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dissertation entitled

LINKING PLANT COMMUNITIES
AND ENVIRONMENTAL VARIABLES
IN SOUTHWESTERN MICHIGAN WETLANDS

presented by

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has been accepted towards fulfillment
of the requirements for the

Ph.D. degree in Zoology

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Major Professor's Signature

1 JULY 2004
Date

LINKING PLANT COMMUNITIES AND ENVIRONMENTAL VARIABLES IN SOUTHWESTERN MICHIGAN WETLANDS

By

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A DISSERTATION

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

DOCTOR OF PHILOSOPHY

W. K. Kellogg Biological Station
Department of Zoology
and
Ecology, Evolutionary Biology & Behavior Program

2004

ABSTRACT

LINKING PLANT COMMUNITIES AND ENVIRONMENTAL VARIABLES IN SOUTHWESTERN MICHIGAN WETLANDS

By

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Plant communities often vary as a function of their abiotic environments; this is especially true in wetlands, where hydrology is of paramount importance. Wetland hydrology remains an elusive concept to measure and relate quantitatively to the composition of plant communities. In an effort to elucidate these relationships I surveyed plant communities across a diverse set of 24 wetlands in southwestern Michigan. I also quantified wetland hydrology at these sites in terms of water sources, seasonal water level variation, and hydrochemical composition. Using major solutes as tracers of water sources, I estimated the relative importance of precipitation and groundwater inputs (i.e., "fraction groundwater"). I monitored water levels, collected soil water from the root zone for hydrochemical analyses, and collected organic soils for soil nutrient analysis. Nutrient accumulation on ion exchange resin was used to estimate nutrient supply to each wetland.

Cluster analysis and indicator species analysis revealed seven different groups of wetland plant communities, which I have distinguished for the purposes of discussion: leatherleaf bogs, bogs, a poor fen, fens, sedge meadow fens, wet swamps, and dry swamps. Ordination using nonmetric multidimensional scaling (NMS) reduced the plant community data down to two synthetic axes (NMS Axes

1 and 2) that explained 64% of the variation. pH, as well as fraction groundwater, soil nutrients, and hydrochemical variables that covaried with pH, and canopy, an estimate of shade cast by tall woody species, were the environmental variables most strongly related to the ordination; water levels were of secondary importance; nutrient supply was of less importance. Fens and sedge meadow fens exhibited higher water levels and lower canopy values (i.e., less shade) than wet and dry swamps. Evaluation of fraction groundwater estimates for these seven groups suggested that fens and swamps, while generally groundwater-fed, are not all strongly groundwater-fed; bogs were all strongly precipitation-fed; the poor fen was intermediate between bogs and fens.

A partial least squares composite variable model was used to test these ordination results and evaluate the relationship between landscape variables and wetland environmental variables. Landscape variables were good predictors of wetland water source (R^2 = 0.60), while water sources and water levels were moderately good predictors of nutrient supply (R^2 = 0.51). Acidity, shade, water levels, and nutrient supply collectively explained 94% and 80% of the variation in NMS Axes 1 and 2, respectively; acidity and shade were stronger predictors of the vegetation differences than water levels and nutrient supply. Based on these results and plant physiology studies, many wetland plant species may be excluded from the acidic bog environment for physiological reasons relating to acid stress instead of nutrient availability per se. This suggests that measures of nutrient availability may be less helpful in explaining why so few wetland plant species may persist in acidic peatlands.

ACKNOWLEDGEMENTS

This was a sizeable undertaking (more so than I anticipated!), and I couldn't have done it alone. First, I would like to thank my dissertation advisor Steve Hamilton for his guidance, constructive criticism, and friendship. No one can talk science while leaping from hummock to hummock in a swamp like Steve can, and I very much have appreciated sharing ideas with him over the last seven years. I would also like to thank the other members of my guidance committee – Kay Gross, Dave Long, and Nathaniel Ostrom – for their comments and support throughout my graduate studies.

Various members of the Hamilton lab were invaluable field and lab assistants, colleagues, and friends: Amy Burgin, Amanda Kurzman, Konrad Kulacki, Madhav Machavaram, Eliza Peterson, Dave Raikow, Nicole Reid, Markus Ruchter, Suzanne Sippel, David Weed, and Stefanie Whitmire. I would especially like to thank Stefanie Whitmire and David Weed for their many contributions to this project.

Others also ventured into wetlands – some frightening places to traverse, to be sure – and I would like to thank these individuals: Kathy Crowley, Nate Dorn, Heather Sahli, Elliot Saunders, Gary Schott, Kristi Sherfinski, Bob Thobaben, and Cordt Thobaben.

There are numerous logistical hurdles in graduate school and research, and Char Adams, Lisa Craft, Nina Consolatti, Alice Gillespie, John Gorentz, Sally

Shaw, and Melissa Yost all helped me run the race more swiftly. Many thanks to them.

Science is the business of ideas, and I received helpful comments and feedback from numerous individuals (in addition to those previously listed), including Tom Getty, Jim Grace, Greg Houseman, Bruce McCune, Ed Rigdon, Rich Smith, Alan Tessier, and Jeremy Wojdak. I would especially like to thank Jeremy Wojdak for our many discussions about ecology and everything else under the sun.

Moral support is always critical when times get tough – and I encountered many such times throughout my graduate studies. My family and friends were irreplaceable in this regard. I would especially like to thank my wife Kristi Sherfinski for her patience and understanding throughout this endeavor, as well as opening my eyes to the world of plants – they're not just green things!

I received financial support from the National Science Foundation, the College of Natural Science, the Graduate School, the Zoology Department, and the MSU Ecology, Evolutionary Biology & Behavior Program.

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CHAPTER 1

INTRODUCTION

Why do species occur in some habitats but not in others? This basic question has fascinated ecologists for over a century (Cowles 1899), and while some answers have been forthcoming, it remains an open question in many ecosystems. Wetlands represent a particularly challenging ecosystem in the context of this question. Myriad wetland plant communities occur in nature, but the environmental variables that support these different plant communities remain unresolved. In this thesis I attempt to answer why different plant communities occur in different types of wetlands in southwest Michigan.

One motivation for studying wetlands is because they represent unique ecosystems that are highly threatened. Over half the wetlands in the United States have been lost or severely modified since European settlement (Dahl 1990). Wetlands are generally lands of low economic value that have been filled and drained for residential, commercial, and agricultural development. While legislation since the 1970s has curbed the rate of wetland degradation, it continues to occur, albeit at a slower rate than before. Wetland creation (mitigation to compensate for losses) often results in a net loss of wetland ecosystem diversity because it is more difficult to create some wetlands (e.g., wet prairies, hardwood swamps) than others (e.g., shallow ponds ringed by cattails). Until strict type-for-type replacement becomes commonplace in wetland mitigation, uncommon wetland types that are challenging to engineer and maintain will continue to become more rare as development ensues.

The values ascribed to wetlands have undergone a dramatic change over the last several decades (Prince 1997). Once considered wasteland, wetlands are now valued for their many ecosystem services and natural features. Wetlands are important to society for many reasons, including temporary floodwater storage, nutrient retention, biomass production for various purposes, and food production for fish and wildlife, which are important for many local economies. Wetlands harbor numerous unique plants, which are valued both for their contribution to regional and global biodiversity and for the provision of habitat for wildlife. Finally, wetlands are valued aesthetically as inspiration for photography, painting, poetry, and other art forms.

In ecological terms, wetlands generally represent a transitional habitat between terrestrial and aquatic ecosystems. The environmental conditions in wetlands are similar and yet distinct from upland and deep water habitats. These unique conditions result in an environment where abiotic drivers are strong, particularly due to the presence of water. The hydrology of wetlands is usually considered to be of greatest importance in determining wetland ecosystem function. Because wetlands are intimately tied to their unique hydrologic conditions, a change in global climate could have strong effects on these hydrologically sensitive ecosystems (Winter 2000, Weltzin et al. 2003).

The position of wetlands in the landscape makes them important in terms of many ecosystem processes. Wetlands are located at interfaces where water is exchanged between surface and ground water, where they intercept runoff from uplands to lakes, streams, and oceans, or where they occur as floodplains fringing rivers. The biogeochemical processes that occur in wetlands are largely those of nutrient transformation, although wetlands also retain and export nutrients. The shallow water level conditions in wetlands provide a setting where the redox potential can vary from oxidizing to strongly reducing over short spatial scales. Anaerobic microbial processes such as denitrification; manganese, iron, and sulfate reduction; and methanogenesis are prevalent in different types of wetland sediments and exemplify how the microbial community catalyzes these biogeochemical transformations. Overall, wetlands are considered to be biogeochemical hot spots in the landscape (Schlesinger 1997).

