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thesis entitled

The Ecology of Coastal Wetpannes near Saugatuck, Michigan and the Effects of the Introduced Austrian Pine (*Pinus nigra*) on their Hydrology and Vegetation

presented by

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has been accepted towards fulfillment
of the requirements for

M.S. degree in Botany

Major professor

Date August 16, 2000

THE ECOLOGY OF COASTAL WETPANNES NEAR SAUGATUCK, MICHIGAN AND THE EFFECTS OF THE INTRODUCED AUSTRIAN PINE (*PINUS NIGRA*) ON THEIR HYDROLOGY AND VEGETATION

By

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A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

MASTER OF SCIENCE

Department of Botany and Plant Pathology

2000

ABSTRACT

THE ECOLOGY OF COASTAL WETPANNES NEAR SAUGATUCK, MICHIGAN AND THE EFFECTS OF THE INTRODUCED AUSTRIAN PINE (*PINUS NIGRA*) ON THEIR HYDROLOGY AND VEGETATION

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Wetpannes, also known as dune slacks, are a type of coastal wetland that are found within sand dune ecosystems worldwide. Twenty-one Lake Michigan wetpannes near Saugatuck, Michigan, U.S.A. were investigated to characterize their hydrology, water chemistry, sediment characteristics, light regime, and plant communities. A chronosequence of aerial photographs of the study site was analyzed using Geographic Information Systems to look at interannual variability in wetpanne water levels. The effects of the introduced Austrian pine (*Pinus nigra*) on wetpanne ecology were examined by comparing the characteristics of wetpannes with and without Austrian pine. The transpiration rates of Austrian pine and the native jack pine (*Pinus banksiana*) were compared to see if Austrian pine has the potential to differentially affect the water table level beneath the wetpannes.

Of the 144 species found within the wetpannes at Saugatuck, only one, *Hypericum kalmianum*, was a Great Lakes endemic and may serve as an indicator species for this particular wetpanne habitat. The distribution of plant species along a complex water gradient was examined. Although many species overlapped, each species occupied a distinct range along the water depth gradient. The water levels within wetpannes were controlled by, but not derived from, Lake Michigan. Consequently, the water levels

fluctuate greatly from year-to-year in step with the lake. The water chemistry of wetpannes as well as the slope of the water table suggests that local groundwater flow feeds the wetpannes.

Overall, wetpannes associated with Austrian pine plantings share similarities with the jack pine wetpannes that are located farther away from the lake. Tree density is positively correlated with shrub cover, woody species diversity, and herbivory, and is negatively correlated with herb diversity and the percentage of wetland species in wetpannes. Austrian pines and jack pines have similar transpiration rates on a per leaf area basis, but, due to a much greater total leaf surface area, Austrian pines have the potential to transpire more water per tree. This result could explain why the water table depth changed more over the course of the season in the wetpannes surrounded by Austrian pine than in the other wetpannes when distance from Lake Michigan was factored out. The Austrian pine plantings may have converted the formerly open, treeless wetpannes near Lake Michigan into forested wetpannes like those that are normally found farther from the lake.

ACKNOWLEDGMENTS

Many thanks to my advisor, Dr. Peter Murphy, for all of the advice and support he has given me throughout the course of this project. I would also like to thank my committee members, Dr. Pat Webber and Dr. Steve Hamilton. Dr. Steve Hamilton provided me with the water chemistry analyses free of charge, lent me field equipment, and helped me interpret the results of the hydrological measurements. I would like to thank all of the students, both graduate and undergraduate, who helped with the field work, especially Jeff Benefiel, who conducted most of the transpiration work. Sandy Halstead helped me obtain GPS coordinates in the field at Saugatuck. Thanks also goes to Ms. Ethel Burns, who graciously opened up her home so that I could live near my field sites. The Denison family generously allowed me to conduct field work on their property. Ms. Connie Deam provided me with historical photos of wetpannes and provided me with water level data of the Kalamazoo River oxbow lake. This work was funded by Sigma Xi, the National Science Foundation Reasearch Training Grant, and the Department of Botany and Plant Pathology.

TABLE OF CONTENTS

Page

LIST OF TABLES

Page

Page

LIST OF FIGURES

Page

Page

Page

Page

Page

Page

Page

Page

Page

CHAPTER ONE

GENERAL INTRODUCTION

A wetpanne is a type of coastal wetland that occurs in sand dune ecosystems. Wetpannes can range from wet, forested depressions that are intermittently flooded to open ponds with up to two meters of standing water. The presence of similar types of wetlands has been documented in coastal areas worldwide, although these wetlands are not always referred to by the same name. In Australia, New Zealand, England, the Netherlands, and most of Europe, wetpannes are known as "dune slacks" (Ranwell, 1959; Van der Laan, 1979; Timms, 1982; Zoladeski, 1991; Wilson and Gitay, 1995). Slack is derived from an old Norse word, "slakki," which means "a small depression between two stretches of rising ground" (Ranwell, 1959). In the United States, a variety of names have been used to refer to the same kind of habitat: "dune ponds" (Barko et al., 1977; Wilcox and Simonin, 1987), "intradunal ponds" (Hiebert et al., 1986), "dune swales" (Voss, 1972; Minc, 1997a), "pannés" (Cole and Taylor, 1995), "pannes" (Hiebert et al., 1986), and "wetpannes" (Leege, 1997). The focus of this study will be specifically on the freshwater wetpannes near Saugatuck, Michigan, which are representative of many Great Lakes wetpannes.

Coastal wetlands of the Great Lakes are subject to annual and interannual variations in water depth (Minc, 1997a) because of multi-year cycles of fluctuating water levels. Cohn and Robinson (1976) proposed that the Great Lakes follow 11, 22, and 36 year cycles of high and low water levels. They also state that lake levels are highest in the summer and lowest in the winter. Minc (1997a; 1997b) and Cole and Taylor (1995) have proposed that the water levels in wetpannes are directly linked to the water levels of the Great Lakes. However, no study has quantitatively documented the link between the Great Lakes' water levels and water depths in wetpannes.

Hydrology is one of the main factors that determines the distribution of wetland vegetation (van der Laan, 1979; Shipley et al., 1991; Brinson, 1993; Wilson et al., 1993; Goslee et al., 1997; Runhaar et al., 1997; Wierda et al., 1997). It has been shown that specific plant species occur at particular water depths, with a complement of species forming zones at certain depths. This phenomenon is assumed to reflect trade-offs between the ability of plants to survive the stressful conditions of a flooded environment and their ability to compete under drier, more aerobic conditions (Shipley et al., 1991). Alternatively, it has been proposed that each plant grows where it does along the water-depth gradient because its physiologic response to flooding is unique to that species (Shipley et al., 1991). It is possible that the fluctuating water levels of the Great Lakes could cause substantial changes in the plant communities of wetpannes if the distribution of plants in wetpannes is linked to hydrology. This relationship between fluctuating water levels and the vegetation of wetpannes of the Great Lakes has never been defined.

In addition to natural fluctuations of water levels in wetpannes, anthropogenic manipulations may affect water depth. Most disturbances result in a lowering of the water table. Drainage of wetlands for the development of homesites, industrial parks, and agriculture seems to be the most widespread type of anthropogenic disturbance. Sand dune ecosystems in particular are under pressure by human development because of the high value of real estate bordering large water bodies. These areas are also in demand for specialized crop cultivation, for shipping, and for recreation. At Indiana Dunes National

Lakeshore, extensive ditching was done to drain the area surrounding the species-rich Cowles Bog for industrial and agricultural use (Wilcox, 1995). In the Netherlands, freshwater coastal dune slacks are used to supply drinking water for several major cities (Runhaar et al., 1996).

Anthropogenic disturbances to the hydrology of an ecosystem can drastically change its plant community. Wilcox (1995) stated that a change in species composition or changes in the relative dominance of plant species in a community are indicators of anthropogenic hydrologic disturbance. Other indicators mentioned were the presence of invasive species, the presence of large mono-specific stands of vegetation, and the absence of sensitive species (Wilcox, 1995). At Indiana Dunes National Lakeshore, Cowles Bog has become overrun by cattails (personal observation). Ehrenfeld and Schneider (1993) found that wetlands in urbanized watersheds had a higher percentage of facultative upland and upland species than wetlands in the undisturbed watersheds. In the Netherlands, the water table has dropped an average of 35 cm in the coastal dune areas since drinking water extraction began (Runhaar et al., 1996). Over 70% of the natural conservation areas surveyed by Runhaar (1996) had a substantial decrease in the number of hydrophytes within their boundaries.

Another way in which humans can alter the water table of an ecosystem is through afforestation. It is a common practice to plant pine plantations in sand dune areas worldwide (Sturgess and Atkinson, 1993). The reasons for doing so are to prevent erosion of sand dunes and to supposedly enhance an area for recreation. Artificial forestation of an area can lower the water table up to several meters (Bell et al., 1990; Sturgess and Atkinson, 1993). In one study in the Netherlands, the groundwater levels of a dune system dropped 0.1 to 2 meters at the site of the pine plantations (Van Dijk and Grootjans, 1993). Sturgess and Atkinson (1993) noted that pine plantings have the potential to dry out the dune slacks and eliminate the indigenous flora and fauna.

Pine plantations may have other detrimental effects on the sand dune ecosystem. Examples of pine plantations that have displaced the native dune vegetation have been documented (Ovington, 1950; Sturgess and Atkinson, 1993). The plantations provide shelter that encourages the growth of woody vegetation beneath the pines (Hill and Wallace, 1989; Sturgess and Atkinson, 1993; Van Dijk and Grootjans, 1993). These plantations also directly eliminate indigenous plant species and the animals that feed on them by producing a thick litter layer, competing for nutrients, lowering water levels, and producing a dense shade (Hill and Wallace, 1989; Sturgess and Atkinson, 1993). Ovington (1950) stated that once the pine canopy closes, the herb layer becomes sparse and woodland species take over.

At Saugatuck Dunes State Park, Michigan, over 25,000 Austrian pines (*Pinus nigra*), a non-native tree, were planted by the previous landowners between 1956 to 1972 in an effort to stabilize the shifting sand. Many of these trees were planted adjacent to the wetpannes in the park and are now beginning to reproduce and become successfully established (Leege, 1997). Leege (1997) was one of the first to suggest that these trees may be drying down the wetpannes at Saugatuck Dunes State Park. The current Michigan Department of Natural Resources Management Plan for Saugatuck Dunes State Park proposes that all Austrian pines surrounding the wetpannes should be removed within five years (Leege, 1998). Proper management of this protected natural area depends on understanding how the Austrian pines are affecting the hydrology of wetpannes, which is one goal of this study. But first, before the effects can be known, the physical and biological components of the wetpannes must be characterized. The focus of Chapter 2 will be on the floristics of the wetpannes of southern Michigan. In Chapter 3, the biotic and abiotic components of wetpannes will be described, and comparisons will be drawn between wetpannes that have been planted with Austrian pine and those without. In Chapter 4, the potential for Austrian pine to use more water via transpiration relative to the native jack pine will be examined. Lastly, the overall conclusions of the study will be given in Chapter 5.

CHAPTER TWO

THE FLORISTICS OF SOUTHERN MICHIGAN WETPANNES

INTRODUCTION

An exhaustive list of plant species that grow in the wetpannes of the Great Lakes has never before been published in the scientific literature. Hiebert et al. (1986) and Wilcox and Simonin (1987) each published a list of only the most common species occurring at sites within Indiana Dunes National Lakeshore. Comer and Albert (1993) produced a government publication on the vegetation of the dune swale type of wetpanne in northern Michigan, including a complete list of the plant species found in over 40 sites. However, the vegetation of wetpannes in the blowout areas (wind- carved areas of sand dune ecosystems) of southwestern Michigan has never been characterized. The purpose of Chapter 2 is to present the complete list of species that occurred in the wetpannes in the Saugatuck area of southwestern Michigan, and to discuss the general features of the plant species that were found.

METHODS

The wetpannes in this study are located in Allegan County at Saugatuck Dunes State Park Natural Area, Michigan, and on private property just south of the park (Fig. 2-1). Lake Michigan lies to the west of these sites. Three types of wetpannes were studied—wetpannes around which Austrian pines have been planted, forested wetpannes that are naturally fringed with the native jack pine, and open wetpannes (wetpannes not surrounded by trees). The open wetpanne and the Austrian pine wetpanne types were both located close to Lake Michigan at low elevations above the level of the lake, whereas the jack pine wetpannes were farther away from the lake at slightly higher elevations (Fig. 2-2). A total of 21 wetpannes was sampled. The wetpannes ranged in size from 10 m^2 to 11,500 m^2 (Table 2-1) and were generally ellipsoid in shape. Ten wetpannes that had been planted with Austrian pine were located on park property about 150 meters east of Lake Michigan (Table 2-1). Five of these wetpannes were part of a large complex of wetpannes that was surrounded by one continuous Austrian pine planting. Some of the wetpannes within this complex were separated by jack pines. Seven jack pine wetpannes were found east of the Austrian pine wetpannes, between 450 to 600 meters east of Lake Michigan (Table 2-1). Finally, four open wetpannes 150 meters east of Lake Michigan were located south of Saugatuck Dunes State Park on private property (Table 2-1). The open wetpannes were more irregularly shaped than the other wetpanne types and had deeper basins. The private property where they were located was bordered by a manmade channel to the north and an oxbow lake to the east. The oxbow lake occupies the original Kalamazoo River bed. It became a lake after the Kalamazoo River was rechannelled in 1906, and sand buried the original river mouth. The oxbow lake is now connected to the Kalamazoo River via a small marshy area.

Table 2-1. The geographic coordinates, dimensions, and areas of the wetpannes studied in the Saugatuck, MI area.

Wetpanne Type	Geographic Coordinates[1] (in UTM)		Dimensions (Long Axis X Short Axis in meters)	Area (m^2)
	Eastings	Northings		
Open				
1D	564543	4724211	116 X 85	8810
2D	564556	4724349	73 X 56	2161
3D	564651	4724524	187 X 140	11570
4D	564664	4724699	88 X 35	2825
Austrian Pine				
3	564869	4725955	93 X 61	3126
4	564835	4726044	42 X 14	456
5	564840	4726114	17 X 9	129
6	564853	4726100	20 X 9	160
7	564881	4725985	22 X 10	174
9	564885	4725959	17 X 11	132
10	564881	4725952	4 X 3	10
11	564878	4726011	21 X 16	225
12	564847	4726260	19 X 14	212
13	564871	4726290	19 X 13	156
Jack Pine				
A	565219	4725784	37 X 12	286
B	565171	4725726	51 X 26	1028
C	565161	4725840	18 X 15	134
D	565140	4725844	22 X 18	252
E	565125	4725816	39 X 19	488
F	565065	4725832	71 X 28	892
G	565238	4725796	17 X 8	136

[1] UTM = Universal Transverse Mercator. Zone 16 – 90 W to 84 W. The projection used was the World Geodetic System 1984. The coordinates give the positions of the mid-wells (monitoring wells in the lowest part of each wetpanne basin).

The vegetation of each wetpanne was completely censused by making a list of all species present within sampling plots used to quantify the vegetation of the wetpannes. Belt transects of 0.25 m^2 plots were used to quantify the herbaceous vegetation, and belt transects of 1 m^2 plots were used to quantify the woody vegetation. The wetpannes were then systematically searched for any species that were missed by the vegetation plots.

Unknown species were collected and pressed for later identification. Plants were identified using Voss (1972, 1985, 1996) and Gleason and Cronquist (1991) as the authorities. Each species was then verified against known specimens at the Beal-Darlington Herbarium at Michigan State University.

Each species was assigned a wetland category based on those given in a special report by the Michigan Department of Natural Resources (Herman et al., 1996) (Table 2-2). These categories are based on the National Wetland Indicator categories given by Reed (1985), and 600 additional species that were assigned categories *de novo* by the Michigan Department of Natural Resources. The preferred habitat and the geographic range of each species were determined using Voss (1972, 1985, 1996) and Gleason and Cronquist (1991). A species' preference toward calcareous or acidic conditions was recorded when mentioned in these references.

Table 2-2. The definitions of the wetland coefficient categories (from Herman et al., 1996). A '+' indicates a wet tendency, and a '-' indicates a dry tendency.

Wetland Coefficient	Wetland Category	Symbol	Probability of Occurring in a Wetland
5	Upland	UPL	< 1%
4		FACU-	
3	Facultative upland	FACU	1-33%
2		FACU+	
1		FAC-	
0	Facultative	FAC	34-66%
-1		FAC+	
-2		FACW-	
-3	Facultative wetland	FACW	67-99%
-4		FACW+	
-5	Obligate wetland	OBL	>99%

Importance values for each species were calculated for each of the three wetpanne types using the frequency, cover, and density values obtained from the vegetation plots as in Brower, Zar, and von Ende (1990). The vegetation plots were pooled into each of the three wetpanne types before the importance values were calculated. The importance value for each species *i* (IV_i) is obtained by adding relative density (RD_i), relative frequency (Rf_i), and the relative cover (RC_i) of that species within each wetpanne type. The importance values of the woody plant species were calculated separately from those of the herbaceous vegetation.

$$IV_i = RD_i + Rf_i + RC_i$$

The importance values range from 0 to 3.00. An importance value of 0 means that the species was not found within the vegetation plots of that particular wetpanne type. An importance value of 3.00 would indicate that the species is the only species found within a wetpanne type. Density (D_i) was calculated by dividing the total number of individuals of species *i* (n_i) by total area (A) sampled:

$$D_i = n_i / A$$

The density of the woody vegetation was determined by counting the total number of stems of each species per plot rather than the number of individuals because it was difficult to define individual plants. For some herbaceous species, the plants were tufted and/or density was difficult to assess. For these species, only relative cover and relative frequency were used to calculate importance values. Therefore, the importance of these species within the wetpanne types was underestimated. These species are demarcated within the Results section (Table 2-4). Densities were determined whenever possible. The relative density of each species *i* was calculated by dividing D_i by the total density for all species:

$$RD_i = D_i / \Sigma D$$

Frequency (f_i) was calculated by dividing the number of plots in which species *i* occurs (j_i) by the total number of plots measured (k):

$$f_i = j_i / k$$

The relative frequency of species *i* was calculated by dividing f_i by the sum of the frequencies for all species:

$$Rf_i = f_i / \Sigma f$$

Cover (C_i) is defined as the proportion of the plot occupied by the above ground portions of species *i* and was calculated by dividing the total area covered by species *i* (a_i) by the total area sampled (A) in each wetpanne type:

$$C_i = a_i / A$$

Relative cover was calculated by dividing C_i by the sum of the covers for all species in each wetpanne type:

$$RC_i = C_i / \Sigma C$$

RESULTS AND DISCUSSION

A total of 144 species was found. Most of the species found in wetpannes were generalists. The species that were found occur in many other habitats (Table 2-3). The only habitat requirement for a third of the plant species was wetness. Only four species strictly preferred wet, calcareous sand. The wetpanne species also have a wide variety of geographic origins (Table 2-3). A large number of species have ranges that extend outside of North America (24%). Only one species is endemic to the Great Lakes region. None of the wetpanne species are presently considered to be endangered or threatened.

The importance values are listed for each species in each of the three types of wetpannes (Table 2-4) as well as presence/absence information for each species in the individual wetpannes. The top five herbaceous species in the open wetpannes (in order from most important to least important) were *Cladium mariscoides* (IV= 0.8151), *Panicum implicatum* (IV= 0.2679), *Andropogon scoparius* (IV= 0.1866), *Utricularia minor* (IV= 0.1647), and *Juncus brachycephalus* (IV= 0.1201). These species reflect the fact that the open wetpannes tended to have standing water year-round—*Cladium mariscoides*, *Utricularia minor*, and *Juncus brachycephalus* are obligate wetland plants. Three of the top five species are known calciphiles—*Cladium mariscoides*, *Panicum implicatum*, and *Utricularia minor*. The dominant herbacous species in the jack pine wetpannes were *Cladium mariscoides* (IV= 0.5501), *Scirpus cyperinus* (IV= 0.3772), *Juncus balticus* (IV= 0.2398), *Solidago canadensis* (IV= 0.2197), and *Calamagrostis canadensis* (IV= 0.2087). The large importance value for *Cladium mariscoides* was because of one jack pine wetpanne that was dominated by that species. The other four jack pine wetpannes sampled had only small quantities of *Cladium mariscoides*. *Scirpus cyperinus* prefers acidic habitats, and its inclusion in the top five species may have been because the jack pine needles have created more acidic conditions in these wetpannes. *Solidago canadensis* is usually found in mesic forest habitats, so it may be able to tolerate the shadier conditions of a forested wetpanne. The most important herbaceous species in the Austrian pine wetpannes was *Juncus balticus* (IV= 0.6352), with *Fragaria virginiana* (IV= 0.2136), *Solidago canadensis* (IV= 0.2106), *Panicum implicatum* (IV= 0.1738), and *Andropogon scoparius* (IV= 0.1307) playing comparatively minor roles. *Fragaria virginana* is also usually found in forests. *Cladium mariscoides* was relatively unimportant in wetpannes where Austrian pine had been planted.

The top three woody species in the open wetpannes were *Hypericum kalmianum* (IV= 1.1783), *Spiraea tomentosa* (IV= 0.8473), and *Salix* spp. (IV= 0.3868). The dominant woody species in the jack pine wetpannes were *Pinus banksiana* (IV= 0.6538), *Rubus* spp. (IV= 0.5384), and *Salix* spp. (IV= 0.3420). The most important species in the Austrian pine wetpannes were *Spiraea tomentosa* (IV= 0.7285), *Salix* spp. (IV= 0.5184), and *Rubus* spp. (IV= 0.4552). *Hypericum kalmianum*, *Spiraea tomentosa*, and *Salix* are the most tolerant of wet conditions. *Rubus* and *Pinus banksiana* seem to be less tolerant of saturated soils and more common in forested areas.

Utricularia minor, filamentous green algae, *Scirpus validus*, *Scirpus americanus*, *Cladium mariscoides*, and *Potamogeton oakesianus* dominated the pools of standing water in the open wetpannes. The forested wetpannes (i.e., the Austrian pine and jack pine wetpannes) generally did not have standing pools of water, so submergent vegetation such as *Utricularia* and *Potamogeton* were absent from these sites. The dominant species in the wettest parts of the jack pine wetpannes were *Calamagrostis canadensis* and *Scirpus cyperinus*, except in wetpanne B, where *Cladium mariscoides* was the dominant species. In Austrian pine wetpannes, the dominant species in the wettest parts were *Carex lanuginosa*, *Carex lacustris*, *Cladium mariscoides,* and *Scirpus cyperinus*.

Outside of the wettest areas of the wetpannes, certain species occurred in narrow, concentric rings along the wetpanne basin, including *Linum striatum*, *Lobelia kalmii*, *Hypericum majus*, *Carex viridula*, *Carex aurea*, *Agalinus purpurea*, *Centaurium erythraea*, and *Hieracium* spp. The regions in which some of these species occurred became particularly apparent when the flowering plants formed an attractive ring of blooms that encircled the wetpanne. Other species occupied wide ranges across the entire wetpanne: *Andropogon scoparius*, *Panicum implicatum*, *Eleocharis elliptica*, *Juncus balticus*, *Panicum virgatum*, *Solidago canadensis*, *Fragaria virginiana*, *Poa compressa*, and *Equisetum hyemale*.

The edge of the wetpanne was defined as the point at which wetland vegetation is replaced by the upland sand dune vegetation. *Salix* shrubs typically formed a ring around the wetpanne at this edge. *Pinus banksiana* (and *Pinus nigra* in the case of the Austrian pine wetpannes) also grew along the wetpanne edge in the forested wetpannes. In the open wetpannes where the surrounding habitat was open sand dune, species typical of the sand dune habitat appeared at the wetpanne edges: *Polygonella articulata*, *Monarda punctata*, *Ammophila breviligulata*, *Hudsonia tomentosa*, and *Prunus pumila*. In both types of forested wetpannes, species more characteristic of the understory of a dry sandy forest or a mesic forest appeared at the wetpanne edges. The dry sandy forest species included *Smilacina stellata*, *Galium pilosum*, and *Chimaphila maculata*. *Maianthemum*

Table 2-3. A list of the 144 species found in the Saugatuck, MI area.

Species Name	Species Abbrev.	Life[1] Form	Wetland[2] Category	Preferred[3] Habitat	pH[4] Tolerance	Geographic Range[5]
Achillea millefolium	Ach mil	f	FACU	disturbed		circumboreal
Agalinus purpurea	Aga pur	f	FACW	wet sand		east
Agrostis gigantea	Agr gig	g	[FAC]	wet		Eurasia
Agrostis hyemalis	Agr hye	g	FAC-	sand dune		east
Algae (filamentous)	Alg spp		OBL	wet		
Amelanchier interior	Ame int	t	UPL	sand forest		northeast
Ammophila breviligulata	Amm bre	g	UPL	sand dune		coastal
Andropogon scoparius	And sco	g	FACU	prairie		e/w US
Apocynum cannabinum	Apo can	f	FAC	disturbed		e/w US
Arabis lyrata	Ara lyr	f	FACU-	sand dune		northeast
Arctostaphylos uva-ursi	Arc uva	s	[UPL]	sand dune		circumboreal
Artemesia caudata	Art cau	f	[FAC]	sand dune		circumboreal
Asclepias incarnata	Asc inc	f	OBL	prairie		east
Asclepias syriaca	Asc syr	f	UPL	disturbed		east
Aster lateriflorus	Ast lat	f	FACW-	wet		east
Aster pilosus	Ast pil	f	FACU+	wet sand	calcareous	east
Betula papyrifera	Bet pap	t	FACU+	disturbed		north
Botrychium dissectum	Bot dis	f	FAC	mesic forest		east
Calamagrostis canadensis	Cal can	g	OBL	prairie		north
Calomovilfa longifolia	Cal lon	g	UPL	prairie		north
Carex spp.	Car spp	g				
Carex alata	Car ala	g	OBL	wet	acidic	southeast
Carex aquatilis	Car aqu	g	OBL	wet	acidic	circumboreal
Carex aurea	Car aur	g	FACW+	wet	acidic	north
Carex crinita	Car crin	g	FACW+	wet		east
Carex cristatella	Car cris	g	FACW+	wet		northeast
Carex eburnea	Car ebu	g	FACU-	wet	calcareous	northeast
Carex lacustris	Car lac	g	OBL	wet	acidic	northeast
Carex lanuginosa	Car lan	g		wet		temperate na
Carex viridula	Car vir	g	OBL	wet	calcareous	circumboreal
Celastrus orbiculata	Cel orb	v	UPL	disturbed		Eurasia
Centaurium erythraea	Cen ery	f	[FACW+]	disturbed		Eurasia
Cephalanthus occidentalis	Cep occ	s	OBL	wet		southeast
Chimaphila maculata	Chi mac	f	UPL	sand forest		east
Cladium mariscoides	Cla mar	g	OBL	wet	calcareous	east
Conzya canadensis	Con can	f	FAC-	disturbed		N. America
Corallorhiza odontorhiza	Cor odo	f	UPL	mesic forest		east
Cornus amomum	Cor amo	s	FACW+	wet		east
Cornus foemina	Cor foe	s	FACW-	wet		northeast
Cornus stolonifera	Cor sto	s	FACW	wet	acidic	north
Cyperus strigosus	Cyp str	g	FACW	wet		e/w US

Table 2-3. (continued)

Species Name	Species Abbrev.	Life[1] Form	Wetland[2] Category	Preferred[3] Habitat	pH [4] Tolerance	Geographic Range[5]
Dianthus armeria	Dia arm	f	UPL	disturbed		Eurasia
Dryopteris spp.	Dry spp	f		mesic forest		
Eleocharis elliptica	Ele ell	g	FACW	wet sand		north
Epilobium coloratum	Epi col	f	OBL	wet		east
Equisetum arvense	Equ arv	f	FACW-	mesic forest		cosmopolitan
Equisetum hyemale	Equ hye	f	FAC	wet		circumboreal
Erigeron annuus	Eri ann	f	FAC-	disturbed		northeast
Eupatorium perfoliatum	Eup per	f	FACW+	wet		east
Fagus grandifolia	Fag gra	t	FACU	mesic forest		east
Fragaria virginiana	Fra vir	f	FAC-	sand forest		N. America
Fraxinus americana	Fra ame	t	FACU	mesic forest		east
Galium pilosum	Gal pil	f	UPL	sand forest		southeast
Galium triflorum	Gal tri	f	FACU+	mesic forest		circumboreal
Gnaphalium obtusifolium	Gna obt	f	UPL	disturbed		east
Hieracium spp.	Hie spp	f	UPL	disturbed		Eurasia
Hudsonia tomentosa	Hud tom	s	UPL	sand dune		coastal
Hypericum kalmianum	Hyp kal	s	FACW-	wet sand	calcareous	Great Lakes
Hypericum majus	Hyp maj	f	FACW	wet sand		east
Hypochaeris radicata	Hyp rad	f	[UPL]	disturbed		Eurasia
Ilex verticillata	Ile ver	s	FACW+	wet		east
Juncus acuminatus	Jun acu	g	OBL	wet sand		e/w US
Juncus alpinus	Jun alp	g	OBL	wet sand	calcareous	circumboreal
Juncus balticus	Jun bal	g	OBL	wet	calcareous	circumboreal
Juncus biflorus	Jun bif	g	FACW	wet sand		southeast
Juncus brachycephalus	Jun bra	g	OBL	wet sand		northeast
Juncus canadensis	Jun can	g	OBL	wet		east
Juncus dudleyi	Jun dud	g	FAC	mesic forest		N. America
Juncus effusus	Jun eff	g	OBL	wet		cosmopolitan
Juncus nodosus	Jun nod	g	OBL	wet	acidic	temperate na
Juncus tenuis	Jun ten	g	FAC	mesic forest		N. America
Juncus torreyi	Jun tor	g	FACW	prairie		temperate na
Juniperus communis	Jun com	s	[FACU]	sand dune		circumboreal
Juniperus virginiana	Jun vir	t	FACU	sand forest	calcareous	east
Lactuca canadensis	Lac can	f	FACU+	disturbed		e/w US
Leersia oryzoides	Lee ory	g	OBL	wet	acidic	cosmopolitan
Linum striatum	Lin str	f	FACW-	wet sand		southeast
Liparis loesellii	Lip loe	f	FACW+	wet	acidic	north
Lithospermum caroliniense	Lit can	f	[UPL]	prairie		east
Lobelia kalmii	Lob kal	f	OBL	wet	calcareous	north
Lonicera spp.	Lon spp	s		disturbed		Eurasia
Lycopodium spp.	Lyd spp	f		mesic forest		

Table 2-3. (continued)

Species Name	Species Abbrev.	Life[1] Form	Wetland[2] Category	Preferred[3] Habitat	pH [4] Tolerance	Geographic Range[5]
Lycopus uniflorus	Lyc uni	f	OBL	wet		north
Lythrum salicaria	Lyt sal	f	OBL	wet		Eurasia
Maianthemum canadense	Mai can	f	FAC	mesic forest		northeast
Melampyrum lineare	Mel lin	f	FAC-	wet	acidic	north
Monarda punctata	Mon pun	f	[UPL]	sand dune		east
Oenothera biennis	Oen bie	f	FACU	disturbed		N. America
Onoclea sensibilis	Ono sen	f	FACW	wet	acidic	east
Osmunda regalis	Osm reg	f	OBL	wet	acidic	circumboreal
Panicum implicatum	Pan imp	g	FAC	wet sand	calcareous	northeast
Panicum virgatum	Pan vir	g	FAC+	prairie		east
Pinus banksiana	Pin ban	t	[FACU]	sand forest		northeast
Pinus nigra	Pin nig	t	[OBL]	sand forest		Eurasia
Pinus strobus	Pin str	t	FACU	sand forest		northeast
Pinus sylvestris	Pin syl	t	UPL	sand forest		Eurasia
Poa compressa	Poa com	g	FACU+	disturbed		Eurasia
Polygonella articulata	Pol art	f	UPL	sand dune		coastal
Polygonum amphibian	Pol amp	f	OBL	wet		cosmopolitan
Polygonum punctatum	Pol pun	f	OBL	wet		e/w US
Polygonum spp.	Poly spp	f		wet		
Pontederia cordata	Pon cor	f	OBL	wet		east
Populus deltoides	Pop del	t	FAC+	prairie		east
Potamogeton oakesianus	Pot oak	f	OBL	wet	acidic	northeast
Prunus pumila	Pru pum	s	UPL	sand dune		northeast
Prunus serotina	Pru ser	t	FACU	disturbed		east
Prunus spp.	Pru spp	t	FACU/ FAC-			
Prunus virginiana	Pru vir	t	FAC-	sand forest		temperate na
Ptelea trifoliata	Pte tri	s	FACU+	sand dune		southeast
Pyrola elliptica	Pyr ell	f	UPL	mesic forest		north
Pyrola spp.	Pyr spp	f		mesic forest		
Quercus rubra/ Quercus velutina	Que spp	t	FACU/ UPL	sand forest		east
Rhynchospora capitellata	Rhy cap	g	OBL	wet	acidic	e/w US
Ribes spp.	Rib spp	s				north
Rosa spp.	Ros spp	s				north
Rubus spp.	Rub spp	s				north
Rumex acetosella	Rum ace	f	FAC	disturbed		Eurasia
Salix spp.	Sal spp	s		wet		north
Sassafras albidum	Sas alb	t	FACU	disturbed		southeast
Scirpus americanus	Sci ame	g	OBL	wet		N. America
Scirpus cyperinus	Sci cyp	g	OBL	wet	acidic	e/w US
Scirpus validus	Sci val	g	OBL	wet	acidic	N. America

Table 2-3. (continued)

Species Name	Species Abbrev.	Life[1] Form	Wetland[2] Category	Preferred[3] Habitat	pH [4] Tolerance	Geographic Range[5]
Smilacina stellata	Smi ste	f	FAC-	sand forest		temperate na
Solidago canadensis	Sol can	f	FACU	mesic forest		N. America
Solidago graminifolia	Sol gra	f	FACW-	wet sand		e/w US
Solidago nemoralis	Sol nem	f	UPL	sand forest		east
Solidago rugosa	Sol rug	f	FAC+	disturbed		southeast
Solidago simplex	Sol sim	f	FACU	sand dune		e/w US
Spiraea alba	Spi alb	s	FACW+	wet		northeast
Spiraea tomentosa	Spi tom	s	FACW	wet	acidic	e/w US
Spiranthes cernua	Spi cer	f	FACW-	wet sand		east
Taraxicum officinale	Tar off	f	FACU	disturbed		Eurasia
Thelypteris palustris	The pal	f	FACW+	wet	acidic	cosmopolitan
Toxicodendron radicans	Tox rad	v	FAC+	disturbed		east
Typha latifolia	Typ lat	g	OBL	wet		cosmopolitan
Unknown #11	Unk 11	f				
Unknown #12	Unk 12	f				
Unknown #6	Unk 6	f				
Unknown #9	Unk 9	f				
Unknown orchid	Unk Orc	f				
Utricularia minor	Utr min	f	OBL	wet	calcareous	circumboreal
Viburnum opulus	Vib opu	s	FACW	wet		north
Viola lanceolata	Vio lan	f	OBL	wet sand	acidic	e/w US
Vitis riparia	Vit rip	v	FACW-	sand forest		northeast

[1] Life forms are forb (f), graminoid (g), shrub (s), tree (t), and vine (v).

[2] Wetland categories from Herman et al. (1996). Bracketed categories refer to a wetland category that has been adjusted for the state of Michigan. Refer to Table 2-2 for a definition of each category.

[3] Habitat information from Voss (1972, 1985, 1996) and Gleason and Cronquist (1991). 'Prairie' = dry and wet prairies; 'sand dune' = sand dunes; 'sand forest' = dry sandy forests; 'mesic forest' = moist forest; 'disturbed' = recently disturbed habitats; 'wet sand' = wet sandy places; and 'wet' = wet places in general, including wet forests.

[4] Tolerance for different pH regimes from Voss (1972, 1985, 1996) and Gleason and Cronquist (1991). 'Calcareous' indicates that the species grows better in calcium-rich areas such as those with limestone rock, and 'acidic' indicates that the species has the ability to tolerate acidic conditions, such as those found in bogs.

[5] The geographic range refers to the center of each species' range. Information from Voss (1972, 1985, 1996) and Gleason and Cronquist (1991). Compass directions refer to ranges within the U.S. 'E/w US' refers to species that have ranges both in the east and in the far west, but not in the Great Plains/ Great Basin regions. 'Coastal' refers to species with ranges along the Atlantic coast. 'N. America' represents species that have ranges spanning North America. 'Temperate na' indicates species that grow only in temperate North America. 'Eurasia' refers to non-native species with their original ranges in Eurasia. 'Circumboreal' refers to species that are found throughout the northern part of the northern hemisphere, and 'comsmopolitan' refers to species that can be found worldwide.

canadense, *Galium triflorum*, *Botrychium dissectum*, *Pyrola elliptica*, and *Lycopodium* spp. represented the mesic forest species. A number of dry sandy forest and mesic forest tree species appeared along the edges of the jack pine wetpannes: *Quercus rubra*, *Quercus velutina*, *Amelanchier interior*, *Pinus strobus*, and *Fagus grandifolia*.

A few weedy species were found in the wetpannes in small quantities, including *Dianthus armeria*, *Hypochaeris radicata*, *Lythrum salicaria*, *Agrostis gigantea*, and *Taraxacum officinale*. *Lythrum salicaria* was represented by only one or two plants and had not yet spread. Most of these weedy species are non-native with their geographic origins in Eurasia (Table 2-3).

Many of the rarer species were found as isolated patches in only one or two wetpannes (Table 2-4). Thirty-five species each appeared only once in a single wetpanne. Of these 35, seven were weedy and/or from Eurasia, and 18 were native wetland species. The patchy wetland species included: *Carex crinita*, *Ilex verticillata*, *Juncus canadensis*, *Carex eburnea*, and *Rhynchospora capitellata*. Small populations of plants such as these may be populations of newly established plants or populations on the verge of extirpation from the site. It is likely that the Eurasian species are newly established populations in areas of disturbance. If the wetpannes are drying out, as suggested by Leege (1997), the small populations of wetland plants may be disappearing from these sites.

The preferred habitat for each species was determined (Gleason and Cronquist, 1991; Voss, 1972, 1985, 1996) (Table 2-3). The preferred habitats of wetpanne plant species include sand dunes, dry sandy forests, mesic forests, disturbed areas, prairies (including wet prairies), wet sandy places, and wet places in general. The largest habitat category was formed bywetpanne species that prefer wet places in general (50 out of 144 total species, or 35%). Not surprisingly, 21 of the 28 species that prefer mesic forests or dry sandy forests were restricted to the forested wetpanne sites. Of the 14 species that prefer wet sandy places, 12 occurred in both open and forested wetpannes.

The pH range that each species can tolerate was then determined (Gleason and Cronquist, 1991; Voss, 1972, 1985, 1996) (Table 2-3). Only 21% of all the species were reported as having preferences for either calcareous or acidic conditions. Of the 11 species reported as calciphiles, 4 of these most often grow in wet sandy habitats. Nine of these calciphiles are found in both forested and open wetpanne sites. Of the 18 species with the ability to tolerate acidic conditions, 10 were unique to the forested wetpannes. This result was expected because the pine needle litter in the forested wetpannes generates more acidic conditions than in the open wetpannes.

Of the total number of species that could be assigned wetland categories, 59% were considered to be wetland indicator species. To be considered a wetland indicator, a species has to be classified in the FAC, FAC+, FACW-, FACW, FACW+, or OBL categories. The remaining species were classified as upland species. More upland species were found among the species that were found only in the forested wetpannes—only 51% were wetland indicators and 49% were upland species. Among those species that were found only in the open wetpannes, 75% were wetland indicators and 25% were upland species.

Table 2-4. The presence of individual species within each wetpanne studied, and the overall importance values (IV) for each wetpanne type.

