ab	0.009
Percent of pebbles and cobbles (0-150 cm)	b	b	b	b	a	b	b	0.007
Elevation (m)	b	d	d	c	a	b	d	0.0001
Depth of depressions or channels (m)	b	b	b	b	a	b	b	0.0001
Average pH (30-150 cm)	c	abc	ab	bc	a	a	abc	0.009
Basal diameter of oak snags (in)	a	a	a	b	a	a	a	0.002
Average height of 1st living JP branch	c	abc	a	ab	a	bc	ab	0.025
Openess class in general area	ab	ab	b	ab	a	a	ab	0.031
Average height of dominant oaks	a	ab	b	ab	a	ab	ab	0.028
Number of oak clumps	c	ab	abc	a	bc	abc	bc	0.023
Number of oak seedlings	a	ab	ab	c	a	a	bc	0.001

1/ Variables with the same letters are not significantly different (= 0.05).
2/ Presence based on singing males and nesting females in the ecosystem types.

The basal diameter (20 cm above ground) of oak snags in type 10 is greater than that of all other types. The average height of the first living branch of jack pine is lowest in type 1. The openness classes of the general area in types 3 and 4 are the lowest. The average height of dominant oaks in types 1 and 4 is typically lower than in other types, whereas type 8 has the highest average height value. The number of oak clumps in type 1 is the lowest, whereas type 10 contains the highest number of these clumps. Similar trends occur for the number of oak seedlings.

Northern pin oak typically has low coverage in ecosystem type 4 and high coverage in types 1 and 8 than in other types. The coverage of *Amelanchier sanguinea* is significantly higher in types 4 and 3. *Gaylussacia baccata* appears only in type 10. *Prunus pumila* has its highest coverage in type 4. *Rosa blanda* is present frequently in type 9. *Aster ptarmicoides* was only recorded in type 6. *Maianthemum canadense* favors type 9. *Senecio pauperculus* is typically found in type 4. Compared with other ecosystems, ecosystem types 1 and 4 support significantly lower numbers of shrub species, and types 1, 6, 10, and 9 have a significantly higher number of lichen species.

Relationships of Physical and Vegetative Factors to the Pattern of Jack Pine Occurrence and the Occupancy of the Kirtland's Warbler

The selected variables were also closely associated with the patterns of jack pine occurrence (Table 4.7). The contagious pattern often appear in areas where there are a high coverage of northern pin oak and a relatively low coverage of *Amelanchier sanguinea* and *Prunus pumila*. Such areas are commonly associated with relatively poor soils, high elevations, and low pH. On the other hand, the random pattern is usually related to low coverage of northern pin oak, high coverage of *Amelanchier sanguinea*, soils having a heavy-textured layer or a layer of pebbles and cobbles, low elevations (outwash channels), and relatively high pH. Several grass species are highly related to the pattern types of jack pine occurrence. The blue stem grasses are often abundant in areas having a contagious pattern of jack pine occurrence, whereas *Oryzopsis asperifolia* and *Schizachne purpurascens* are often more prevalent in ecosystems with a random pattern.

Plant species that were observed to be unevenly distributed are probably the major direct causal factors of the pattern of the jack pine occurrence. Such plant species are typically those that regenerate vegetatively by rhyzomes or roots and form clones. Species that tend to exhibit such an uneven distribution include northern pin oak, low sweet blueberry, sweet fern, blue stem grasses, bearberry, and wintergreen. Although these species may grow together throughout the burn, the former three tend to occur on the high-level outwash terraces and ice-contact terrain, and the latter three on the low-level outwash terrain. Jack pine appears to have difficulty in establishing and competing with these species when it grows together with them, but jack pine is easy to establish in areas not having these species, especially in bare ground. Hence, a contagious pattern of jack pine occurrence tends to develop in areas with a mosaic spatial arrangement of bare ground and these species.

The physiography-soil variables indirectly affect the pattern of jack pine occurrence. These variables affect plant species composition and spatial vegetative structureand hence the pattern of jack pine occurrence. More species and a higher plant coverage were present in ecosystem types 3, 9 (having a layer of heavy-textured soil), and 4 (outwash channel) than that in other ecosystem types. Hardly any bare ground is found in these types. Competition for jack pine is severe but evenly distributed. As a result, jack pine appeares to occurs in a more random pattern in these types than in types that have bare ground interspersed in the area, including types 1, 6, 7, 8, and 10.

Site conditions in depressions and channel areas are different from the surrounding terrain. Because of the damage of freezing temperatures in the early growing season, northern pin oak is often absent. The coverage of plants is also higher and more evenly distributed than those in the highly-elevated areas because of the moister soil. Therefore, the occurrence of jack pine again tend to be random. Other factors such as prefire management history and species composition and severity of burning may also affect the pattern of jack pine occurrence.