Some of these biogeochemical transformations could have potentially adverse effects on members of the plant community. Several of the reduced products of these reactions, including Mn^{2+}, Fe^{2+}, and S^{2-}, are readily subject to root uptake and toxic to plants at low levels (Ernst 1990). In addition to these reduced geochemical species, anaerobic decomposition of organic matter produces a wide range of differentially phytotoxic organic compounds, including acetic and butyric acids (Ponnamperuma 1984, Cronk and Fennessy 2001). To avoid these toxins that develop under anoxic conditions, plants that can transport oxygen to their roots exhibit radial oxygen loss, which oxidizes the surface of their roots (Koncalova 1990). This may be one adaptation that many wetland plants possess in contrast to species that are restricted to upland habitats.

Another stress for plants is the low oxygen conditions that are commonly associated with waterlogged soils. Atmospheric oxygen diffuses 10^4 times slower through water-filled soil pores than through unsaturated sediments (Greenwood 1961). After flooding, the oxygen demand by heterotrophic microbes and plant root respiration quickly depletes any oxygen remaining in the soil solution (Ponnamperuma 1984). Insufficient oxygen results in the loss of root function, including water and nutrient uptake, which may cause leaf chlorosis, growth inhibition, and eventually death (Pezeshki 1994). Wetland plants possess many different adaptations that help them cope with anoxia in waterlogged soils. These include aerenchymous tissue for transporting oxygen from the leaves down the stem to the roots; hypertrophied stems and lenticels, which increase gas exchange between the plant and its environment; and shallow and adventitious rooting systems that serve to avoid hypoxic or anoxic conditions deeper in the soil (Tiner 1999).

The ability of a plant to tolerate flooded conditions is thus a complex set of physiological responses to myriad potential stressors in the soil solution. With so many potential stressors acting, many simultaneously, it is difficult to elucidate which environmental factors may be having the greatest influence in determining wetland plant communities. Furthermore, although experimental research has been restricted more to flooded vs. unflooded treatments, the range of potential water level conditions in nature is infinite. Because variability in plant community composition exists outside of the realm of flooded vs. unflooded conditions, subsequent experiments will need to address various water level conditions below the soil surface in addition to flooded treatments. This is especially true if low subsurface water levels during the growing season, a temporal window for growth, turn out to be one of the more important hydrologic factors influencing the establishment and maintenance of different wetland plant communities.

One difficulty in evaluating the linkages between environmental variables and wetland plant communities is the interdisciplinary nature of the topic. Many wetland ecologists are trained primarily as plant ecologists or hydrologists, but a strong understanding of both fields is necessary to best address these complex plant-environment interactions. In addition, a strong background in biogeochemistry is helpful if there is an interest in evaluating whether the reduced geochemical species may be adversely affecting the plants under natural conditions. Therefore, these questions will remain challenging because it is unusual to find ecologists with the interest and the necessary training in these somewhat disparate fields.

In the chapters that follow I investigate which environmental variables are most important in determining the differences in wetland plant communities in southwest Michigan. In Chapter 2 I quantify different aspects of wetland hydrology and report additional environmental measurements that could be influencing the plants in these communities. In Chapter 3 I use multivariate analyses to distinguish which environmental variables are most strongly related to differences in plant community composition. Chapter 4 presents a statistical model to link landscape-level variables to the proximate environmental variables which directly affect the plants. In Chapter 4 I also evaluate which environmental variables best explain differences among these wetland plant communities.

Finally, I draw several conclusions from the overall research project in Chapter 5.

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CHAPTER 2

THE HYDROLOGY, HYDROCHEMISTRY, AND SOILS OF SOUTHWESTERN MICHIGAN WETLANDS

INTRODUCTION

It is widely acknowledged that understanding wetland hydrology is key to understanding the ecological patterns and processes of wetlands (Brinson 1993b, Mitsch and Gosselink 2000). The hydrologic environment determines when and to what degree the soils in a wetland are saturated and when standing waters are present. Soil saturation in turn controls oxygen availability, redox status, and critical steps in the biogeochemical cycling of nutrients and other elements, affecting ecosystem functions as well as conditions for plant growth (Ernst 1990, Laanbroek 1990). Plant community composition and productivity vary largely as a function of wetland hydrology (Wilcox 1995, Megonigal et al. 1997, Clawson et al. 2001, Wassen et al. 2003). Wetland faunal communities are influenced both by the presence of surface water and by the nature and productivity of the vegetation (Wilcox and Meeker 1992, Acosta and Perry 2002, de Szalay et al. 2003, Batzer et al. 2004), which demonstrates how hydrology affects the biota both directly and indirectly. Thus, hydrology is one of the key drivers of wetland ecosystem structure and function.

One reason hydrology is considered to be so important in wetland ecology is because the term embodies many environmental variables, including water depth (above or belowground), seasonal and interannual variability in water levels, the timing and duration of flooding, hydraulic residence time, connectivity to other surface waters, and water source. These hydrologic variables differ in how they affect wetland ecosystems. The duration of flooding can have marked effects on the availability of oxygen and other terminal electron acceptors in surface waters (Turner and Patrick 1968). Interannual variability in water levels near the soil surface contributes to the development of wetland soils (Tiner 1999). A wetland's water sources and soils interact to determine the hydrochemistry of and nutrient supply to wetlands (Vitt et al. 1995). All of these ecosystem processes are due in part to specific hydrologic causes, although they are often ascribed to hydrology in general. In fact, most aspects of wetland ecology are related to hydrology in some way, which explains why the term enjoys such broad usage.

However, while the term hydrology readily conveys a general meaning, invoking the broad concept of hydrology for explanatory purposes does little to elucidate what may be driving a wetland phenomenon. For example, plant communities in wetlands vary not as a function of hydrology, but as a function of water depth, the timing and duration of flooding, and the hydrochemistry of that water. These hydrologic variables, together with other abiotic variables such as light and nutrient availability, interact to set the context within which plant competition occurs. Specificity allows us to tease apart which hydrologic variables are most important to a given ecological question; general terminology does not. One of the remaining challenges for the field of wetland ecology is to specify and quantify hydrology in more rigorous terms that are also relevant to the ecological question of interest. A more mechanistic understanding of plant-hydrology relations would greatly aid efforts to create and restore wetlands.

The overarching goal of this study was to describe environmental variables that may help explain the variability in plant community composition across a diverse set of wetlands in southwest Michigan. In this chapter I present all of the environmental variables that were measured in this study. I evaluate three hydrologic properties of wetlands: water sources, water levels, and surface water connectivity. Water levels are commonly measured in wetland studies (Cole and Brooks 2000). Water sources are sometimes inferred (Goslee et al. 1997), but rarely estimated quantitatively (Hunt et al. 1998, Winter et al. 2001). The importance of surface water connectivity is increasingly acknowledged (Brinson 1993a, Bedford and Godwin 2003), and I explore its relationship with water sources and water levels. I also characterize the hydrochemistry of wetland porewaters and the chemical composition of wetland soils. Finally, I present a measure of nutrient availability (ammonium, nitrate, and phosphate) in the rooting zone for wetlands.

This study is unique because it includes a hydrochemically diverse set of wetlands that are all located in a relatively small area. This proximity facilitates comparisons across wetland types because the study sites share a similar underlying geology and are subject to the same climate.

METHODS

Study sites

All wetlands in this study are located within 30 km of the W.K. Kellogg Biological Station (KBS), an academic unit of Michigan State University. KBS is located 20 km northeast of Kalamazoo, MI, in a mosaic of agricultural fields (40% areal coverage), forests (20%), open space (mostly abandoned farmland – 12%), wetlands (12%), residential areas (9%), lakes and ponds (6%), and commercial and industrial areas (1%) (WMU GIS Research Center 1996). The underlying geology of this area is dominated by glacial till that contains significant calcite and dolomite, and local groundwater is ionically rich with high alkalinity. Mean annual precipitation for Kalamazoo is 89 cm (Rheaume 1990).