Species[1] Abbrev.	Open Wetpannes				Jack Pine Wetpannes						Austrian Pine Wetpannes									
	1D	2D	4D	Overall[2] IV	B	C	D	E	G	Overall[2] IV	3	4	5	6	7	9	11	12	13	Overall[2] IV
Herbaceous Species																				
Ach mil				0.0000				+		0.0000	+									0.0000
Aga pur	+	+	+	0.0299	+					0.0000	+						+			0.0026
Agr gig				0.0000						0.0000								+		0.0019
Agr hye	+	+	+	0.0451*	+	+	+	+	+	0.0607*	+	+	+	+	+	+	+	+		0.0440*
Alg spp	+		+	0.1097*						0.0000*										0.0000*
Amm bre	+	+	+	0.0939	+					0.0094	+	+	+	+	+		+	+	+	0.0693
And sco	+	+	+	0.1866*	+	+	+	+	+	0.0879*	+	+	+	+	+	+	+	+	+	0.1307*
Apo can				0.0000			+			0.0000										0.0000
Ara lyr	+	+		0.0073						0.0000			+							0.0012
Arc uva				0.0000		+	+	+		0.0176					+					0.0007
Art cau	+	+		0.0047	+					0.0012										0.0000
Asc inc				0.0000						0.0000	+									0.0000
Asc syr				0.0000				+		0.0000										0.0000
Ast lat				0.0000					+	0.0163	+									0.0000
Ast pil	+		+	0.0141	+	+	+	+		0.0143	+	+	+	+	+	+	+	+	+	0.0683
Bot dis				0.0000		+		+	+	0.0121										0.0000
Cal can	+	+		0.0485*	+	+	+	+		0.2087*	+		+							0.0248*
Cal lon	+	+	+	0.0661	+	+	+	+	+	0.0523	+	+	+	+	+	+	+	+	+	0.0592
Car spp				0.0000					+	0.0029										0.0000
Car ala				0.0000						0.0000	+	+								0.0046
Car aqu	+		+	0.0153						0.0000	+									0.0091
Car aur				0.0000				+	+	0.0177	+	+	+			+	+	+		0.0683
Car crin				0.0000				+		0.0000										0.0000
Car cris				0.0000						0.0000								+		0.0062
Car ebu				0.0000						0.0000							+			0.0019
Car lac				0.0000						0.0000	+									0.0385
Car lan		+		0.0112*						0.0000*	+	+			+				+	0.1132*
Car vir	+	+	+	0.0776		+		+	+	0.0202	+	+	+	+			+			0.0414
Cen ery		+		0.0009	+		+	+		0.0111	+	+	+	+	+	+	+	+	+	0.1116

Table 2-4. (continued)

Species[1] Abbrev.	Open Wetpannes				Jack Pine Wetpannes						Austrian Pine Wetpannes									
	1D	2D	4D	Overall[2] IV	B	C	D	E	G	Overall[2] IV	3	4	5	6	7	9	11	12	13	Overall[2] IV
Chi mac				0.0000		+	+		+	0.0094				+		+		+	+	0.0047
Cla mar	+	+	+	0.8151	+			+		0.5501	+	+			+		+			0.0516
Con can	+	+	+	0.0064						0.0000			+							0.0000
Cor odo				0.0000			+			0.0000						+		+	+	0.0003
Cyp str	+			0.0000						0.0000										0.0000
Dia arm				0.0000						0.0000								+		0.0017
Dry spp				0.0000						0.0000				+						0.0000
Ele ell	+	+	+	0.0641*	+	+	+	+	+	0.1250*	+	+	+		+	+	+	+		0.0503*
Epi col	+			0.0000						0.0000										0.0000
Equ arv				0.0000						0.0000								+		0.0000
Equ hye	+	+	+	0.0056	+					0.0208	+	+	+	+				+	+	0.0940
Eri ann				0.0000	+	+			+	0.0076	+	+			+	+			+	0.0045
Eup per	+	+	+	0.0075	+				+	0.0025	+	+	+	+	+	+	+	+		0.0781
Fra vir	+	+	+	0.0340	+	+	+	+	+	0.0662	+	+	+	+	+	+	+	+	+	0.2136
Gal pil				0.0000	+		+	+		0.0016	+	+		+	+	+	+			0.0040
Gal tri				0.0000					+	0.0008		+								0.0010
Gna obt	+	+	+	0.0109				+		0.0000	+	+	+	+	+	+	+	+		0.0025
Hie spp	+			0.0010	+	+	+	+	+	0.0521	+	+	+	+	+	+	+	+	+	0.0517
Hyp maj	+	+	+	0.1196	+	+			+	0.0037	+	+		+		+	+			0.0242
Hyp rad				0.0000				+		0.0120	+		+					+		0.0011
Jun acu		+	+	0.0170		+		+	+	0.0118	+	+		+			+	+	+	0.0274
Jun alp	+	+	+	0.0041					+	0.0028	+		+			+	+	+		0.0078
Jun bal	+	+	+	0.0456	+	+	+	+	+	0.2398	+	+	+	+	+	+	+	+	+	0.6352
Jun bif	+	+		0.0009						0.0000										0.0000
Jun bra	+	+	+	0.1201	+				+	0.0091	+		+			+	+			0.0488
Jun can				0.0000						0.0000								+		0.0013
Jun dud	+	+		0.0399						0.0000										0.0000
Jun eff		+		0.0000				+		0.0000	+	+						+		0.0050
Jun nod		+		0.0028						0.0000	+									0.0022
Jun ten				0.0000						0.0000									+	0.0038
Jun tor	+			0.0000						0.0000							+			0.0000
Lac can				0.0000				+		0.0000	+	+				+		+		0.0028

Table 2-4. (continued)

Species[1] Abbrev.	Open Wetpannes				Jack Pine Wetpannes						Austrian Pine Wetpannes									
	1D	2D	4D	Overall[2] IV	B	C	D	E	G	Overall[2] IV	3	4	5	6	7	9	11	12	13	Overall[2] IV
Lee ory				0.0000						0.0000	+	+								0.0065
Lichens	+	+		0.0062*	+	+	+	+	+	0.1726*	+	+	+	+	+	+	+	+	+	0.0578*
Lin str	+	+	+	0.0289	+	+			+	0.0617	+	+	+			+	+	+		0.0413
Lip loe				0.0000		+				0.0037					+	+				0.0028
Lit can				0.0000						0.0008			+					+	+	0.0013
Lob kal	+	+	+	0.0092	+			+	+	0.0082	+	+	+		+	+	+	+		0.0128
Lyd spp				0.0000	+					0.0015										0.0000
Lyc uni			+	0.0019	+			+		0.0259	+		+		+	+	+	+		0.0486
Lyt sal				0.0000						0.0000	+									0.0000
Mai can				0.0000	+	+	+			0.0290										0.0000
Mel lin				0.0000				+		0.0024								+	+	0.0016
Mon pun	+	+	+	0.0271	+			+		0.0023				+						0.0003
Moss	+	+	+	0.0352*	+	+	+	+	+	0.0729*	+	+	+	+	+	+		+	+	0.0577*
Oen bie	+		+	0.0000						0.0000	+		+		+					0.0007
Ono sen		+		0.0011	+					0.0019						+				0.0003
Osm reg				0.0000						0.0000						+				0.0004
Pan imp	+	+	+	0.2679	+		+	+	+	0.0751	+	+	+	+	+	+	+	+	+	0.1738
Pan vir	+	+		0.0895	+	+	+	+	+	0.0465	+	+	+	+	+	+	+	+	+	0.0539
Poa com	+	+		0.0029*	+	+	+	+	+	0.0560*	+	+	+	+	+	+	+	+		0.0491*
Pol amp		+		0.0000						0.0000	+									0.0000
Pol art	+		+	0.0216						0.0000										0.0000
Pol pun		+		0.0129						0.0000										0.0000
Pol spp				0.0000						0.0000	+									0.0000
Pon cor			+	0.0000						0.0000										0.0000
Pot oak	+	+	+	0.0926*						0.0000*										0.0000*
Pyr ell				0.0000						0.0000				+						0.0000
Pyr spp				0.0000					+	0.0009										0.0000
Rhy cap		+		0.0000						0.0000										0.0000
Rum ace		+	+	0.0066	+		+	+		0.0210	+	+								0.0058
Sci ame	+		+	0.1168						0.0000										0.0000
Sci cyp				0.0000		+	+	+	+	0.3772	+	+		+	+	+		+		0.0527
Sci val	+		+	0.0292						0.0000										0.0000

Table 2-4. (continued)

Species[1] Abbrev.	Open Wetpannes				Jack Pine Wetpannes						Austrian Pine Wetpannes									
	1D	2D	4D	Overall[2] IV	B	C	D	E	G	Overall[2] IV	3	4	5	6	7	9	11	12	13	Overall[2] IV
Smi ste				0.0000	+	+	+	+	+	0.0423		+					+	+		0.0037
Sol can	+	+	+	0.0358	+	+	+	+	+	0.2197	+	+	+	+	+	+	+	+	+	0.2106
Sol gra	+	+	+	0.0192	+	+	+	+		0.0170	+	+	+	+	+	+	+	+		0.0652
Sol nem	+	+		0.0086				+		0.0000										0.0000
Sol rug				0.0000	+					0.0099			+			+			+	0.0016
Sol sim	+			0.0000						0.0000										0.0000
Spi cer		+		0.0000		+		+	+	0.0045	+	+	+			+	+	+	+	0.0176
Tar off	+			0.0009	+	+	+		+	0.0090	+	+	+	+	+	+		+		0.0081
The pal		+		0.0157	+			+		0.0061	+				+	+				0.0085
Typ lat				0.0000						0.0000	+	+								0.0004
Unk 11				0.0000		+			+	0.0032				+						0.0003
Unk 12				0.0000	+					0.0012		+								0.0007
Unk 6				0.0000						0.0000		+							+	0.0008
Unk 9				0.0000		+		+		0.0081									+	0.0004
Unk Orc				0.0000						0.0000								+		0.0000
Utr min	+		+	0.1647*						0.0000*										0.0000*
Vio lan				0.0000			+			0.0718										0.0000
Woody Species																				
Ame int				0.0000		+	+	+	+	0.0546	+			+	+					0.0059
Bet pap	+	+		0.0000		+	+		+	0.0656	+	+								0.0019
Cel orb				0.0000		+				0.0093										0.0000
Cep occ	+	+		0.0063						0.0000	+									0.0000
Cor amo			+	0.0063						0.0000										0.0000
Cor foe	+			0.0000						0.0000										0.0000
Cor sto				0.0000	+	+	+	+	+	0.2176	+	+		+	+	+	+	+	+	0.2748
Fag gra				0.0000				+	+	0.0063	+									0.0000
Fra ame				0.0000		+	+	+	+	0.0708								+		0.0019
Hud tom	+		+	0.0686						0.0000										0.0000
Hyp kal	+	+	+	1.1783	+	+	+	+	+	0.2523	+	+	+	+	+	+	+	+	+	0.2478
Ile ver				0.0000		+				0.0056										0.0000
Jun com			+	0.0045		+	+	+		0.0089	+					+				0.0038

Table 2-4. (continued)

Species[1] Abbrev.	Open Wetpannes				Jack Pine Wetpannes						Austrian Pine Wetpannes									
	1D	2D	4D	Overall[2] IV	B	C	D	E	G	Overall[2] IV	3	4	5	6	7	9	11	12	13	Overall[2] IV
Jun vir	+			0.0000						0.0000	+	+							+	0.0000
Lon spp				0.0000	+				+	0.0489						+				0.0020
Pin ban				0.0000	+	+	+	+	+	0.6538	+	+	+	+	+	+	+	+	+	0.4208
Pin nig				0.0000						0.0000	+	+	+	+	+	+	+	+	+	0.1896
Pin str				0.0000	+	+	+			0.0160										0.0000
Pin syl	+			0.0000						0.0000										0.0000
Pop del		+		0.0146						0.0000	+									0.0059
Pru pum	+	+	+	0.1362						0.0000										0.0000
Pru ser				0.0000		+	+			0.0166				+				+		0.0034
Pru spp				0.0000	+	+				0.0294										0.0031
Pru vir				0.0000		+	+			0.0316				+		+		+		0.0091
Pte tri				0.0000						0.0000				+						0.0014
Que spp		+		0.0000	+	+	+	+	+	0.1757	+	+		+	+	+	+	+	+	0.0321
Rib spp				0.0000	+					0.0037				+						0.0014
Ros spp	+	+		0.2029	+	+				0.0123	+									0.0025
Rub spp	+	+		0.1481	+	+	+	+	+	0.5384	+	+	+	+	+	+		+		0.4552
Sal spp	+	+	+	0.3868	+	+	+	+	+	0.3420	+	+	+	+	+	+	+	+	+	0.5184
Sas alb				0.0000	+	+	+		+	0.0871	+	+	+	+				+		0.0145
Spi alb		+		0.0000						0.0000										0.0000
Spi tom		+	+	0.8473	+	+	+	+	+	0.2479	+	+	+		+	+	+			0.7285
Tox rad				0.0000		+	+	+	+	0.0558		+		+					+	0.0073
Vib opu				0.0000						0.0000						+	+			0.0047
Vit rip				0.0000	+	+	+	+	+	0.0498	+	+	+	+	+	+	+	+	+	0.0640

[1] See Table 2-3 for the full species names.
[2] The importance values range from 0 to 3. The importance values of the herbaceous vegetation are calculated separately from those of the woody vegetation.
* Indicates the importance values were calculated with relative cover and relative frequency values only and are therefore underestimated.

The geographic range of each species was determined and the center of its range was listed (Gleason and Cronquist, 1991; Voss, 1972, 1985, 1996) (Table 2-3). The ranges of wetpanne plant species are centered in a variety of locations in the United States, including the north, northeast, east, southeast, Atlantic coast, and temperate areas (excludes subtropical areas). Some species are distributed in the eastern and the western United States but are not found in the Great Plains region. Other species have more widespread distributions, which include North America, Eurasia, and circumboreal areas. Some of the species had cosmopolitan distributions. The highest percentages of species are from the east (23%) and the north (14%) (Table 2-5). The rest of the species are relatively evenly distributed among the ten other geographic ranges. Only one species found in the wetpannes is a Great Lakes endemic, *Hypericum kalmianum*. It was found in every wetpanne at Saugatuck. Its preferred habitat is calcareous, wet sand (Voss, 1985). Since it is rarely found in other wetland types, *Hypericum kalmianum* is a good indicator species for wetpannes of the Great Lakes region.

None of the plants found in the wetpannes are listed as endangered or threatened in the United States. None of the plants are listed as endangered, threatened, or of special concern to the state of Michigan either, although some species that were found are considered to be in decline there. *Spiranthes cernua* is a species of orchid with creamy white flowers that spiral up its stem. *Melampyrum lineare*, a partial root parasite, is listed as "threatened" in the state of Indiana. *Carex eburnea* is also listed as "threatened" in Indiana.

Table 2-5. The geographic origins of different wetpanne plant species.

Geographic Range	% Total
East	23%
North	14%
Northeast	11%
Eurasia	10%
Circumboreal	9%
E/W U.S.	9%
North America	6%
Southeast	6%
Cosmopolitan	5%
Temperate North America	4%
Atlantic Coast	2%
Great Lakes	1%

Figure 2-1. A photograph of the study site taken in 1988 (scale 1:24,000). Three types of wetpannes (Wps) were studied: Austrian pine wetpannes, jack pine wetpannes, and open, treeless wetpannes. The squared off portion represents the area that encompasses the Austrian pine and the jack pine wetpannes within Saugatuck Dunes State Park, Michigan.


Austrian Pine
Wps
Jack Pine Wps
Open Wps
0
500
1000
1500
2000 Meters
N

Figure 2-1.

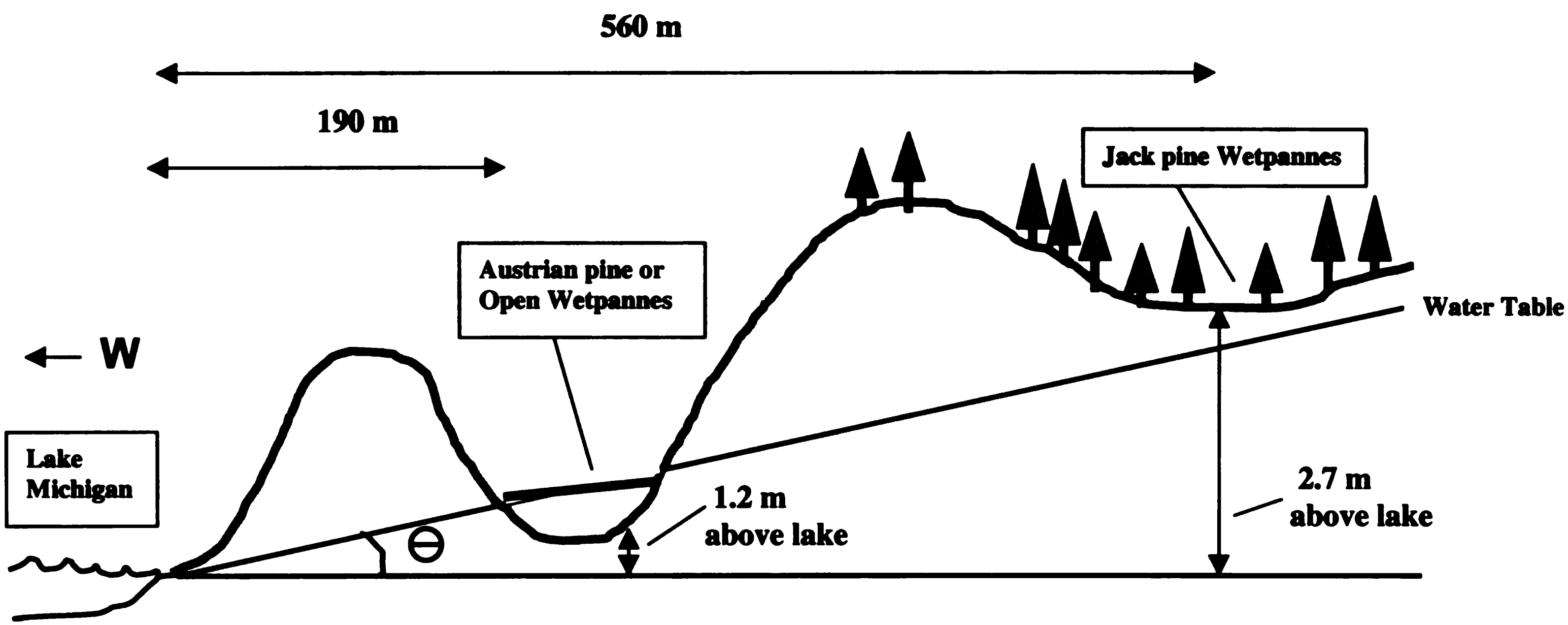


Figure 2-2. A profile of the study site showing the relative positions of the different wetpanne types. Average distances from Lake Michigan and the average elevations above the lake level are given.

CHAPTER THREE

A COMPARISON OF THE BIOTIC AND ABIOTIC CHARACTERISTICS OF WETPANNES WITH AND WITHOUT AUSTRIAN PINE (*PINUS NIGRA*)

INTRODUCTION

Wetpannes have been recognized as a type of coastal wetland that has become a priority on the international conservation agenda (Grootjans et al., 1998). Wetpannes are considered to be a globally rare ecosystem. The Michigan Natural Features Inventory (1993) has listed interdunal wetpannes as having a "G2" global status, which means they are imperiled globally because of their rarity or because of some other factor that make them vulnerable to extinction throughout their range. Wetpannes were first studied in Europe in the 1950s. Since then, researchers have studied several aspects of wetpanne ecology: hydrology and water chemistry (Timms, 1982; Bakker, 1990; Noest, 1991; Grootjans et al., 1996; Sival and Grootjans, 1996); factors influencing the distribution of vegetation (Ranwell, 1959; Willis et al., 1959; Jones and Etherington, 1971; Onyekwelu, 1972; van der Laan, 1979; Zoladeski, 1991; Wilson and Gitay, 1995); and hydrarch succession (Sival, 1996). Grootjans et al. (1998) summarized the results of these studies in a review of European wetpannes. They described wetpannes as "low-lying areas within coastal dune systems where the water table is near the surface but has high seasonal fluctuations." They stated that the depth to the water table can vary up to 2 meters. The vegetation of wetpannes varies greatly in species composition, but the distribution of the species that grow in each slack is related to the groundwater regime

(Grootjans et al., 1998). Calcareous groundwater supports calciphiles, and wetpannes that are close to the sea are often brackish (Grootjans et al., 1998).

It is remarkable that wetpannes have been so well studied in Europe, but virtually ignored in the United States. They have been especially neglected in the Great Lakes region. Very few studies have been done on freshwater wetpannes, and of those that have been done, most have been restricted to Indiana Dunes National Lakeshore. Henry C. Cowles (1899), famous for his pioneering theories on vegetation succession, was one of the first to describe wetpannes at Indiana Dunes, although his comments on them were restricted to a few short notes. He noticed "a number of swamps that run more or less parallel with the lakeshore." He described two types of swamps—the "bulrush swamp" which was "more or less continuously surrounded by a marginal fringe of willows and dogwoods," and the "pine bottom," a "very distinct type of coniferous forest…in low depressions between dunes" where Jack pines (*Pinus banksiana*) were commonly found growing around "the gently sloping margin of an undrained swamp." In 1911, Cowles' colleague, V.E. Shelford, studied succession in animal communities of the wetpannes, and recognized as many as 58 linear rows of ponds at Indiana Dunes, most of which have since been destroyed by development (Wilcox and Simonin, 1987). The wetpannes of the Great Lakes were not studied again until many years after Cowles' initial description.

In 1977, Barko et al. studied primary productivity in a single dune pond near Saugatuck, Michigan, but no attempt was made to characterize more than that one pond. In 1986, the first attempt to quantitatively characterize the wetpanne habitat was made at Indiana Dunes National Lakeshore (Hiebert et al., 1986). Hiebert et al. (1986) measured the water chemistry in five dune ponds, and attempted to quantify the distribution of plant species along a water depth gradient. Wilcox and Simonin (1987), Jackson et al. (1988), and Cole and Taylor (1995) used the wetpannes of Indiana Dunes to study hydrarch succession in wetpannes. In 1993, the first survey of wetpannes outside of the Indiana dunes area was conducted by the Michigan Natural Features Inventory (Comer and Albert, 1993). Leege and Murphy (2000) studied the effects of an exotic planted tree species, the Austrian pine (*Pinus nigra*), on the dune vegetation at Saugatuck Dunes State Park, Michigan. They looked at its effects across several different dune habitat types, one of which was the wetpanne. They found that light levels and soil moisture levels were reduced in wetpannes planted with Austrian pine. They also found a greater cover of woody vegetation in Austrian pine wetpannes. Their suggestion that the Austrian pines may be drying down the wetpannes led to the basis of this study.

There is disagreement in the literature as to what a wetpanne is. The confusion may be related to the different ways that wetpannes of the Great Lakes are formed. One way that wetpannes may be formed is by strong winds that carve out large areas of sand down to the water table (Cole and Taylor, 1995). This type, often referred to as a "panne", is found primarily in Indiana and southwestern Michigan where large blowouts have occurred. Blowouts are much more common on the eastern sides of the Great Lakes due to the fact that the prevailing westerly winds gain energy during their unimpeded flow across the surface of the Great Lakes (Dorr and Eschman, 1970). Wetpannes can also be formed another way. In years when lake levels recede, sand is blown from the newly exposed beach to form a low ridge. Over several cycles of fluctuating lake levels, many low beach ridges are formed in succession parallel to the lakeshore (Dorr and Eschman, 1970). The wetpannes occur in the troughs between these beach ridges (Comer and Albert, 1993). Wetpannes formed in this manner are usually called "dune swales." In the Michigan Natural Features Inventory survey of wetpannes, the "panne" type of wetpanne in southwestern Michigan was omitted (Comer and Albert, 1993). Although the panne and dune swale wetpanne types have different origins, they share many of the same characteristics. Both are described as permanent or intermittent ponds that can contain up to 2 meters of water (Comer and Albert, 1993; Wilcox and Simonin, 1987). Both types have sandy substrates. They even share many of the same calciphilous plant species (Comer and Albert, 1993; Wilcox and Simonin, 1987). They seem to be similar systems, despite their different origins.

A second debate is related to when the wetpannes were formed. Some researchers believe wetpannes to be of relatively recent origin. Hiebert et al. (1986) and Barko et al. (1977) state that the wetpannes they studied were probably formed about the turn of the century during an extremely dry period. They implied that the low water tables during this period caused the sand to dry out and allowed the current wetpannes to be carved out by strong winds. Olson (1958), who followed up H.C. Cowles' initial studies on dune succession at Indiana Dunes National Lakeshore, also believed wetpannes to be a temporary phase in dune formation (Menges and Armentano, 1985) and did not include them in his study of dune succession. He may have been led to think that wetpannes were unimportant in dune succession by Cowles, who implied that existing wetpannes would be buried by advancing dune ridges over a time scale of a few years (Cowles, 1899). More recent evidence has shown that wetpannes are much more stable than was previously believed. Jackson et al. (1988) dated the bottom layer of sediment cores taken from the ponds at Indiana Dunes. They discovered that wetpannes that were the farthest from Lake Michigan were about 3,000 years old, those in the middle were about 2,100 years old, and those nearest the lake were 300 years old (Jackson et al., 1988). The explanation for this is that the wetpannes were formed sequentially in rows parallel to the Lake Michigan shoreline as lake levels dropped. The Great Lakes' water levels were at their highest level about 4,000 years ago during the Nipissing Stage and have since dropped about 25 feet (Dorr and Eschman, 1970). Wilcox and Simonin (1987) and Cole and Taylor (1995) used this information to study vegetation succession in these wetpannes.

The purpose of Chapter 3 is to investigate the biotic and abiotic characteristics of the blowout type of wetpanne that is found along the southeastern shore of Lake Michigan. Ponded, treeless wetpannes and those that are forested with jack pine are included in this study. The ecological characteristics of these wetpannes are then compared to wetpannes that have been planted with Austrian pine. The objectives of this chapter are as follows:

1. To explore the biotic and abiotic features common to all of the wetpannes in the study.
    A. To determine if the observed distribution pattern of plant species in wetpannes is linked to water table levels.
    B. To look for seasonal patterns in water table levels within wetpannes, and to determine what factors may be influencing the observed water levels.
    C. To determine the source of the wetpanne water (precipitation, groundwater, or backflow from Lake Michigan) using water chemistry analyses.

D. To use the depth, pH, and moisture content of the sediment layer underlying the wetpannes to infer the age and the hydrology of wetpannes.

E. To look for year-to-year patterns in the aboveground water levels of wetpannes and use historical records to decide whether lake level, precipitation, or temperature is the best predictor of wetpanne water level.

2. To make comparisons between open, treeless wetpannes and those that are forested with jack pine or are planted with the non-native Austrian pine.

   A. To compare plant community characteristics among wetpanne types, and to determine how tree density, elevation of the wetpanne above the water table, and distance from Lake Michigan affect these characteristics.

   B. To compare seasonal patterns in water table levels among wetpanne types, and to determine if the tree species surrounding the wetpanne is correlated with the water table level.

   C. To compare light regimes in the jack pine and Austrian pine wetpannes.

METHODS

Biotic Characteristics

DISTRIBUTION PATTERN OF PLANT SPECIES

The plant community composition of each wetpanne was determined to examine the relationship between water table depth and the distribution pattern of plant species within the wetpannes. It was believed that each plant species would be found in a particular range along the water depth gradient. Water table depth was measured by installing a well in the deepest part of each wetpanne. Belt transects that intersected the position of the well were used to sample the plant community. The shape of the wetpanne basin was then measured along the same belt transects. This allowed for the calculation of the water table depth for all of the vegetation plots along the transect line.

The geometry of the wetpanne basin was estimated by stretching taut, level lines over the wetpanne and measuring the distance from the lines to the basin bottom (Fig. 3-1). Basin depth was measured relative to the deepest area of each wetpanne, where a well was installed. At least one transect line crossed over this point of the wetpanne basin. The distance from the level line to the bottom of the basin was measured every 50 cm along the transect lines. These measurements coincided with the center of each of the $0.25m^2$ vegetation plots.

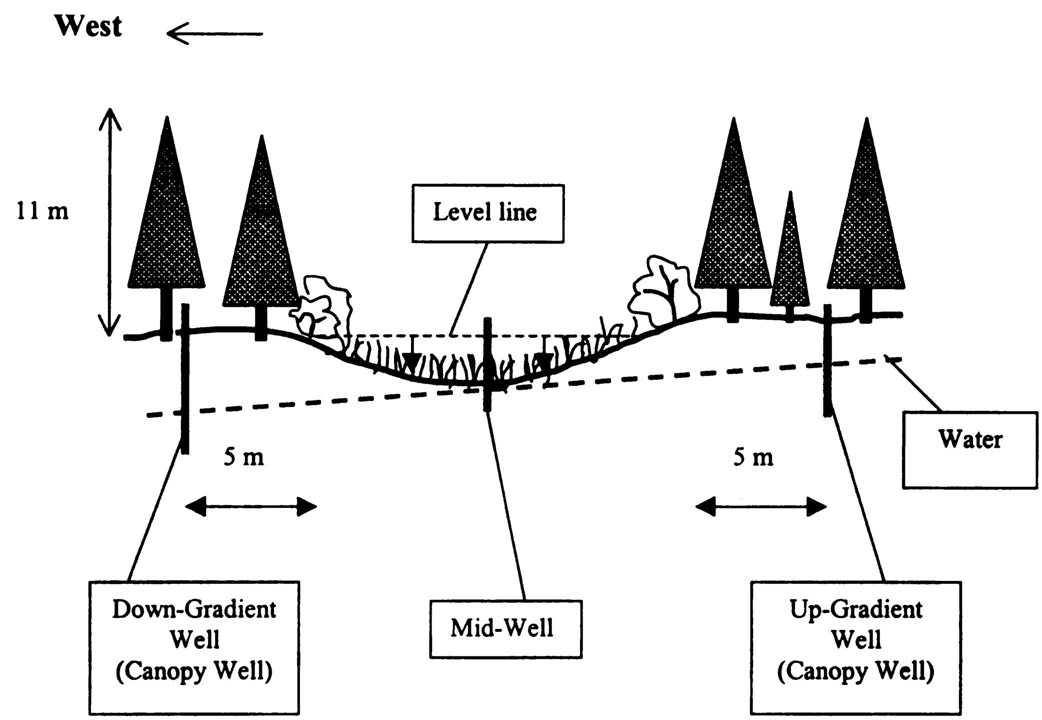


Figure 3-1. Profile of a typical wetpanne, showing how a taut, level line was used to measure basin depth and the placement of the wells. The canopy wells were placed 5 m from the eastern edge and 5 m from the western edge of the wetpanne. The average height of the surrounding tree canopy of the forested wetpanne types was 11 m.

The water depths in the wells were measured biweekly from 1 June 1998 to 6 September 1998. All calculations of water table depth in the vegetation plots were made relative to the 1 June 1998 water depth measurement because it was assumed that the inland water table would be highest in the spring. Spring flooding may determine where each plant species can grow within the wetpanne basin. Based on the literature (Shedlock, 1993; Lichter, 1995), it was assumed that the water table flows as a plane west toward Lake Michigan. Additional measurements of water table depth were made just outside the eastern and western edges of each wetpanne to estimate the slope of this plane

(Fig. 3-1). In most wetpannes, the water table did slope west, although in a few cases, the water table flattened out slightly as it flowed under or through the wetpanne. The distance of this plane from the lowest point of the wetpanne basin was calculated using the water level measured in the well. The basin depth measurements were used to calculate the distance from the bottom of the basin to the water table at each vegetation plot. Corrections were made for the slope of the water table in the transects that ran from east to west. When applicable, the depth of standing water in each plot was measured at the midpoint of each $0.25m^2$ plot along the vegetation transect line.

The wetpanne vegetation was sampled in July and August of 1998 using belt transects that coincided with the basin depth measurements (Fig. 3-2). The purpose of using belt transects was to detect patterns in the distribution of the plant species. Each transect extended 2 meters beyond either edge of the wetpanne. The edge of the wetpanne was defined as the place where wetland plant species were replaced by upland, sand dune plant species. Additional stratified-random transects were added as necessary based on the size of the individual wetpanne.

To quantify the herbaceous vegetation, contiguous, $0.25m^2$ plots (0.5m x 0.5m square) were laid along each transect line. In wetpannes that had an area greater than 1000 m^2, only every other plot was measured. To quantify the woody vegetation, contiguous, $1m^2$ (1m x 1m square) plots were nested over every other $0.25m^2$ plot on each transect line. The cover and density of each plant species were determined in each plot. Cover, a measure of the proportion of area occupied by the above ground portion of an individual plant species relative to the total area in the plot, was estimated using the following cover classes: >0-5%; >5-25%, >25-50%, >50-75%, >75-95%, >95-100%.

Overhanging canopies of vegetation were included in the cover estimates of the woody vegetation, but only plants that were actually rooted within the plots were used to estimate the cover of the herbaceous vegetation. Density, a measure of the number of individual plants per unit area, was determined by counting the number of individualss rooted within the plot and dividing by the plot area. The density of the woody vegetation was determined by counting the total number of stems of each species per plot rather than the number of individuals because it was difficult to define individual plants. In addition to the vegetation plots, each wetpanne was systematically searched for any species that were missed by the belt transects to determine the overall species richness in each wetpanne.

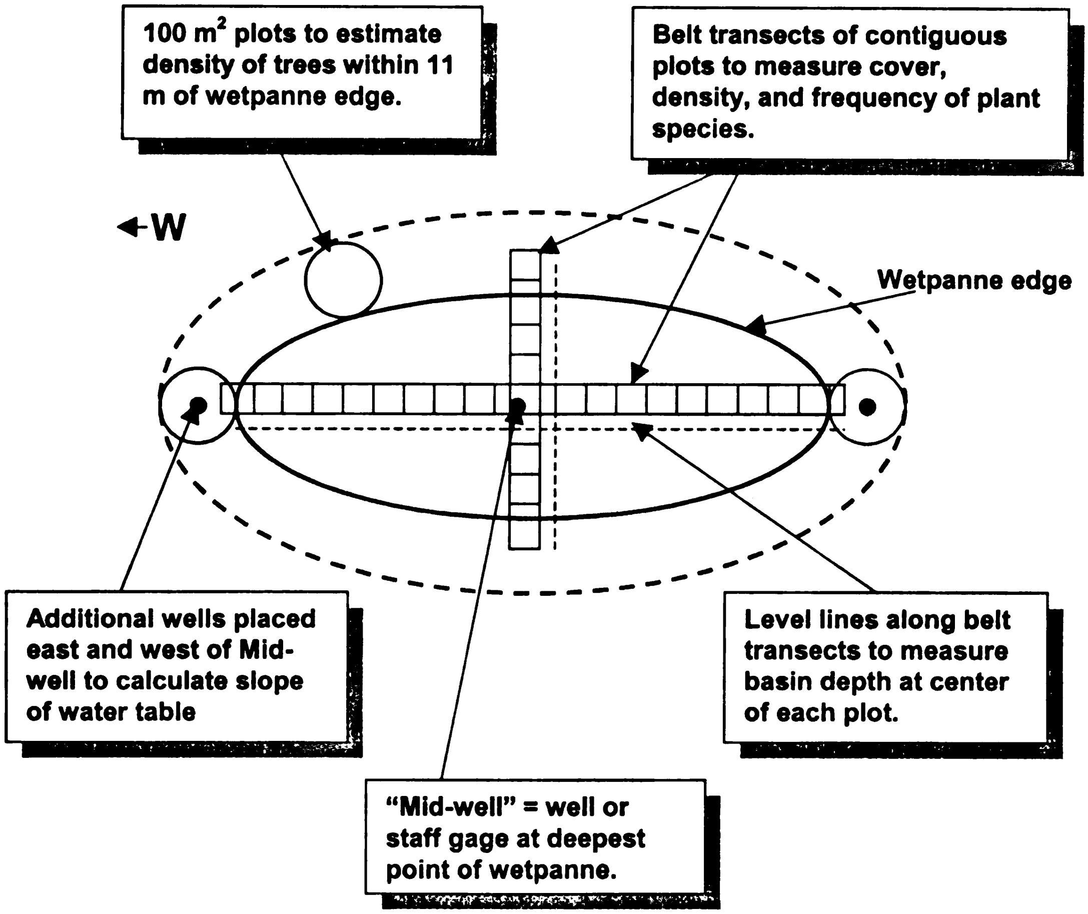


Figure 3-2. A bird's eye view of a wetpanne illustrating the sampling methods used.

The vegetation plots were first grouped together by wetpanne type—open wetpannes, jack pine wetpannes, and Austrian pine wetpannes. The plots were then separated into classes based on water table depth in each plot, with each class defined by successive 10 cm increments of depth. The classes ranged from 0 to 13 (Table 3-1). Low water depth classes indicated drier conditions in the plots. Higher water depth classes indicated plots with wetter conditions. A water depth class of zero represented plots that were within 2 meters outside the wetpanne edge, because water table depth was not determined for plots outside of the wetpannes. Water depth classes between 1 and 7 represented plots in which the water table was below ground. Water depth classes of 8 to 13 represented plots that had standing water. All water depth classes represented the water table level on 1 June 1998.

Table 3-1. The definitions of the water depth classes.

Water Depth Class	Depth from ground level to water table	Position of Water Table
0	Plots outside wetpanne perimeter	Below ground
1	> -60 cm	Below ground
2	-50 to -59.9 cm	Below ground
3	-40 to -49.9 cm	Below ground
4	-30 to -39.9 cm	Below ground
5	-20 to -29.9 cm	Below ground
6	-10 to -19.9 cm	Below ground
7	0 to -9.9 cm	Below ground
8	+0.1 to +9.9 cm	Above ground
9	+10 to +19.9 cm	Above ground
10	+20 to +29.9 cm	Above ground
11	+30 to +39.9 cm	Above ground
12	+40 to +49.9 cm	Above ground
13	> +50 cm	Above ground

Importance values for each species were calculated for the species found in each of the fourteen water depth classes using the cover and density values obtained from the vegetation plots, and a third metric, frequency. Frequency is a measure of the chance of finding a given species within a plot, and was calculated for each species in each water depth class. The importance value for each species *i* (IV_i) was obtained by adding the relative density (RD_i), the relative frequency (Rf_i), and the relative cover (RC_i) of that species within each water depth class as in Brower, Zar, and von Ende (1990):

$$IV_i = RD_i + Rf_i + RC_i$$

The importance values of the woody vegetation were calculated separately from the importance values of the herbaceous vegetation. The importance values ranged from 0 to 3.00. An importance value of 0 indicated that the species was not found within the vegetation plots of that particular water depth class. Higher importance values for a species indicated that the species is dominant relative to other species in that water depth class. An importance value of 3.00 indicated that a species is the only species found within the water depth class.

Density (D_i) was calculated by dividing the total number of individuals of species i (n_i) by the total area (A) sampled within each water depth class:

$$D_i = n_i / A$$

Densities were determined whenever possible; however, for some herbaceous species, the plants were tufted and/or density was difficult to assess. For these species, only relative cover and relative frequency were used to calculate importance values. Therefore, the importance of these species within each water depth class was underestimated. These species are demarcated within the Results section (Tables 3-3; 3-4; 3-5). The relative density of each species i was calculated by dividing D_i by the total density for all species:

$$RD_i = D_i / \Sigma D$$

Frequency (f_i) was calculated by dividing the number of plots in which species *i* occurs (j_i) by the total number of plots measured (k) in each water depth class:

$$f_i = j_i / k$$

The relative frequency of species *i* was calculated by dividing f_i by the sum of the frequencies for all species:

$$Rf_i = f_i / \Sigma f$$

Cover (C_i) was calculated by dividing the total area covered by species *i* (a_i) by the total area sampled (A) in each water depth class:

$$C_i = a_i / A$$

Relative cover was calculated by dividing C_i by the sum of the covers for all species in each water depth class:

$$RC_i = C_i / \Sigma C$$

The importance values of the dominant species in each water depth class are arranged in a table for each wetpanne type for both the woody and the herbaceous vegetation (Tables 3-3; 3-4; 3-5; 3-6; 3-7; 3-8). To be considered dominant, a species had to have an overall importance value that was greater than 0.01 in at least one of the wetpanne types. The species are arranged in the order in which they appear along a water depth gradient from dry to wet for each of the three wetpanne types. Overall importance values were also calculated for each of the three wetpanne types as described in Chapter 2 (Table 2-4).

In order to show that the plant species were arranged within the wetpanne basin based on their affinity for wet conditions, a weighted average ordination was performed on the samples using a wetland coefficient value to weight each species. Wetland coefficient values are values that have been assigned by the Michigan Department of Natural Resources and indicate how often a particular plant species is found in a wetland (Herman et al., 1996). These categories are based on the National Wetland Indicator categories given by Reed (1985), and 600 additional species that were assigned categories *de novo* by the Michigan Department of Natural Resources. Negative wetland coefficient values represent species that have a higher probability of being found in a wetland, and positive values represent species that are found more often in upland conditions. The wetland coefficients range from +5 for upland species to –5 for obligate wetland species (Table 3-2).

Table 3-2. The definitions of the wetland coefficient categories (from Herman et al., 1996). A '+' indicates a wet tendency, and a '-' indicates a dry tendency.

Wetland Coefficient	Wetland Category	Symbol	Probability of Occurring in a Wetland
5	Upland	UPL	< 1%
4		FACU-	
3	Facultative upland	FACU	1-33%
2		FACU+	
1		FAC-	
0	Facultative	FAC	34-66%
-1		FAC+	
-2		FACW-	
-3	Facultative wetland	FACW	67-99%
-4		FACW+	
-5	Obligate wetland	OBL	>99%

The weighted average ordination score was calculated for each plot by multiplying the cover class of each species by its wetland coefficient value. These values were summed for each plot and the sum was divided by the total cover of all species in the plot to get an ordination score for that sample. The formula follows:

$$S_j = \frac{\Sigma c_{ij} w}{\Sigma c_{ij}}$$

For all species *i* in plot *j*.
[c = cover and w = wetland coefficient for species *i*].

The ordination scores were first separated by wetpanne type, and then each ordination score was plotted against the water table depth or the basin depth in the vegetation plot. A correlation was run to determine whether water table depth or basin depth better described the arrangement of samples along the ordination axis.

PLANT COMMUNITY DIFFERENCES AMONG WETPANNE TYPES

The vegetation data were also analyzed at the whole wetpanne level to be able to make comparisons among the plant communities of open wetpannes, those that are forested with jack pine, and those planted with Austrian pine. A variety of plant community characteristics were compared. Species diversity, species richness, and the relative number of wetland indicator species were compared among the three wetpanne types. The average total cover of woody vegetation was compared to see if the total cover was greater in the Austrian pine wetpannes than in the other two wetpanne types. An herbivory index was devised to compare the impact of herbivory on the woody vegetation across wetpanne types. Then, all of the relationships between species diversity, species richness, the percent wetland indicator species, total cover of woody vegetation, the herbivory index values, tree density, wetpanne area, the elevation of the wetpanne basin above the water table, and the distance from Lake Michigan were explored. The elevation of the wetpanne basin above the water table is defined as the distance of the water table to the lowest point of the wetpanne basin as measured on 1 June 1998. Finally, the density of juvenile Austrian pine trees and jack pine trees in each of the forested wetpanne types was determined to estimate the relative establishment of the two tree species within the wetpannes.

The overall differences among wetpanne types were determined by using a Kruskal-Wallis test because the available number of each wetpanne type was small. For open wetpannes, n=3; for jack pine wetpannes, n=5; and for Austrian pine wetpannes, n=9. A Dunn's multiple comparison test was then used to look for differences among wetpanne types at a 15% experimentwise error level (Daniel, 1978). An experimentwise error level larger than the traditional level of 5% used for single comparison tests was recommended by Daniel (1978) because of the difficulty in detecting differences among samples when making multiple comparisons.

The species diversity was calculated using the Shannon-Weaver diversity index (H') using the equation described in Pielou (1975). Species richness is defined as the number of species found in each wetpanne. The relative number of wetland indicator species per wetpanne was calculated by dividing the number of species that fell into the FAC, FAC+, FACW-, FACW, FACW+, and OBL wetland categories by the total number of species in each wetpanne. Wetland categories are assigned as in Herman et al. (1996) (Table 3-2). An herbivory index was designed to quantify the amount of damage to woody vegetation by herbivory in each plot. The index ranged from 0, representing no damage, to 3, indicating the most severe amount of damage to the plants. A value of 1 was assigned to plots with plants that sustained only small amounts of damage (i.e., bite marks visible in the foliage). A value of 2 was assigned to plots where moderate amounts of damage were incurred by the plants (i.e., obvious damage to foliage such as stems that were bitten off). A value of 3 was assigned to plots with plants that were severely stunted or deformed (i.e., multiple stem sprouts because plant apex had been repeatedly chewed off). The average of the herbivory index values was calculated for each wetpanne to get an idea of the overall herbivory at each site. The primary herbivores at the study site were deer and rabbits.

Several correlations were run to look for relationships between the different variables related to wetpanne type and tree density, elevation of the wetpanne basin above the water table, and distance from Lake Michigan. Sequential Bonferroni corrections were applied to the p-values to determine the experimentwise significance level for each correlation and to avoid correlations that were significant by chance alone (Type I error).

The number of juvenile trees of each pine species growing within the wetpanne interior was counted for each wetpanne. A juvenile tree is defined as having a DBH (diameter at breast height) of less than 2.5 cm. The density of trees in the wetpannes was calculated by dividing the total number of trees in each wetpanne by the area of that wetpanne. The total area of each wetpanne was calculated either by aerial photograph analysis in ArcView (Environmental Systems Research Institute, Inc., Redlands, CA) or by mapping the boundaries of the wetpanne on graph paper and then counting the number of occupied squares of graph paper.

Abiotic Characteristics

HYDROLOGY

Hydrological measurements were made to describe seasonal patterns in water table levels within the wetpannes and learn what factors may be influencing these patterns. Comparisons were made between seasonal patterns of water table levels in wetpannes with and without Austrian pine to determine if the introduced Austrian pine has the ability to depress water table levels more than the native jack pine.

Depth of surface water or depth to groundwater in the wetpannes was measured biweekly over the months June through September, 1998. A combination of staff gages and wells were used. Staff gages were placed in the deepest parts of all the wetpannes that had standing pools of water at the beginning of the growing season. Staff gage measurements were also taken in the fall of 1997 and in the spring of 1999. Wells were installed in the lowest point of each wetpanne basin (hereafter referred to as a "mid-well") (Figs. 3-1). Wells were also installed up-gradient and down-gradient of the mid-wells based on the assumption that groundwater flows west towards Lake Michigan. One well was placed 5 meters from the wetpanne edge to the east, and the other was placed 5 meters from the edge of the wetpanne to the west (Fig. 3-1). These wells are referred to as "canopy wells" because their purpose was to measure water table levels directly beneath the canopy of Austrian pine or jack pine trees that bordered the edges of the wetpannes, and to determine the effects of tree density on the water levels of individual wells. The complex of Austrian pine wetpannes was treated as one hydrological unit and received only one up-gradient and one down-gradient well, although each unit in the complex had its own well at its lowest point. This was done because each wetpanne within the complex was so close together that their up-gradient and down-gradient wells would have fallen into the interior of a neighboring wetpanne rather than under a canopy of trees.