In summary, the warblers prefer areas having a contagious jack pine distribution that is found in ecosystem types 1, 6, 7, 8, and 10. These ecosystem types are characterized by one or more of the following features: 1) rolling or level topography; 2) Grayling, Graycalm, Montcalm, and Rubicon soil series; 3) uplands which have warm microclimate; 4) vegetation dominated by the northern pin oak, low sweet blue berry, and blue stem grasses, or combinations of these species; and 5) relatively tall, dense, and patchy jack pine. In contrast, the warblers avoid areas having random pattern found in ecosystem types 2, 3, 4, 5, 9, and 11. These ecosystem types are characterized either by one or more of the following: 1) depressions and outwash channels; 2) rich soil series such as Manistee series (heavy-textured layer greater than 10 cm thick); 3) relatively cold microclimate having freezing temperatures in the early growing season; 4) ground-cover species dominated by species such as Oryzopsis asperifolia, and Schizachne purpurascens; and 5) relatively short, sparse, and randomly distributed jack pines.

Relationships of Canonical Variates to Physical and Vegetative Factors

Marked difference among the ecosystem types were demonstrated by canonical variate analysis using the first 20 principal components (Fig. 4.1, 4.2; Table 4.8). The cumulative variation for the first 20 principal components was 90.8 %, and that for the first 3 canonical variates was 90.1 %. A total of 81.8 % of the information in the 56 variables is contained in the first three canonical variates.

High values of the first canonical variate were mainly associated with high values of principal components 1, 5, 6, and 12 and with the low value of principal component 7 (Table 4.8). These values were associated with the topography of the high-level outwash terraces and