The wetlands in this area are notably diverse and include bogs, marshes, fens, swamps, vernal pools, and ponds. I selected study sites with an intent to span both the terrestrial end of this wetland gradient (i.e., wetlands with little standing water) and a water source gradient, from precipitation-fed to more groundwater-fed wetlands. Wetlands with permanent or semi-permanent standing water (ponds, littoral zones of lakes) were purposely excluded in order to restrict comparisons across emergent plant communities. In 1999, using National Wetlands Inventory (NWI) maps (U.S. Fish and Wildlife Service 1995), I selected three wetlands from each of four NWI subclasses: PSS3 (palustrine scrub shrub wetland, broad-leaved evergreen), PEM (palustrine emergent wetland), PSS1 (palustrine scrub shrub wetland, broad-leaved deciduous), and PFO (palustrine forested wetland). After one year of study, these first 12 wetlands appeared to be either strongly precipitation-fed or strongly groundwater-fed, with none in between. In 2000 I selected 12 additional wetlands (for a total of 24 study sites), three from each of the four NWI subclasses above, but I deliberately included wetlands that I suspected might receive more intermediate contributions of groundwater and precipitation.

Wetland classification is not a simple exercise because of the variability in terminology. I considered using three different classification systems: the Canadian system (National Wetlands Working Group 1997), the U.S. Fish and Wildlife Service (USFWS) system (Cowardin et al. 1979), and the hydrogeomorphic (HGM) approach (Brinson 1993b). I follow the Canadian wetland classification system for three reasons: 1) the Canadian classes are most specific and applicable to wetlands in southwest Michigan; 2) they convey meaning of both basin geomorphology and physiognomy; and 3) the Canadian system's terminology is most communicable, which facilitates relating research findings to others. I list study sites according to the Canadian and USFWS systems (Table 2.1) as well as the HGM approach (Table 2.2), although the Canadian terminology is retained for all other purposes.

I list other general information for each study site in Table 2.3. In Table 2.3 relative elevation reflects the position of the wetland relative to its upper catchment boundary (1) and the topographic low (0) in that wetland's local hydrologic flow system. Thus, wetlands located relatively high in their local

Table 2.1: Canadian and U.S. Fish and Wildlife Service (USFWS) classifications of the 24 wetlands in southwest Michigan that are included in this study (Cowardin et al. 1979, National Wetlands Working Group 1997). NWI refers to the National Wetlands Inventory. NWI categories are hierarchical and all fall under the system Palustrine (P); classes include Emergent (E), Scrub Shrub (SS), and Forested (FO); subclasses include Broad-leaved deciduous (1), Broad-leaved evergreen (3), and Deciduous (6); water regime modifiers include Temporarily flooded (A), Saturated (B), Seasonally flooded (C), and Semipermanently flooded (F); special modifiers include Partially drained, ditched (d).

site	class	form	type	NWI
Blachman Bog	bog	basin	mixed shrub	PSS3/6B
Purdy Bog	bog	basin	low shrub	PSS3B
Kidd Bog	bog	basin	mixed shrub	PSS3B
Leatherleaf Bog	bog	basin	mixed shrub	PSS3B
Chainfern Bog	bog	basin	forb	PSS1B
Blueberry Bog	bog	basin	mixed shrub	PSS3B
Longman Road Bog	bog	basin	low shrub	PSS3B
Chokeberry Bog	bog	basin	tall shrub	PSS1/3B, PSS1F
Winterberry Fen	fen	basin	grass	PSS1B
Lang Fen	fen	basin	sedge	PEMF
Glasby Fen	fen	shore	tall rush	PEMFd
Cemetery Fen	fen	stream	sedge	PSS1C
Butterfield Fen	fen	shore	sedge	PEMC
Balker Lake Swamp	swamp	basin	mixed treed	PFO1C
Otis Pond Swamp	swamp	basin	hardwood treed	PFO6/SS1B
Stafford Fen	fen	stream	sedge	PSS1C
Sherriff Fen	fen	floating	forb	PEMF
Mott Road Fen	fen	stream	sedge	PEMC
Starflower Swamp	swamp	basin	mixed treed	PFO6B
Serbin Swamp	swamp	seepage	mixed treed	PFO6B, PFO1C
Turner Creek Fen	fen	stream	tall shrub	PEMCd
Stafford Swamp	swamp	riverine	hardwood treed	PFO1C
Prairieville Creek Fen	fen	spring	tall shrub	PSS1C
Kalamazoo River Swamp	swamp	floodplain	hardwood treed	PFO1C, PFO1A

Table 2.1

Table 2.2: Hydrogeomorphic classification of the 24 wetlands in southwest Michigan included in this study (Brinson 1993b). Geomorphic setting classes include depressional (d) and riverine (r) wetlands. Water sources are precipitation (p), intermediate (p/g), and groundwater (g) and were determined based on a linear mixing model using [Mg^{2+}]. Hydrodynamic categories are vertical fluctuation (v f) and unidirectional fluctuation (u f). Hydrodynamic fluctuations are seasonal (s) and nearly constant (n c).

site	geomorphic setting		water source	hydrodynamics	
	category	surface water connectivity		category	fluctuations
Blachman Bog	d	no inlet or outlet	p	v f	s
Purdy Bog	d	no inlet or outlet	p	v f	s
Kidd Bog	d	no inlet or outlet	p	v f	s
Leatherleaf Bog	d	no inlet or outlet	p	v f	s
Chainfern Bog	d	no inlet or outlet	p	v f	s
Blueberry Bog	d	no inlet or outlet	p	v f	s
Longman Road Bog	d	no inlet or outlet	p	v f	s
Chokeberry Bog	d	no inlet or outlet	p	v f	s
Winterberry Fen	d	no inlet or outlet	p/g	v f	s
Lang Fen	d	no inlet or outlet	p/g	v f	s
Glasby Fen	d	surface outlet	p/g	v f	s
Cemetery Fen	d	peripheral surface inlet and outlet	p/g	v f	n c
Butterfield Fen	d	peripheral surface inlet and outlet	p/g	v f	s
Balker Lake Swamp	d	surface outlet	p/g	v f	s
Otis Pond Swamp	d	surface outlet	p/g	v f	s
Stafford Fen	d	peripheral surface inlet and outlet	p/g	v f	s
Sherriff Fen	d	surface inlet and outlet	g	v f	s
Mott Road Fen	d	surface inlet and outlet	g	v f	n c
Starflower Swamp	d	surface outlet	g	v f	s
Serbin Swamp	d	surface outlet	g	v f	n c
Turner Creek Fen	d	surface inlet and outlet	g	v f	s
Stafford Swamp	d	surface inlet and outlet	g	v f	s
Prairieville Creek Fen	d	surface outlet	g	v f	s
Kalamazoo River Swamp	r	low-gradient alluvial	g	u f	s

Table 2.2

Table 2.3: General characteristics of 24 wetlands in southwest Michigan. Area is measured in hectares. Elevation is measured in meters above sea level and was estimated visually using the MSU Institute of Water Research Interactive Watershed Mapping tool (http://www.iwr.msu.edu/gis/gisfp.html). Relative elevation is the position of the wetland relative to its upper catchment boundary (1) and the topographic low (0). Wetlands lie in either the Kalamazoo (K) or Thornapple (T) watersheds. Land ownership categories are as follows: private (pr), public (pub), military (m), and national cemetery (n c). Distance from KBS is measured in kilometers.

site	area	elevation	relative elevation	watershed	land ownership	distance from KBS
Blachman Bog	54.3	283.0	0.82	K	pr	10.6
Purdy Bog	17.6	276.9	0.78	K	pr	6.8
Kidd Bog	5.0	279.1	0.71	K	pr	7.5
Leatherleaf Bog	2.6	228.4	0.94	K	pub	26.4
Chainfern Bog	1.5	228.4	0.94	K	pub	26.2
Blueberry Bog	14.9	280.0	0.84	K	pr	5.3
Longman Road Bog	1.9	282.1	0.65	K	m	15.3
Chokeberry Bog	12.8	276.0	0.81	K	pr	3.8
Winterberry Fen	0.7	261.4	0.85	T	pub	21.8
Lang Fen	6.0	273.0	0.70	K	pr	6.9
Glasby Fen	44.2	282.4	0.81	K	pr	7.6
Cemetery Fen	22.5	242.5	0.17	K	n c	9.8
Butterfield Fen	7.6	260.5	0.54	K	pr	5.1
Balker Lake Swamp	30.2	279.4	0.85	K	pr	10.4
Otis Pond Swamp	13.1	261.4	0.85	T	pub	22.0
Stafford Fen	14.4	263.8	0.51	K	pr	5.1
Sherriff Fen	64.5	261.4	0.46	K	pr	5.8
Mott Road Fen	10.6	260.8	0.33	K	m	13.3
Starflower Swamp	9.5	228.1	0.80	K	pub	26.3
Serbin Swamp	6.6	228.8	0.38	K	pub	22.8
Turner Creek Fen	0.8	228.4	0.10	T	pub	28.1
Stafford Swamp	115.4	263.2	0.49	K	pr	6.3
Prairieville Creek Fen	27.9	276.0	0.67	K	pr	4.4
Kalamazoo River Swamp	14.6	239.4	0.00	K	pub	9.9

Table 2.3

watershed have relative elevation values that approach 1. Elevation values were estimated visually using the MSU Institute of Water Research Interactive Watershed Mapping tool (http://www.iwr.msu.edu/gis/gisfp.html). Elevation values for wetlands and their upper catchment boundaries were estimated using the midpoint value of each elevation color contour (each elevation contour generally spanned 8 m in elevation). The elevation value used for the topographic low reflects where that wetland's local hydrologic flow system enters either the Kalamazoo River or the Thornapple River, depending on in which watershed the wetland lies. Relative elevation is meant to approximate the position of the wetland along the maximum hydrologic flow path from the highest point in the wetland's watershed to the local topographic low. The location of each wetland study site is shown in Figure 2.1. A description of each study site follows.