Wells were constructed of 1 ¼" PVC pipe cut long enough to extend at least 50 cm below the spring water table level. The bottoms of the wells were covered with a durable cotton fabric that allowed water into the wells, but kept sand out. The wells were installed using a soil bucket auger. The elevation of the ground surface at each well was measured relative to the level of Lake Michigan using a laser level. The distance from the top of the well to the water table was measured electronically with a set of wires that sounded a warning tone when they touched the water surface or by blowing air down a length of Tygon tubing and recording the depth at which bubbling was first heard.

The density and total basal area of each tree species that grew within the wetpanne interior and just outside of the wetpanne edge were determined and used to examine the relationships between tree density and tree size on water levels within the wetpannes. More or larger trees may use more water than fewer or smaller trees, thus lowering water table levels more. The number of each tree species that grew inside the boundary of each wetpanne was counted and divided by the total wetpanne area to obtain a measure of interior tree density. The density of trees that grew around the edges of the wetpannes was estimated by placing at least three 100 m^2 circular plots tangential to the edge of each wetpanne (Fig. 3-2). The first two circular plots were centered over the canopy wells so that the effects of tree density on water levels in these wells could be determined, and the third plot was randomly chosen around the edge of the wetpanne. The numbers of Austrian pines and jack pines in the plots were counted and divided by the total area sampled to estimate the total density of trees growing in an 11.3 meter wide strip around the edge of each wetpanne. This strip was considered wide enough to contain all trees with roots that touch the wetpanne interior since the average canopy height surrounding the wetpanne was 11.2 meters, and the average spread of Austrian and jack pine root systems is less than their height (Strong and La Roi, 1983). The diameter at breast height (DBH) was used to calculate the basal area of each tree, and the total basal area of all the trees were summed and divided by the total area sampled to estimate total basal area. Only larger trees (DBH >2.5 cm) in the circular plots were measured or counted.

The relationships between the total change in water table depth from 1 June 1998 to 6 September 1998 and the distance of the well from Lake Michigan, the elevation of the well relative to Lake Michigan, and total wetpanne area were also explored. The relationship between the change in water table level and distance from, or elevation above, Lake Michigan was explored because the slope of the water table was thought to influence water levels in wetpannes. Total wetpanne area was examined because the effects of trees that surround the wetpannes on the water levels in the mid-wells should be less if total wetpanne area is large.

WATER CHEMISTRY

The chemical composition of the wetpanne water was assayed because its water chemistry can be used to determine the predominant source of water in the wetpannes. The chemical compositions of precipitation, of groundwater, and of Lake Michigan are distinctive, and by comparing the water chemistry of wetpannes to these potential water sources, one can determine from where the water in the wetpannes is derived. Two other reasons for measuring water chemistry were to compare the Saugatuck wetpanne characteristics to the wetpanne studies at Indiana Dunes National Lakeshore and to examine any differences among the three types of wetpannes within the Saugatuck area.

Surface waters from the center of the ponded wetpannes (n=3) and from Lake Michigan and the oxbow lake were collected twice during summer of 1998 (on 1 July 1998 and again on 20 September 1998). In the dry wetpannes, water from the mid-wells was sampled once on 1 July 1998. Six jack pine wetpannes and eight Austrian pine wetpannes were sampled this way. Sample bottles were stored on ice and brought back to the lab the same day. Samples were analyzed at Kellogg Biological Station in Hickory Corners, Michigan in the laboratory of Dr. Steve Hamilton. The parameters measured were specific conductance, pH, alkalinity, Ca^{2+}, Mg^{2+}, Na^{+}, Cl^{-}, K^{+}, SO_4^{2-}, NH_4^{+}-N, total dissolved phosphorus (TDP), NO_3-N, and silica. The pH measurements, filtration, and the preservation of subsamples were performed within 24 hours of collection. The pH was determined using a closed-system measurement with a low-ionic strength electrode as described by Hamilton (1994). Samples were vacuum filtered using a Gelman Supor membrane filter (0.45 μm pore size). The specific conductance, alkalinity, and concentration of the nutrients NO_3-N, NH_4^{+}-N, and TDP were measured within two weeks of sample collection. The specific conductance was corrected to 25°C. Alkalinity as HCO_3^{-} was measured using Gran titration between pH 4 and 3 as in Cantrell et al. (1990). NO_3-N was determined via cadmium reduction and colorimetric analysis (Wetzel and Likens, 1991). NH_4^{+}-N was determined with the phenolhypochlorite colorimetric method (Wetzel and Likens, 1991). TDP was measured using persulfate digestion and the molybdate blue colorimetric analysis (Valderrama, 1981). The concentrations of Cl^- and SO_4^{2-} were determined by ion chromatography. Flame atomic absorption was used to measure the concentrations of Na^+, K^+, Mg^{2+}, and Ca^{2+}. Finally, the amount of soluble silica (Si) was measured using the molybdenum blue method (Wetzel and Likens, 1991).

SEDIMENT DEPTH

The depth of the organic sediment layer may indicate the relative age of a wetpanne. Deeper sediment layers may indicate older wetpannes. It was predicted that the wetpannes farther away from Lake Michigan were older and would have a deeper organic sediment layer than those that were closer to the lake. Sediment cores were also examined for hydric soil characteristics, because in order for a habitat to be considered a wetland, its soil must show signs of having been saturated at one time (Tiner, 1999). The depth of the organic layer in each wetpanne was sampled once near the end of the 1998 growing season. A one-inch diameter soil corer was used to take a core from the soil surface, and the depth of the black organic layer was measured. A soil core was removed from the deepest part of each wetpanne. The pH of the soil in this core was assayed because it was believed that the pH of the forested wetpanne soil would be more acidic than the unforested wetpannes due to the input of pine needle litter. The pH was measured by dissolving the soil samples in distilled water for ten minutes and then inserting a calibrated pH electrode into the soil solution. Additional cores were taken every 2 to 10 meters along transects crossing the length of the wetpannes. Along a transect in one wetpanne, the moisture levels in the cores were determined. The cores were sampled in the early afternoon on a sunny September day. Each core was split into two 10 cm layers, and the moisture content was determined separately in the upper 10 cm layer and in the lower 10 cm layer. This helped in determining whether the organic layer in the upper 10 cm had a greater moisture holding capacity than the sand in the lower 10 cm. The moisture levels were determined by drying the samples overnight in a 60° C oven and subtracting the dry weight of the samples from their initial weight.

LIGHT REGIME

Because Austrian pine trees have fuller, denser profiles than jack pines of similar stature, it was believed that Austrian pines would reduce light levels in wetpannes more than jack pines. Low light levels may negatively affect herbaceous vegetation in wetlands. Therefore, the light regime of the wetpannes was documented and comparisons were made between wetpannes with Austrian pine and wetpannes with jack pine. Tree density effects on light level were also evaluated.

Fish-eye photography was used to estimate percent open sky in the canopy above each wetpanne and percent transmission of global photosynthetically active radiation (PAR) through the canopy. A camera with a fish-eye lens was set horizontally on a tripod at one meter above ground level in the middle of each wetpanne. Since the fish-eye lens photographs everything within a 180° angle, corrections did not need to be made for large wetpannes. The canopy of each wetpanne was photographed on a single day in July of 1998. The photographs were taken early in the morning when the sun was low in the sky so that sun bursts on the exposure could be avoided. The photographs were then scanned into a computer and digitized using image analysis software. A threshold gray level was determined for each photograph and used to distinguish pixels containing foliage from pixels containing sky. The latitude of the study site, the length of the growing season at the study site, and the percent open sky visible in each photograph was used by the software to calculate a gap light index (GLI). The GLI represents the amount of light that can penetrate the canopy gap over the course of the growing season as a percentage of the total amount of light that reaches the top of the tree canopy during the same period (Canham et al., 1990). The GLI can be used to calculate the direct beam radiation, diffuse radiation, or global radiation (which is a combination of both direct and diffuse light) (Canham et al., 1990)). Global radiation is expressed as the percent transmission of photosynthetically active radiation through the canopy gap over the course of a growing season (Canham et al., 1990).

A direct measurement of light intensity in the Austrian pine and jack pine wetpannes was taken with a light meter. Measurements were taken once in spring, summer, and fall to examine potential seasonal differences between the two wetpanne types. These days occurred one month before summer solstice (May), one month after summer solstice (July), and on the fall equinox (September). Light intensities were measured every 2 meters along line transects that bisected the wetpannes into eastern and western and northern and southern halves. Each transect extended 6 meters into the surrounding tree canopy beyond the edge of the wetpanne. All measurements were taken on bright, cloudless days between 9:30am and 2pm daylight savings time. To serve as a control, measurements of the light intensity were taken in a nearby open area after each wetpanne was surveyed.

HISTORICAL CHANGES IN WETPANNE HYDROLOGY

A chronosequence of aerial photographs was analyzed using geographic information systems (GIS) to look for interannual variation in the aboveground water levels in wetpannes in the Saugatuck area. These patterns were then compared to historical records of precipitation, temperature, or level of Lake Michigan to determine which best predicts water levels in wetpannes. Aerial photographs (scale = 1:24,000) of the study site taken between the months of June and September were available for the years 1938, 1950, 1955, 1960, 1967, 1974, 1978, 1980, 1988, and 1992. Four treeless wetpannes (1D, 2D, 3D, and 4D) were analyzed. Only one of the studied jack pine wetpannes (JpB) was visible in the photos, but two additional jack pine wetpannes (JpH, JpI) on private property were visible. Of the Austrian pine sites, the complex was the only wetpanne visible at this scale (Fig. 3-3). The photographs taken before 1967 show the area before Austrian pines were planted around some of the wetpannes.

The aerial photographs were scanned into a computer at 600 dots per inch (dpi) and saved as uncompressed TIF files. A global positioning system (GPS) was used to determine the coordinates of ten reference points (i.e., buildings, road intersections) that were visible in all photographs in all years. Differential corrections of the coordinates were made against readings from a GPS unit at a base station of known location at Kellogg Biological Station, Hickory Corners, MI. The photographs were then registered to the reference points and rectified by entering the coordinates into Arc/INFO (Environmental Systems Research Institute, Inc., Redlands, CA). The coordinate system used was the World Geodetic System 1984, and the projection used was World Geographic.

The rectified photographs were then opened in ArcView (Environmental Systems Research Institute, Inc., Redlands, CA) for the analysis of the wetpannes. The individual wetpannes were digitized directly on the computer screen in ArcView. The perimeters of the wetpannes were traced for each year by outlining the area where the emergent vegetation of the wetpanne was bounded by the relatively unvegetated sand dunes. The total area occupied by each wetpanne was calculated in ArcView. An area:perimeter ratio was calculated for each wetpanne by dividing the area of each wetpanne by its perimeter. This gives a measure of how much "edge" a wetpanne has relative to its total area. A lower area:perimeter ratio indicates a wetpanne that has greater edge length relative to its total area. Wetpannes with a greater amount of edge would have more habitat for emergent vegetation. The perimeters of all pools of open surface water were traced to distinguish these areas from the parts of wetpannes that contained emergent vegetation. A pool was defined as an area covered by water, but devoid of emergent vegetation. The boundaries between the pools and the emergent vegetation were readily visible on the aerial photographs. The area occupied by a pool of open water was divided by the total wetpanne area in order to calculate a "percent open water" value. This value is considered a proxy for changes in water depth. When the water levels in a wetpanne arehigher, its percent open water value is usually larger.

The parameters that were calculated in ArcView were compared to historical lake level measurements of Lake Michigan (U.S. Army Corps of Engineers, 2/3/2000) to explore correlations between lake level and wetpanne water levels. The lake level data were also compared to the hydrological data from this study. Historical precipitation and temperature records were also examined. The sum of the precipitation data from three months prior to the date each photograph was taken was used to take into account the lag period between when the precipitation event occurred and when the water levels in the wetpannes responded to the increase in the water table. Precipitation and temperature data were obtained from the nearest weather station in South Haven, Michigan (NOAA, 1971; NOAA, 1996).

RESULTS

Throughout the Results section, unless otherwise stated, all means are reported with a 95% confidence interval (which is equivalent to two standard errors of the mean).

Biotic Characteristics

DISTRIBUTION PATTERN OF PLANT SPECIES

The individual species' distributions peaked at various points along the water depth gradient, and their distributions were often limited to particular ranges of water depth as predicted. The distributions of many individual species overlapped; however, distinct zones of plant species were not apparent along the water depth gradient. The order that each species occurred along the water depth gradient stayed relatively consistent from one wetpanne type to another.

The importance values of 52 of the most dominant herbaceous species in the wetpannes were calculated for each water depth class in each wetpanne type. These importance values were arranged in tabular form in the order in which they appeared along the water depth gradient from dry to wet (Tables 3-3; 3-4; 3-5). Based on comparisons of importance values within each water depth class, different species were dominant at different places along the water depth gradient. The particular species that had the highest importance values for each class varied among the three different wetpanne types. In the open wetpannes, *Ammophila breviligulata* had the highest importance value in classes 0 and 1 (Table 3-3). It was replaced by *Panicum implicatum* as the dominant species in class 2. *Cladium mariscoides* replaced *Panicum implicatum* as the dominant species in class 4 and remained dominant until it was replaced by *Utricularia* in class 12. In the jack pine wetpannes, *Juncus balticus* was dominant in classes 0 through 2, *Scirpus cyperinus* was dominant in classes 3 through 6, and *Cladium mariscoides* had the highest importance value in classes 7 through 9 (Table 3-4). In the Austrian pine wetpannes, *Juncus balticus* had the highest importance value in all of the water depth classes (Table 3-5).

Some species occupied narrow ranges along the water depth gradient, occurring in only four or five consecutive water depth classes. For example, in the jack pine wetpannes, *Hieracium* was found in water depth classes 0 through 4, *Carex aurea* was found in classes 2 through 6, *Hypericum majus* was in classes 4 through 7, and *Lycopus uniflorus* was in classes 5 through 8 (Table 3-4). The same pattern was observed in the Austrian pine wetpannes. In the open wetpannes, certain species were limited to pools of standing water and were only found in water depth classes 9 through 13 (Table 3-3). Among these were *Utricularia minor*, *Scirpus validus*, *Scirpus americanus*, and *Potamogeton oakesianus.* The open wetpannes were the only wetpannes that could support these species because only they had standing water during the 1998 growing season. Other species occupied wider ranges along the water depth gradient, such as *Panicum implicatum,* which was found in classes 0 through 8 in the jack pine wetpanne type. *Eleocharis elliptica*, *Juncus balticus*, *Panicum virgatum*, *Solidago canadensis*, and *Fragaria virginiana* all occurred in classes 0 through 7 in the jack pine wetpannes (Table 2-4).

Table 3-3. Distribution of herbs in open wetpannes. Species' importance values are given for each water depth class. An '*' marks the species whose importance values were calculated with frequency and cover only.

Species Abbrev.	Wetland Coeffic-ient	Water Depth Class (Mean Weighted Average Ordination Scores)													
		0	1	2	3	4	5	6	7	8	9	10	11	12	13
		(4.27)	(2.40)	(1.73)	(1.16)	(0.35)	(-2.35)	(-2.38)	(-2.50)	(-2.22)	(-3.96)	(-4.59)	(-4.96)	(-5.00)	(-5.00)
Arc uva	5														
Amm bre	5	1.260	0.731	0.380	0.081	0.140		0.021							
Mon pun	5	0.181	0.204	0.272	0.017	0.024	0.022	0.018							
Cal lon	5	0.452	0.120	0.065	0.192	0.141	0.091	0.088	0.041	0.011					
Mai can	0														
Rum ace	0	0.026	0.053	0.104	0.015										
Smi ste	1														
Lichens*	5	0.053			0.023			0.033							
Hie spp	5						0.018								
Pol art	5	0.190		0.023	0.023	0.061	0.028	0.020	0.013						
Equ hye	-2	0.032	0.061			0.016		0.014							
Poa com*	2		0.147			0.006									
Fra vir	1	0.029	0.105	0.026		0.069	0.064	0.068	0.074	0.036	0.016				
Sol can	3		0.107	0.168	0.030	0.063	0.052	0.095	0.048	0.019					
Gna obt	5	0.026				0.021		0.031		0.020		0.018			
Moss*	1		0.082	0.162	0.060	0.085	0.022	0.040	0.032	0.048					
Jun dud	0			0.172	0.205	0.067	0.032	0.014	0.013	0.064					
Cen ery	-4				0.015										
Ast pil	2	0.026				0.040	0.020	0.034	0.038	0.007					
Pan vir	-1			0.211	0.168	0.130	0.143	0.252	0.143	0.095	0.034				
Sol gra	-2		0.053		0.015	0.074	0.042	0.010	0.023	0.020					
Aga pur	-3				0.183	0.097		0.020	0.011	0.037					
Car aur	-4														
Agr hye*	1		0.082	0.036	0.149	0.079	0.028	0.059	0.044	0.084	0.038				
Car vir	-5		0.189	0.129	0.262	0.079		0.188	0.125	0.122	0.017				
Vio lan	-5														

Table 3-3. (continued)

Species Abbrev.	Wetland Coefficient	Water Depth Class (Mean Weighted Average Ordination Scores)													
		0	1	2	3	4	5	6	7	8	9	10	11	12	13
		(4.27)	(2.40)	(1.73)	(1.16)	(0.35)	(-2.35)	(-2.38)	(-2.50)	(-2.22)	(-3.96)	(-4.59)	(-4.96)	(-5.00)	(-5.00)
Jun acu	-5			0.023	0.050	0.038	0.038	0.030	0.030	0.008					
Jun bal	-5	0.041			0.023	0.009	0.128	0.057	0.175	0.053	0.059	0.011			
Ele ell*	-3	0.019	0.046	0.055	0.178	0.125	0.095	0.082	0.111	0.078	0.019	0.018			
Ast lat	1														
Hyp maj	-3			0.201	0.181	0.164	0.066	0.159	0.082	0.238	0.152	0.053			
Lob kal	-5				0.030	0.009		0.036		0.021					
Eup per	-4			0.049	0.032	0.016		0.010		0.006					
Spi cer	-2														
Dry the	-4							0.130	0.063						
Jun bre	-5	0.058	0.143		0.147	0.132	0.073	0.197	0.259	0.273	0.077	0.022			
Pan imp	0	0.245	0.650	0.544	0.625	0.373	0.181	0.377	0.396	0.373	0.123	0.068	0.028		
And sco*	3	0.019	0.173	0.126	0.202	0.377	0.346	0.093	0.332	0.306	0.242	0.037	0.014		
Lin str	-2	0.045	0.053	0.023	0.025			0.032	0.088	0.055	0.022	0.035	0.020		
Car lan*	-5						0.096	0.058	0.010						
Sci cyp	-5														
Cal can*	-5					0.020		0.270	0.271	0.024			0.022		
Lyc uni	-5									0.007		0.010			
Pol pun	-5									0.087					
Car aqu	-5									0.020	0.086	0.025			
Car lac	-5														
Cla mar	-5	0.150		0.049		0.512	1.333	0.372	0.534	0.775	1.718	1.507	1.493	0.850	0.813
Sci acu	-5										0.052	0.068	0.093	0.181	0.091
Sci ame	-5										0.108	0.468	0.481	0.451	0.387
Pot oak*	-5								0.028	0.096	0.093	0.158	0.144	0.405	0.343
Alg spp*	-5										0.142	0.413	0.454	0.199	0.232
Utr spp*	-5											0.088	0.251	0.914	1.134

Table 3-4. Distribution of herbs in jack pine wetpannes. Species' importance values are given for each water depth class. An '*' marks the species whose importance values were calculated with frequency and cover only.

Species Abbrev.	Wetland Coefficient	Water Depth Class (Mean Weighted Average Ordination Scores)													
		0	1	2	3	4	5	6	7	8	9	10	11	12	13
		(2.24)	(1.24)	(0.88)	(-1.70)	(-2.57)	(-2.75)	(-3.74)	(-4.25)	(-4.92)	(-5.00)	--	--	--	--
Arc uva	5	0.129	0.060	0.005	0.011										
Amm bre	5	0.081				0.009									
Mon pun	5	0.022													
Cal lon	5	0.329	0.142	0.070	0.014										
Mai can	0	0.119	0.129		0.031	0.015		0.027							
Rum ace	0	0.029	0.044	0.092	0.005										
Smi ste	1	0.054	0.098	0.068	0.033	0.050	0.050	0.012							
Lichens*	5	0.327	0.302	0.368	0.172	0.107	0.064	0.027							
Hie spp	5	0.074	0.080	0.108	0.128	0.011									
Pol art	5														
Equ hye	-2	0.007	0.090	0.055	0.024	0.008	0.012								
Poa com*	2	0.123	0.124	0.066	0.045	0.047	0.050	0.021							
Fra vir	1	0.144	0.078	0.043	0.011	0.126	0.055	0.091	0.050						
Sol can	3	0.296	0.278	0.252	0.308	0.322	0.192	0.087	0.013						
Gna obt	5														
Moss*	1	0.226	0.071	0.062	0.012	0.045	0.118	0.133	0.041						
Jun dud	0														
Cen ery	-4		0.012	0.028	0.021	0.012									
Ast pil	2	0.007	0.024	0.015	0.007	0.037	0.019								
Pan vir	-1	0.066	0.187	0.026	0.057	0.037	0.026		0.056						
Sol gra	-2	0.022		0.037	0.026	0.010	0.019		0.017						
Aga pur	-3														
Car aur	-4			0.049	0.020	0.010	0.062	0.022							
Agr hye*	1		0.040	0.125	0.067	0.060	0.094	0.064	0.049	0.029					
Car vir	-5	0.015		0.017	0.037	0.033	0.057								
Vio lan	-5			0.026	0.345	0.077									

Table 3-4. (continued)

Species Abbrev.	Wetland Coefficient	Water Depth Class (Mean Weighted Average Ordination Scores)													
		0	1	2	3	4	5	6	7	8	9	10	11	12	13
		(2.24)	(1.24)	(0.88)	(-1.70)	(-2.57)	(-2.75)	(-3.74)	(-4.25)	(-4.92)	(-5.00)	--	--	--	--
Jun acu	-5			0.012	0.022	0.010	0.043	0.026							
Jun bal	-5	0.485	0.712	0.726	0.157	0.099	0.092	0.090	0.051						
Ele ell*	-3	0.081	0.081	0.110	0.082	0.201	0.196	0.250	0.028						
Ast lat	1					0.042	0.124								
Hyp maj	-3					0.006		0.024	0.013						
Lob kal	-5				0.005	0.004	0.024	0.024	0.039	0.030					
Eup per	-4								0.033						
Spi cer	-2					0.011	0.029								
Dry the	-4	0.013						0.019	0.020	0.041					
Jun bre	-5							0.041	0.063	0.039					
Pan imp	0	0.018	0.066	0.195	0.126	0.032	0.053	0.077	0.052	0.063					
And sco*	3	0.129	0.182	0.104	0.141	0.070	0.035	0.037							
Lin str	-2	0.031		0.026	0.016	0.012	0.050	0.048	0.340	0.088					
Car lan*	-5														
Sci cyp	-5	0.016	0.022	0.055	0.514	0.758	0.739	1.184							
Cal can*	-5	0.024	0.073	0.057	0.310	0.435	0.282	0.043	0.118	0.036					
Lyc uni	-5						0.034	0.044	0.207	0.157					
Pol pun	-5														
Car aqu	-5														
Car lac	-5														
Cla mar	-5			0.100	0.193	0.200	0.386	0.475	1.705	2.487	3.000				
Sci acu	-5														
Sci ame	-5														
Pot oak*	-5														
Alg spp*	-5														
Utr spp*	-5														

Table 3-5. Distribution of herbs in Austrian pine wetpannes. Species' importance values are given for each water depth class. An '*' marks the species whose importance values were calculated with frequency and cover only.

Species Abbrev.	Wetland Coeffic-ient	Water Depth Class (Mean Weighted Average Ordination Scores)													
		0	1	2	3	4	5	6	7	8	9	10	11	12	13
		(1.75)	(1.78)	(1.31)	(0.46)	(-0.41)	(-1.56)	(-2.30)	(-3.54)	(-3.45)	(-4.44)	--	--	--	--
Arc uva	5			0.008											
Amm bre	5	0.395	0.227	0.106	0.097	0.036	0.040								
Mon pun	5					0.001									
Cal lon	5	0.365	0.095	0.195	0.040	0.025	0.031	0.002							
Mai can	0														
Rum ace	0			0.010	0.014	0.009	0.003	0.003							
Smi ste	1	0.022				0.008	0.002								
Lichens*	5	0.152	0.221	0.204	0.120	0.039	0.011								
Hie spp	5	0.065	0.188	0.113	0.096	0.060	0.024	0.010	0.011						
Pol art	5														
Equ hye	-2	0.202	0.096	0.116	0.083	0.065	0.078	0.104	0.117						
Poa com*	2	0.038	0.041	0.034	0.066	0.093	0.055	0.009	0.005						
Fra vir	1	0.095	0.272	0.169	0.185	0.301	0.266	0.164	0.147	0.146					
Sol can	3	0.187	0.069	0.162	0.233	0.254	0.189	0.224	0.205	0.359					
Gna obt	5			0.006	0.012	0.000	0.001								
Moss*	1	0.115	0.164	0.100	0.062	0.024	0.036	0.067	0.069						
Jun dud	0														
Cen ery	-4	0.023	0.217	0.091	0.109	0.190	0.150	0.063	0.007						
Ast pil	2	0.010	0.097	0.052	0.091	0.090	0.086	0.069	0.004	0.050					
Pan vir	-1	0.026	0.243	0.096	0.094	0.052	0.047	0.021	0.025						
Sol gra	-2	0.020	0.031	0.022	0.052	0.083	0.108	0.070	0.017	0.073					
Aga pur	-3					0.003	0.006	0.005							
Car aur	-4	0.014			0.017	0.054	0.136	0.126	0.068						
Agr hye*	1	0.031	0.018	0.024	0.054	0.037	0.041	0.074	0.046						
Car vir	-5	0.004		0.019	0.006	0.027	0.082	0.097	0.003		0.108				
Vio lan	-5														

Table 3-5. (continued)

Species Abbrev.	Wetland Coeffic-ient	Water Depth Class (Mean Weighted Average Ordination Scores)													
		0	1	2	3	4	5	6	7	8	9	10	11	12	13
		(1.75)	(1.78)	(1.31)	(0.46)	(-0.41)	(-1.56)	(-2.30)	(-3.54)	(-3.45)	(-4.44)	--	--	--	--
Jun acu	-5			0.068	0.027	0.046	0.031	0.006	0.007		0.033				
Jun bal	-5	0.903	0.675	0.858	0.732	0.706	0.411	0.447	0.592	1.351	1.227				
Ele ell*	-3	0.029	0.089	0.008	0.023	0.032	0.058	0.091	0.079		0.185				
Ast lat	1														
Hyp maj	-3		0.012	0.045	0.036	0.044	0.024	0.002							
Lob kal	-5				0.017	0.013	0.025	0.012	0.004						
Eup per	-4			0.006	0.026	0.094	0.137	0.098	0.093		0.067				
Spi cer	-2	0.021		0.003	0.002	0.011	0.015	0.025	0.069						
Dry the	-4						0.012	0.040							
Jun bre	-5	0.014		0.006	0.016	0.032	0.033	0.119	0.117		0.443				
Pan imp	0	0.032	0.029	0.249	0.343	0.150	0.208	0.119	0.033	0.187	0.256				
And sco*	3	0.048	0.153	0.116	0.175	0.166	0.124	0.156	0.062						
Lin str	-2	0.048		0.006	0.010	0.054	0.056	0.075	0.016						
Car lan*	-5		0.009	0.018	0.052	0.046	0.187	0.175	0.211	0.391	0.111				
Sci cyp	-5			0.007	0.005	0.055	0.083	0.079	0.104						
Cal can*	-5							0.036	0.175	0.229					
Lyc uni	-5				0.008	0.013	0.041	0.074	0.254		0.284				
Pol pun	-5														
Car aqu	-5							0.022	0.054	0.111					
Car lac	-5						0.010	0.039	0.316	0.102					
Cla mar	-5					0.010	0.073	0.209	0.031						
Sci acu	-5														
Sci ame	-5														
Pot oak*	-5														
Alg spp*	-5														
Utr spp*	-5														

The importance values of the woody species in the wetpannes were also listed in tabular form as done for the herbaceous species (Tables 3-6; 3-7; 3-8). Again, individual species often were restricted to certain ranges along the water depth gradient, and some of the ranges overlapped. The upland tree species such as *Pinus strobus, Fagus grandifolia,* and *Prunus serotina* were restricted to the drier plots closer to the edges of the wetpannes (classes 0 through 4) (Tables 3-7; 3-8). *Fraxinus americana*'s range extended into slightly wetter areas (classes 0 through 5) (Table 3-7). The other species occupied wide ranges along the water depth gradient. Surprisingly, juvenile (DBH < 2.5 cm) *Pinus banksiana* and *Pinus nigra* trees were able to grow in very wet conditions as well as in upland conditions—Pinus banksiana occurred in classes 0 through 8, and Pinus nigra occurred in classes 0 through 7 (Table 3-8). Even adult trees of these two species were occasionally found within the wetpanne interiors. *Rubus* was found over a range of 0 to 8 (Table 3-8). *Spiraea tomentosa* and *Hypericum kalmianum* were found in classes 0 through 10 (Table 3-6). *Salix* spp. was found in classes 0 through 9, and was once found in class 11 (Table 3-6). No woody species could tolerate the standing water levels of classes 12 or 13, which had at least 30 or 40 cm of standing water as of 1 June 98. The weighted average ordination scores were negatively correlated with both water table depth and basin depth in all three wetpanne types. As the water table became shallower (and the wetpanne basin became deeper), the ordination scores became more negative (Figs. 3-4; 3-5; 3-6; 3-7; 3-8; 3-9). Negative ordination scores close to –5 represented plots that are dominated by obligate wetland plant species, and positive ordination scores near +5 represented plots dominated by upland plant species. The change from upland plants to wetland plants occurred gradually over the water depth gradient. The switch from dominance by upland plant species to dominance by wetland plant species occurred when the water table was between 30 to 50 cm below ground level (Figs. 3-4; 3-6; 3-8).

The weighted average ordination scores were better correlated with water table depth than with basin depth for the jack pine wetpannes and the Austrian pine wetpannes. The correlations between water table depth and the ordination scores were $r = -0.671$ ($p < 0.001$) (Fig. 3-4) for jack pine wetpannes and $r = -0.675$ ($p < 0.001$) (Fig. 3-6) for Austrian pine wetpannes. The correlations between basin depth and the ordination scores were $r = -0.626$ ($p < 0.001$) (Fig. 3-5) for jack pine wetpannes and $r = -0.629$ ($p < 0.001$) (Fig. 3-7) for Austrian pine wetpannes. In open wetpannes, the correlation between the ordination scores and water table depth was slightly weaker than that for basin depth—$r = -0.700$ ($p < 0.001$) (Fig. 3-8) compared to $r = -0.803$ ($p < 0.001$) (Fig. 3-9). Since vegetation composition in two of the three wetpanne types was better explained by water table depth than by basin depth, water table depth was used to describe the distribution pattern of the vegetation.

The mean weighted average ordination score per class was calculated for each of the three wetpanne types. The mean ordination scores are listed below each water depth class in the tables of importance values (Tables 3-3; 3-4; 3-5) so that the plant assemblages within each water depth class could be compared to the weighted average ordination scores. In the open wetpanne type, the mean ordination score for water depth class 0 was 4.27, which means this class was dominated by upland plant species. The switch from dominance by upland species to a dominance by wetland species, which is signified by a change from a positive to a negative mean ordination score, occurred in class 5 (Table 3-3). The mean ordination score decreased steadily until it became 5.00 in class 12, where the plots were dominated by obligate wetland plant species. In the jack pine wetpanne type, the mean ordination score for class 0 was 2.24, first became negative in class 3, and reached –5.00 in class 9 (Table 3-4). In the Austrian pine wetpanne type, the mean ordination score for class 0 was 1.75, first became negative in class 4, and reached –4.44 in class 9 (Table 3-5). The variations in mean scores for each class among wetpanne types may be due to slight differences in species composition. The shade and the litter at the edges of the Austrian and jack pine wetpannes allow the soil to hold more moisture, which would allow more facultative plants to survive than in the dry, sandy edge plots of the open wetpanne types. The variations in mean ordination scores may also be related to how steep the water depth gradient is in each wetpanne type. The jack pine wetpannes have the steepest gradient because the mean ordination scores change more over fewer water depth classes.

The range that each species occupied along the water depth gradient is related to each species' tolerance to soil saturation and water depth. This range can be used to evaluate how well the wetland coefficients describe each plant species. The wetland coefficients are listed beside each species on each importance value table (Tables 3-3 through 3-8). The wetland coefficients tended to decrease going down the column of each table. The species that are found in the drier water depth classes have positive wetland coefficient values, and the species found in wetter classes have increasingly negative values. However, in a few cases, the wetland coefficient value does not match the range of classes a species occupies very well. For example, *Andropogon scoparius* is found in classes 0 through 11 in the open wetpanne types, which corresponds to the mean ordination scores of 4.27 to –4.96. In the jack pine wetpanne types, it was found in classes 0 through 6, which correspond to mean scores of 2.24 to –3.74. In the Austrian pine wetpanne types, it was found in classes 0 through 7, which correspond to mean scores of 1.75 to –3.54. However, *Andropogon scoparius* was assigned a wetland coefficient of +3 (Herman et al., 1996). The results of this study suggest that it should have a wetland coefficient of 0 to reflect the equal probability of finding it in upland and wetland conditions. Another example is *Juncus balticus*, which has a wetland coefficient of –5. It had high importance values in several of the upland water depth classes. It had the highest importance values in classes 1 and 2 of the jack pine wetpannes (Table 3-4). In the Austrian pine wetpannes (Table 3-5), it had high importance values in classes 0 through 2, and then again in classes 8 and 9. The evidence suggests that its wetland coefficient should be somewhat higher than it is.

Table 3-6. Distribution of woody plants in open wetpannes. Species' importance values are given for each water depth class.

Species Abbrev.	Wetland Coefficient	Water Depth Class													
		0	1	2	3	4	5	6	7	8	9	10	11	12	13
Pte tri	2														
Fag gra	3														
Jun com	3	0.079													
Pru ser	3														
Pru vir	1														
Sas alb	3														
Pin str	3														
Tox rad	-1														
Vit rip	-2														
Hud tom	5	1.135			0.058	0.037	0.046								
Que spp	3 or 5														
Ame int	5														
Bet pap	2														
Cel orb	5														
Ile ver	-4														
Vib tri	-3														
Fra ame	3														
Pop del	-1		0.438				0.077								
Lon spp															
Pin nig	-5														
Pin ban	3														
Pru pum	5	0.386		0.987	0.670				0.040			0.150			
Cor amo	-4									0.041					
Cep occ	-5									0.041					
Cor sto	-3														
Ros spp					0.076	0.191	0.650	0.205	0.235	0.031	0.445				
Rub spp							0.472	0.141	0.047	0.376	0.193				
Sal spp		0.139			0.619	0.482	0.338	0.407	0.682	0.189	0.286		3.000		
Hyp kal	-2	1.116	2.562	1.748	1.528	1.575	0.430	1.246	0.620	0.953	1.700	1.827			
Spi tom	-3	0.145		0.265	0.048	0.715	0.987	1.000	1.376	1.369	0.376	1.023			

Table 3-7. Distribution of woody plants in jack pine wetpannes. Species' importance values are given for each water depth class.

Species Abbrev.	Wetland Coefficient	Water Depth Class													
		0	1	2	3	4	5	6	7	8	9	10	11	12	13
Pte tri	2														
Fag gra	3	0.020			0.018										
Jun com	3	0.016		0.028	0.018										
Pru ser	3	0.016	0.107	0.020											
Pru vir	1	0.046	0.172	0.035											
Sas alb	3	0.204	0.117	0.221	0.036										
Pin str	3	0.010	0.027	0.063		0.012									
Tox rad	-1	0.156	0.146	0.047	0.022	0.024									
Vit rip	-2	0.121	0.152	0.047	0.018	0.024									
Hud tom	5														
Que spp	3 or 5	0.366	0.236	0.297	0.111	0.055		0.155							
Ame int	5	0.089	0.049	0.139	0.054	0.035									
Bet pap	2	0.036		0.161	0.100	0.111									
Cel orb	5		0.056			0.017									
Ile ver	-4				0.018	0.014									
Vib tri	-3														
Fra ame	3	0.152	0.153	0.040	0.057	0.047	0.040								
Pop del	-1														
Lon spp		0.143						0.370	0.070						
Pin nig	-5														
Pin ban	3	0.668	0.582	1.026	0.817	0.601	0.453	0.353	0.153						
Pru pum	5														
Cor amo	-4														
Cep occ	-5														
Cor sto	-3	0.148	0.187		0.186	0.288	0.366	0.411	0.427						
Ros spp					0.026				0.139						
Rub spp		0.483	0.741	0.327	0.675	0.684	0.274	0.555	0.627						
Sal spp		0.208	0.153	0.202	0.308	0.258	0.903	1.000	0.542						
Hyp kal	-2	0.020	0.122	0.273	0.346	0.173	0.382	0.068	1.042	3.000					
Spi tom	-3			0.027	0.145	0.647	0.582	0.087							

Table 3-8. Distribution of woody plants in Austrian pine wetpannes. Species' importance values are given for each water depth class.

Species Abbrev.	Wetland Coefficient	Water Depth Class													
		0	1	2	3	4	5	6	7	8	9	10	11	12	13
Pte tri	2	0.014													
Fag gra	3														
Jun com	3				0.019										
Pru ser	3	0.036													
Pru vir	1	0.014		0.028	0.015	0.024									
Sas alb	3	0.032			0.050	0.018	0.007	0.012							
Pin str	3														
Tox rad	-1	0.054				0.009									
Vit rip	-2	0.202	0.103	0.093	0.217	0.043		0.034							
Hud tom	5														
Que spp	3 or 5	0.061	0.240		0.032	0.052	0.009	0.009	0.012						
Ame int	5	0.027				0.017									
Bet pap	2						0.009								
Cel orb	5														
Ile ver	-4														
Vib tri	-3				0.023		0.012								
Fra ame	3			0.034											
Pop del	-1								0.051						
Lon spp			0.075												
Pin nig	-5	0.220	0.427	0.681	0.194	0.079	0.101	0.185	0.168						
Pin ban	3	0.933	0.351	0.637	0.710	0.331	0.355	0.194	0.089	0.224					
Pru pum	5														
Cor amo	-4														
Cep occ	-5														
Cor sto	-3	0.507	0.615	0.303	0.213	0.370	0.285	0.110	0.127						
Ros spp									0.022						
Rub spp		0.267		0.149	0.407	0.712	0.593	0.582	0.181	0.449					
Sal spp		0.470	1.062	0.738	0.560	0.739	0.462	0.372	0.445						
Hyp kal	-2	0.085	0.129	0.272	0.200	0.305	0.293	0.262	0.305	0.130					
Spi tom	-3	0.047		0.042	0.360	0.292	0.874	1.240	1.599	2.196	3.000				

PLANT COMMUNITY DIFFERENCES AMONG WETPANNE TYPES

Of the 55 relationships among plant community attributes tested, 28 were significant at the 5% level before correcting for experiment level error (Table 3-9). After the sequential Bonferroni corrections were applied, two correlations remained significant at the 5% level (Table 2-9). The individual, uncorrected p-values are listed in the figures and the text. The correlations were used to help explain the differences in the plant community attributes of the three wetpanne types. The relationships between the plant community attributes and the density of trees surrounding each wetpanne type was of particular interest, since the focus of this study is on the effects of an artificially planted tree species on the wetpanne plant community.

The density of trees surrounding each wetpanne was positively correlated with the density of trees within the wetpanne interiors ($r = 0.629$; $p = 0.012$). The density of trees surrounding the wetpannes was negatively correlated with the elevation of the wetpanne basin above the water table ($r = -0.683$; $p = 0.005$) (Fig. 3-10), which means there were more trees around wetpannes that were drier.

There was no significant difference between total shrub cover within Austrian pine or jack pine wetpannes (Table 3-10). The particular species of the tree surrounding each wetpanne seemed to be unimportant. The total cover by woody plants was significantly lower within the interiors of the open wetpannes. Total shrub density (# stems/m^2) was not analyzed because shrub cover was a more accurate measure of the woody plants in wetpannes. This was because some species had many stems that covered only a small area, whereas other species had few stems that covered a large area.

Herbivory on the woody species exacerbated this problem by reducing shrub cover and increasing the number of stems per plant.

Shrub cover was positively correlated with the density of trees surrounding each wetpanne ($r = 0.396$; $p = 0.143$) (Fig. 3-11) although not significantly so at the experiment level (Table 3-9). Shrub cover was also positively correlated with the diversity of woody species within the wetpannes ($r = 0.617$; $p = 0.014$) (Fig. 3-12). Shrub cover was negatively correlated with the elevation of the wetpanne basin above the water table, meaning there was greater shrub cover when the wetpanne basin was higher above the water table ($r = -0.545$; $p = 0.036$) (Fig. 3-13). Shrub cover was also negatively correlated with the percentage of wetland indicator species within the wetpannes ($r = -0.510$; $p = 0.052$).

The herbaceous species diversity was negatively related to the density of adult trees surrounding the wetpannes ($r = -0.660$; $p = 0.007$) (Fig. 3-14); however, tree species was important in this case. The species diversity of herbaceous vegetation was significantly lower in the jack pine wetpannes than in the Austrian pine wetpannes (Table 3-10). Herbaceous species diversity was highest in the open wetpannes, however (Table 3-10). The herbaceous species diversity decreased with increasing interior tree density ($r = -0.654$; $p = 0.009$), and with increasing elevation of the basin above the water table ($r = 0.680$; $p = 0.005$) (Fig. 3-15) (i.e., the herbaceous species diversity was highest when the water table was aboveground). The woody species diversity, on the other hand, was significantly higher in jack pine wetpannes than in open wetpannes (Table 3-10). The woody species diversity in the Austrian pine

Table 3-9. Correlations between plant community characteristics of wetpannes. The shaded cells represent correlations with uncorrected p-values of less than 0.05.