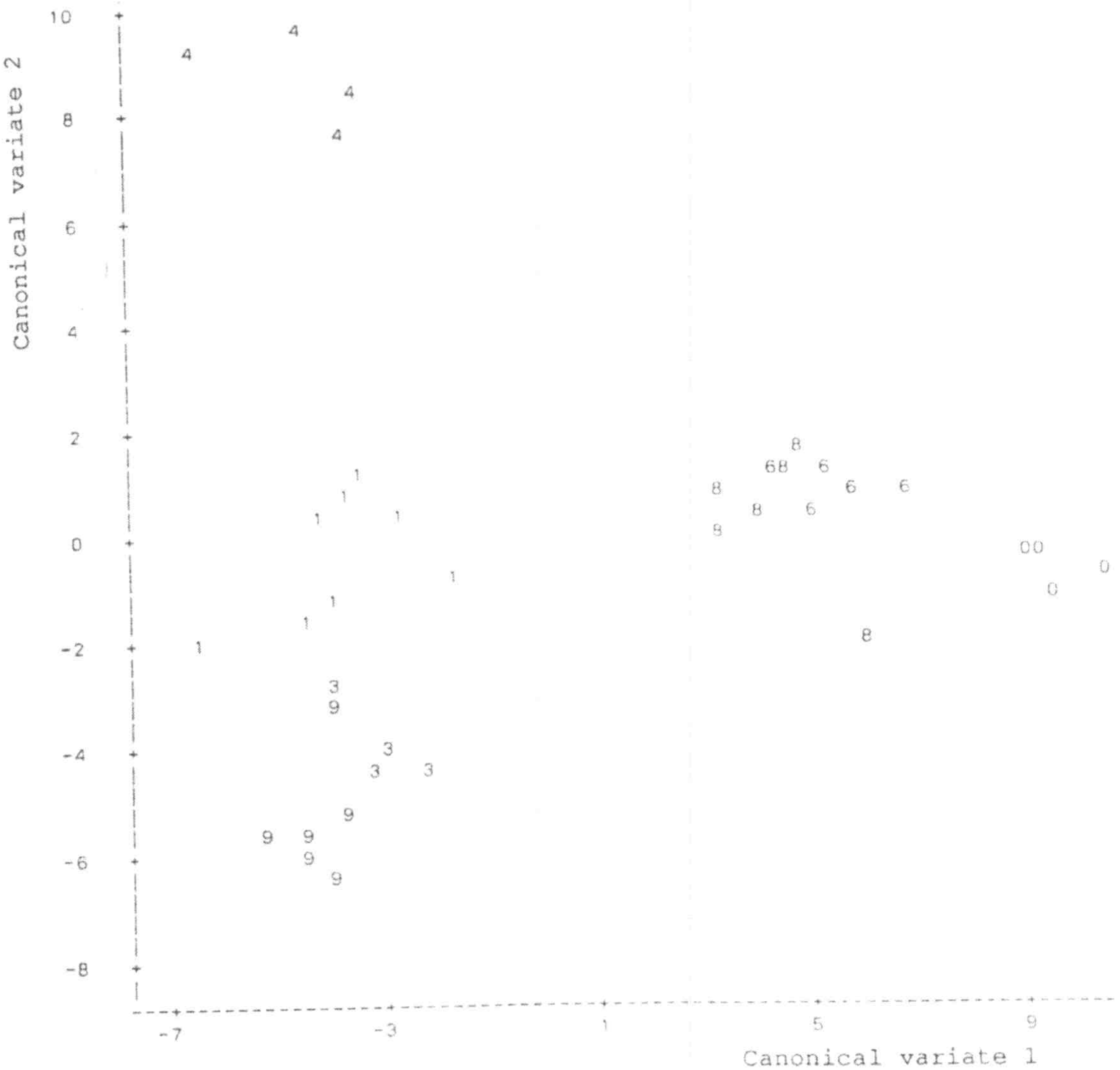


Fig. 4.1. Ordination of samples of the selected local landscape ecosystem types along the first two canonical variates using the first twenty principal components. Number 0 stands for ecosystem type 10.

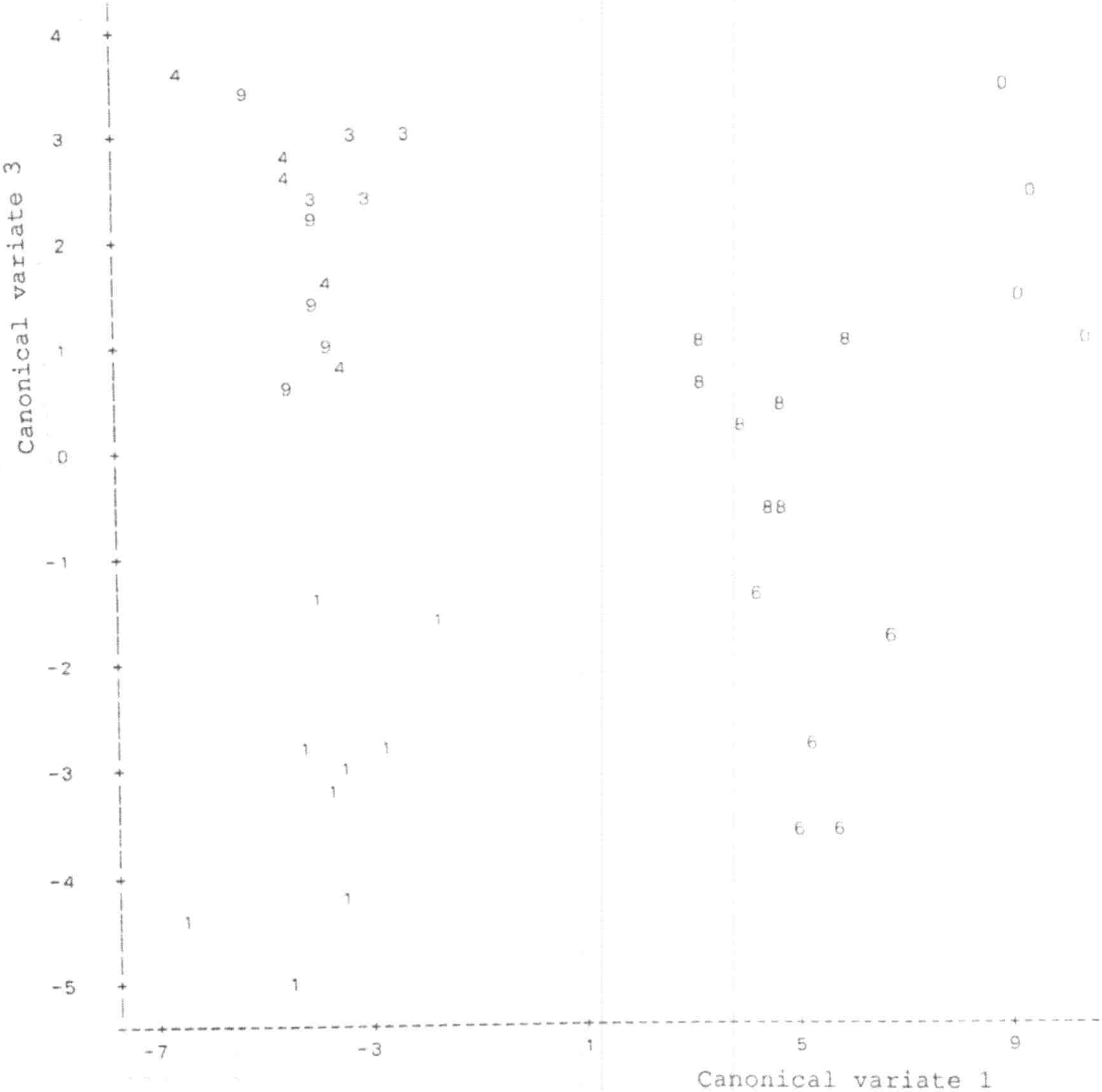


Fig. 4.2. Ordination of samples of the selected local landscape ecosystem types along the first and the third canonical variates using the first twenty principal components. Number 0 stands for ecosystem type 10.