Study site descriptions

Blachman Bog is the northernmost wetland in this study that still lies in the Kalamazoo River watershed (before crossing over to the Thornapple watershed to the north). Like most bogs in the Kalamazoo River watershed, Blachman Bog is a basin bog (Table 2.1) that is perched relatively high in the watershed (relative elevation = 0.61; Table 2.3). The study area is the eastern lobe of the basin, which is northeast of Pleasant Lake. Prior to road development, it appears that the greater hydrologic basin ran from one large depression in the north

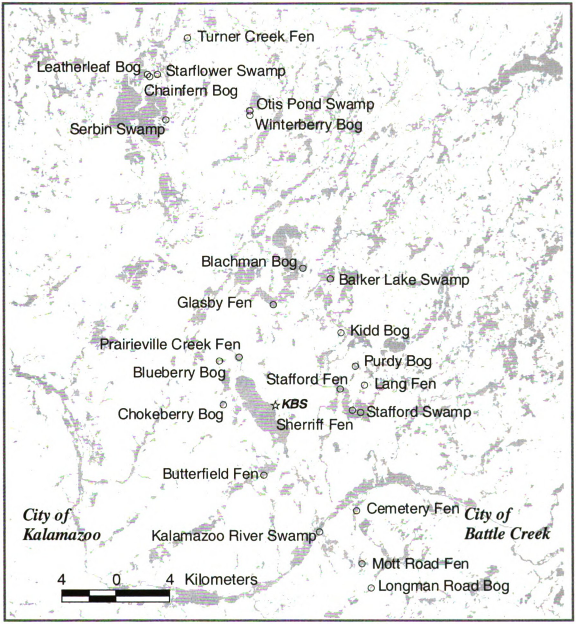


Figure 2.1: Locations of 24 wetland study sites in southwest Michigan. Note the extensive wetlands and lakes (shaded areas) in the region. The W.K. Kellogg Biological Station (KBS) and the cities of Kalamazoo and Battle Creek are shown for reference.

(Blachman Bog), through Pleasant Lake and south to Mud Lake and its peripheral bogs, then west to the Glasby Lake basin, and eventually ending at the Crooked Lake system. A smaller subsystem ran north from Blachman Bog to Wall Lake. *Vaccinium corymbosum* (highbush blueberry) and *Chamaedaphne calyculata* (leatherleaf), shrubs typical of local bogs, dominate the well-developed *Sphagnum* hummocks.

Purdy Bog lies in a basin whose shape resembles a pair of human lungs. Purdy Lake, a small softwater lake, is located in the middle of the eastern lobe; a wetter area is similarly located in the middle of the western lobe. The vegetation in these wetter areas is characterized by the sedges *Carex oligosperma* (running bog sedge) and *Rhynchospora alba* (white beak-rush), although one may also find carnivorous plants such as *Sarracenia purpurea* (pitcher plant) and *Drosera rotundifolia* (round-leaved sundew), especially near the lake. Most parts of this basin bog are dominated by the low ericaceous shrub *Chamaedaphne calyculata* (leatherleaf). Like most bogs in the area, this site has a well-defined lagg, or moat, around its perimeter.

Kidd Bog, like Purdy Bog, is a basin bog with a small pond in its center. The wetter areas near the pond share the same sedge and carnivorous species as those for Purdy Bog. However, a stand of *Larix laricina* (tamarack) encircles the pond. While *Larix* is frequently found in bogs in the U.S. and across Canada, many of the bogs in this study lack *Larix*. The vegetation in most parts of the bog include low shrub and mixed shrub areas, which are typically dominated by

Chamaedaphne calyculata (leatherleaf) and *Vaccinium corymbosum* (highbush blueberry), respectively.

Leatherleaf Bog is a basin bog that is located in the Yankee Springs State Recreation Area (Table 2.3). This area comprises part of the interlobate region, an area where several glacial lobes came together during the last glaciation (Kehew and Brewer 1992). Sandy soils are common in the area. The vegetation in Leatherleaf bog is a mixed shrub community dominated by *Vaccinium corymbosum* (highbush blueberry) and *Chamaedaphne calyculata* (leatherleaf).

Chainfern Bog is a basin bog located just across the road from Leatherleaf Bog, less than 1 km northeast of the trailhead to the Long Lake Nature Trail. What distinguishes this bog from other bogs in this study is its expansive *Sphagnum* carpet that has not yet developed the characteristic hummock-hollow structure that is more typical of local bogs. Consequently, the bog is much more homogeneously wet, although the peat surface can dry entirely during the summer. Much of the bog is a *Sphagnum* lawn dominated by *Woodwardia virginica* (Virginia chainfern), although shrubs also occur in some areas.

Blueberry Bog is located 2 km northwest of Gull Lake in an irregularly shaped depression that runs west-east. The well-developed lagg is dominated by *Carex rostrata* (beaked sedge), while most of the bog is densely covered by *Vaccinium corymbosum* (highbush blueberry). The southwestern lobe of the overall basin, which was not included in this study, grades into a lower area that is usually inundated or, when sufficiently dry, covered by *Phalaris arundinacea* (reed canary grass).

Longman Road Bog is a basin bog that is located in the Fort Custer Training Center, east of Augusta, MI. *Cephalanthus occidentalis* (buttonbush) occupies most of this bog's lagg. The overall basin has relatively steep sides and runs northeast to southwest. The wetter area in the southwest, which does not have characteristic bog-like vegetation, was not included in this study. Like Purdy Bog, the dominant plant in this bog is the low shrub *Chamaedaphne calyculata* (leatherleaf), which grows on a *Sphagnum* complex of moderately developed hummocks and hollows.

Chokeberry Bog is a basin bog located 2 km west of Gull Lake. Chokeberry bog is somewhat unusual for local bogs in that it has a well-developed raised mound in its middle, which is sufficiently dry to support a small island of trees. However, much of the bog vegetation is dominated by a dense stand of tall, slender-stemmed shrubs – most notably *Aronia prunifolia* (chokeberry) and *Ilex verticillata* (winterberry), which are not the dominant shrub species in other local bogs. Between the inner shrub zone and the lagg lies a swath of *Decodon verticillata* (swamp loosestrife) that is extremely dense (and *very* difficult to walk through!).

Winterberry Fen is distinctive due to its more intermediate plant community composition and soil acidity. Located 1 km south-southwest of Otis Lake in Barry State Game Area, Winterberry Fen lacks surface inflows and outflows and is the only poor fen included in this study. Sparse *Sphagnum* (relative to local bogs) and several species of shrubs are scattered throughout this small depression.

The grass *Calamagrostis canadensis* (blue-joint) is the most abundant plant species.

Lang Fen is a basin fen – an unusual fen type for this area because it lacks surface inflows and outflows. Baseline Road separates the northernmost tip of this wetland from the remainder of the depression, which is the focal area of this study. The plant community varies between shrubby areas of *Salix discolor* (pussy willow) and areas that are dominated by various sedges and forbs. A population of *Lythrum salicaria* (purple loosestrife), an invasive species, exists near the road. According to Mahan (1980), Lang Fen lies just outside the Augusta Creek watershed. While this may be true topographically, it is more likely that water in this depression percolates down and flows south-southwest belowground to emerge as an intermittent stream that flows into Stafford Swamp (described below), which is a part of the Augusta Creek drainage system.

Glasby Fen is a large shore fen that borders Glasby Lake. The study area is the most southeastern portion of the fen, which is farthest from the lake. *Typha latifolia* (common cattail) is the dominant species throughout the wetland. Although only 2 km south of Delton, MI, Glasby Lake is actually quite remote; only one property owner has lake access via a dock (in part because the marsh is so extensive around the lake's perimeter). As a result, this marsh and the lake are likely good breeding habitat for waterfowl and other bird species. A sewage treatment plant is located downgradient of the lake and, therefore, likely has no effect on the plant community in this study. This basin has no surface inflows, although it may have had inflow from Mud Lake prior to road construction at its eastern end.