	Distance from lake	Wetpanne area	Exterior tree density	Shrub cover	Interior tree density	Shannon diversity of herbaceous species	Total species number	%Wetland Species	Shannon diversity of woody species	Herbivory Index (0 to 3)	Elevation above water table
Distance from lake	1.000 --										
Wetpanne area	-0.207 0.459	1.000 --									
Exterior tree density	0.583 0.022	-0.549 0.034	1.000 --								
Shrub cover	0.357 0.192	-0.536 0.039	0.396 0.143	1.000 --							
Interior tree density	0.331 0.228	-0.200 0.474	0.629 0.012	0.312 0.257	1.000 --						
Shannon diversity of herbaceous species	-0.552 0.033	0.529 0.043	-0.660 0.007	-0.366 0.180	-0.648 0.009	1.000 --					
Total species number	0.024 0.932	0.706 0.003**	-0.318 0.248	0.014 0.960	-0.103 0.716	0.573 0.026	1.000 --				
%Wetland Species	-0.375 0.169	0.518 [illegible]	-0.630 0.012	-0.510 0.052	[illegible] 0.001**	0.753 0.001**	0.397 0.142	1.000 --			
Shannon diversity of woody species	0.441 0.100	-0.151 0.592	0.229 0.411	0.617 0.014	0.456 0.088	-0.214 0.444	0.344 0.209	-0.319 0.247	1.000 --		
Herbivory Index (0 to 3)	[illegible] [illegible]	-0.456 0.087	-0.564 0.029	0.649 0.009	0.474 0.075	[illegible] 0.028	-0.038 0.894	-0.627 0.012	[illegible] [illegible]	1.000 --	
Elevation above water table	-0.232 0.405	0.793 0.000***	-0.683 0.005*	-0.545 0.036	[illegible] 0.008	0.680 0.005*	0.596 0.019	0.651 0.009	-0.262 0.345	-0.500 0.058	1.000 --

*** indicates an experimentwise p-value of < 0.05; ** indicates an experimentwise p-value of < 0.10; * indicates an experimentwise p-value of < 0.25. Experimentwise p-values were calculated using sequential Bonferroni corrections.

wetpannes was not significantly different from woody species diversity in the open wetpannes or the jack pine wetpannes.

The average number of woody species in the jack pine wetpannes, 16, was significantly higher than either the average number of woody species in the Austrian pine wetpannes, 12, or the average number of woody species in the open wetpannes, 9 (Table 3-10). There was an average of 43 herb species in the open wetpannes, 36 in the Austrian pine wetpannes, and 33 in the jack pine wetpannes, but the differences among wetpanne types were not significant (Table 3-10). The total number of species was not statistically different in the three wetpanne types (Table 3-10). The total number of species per wetpanne was correlated with the natural logarithm of total wetpanne area ($r = 0.706$; $p = 0.003$) (Fig. 3-16).

The average herbivory index values and the total shrub cover values were correlated ($r = 0.649$; $p = 0.009$) (Fig. 3-17). The estimated amount of damage by herbivory was positively correlated with distance from Lake Michigan ($r = 0.809$; $p < 0.001$) (Fig. 3-18). The estimated amount of herbivory was significantly less in the open wetpannes, but no differences between Austrian pine and jack pine wetpannes were detected (Table 3-10). This result is probably related to the fact that shrub cover was much lower in the open wetpannes.

Table 3-10. Kruskal-Wallis tests for differences in vegetation characteristics of the three wetpanne types. The means are given with 95% confidence intervals for each parameter. Different letters indicate significant differences between wetpanne types at the 15% level.

	Wetpanne Type:			Overall Significance
	Open n=3	Austrian pine n=9	Jack pine n=5	
Total Shrub Cover	0.071 ± 0.057^a	0.496 ± 0.122^b	0.529 ± 0.183^b	$p < 0.05$
Shannon Diversity of:				
Woody species	1.348 ± 0.204^a	1.515 ± 0.160^{ab}	1.807 ± 0.270^b	$p < 0.10$
Herbs	2.466 ± 0.212^a	2.060 ± 0.334^a	1.450 ± 0.328^b	$p < 0.05$
Species Richness:				
Woody	9.0 ± 2.0^a	12.0 ± 2.4^a	16.4 ± 3.2^b	$p < 0.05$
Herbaceous	43.0 ± 6.3	36.1 ± 5.8	33.2 ± 5.2	n.s.
Total	52.0 ± 8.2	48.1 ± 7.6	49.6 ± 3.3	n.s.
Herbivory Index (0 to 3)	0.102 ± 0.047^a	0.708 ± 0.217^b	1.467 ± 0.633^b	$p < 0.05$
% Wetland Indicators	$64.1 \pm 7.5\%^a$	$54.4 \pm 4.8\%^{ab}$	$49.5 \pm 5.8\%^b$	$p < 0.10$
Density of Juvenile Trees (# trees/m^2):				
Pinus nigra	0^a	0.082 ± 0.054^b	0^a	$p < 0.05$
Pinus banksiana	0^a	0.148 ± 0.093^b	0.253 ± 0.130^b	$p < 0.05$

There was a significantly higher percentage of wetland species in the open wetpannes than in the jack pine wetpannes. The percent wetland species was negatively correlated with the density of trees surrounding each wetpanne ($r = -0.630$; $p = 0.012$) (Fig. 3-19), and with the density of trees within the wetpannes ($r = -0.744$; $p < 0.001$). The percent wetland species is positively correlated with the elevation of the wetpanne basin above the water table ($r = 0.651$; $p=0.009$) (Fig.3-20). The higher the wetpanne basin was above the water table, the fewer number of wetland species were found in a particular wetpanne. Wetpanne area was also correlated with the elevation of the wetpanne basin above the water table ($r = 0.793$; $p < 0.001$). Wetpannes of larger area tended to have deeper basins, and thus, a greater proportion of wetland species.

There were zero juvenile pine trees in the open wetpannes (Table 3-10). There were no Austrian pine trees in the jack pine wetpannes. Within the Austrian pine wetpannes, the density of juvenile jack pine trees was not significantly different from the density of juvenile Austrian pine trees (0.148 trees/m^2 vs. 0.082 trees/m^2) ($p = 0.245$). The density of juvenile jack pine trees in the jack pine wetpannes was 0.253 trees/m^2, slightly higher than their density in the Austrian pine wetpannes (0.148 trees/m^2), but not significantly so (Table 3-10). When adult Austrian pines were present as a seed source, the juvenile Austrian pines seemed to be competing for space with the juvenile jack pines in the wetpannes.

Abiotic Characteristics

HYDROLOGY

The groundwater table dropped an average of 23 ± 3 cm over the 1998 growing season in the mid-wells of all wetpannes. The water table sloped towards Lake Michigan at an angle of 0.24 ° on 1 June 1998 and decreased to 0.22 ° by 6 September 1998. The overall slope was calculated on each date by dividing the elevation of the water table in the well that was furthest inland by its distance from Lake Michigan and then taking the inverse tangent of that number (Fig. 3-21). This method assumes that there are no perched basins.

$$\theta = \tan^{-1}\left(\frac{\text{elevation}}{\text{distance}}\right)$$

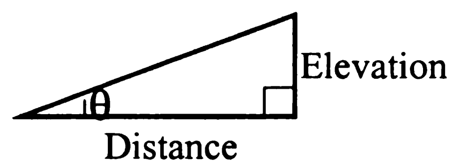


Figure 3-21. The slope of the water table was calculated by dividing the elevation of the water table by the well's distance from Lake Michigan and then taking the inverse tangent of that number.

The slope of the water table in each individual wetpanne was calculated the same way by subtracting the elevation of the water table in the down-gradient well from the elevation of the water table in the up-gradient well, and dividing by the distance between the two wells. The individual wetpanne slopes were found to vary from 0.84° to –0.01° (a negative slope indicates that the water table slopes away from the lake). These slopes tended to decrease slightly over the course of the season, although not significantly so (Table 3-11).

Table 3-11. The individual slope of the water table for each wetpanne in spring and late summer. (Jp= jack pine site, Op= open, treeless site, Ap= Austrian pine site).

Wetpanne ID	Water Table Slope 6/1/98	Water Table Slope 9/6/98
JpA	0.54°	0.41°
JpC	0.22°	0.19°
JpD	0.14°	0.11°
JpE	0.26°	0.25°
JpF	0.21°	0.19°
Op1	-0.01°	0.02°
Op2	-0.01°	0.02°
Ap3	0.45°	0.42°
Ap4	0.10°	0.09°
Ap5	0.27°	0.32°
Ap6	0.44°	0.44°
Ap12	0.84°	0.75°
Ap13	0.52°	0.46°

The water table dropped more under the wetpannes that were farther away from Lake Michigan (Fig. 3-22). There was a significant negative correlation between the change in the water table over the season (between 1 June 1998 and 6 September 1998) and the distance of the wetpanne from Lake Michigan ($r = -0.630$; $p=0.0029$) (Fig. 3-23). Elevation was negatively correlated with the total change in the water table over the season ($r= -0.660$; $p<0.0001$) (Fig. 3-24), which means that the higher elevation sites experienced a greater decline in water table levels. The further a wetpanne was from Lake Michigan, the higher its elevation was relative to the lake. Accordingly, distance and elevation were highly positively correlated with each other ($r=0.945$; $p<0.0001$) (Fig. 3-25).

The stand characteristics of the trees surrounding the Austrian pine and jack pine wetpanne types were compared because total water use by trees may be different in stands with varying tree sizes or densities. The average height of the tree canopy surrounding the Austrian pine wetpannes was 11.7 m, and the average diameter at breast height (DBH) of the trees was 12.9 cm. The average height of the tree canopy surrounding the jack pine wetpannes was 10.6 m, and the average DBH of the trees was 8.6 cm. Differences in tree densities between jack pine and Austrian pine wetpanne types were compared with a t-test (Table 3-12). The total tree density within the wetpanne interiors and surrounding the wetpannes was not significantly different in the Austrian pine and jack pine wetpannes. The total basal area of trees surrounding the wetpannes was also not significantly different between wetpanne types. The density and total basal area of jack pine trees were significantly higher in the jack pine wetpannes than in the Austrian pine wetpannes. The density and total basal area of Austrian pines in the jack pine wetpannes were zero. Total density and basal area in the Austrian pine and jack pine wetpannes were also not significantly different in the plots that were centered over the individual canopy wells.

The relationships between tree density or total basal area and water table depth were examined. The change in the water table was correlated with the tree density. The water levels in the canopy wells were significantly correlated ($r = -0.591$; $p = 0.0015$) with the total tree density surrounding each individual well (Fig. 3-26). The change in the water table level in the mid-wells was also significantly correlated ($r = -0.561$; $p = 0.0367$) with the total tree density surrounding each wetpanne (Fig. 3-27). In other words, the water levels in the mid-wells dropped more over the season in wetpannes that had a greater density of trees surrounding them. The relationships between the basal area of the trees and changes in water table were not significant.

Table 3-12. The total mean tree density and basal area/ total area values for each wetpanne type, and the mean tree density and basal area/ total area values by species in each wetpanne type.

Mean Density (trees/m^2) and Basal Area/ Total Area Values:	**Wetpanne Type**		**T-test**
	Austrian pine	**Jack pine**	**(p values)**
Total Interior Tree Density	0.032	0.085	0.072
Pinus nigra	0.011	0	0.231
Pinus banksiana	0.021	0.082	0.024
Total Exterior Tree Density	0.119	0.168	0.087
Pinus nigra	0.069	0	0.012
Pinus banksiana	0.042	0.129	0.003
Total Exterior Tree Basal Area	0.0017	0.0013	0.112
Pinus nigra	0.0014	0	<0.001
Pinus banksiana	0.0003	0.0009	<0.001
Total Tree Density Around Canopy Wells	0.123	0.178	0.115
Pinus nigra	0.078	0	0.009
Pinus banksiana	0.043	0.117	0.010
Total Basal Area Around Canopy Wells	0.0018	0.0013	0.164
Pinus nigra	0.0015	0	0.001
Pinus banksiana	0.0003	0.0010	<0.001

Since both the distance from Lake Michigan and the density of trees surrounding each wetpanne were correlated with how much the water table changed over the season, a stepwise multiple linear regression was run on water levels for both the mid-wells and the canopy wells. This was done to assess the relative importance of distance and tree density as predictors of water levels. Additional factors that may affect the total change in water level over a season were included in the regression. Several factors were included in the regression for the mid-wells: distance of the well from Lake Michigan, elevation of the well above Lake Michigan, logarithm of the total wetpanne area, density of trees within the wetpanne interiors, density of Austrian pines surrounding the wetpannes (i.e., exterior density), density of jack pines surrounding the wetpannes, total basal area of Austrian pines surrounding the wetpannes (i.e., exterior basal area), and total basal area of jack pines surrounding the wetpannes. Many of the same factors were included in the regression for the canopy wells: distance of the well from Lake Michigan, elevation of the well above Lake Michigan, the density and total basal area of Austrian pines in the $100m^2$ plot around each well, and the density and total basal area of jack pines around each well. In the mid-well regression, only distance from Lake Michigan and the exterior basal area of Austrian pines were accepted in the model. The total variation explained was $R^2 = 0.629$ with distance explaining 49% of the variation and the exterior basal area of Austrian pines explaining 14% of the variation (Table 3-13). In the canopy well regression, the distance from Lake Michigan, the density of jack pines, and the density of Austrian pines were accepted in the stepwise regression. The R^2 of the model was 0.638. Distance from the lake explained 54%, the density of Austrian pines explained 4.7%, and the density of jack pines explained 4.3% of the variation (Table 3-13).

Table 3-13. Summary of the mid-well and canopy-well stepwise regressons.

Step	Variable Entered	Partial R-Square	Model R-Square	F Value	P-value
Mid-wells:					
1	Distance	0.4872	0.4872	11.40	0.0055
2	Exterior basal area of *P. nigra*	0.1416	0.6288	4.20	0.0651
Canopy-wells:					
1	Distance	0.5482	0.5482	29.12	<.0001
2	Exterior density of *P. nigra*	0.0471	0.5953	2.67	0.1156
3	Exterior density of *P. banksiana*	0.0426	0.6379	2.59	0.1219

The mean total change in water levels in the jack pine wetpannes was -28 cm, in Austrian pine wetpannes was -23 cm, and in open wetpannes was -12 cm. Since distance explained the majority of the variability in the change in water levels in both regression models, an analysis of covariance (ANCOVA) was run using distance as the covariate to test the effects of wetpanne type on the total change in water levels (Table 3-14). The open, treeless wetpannes were grouped with the jack pine wetpannes to act as a control for the Austrian pine wetpannes. The two types of wetpannes compared were then wetpannes with Austrian pines, and those without Austrian pines. The height of the regression line (i.e., the y-intercept) for wetpannes with Austrian pines was significantly lower than that for the wetpannes without Austrian pines by about 10 to 15 cm ($p<0.0001$) (Fig. 3-28). This means that the water table dropped significantly more in wetpannes planted with Austrian pine. The same result was reached when the open wetpanne data points were omitted from the analysis. Since tree density and total basal area surrounding Austrian pine sites and jack pine sites were not significantly different from one another (Table 3-12), there should have been no difference between wetpanne types if tree density or size were the only factors determining water table levels. These results suggest that Austrian pines may have the ability to lower water levels in wetpannes more than the jack pines. If the analysis is run without distance as the covariate, the change in water levels was not significantly different between wetpannes with Austrian pines and those without (Table 3-14).

Table 3-14. Results of the ANCOVA for the effects of wetpanne type on change in water table level, with distance from Lake Michigan as the covariate.

Source	DF	Type III SS	F Value	Pr > F
With Covariate:				
Wetpanne type (Intercept)	1	411.68	35.71	<.0001
Distance (Slope)	1	751.95	65.22	<.0001
Testing Homogeneity of Slopes:				
Distance*Wetpanne type	1	1.72	0.08	0.7769
Without Covariate:				
Wetpanne type	1	2.63	0.05	0.8185

WATER CHEMISTRY

The data points for individual wetpannes were plotted as vertical dot plots for each ion or nutrient measured (Fig. 3-29 through 3-41). The data points were broken down into categories to show differences among water collection sites. "Mid Ap" refers to groundwater samples taken from the mid-well of Austrian pine wetpannes. "Mid Jp" refers to groundwater samples taken from the mid-well of jack pine wetpannes. "Op Surface" refers to the surface water sampled from the center of open wetpannes. "LMich" and "River" refer to surface waters taken from Lake Michigan and the Kalamazoo River oxbow lake, respectively.

The most striking observation was that there were large amounts of variability within each category for almost all parameters tested, shown by a large amount of scatter in the vertical dot plots (Figs. 3-29 through 3-41). This variability was also reflected by the large standard deviations for each parameter (Table 3-15). There were two outliers for several parameters within the Mid Jp category which corresponded to wetpannes 'E' and 'F'. Values for E and F were particularly low for specific conductance, alkalinity, pH, Ca^{2+}, and Mg^{2+} (Fig. 3-29; 3-30; 3-31; 3-32; 3-33). Values were higher than expected for Na^{+}, K^{+}, TDP, and NH_4^{+}-N (Fig. 3-35; 3-37; 3-39; 3-40). Low pH, alkalinity, and concentrations of $Ca^{2+}$and Mg^{2+} are evidence that the major source of water for these wetpannes is precipitation.

Differences among categories were also apparent. First, specific conductance, alkalinity, Ca^{2+}, and Mg^{2+} values were higher for Mid Ap sites than for the other categories (Fig. 3-29; 3-30; 3-32; 3-33). Second, the pH of Lake Michigan and the Kalamazoo oxbow waters tended to be higher than that of the wetpanne categories (Fig. 3-31). Third, the concentrations of the relatively conservative ions, Na^{+} and of Cl^{-}, were higher in Lake Michigan and the oxbow lake than in the wetpannes (Fig. 3-35; 3-36), indicating that wetpannes do not contain water primarily from the river or the lake.

In general, Ap, Jp, and Op wetpannes have a chemical composition that is similar to the groundwater chemistry of southwestern Michigan (Table 3-15). They have relatively high Ca^{2+}, Mg^{2+}, alkalinity, and specific conductance, which result from the dissolution of calcium and magnesium carbonates along groundwater flow paths. Their

Table 3-15. The water chemistry values of wetpannes. Standard deviations are in parentheses.

Source	pH	Specific Conductance (uS/cm)	Alkalinity (meq/L)	Ca^{2+} (mg/L)	Mg^{2+} (mg/L)	Na^{+} (mg/L)	Cl^{-} (mg/L)	K^{+} (mg/L)	Si (mg/L)	SO_4^{2-} (mg/L)	NO_3-N (mg/L)	NH_4^{+}-N (mg/L)	TDP (mg/L)
Hiebert et al., 1986													
Indiana Dunes National Lakeshore (West Beach Unit)													
Surface water	7.4 (0.4)	409 (96)	3.837 (0.799)	67 (16)	11.7 (5.4)	---	---	0.81 (0.39)	---	---	0.42 (0.57)	0.52 (0.50)	0.01 (0.01)
Wilcox & Simonin, 1987													
Indiana Dunes National Lakeshore (Miller Unit)													
Surface water	8.00	419 (33)	3.317 (0.639)	53.9 (12.8)	12.1 (4.0)	---	---	2.1 (0.9)	---	---	---	0.25 (0.14)	0.004 (0.001)
This Study:													
Saugatuck, Michigan													
Mid JP-Groundwater	6.61 (0.93)	211 (77)	1.743 (1.173)	28.7 (17.0)	7.7 (2.6)	5.3 (3.7)	4.1 (5.2)	1.2 (0.9)	4.2 (0.6)	7.8 (2.1)	0.01 (0.01)	0.070 (0.089)	0.010 (0.012)
Mid AP-Groundwater	7.16 (0.24)	414 (48)	4.136 (0.670)	65.2 (9.4)	18.2 (3.5)	3.3 (1.3)	3.9 (2.2)	0.7 (0.3)	4.3 (0.5)	14.6 (5.8)	0.5 (0.7)	0.054 (0.050)	0.005 (0.002)
Mid OP-Surface water	7.49 (0.18)	283 (36)	2.852 (0.473)	40.1 (8.9)	15.8 (4.7)	1.0 (0.1)	1.3 (0.4)	1.7 (1.2)	5.4 (4.1)	3.9 (0.4)	<0.02	0.015 (0.004)	0.010 (0.003)

Table 3-15. (continued)

Source	pH	Specific Conductance (µS/cm)	Alkalinity (meq/L)	Ca^{2+} (mg/L)	Mg^{2+} (mg/L)	Na^{+} (mg/L)	Cl^{-} (mg/L)	K^{+} (mg/L)	Si (mg/L)	SO_4^{2-} (mg/L)	NO_3-N (mg/L)	NH_4^{+} (mg/L)	TDP (mg/L)
This Study:													
Saugatuck, Michigan													
Lake Michigan-Surface water	7.87 (0.01)	310	2.071 (0.351)	38.8 (2.3)	11.7 (0.2)	8.3 (0.4)	13.1 (1.2)	1.5 (0.03)	0.2 (0.1)	25.3 (0.6)	0.2 (0.1)	0.013 (0.009)	0.006 (0.004)
Kalamazoo Oxbow-Surface water	8.10 (0.11)	320 (1)	2.352 (0.152)	28.9 (1.1)	21.2 (0.05)	11.6 (0.7)	20.9 (0.1)	1.4 (0.1)	2.0 (1.3)	16.7 (3.9)	<0.02	0.005 (0.005)	0.007 (0.003)
From Rheaume (1990), Kehew and Brewer (1992), and the National Atmospheric Deposition Program (2/12/97):													
Range of Values for Southwestern Michigan													
Precipitation	4.3 to 4.45	26.1 to 34.0	0	0.19 to 0.22	<0.01 to 0.05	<0.2 to 0.10	0.16 to 0.25	<0.1 to 0.02	0	2.72 to 3.5	0.42 to 0.61	0.33 to 0.56	0.03
Range of Values for Southwestern Michigan													
Groundwater	7.34	403 to 587	3.933 to 4.243	69.83 to 81.0	22.50 to 25.0	4.33 to 9.30	>0 to 11.0	1.0 to 1.60	6.5 to 12.0	22.47 to 35.00	0 to 3.36	0.03 to 0.06	0.01

chemistry is not like that of precipitation, which is ion-poor. In addition, the wetpannes of Saugatuck have water chemistries similar to those reported for Indiana Dunes National Lakeshore (Hiebert et al., 1986; Wilcox and Simonin, 1987), except that the Indiana wetpannes have higher values of NH_4^+-N (Table 3-15).

SEDIMENT DEPTH

The depth of the organic layer, its pH and moisture content, and the general character of the soil profile in the wetpanne basins were investigated. The mean depth of the organic layer for all wetpannes was 3.8 ± 1.0 cm. A 5 to 10 cm layer of gray sand was found beneath the organic layer. Relatively unaltered lake sand was found below this gray layer. Occasionally, small (<5x5cm) orange-red and gray patches were discovered embedded within this last layer.

The mean organic soil depth underlying pools of standing water was 10.7 ± 1.1 cm, whereas the mean organic soil depth for wetpannes that dried out over the course of a season was 3.0 ± 0.5 cm (Fig. 3-42). A t-test showed these depths to be significantly different ($p < 0.0001$). Differences in the organic layers among wetpanne types were also observed. The mean depth of the organic layer in the Austrian pine wetpannes was 2.7 ± 0.8 cm. The mean depth for the jack pine wetpannes was 3.8 ± 1.0 cm. The mean depth for open, treeless wetpannes (which included some measurements of sediment beneath pools of standing water) was 6.2 ± 5.1 cm (Fig. 3-43). A Kruskal-Wallis test showed that there were significant differences among the organic soil depths of the three different wetpanne types ($p<0.05$). A Dunnett's multiple comparison test at a 15% experimentwise error rate showed that organic layer of the open wetpannes was significantly deeper than the organic layer in Austrian pine wetpannes. The open and jack pine wetpanne organic layers, and the jack pine and Austrian pine wetpanne organic layers were not significantly different from one another.

The average pH of the organic layer was 5.9 ± 0.4 for all wetpannes except those that had standing water at the time of sampling. Although sample size was not large enough to show significance, the pH of the organic layer under standing pools of water was less acidic than in wetpannes that were dry. The pH of submerged soils often approaches neutral after a few weeks of submergence (Ponnamperuma, 1972). The organic layer of soil was found to have a pH of 7.6 in one wetpanne and 6.9 ± 0.8 in another. The pH of the water column above the organic soil of these two wetpannes were 8.2 ± 0.1 and 7.1 ± 0.5, respectively. The mean pH of the organic layer of Austrian pine (6.2 ± 0.6) and of jack pine (5.5 ± 0.5) wetpannes were not significantly different from one another ($p=0.067$), although the organic layer in the jack pine wetpannes tended to be more acidic.

Higher percent moisture levels were found in the upper 10 cm layer of soil than in the 10 cm layer of soil beneath it. The mean percent moisture in the top 10 cm layer of soil was 26.2 ± 2.8 %, and the mean percent moisture in the 10 to 20 cm layer beneath it was 19.1 ± 0.6 %. A paired t-test showed this difference to be significant ($p=0.0001$). However, this difference may have been exaggerated because the sand particles in the lower layer are denser than the organic soil particles in the upper layer. Percent moisture levels were higher near the center of the wetpanne in the 10 to 20 cm layer than they were near the edges of the wetpannes (Fig. 3-44).

LIGHT REGIME

There were no significant differences in seasonal light interception by tree canopies in Austrian pine or jack pine wetpannes as estimated by the analysis of the fish-eye photographs. The mean percent open sky visible in the jack pine wetpannes was 40 ± 15%, and the mean percent open sky in the Austrian pine wetpannes was 44 ± 11%. The mean percent global light transmission in the jack pine wetpannes was 60 ± 25%, and in the Austrian pine wetpannes, it was 66 ± 13%. The percent open sky and percent global light transmission were both highly correlated with the log of the total area of each wetpanne. For percent open sky, $r = 0.803$ ($p=0.0008$) (Fig. 3-45), and for percent global light, $r = 0.688$ ($p=0.0008$) (Fig. 3-46).

There were significant relationships between seasonal light interception by tree canopies and the density and total basal area of the trees surrounding each wetpanne. The percent open sky was negatively correlated with density ($r= -0.673$; $p=0.0043$; Fig. 3-47) and with the total basal area of the surrounding trees ($r= -0.638$; $p=0.0078$; Fig. 3-48). The percent global light received was also negatively correlated with density ($r= -0.49117$; $p=0.0534$; Fig. 3-49) and basal area ($r= -0.443$; $p=0.0855$; Fig. 3-50), but not significantly so. The relationship between seasonal light interception by tree canopies and tree density within the wetpanne interiors was not significant.

Light intensity within the wetpanne interiors was directly measured with a light meter along east-west and north-south transects in spring, summer, and fall. Values ranged from 18,500 lux in the center of the wetpannes to only 100 lux beneath the canopy of trees at the edges of the wetpannes. Comparisons between different wetpannes were made using the percent of light transmitted to the wetpanne surface relative to a reference measurement made in a nearby treeless area. Repeated measures analyses were run on the absolute value of the light intensity reaching the center of the wetpannes, the percent light intensity reaching the center of the wetpannes, and the percent light intensity reaching the edges of the wetpannes. The percent values were first square-root transformed before running the analysis to normalize the data. There was no difference in the percent light intensity penetrating the canopy of trees at the edge of the wetpannes in jack or Austrian pine sites (Table 3-16). The mean percent light reaching the edges of the wetpannes was 25% of the reference value. The wetpanne type*time interaction was significant for both the analysis of the absolute value of light and the analysis of percent light transmitted to the center of the wetpannes, so the interactions were then sliced by time. The difference between the absolute amount of light penetrating the center of the wetpannes was significantly greater in the Austrian pine wetpannes in July ($p = 0.0012$), but on no other date (Table 3-16). The least square mean light intensity in July was 13772 lux in the Austrian pine wetpannes and 6654 lux in jack pine wetpannes. The percent light penetrating the center of the wetpannes was not significantly different on any date.

Table 3-16. Results of the repeated measures analyses of light meter data.

Parameter	Effect	Least Square Means		F Value	Pr > F
		Austrian	Jack pine		
Percent Edge	Wp type	--	--	0.39	0.5435
	Time	--	--	1.91	0.1511
	Wp type*Time	--	--	0.52	0.5978
Absolute Center (lux)	Wp type*Time	lux	lux		
	Sliced by May	8862	6522	1.06	0.3041
	Sliced by July	13772	6654	10.90	0.0012
	Sliced by Sept.	5659	2779	1.93	0.1673
Percent Center	Wp type*Time	%	%		
	Sliced by May	68.55	63.34	0.00	0.9523
	Sliced by July	80.48	53.58	2.26	0.1346
	Sliced by Sept.	48.53	52.32	0.17	0.6849

Even though there were no differences in the percent light transmitted to the center of wetpannes or through the canopy at the edges, there were significant differences in percent light intensity at various locations along the transects between the edges and the centers of the wetpannes. T-tests were run at each position along the transects to look for differences in light intensity in Austrian pine and jack pine wetpannes in each season. In July, the percent light transmitted at 0, 2, 4, 6, 8, and 10 meters along the transects were significantly higher in Austrian pine wetpannes than in jack pine wetpannes (Fig. 3-52). Within the canopy at the edge of the wetpannes, at -6, -4, and -2 meters along the transects, there were no significant differences between wetpanne types. Beyond 10 meters along the transects and into the centers of the wetpanne, the differences between wetpanne types were insignificant. The same phenomenon was observed in May (Fig. 3-

51), although the light intensity was higher in only the 4, 6, and 8 meter locations along the transects in the Austrian pine wetpannes. In September, the percent light transmitted in Austrian pine sites was also higher from 0 to 10 meters, but not significantly so (Fig. 3-53).

HISTORICAL CHANGES IN WETPANNE HYDROLOGY

The aerial photograph analysis of the study site showed that the size and shape of wetpannes remained relatively constant from photograph to photograph. The area of each wetpanne changed by no more than 33% from one photograph to the next photograph in the chronosequence, except for the area of wetpanne JpI, which dropped about 56% in 1960 (Fig. 3-54). Despite slight changes in wetpanne area, each wetpanne in this study maintained the same overall shape in all photographs, except in dry years when some of the wetpannes became fragmented. The area:perimeter ratio of each wetpanne was relatively consistent from photograph to photograph, but dropped in the years 1960 and 1992 (Fig. 3-55). The decrease in the area:perimeter ratios indicates that the edges of the wetpannes increased in those years. These two years were particularly dry, and wetpannes JpH, JpI, and 2D became fragmented into two or more separate areas in those years. Surface water was present in at least some of the wetpannes in all of the photographs in the chronosequence, even in 1960 and 1992. In 1999, the last year of this study, all of the wetpannes dried up completely, possibly for the first time in many years. It is unknown if the wetpannes dried up at any time before 1999 since aerial photographs were not available for all years.

Seasonal trends in the water levels of wetpannes were masked by the large year-to-year variability in water levels. In 1997, water levels were high in all wetpannes at the end of the growing season. Some wetpannes had up to 70 cm of surface water. Water levels started to decrease that fall and fell continuously through 1998 and into the spring of 1999, by which time all the wetpannes had become dry (Fig. 3-56). The only potentially seasonal trend observed was a slight rise in water levels in wetpannes B, 3, A, and G that coincided with the spring of 1998. The percent open water in each wetpanne changed greatly from year-to-year (Fig. 3-57). Almost all wetpannes had the highest percent open water in 1955 and in 1978. They had the lowest percent open water in 1960 and in 1992. These trends become clearer when the average percent open water for all wetpannes is calculated for each year (Fig. 3-58).

Mechanisms behind the year-to-year variability in wetpannes were investigated. The average percent surface water was plotted against the sum of precipitation that fell three months prior to the date when each photograph was taken (Fig. 3-59). There was no correlation between precipitation and percent open water ($r= -0.098$; $p= 0.8021$). The average percent open water was plotted against the average level of Lake Michigan for the month each photo was taken (Fig. 3-60). In this case, there was a slight positive relationship ($r= 0.303$), but it was not significant ($p= 0.3949$). Very little of the variability in wetpanne water levels could be accounted for with linear relationships. Other relationships were then explored graphically.

First, the average percent open water in the wetpannes was plotted alongside historical climate data to look for trends. There was no relationship between the total annual precipitation and percent open water, or the mean annual temperature and percent open water. There was a relationship, however, between percent open water and the level of Lake Michigan. Here, the peaks in lake level roughly corresponded to the peak percent open water values in the wetpannes (Fig. 3-61).

Second, precipitation-event data from the South Haven weather station for the summer of 1998 were plotted alongside the biweekly water table measurements in the wetpannes (Fig. 3-62). This provided evidence that larger precipitation events can temporarily increase the water levels in wetpannes. A large rain event on August 5th (Day 66) seemed to produce an increase in the water levels of the wetpannes five days later (Day 71). The water levels receded to pre-rain event levels within a few days after that. This same phenomenon was qualitatively observed in 1997—the surface water levels of the wetpannes increased significantly after a heavy rainstorm. Precipitation was probably responsible for the peak in the percent open water values in 1978 (Fig. 3-57). It rained 12.54 inches in September 1978, the month the photograph was taken (NOAA, 1996). The average rainfall for September at the study site is 3.05 inches (NOAA, 1971).

Third, the levels of Lake Michigan were plotted alongside the wetpanne water levels (Fig. 3-56 and Fig. 3-63). Surface water levels in wetpannes fell at nearly the same rate as the level of Lake Michigan (Fig. 3-56). The groundwater levels in wetpannes lacking surface water also dropped concomitantly with the level of Lake Michigan over the period from 1 June 1998 to 6 September 1998 (Fig. 3-63). In addition to these two plots, anecdotal evidence that wetpanne water levels are tied to the level of Lake Michigan was available from a resident who lives near the study site (C. Deam, personal communication). Her family noted high water levels in the oxbow lake since the time when they moved into their home in 1951. The family record of high water levels in the oxbow lake before 1985 matched the historical lake level data surprisingly well. When the record stated that oxbow lake levels were particularly high, the historical lake level was also high. In 1985, she started measuring the level of the oxbow lake relative to a permanent iron stake every September. September levels of Lake Michigan for the same years (Fig. 3-64) follows the same trends as her data (Fig. 3-65). It is not unreasonable to suggest that the wetpannes near the oxbow lake also followed the level of Lake Michigan over these years.

Differences in the hydrological variability among wetpanne types over time could not be differentiated. The sample size for each wetpanne type visible on the aerial photograph was too small. There were three jack pine wetpannes and four open wetpannes. Only one Austrian pine wetpanne, the Austrian pine complex, was visible in the photographs. The other Austrian pine wetpannes were too small to be detected at the scale of the photographs. The percent open water of the Austrian pine complex did seem to decrease over time (Fig. 3-57), but the growth of the pines obscured the view of the wetpanne in later years and made it difficult to see the surface of the wetpanne accurately.

DISCUSSION

General Features of Wetpannes

The wetpannes of this study held many features in common, regardless of whether they had been planted with Austrian pine or not.

Many species occurred in specific ranges along the water depth gradient according to their tolerance to wet conditions as was predicted. These ranges often overlapped, although the areas of overlap were not distinct enough for the vegetation assemblages to be considered discreet zones within the wetpanne basin. In addition, the ranges of some species along the water depth gradient were much wider than others. These particular species seem to be able to tolerate varying amounts of wetness. Detailed information about the distribution of individual species within wetpannes is presented in the Results section of this chapter.

Although the weighted average ordination approach is somewhat circular, it was useful for showing the patterns of the distribution of plant species along the water depth gradient. Upland plant species dominated the edges of wetpannes and were more or less gradually replaced by species that were considered to be wetland indicator species. Wetland plant species replaced the upland plant species when the early June water table was between 30 to 50 cm below the ground level, and the wetland species maintained dominance in shallower water tables. Obligate wetland species often were dominant in the deepest parts of the wetpanne basins. The same pattern was observed in the open, jack pine, and Austrian pine wetpanne types.

The ramifications of these findings are that the shape of the wetpanne basin and the absolute distance of the basin to the water table will largely determine the proportion of wetland species found within the wetpanne at any particular time. A gradually sloping basin will have upland plant species that are gradually replaced by wetland plant species as the basin gets deeper (and closer to the water table). A wetpanne with a deep, steeply sloped basin will have fewer upland species that will be more quickly replaced by wetland plant species. For example, the open wetpannes had deeper wetpanne basins that contained standing water and could therefore support some submersed aquatic species (Table 3-3).

Factors other than the water depth gradient may also be determining the distribution of plant species within the wetpanne basin. Competition among plant species may cause some species to occupy a much narrower range along the water depth gradient than they would in the absence of competitors. Dispersal limitation may limit which species colonize a particular wetpanne. This could affect the distribution pattern because a species that reached a wetpanne first may have gained a competitive advantage over other species that arrive later. Light may be another one of the other factors that determine the distribution pattern. Some species may not be able to tolerate the shaded conditions of the forested wetpannes and will be less able to compete with other species along the water depth gradient under these conditions than under full sun conditions. The depth of the litter layer in forested wetpannes may limit which species can become established in the wetpanne. Often, the edges of the forested wetpanne interiors were buried under 3 or 4 cm of pine needles. Some of the seeds of the wetpanne plant species may get caught in the litter layer and become desiccated before their roots reach the soil layer beneath. Other seedlings may simply be unable to penetrate the litter layer. Because both the light level and litter depth gradients parallel the water depth gradient, their effects were confounded with the water depth gradient and could not be teased apart in the absence of experimental manipulation. Since this was an observational study with the purpose of describing the pattern of vegetation seen within the wetpannes, further study is needed to tease apart these and other factors.

Another distinctive feature shared by the wetpannes in this study is that their water levels are controlled by, but not derived from, Lake Michigan. The fact that the water chemistry of most wetpannes resembled groundwater of southwestern Michigan (Table 3-15) strongly suggests that these systems' water source is primarily groundwater. The wetpannes at Indiana Dunes National Lakeshore also share the characteristics of groundwater. Even the chemistry of the surface water of the open, treeless wetpannes was like that of groundwater. The high dissolved ion concentrations eliminate the possibility that these systems are fed by precipitation alone. The only exceptions were wetpannes E and F, which had water chemistry consistent with that of precipitation. The large amount of variability within and among sites suggests that the water source for wetpannes is local groundwater flow rather than regional flow. Local groundwater flow could explain the variability because different flow paths may pick up varying concentrations of ions and nutrients. The relative contribution of groundwater to wetpannes E and F may be less than that to the other wetpannes, which would account for the difference in their water chemistry. Theoretically, water could backflow from Lake Michigan into the wetpannes and mix with the groundwater, but this is not likely the case since the wetpannes are elevated above the lake level, and the levels of the relatively conservative ions, Na^+ and Cl^-, are much lower than those of Lake Michigan. There is probably no inflow of water from the Kalamazoo River oxbow lake into the wetpannes either, because the oxbow lake water also has large concentrations of Na^+ and Cl^-, probably from road salt and other contaminants that have run off from the watershed.

The results of this study show that the water levels of wetpannes are controlled by Lake Michigan. Although the wetpannes do not actually derive their water from the lake, the lake sets the level of the water table within the wetpannes. The phenomenon is related to the fact that the water table slopes towards Lake Michigan near the coast (Shedlock, 1993; Lichter, 1995). This slope varies over the course of theyear. If the level of Lake Michigan drops, the slope has the potential to become steeper, assuming constant recharge from upland areas. If the level of Lake Michigan rises, then this slope should become shallower. The level of Lake Michigan is not the only factor that determines the slope of the water table, however; the input of precipitation to the watershed at any given time is also important. More precipitation creates higher groundwater recharge and thus raises the water table. At any given level of Lake Michigan, higher water tables inland have a greater elevation to fall towards Lake Michigan than lower inland water tables do. Therefore, the slope of the water table flowing towards Lake Michigan would be steeper when the water table levels are higher inland. In the winter and spring, large amounts of precipitation raise the water table of the watershed, and the slope of the water table flowing towards the lake is steeper. When the water table becomes lower in the fall, the slope of the water table flowing towards Lake Michigan becomes flatter (Fig. 3-22). In this study, the level of Lake Michigan dropped 19 cm and the slope of the water table decreased from 0.24 ° to 0.22 ° over the period from 1 June 1998 to 6 September 1998.

This reflected the relatively low amount of precipitation in the region over this time period because the inland water table dropped over the same period of time that the level of Lake Michigan dropped. The end result was that the water levels of the wetpannes that were farther away from the lake dropped more over this time period than the water levels of the wetpannes that were closer to the lake.

Because the level of Lake Michigan controls the water level of the wetpannes, the water levels of wetpannes follow the same cycles of fluctuating water levels that Lake Michigan does. The analysis of the aerial photographs showed two cycles of high and low water levels in wetpannes that lasted about 25 to 30 years (Fig. 3-61). Caution must be used in interpreting the graphs, however, since not all years were represented in the collection of aerial photographs. In 1986, the level of Lake Michigan was the highest it had been in the past 100 years, yet the water levels seem to be decreasing over the period from 1980 to 1988 based on the aerial photograph analysis (Fig. 3-62) because there was no photograph available for 1986. Since the aerial photograph record is incomplete, other particularly high or low water levels may also have been missed. If this is the case, then the cycles may have been shorter than the proposed 25 or 30 year interval. Another caution to be heeded in the interpretation of the aerial photographs is that although wetpanne water level and percent open water were positively correlated, the relationship was not linear. The wetpannes have irregularly shaped basins and therefore, only a complex function would be able to describe the relationship between wetpanne water depth and percent open water. At some point, a small change in depth may be accompanied by a large change in area. This is probably why the correlation between percent open water and lake level was not significant (Fig. 3-60).

The year-to-year variability in wetpanne water level was greater than seasonal trends in water levels. The water levels of wetpannes at the study site dropped up to 70 cm during the three year study period, and only showed slight increases in the spring of 1998 (Fig. 3-56). The large amount of year-to-year variability in the wetpanne water levels can have an effect on the vegetation. When the water levels were low, the perimeter of the wetpannes increased (Fig. 3-55), allowing more of the wetpanne edge to become available for emergent vegetation. At the same time, the amount of habitat available for submersed vegetaton was reduced. Water lilies that were present in 1997 disappeared when water levels dropped the following year. High water levels may negatively affect other plant species. Several *Betula papyrifera* trees that had trunks under 10 cm of water in 1997 died by 1998. The high water levels also killed some of the herbaceous vegetation. In 1998, wide swaths of dead *Cladium mariscoides* plants were found in plots that had been flooded the previous year.

Indirect evidence that the water table had fluctuated greatly in wetpannes also existed in the wetpanne sediment. The wetpanne sediment displayed hydric characteristics. Hydric characteristics are evidence that the soil has been saturated at some time in the past (Tiner, 1999). The requirement for a sandy soil to be considered hydric is that it must have a 2 cm layer of muck within 15 cm of the surface (Tiner, 1999). The sandy wetpanne soils had organic layers ranging from 2 to 10 cm deep. Mottling, another hydric soil attribute, was also observed in the wetpanne soils. Mottling occurs when anerobic conditions cause the iron in the soil to be reduced and subsequently mobilized within the soil solution (Tiner, 1999). The iron moves vertically or horizontally within the soil profile and reprecipitates as patches of iron-rich soil. The patches of soil that have been depleted of iron are gray-colored. Later, if the water table fluctuates and oxygen becomes available, the iron-rich patches are oxidized and turn a reddish-orange color. Both orange and gray mottles were found within 50 cm of the soil surface in the wetpannes, indicating that the water table has fluctuated in the past.

The results of this study suggest that wetpannes are a permanent part of the sand dune landscape. The wetpannes of this study have persisted for at least 60 years, since they were visible in the 1938 aerial photographs. Wilcox and Simonin (1987) showed that wetpannes near Lake Michigan at Indiana Dunes National Lakeshore were up to a few hundred years old. It is possible, however, that the wetpannes at Saugatuck have become artificially stabilized by the Austrian pine plantings or by the channelization of the Kalamazoo River mouth.

Differences in Wetpannes With and Without Austrian Pine

Despite the many features that wetpannes have in common, differences between the open, treeless wetpannes and the forested wetpanne types were observed. Trees within and around the wetpannes affected several aspects of wetpanne ecology. The effects of Austrian pine in particular were observed.