Table 4.8 Eigenvalues, cumulative proportion of explained variance, and variance coefficients of the first three canonical variates of an analysis of the first 20 principal components.

Canonical variate	1	2	3
Eigenvalue	31.2	19.5	6.4
% of cumulative variance	49.2	80.0	90.1
Principal component 1	.655	-.353	-.166
Principal component 2	.057	-.556	.464
Principal component 3	-.018	.038	.157
Principal component 4	.008	-.100	.126
Principal component 5	.221	.384	.109
Principal component 6	.368	.132	.418
Principal component 7	-.224	-.101	.358
Principal component 8	-.042	.074	-.080
Principal component 9	.042	-.028	.277
Principal component 10	-.030	.045	.126
Principal component 11	.189	-.186	-.262
Principal component 12	.212	-.016	-.094
Principal component 13	.087	.024	.115
Principal component 14	.136	.054	.295
Principal component 15	.076	.129	.050
Principal component 16	.361	.367	.165
Principal component 17	.198	.009	-.129
Principal component 18	-.063	-.055	-.021
Principal component 19	.182	.005	-.208
Principal component 20	-.005	.193	-.185

Table 4.9 Eigenvalues, cumulative proportion of explained variance, and variable coefficients of 10 selected principal components of an analysis of 56 variables of physiography-soil, tree species, and ground-cover vegetation determined by stepwise discriminant analysis

Component	1	2	3	5	6	7	9	12	14	16
Eigenvalue	7.7	5.7	4.8	3.4	3.2	2.9	2.5	1.9	1.7	1.3
% of cumulative variance	13.1	22.9	31.0	36.8	42.2	47.1	51.4	54.7	57.6	59.8
Variable										
Percent medium sand (10-150 cm)	.071	-.209	-.256	.218	-.074	.052	.009	-.013	-.022	.025
Percent very fine sand (10-150 cm)	-.116	.218	.209	-.082	.032	-.100	-.056	.070	.076	.069
Thickness of A1 horizon (cm)	-.022	-.073	-.122	.167	.066	.121	-.005	.070	-.012	-.082
Depth to clay or loam (cm)	.156	-.265	.028	.084	.008	-.157	-.039	.144	-.064	.192
Thickness of clay or loam (0-150 cm) (cm)	-.062	.274	-.056	-.147	-.075	.141	-.065	-.063	.050	-.198
Depth to lamellae (cm)	-.050	-.189	-.270	.157	-.064	-.017	-.070	-.076	-.027	-.146
Percent pebbles and cobbles(0-150 cm)	-.122	-.163	.063	.178	-.036	.133	.054	-.062	-.069	.113
Elevation (m)	.266	.139	-.077	-.056	.127	-.070	-.067	.085	.035	-.033
Slope aspect of slope	.078	-.086	.020	-.018	.061	-.035	.301	-.097	-.111	-.068
Depth of depressions or channels (m)	-.218	-.064	.174	.141	.088	-.018	.036	-.139	.105	.153
Average pH (30-150 cm)	-.164	.090	-.005	-.026	.094	.164	.152	-.044	-.088	.256
Number of oak seedlings	.207	.199	.018	.053	.089	.162	-.113	-.061	.094	.123
Basal diameter of oak snags (in)	.236	.033	.092	.051	.269	.059	-.019	-.087	.053	-.126
Average height of 1st living JP branch (cm)	.039	.122	.178	.270	-.043	-.076	.033	.062	.053	.134
Openness class in plot	.189	-.051	.258	.057	-.209	.005	.096	.141	-.010	-.003
Openness class in general area	.218	.016	.211	.033	-.205	-.011	-.009	.176	-.100	-.140
Average height o f dominant oaks (cm)	.196	.185	.037	.107	-.061	.087	.039	-.100	.068	.142
Number of oak clumps	.215	.101	-.034	.237	.090	.121	-.058	-.125	-.004	.173
Number of JP in selected two subplots	.218	-.064	.203	.071	-.116	-.099	.059	-.075	-.013	-.097

Table 4.9 (continued).