Cemetery Fen is a stream fen located on the western end of the Fort Custer National Cemetery in Augusta, MI. While a stream fen in the broadest sense, this wetland is only marginally connected to Eagle Creek, which flows by the southwestern corner of the fen. Evidence of manmade drainage channels is apparent in this wetland. A channel in the southern part of the fen flows toward the creek. The excavated spoils appear to have been piled adjacent to the dugout channel, and several upland species, including *Prunus serotina* (black cherry), have colonized these local dry patches. Despite these drainage attempts, the fen remains relatively wet, and much of the fen is inundated throughout the year. *Lythrum salicaria* (purple loosestrife) and *Typha latifolia* (common cattail) are abundant near the road and along the dugout channel. The study area lies just north of the dugout channel. Dominant species include *Carex stricta* (tussock sedge) and *Aster puniceus* (purple-stemmed aster). Also noteworthy is the diversity of shrub species in this fen (11 shrub species occurred on the vegetation transects).

Butterfield Fen is a shore fen, and the area of study is positioned along the southern shore of Butterfield Lake and its outflow channel, which are part of the Gull Creek system. The watershed for the study area is actually quite small; a topographic rise < 0.2 km to the southeast defines the watershed boundary. Groundwater in this part of the Kalamazoo River watershed generally flows north to south (Baker 2001). As a result, the groundwater emerging along the northern shore of Butterfield Lake likely has flown underground longer than the groundwater emerging along the southern shore of the lake and outflow channel. This could result in geochemically different groundwater in the northern and southern shore fens. Thus, the results of this study are meant to characterize only the southern shore fen. The plant community in Butterfield fen is dominated by *Carex stricta* (tussock sedge), although shrubs become more prevalent towards the wetland-upland border. Two species of note are *Lythrum salicaria* (purple loosestrife) and *Phragmites australis* (common reed), both of which are considered to be invasive species. *Lythrum* occurs in abundance at the lake-fen interface. The *Phragmites* population, which appears to be the non-native, aggressive genotype (Blossey 2002, Saltonstall 2002), appears to be slowly spreading (< 0.5 m per year, personal observation) from the southern tip of the fen northward.

Balker Lake Swamp is located high in the watershed (relative elevation = 0.57; Table 2.3) and represents the headwaters of the Augusta Creek drainage system. The Balker Lake outflow to Gilkey Lake is the only surface water that, at least distally, drains the swamp. This swamp is perennially wet, with *Sphagnum*-covered hummocks occurring throughout. The study area lies east of the lone upland island in the swamp's interior. *Acer rubrum* (red maple) and *Ulmus americana* (American elm) are the dominant tree species in the study area, although *Larix laricina* (tamarack) is quite common in the eastern portion of the swamp. The most abundant graminoid and forb species are *Carex lacustris* (lakeshore sedge) and *Osmunda regalis* (royal fern), respectively. This is the only non-bog site where *Chamaedaphne calyculata* (leatherleaf) occurred, albeit in very low abundance.

Otis Pond Swamp is a basin swamp located east of a permanent pond that is southwest of Otis Lake. Winterberry Fen lies just over a low saddle to the south of this depression. Like Balker Lake Swamp, this a perennially wet hardwood swamp with *Sphagnum*-covered hummocks scattered throughout the swamp. Several orchid species occur on these hummocks, including *Cypripedium acaule* (pink lady-slipper) and *Habenaria clavellata* (club-spur orchid). The dominant tree species include *Ulmus americana* (American elm) and *Acer rubrum* (red maple). *Osmunda cinnamomea* (cinnamon fern) covers nearly all the hummocks and is the herbaceous community dominant. The quiet seclusion and cool shade of this swamp made it one of my favorite sites to visit.

Stafford Fen is a stream fen that borders Augusta Creek, albeit peripherally. This area has features of a glacial moraine: the property owner, an excavator by trade, excavates large stones (some 1 m in diameter!) and uses them for landscaping. In the 1960s, this property owner, noticing the springs on his land, dug out 7 ponds in which to raise trout. The trout contracted a disease and had to be exterminated, although the ponds remain. The study area is located north of these ponds and runs west toward the creek. This fen is really a mixture of several plant communities that grade from a shrubby zone to a *Typha* zone and finally to a sedge meadow closer to the stream. *Cornus foemina* (gray dogwood) and *Cornus stolonifera* (red-osier dogwood) are the most abundant shrub species.

Sherriff Fen is a locally large, floating fen (64.5 hectares; Table 2.3) with a well-developed quaking mat that floats 10-80 cm above more consolidated organic sediments. A small dam, which was installed in the early 1950s, regulates outflow at the downstream end of the fen. A tributary of Augusta Creek flows into the fen from the east (from Stafford Swamp, described later) and joins a smaller tributary from the north in the central portion of the fen before flowing out to the west. The eastern tributary is slow-flowing and choked with *Nymphaea odorata* (water-lily) and *Nuphar advena* (pond-lily). During the late spring and early summer the mat floats, and the wetland acts as a temporary reservoir for waters flowing through this part of the Augusta Creek drainage system. Thus, this depression is locally important for temporary floodwater retention. There are several shallow ponds (< 3 m deep) in the fen's interior that are best reached by canoe. The plant community at Sherriff Fen is a mixture of herbaceous species: *Pilea pumila* (clearweed) and *Typha latifolia* (common cattail) are the dominant forbs, while *Carex lacustris* (lakeshore sedge), *Eleocharis erythropoda* (creeping spike-rush), and *Leersia oryzoides* (cut grass) are the most widespread graminoids. Flocculent iron oxide precipitates are common in the surface waters.

Mott Road Fen is a stream fen located in the Fort Custer Training Center. The area of study is the fen north of Mott Road on the east side of the stream. This area has been subject to several hydrologic alterations: the stream is channelized and runs linearly; beaver have constructed dams in different places along the stream (three different places during the past three years of study); and a culvert under Mott Road impedes water flow from the fen south of the road to the fen north of the road. Because of the riparian nature of the fen, water levels in the wetland vary as a function of water levels in the stream. There are two distinct plant communities included in this study: the sedge meadow near the stream, which is more typical of local fen communities, and a wet prairie community positioned upgradient of the sedge meadow. The Michigan Natural Features Inventory has designated this wet prairie as a "high quality" community (Legge et al. 1995). *Carex stricta* (tussock sedge) dominates the community near the stream, while *Potentilla fruticosa* (shrubby cinquefoil) characterizes the wet prairie community. A rare find in the wet prairie is *Gentianopsis crinita* (fringed gentian).

Starflower Swamp is a basin swamp located on the Long Lake Nature Trail in the Yankee Springs State Recreation Area. Chainfern Bog and Leatherleaf Bog lie < 1 km west-southwest of this basin. This study site is another swamp that is perennially wet with many *Sphagnum*-covered hummocks. A small, semi-permanent stream drains from the central portion of the swamp into the northern end of Long Lake. *Acer rubrum* (red maple), *Ulmus americana* (American elm), and *Pinus strobus* (white pine) characterize the tree community. *Lindera benzoin* (spicebush) dominates the shrub community, while *Osmunda cinnamomea* (cinnamon fern) is the most common herbaceous species. In late May or early June the boardwalk through this swamp provides easy access to blooming orchids such as *Cypripedium calceolus* (yellow lady-slipper) and *Cypripedium acaule* (pink lady-slipper) as well as *Trientalis borealis* (star-flower), for which this site is named.

Serbin Swamp is a seepage swamp located in the Yankee Springs State Recreation Area. The southern perimeter of this basin is very steep, and the large break in slope generates the seeps that flow continuously into the swamp. Hastings Point Road, which runs along the northwestern edge of the swamp, hydrologically separates the swamp from the wetland areas and Gun Lake to the northwest. A stream that enters and flows through the northern edge of the swamp joins the waters draining from the swamp and together flow through the culvert at the northwestern edge of the wetland. This swamp is a wet mixed swamp with *Sphagnum*-covered hummocks scattered throughout. *Fraxinus nigra* (black ash) and *Larix laricina* (tamarack) are the most widespread tree species, while *Lindera benzoin* (spicebush) dominates the shrub community. The herbaceous community is diverse and characterized by *Osmunda cinnamomea* (cinnamon fern), *Typha latifolia* (common cattail), and *Carex lacustris* (lakeshore sedge). *Drosera rotundifolia* (round-leaved sundew) occurs on hummocks in the southern area of the swamp. On one occasion I had the pleasure of finding and photographing a lone *Calopogon tuberosus* (grass-pink).