THE EFFECTS OF TREES ON WETPANNE ECOLOGY

Forested wetpannes are different from unforested wetpannes in several ways. The forested wetpannes were always drier than the unforested wetpannes. However, it remains unknown whether the trees are lowering water tables in these wetpannes, or if the trees became established in these wetpannes because they were initially drier. Tree density was correlated with the total change in water table depth during the 1998 growing season, although there was a much stronger relationship between the total change in water table depth and the distance of the wetpanne from Lake Michigan. The trees in the forested wetpannes reduce light levels at the edges of a wetpanne and up to 10 meters into the wetpanne interior. Trees cause an increase the depth of the litter layer, creating more acidic conditions in the wetpanne sediment relative to the sediment of the open wetpannes. The sediment layer is thinner in the forested wetpannes than in the open wetpannes, probably because the drier conditions allow the aerobic decomposers to more quickly break down the organic material.

Tree density was also correlated with a number of plant community characteristics within the wetpannes. An increase in tree density surrounding the wetpannes was correlated with an increase in shrub cover in the wetpannes, an increase in the number and diversity of woody species, an increase in the amount of herbivory, a decrease in the diversity of herbaceous species, and a decrease in the percentage of wetland indicator species. Since tree density was also positively correlated with the distance from Lake Michigan and negatively correlated with the distance of the wetpanne basin to the spring water table level, the effects of tree density on the wetpanne plant community was confounded with these other variables. Tree density may explain some of the trends better than distance from the lake or distance to the water table, however. Woody species may increase in wetpannes with a greater density of trees because these species more successfully compete for light or water than the herbaceous plant species do. The amount of damage due to herbivory may increase in wetpannes with a greater number of trees because the trees provide cover for the herbivores. On the other hand, the elevation of the wetpanne basin above the water table may better explain some of the other trends in the wetpanne plant community. Herbaceous species diversity and the percent wetland indicator species were higher in wetpannes that were closer to the water table because high water tables may limit the establishment of woody species and allow the more flood-tolerant herbaceous species to flourish. The amount of shrub cover and the number and diversity of woody species decreased in wetpannes that were closer to the water table.

The fact that density of trees, the shrub cover, and the woody species diversity increased with increasing distance from Lake Michigan, may indicate that succession is more advanced in wetpannes that are farther away from the lake (i.e, the jack pine wetpannes). Successional stages in the upland areas of the sand dunes become more advanced with greater distance from the lake (Cowles, 1899; Olson, 1958; Lichter, 1995), so perhaps succession in the wetpannes also becomes more advanced with increasing distance from the lake. The mechanism for succession in wetpannes may be linked to the fact that the water table drops more in wetpannes further from Lake Michigan over the course of a season. Even though the elevation of the wetpanne basin above the water table is not correlated with distance from the lake, the greater overall drop in water levels in sites far away from the lake may be enough to allow woody vegetation to get established during dry periods.

THE EFFECTS OF AUSTRIAN PINE COMPARED TO THE NATIVE JACK PINE

In wetpannes that have been planted with Austrian pines, the Austrian pines are colonizing the wetpannes at the same rate as the native jack pines, based on the number of juvenile trees of each species in these wetpannes. Because Austrian pine has a lifespan that is at least twice as long as the jack pine (300 years compared to 80-150 years) (Vergas, 1985; Rudolph and Laidly, 1990; Vidakovic, 1991), its ability to alter the wetpanne ecosystem may ultimately be greater than that of the jack pine.

The characteristics of the Austrian pine wetpannes are intermediate between the characteristics of the open wetpannes and the wetpannes forested with jack pine. The mean values of shrub cover, species richness, species diversity, percent wetland plants, and estimated herbivory for the Austrian pine wetpannes all fell between the mean values for the open wetpannes and the jack pine wetpannes. Before the Austrian pines were planted, these wetpannes were relatively open, based on the early aerial photographs. It seems that the main effect of the Austrian pine on the ecology of wetpannes is to make the wetpannes more like the forested wetpannes located farther from Lake Michigan, in areas that were previously unforested. The extent to which the Austrian pine wetpannes resemble the jack pine wetpannes may be a function of how long each type has been forested. The jack pine wetpannes were forested well before the Austrian pines were planted. This is reflected in the sediment layer of the wetpannes—the organic layer in the jack pine wetpannes was more acidic and slightly deeper than the organic layer in the Austrian pine wetpannes, suggesting that these wetpannes have been surrounded by pine trees for a longer period of time.

Austrian pines seem to be having a bigger impact than the jack pines on the hydrology of the wetpannes, although the evidence is only correlative. When the distance of the wetpanne from Lake Michigan was factored out, it was found that the water levels dropped more over the course of the season in the Austrian pine wetpannes than in the jack pine wetpannes. This difference was not a result of a difference in tree density between the two wetpanne types. It may be indirectly related to the fact that the average DBH of the trees surrounding the Austrian pine wetpannes was slightly higher than the DBH of the trees surrounding the jack pine wetpannes. One problem with the analysis was that there were no data points for Austrian pine wetpannes in the 400 to 600 meter range (Fig. 3-28), so the regression extends beyond the available data points. However, there were no wetpannes planted with Austrian pine at that distance. Since this was not an experimental manipulation of wetpannes where the only variable was the presence or absence of Austrian pines, one cannot say for certain that the Austrian pines themselves are responsible for lowering the water table in these wetpannes. Some other factor that was not controlled for may have been responsible for the change in the water table.

The analysis of the aerial photographs revealed very little about the effects of the Austrian pines on the wetpanne water levels. Photographs were available for years both before and after the pines were planted in the 1960's, but the wetpannes with Austrian pines were generally too small to be seen at the scale of photographs available. Only one of the Austrian pine wetpannes could be seen at that scale, and the trees obscured the view of even that wetpanne in later years. It became difficult to see the surface of the wetpanne once the trees started to get larger. Although not entirely conclusive, the results suggest that the water levels of the Austrian pine complex became reduced after the trees became established after 1967.

In this study, no difference was found between the ability of Austrian pine and the ability of jack pine to reduce light in the wetpannes, except in July, when jack pine reduced light more than Austrian pine within the interior of the wetpannes. In contrast, Leege (1997) found that light intensities were consistently lower under Austrian pine canopies than under jack pine canopies at the edges of wetpannes. The discrepancy between studies can be explained by the methods used in each.

Leege (1997) looked at the effects of Austrian or jack pines at a smaller scale. She laid her transects across microsites where a thick canopy of trees bordered the wetpanne edge and measured light intensity with a light meter. In this study, the whole wetpanne was examined rather than particular microsites. Because the distribution of trees around the wetpanne edge is patchy the transects in this study sometimes crossed open areas along the wetpanne edges. These light intensities were included in the calculation of the average light intensity for each position along the transect. Also in this study, fish-eye photography was used to estimate the total amount of light reaching the wetpanne surface. Therefore, in this study, the light intensity was measured at the scale of the entire wetpanne, which was appropriate because the goal of this study was to examine the effects of Austrian pine on wetpannes as a whole. This accentuates the importance of scale in making ecological measurements.

So, at the scale of the entire wetpanne, the average amount of light was the same regardless of whether the wetpanne was surrounded by Austrian pines or by jack pines. The larger the wetpanne, the less effect the surrounding trees had on the wetpanne interior. The amount of light reaching the wetpanne surface was negatively correlated with tree density. Therefore, the density of trees and the size of the wetpanne were much more important than whether the trees were Austrian pine or jack pine.

Seasonal differences between Austrian pine and jack pine wetpannes became evident when measurements were taken with the light meter. Austrian pine and jack pine canopies let in the same percent of light on average in the edge positions of the transects.

The reason that light intensities were higher at some positions along the transects within Austrian pine wetpannes could have been due to the angle of sun when these wetpannes were measured. Most jack pine wetpannes were measured earlier in the day when the sun's angle was lower, from 9:30 am to 12:00pm daylight savings time. The Austrian pine wetpannes were measured closer to midday, from 12:00 to 2:30 pm. This was done in order to measure all sites in one day. The light intensities were analyzed as a percent of the total light of a control measurement taken after each wetpanne was measured. However, this may not have been enough to correct for the differences in the angle of the sun. Trees cast longer shadows in the morning hours and this may have caused the jack pine sites to show reduced light intensities in areas that were shaded. The seasonal differences in the sun's angle would only accentuate the difference between morning and afternoon. The overall light intensity would have been even greater in the afternoon in July. It would have better to take the measurements over several days between 12 and 2pm daylight savings time rather than measuring all sites on the same day. This demonstrates the benefits of using fish-eye photography for measuring light differences—the light intensities are calculated for an entire season rather than for a single instant as by a light meter.

The purpose of this chapter was to describe the plant community and hydrological patterns seen in the wetpannes. Trees in general seem to have an effect on water table levels in wetpannes, and Austrian pines specifically may use more water than the native jack pines do in wetpannes. The focus of the next chapter is to see if differences in transpiration rates, leaf surface area, and root structure of the two pine species can explain this phenomenon.

Figure 3-3. An example of a digitized aerial photograph. Wetpannes 1D, 2D, 3D, and 4D are open, treeless wetpannes; JpH, JpI, and JpB are jack pine wetpannes; and ApComplex is the only visible Austrian pine wetpanne. The wetpanne boundaries are traced in black.

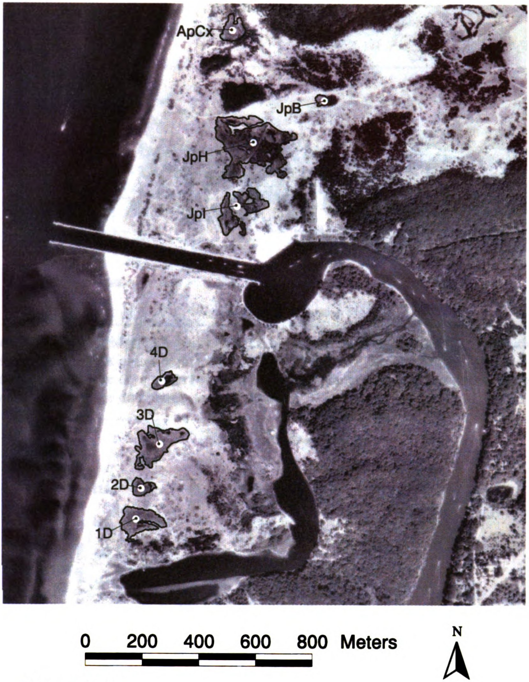


Figure 3-3.

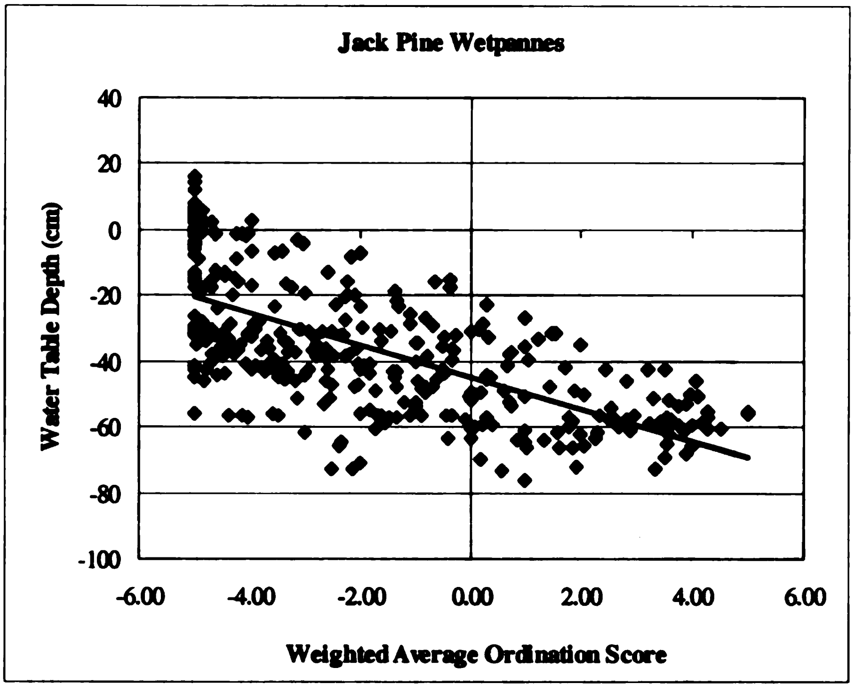


Figure 3-4. The relationship between water table depth and weighted average ordination scores for the jack pine wetpannes ($r = -0.671$; $p<0.001$). Low ordination scores mean the plots are dominated by obligate wetland plants, and high ordination scores mean the plots are dominated by upland plants.

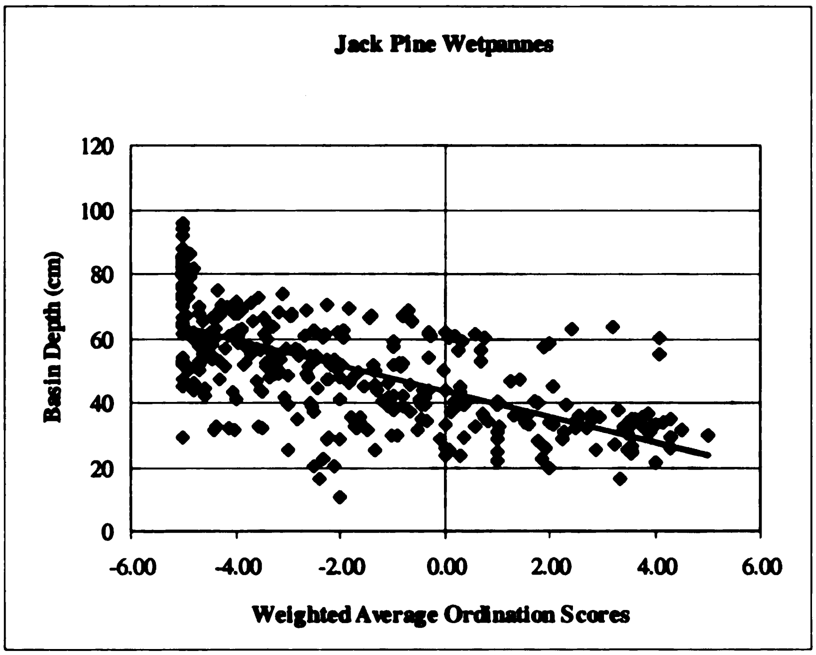


Figure 3-5. The relationship between basin depth and weighted average ordination scores for the jack pine wetpannes ($r = -0.626$; $p<0.001$). Low ordination scores mean the plots are dominated by obligate wetland plants, and high ordination scores mean the plots are dominated by upland plants.

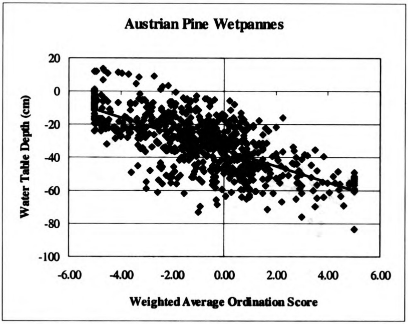


Figure 3-6. The relationship between water table depth and weighted average ordination scores for the Austrian pine wetpannes (r = -0.675; p<0.001). Low ordination scores mean the plots are dominated by obligate wetland plants, and high ordination scores mean the plots are dominated by upland plants.

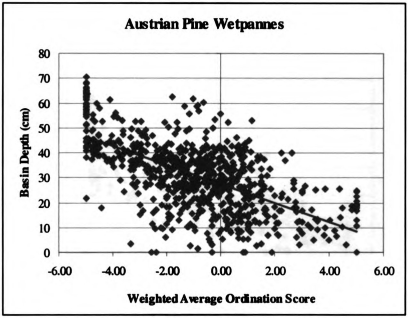


Figure 3-7. The relationship between basin depth and weighted average ordination scores for the Austrian pine wetpannes (r = -0.629; p<0.001). Low ordination scores mean the plots are dominated by obligate wetland plants, and high ordination scores mean the plots are dominated by upland plants.

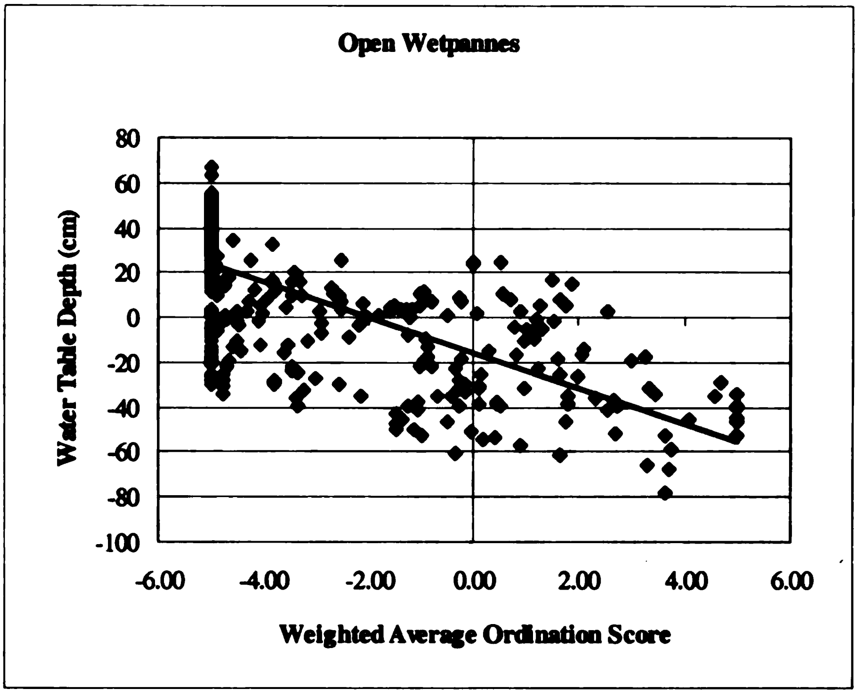


Figure 3-8. The relationship between water table depth and weighted average ordination scores for the open wetpannes ($r = -0.700$; $p<0.001$). Low ordination scores mean the plots are dominated by obligate wetland plants, and high ordination scores mean the plots are dominated by upland plants.

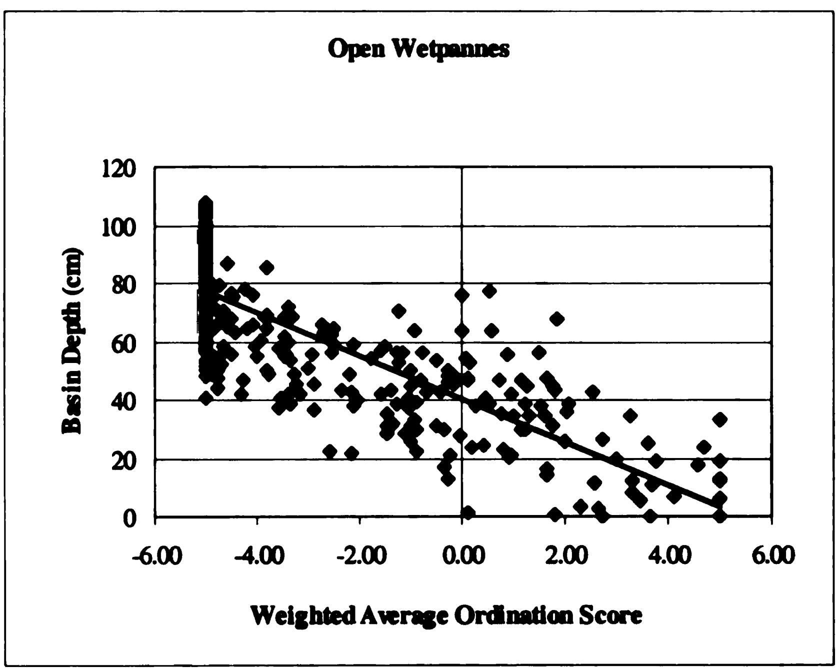


Figure 3-9. The relationship between basin depth and weighted average ordination scores for the open wetpannes ($r = -0.803$; $p<0.001$). Low ordination scores mean the plots are dominated by obligate wetland plants, and high ordination scores mean the plots are dominated by upland plants.

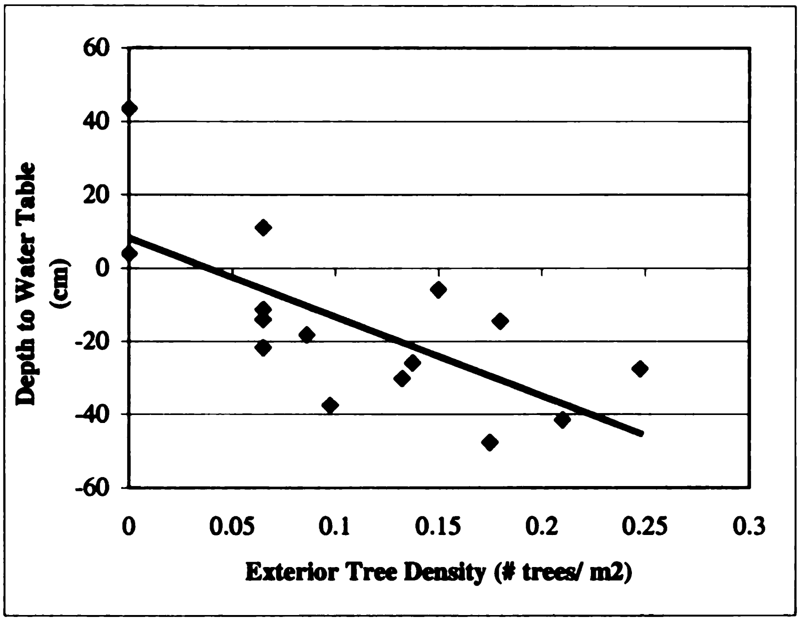


Figure 3-10. The relationship between the elevation of the wetpanne basin relative to the water table and the estimated tree density within an 11.3 m belt surrounding each wetpanne (r = -0.683; p=0.005). Negative numbers represent water levels below ground, and positive values indicate surface water.

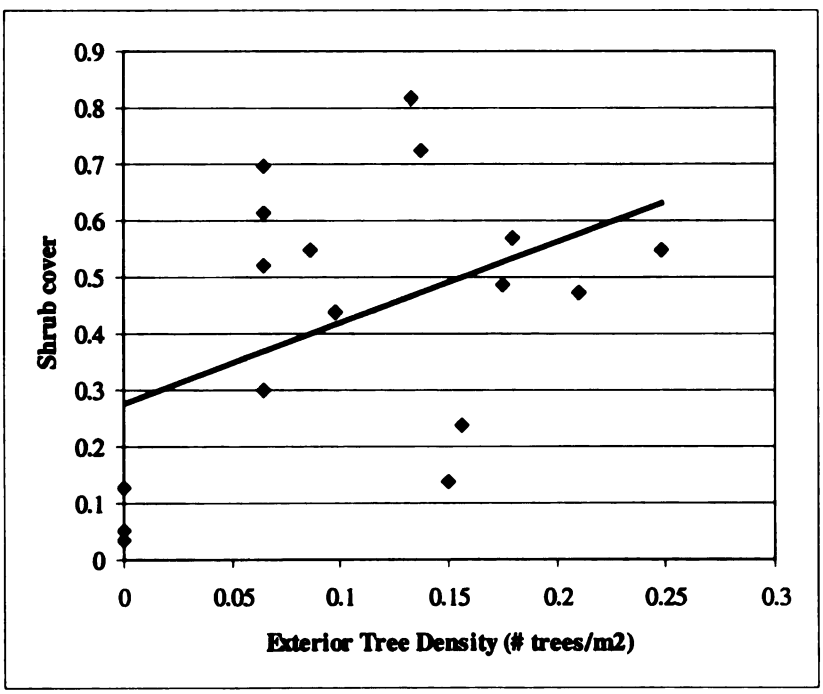


Figure 3-11. The relationship between total shrub cover and the estimated tree density within an 11.3 m belt surrounding each wetpanne (r = 0.396; p=0.143).

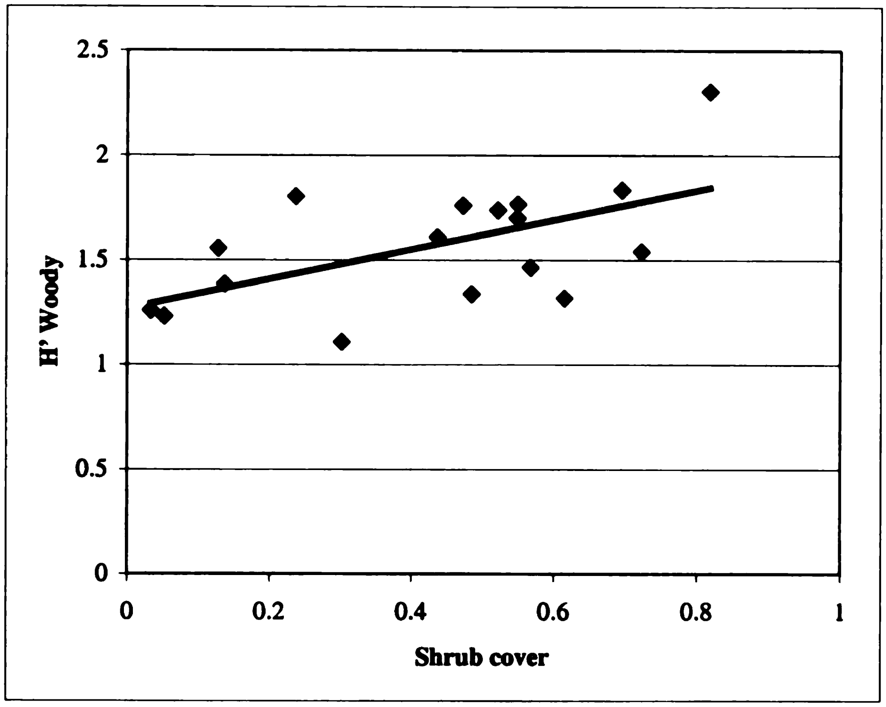


Figure 3-12. The relationship between the Shannon diversity (H') of woody vegetation and the total shrub cover within each wetpanne (r = 0.617; p=0.014).

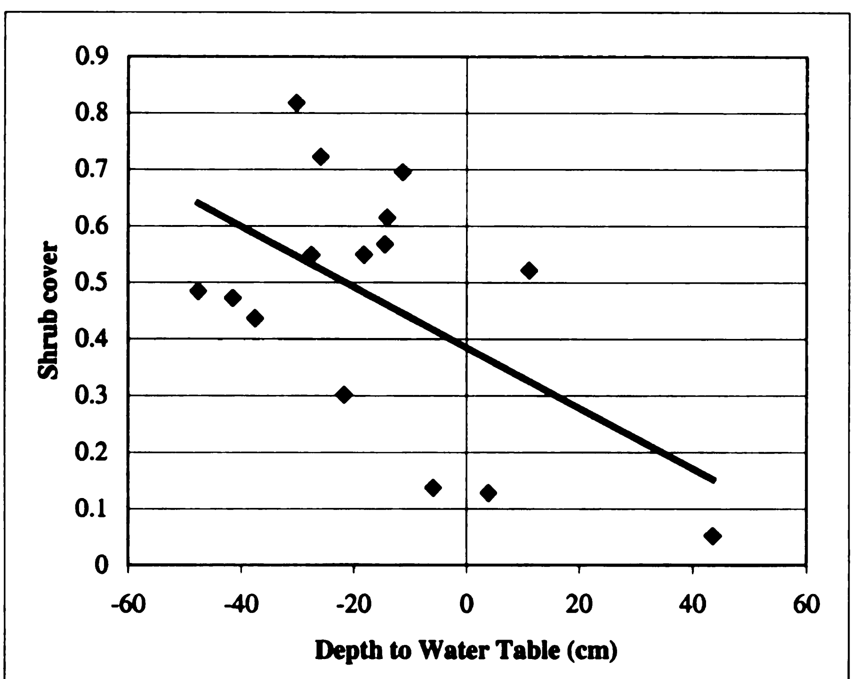


Figure 3-13. The relationship between total shrub cover and the elevation of the wetpanne basin relative to the water table (r = -0.545; p=0.0.36). Negative numbers represent water levels below ground, and positive values indicate surface water.

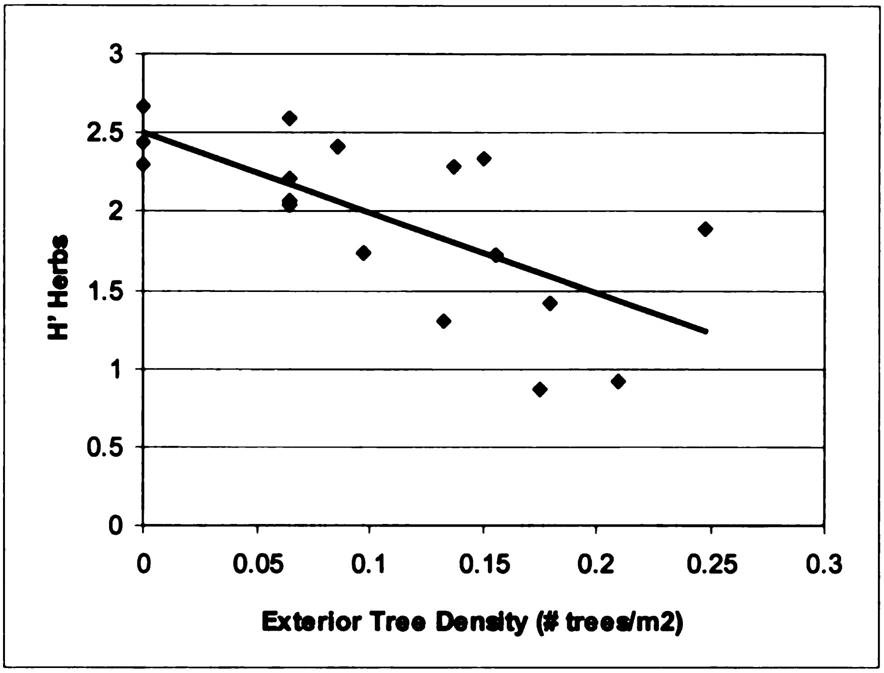


Figure 3-14. The relationship between the Shannon diversity (H') of the herbaceous vegetation and the estimated density of trees within an 11.3 m belt surrounding each wetpanne ($r = -0.660$; $p=0.007$).

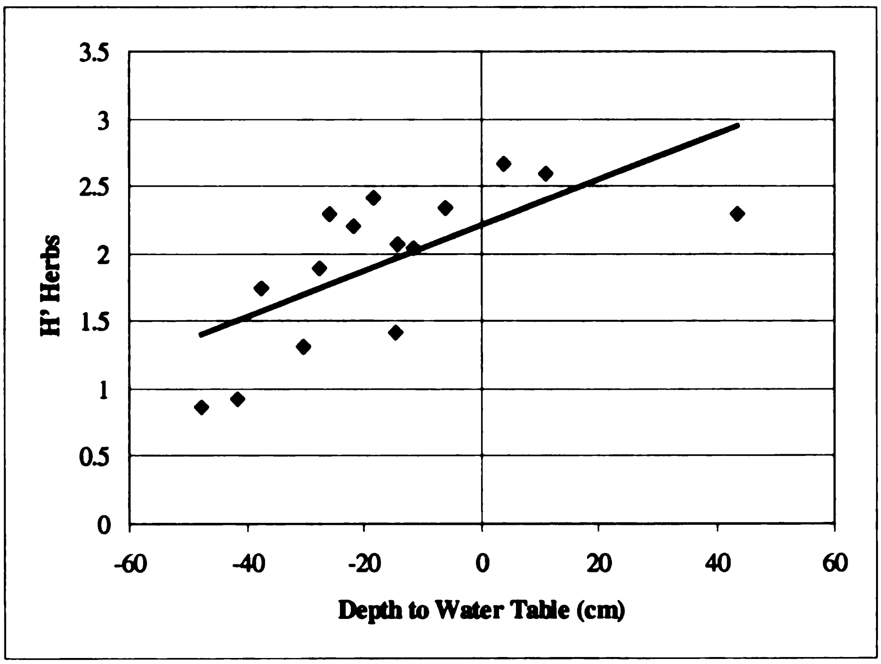


Figure 3-15. The relationship between the Shannon diversity of the herbaceous vegetation and the elevation of the wetpanne basin relative to the water table ($r = 0.680$; $p=0.005$). Negative numbers represent water levels below ground, and positive values indicate surface water.

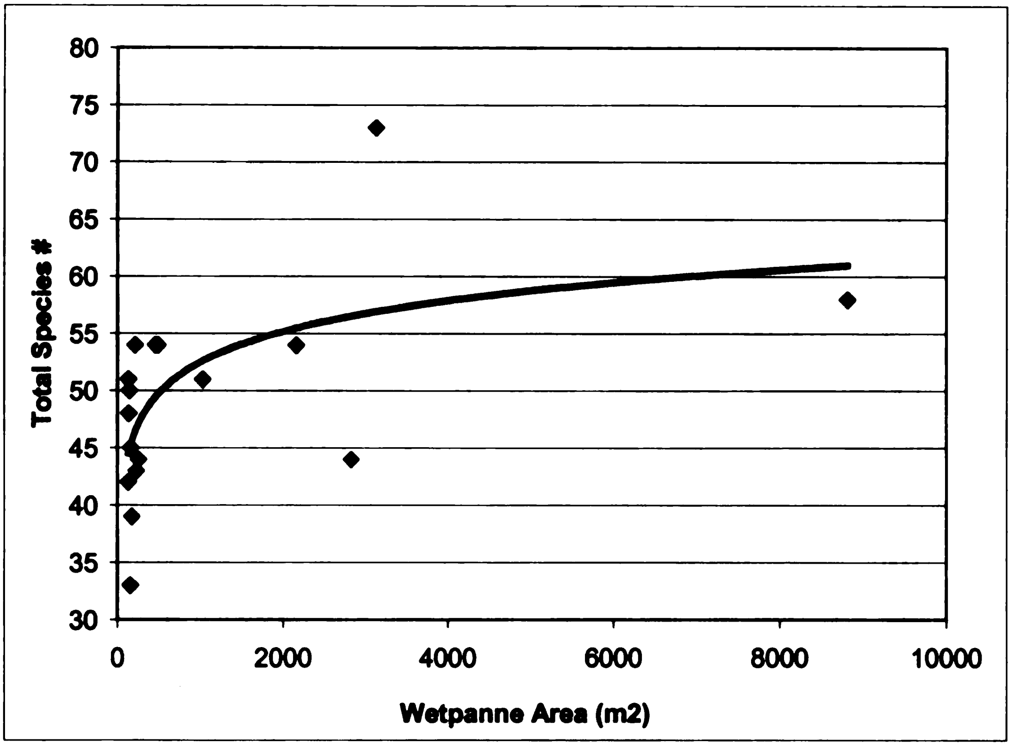


Figure 3-16. The relationship between the total number of species per wetpanne and the wetpanne area ($r = 0.706$; $p=0.003$).

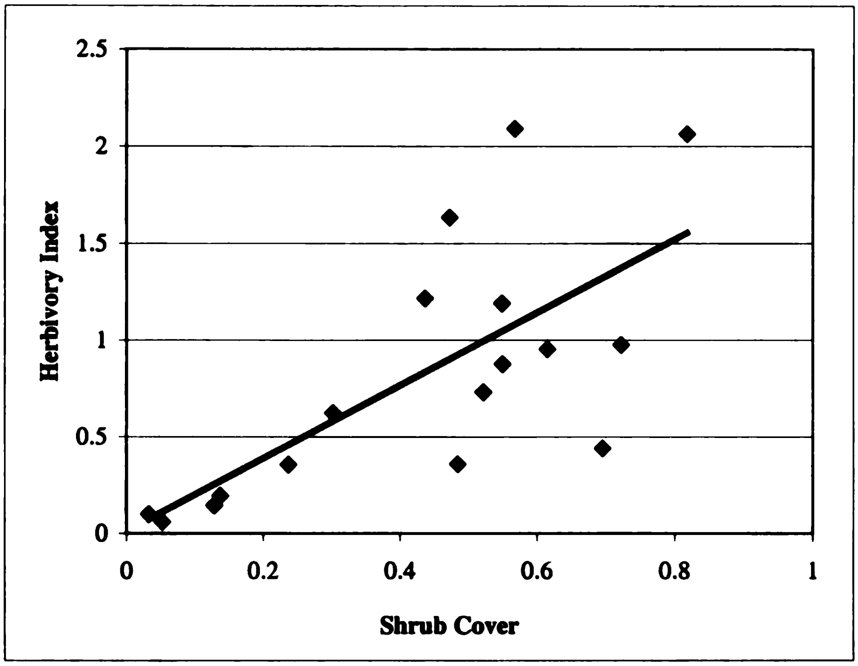


Figure 3-17. The relationship between the index of herbivory and the total shrub cover in each wetpanne (r = 0.649; p=0.009). The herbivory index ranges from 0 = "undamaged" to 3 = "severely stunted."

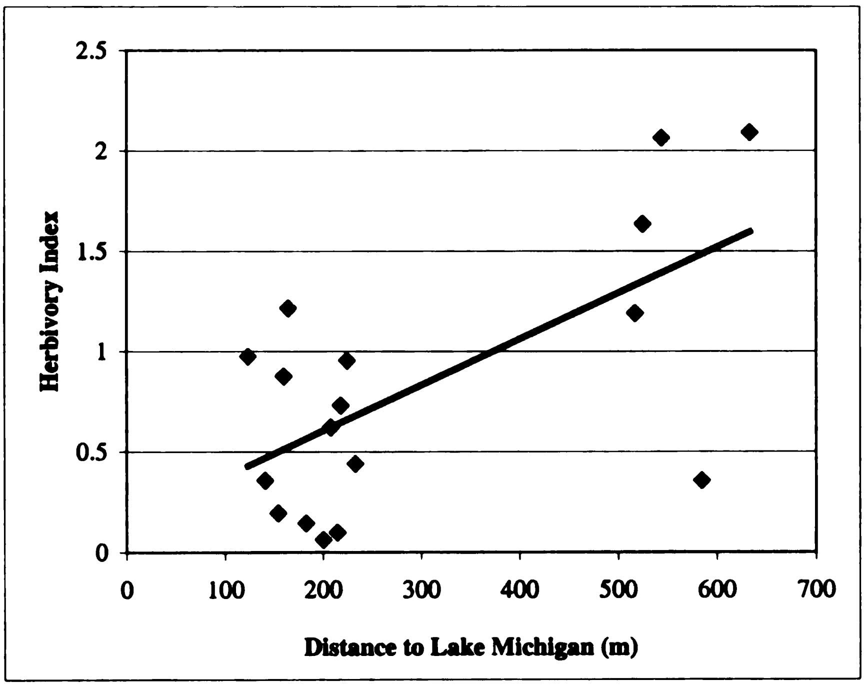


Figure 3-18. The relationship between the index of herbivory and the distance to Lake Michigan (r = 0.809; p<0.001). The herbivory index ranges from 0 = "undamaged" to 3 = "severely stunted."

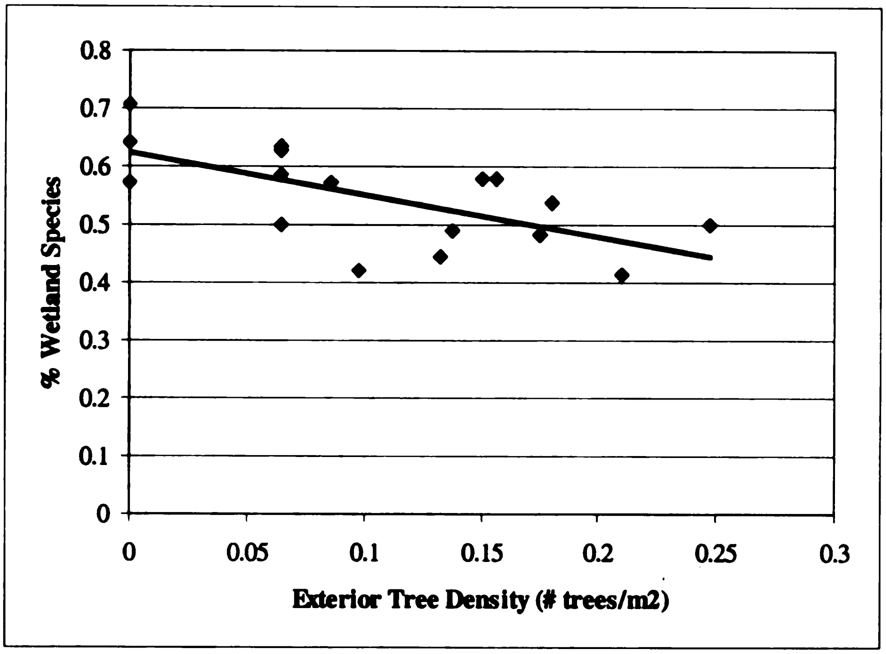


Figure 3-19. The relationship between the percent wetland indicator species and the estimated total tree density within an 11.3 m belt surrounding each wetpanne (r = -0.630; p=0.012).

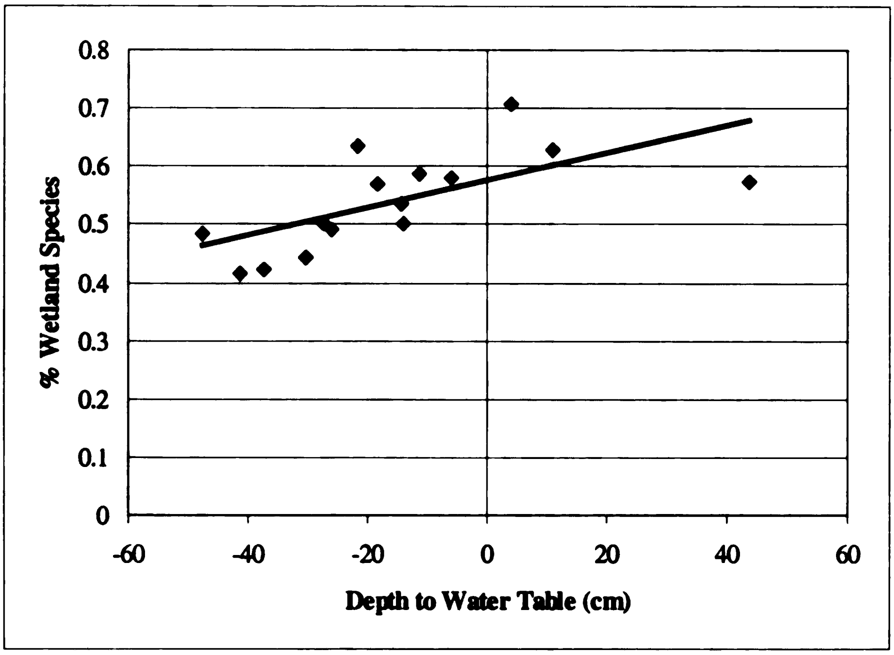


Figure 3-20. The relationship between the percent wetland indicator species and the elevation of the wetpanne basin relative to the water table (r = 0.651; p=0.009). Negative numbers represent below ground water levels, and positive values indicate surface water.