Component	1	2	3	5	6	7	9	12	14	16
Pinus banksiana	.149	-.062	.241	.067	-.207	.036	.048	.228	.002	.020
Populus grandidentata	.155	.020	.141	.077	.072	-.135	.060	-.320	.060	-.088
Quercus ellipsoidalis	.251	.062	.048	.048	.260	.105	.063	.065	.051	.001
Amelanchier sanguinea	-.205	-.020	.129	.107	.170	.226	-.072	.054	.092	-.077
Arctostaphylos uva-ursii	.069	-.106	-.032	-.012	.119	-.229	.059	-.237	.139	-.040
Cretaegus spp.	-.039	.172	-.196	.053	-.055	-.089	.205	.084	-.124	.112
Gaylussacia baccata	.150	.028	.110	.094	.115	-.125	.009	-.360	.130	-.114
Prunus alleghaniensis	-.009	-.026	-.174	.037	.174	-.209	.275	.221	.316	.032
Prunus pumila	-.149	-.219	.015	.109	.044	.191	-.014	-.107	.053	.127
Rhus aromatica	-.093	-.088	.091	.209	.031	.163	-.126	.171	.132	-.028
Rosa blanda	-.122	.257	-.030	.005	-.060	-.017	.105	-.027	-.130	-.069
Symphoricarpus albus	-.180	.120	.126	.006	.190	.042	.038	-.016	-.013	-.154
Vaccinium angustifolium	.056	-.000	-.113	-.058	.194	.210	-.093	.076	.088	.031
Antennaria plantaginifolia	.053	.017	.008	-.009	-.035	-.095	-.214	.299	.042	.070
Aster macrophyllus	.005	.188	-.008	-.086	-.110	.088	-.042	-.028	.149	.012
Aster ptarmicoides	-.015	.003	-.122	.049	-.023	-.162	-.262	.213	.100	-.055
Cirsium hillii	-.167	.121	.206	.146	.066	-.242	.067	.002	-.043	.011
Erigeron strigosus	-.166	.120	.212	.146	.073	-.232	.048	-.007	-.022	-.011
Fragaria virginiana	.006	.057	-.145	.216	-.031	.181	.253	-.005	.001	-.130
Helianthus canadensis	-.081	-.181	.129	-.045	-.107	.033	.111	-.084	.214	-.013
Krigia virginica	.019	-.100	.031	.118	-.166	.098	-.037	.075	.142	-.291
Maianthemum canadense	-.032	.264	-.070	-.129	-.189	.110	-.002	-.070	.119	.099
Melampyrum lineare	.159	.051	-.014	.218	.166	.052	-.054	-.000	-.238	.097
Senecio pauperculus	-.182	.025	.197	.279	.077	-.058	-.079	.123	.065	-.032
Smilacina racemosa	-.005	-.025	-.171	.038	.176	-.211	.277	.217	.314	.033
Solidago spp.	.019	-.079	-.040	.122	-.202	.064	-.135	-.074	.285	.030
Solidago spathulata	-.199	.017	.133	.055	.183	.204	-.018	.026	.035	-.108
Solidago speciosa	-.022	-.122	.036	-.031	-.118	-.052	.052	-.100	.159	.085
Streptopus roseus	.110	-.045	.064	-.099	.225	.127	-.002	.192	.059	-.176
Taraxacum ifficinale	.049	.064	-.020	.096	-.124	.232	.328	.053	.086	-.051
Viola pedata	-.019	-.136	.089	-.144	-.120	-.026	.138	-.077	.121	-.091
Grasses and sedges	-.105	-.006	.025	.003	-.161	-.065	.165	.041	-.216	-.035
Lichens	.056	-.126	.119	-.237	.166	.111	.064	.116	.115	-.048
Woody debris	-.050	.167	-.010	.212	-.170	-.011	-.211	.019	.175	-.176
Bare ground	-.042	-.198	-.037	.011	.133	.011	-.084	-.025	-.177	-.044
Number of shrub species	-.041	.195	-.173	.206	.025	-.157	.070	.144	.055	.111
Number of lichen species	.038	-.081	.207	-.187	.017	.148	.068	.136	-.005	.453

the ice-contact terrain, the presence of abundant oaks, the soil without loam or clay bands, the high patchiness of jack pine occurrence, the high coverage of the bearberry, and the low coverage of Amelanchier sanguinea (Table 4.9).

High values of the second canonical variate were mainly associated with high values in principal components 5 and 16 and low values in components 1 and 2, which were associated with the depressions or outwash channels, the presence of pebble and cobble layers, the low coverage of bearberry and Gaylussacia baccata, and the high coverage of Rhus aromatica, Fragaria virginiana, and Senecio pauperculus. Low values in canonical variate 2 were mainly determined by the presence of a layer of heavy-textured soil and the absence of the northern pin oaks.

High values of canonical variate 3 were highly associated with high values in principal components 2, 6, 7, 9, and 14, that were related to the presence of a layer of heavy-textured soil, hilly topography, high coverage of Prunus alleghaniensis, Fragaria virginiana, Smilacina racemosa, and relatively low coverage of Melampyrum lineare, grasses and Carex pennsylvanica.