Turner Creek Fen is a stream fen located in the Barry State Game Area. This site is a narrow strip of fen that lines a channelized stream. Springs emerge in several places along the fen, and seeps flow sufficiently to generate small drainage tracks that flow to the stream. *Onoclea sensibilis* (sensitive fern) dominates the forb community, while *Carex stricta* (tussock sedge) and *Leersia oryzoides* (cut grass) are the dominant graminoids.

Stafford Swamp is a riverine swamp in the Augusta Creek watershed that lies downstream of Hamilton Lake and upstream of Sherriff Fen. The stream that flows through the swamp flows very slowly; *Nymphaea odorata* (water-lily) and *Nuphar advena* (pond-lily) grow in portions of the stream channel. 45th Street, the western border of the swamp, constrains surface flow from the swamp, although two culverts (the main stream channel and a smaller culvert located 100 m to the north) facilitate surface water outflow. This basin is quite broad, and the stream does not appear to flood back into the swamp very frequently. Instead, when subsurface water levels rise following a rain event, it is likely due to an increase in stream stage, which temporarily impedes drainage from the swamp. Unlike several of the swamps in this study, Stafford Swamp is relatively dry. The most abundant tree species is *Betula alleghenensis* (yellow birch), although *Fraxinus nigra* (black ash) and *Ulmus americana* (American elm) are also common. *Carpinus caroliniana* (blue-beech) is the most prevalent shrub. The shady understory is dominated by *Laportea canadensis* (wood nettle) and *Carex bromoides* (brome hummock sedge). Several groundwater seeps emerge in the swamp, and iron oxide precipitation readily occurs in these waters.

Prairieville Creek Fen is a spring fen located just north of Gull Lake. This site is unique because of its landscape position and landscape context. First, the basin is positioned relatively high in the watershed (relative elevation = 0.52; Table 2.3) at an elevation more typical of bog systems (see Blueberry Bog, which lies 1.5 km to the west). Second, there is no drainage network directly upgradient of the Prairieville Creek basin; the Crooked Lake system to the north-

northwest has no outflow streams. Instead, water from the Crooked Lake system and precipitation that infiltrates the predominantly agricultural land to the north likely flow underground and discharge into the Prairieville Creek basin. This hydrogeomorphic context has important consequences for the wetland. Numerous groundwater springs emerge in the fen and converge to form various drainage channels (these channels flow first to a small lake and then south to Gull Lake), which maintain relatively low water levels. The springs emerging in the basin are very high in nitrate (3-13 mg NO_3-N/L for the spring nearest the study area; n=6 sampling dates), which is likely a function of the widespread agricultural land use upgradient of the fen. Thus, altogether, this fen has well-drained surface soils and receives constant supplies of nitrogen-rich groundwater below the rooting zone. A dense stand of *Rhamnus frangula* (glossy buckthorn), an invasive, exotic shrub species, shades the fen understory. While once a sedge meadow community (remnants persist north of Hickory Road), this fen now supports shade-tolerant understory species such as the current community dominants *Onoclea sensibilis* (sensitive fern) and *Carex bromoides* (brome hummock sedge). Anyone who enters this wetland is well advised to take a compass or GPS unit!

The Kalamazoo River Swamp is a floodplain swamp located 2 km south-southwest of Augusta, MI, in the Fort Custer State Recreation Area. The study area is bounded by a large meander in the river to the north, west, and south and a moderately steep slope to the east. Seeps emerge in several places along this escarpment. The floodplain topography is heterogeneous – more so than any of the other study sites. The particular area studied begins at the escarpment, crosses through a relatively wet area subject to groundwater discharge, and ends in a drier section closer to the river. *Acer saccharinum* (silver maple) and *Fraxinus pennsylvanica* (green ash) are the dominant tree species, although they are much more prevalent in the drier area near the river. *Laportea canadensis* (wood nettle) and *Carex bromoides* (brome hummock sedge) dominate the understory. While the floodplain offers frequent mosquito visits, avid botanists and photographers may enjoy seeking out the beautiful flowers of *Habenaria psycodes* (purple fringed orchid) and *Lobelia cardinalis* (cardinal flower) in June and August, respectively.

Hydrochemical characterization of wetland and source waters

I characterized the hydrochemistry of wetland surface waters and porewaters across this suite of wetlands, as well as local groundwater in the form of seeps, springs, and streams. To characterize seasonal variability, I sampled surface waters (in hollows and low areas), seeps, springs, and porewaters during the fall (Oct 2000), spring (May 2001), and late summer (Sep 2001). Samples from surface waters, seeps, and springs were collected using a plastic dipper. To sample shallow and deeper porewaters at each wetland, I installed ¾-inch PVC mini-piezometers (Lee and Cherry 1979) with 10-cm length screens at the following depths: 0-10 cm, 10-20 cm, and 45-55 cm. Wetland water levels decline during the late summer, but by sampling at these three depths, I could sample the most surficial porewaters at all times of the year. Occasionally seepage into the mini-piezometers was prohibitively slow, and it was necessary to sample porewaters from the monitoring wells (described below under *Water level variability*), which span 0-100 cm depth. Between sampling periods mini-piezometers remained capped with syringe barrels, which allowed pressure equilibration (and therefore water flow into the mini-piezometer), but prevented rainwater from entering the mini-piezometer. Porewaters were collected by pumping water out of the mini-piezometer three times (to flush out any residual porewaters that had collected inside the mini-piezometer), then pumping out water a fourth time and collecting the sample in a Nalgene bottle. All samples were put on ice following collection. Upon return to the lab, samples were refrigerated (alkalinity, conductivity) or filtered through Gelman Supor 0.47-μm membrane filters and then refrigerated (anions, silica) or acidified with 8 N HNO_3 (cations) until analysis. Some mini-piezometers yielded only small volumes of sample water; these samples were diluted with deionized water prior to analysis to ensure sufficient sample volume for all hydrochemical analyses.

Conductivity was measured in the lab using an Orion model 135 conductivity meter (Analytical Technology, Inc.). Ca^{2+}, Mg^{2+}, Na^+, and K^+ were measured by flame atomic absorption spectrometry. Alkalinity, which generally represents HCO_3^- in local waters, was determined by titration with 0.3 N HCl and calculation of the Gran function (Cantrell et al. 1990). SO_4^{2-}, Cl^-, and NO_3^- were measured by ion chromatography. Si was measured colorimetrically by the ammonium molybdate method (Wetzel and Likens 2000).

Other nutrients were measured for samples from the Oct 2000 and May 2001 sampling periods. NH_4^+ was measured colorimetrically following an adapted version of the phenylhypochlorite method (Aminot et al. 1997). Soluble reactive phosphorus (PO_4-P) and total dissolved phosphorus (TDP) were measured colorimetrically following the acid molybdate method (Wetzel and Likens 2000); the TDP colorimetric analysis was preceded by a persulfate digestion to decompose organically bound P (Valderrama 1981).

A separate set of pH measurements was made for all wetland porewaters in Aug 2003. These samples were collected from three different locations within each wetland (near each of the three monitoring wells in most cases) to describe any spatial variability in pH at each site. A metal rod was inserted into the soil to make a small hole into which porewater seeped. Using a 3-mL syringe, water samples were collected from the upper 15 cm of the soil (deeper when necessary), capped, and put on ice until return to the lab. pH was then measured by injecting the porewater into a piece of Tygon tubing that connected to the electrode tip of the pH meter. By using this method, I avoided loss of dissolved CO_2 from the samples, which would have changed their pH. All pH measurements were made using an Accumet 1003 pH meter (Fisher Scientific) with a Ross combination pH electrode calibrated to pH 4 and 7 buffers.

Hydrochemical data for local precipitation were generated by the National Atmospheric Deposition Program/National Trends Network (NADP/NTN 2003). Values reported are the means of annual volume-weighted means for 1979-2002 from the KBS station (MI26).

Water sources

Precipitation, groundwater, and surface inflows constitute the potential water sources for non-tidal wetlands (Mitsch and Gosselink 2000). For inland, depressional wetlands, the predominant surface inflow is overland flow, although riverine overflow may be important for floodplain wetlands. The KBS vicinity is rural with few impervious surfaces relative to more urban environments (WMU GIS Research Center 1996). In addition, the sandy loam soils in this area facilitate infiltration and reduce the frequency of overland flow events (Rheaume 1990). Thus, in the KBS area overland flow is likely less important than precipitation and groundwater in terms of wetland source waters. Consequently, I have simplified the water source calculations that follow by excluding overland flow. This does not mean overland flow is unimportant; it can become important during large rain events or when rain or snowmelt flow over frozen soils. The hydrochemistry of such overland flow would likely resemble precipitation. Thus, if I underestimate the relative importance of overland flow in any calculations that follow, it would most likely manifest itself by making the wetland appear more precipitation-fed.