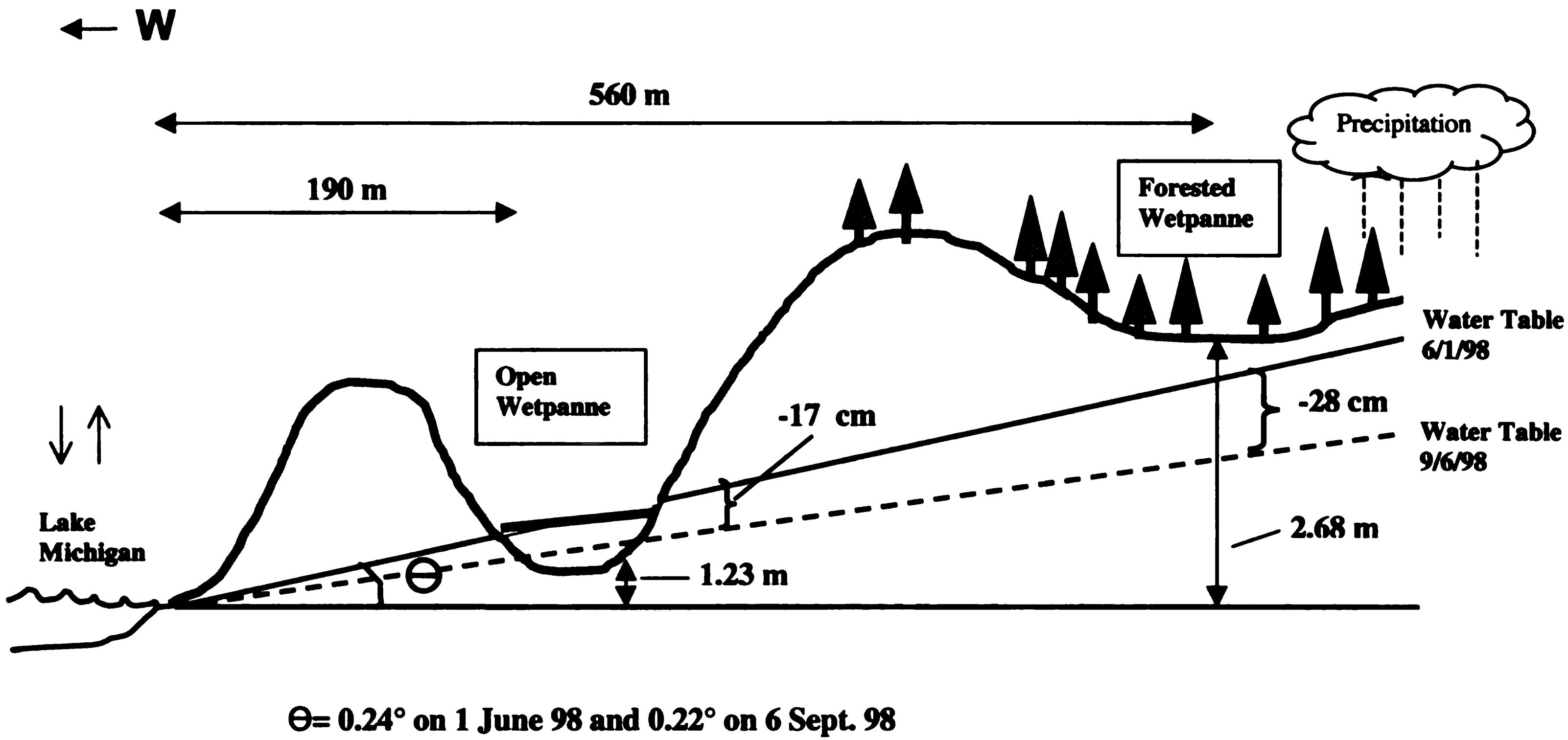


Figure 3-22. A profile of the water table. Note that the water table slopes towards Lake Michigan. Also note that the drop in water table over the course of a season is greater in sites that are further from the lake.

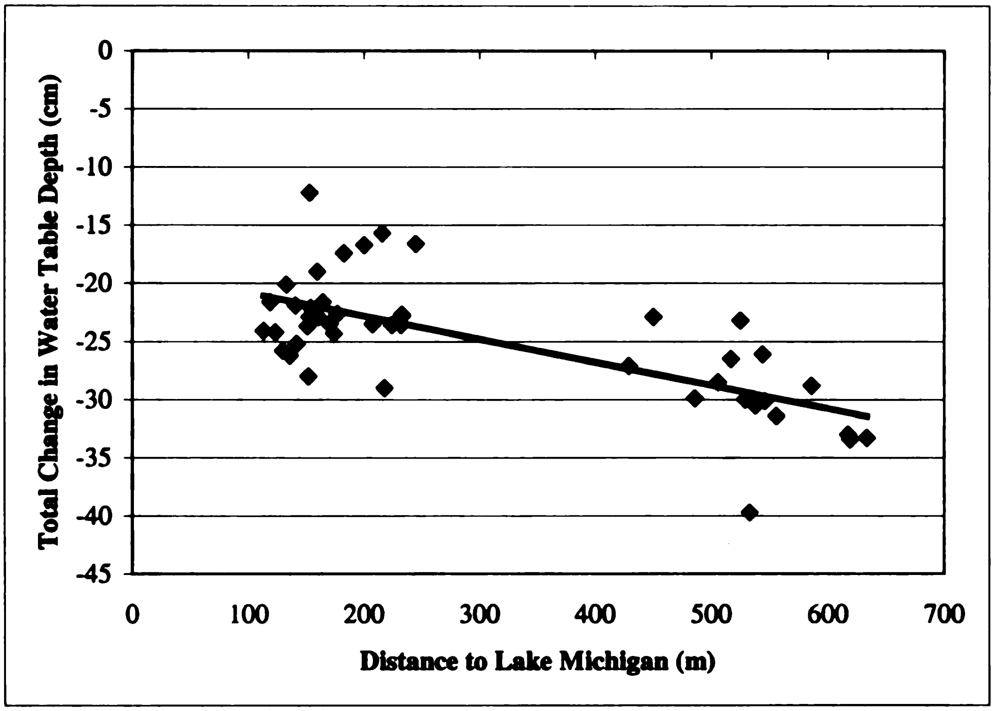


Figure 3-23. The relationship between the total change in water table depth from 1 June 1998 to 6 September 1998, and the distance to Lake Michigan ($r = -0.630$; $p = 0.0029$). A negative change indicates a drop in water level.

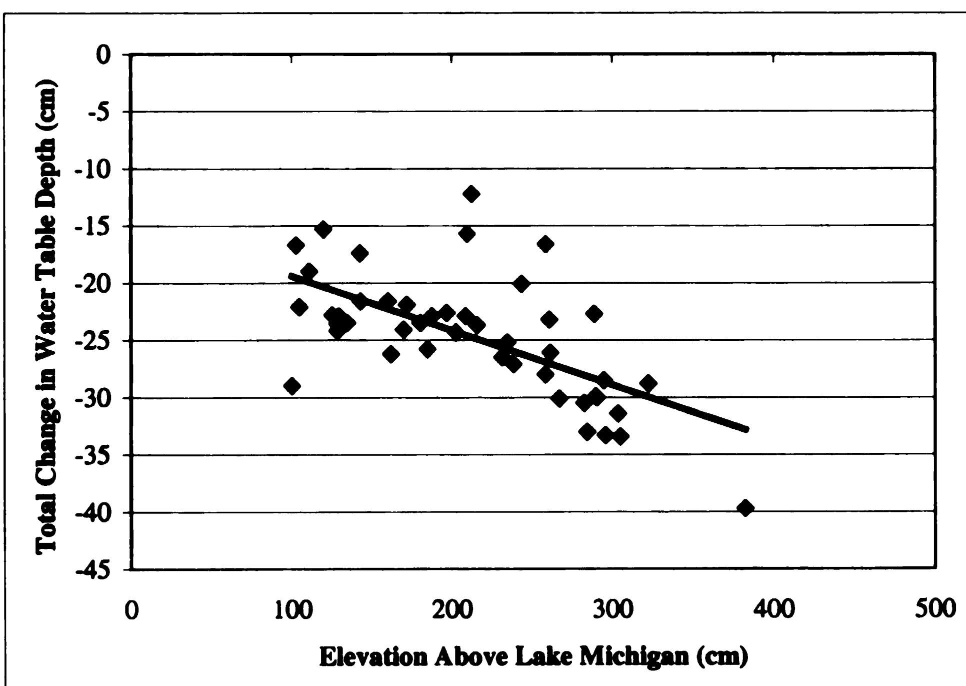


Figure 3-24. The relationship between the total change in water table from 1 June 1998 to 6 September 1998, and the elevation of the ground surface above Lake Michigan ($r = -0.660$; $p < 0.0001$). A negative change indicates a drop in water level.

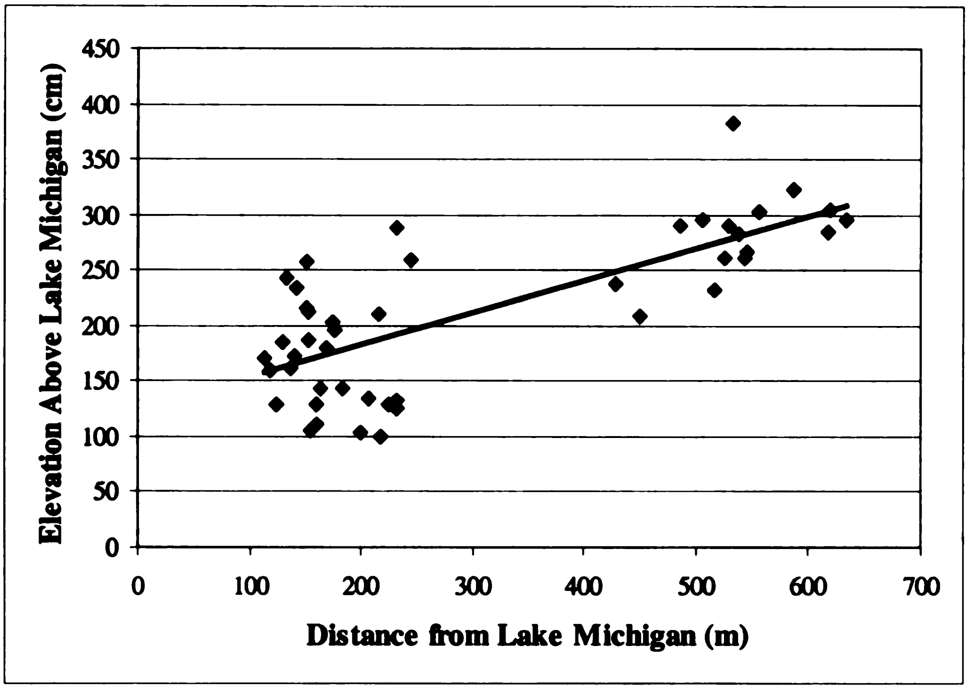


Figure 3-25. The relationship between the elevation of a well above the surface of Lake Michigan and its distance from Lake Michigan ($r = 0.945$; $p < 0.0001$).

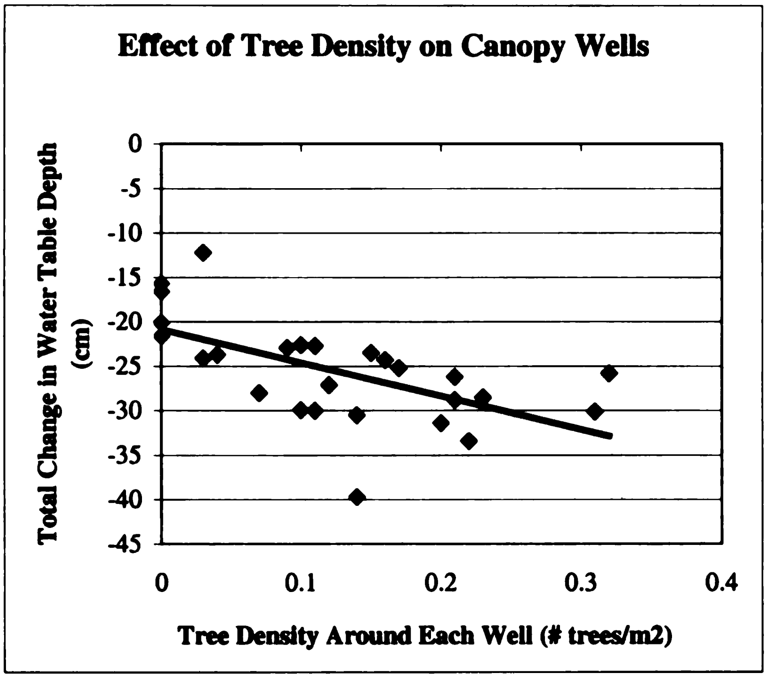


Figure 3-26. The relationship between the total change in water table depth from 1 June 1998 to 6 September 1998, and the density of trees within a 100 m^2 plot surrounding each canopy well ($r = -0.591$; $p = 0.0015$).

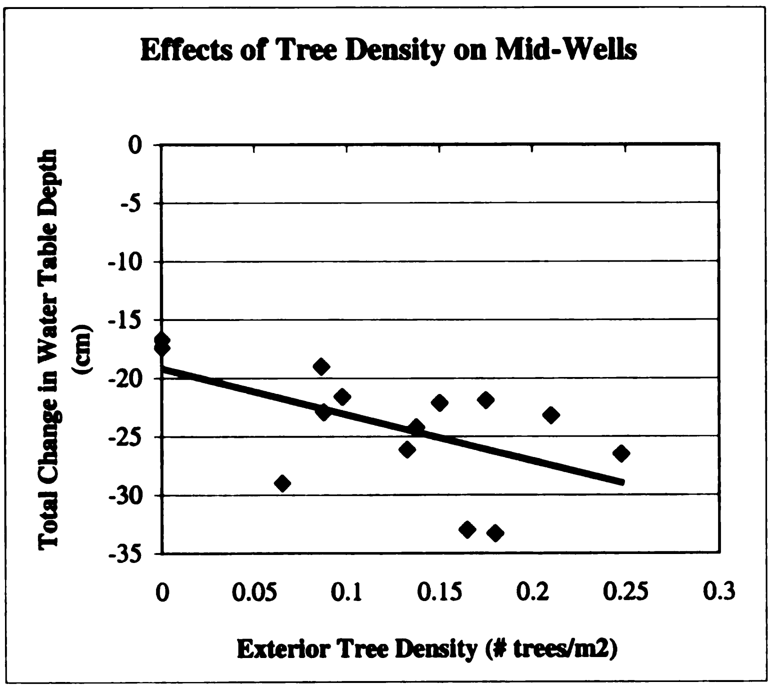


Figure 3-27. The relationship between the total change in water table depth from 1 June 1998 to 6 September 1998 in the mid-wells, and the estimated density of trees within an 11.3 m belt surrounding each wetpanne ($r = -0.561$; $p = 0.0367$).

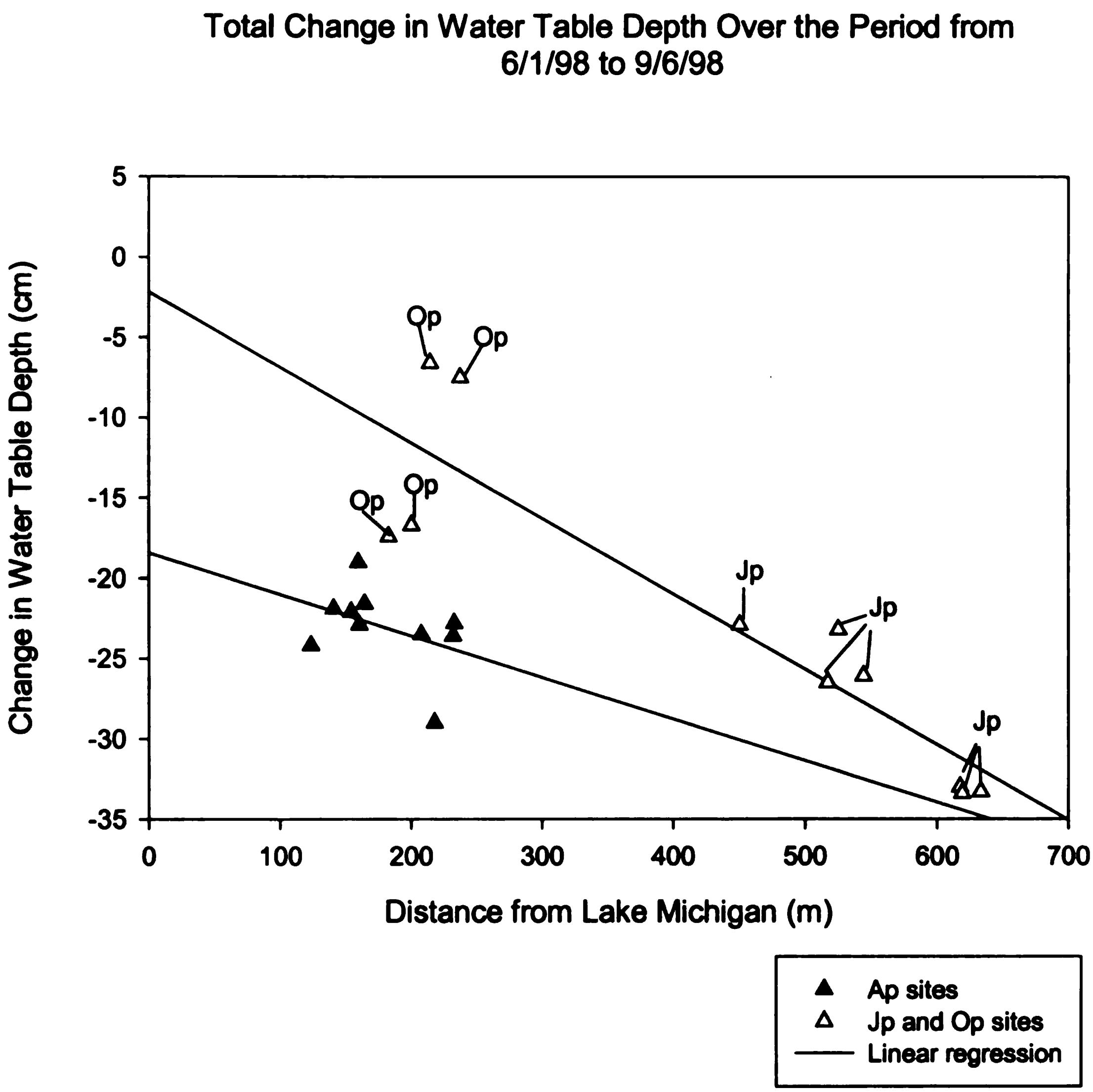


Figure 3-28. An ANCOVA using distance from Lake Michigan as the covariate to test for differences in the total seasonal change in water table depth in Austrian pine wetpannes and in wetpannes without Austrian pines. The elevation of the regression line for Austrian pine (Ap) wetpannes is significantly higher than the regression line for the jack pine (Jp) and open (Op) wetpannes ($p < 0.0001$). The interaction between the slopes of the lines was not significant.

Figure 3-29. Specific conductance values for all wetpannes. Wetpannes E and F have distinctly lower values. (Mid Ap = groundwater sample from the mid-wells in the Austrian pine wetpannes; Mid Jp = groundwater samples from mid-wells in jack pine wetpannes; Op Surface = surface water samples from open wetpannes; Lmich = surface water from Lake Michigan; and River = surface water from the Kalamazoo River oxbow lake.)

Figure 3-30. Alkalinity concentrations for all wetpannes. Wetpannes E and F have distinctly lower values. (Mid Ap = groundwater sample from the mid-wells in the Austrian pine wetpannes; Mid Jp = groundwater samples from mid-wells in jack pine wetpannes; Op Surface = surface water samples from open wetpannes; Lmich = surface water from Lake Michigan; and River = surface water from the Kalamazoo River oxbow lake.)

Figure 3-31. The pH values for all wetpannes. Wetpannes E and F have distinctly lower values. (Mid Ap = groundwater sample from the mid-wells in the Austrian pine wetpannes; Mid Jp = groundwater samples from mid-wells in jack pine wetpannes; Op Surface = surface water samples from open wetpannes; Lmich = surface water from Lake Michigan; and River = surface water from the Kalamazoo River oxbow lake.)

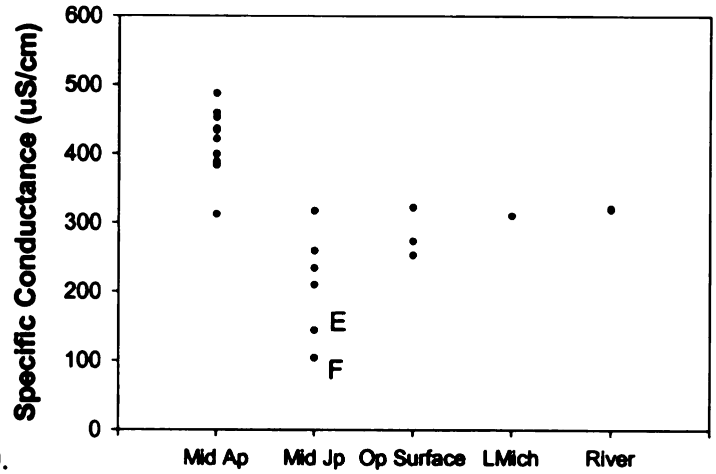


Figure 3-29.

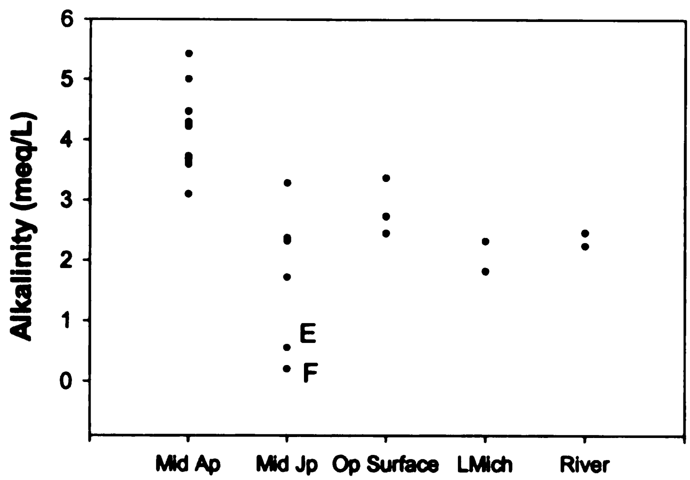


Figure 3-30.

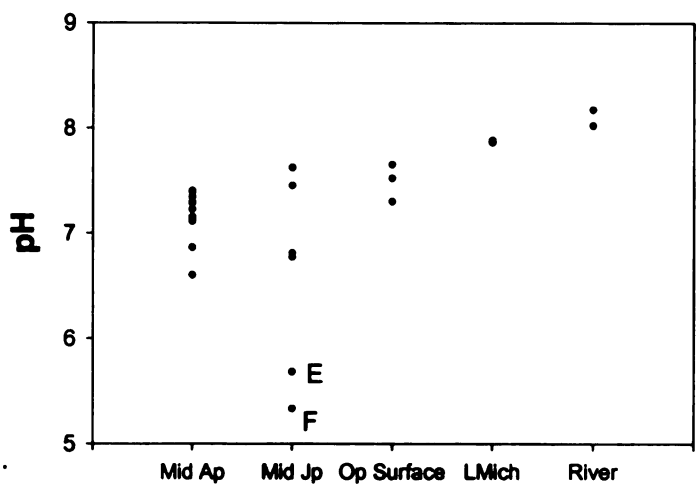


Figure 3-31.

Figure 3-32. Concentration of calcium ions (Ca^{2+}) for all wetpannes. Values for wetpannes E and F are distinctly lower. (Mid Ap = groundwater sample from the mid-wells in the Austrian pine wetpannes; Mid Jp = groundwater samples from mid-wells in jack pine wetpannes; Op Surface = surface water samples from open wetpannes; Lmich = surface water from Lake Michigan; and River = surface water from the Kalamazoo River oxbow lake.)

Figure 3-33. Concentration of magnesium ions (Mg^{2+}) for all wetpannes. Values for wetpannes E and F are distinctly lower. (Mid Ap = groundwater sample from the mid-wells in the Austrian pine wetpannes; Mid Jp = groundwater samples from mid-wells in jack pine wetpannes; Op Surface = surface water samples from open wetpannes; Lmich = surface water from Lake Michigan; and River = surface water from the Kalamazoo River oxbow lake.)

Figure 3-34. Concentration of silica (as mg Si/L) for all wetpannes. (Mid Ap = groundwater sample from the mid-wells in the Austrian pine wetpannes; Mid Jp = groundwater samples from mid-wells in jack pine wetpannes; Op Surface = surface water samples from open wetpannes; Lmich = surface water from Lake Michigan; and River = surface water from the Kalamazoo River oxbow lake.)

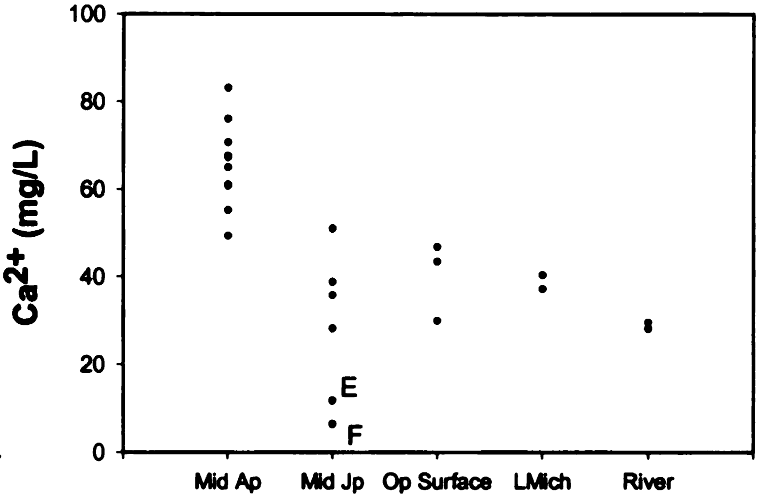


Figure 3-32.

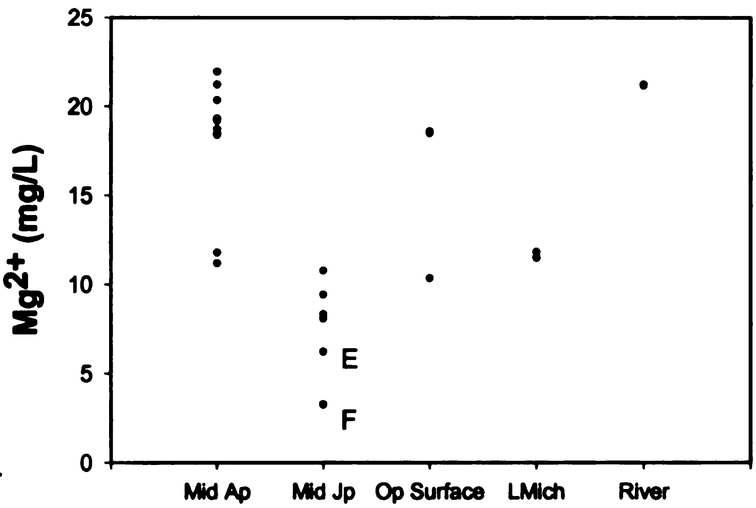


Figure 3-33.

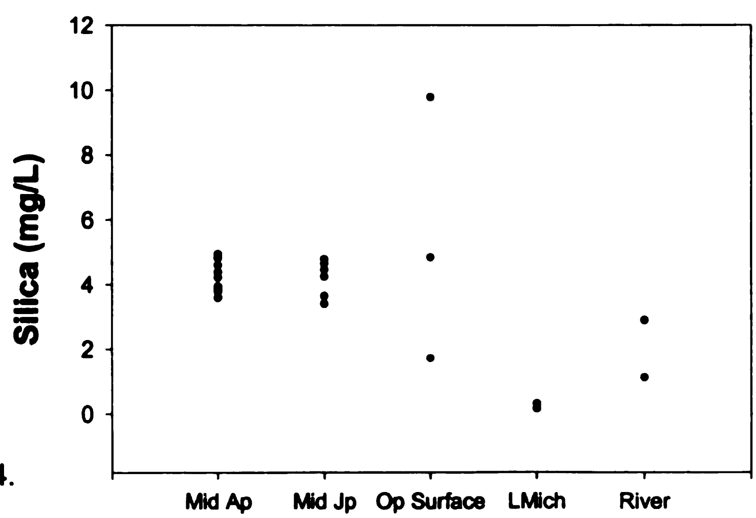


Figure 3-34.

Figure 3-35. Concentration of sodium ions (Na^+) for all wetpannes. Values for wetpannes E and F are distinctly higher. (Mid Ap = groundwater sample from the mid-wells in the Austrian pine wetpannes; Mid Jp = groundwater samples from mid-wells in jack pine wetpannes; Op Surface = surface water samples from open wetpannes; Lmich = surface water from Lake Michigan; and River = surface water from the Kalamazoo River oxbow lake.)

Figure 3-36. Concentration of chloride ions (Cl^-) for all wetpannes. (Mid Ap = groundwater sample from the mid-wells in the Austrian pine wetpannes; Mid Jp = groundwater samples from mid-wells in jack pine wetpannes; Op Surface = surface water samples from open wetpannes; Lmich = surface water from Lake Michigan; and River = surface water from the Kalamazoo River oxbow lake.)

Figure 3-37. Concentration of potassium ions (K^+) for all wetpannes. Values for wetpannes E and F are distinctly higher. (Mid Ap = groundwater sample from the mid-wells in the Austrian pine wetpannes; Mid Jp = groundwater samples from mid-wells in jack pine wetpannes; Op Surface = surface water samples from open wetpannes; Lmich = surface water from Lake Michigan; and River = surface water from the Kalamazoo River oxbow lake.)

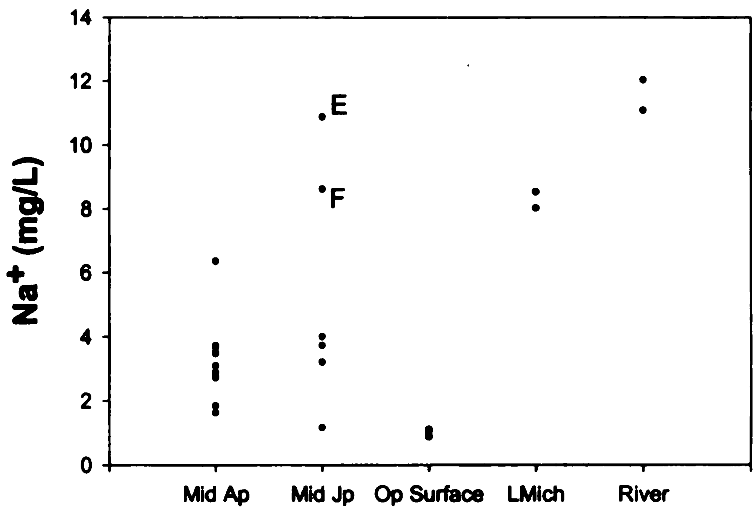


Figure 3-35.

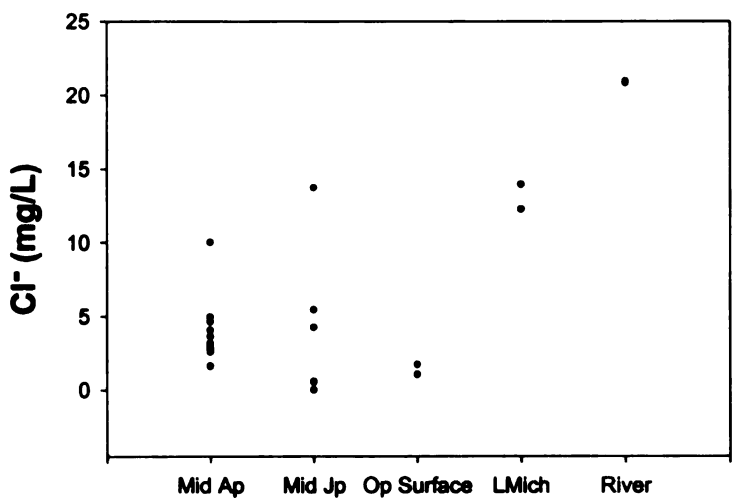


Figure 3-36.

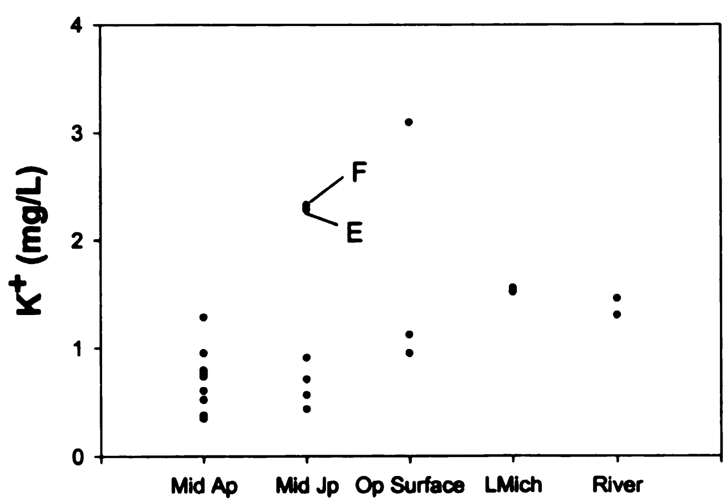


Figure 3-37.

Figure 3-38. Concentration of sulfate (SO_4^{2-}) for all wetpannes. (Mid Ap = groundwater sample from the mid-wells in the Austrian pine wetpannes; Mid Jp = groundwater samples from mid-wells in jack pine wetpannes; Op Surface = surface water samples from open wetpannes; Lmich = surface water from Lake Michigan; and River = surface water from the Kalamazoo River oxbow lake.)

Figure 3-39. Concentration of total dissolved phosphorus (TDP) for all wetpannes. Values for wetpannes E and F are distinctly higher. (Mid Ap = groundwater sample from the mid-wells in the Austrian pine wetpannes; Mid Jp = groundwater samples from mid-wells in jack pine wetpannes; Op Surface = surface water samples from open wetpannes; Lmich = surface water from Lake Michigan; and River = surface water from the Kalamazoo River oxbow lake.)

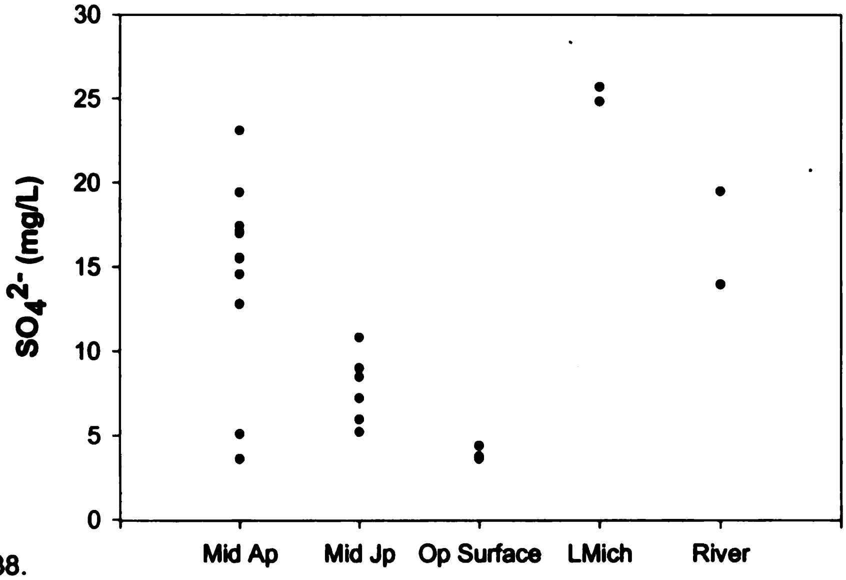


Figure 3-38.

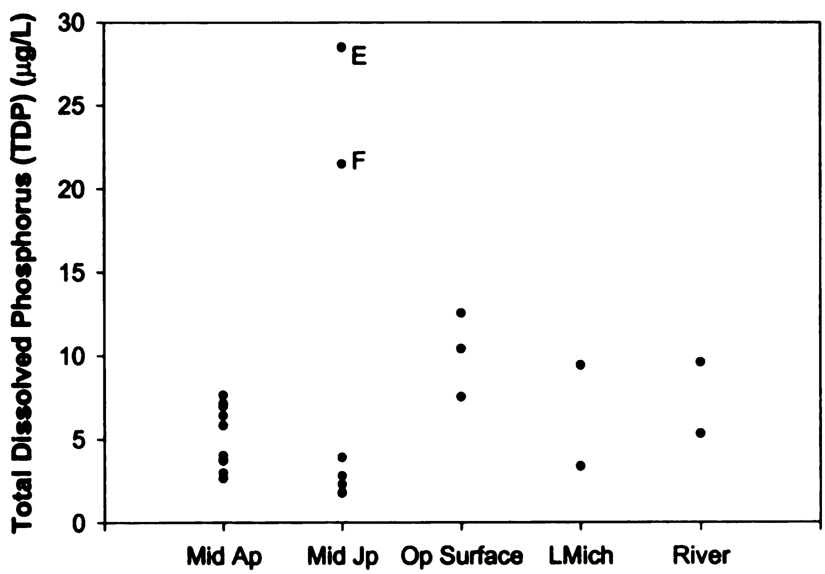


Figure 3-39.

Figure 3-40. Concentration of ammonium (NH_4^+-N) for all wetpannes. Values for wetpannes E and F are distinctly higher. (Mid Ap = groundwater sample from the mid-wells in the Austrian pine wetpannes; Mid Jp = groundwater samples from mid-wells in jack pine wetpannes; Op Surface = surface water samples from open wetpannes; Lmich = surface water from Lake Michigan; and River = surface water from the Kalamazoo River oxbow lake.)

Figure 3-41. Concentration of nitrate (NO_3-N) for all wetpannes. (Mid Ap = groundwater sample from the mid-wells in the Austrian pine wetpannes; Mid Jp = groundwater samples from mid-wells in jack pine wetpannes; Op Surface = surface water samples from open wetpannes; Lmich = surface water from Lake Michigan; and River = surface water from the Kalamazoo River oxbow lake.)

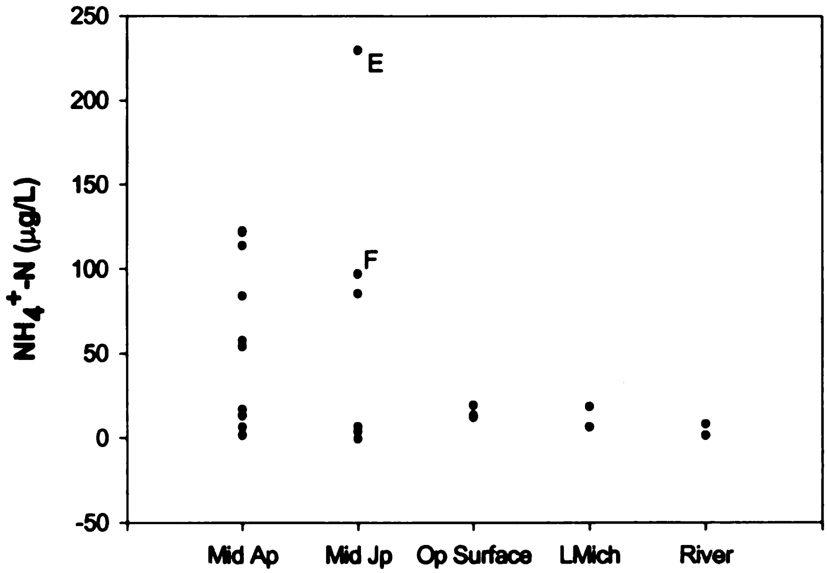


Figure 3-40.

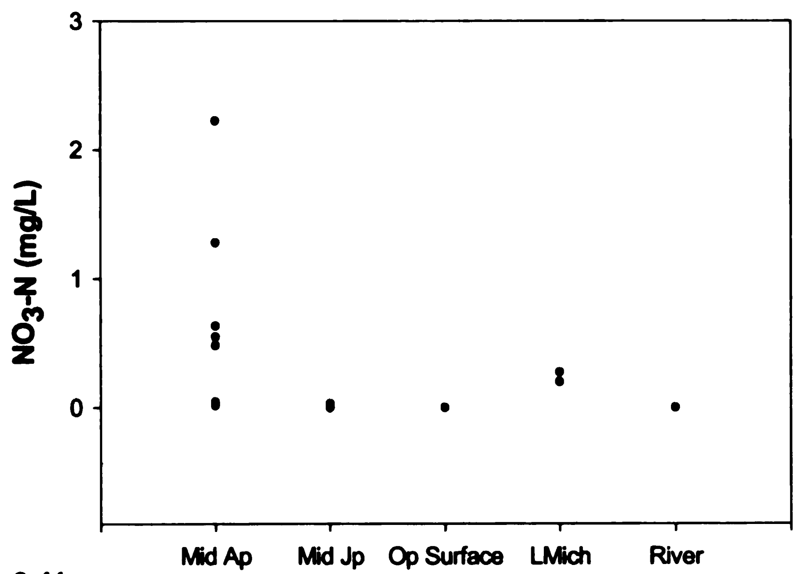


Figure 3-41.

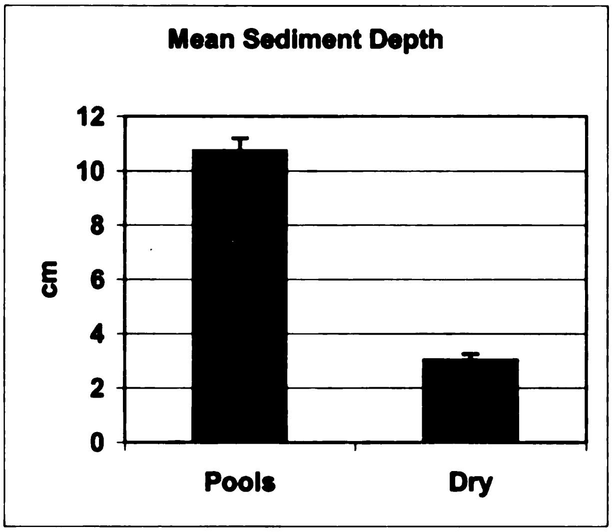


Figure 3-42. The mean sediment depths of all wetpannes that had standing water ("Pools") and of those that were dry ("Dry") during the 1998 growing season. Standard error bars are shown.

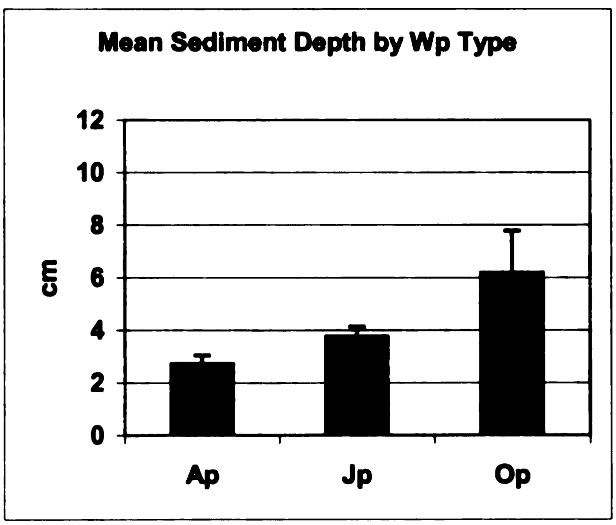


Figure 3-43. The mean sediment depths of the different wetpanne types. (Ap= Austrian pine wetpannes; Jp= Jack pine wetpannes; Op= Open, treeless wetpannes). Standard error bars are shown.