The contagious pattern of jack pine occurrence and the presence of the warbler are associated with medium values of canonical variate 2 (Fig. 4.1; ecosystem types 1, 6, 8, and 10). Plots having either too high or too low a value for the second canonical variate are frequently associated to a random pattern of jack pine occurrence and were not occupied by warblers in 1986 and 1987 (Fig. 4.1; ecosystem types 3, 4, and 9). Thus, ecosystem types with medium values of canonical variate 2 appear to be favorable summer habitat of the warbler, whereas ecosystem types with either too high or too low a value are less favorable summer habitat of the warbler. Plots giving high values for canonical variate 3 as well as low values to canonical variate 1 (Fig. 4.2; types 3, 4, and 9) are also recognized as less favorable summer habitat. However, plots with either low values of canonical 3 and/or high values of canonical 1 (Fig. 4.2; types 1, 6, 8, and 10) are favored by warblers.

CHAPTER V

SUMMARY AND CONCLUSIONS

Background, Hypothesizes, and Objectives

Following the initial work of Gleason and Svedberg in 1920, the study of pattern of vegetation was developed in various ways. Marked progress has been made in the past decades. The early work led to the establishment of models for determining pattern types of a species population using a method of quadrat sampling. In 1952, Dice first used the "plotless sampling" method to measure departure of a species population from randomness. By using this method, the effect of quadrat size on pattern types was minimized or even avoided. Due to the advantage of plotless sampling, many new models to determine pattern of a species population have been developed. Recent work has emphasized causal factors of different patterns.

Previous studies have been restricted to the entire population level within a species or to the community level of several species. No reports are available where the study of pattern has been carried out at the landscape ecosystem level for a species. It has been widely accepted that different ecosystem types differ in physiography, soil and vegetation. Thus, a primary working hypothesis is that the types of plant patterns in different ecosystems may also differ.

In 1986 and 1987, Dr. B. V. Barnes and teams of graduate students from the University of Michigan conducted a study of the local landscape ecosystem types of the Mack Lake area, Oscoda County, northern lower Michigan. Eleven ecosystem types were identified, their characteristics were described, and the occurrence of the Kirtland's warbler in 1986 and 1987 in the area were plotted. I participated briefly in this study in 1986 and was a research assistant in 1987. The Mack Lake area is the center of the summer habitat of an endangered species--the Kirtland's warbler. This area was burned in the summer of 1980, and jack pine regenerated throughout much of the area. The burn provides a unique opportunity to study the local landscape ecosystems in relation to the colonization by the Kirtland's warbler. The study of pattern of jack pine occurrence in different ecosystems was also part of this overall investigation.

The Kirtland's warbler is one of the most rare and endangered songbirds in the world. Restricted to northern lower Michigan, its summer habitat comprises an area about 120 x 160 km. All nests have been found within 13 counties. Censuses of its population have been carried out in 1951, 1961, and every year since 1971. Although strong efforts have been made in management activities to recover the warbler population, including control of the brown-headed cow bird, prescribed burning, and establishment of jack pine plantations, the male population of the warbler has not increased. The reasons are not well known.

It has long been known that the warbler requires numerous small openings interspersed among dense seedling and sapling patches of jack pines. Thus, a second working hypothesis is that there is a relationship between pattern of jack pine occurrence in an area and the degree of occupancy of the Kirtland's warbler.

The specific objectives of this study were: 1) to determine the pattern of jack pine occurrence in selected landscape ecosystem types of the Mack Lake burn, and 2) to examine the relationship of the pattern of jack pine distribution to: (i) the local landscape ecosystem types of the burn, (ii) the spatial occurrence of the singing and nesting warblers in 1986 and 1987, and (iii) the specific components (physiography, soil, and vegetation) of the local landscape ecosystem types and of the occupancy of the Kirtland's warbler.

Methods

Twenty-five plot samples were taken in 7 local landscape ecosystem types (1, 3, 4, 6, 8, 9, and 10). Fifteen plots were located in ecosystem types (1, 6, 8, and 10) where warblers were singing or nesting, and 10 were located in ecosystem types (3, 4, and 9) without warblers. Twenty-two samples were obtained from ecosystem sample plots. Three other plots were also established: one plot was located in a jack pine plantation with created openings, one in a red pine plantation, and one in the 1966 burn. The plot size used in the jack pine plantation was 100 x 100 m. All other plots were 10 x 20 m. Three male warblers were separately found in the jack pine plantation and the red pine plantation. Warblers had been found before 1985 in the 1966 burn but have not been found in the area since then.

A total of 190 variables was collected. Among them 38 are variables of physiography-soil attributes, 32 are tree species, and 120 are coverage of ground-cover species or other trails.