To estimate the relative importance of precipitation and groundwater as wetland water sources, I used dissolved Mg^{2+} as a semi-conservative geochemical tracer. An ideal tracer is conservative and differs broadly among the sources one wishes to distinguish. Mg^{2+} is minimal in local precipitation (24-year mean = 0.05 mg/L for the period 1979-2002; NADP/NTN 2003), but is relatively high in local groundwaters (Kalamazoo county mean = 23 mg/L; Rheaume 1990). Mg^{2+} is greater in local groundwaters because as rainwater percolates into the soil and moves through the aquifer, it comes to equilibrium with the dolomite in the glacial till. While no geochemical tracer is truly conservative, Mg^{2+} behaves relatively conservatively in this area because it is not readily subject to reprecipitation (Stauffer 1985) and is not detectably altered by biological uptake (Wetzel and Otsuki 1974).

I used a linear mixing model with precipitation and groundwater as the endmembers to estimate the relative importance of wetland source waters. If these are the only two source waters, and the Mg^{2+} is known in a representative sample of the wetland and the potential source waters, we can solve the following two equations with two unknowns:

$$f_{groundwater} + f_{precipitation} = 1$$

$$f_{groundwater} * [Mg^{2+}]_{groundwater} + f_{precipitation} * [Mg^{2+}]_{precipitation} = [Mg^{2+}]_{wetland}$$

where $f_{groundwater}$ = the fraction of wetland water derived from groundwater

$f_{precipitation}$ = the fraction of wetland water derived from precipitation

$[Mg^{2+}]_{groundwater}$ = the concentration of Mg^{2+} in local groundwater

$[Mg^{2+}]_{precipitation}$ = the concentration of Mg^{2+} in local precipitation

$[Mg^{2+}]_{wetland}$ = the concentration of Mg^{2+} in the wetland

Because $f_{groundwater}$ and $f_{precipitation}$ must sum to unity, we can describe the relative importance of both by simply referring to one. Henceforth I refer to fraction groundwater (f_{gw}), where f_{gw} values range from 0 (strongly precipitation-fed) to 1 (strongly groundwater-fed).

Evapoconcentration

The water source calculations above could have been affected by evapoconcentration. The water samples that were used for these calculations were collected from the rooting zone in order to describe the hydrochemical conditions from the perspective of the plant community. However, water uptake by plants may concentrate solutes in the rooting zone of wetlands. In terms of the f_{gw} calculations, an increase in Mg^{2+} would make sites appear to be more groundwater-fed than they actually were.

Fortunately, I was able to sample both shallow (0-10 or 10-20 cm depth) and deeper (45-55 cm depth; occasionally 0-100 cm depth) porewaters whenever possible throughout the hydrochemical sampling period. Plant roots – even the roots of large trees – rarely penetrated deeper than 30 cm in local wetland soils, and the roots of herbaceous plants were predominantly located in the upper 10 cm of the soil (personal observation). Therefore, if evapoconcentration were to occur in shallow porewaters, it likely would not have been apparent in the deeper porewaters that I collected at 45-55 or 0-100 cm depth. By comparing the Mg^{2+} in shallow vs. deeper porewaters on a given date as well as across seasons, it was possible to evaluate whether evapoconcentration may have been affecting the f_{gw} estimates. In the calculations that follow I assumed that if Mg^{2+} was higher in shallow vs. deeper porewaters that it was due only to evapoconcentration of shallow porewaters and that it should be corrected for in the f_{gw} calculations.

Evapoconcentration of shallow porewaters did appear to have occurred at several sites on certain dates (Figure 2.2). In Figure 2.2 the Mg^{2+} in shallow porewaters and their corresponding deeper porewaters is plotted for all three sampling dates. If shallow and deeper porewaters have equal Mg^{2+}, they plot on the 1:1 line. If shallow porewaters have higher Mg^{2+} than their corresponding deeper porewaters (indicating evapoconcentration of shallow porewaters), they plot to the right of the 1:1 line. If deeper porewaters have higher Mg^{2+} than their corresponding shallow porewaters (likely indicating a greater influence of precipitation on the shallow porewaters), they plot to the left of the 1:1 line. Of these three conditions, only the second condition (evapoconcentration) is problematic in terms of the f_{gw} calculations; the other two conditions are both theoretically possible and pose no problems for the f_{gw} calculations.

To evaluate the degree to which evapoconcentration increased the f_{gw} estimates, I recalculated all f_{gw} values for points plotting to the right of the 1:1 line in Figure 2.2. For these recalculations I used the Mg^{2+} in the deeper porewaters instead of the Mg^{2+} in the shallow porewaters. Half of these recalculated f_{gw} values changed very little (< 0.03) and were deemed unnecessary; the remaining

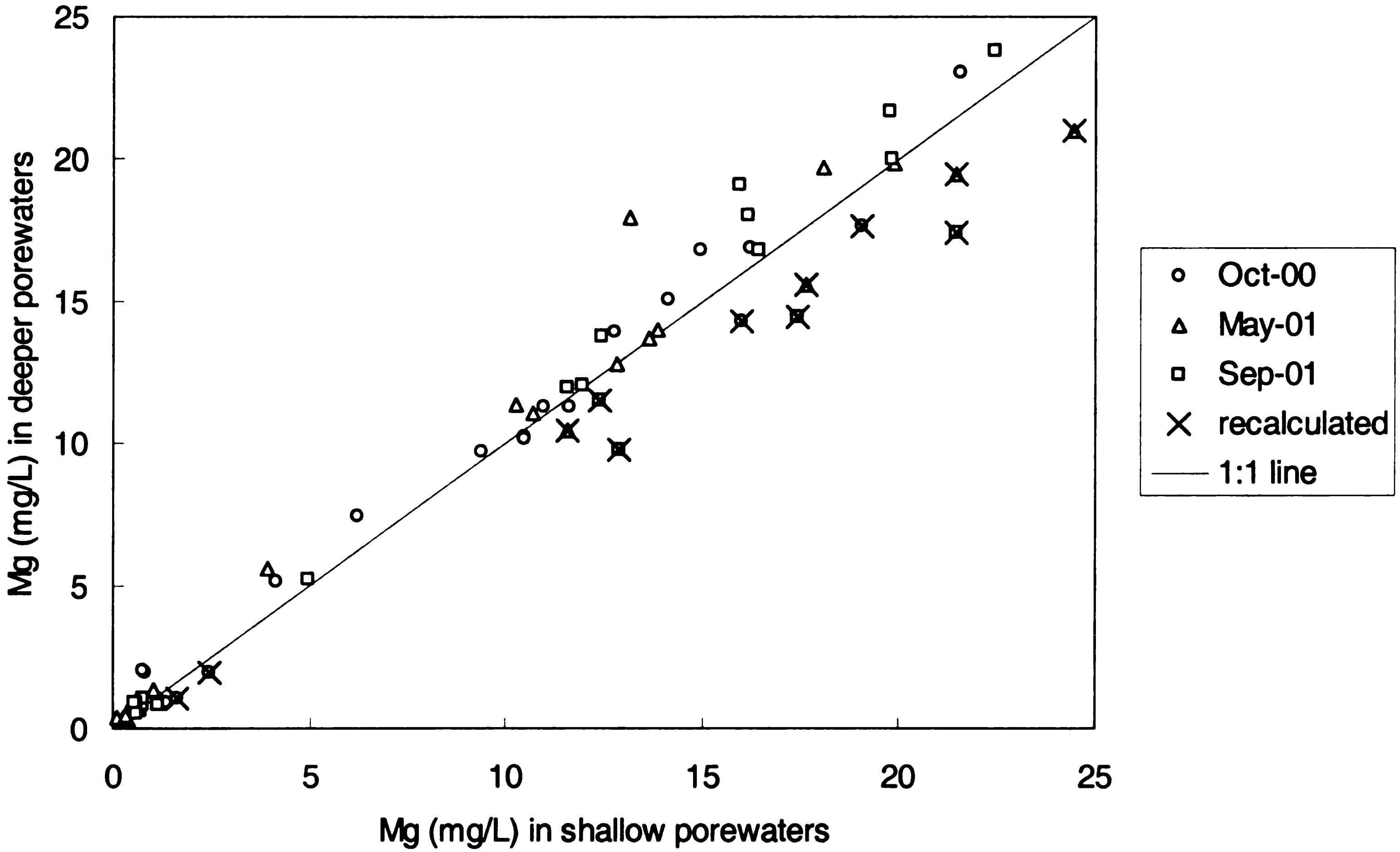


Figure 2.2: A plot of Mg^{2+} in shallow vs. deeper porewaters from 24 wetlands from three sampling periods. Shallow porewaters that were subject to evapoconcentration (relative to their corresponding deeper porewaters) plot to the right of the 1:1 line. For samples that were substantially affected by evapoconcentration, f_{gw} values were recalculated by using the Mg^{2+} in the deeper porewaters instead of the Mg^{2+} in the shallow porewaters.

f_{gw} values changed more and were retained for all subsequent analyses (marked as "recalculated" in Figure 2.2).