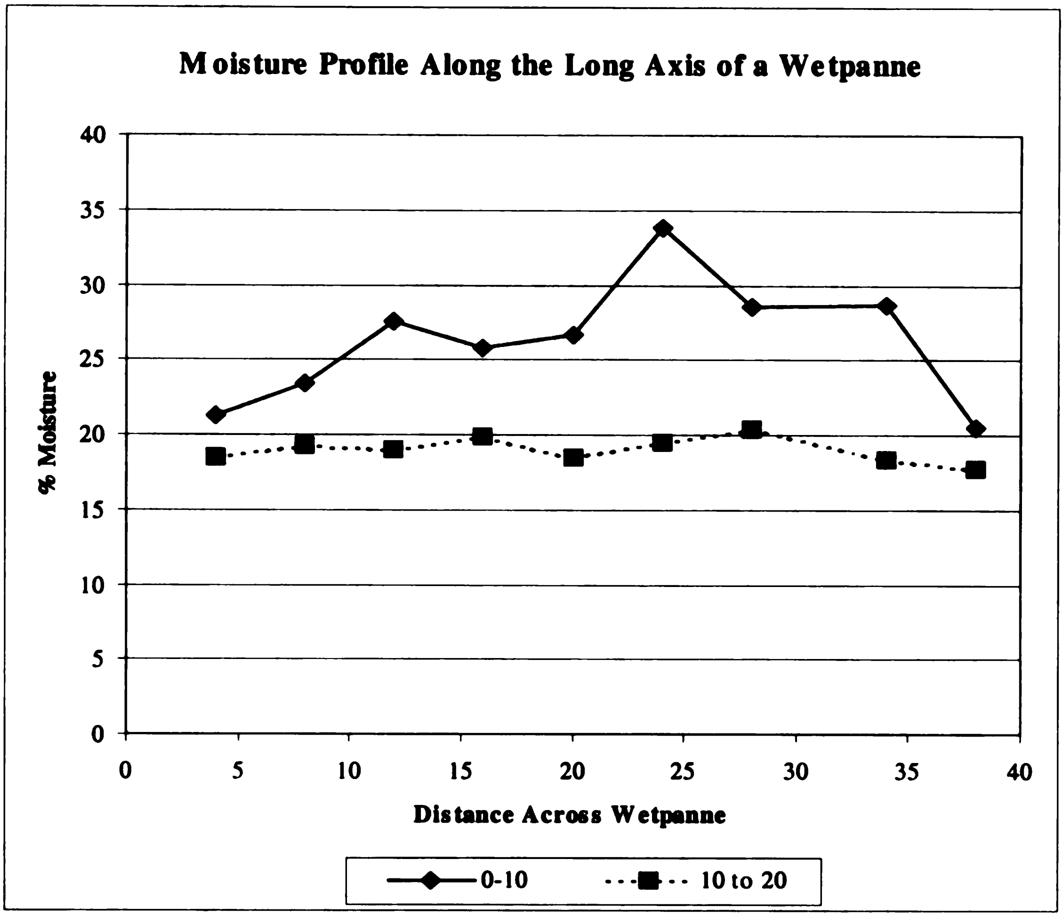


Figure 3-44. The percent moisture values of wetpanne sediment at different depths along a transect bisecting the long axis of a single wetpanne. Moisture levels were higher in the top 10 cm of the wetpanne sediment than in the lower 10 cm of sediment (>10 to 20 cm).

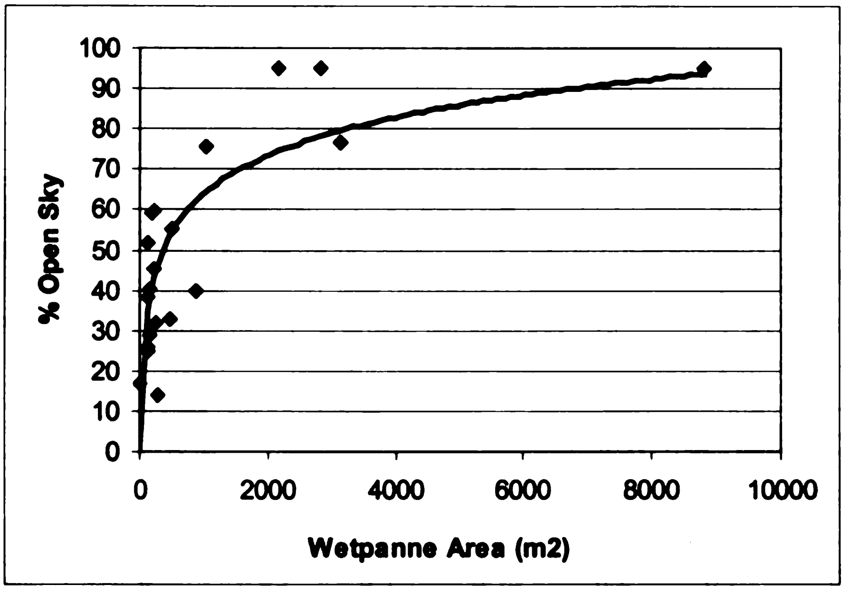


Figure 3-45. The relationship between the percent open sky in the center of the wetpanne and wetpanne area ($r = 0.803$; $p = 0.0008$). Percent open sky was measured using fish-eye photography.

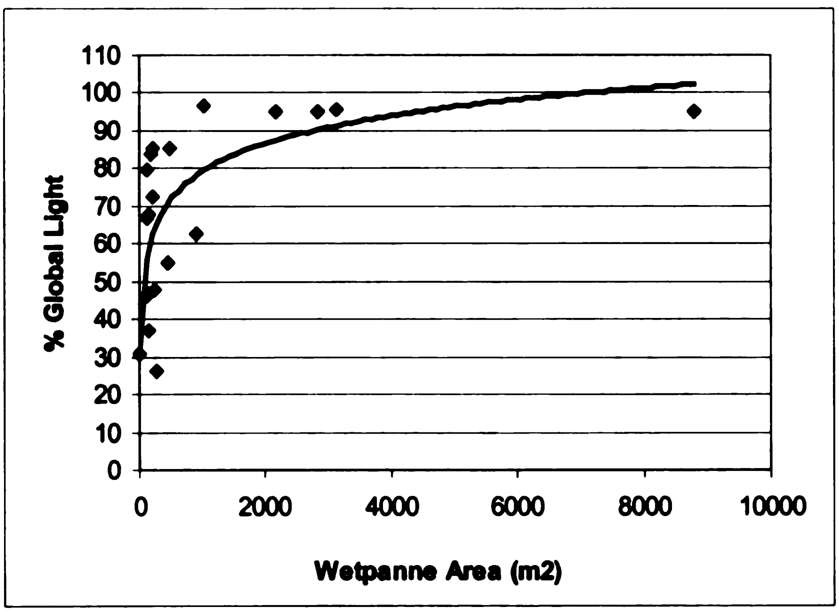


Figure 3-46. The relationship between the percent global light reaching each wetpanne and total wetpanne area ($r = 0.688$; $p = 0.0008$). Global light was measured using fish-eye photography.

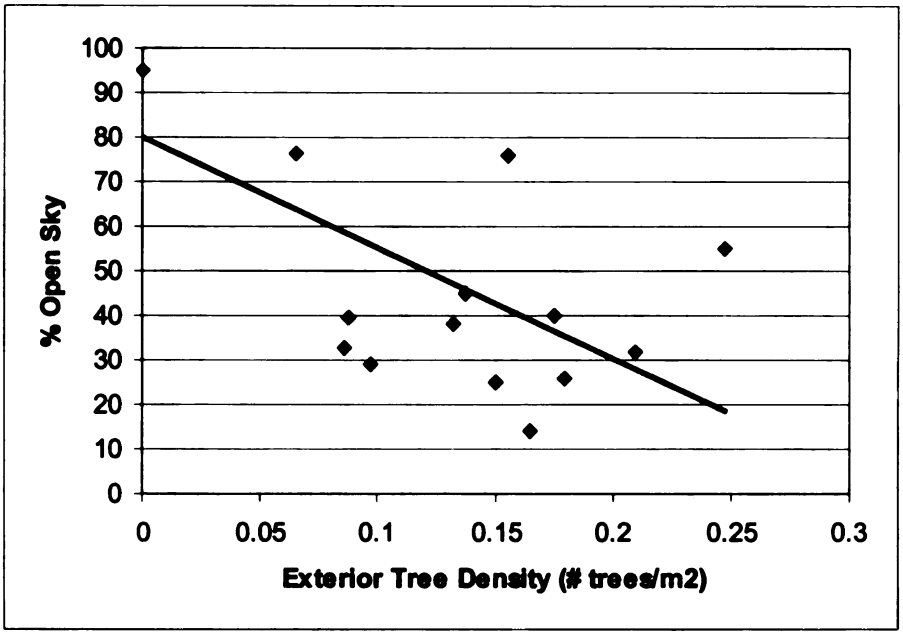


Figure 3-47. The relationship between percent open sky and the estimated density of trees within an 11.3 m belt surrounding each wetpanne ($r = -0.673$; $p = 0.0043$).

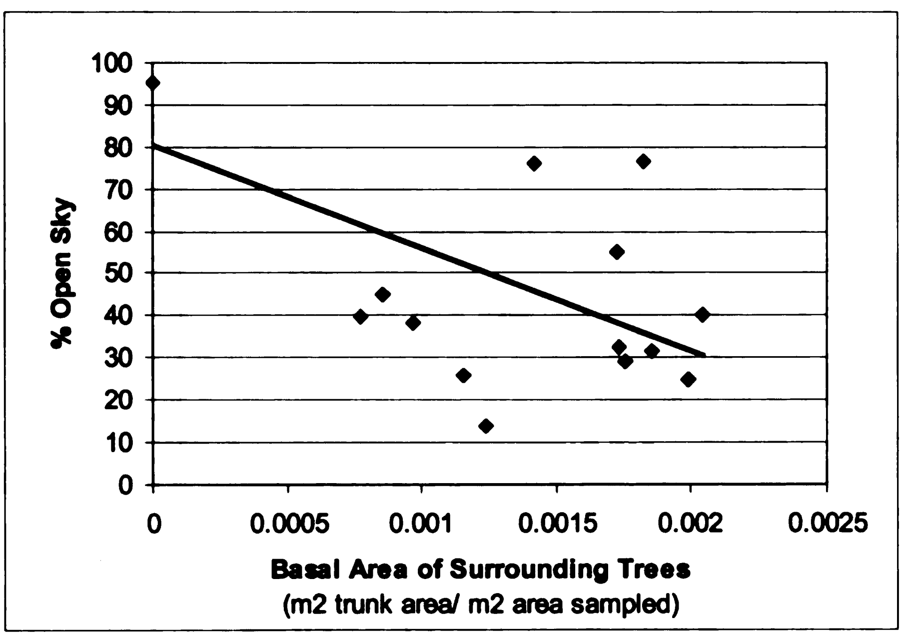


Figure 3-48. The relationship between percent open sky and estimated basal area of trees within an 11.3 m belt surrounding each wetpanne ($r = -0.638$; $p = 0.0078$).

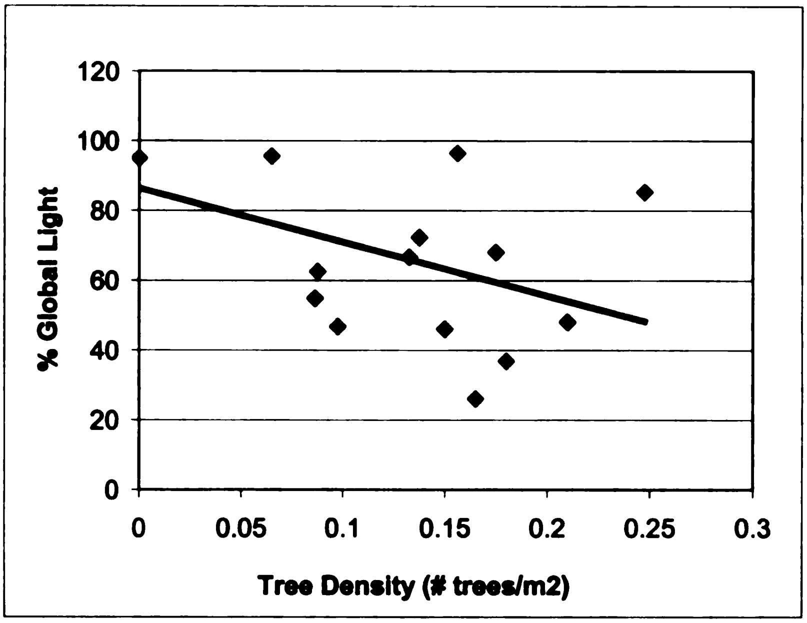


Figure 3-49. The relationship between percent global light and the estimated density of trees within an 11.3 m belt surrounding each wetpanne (r = -0.491; p = 0.0534).

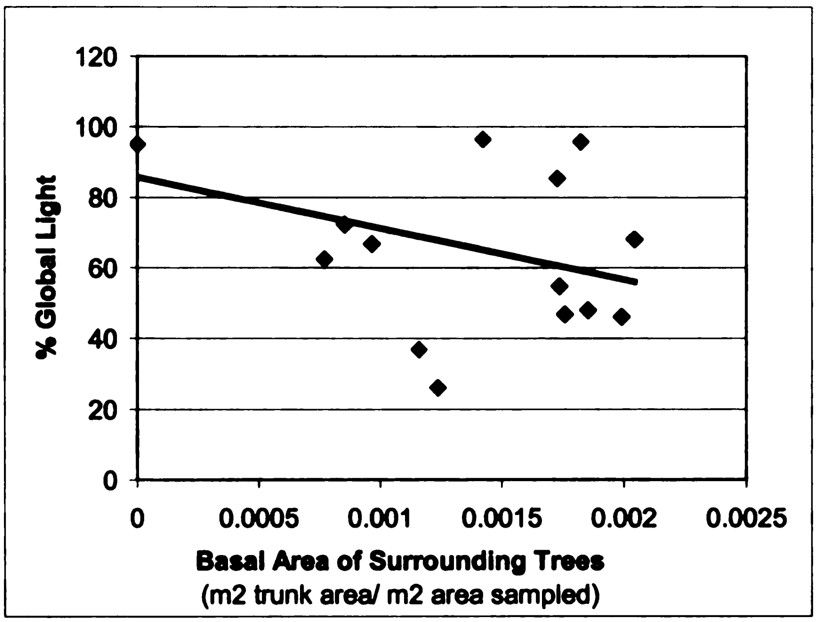


Figure 3-50. The relationship between percent global light and estimated basal area of trees within an 11.3 m belt surrounding each wetpanne (r = -0.443; p = 0.0855).

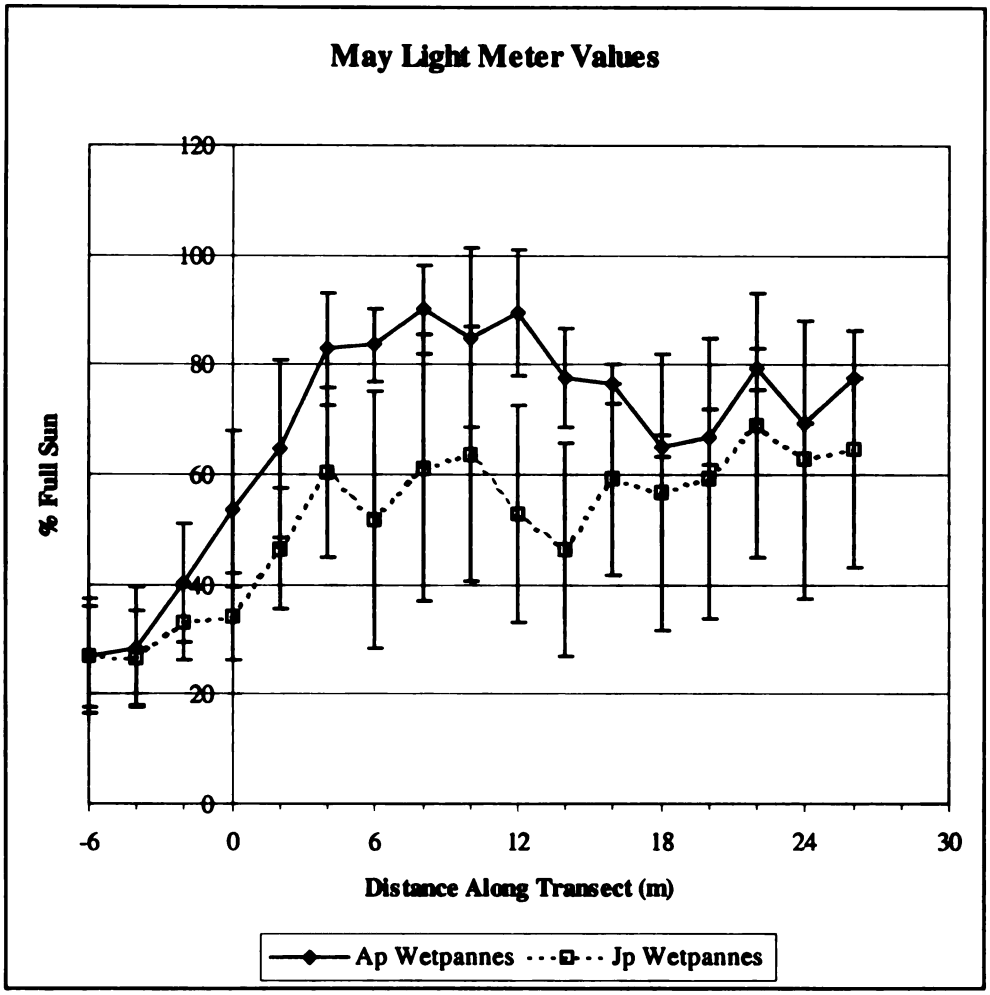


Figure 3-51. Percent full sunlight reaching the wetpanne surface in May. Positions at -6, -4, and -2 meters along the transects are under the surrounding canopy of trees, and the other positions along the transects extend out to the center of the wetpannes. 95% confidence intervals are plotted for each position along the transect. A t-test showed that the light levels in Austrian pine (Ap) wetpannes (n=10) were significantly higher than those in the jack pine (Jp) wetpannes (n=7) at the 4, 6, and 8 meter positions along the transect.

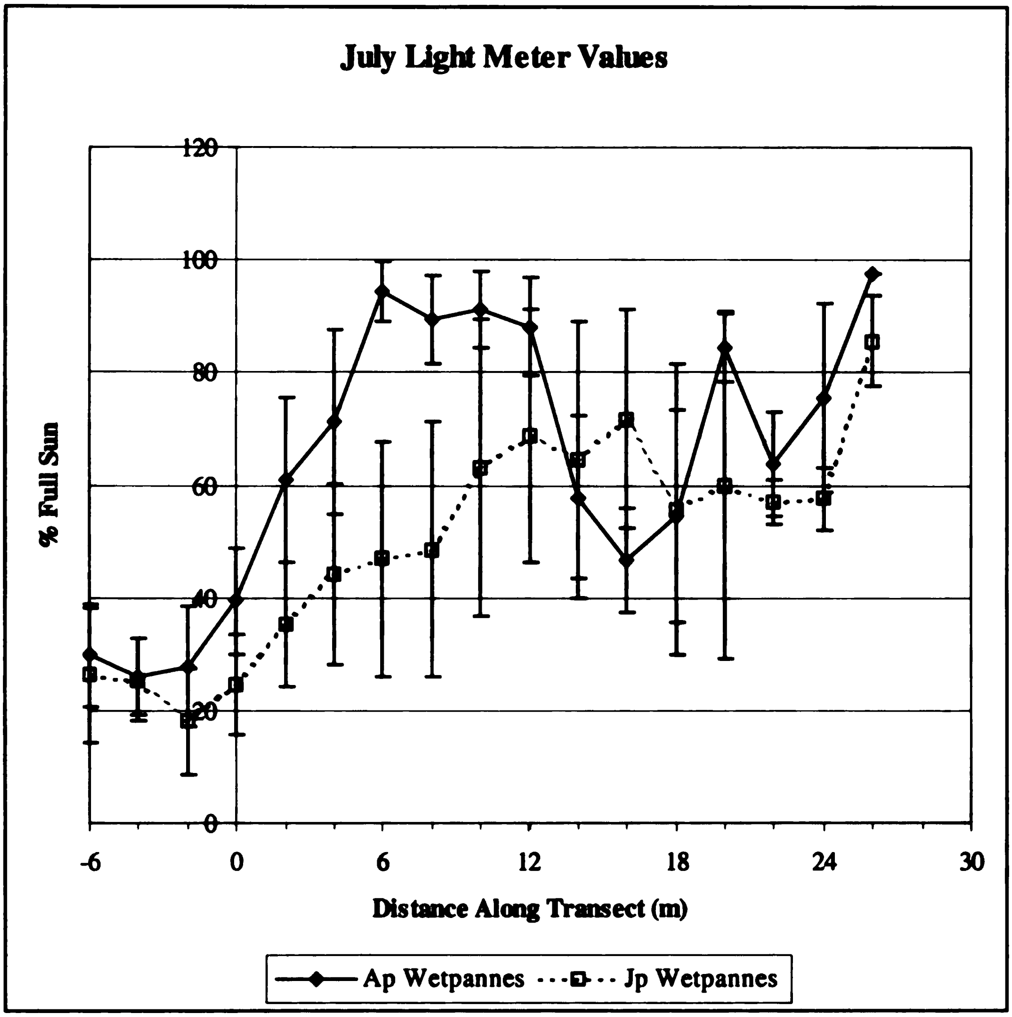


Figure 3-52. Percent full sunlight reaching the wetpanne surface in July. Positions at -6, -4, and -2 meters along the transects are under the surrounding canopy of trees, and the other positions along the transects extend out to the center of the wetpannes. 95% confidence intervals are plotted for each position along the transect. A t-test showed that the light levels in Austrian pine (Ap) wetpannes (n=10) were significantly higher than those in the jack pine (Jp) wetpannes (n=7) at the 0, 2, 4, 6, 8, and 10 meter positions along the transect.

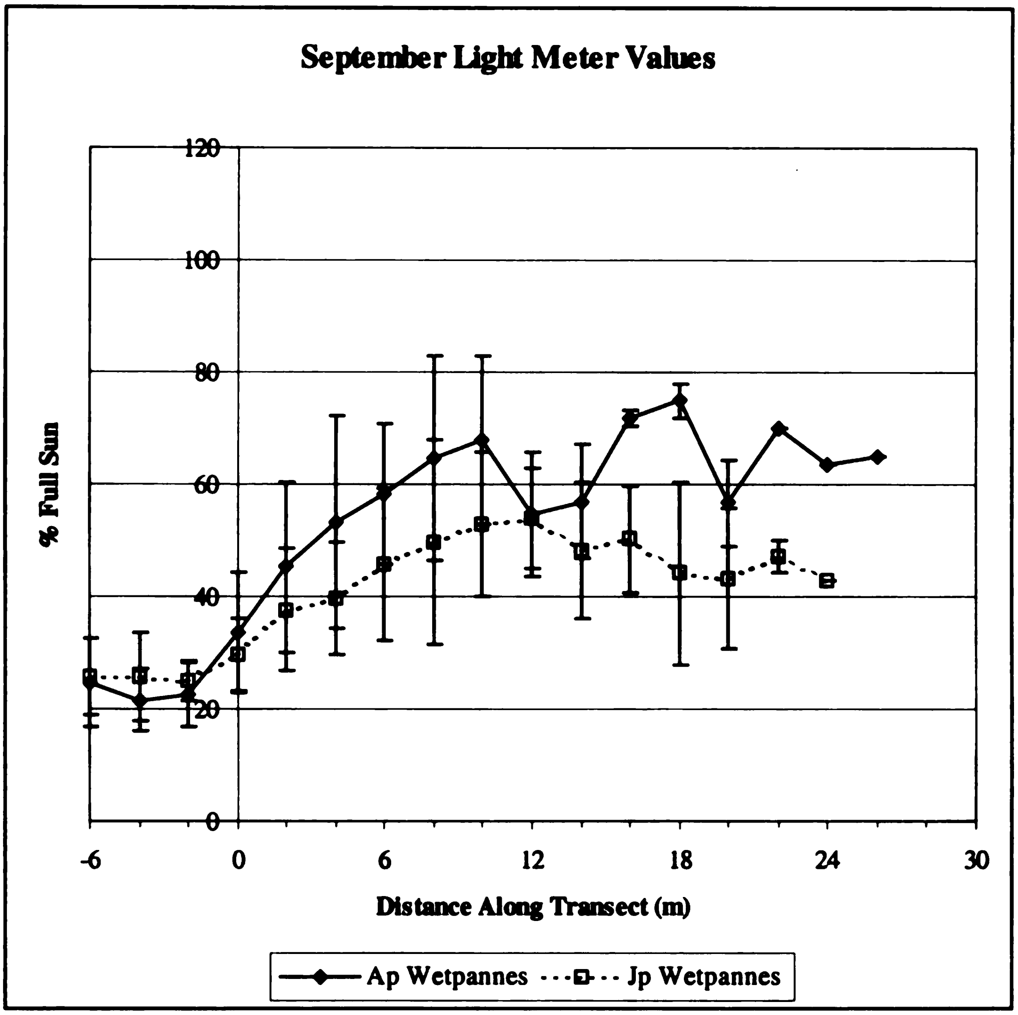
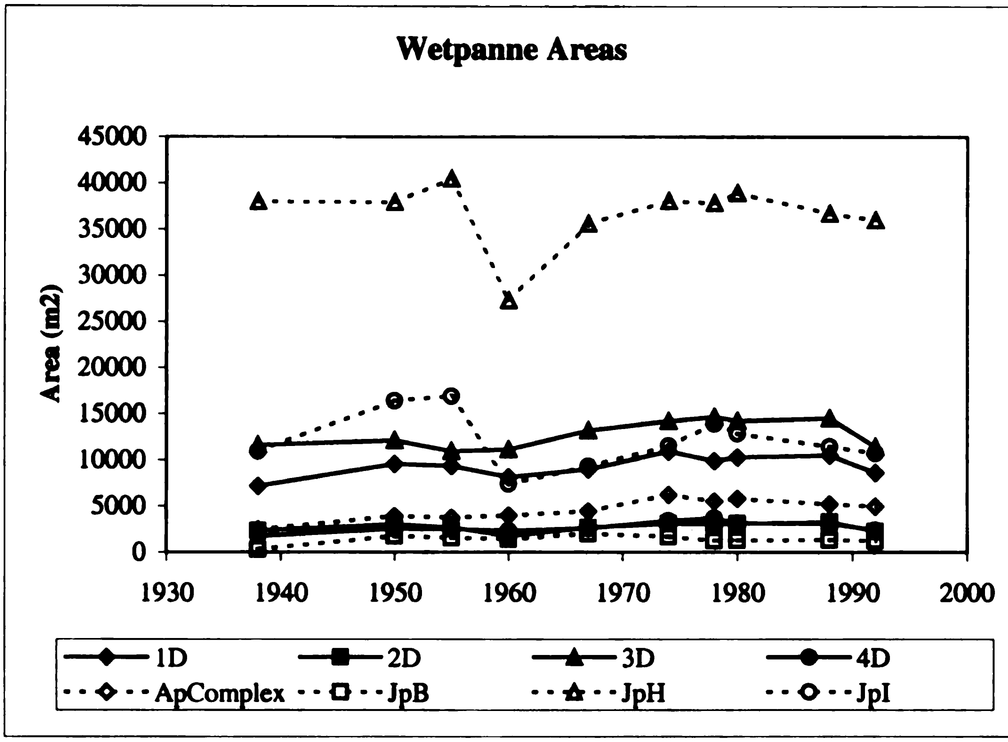


Figure 3-53. Percent full sunlight reaching the wetpanne surface in September. Positions at -6, -4, and -2 meters along the transects are under the surrounding canopy of trees, and the other positions along the transects extend out to the center of the wetpannes. 95% confidence intervals are plotted for each position along the transect. A t-test showed that the light levels in Austrian pine (Ap) wetpannes (n=10) were not significantly higher than those in the jack pine (Jp) wetpannes (n=7) at any position along the transect.

Figure 3-54. Changes in wetpanne areas over time. (1D, 2D, 3D, and 4D are open, treeless wetpannes. ApComplex is the Austrian pine wetpanne. JpB, JpH, and JpI are jack pine wetpannes.)

Figure 3-55. Change in area:perimeter ratios for each wetpanne over time. The area:perimeter ratio is the total area of the wetpanne divided by the length of its perimeter. (1D, 2D, 3D, and 4D are open, treeless wetpannes. ApComplex is the Austrian pine wetpanne. JpB, JpH, and JpI are jack pine wetpannes.)



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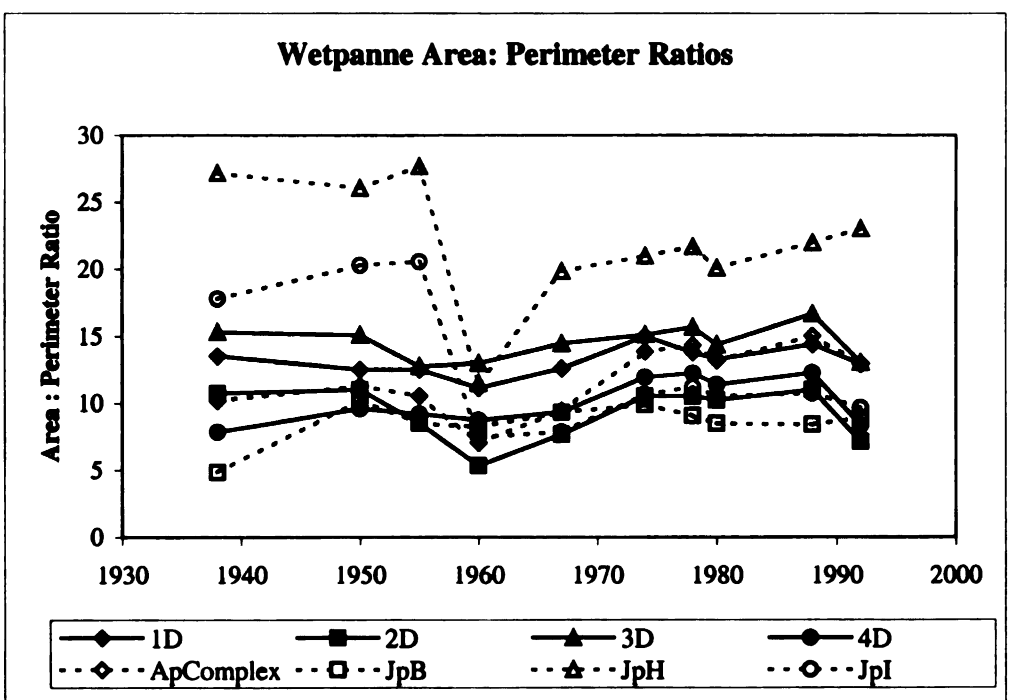

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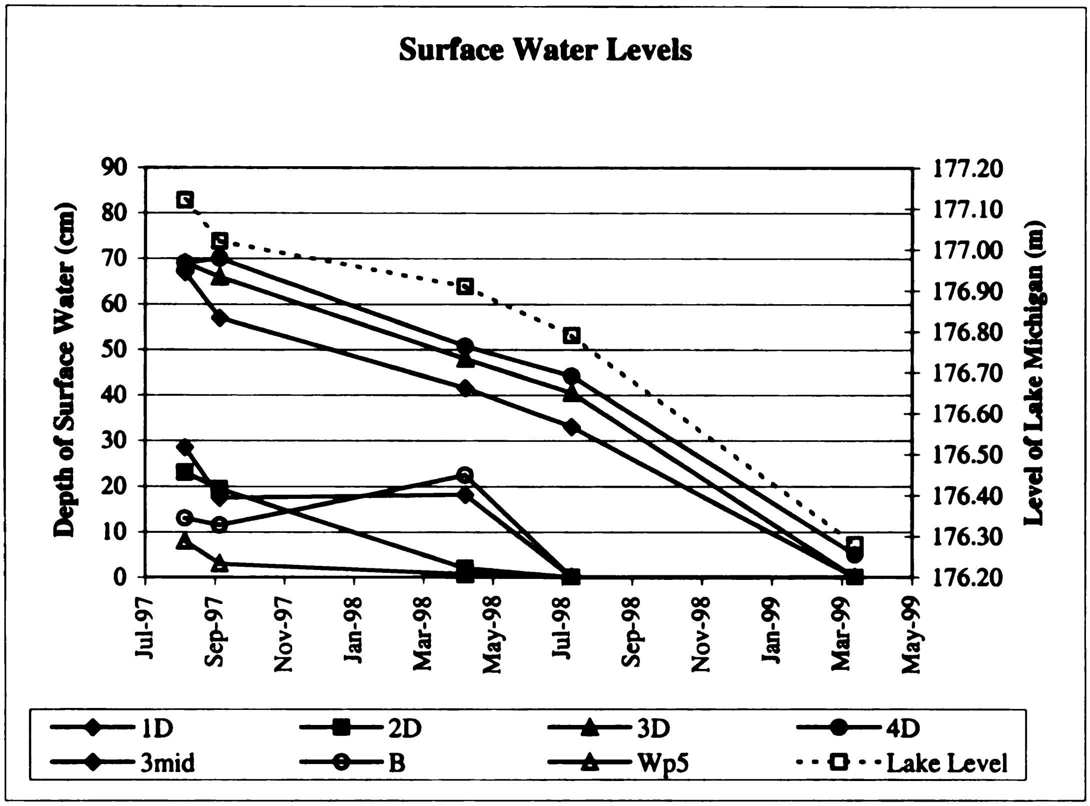
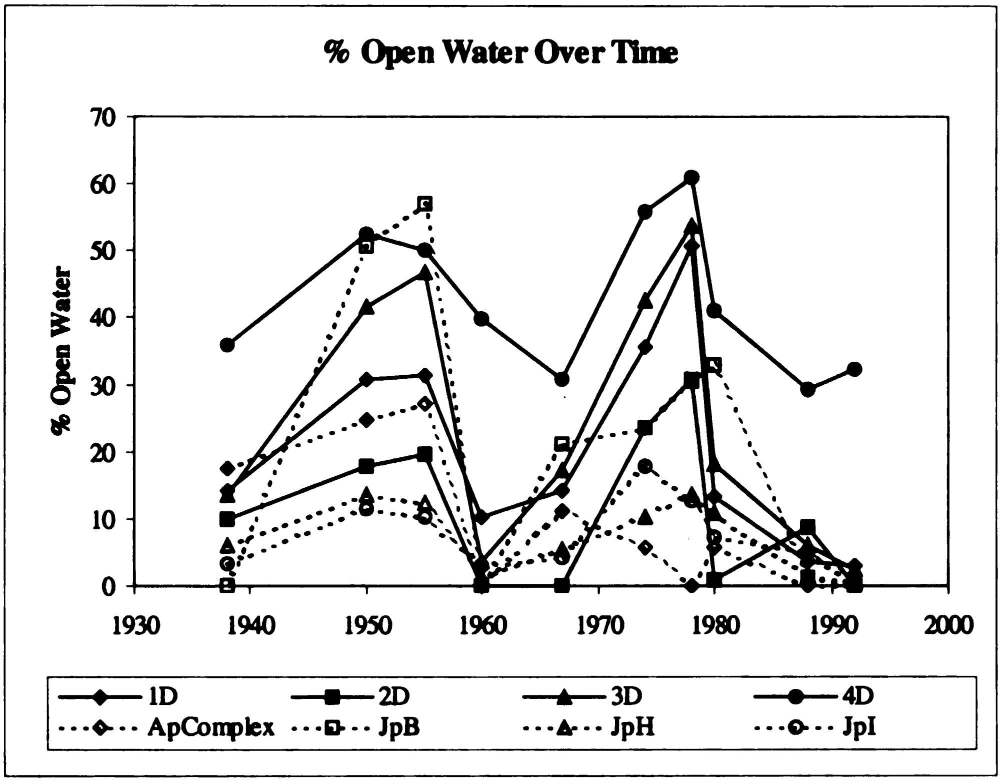


Figure 3-56. Change in surface water levels in wetpannes over the study period. 1D, 2D, 3D, and 4D are open, treeless wetpannes, B is a jack pine wetpanne, and 3mid and Wp5 are Austrian pine wetpannes. The dotted line shows the level of Lake Michigan in meters above sea level (U.S. Army Corps of Engineers, 2/3/3000).

Figure 3-57. Percent open water for each wetpanne over time. Percent open water is the area of open pools of water divided by the total wetpanne area. (1D, 2D, 3D, and 4D are open, treeless wetpannes. ApComplex is the Austrian pine wetpanne. JpB, JpH, and JpI are jack pine wetpannes.)

Figure 3-58. The average percent open water for all wetpannes is shown to clarify the overall trend from year-to-year. (1D, 2D, 3D, and 4D are open, treeless wetpannes. ApComplex is the Austrian pine wetpanne. JpB, JpH, and JpI are jack pine wetpannes.)



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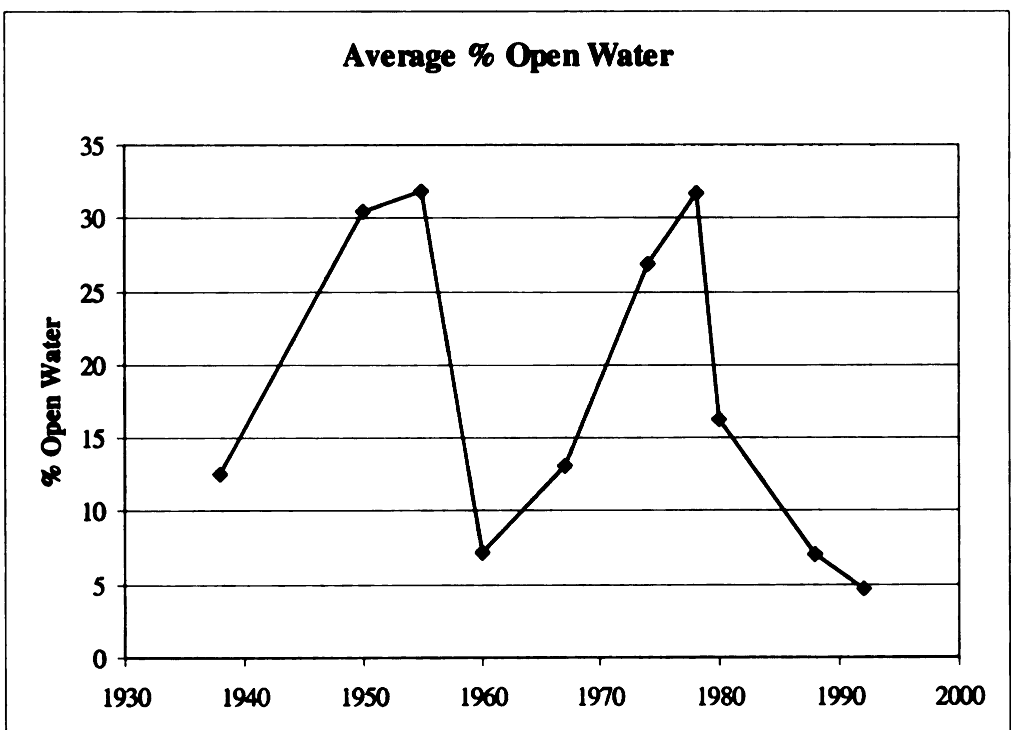

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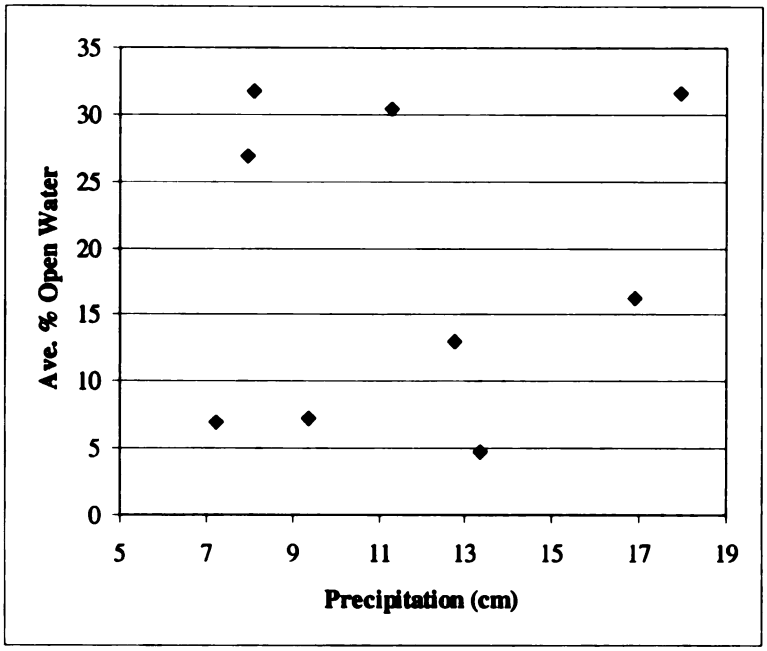


Figure 3-59. The relationship between the average percent open water and precipitation. Precipitation levels were summed over the three months' prior to when each photograph was taken. The correlation is not significant.

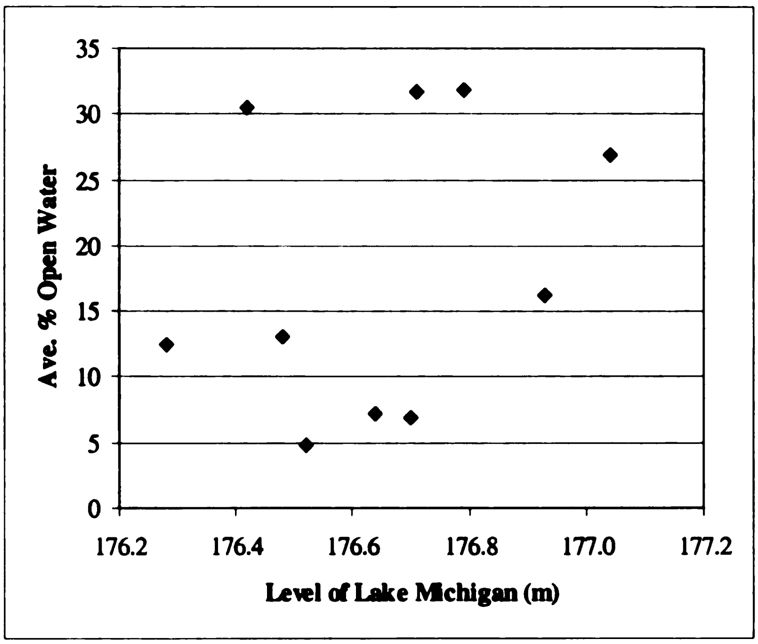


Figure 3-60. The relationship between the average percent open water and the level of Lake Michigan the day each photograph was taken. Lake levels are in meters above sea level. The correlation is not significant.