The methods of Hopkins-Skellam, Clark-Evans, and Pielou-Mountford were used to test the pattern of jack pine occurrence. Two-way analysis of variance (ANOVA) was used to test for significances of differences in the patterns of jack pine occurrence among the three methods and between ecosystems where the warbler was presented in 1987 and ecosystems where the warbler was absent.

Ecosystem types were contrasted by using physiography-soil variables, tree species variables, and ground-cover variables. A two-stage method was used whereby variables were first selected by stepwise discriminant analysis followed by analysis of variance and canonical variate analysis. In addition, variables for canonical variate analysis were obtained from principal component analysis using the selected variables of physiography-soil, tree species, and ground-cover species.

Results and Conclusions

The pattern of jack pine occurrence varied markedly by ecosystem types. Contagious patterns of jack pine occurrence are typically found in ecosystem types 1, 6, 8, and 10, whereas random patterns are frequently associated with ecosystem types 3, 4, and 9. Study of warbler occurrence in 1986 and 1987 showed that warbler favor the former group of ecosystems were absent in the latter group.

The uneven and patchy distribution of clonal plant species probably is the major direct causal factor of contagious pattern of jack pine occurrence. Such plant species include northern pin oak, low sweet blueberry, sweet fern, blue stem grasses, bearberry, and wintergreen. Areas with evenly distributed vegetation tend to have a random pattern. Physiography and soil features affect plant composition and vegetation structure, hence are the indirect causal factors of contagious pattern of jack pine occurrence. Areas in outwash channel or with a layer of heavy-textured soil tend to have a random pattern.

The relationships of the pattern of jack pine occurrence to the specific ecosystem variables (physiography, soil, and vegetation) were described. A contagious pattern of jack pine occurrence is often associated with relatively high elevation, relatively low soil pH, presence of abundant northern pin oaks, low sweet blueberry, and blue stem grasses, and absence of a layer of heavy-textured soil. A random pattern is frequently related to lower elevation in channels, relatively high soil pH, relatively high coverage of Oryzopsis asperifolia, Schizachne purpurascens, Amelanchier sanguinea, Fragaria virginiana, Rhus aromatica, and Prunus alleghaniensis, and presence of a thick layer of heavy-textured soil.

Warblers prefer areas having a contagious pattern of jack pine occurrence. These areas are chracterized by following features: 1) rolling or level topography, 2) Grayling, Graycalm, Montcalm, and Rubicon soil series, 3) upland areas which have warm microclimate, 4) relatively tall, dense, and patchy jack pines, and 5) vegetation dominated by the northern pin oak, low sweet blueberry, and blue stem grasses, or combinations of these species. In contrast, the warblers avoid areas having a random pattern of jack pine occurrence. Such areas are characterized by one or more of the following features: 1) depressions and outwash channels, 2) rich soil series such as Manistee series (a layer of clay or loam thicker than 10 cm), 3) relatively cold microclimate having freezing temperatures in the early growing season, 4) relatively short, sparse, and randomly distributed jack pines, and 5) ground-cover species dominated by species such as Oryzopsis asperifolia, Schizachne purpurascens, Amelanchier sanguinea, Fragaria virginiana, Rhus aromatica, and Prunus alleghaniensis.

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Appendix I. Plot forms used to sample variables of physiography-soil, tree species, and ground-cover vegetation.

Appendix II. Original 190 variables of physiography-soil, tree species, and ground-cover vegetation used in multivariate analysis.

Variables of ground-cover species

coverage of

1. Acer rubrum
2. Pinus banksiana
3. Populus grandidentata
4. P. tremuloides
5. Quercus alba
6. Q. ellipsoidalis
7. Amelanchier spp.
8. A. arborea
9. A. interior
10. A. santuinea
11. A. spicata
12. Arctostaphylos Uva-ursii
13. Ceonthus ovatus
14. Comptonia peregrina
15. Cretaegus spp.
16. Diervilla lonicera
17. Epigaea repens
18. Gaultheria procumbens
19. Gaylussacia baccata
20. Lonicera dioica
21. Prunus allehganiensis
22. P. pensylvanica
23. P. pumila
24. P. serotina
25. P. virginiana
26. Rhus aromatica
27. Rhus typhina
28. Ribes cynosbati
29. Rosa blanda
30. Rubus spp.
31. R. flagellaris
32. Salix humilis
33. Spiranthes lacera
34. Symphoricarpus albus
35. Vaccinium angustifolium
36. V. Myrtilloides
37. Spiranthes gracilis
38. Anemone cylindrica
39. A. quinquefolia
40. Antennaria neglecta
41. A. plantaginifolia
42. Apocynum androsaemifolium
43. Arabis glabra
44. Aster spp.
45. Aster laevis
46. A. Macrophyllus
47. A. ptarmicoides

48. A. sagittifolius
49. Campanula rotundifolia
50. Chrysanthemum leucanthemum
51. Cirsium hillii
52. Convolvulus spithamaeus
53. Erigeron annuus
54. E. strigosus
55. Fragaria virginiana
56. Galium triflorum
57. Gnaphalium spp.
58. Helianthus canadensis
59. H. divaricatus
60. H. occidentalis
61. H. aurantiacum
62. H. canadense
63. H. scabriusculum
64. H. venosum
65. Houstonia longifolia
66. Krigia virginica
67. Lechea intermedia
68. Liatris cylindracea
69. L. novae-angliae
70. L. spicata
71. Liliaceae
72. Lilium philidelphicum
73. Linaria canadensis
74. Lithospermum croceum
75. Lysimachia quadrifolia
76. Maianthemum canadense
77. Melampyrum lineare
78. Monarda fistulosa
79. Pediculaaris canadensis
80. Physalis virginiana
81. Polygala polygama
82. Potentilla arguta
83. P. norvegica
84. P. simplex
85. P. tridentata
86. Prenanthes spp.
87. P. trifoliolata
88. Pyrola elliptica
89. Rumex acetosella
90. Sanicula marilandica
91. Senecio pauperculus
92. Smilacina racemosa
93. Solidago spp.
94. S. canadensis
95. S. hispida
96. S. juncea
97. S. nemoralis
98. S. spathulata
99. S. speciosa
100. Streptopus roseus
101. Taenidia integerrima
102. Taraxacum officinale
103. Verbascum thapsus
104. Viola adunca
105. V. pedata

106. Graminae and Carex pensylvanica
107. Pteridium aquilinum
108. Mosses
109. Lichens
110. Lycopodium
111. Large woody debris
112. Bare ground

Number of
113. tree species
114. shrub species
115. forb species
116. grasses and sedges
117. fern species
118. moss species
119. lichen species
120. total plant species

Variables of soil-physiography

1. % of sand from 10-30 cm
2. % of very coarse sand from 10-30 cm
3. % of coarse sand from 10-30 cm
4. % of very coarse and coarse sand from 10-30 cm
5. % of medium sand from 10-30 cm
6. % of fine sand from 10-30 cm
7. % of very fine sand from 10-30 cm
8. % of fine and very fine sand from 10-30 cm
9. % of silt from 10-30 cm
10. % of clay from 10-30 cm
11. % of silt and clay from 10-30 cm
12. % of sand from 10-150 cm
13. % of very coarse sand from 10-150 cm
14. % of coarse sand from 10-150 cm
15. % of very coarse and coarse sand from 10-150 cm
16. % of medium sand from 10-150 cm
17. % of fine sand from 10-150 cm
18. % of very fine sand from 10-150 cm
19. % of very fine and fine sand from 10-150 cm
20. % of silt from 10-150 cm
21. % of clay from 10-150 cm
22. % of silt and clay from 10-150 cm
23. Average thickness of A1 horizon (cm)
24. Average field pH of upper 10 cm
25. Depth to field pH of 7 or greater (cm)
26. Maximum depth of rooting (cm)
27. Depth to clay or loam (cm)
28. Thickness of fine textured bands from 0-150 cm (cm)
29. Thickness of fine textured bands from 150-400 cm (cm)
30. Depth to lamellae (cm)
31. % of pebbles and cobbles from 0-150 cm
32. Elevation of plot (m)
33. Aspect of plot using azimuth
34. % of slop on plot
35. Maximum % slope on plot
36. Depth of depressions and channels (m)
37. Weighted pH from 10-30 cm

38. Weighted pH from 30-150 cm

Variables of tree species

1. # of jack pine stems per plot
2. Average height of jack pine (cm)
3. Average growth of jack pine in 1985
4. Average growth of jack pine in 1984
5. Average growth of jack pine in 1983
6. Average growth of jack pine from 1980-1982
7. Average growth of jack pine from 1984-1986
8. Average maximum crown area (cm x cm)
9. Average height of 1st living JP branch (cm)
10. Plot openess class
11. General area openess class
12. Largest opening (m x m)
13. # of jack pine snags
14. Average basal diameter of jack pine snags (in)
15. Average height of jack pine snags (ft)
16. # of red pine snags
17. Average basal diameter of red pine snags (in)
18. Average height of red pine snags (ft)
19. # of oak snags
20. Average basal diameter of oak snags (in)
21. Average height of oak snags (ft)
22. Total # of oak clumps
23. Average # of stems per clump
24. Total # of oak seedlings
25. Average height of dominant oaks
26. Average jack pine coverage (%)
27. Average oak coverage (%)
28. Average oak and pine coverage (%)
29. # of jack pine in two subplots
30. Salvage status
31. # of jack pine in understory
32. # of oak in understory