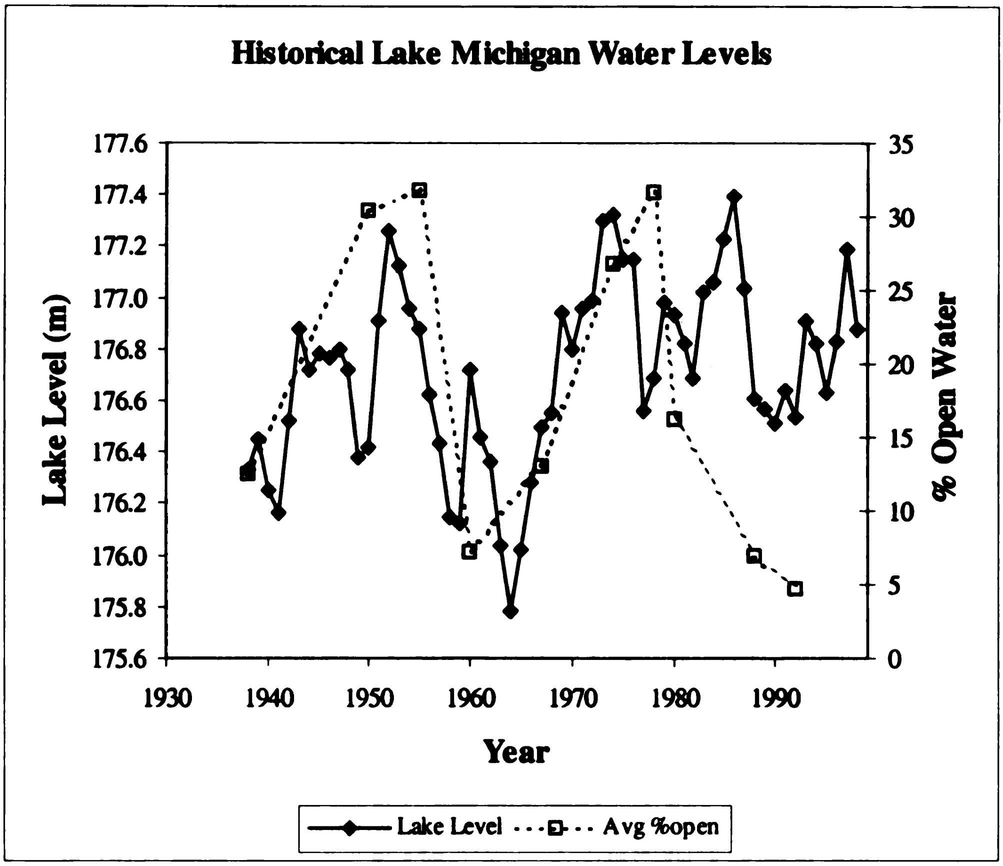
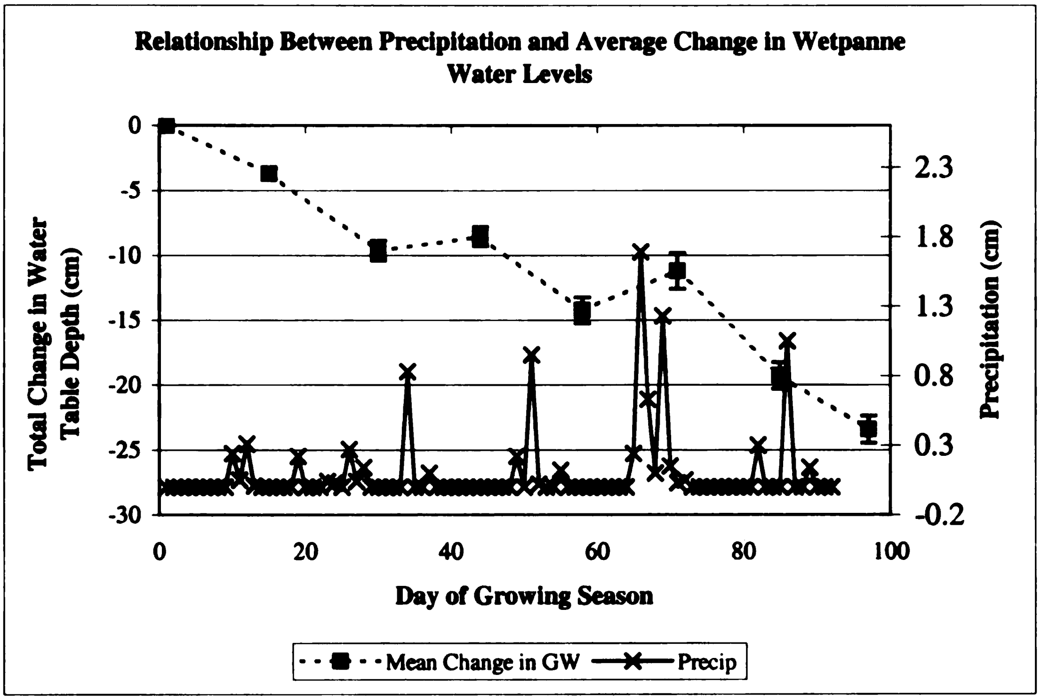


Figure 3-61. The average percent open water of wetpannes overlaid on historical lake level data from Lake Michigan. Lake levels are in meters above sea level (U.S. Army Corps of Engineers, 2/3/00).

Figure 3-62. The average change in the water table depth (dotted line) overlaid on the precipitation events that occurred during the 1998 growing season. Day 1 is defined as the start of the growing season (1 June 1998). The standard error of the means are plotted for the average change in water table. A negative change indicates a drop in water level. Precipitation data from the National Oceanic and Atmospheric Administration (1998a).

Figure 3-63. The average change in the water table depth (dotted line) overlaid on the level of Lake Michigan during the 1998 growing season. Day 1 is defined as the start of the growing season (1 June 1998). The standard error of the means are plotted for the average change in water table level. A negative change indicates a drop in water level. Lake levels are in meters above sea level (U.S. Army Corps of Engineer, 11/12/99).



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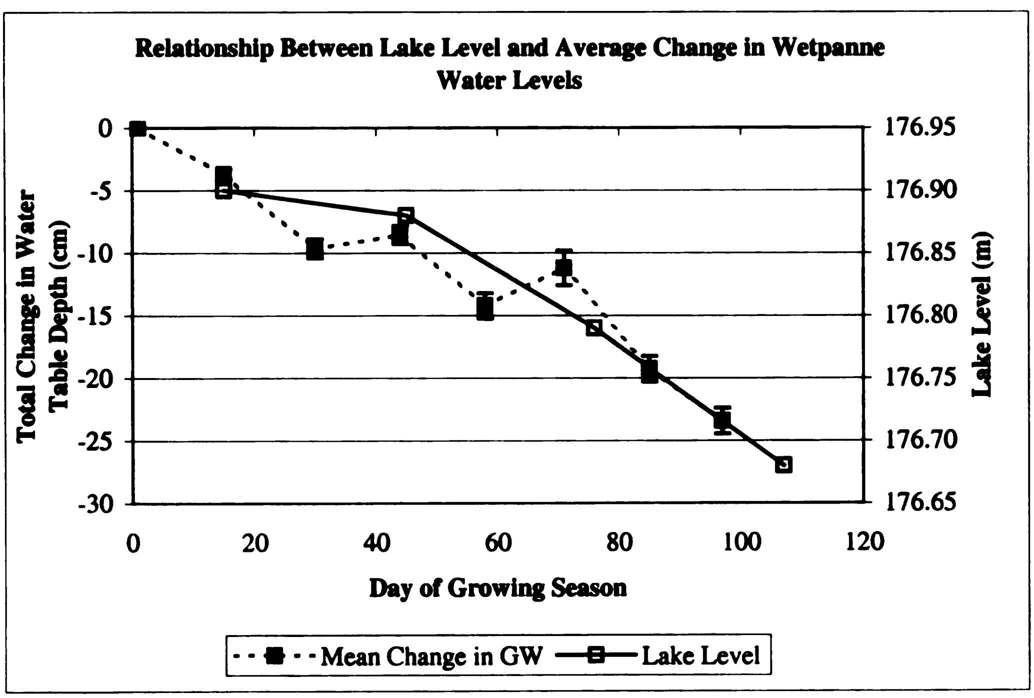
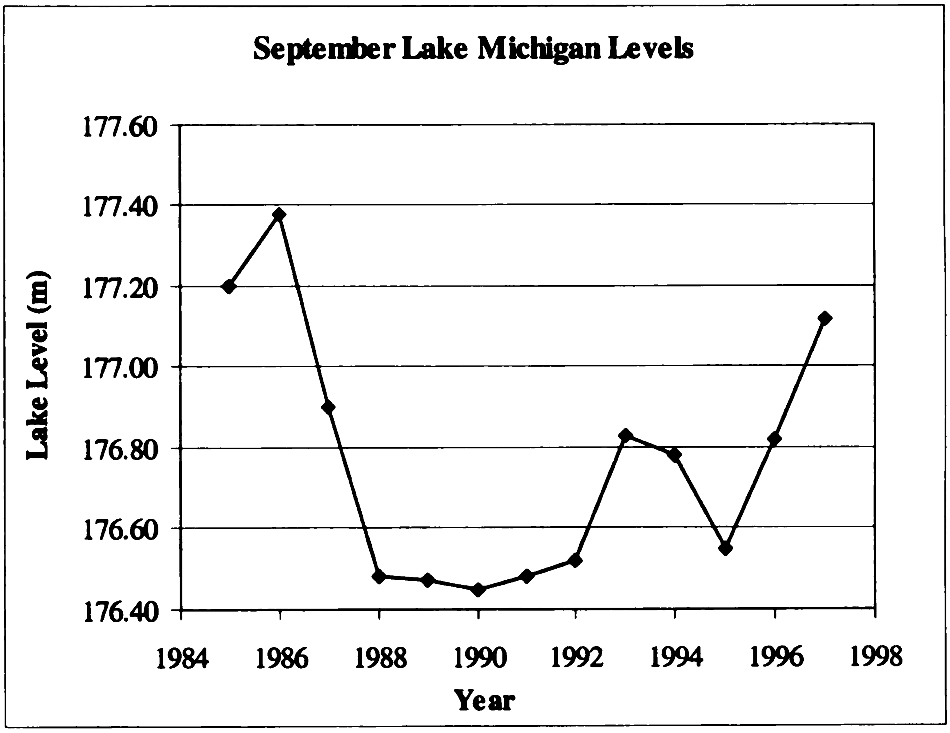


Figure 3-63.

Figure 3-64. Mean September lake levels for Lake Michigan during the last ten years. Lake levels are in meters above sea level (U.S. Army Corps of Engineers, 2/3/00).

Figure 3-65. Relative levels of the Kalamazoo River oxbow lake. Readings were taken by a private resident approximately every September for the past ten years (Deam, pers. comm.).



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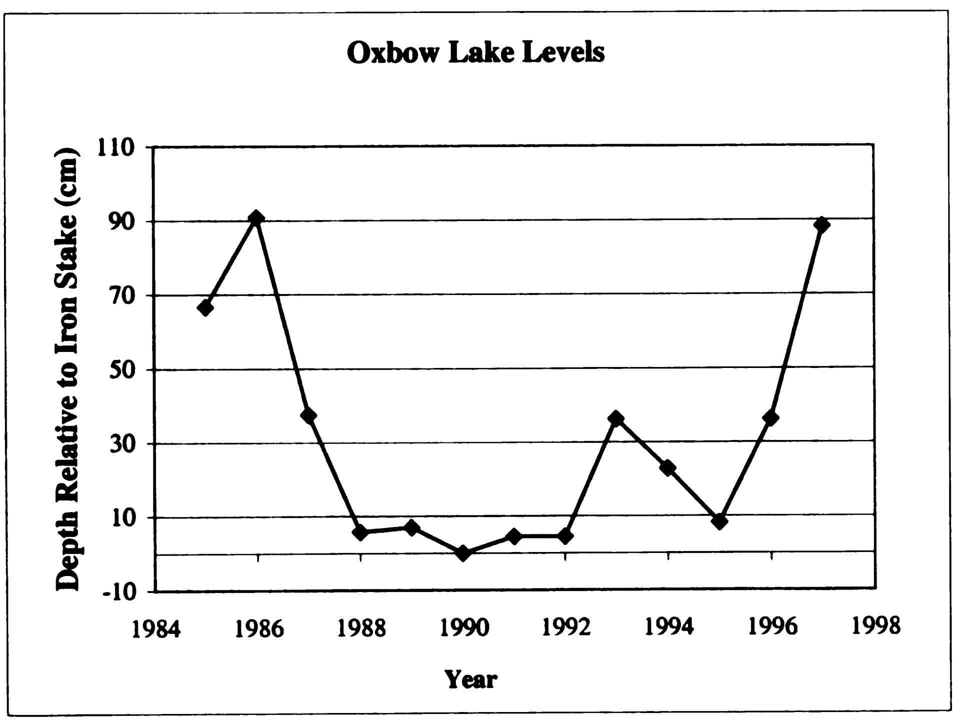


Figure 3-65.

CHAPTER FOUR

THE POTENTIAL FOR AUSTRIAN PINE (*PINUS NIGRA*) TO TRANSPIRE MORE THAN THE NATIVE JACK PINE (*PINUS BANKSIANA*)

INTRODUCTION

Austrian pine (*Pinus nigra*) appears to be having an impact on the wetpannes in the Saugatuck area. It is producing dense shade, dropping a thick litter layer, and acidifying the soil. It may be fostering the development of woody vegetation within wetpannes that would otherwise be unforested. The Austrian pine may also have the capacity to alter the hydrology of wetpannes more than the native jack pine. Other tree species have been known to produce such an ecosystem-level effect. *Tamarix*, a genus introduced to both the U.S. southwest and Australia, is responsible for drawing down the water table in many riparian and wetland sites (Rejmanek, 1995). *Melaleuca quinquenervia* is another tree species that forms dense monocultures in the Florida Everglades. It is believed to have the capacity to transpire at a rate that is 3 to 6 times that of the native vegetation (Allen et al., 1997). It is feared that it may dry down the Everglades, although this viewpoint is somewhat controversial (Allen et al., 1997).

The potential for the genus *Pinus* to affect the hydrology of an ecosystem has been described in many pine plantations throughout the world. Pine plantations were introduced to coastal sand dune areas to stabilize the sand, to prevent erosion, and to increase an area's recreation value. The ability of pine plantations to lower the water table has been previously documented (Bell et al., 1990; Sturgess and Atkinson, 1993; Van Dijk and Grootjans, 1993). Van Dijk and Grootjans (1993) gave four examples of water table reduction in the Netherlands that were due to pine plantings. The plantings caused reductions in the water table ranging from 0.1 meter to 2 meters. One of the pine plantations was planted near a group of wetpannes and caused water table levels to drop 1 meter and all of the wetpannes to completely dry up (Van Dijk and Grootjans, 1993).

Austrian pine (*Pinus nigra*) in particular may have the ability to reduce water table levels in the sand dune ecosystem. Its ability to lower water tables has already been documented in 20 to 40 year old plantations at Newborough Forest and at Culbin Sands, Britain (Ovington, 1950; Hill and Wallace, 1989). Leege (1997) demonstrated the invasiveness of *Pinus nigra* at Saugatuck Dunes State Park, Michigan, and showed that it is successfully reproducing in the sand dune habitat. She also showed that primary establishment is most successful, and growth rate is highest, in the wetpannes. Leege (1997) projected that the number of Austrian pines would increase 17-fold in the wetpannes in the next 15 years, although the actual number of juvenile Austrian pines found in wetpannes had decreased somewhat in the two years between her study and the beginning of this study. In wetpannes where *P. nigra* was already established, the percent moisture level of the soil was lower and the shrub cover was greater than in wetpannes without *P. nigra* (Leege, 1997). If *P. nigra* is indeed lowering the water table levels in wetpannes, it has the potential to cause a drastic ecosystem-level effect which will be compounded if its numbers do increase to the extent projected by Leege (1997). The wetland vegetation of the wetpannes will be lost as the wetpannes dry out, a phenomenon that is not without precedent. Hill and Wallace (1989) mentioned that "...the tendency of slacks [wetpannes] in the forest to dry out and develop scrub will persist..." in the continued presence of *Pinus nigra* trees at Newborough Forest. Ovington (1950) stated that the "lochs" in the dunes at Culbin Sands have become dried up or less extensive since the Austrian pines were planted. In the previous chapter, site differences between wetpannes with and without Austrian pines were explored. The objective of this chapter is to determine if *Pinus nigra* has the potential to use more water in wetpannes than the native *Pinus banksiana*. This will be attempted by comparing the total needle surface area per tree, the transpiration rate per unit surface area, and the root structure of *Pinus nigra* to that of *Pinus banksiana*.

METHODS

Total Needle Surface Area Per Tree

The total surface area of the leaves of each species was estimated so that transpiration rates could be calculated at the level of a whole tree (Fig. 4-1). A total of three open-grown Austrian pines and three open-grown jack pines that were approximately 10 meters tall were randomly chosen from several wetpanne sites. The total number of needles per tree was calculated by estimating the total branch length bearing needles and multiplying by the average number of needles per branch length, or the packing density. The lengths of all branches that were within reach from the ground were measured, and the lengths of the branches that were out of reach were estimated. The parts of the branches that did not bear needles were not included in the measurements. The average number of needles per centimeter of branch length was estimated by counting the needles of several branches, and dividing by the total branch length that bore needles.

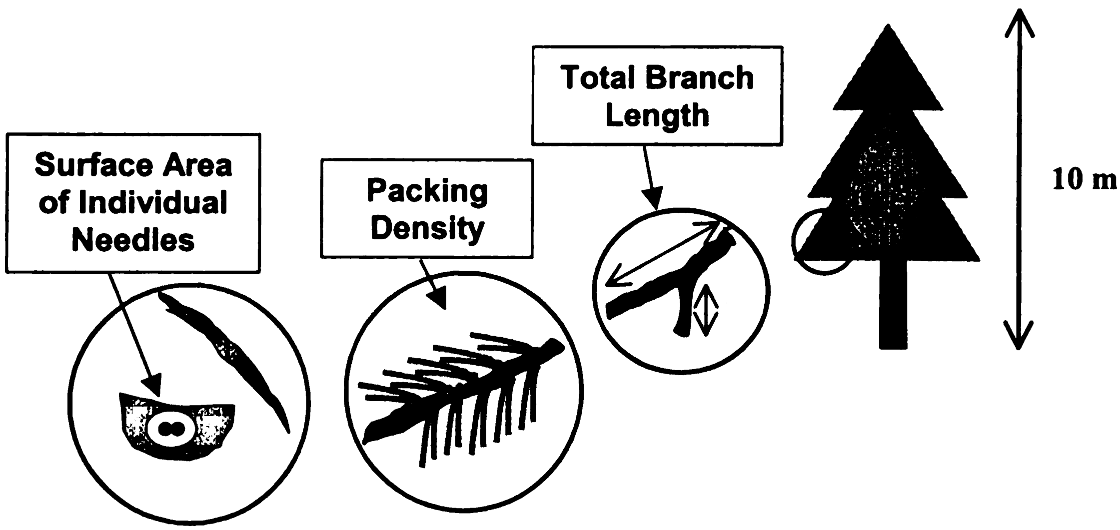


Figure 4-1. The total needle surface area per tree was determined by estimating the total number of needles on a 10 m tall tree, and then multiplying that number by the average surface area per needle. The total number of needles was estimated by measuring the total length of needle-covered branches and multiplying that number by the average number of needles per unit length (packing density).

Needles were plucked from various locations within each tree and their lengths measured. The average needle length was calculated for *P. nigra* (n=270) and for *P. banksiana* (n=370). Pine needles grow within bundles of needles referred to as fascicles. Both Austrian pines and jack pines have two needles per fascicle. The average surface area per fascicle was estimated by the volumetric displacement method described by Johnson (1984). Bundles of 10 fascicles were tied together with a thread and submersed in a graduated cylinder of water. The volume of water displaced was recorded. The surface area per fascicle was then calculated with the following equation:

$$A = 2L\,[1 + \pi/n]\,\sqrt{(Vn)/(\pi L)}$$

A is the total surface area (cm^2), *V* is the displaced volume (cm^3), *n* is the number of needles per fascicle, and *L* is the cumulative needle length of the needles in the sample (cm) (Johnson, 1984). A total of 27 bundles of jack pine fascicles and 37 bundles of Austrian pine fascicles were submersed. The average surface area per fascicle was calculated for each species. The results were divided by two to obtain the average surface areas per needle. The average surface area per needle was multiplied by the average number of needles on each tree in order to estimate the total surface area of needles per tree for each species.

Transpiration Rates

Transpiration rates were measured to estimate how much water an Austrian pine uses relative to an individual jack pine. Transpiration rates per unit leaf area were measured using a LI-COR 1600 steady-state porometer (Li-Cor Inc., Lincoln, NE) with a chamber that was designed for conifer needles. The porometer measured the water given off by the leaves in the chamber by comparing the humidity inside the chamber to the relative humidity of the atmosphere. Several live needles were inserted into the chamber and the transpiration rate reading was taken in units of mmol H_2O m^{-2} s^{-1}. Nine trees of each species were measured on bright, cloudless days. The measurements were taken on

14 August 1998, 16 August 1998, and 22 August 1998. The trees were chosen by randomly selecting three of the Austrian pine wetpanne sites. Three trees of each species were then randomly chosen within each wetpanne. All measurements were taken between noon and 2pm daylight savings time each day to obtain estimates of maximum transpiration rates. On each day, three measurements per tree were taken at breast height (1.4 m), choosing only those leaves that were exposed to direct sunlight. Because the opening of the porometer chamber had a different surface area than the needles that were inserted into it, each measurement needed to be corrected by dividing by the total surface area of the needles that were inserted into the chamber. To look for differences in the transpiration rates between the two species, a repeated measures analysis was run on SAS (SAS Institute, Inc., Cary, NC) using wetpanne as a blocking factor.

Root Structure

The root structure of each species was examined to compare the depths at which the two species can obtain water from the soil. If the roots of one species grew deeper than the other, one can assume that the species can draw on deeper soil water in times of drought. The roots of two Austrian pines and one jack pine were excavated, measured, and then reburied. Additional root measurements were made on two Austrian pines and on five jack pines that had tipped over naturally. The number of lateral roots and the number of vertical roots were counted for each tree. A lateral root was defined as a root that grew at an angle less than 45° from the ground surface. Vertical roots grew at an angle of 45° or greater from the ground surface. The length of each root and its diameter at the base of the tree bole were measured.

RESULTS

Total Needle Surface Area Per Tree

The average whole-tree needle surface area for a 10 meter tall, open grown Austrian pine was estimated to be 100 ± 49 m^2. The average whole-tree surface area for a 7.5 m tall jack pine was 1.4 ± 0.2 m^2. Estimates from 10 m tall jack pines were unavailable, so a scaled-up estimate for a 10 meter tall jack pine tree was determined by assuming there was a linear relationship between the surface area of the needles and the height of the tree. A linear relationship was used because it was assumed that although the length of the branches on the lower part of the tree were longer than the branches at the top of the tree, the absolute length of branch which bore needles was about the same. This was because the lower branches lose many of their needles due to internal shading. A 10 meter tall jack pine tree was estimated to have approximately 1.9 m^2 of total needle surface area. The total leaf surface area of Austrian pines was still 50 times that of a jack pine of similar stature. This difference is due to the fact that Austrian pine needles are much longer than jack pine needles, and are more closely packed on their branches (Table 4-1).

Table 4-1. The transpiration rates and needle characteristics of Austrian and jack pine.

Parameters for 7-10 meter Tall Trees	Mean ± 95% Confidence Interval		T-test p-value
	Austrian Pine	Jack Pine	
Needle Length (cm)	7.61 ± .22	2.01 ± .16	< 0.0001
# Needles/ fascicle	2	2	
Surface Area/ Fascicle (cm^2)	5.31 ± 0.20	0.89 ± 0.08	< 0.0001
# Fascicles/ Branch length(cm)	8.7 ± 0.3	3.7 ± 0.2	< 0.0001
Total Length of Needle-covered Branches (m)	215.7 ± 106.3	4.3 ± 0.6	0.0854
Total Needle Surface Area per Tree (m^2)	100.1 ± 49.3	1.4 ± 0.2	0.0593
Transpiration Rate (mmol H_2O m^{-2} s^{-1}) per m^2 of Needle Surface Area	0.996 ± 0.084 †	0.902 ± 0.084 †	n.s.
Total Transpiration Rate per Tree (mmol H_2O s^{-1})	99.7 ± 49.1	1.3 ± 0.2	0.0593

†= The least-square means and their standard errors are reported here.

Transpiration Rates

The overall means of Austrian pine and jack pine transpiration rates were not significantly different from one another (Table 4-1). However, the mean transpiration rates of the Austrian pines were slightly different than that of jack pines when the rates were analyzed separately by time and by wetpanne (Table 4-2). Because the species*time interaction was significant, the main effects of species and time could not be interpreted and the interaction had to be sliced. The transpiration rates of Austrian pine and jack pine were not significantly different on 14 August 1998 or 16 August 1998, but were significantly different on 22 August 1998. The transpiration rate of Austrian pine was higher on this date. The transpiration rates per unit needle surface area of the two species did not vary significantly in Wetpannes 6 and 13, but were significantly different in

Wetpanne 12. Austrian pine had higher transpiration rates than jack pine in Wetpanne 12 (Table 4-2).

Table 4-2. The results of the repeated measures analysis of Austrian pine and jack pine transpiration rates. Species refers to Austrian pine or jack pine, Time is the day of the measurement, and Wetpanne is the blocking factor.

Effect	Time	Wet-panne ID	Least Squares Means of Transpiration Rates (mmol H_2O m^{-2} s^{-1})		F Value	Pr > F
			Austrian	Jack pine		
Species			0.996	0.902	7.01	0.0213
Time					128.60	< .0001
Wetpanne					18.96	0.0002
Species*time					27.91	<.0001
Sliced by	8/14		1.182	1.230	0.36	n.s.
Sliced by	8/16		1.037	0.991	0.29	n.s.
Sliced by	8/22		0.898	0.430	37.45	<.0001
Species* wetpanne					5.43	0.0210
Sliced by		6	0.938	0.963	0.07	n.s.
Sliced by		12	1.400	0.976	17.12	0.0014
Sliced by		13	0.779	0.712	0.44	n.s.

Root Structure

The Austrian pines had longer vertical roots than the jack pines, even though the average diameter at breast height (DBH) of the Austrian pines that were measured was smaller than that of the jack pines (Table 4-3). If the length of the roots were a function of tree size, then the jack pine roots should have been longer. Neither species had a tap root—a vertical root that is significantly larger than any other root. Both species had several lateral roots and several vertical roots of equal diameter. The Austrian pines had roots that were relatively unbranched along their length (Fig. 4-2). The jack pine roots, particularly the vertical ones, were dichotomously branched into more finely divided roots about halfway down their length (Fig. 4-2).

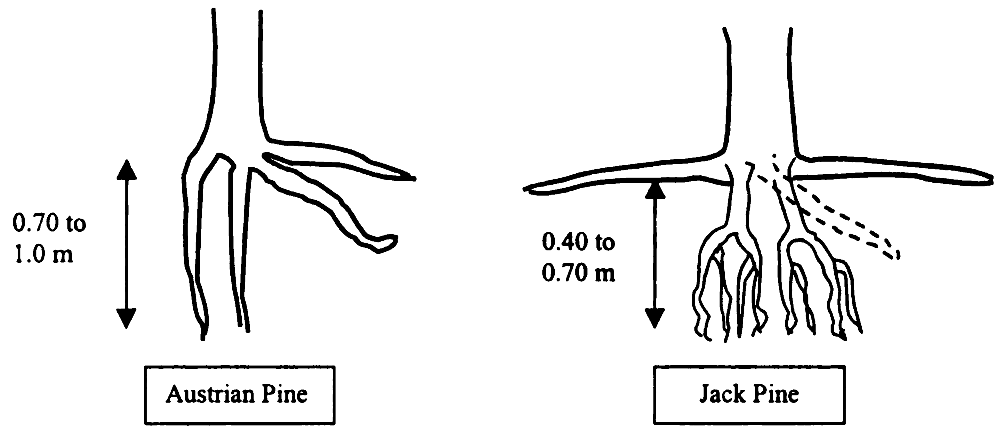


Figure 4-2. Typical root architecture of Austrian pine and jack pine at Saugatuck Dunes State Park, MI.

The root structure of Austrian pines was more plastic than that of jack pines. All of the jack pines had three or four lateral roots and one or two vertical roots. The ratio of lateral to vertical roots varied greatly from tree-to-tree in the Austrian pines. One Austrian pine had four lateral roots and one vertical root, another had two lateral roots and two vertical roots, a third had six lateral roots and three vertical roots, and the last had three lateral roots and four vertical roots. A lateral root of one Austrian pine curved toward the edge of a wetpanne, perhaps growing toward this source of moisture. Root connections were observed between the lateral roots of one Austrian pine and the lateral roots of another Austrian pine 3 meters away.

Table 4-3. Structural differences of Austrian pine and jack pine root systems at Saugatuck Dunes State Park, Michigan.

Variable Measured	Austrian Pine (n=4)	Jack Pine (n=6)
Average DBH	12 cm	18 cm
# of Lateral Roots[1]	2-6	3-4
# of Vertical Roots[1]	1-4	2-3
Average Root Diameter[2]	6 cm	10 cm
Length of Lateral Roots[3]	1-2 m	1.5-3 m
Length of Vertical Roots[3]	0.70-1.0 m	0.40-0.70 m

[1] Roots at an angle less than 45° from the ground surface were counted as lateral roots, and roots at an angle greater than or equal to 45° from the ground surface were counted as vertical roots.
[2] The diameter of each root was measured where the root was connected to the tree bole.
[3] The length of each root was measured from where the root was connected to the tree bole to the tip of the root.

DISCUSSION

The estimated total leaf surface area for a single Austrian pine tree was 50 to 70 times greater than the total leaf surface area of a jack pine tree of similar stature. This was because Austrian pine needles are significantly longer than jack pine needles, and are more closely packed on the tree's branches. Because the average transpiration rate per unit surface area of Austrian pine was slightly greater than that of jack pine (Table 4-1), a single Austrian pine tree has the capacity to transpire up to 79 times more water per second than a jack pine tree, assuming that all needles transpire at the same rate. The vertical roots of the Austrian pine trees were generally longer than the vertical roots of the jack pine trees, indicating that Austrian pine trees are better able to access groundwater in times of drought. These findings support the hypothesis that Austrian pines have the potential to lower water tables under wetpannes more than the native jack pines.

The transpiration rate of jack pine was similar to rates reported in the literature. The transpiration rates for jack pine varied from 0.5 to 1.4 mmol H_20 m^{-2} s^{-1} at midday

(Blake and Yeatman, 1989; Saugier et al., 1997; Sullivan et al., 1997), compared to a mean of 0.9 mmol H_20 m^{-2} s^{-1} in this study. Transpiration rates per unit leaf area were unavailable from the literature for Austrian pine, but estimates of the rate of sap flow per day were available. Rates estimated using this method cannot be converted into mmol H_20 m^{-2} s^{-1}, however. In the sap flow method, the rate of sap flow through a tree's bole is estimated by injecting a heat pulse into its xylem and measuring the amount of time it takes for the heat to dissipate. Based on the sap flow method, *Pinus nigra* transpired 2.31 mm water/day in a sand dune plantation in England (Roberts et al., 1982). For comparison, *Pinus banksiana* transpired only 1.6 mm water/day in a Canadian boreal forest based on the same method (Saugier et al., 1997). However, the results of these studies may not be directly comparable because the sap flow measurements were made under different conditions, and transpiration rates can vary greatly from site-to-site and from day-to-day (Pallardy et al., 1995).

There are several potential sources of error that can occur when estimating whole tree transpiration rates with a porometer. The whole tree transpiration rates in this study were estimated using the assumption that all the needles on a tree transpire at the same rate. In reality, the transpiration rate of a single needle varies with its position on the tree—needles at the crown transpire at higher rates than those on the lower branches. A shaded needle transpires much less than a needle that is in direct sunlight (Pallardy et al., 1995). Transpiration rates also vary throughout the day, with the highest rates occurring at midday (Pallardy et al., 1995). The transpiration rates also depend on the weather conditions. Needles transpire at greater rates under low levels of humidity than under higher levels (McDermitt, 1990). Windy conditions can reduce the boundary layer of air surrounding the needles and increase transpiration rates (Pallardy et al., 1995). Transpiration rates may decrease during periods of drought (Pallardy, et al., 1995). Furthermore, the act of sealing the porometer chamber around the needles may alter the boundary layer and the water vapor difference that the needles would experience under ambient conditions (McDermitt, 1990). To avoid some of this variation, the transpiration rates in this study were measured at the same position on each tree in direct sunlight under similar weather conditions.

Errors are also associated with scaling up from whole tree transpiration rates to the transpiration rates of a stand of trees. Therefore, although the transpiration rates of individual Austrian pine trees may be greater than similarly sized jack pine trees at Saugatuck, a stand of jack pine trees surrounding a wetpanne may collectively transpire more than a stand of Austrian pine trees under certain conditions. Stand level transpiration rates vary with the relative size of the trees within the stand. Smaller trees transpire at lower rates than larger trees due to reduced access to groundwater (Dawson, 1996). Larger trees shade out smaller trees in a stand, further reducing the transpiration rates of the small trees. Despite these factors, uneven-aged stands may transpire more than even-aged stands because a few small trees interspersed throughout a stand allow for more large trees to be exposed to light and wind (Pallardy et al., 1995). The jack pine stands in this study tended to be more uneven-aged than the Austrian pine stands, with the smallest trees closest to the wetpannes and the larger trees further upland. Therefore, the jack pine stands surrounding wetpannes contained more trees in smaller size classes than the Austrian pine stands that surrounded wetpannes (Table 4-4). The Austrian pines were all approximately in the same size class (Table 4-4) because they were planted at about the same time. Because of this, the jack pine stands surrounding the wetpannes at Saugatuck could actually transpire at a greater rate than the Austrian pine stands that surround wetpannes. On the other hand, transpiration does not account for all of the water loss from a stand. Some precipitation is intercepted by foliage and branches and evaporates before it even hits the ground (Pallardy et al., 1995). Austrian pines have much fuller profiles than jack pines and could intercept more precipitation. This would contribute to the ability of a stand of Austrian pine trees to lower water levels within a wetpanne.

Table 4-4. The percent of all trees in different size classes that grow within an 11.3 meter border surrounding the edges of the wetpannes.

	Size Class (in cm DBH)						
	2.5-4.9	**5-9.9**	**10-14.9**	**15-19.9**	**20-24.9**	**25-29.9**	**>30**
Jack pine stands	33.8%	31.4%	19.5%	9.3%	5.1%	0.3%	0.6%
Austrian pine stands	5.9%	19.3%	25.9%	23.7%	17.8%	4.4%	3.0%

Another potential source of error in the whole tree transpiration estimation is that the surface area of jack pine may have been underestimated. One problem is that the surface area was estimated on jack pine trees that averaged 7.5 m tall, whereas the surface area of Austrian pine was estimated using 10 m tall trees. An attempt was made to scale up the surface area of the jack pines for a 10 m tall tree by assuming the surface area varied linearly with tree height. This assumption is probably not completely accurate. Another reason why the surface area of jack pines was underestimated is because jack pines form short spur branches along their main branches, making it difficult to estimate the total branch length. Because the estimated surface area of Austrian pine was so high relative to jack pine, it is likely that the difference between the two species is real, but it may not be as pronounced as the calculations show.

The plasticity of Austrian pine roots may allow them to take advantage of water sources that jack pines cannot access. It is possible that the Austrian pines can adapt their root structure to its particular habitat, maximizing its ability to obtain water or maximizing its stability in the substrate. Austrian pine's adaptability has been documented in other studies. In one study, the root systems of Austrian pines varied with differences in soil texture. In rocky soils, the pines only had a lateral root system, in deep fertile soils the pines had well developed tap roots, and in clayey soils the trees had a combination of well-developed lateral and tap roots (Kovaleva, 1988). In contrast, Jack pines have a relatively consistent root form, with a few minor variations (Strong and La Roi, 1983). The Austrian pines at Saugatuck seemed to have the ability to grow toward water sources. They also could make root connections with other trees, which would allow a tree that cannot access the water table to share resources with a tree that can reach water.

Based on the evidence, it is likely that it is the greater total leaf surface area and the longer roots of Austrian pine trees give them the ability to use more water than jack pines of similar size. This may explain why there is a greater decrease in water table levels in Austrian pine wetpannes than in jack pine wetpannes.

CHAPTER FIVE

CONCLUSIONS

A total of 144 plant species were found in the wetpannes in the Saugatuck, MI area. Of these, 59% are wetland indicator species. The ranges of most of the species are centered in the eastern and northern United States. None of the plants found were listed as endangered or threatened on the Michigan state list or the federal list. Only one plant species, *Hypericum kalmianum*, is endemic to the Great Lakes region. It may serve as an indicator species for the wetpanne habitat because it was found in all of the wetpannes in this study, and it only rarely occurs in other habitats.

The individual plant species occupied specific ranges along the water depth gradient. Although these individual ranges often overlapped, definable assemblages of species were not found. This pattern was evident for the herbaceous species as well as for the woody species, and was consistent from one wetpanne type to another. Wetpannes have the potential to contain upland plant species near their edges, and obligate wetland species at their centers. The relative amounts of upland and wetland plant species in a particular wetpanne depend on the shape of the wetpanne basin and the distance of the bottom of the basin to the water table.

The water levels in the wetpannes are controlled by, but the water is not derived from, Lake Michigan. The lake water contained high concentrations of Na^+ and Cl^-, two relatively conservative ions, but the wetpannes had lower concentrations of these ions. The water chemistry of most of the wetpannes was consistent with that of groundwater rather than Lake Michigan or precipitation.

The level of Lake Michigan determines the base level for the water table in the dunes. A higher lake level results in a higher water table, which then raises the water levels in the wetpannes. The sloping water table also results in a greater seasonal change in the water levels of the wetpannes that are farther from Lake Michigan.

Because Lake Michigan exerts its influence on the water levels of the wetpannes, the water levels fluctuate greatly from year-to-year in response to the changing lake levels. The wetpannes experience 25-30 year cycles of high and low water levels. Evidence that the water levels have fluctuated in the wetpannes was also found in the wetpanne sediment. Orange and gray mottles, hydric soil features characteristic of fluctuating water tables, were found.

The wetpannes of this study were not transient features of the landscape. The aerial photograph record shows the current wetpannes to date back at least 60 years. It is possible that the Austrian pine plantings and the channelization of the Kalamazoo River have artificially stabilized the wetpannes in the area, however, radiocarbon dating of wetpanne sediments at Indiana Dunes National Lakeshore suggest that wetpannes are naturally stable (Jackson et al., 1988).

Trees generally have several effects on the ecology of wetpannes. They reduce light levels, increase the depth of wetpanne sediment, increase litter depth, and draw down the water table (Fig. 5-1). The average density of trees surrounding the Austrian pine wetpannes was not significantly different from the density of trees surrounding the jack pine wetpannes (Fig. 5-1). Tree density was correlated with the total change in water table depth over the growing season, but it only explained a small amount of the variability in water levels compared to the distance of the wetpannes from Lake

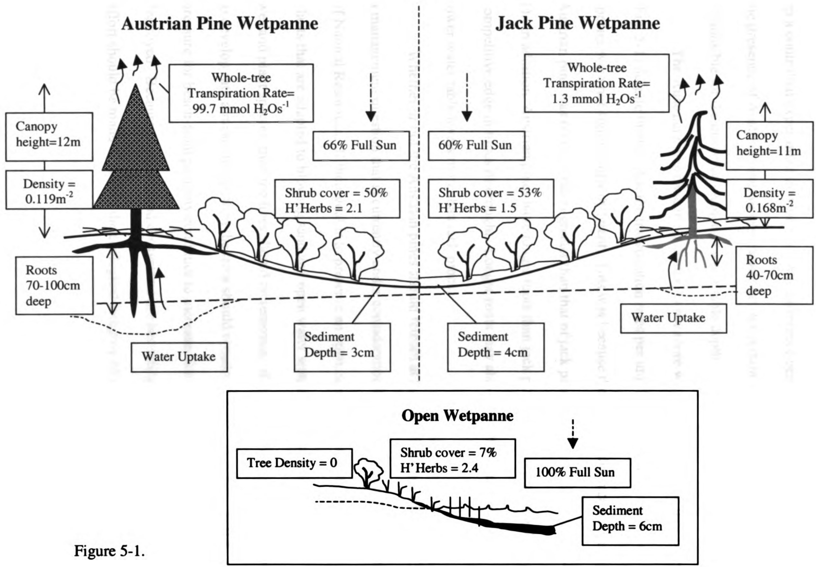
Michigan. Tree density was positively correlated with shrub cover, the number and diversity of woody species, and amount of damage by herbivores in wetpannes. It was negatively correlated with the diversity of herbaceous species and the percentage of wetland indicator species.

In wetpannes that were planted with Austrian pine, the density of juvenile Austrian pines is about half the density of juvenile jack pines. Juvenile Austrian pines were not found in the jack pine or open wetpanne types, so Austrian pine seems to be limited by its ability to disperse. Despite these numbers, the Austrian pines have the potential to affect the wetpannes that they surround more over time than the jack pines because Austrian pines have a longer lifespan and reach larger sizes (Rudolph and Laidly, 1990; Leege, 1997) than the jack pines.

The characteristics of the vegetation of the Austrian pine wetpannes were intermediate between those of the jack pine and the open wetpannes. The mean values of shrub cover, species richness, species diversity, percent wetland plants, and estimated herbivory may reflect the length of time the wetpannes have been forested. The Austrian pine wetpannes have not been forested as long as the jack pine wetpannes; therefore, the characteristics of the vegetation of the Austrian pine wetpannes do not match those of jack pine wetpannes. However, at present, they more closely resemble the jack pine wetpannes than the open, treeless wetpannes (Fig. 5-1).

The results of the analysis of covariance, using distance from the lake as the covariate, showed that the water table dropped more in the Austrian pine wetpannes than

Figure 5-1. A conceptual diagram summarizing the effects of trees on wetpanne ecology and the differences among wetpanne types. Average values are given in each box.



Austrian Pine Wetpanne
Jack Pine Wetpanne
Whole-tree Transpiration Rate= 99.7 mmol H_2Os^{-1}
Whole-tree Transpiration Rate= 1.3 mmol H_2Os^{-1}
Canopy height=12m
Density = $0.119m^{-2}$
Roots 70-100cm deep
66% Full Sun
60% Full Sun
Shrub cover = 50%
H'Herbs = 2.1
Shrub cover = 53%
H'Herbs = 1.5
Canopy height=11m
Density = $0.168m^{-2}$
Roots 40-70cm deep
Water Uptake
Sediment Depth = 3cm
Sediment Depth = 4cm
Water Uptake
Open Wetpanne
Tree Density = 0
Shrub cover = 7%
H'Herbs = 2.4
100% Full Sun
Sediment Depth = 6cm

Figure 5-1.

in the jack pine wetpannes located farther from Lake Michigan. It was not feasible to set up a controlled experiment in which the only difference between the wetpanne types was the presence of Austrian pine, so one cannot say for certain that the Austrian pines were responsible for the observed change in water table depth.

The Austrian pines have the potential to use more water than the native jack pine (Fig. 5-1) despite the fact that the transpiration rates per unit leaf surface area of the two species were not significantly different. This was because the total needle surface area of Austrian pine was 60 to 70 times greater than that of jack pines of similar height (Fig. 5-1). In addition, Austrian pines have longer roots than jack pines (Fig. 5-1), giving them a competitive edge in times of drought. Longer roots may also allow Austrian pines to lower water table levels more than jack pines.

Whether or not the Austrian pines should remain at Saugatuck Dunes State Park is a management question that is currently under consideration by the Michigan Department of Natural Resources. If their goal is to preserve an open, sand dune ecosystem with plants that are adapted to blowing sand and open water wetpannes with a variety of wetland plant species, then the trees should be removed. If their goal is to allow the land to develop into a mesic forest, then the trees should remain in place. However, as the pressure for beach-front property continues to increase, the wetpanne habitat is being destroyed. Because these wetland ecosystems are becoming increasingly rare, every effort should be made to protect the ecological integrity of wetpannes.

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