Following these recalculations, one f_{gw} value > 1 remained, which is theoretically impossible. Prairieville Creek Fen was somewhat unusual in that mini-piezometers at 0-10 and 10-20 cm depth never yielded water, and the mini-piezometer at 45-55 cm depth and the monitoring well (0-100 cm depth) were sampled to characterize shallow and deeper porewaters, respectively. Using samples collected from both these depths in Oct 2000, the calculated f_{gw} values were both > 1 (1.26, 1.18). This suggested evapoconcentration in relatively deep porewaters or a groundwater endmember that was poorly defined. In either case, I lacked sufficient information to generate a better f_{gw} estimate, so this f_{gw} value was reported as 1.00.

It is important to note that this recalculation procedure had no effect on the overall interpretation of any sites. If sites were ranked by mean f_{gw} (mean for the three sampling dates), the order remained unchanged or only changed by one place as a result of these recalculations. The impetus behind these recalculations was simply to provide a more accurate f_{gw} estimate for sites based on theoretical grounds (i.e., recalculating a f_{gw} value that was erroneously high due to evapoconcentration of Mg^{2+}).

Water level variability

To measure water levels, I constructed monitoring wells using 1-inch diameter PVC tubing (Figure 2.3). Three wells were installed at each study site generally at 0, 100, and 200 m along a transect through the middle of the wetland, which corresponded with vegetation transects (exceptions: 4 wells were installed at Serbin Swamp; 5 wells were installed at the Kalamazoo River Swamp). GPS coordinates (latitude-longitude) for each monitoring well are listed in Appendix Table 1. Water levels were measured approximately monthly using a beeping water level indicator (K-V Associates, Inc.) affixed with metric ruler tape. The water level indicator required constant maintenance due to corrosion of the wire tips.

Soil characterization

Soil samples were collected at 3 locations in each wetland (near each of the 3 water monitoring wells) to a depth of 15 cm by cutting and removing a 3x15 cm cylinder of soil using a serrated knife. Soil samples were then placed in plastic bags and stored on ice; upon return to the lab, samples were refrigerated for one month. Soil pH was determined by mixing fresh (undried) soil and deionized water in a 1:2 ratio and measuring the pH of the resulting soil slurry (Robertson et al. 1999). Soil color was determined by visual inspection using the Munsell soil color charts (GretagMacbeth 2000). Soils were further characterized by the

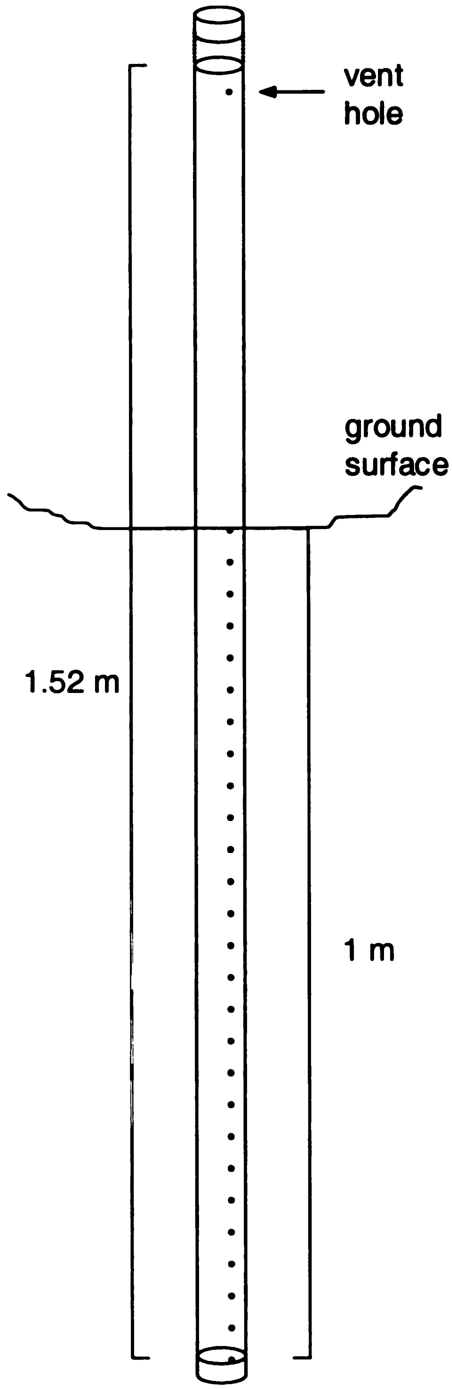


Figure 2.3: Diagram of water level monitoring well.

fraction of identifiable plant material in the soil after gentle rubbing: muck (<16.6% identifiable material); peaty muck (16-45.8%); mucky peat (45.8-75%); and peat (>75%) (Tiner 1999). All three soil samples from each site were then composited in relatively equal amounts, dried at 60°C for 48 hours, ground in a rotary grinder, and analyzed for major nutrients by inductively coupled plasma-atomic emission spectrometry (ICP-AES) at A&L Great Lakes Laboratories (AOAC 975.03B(b)/985.01, 17th Edition, Association of Analytical Communities International 2000).

Nutrient supply

I used ion exchange resin (IER) to estimate ammonium, nitrate, and phosphate nutrient supply at each wetland (Giblin et al. 1994). A 7-mL volume of Dowex HCR-W2 cation exchange resin (H^+ form, 16-40 mesh spherical beads) or IONAC A-554 anion exchange resin (Cl^- form, type II, 16-50 mesh spherical beads) was placed inside a 7x7 cm nylon mesh bag, which was then sewn shut. Resin bags were washed in 1.2 M HCl for 1 hour and thoroughly rinsed with deionized water. After making a small hole outside the seam on the resin bag, fishing line was used to attach the resin bags to a plastic disc, which served as a label tag. Resin bags were then stored in labeled Ziploc bags until deployment.

One anion and one cation resin bag were deployed near each of the three water monitoring wells at each study site. A visual estimate of the location of the resin bag (distance, compass bearing) relative to the monitoring well facilitated finding the resin bags upon collection. Using a serrated knife, three sides of a 10x10 cm square were cut into the soil. The soil was lifted using pasta tongs to create a small space at 5 cm depth into which the resin bag was carefully inserted. Resin bags were incubated for approximately 4 weeks during Jul-Aug 2003. Upon collection, resin bags were stored in individual 1-quart Ziploc bags, put on ice, and frozen upon return to the lab.

I followed the protocol suggested by Giblin et al. (1994) to extract nutrients from the IER. Resin bags were thoroughly rinsed with distilled water to remove any soil particles. The resin bag was then inserted into the bottom of a 30-mL syringe barrel. The extraction apparatus comprised of a series of parts in this order: a funnel, Tygon tubing, a 2-way syringe stopcock, a rubber stopper with a hole, the syringe barrel with the resin bag, Tygon tubing, and another 2-way syringe stopcock. The flow rate of the extractant was regulated using the two 2-way syringe stopcocks. 100 mL of 2 M NaCl in 0.1 M HCl was dripped through the syringe over approximately 2 hours: the first 50 mL in three ~15 mL "pulses" followed by continuously dripping the remaining 50 mL. This technique appeared to provide better recovery rates than a single continuous 100 mL drip. The extract was collected in a Nalgene bottle and refrigerated. Ammonium was measured colorimetrically following an adapted version of the phenylhypochlorite method (Aminot et al. 1997). Phosphate was measured colorimetrically following the acid molybdate method (Wetzel and Likens 2000). Nitrate was measured by ion chromatography (IC). Prior to IC analysis, samples were diluted by a factor of 10 to diminish the chloride peaks and make the nitrate peaks more visible. Even with this dilution the nitrate detection limit remained somewhat elevated (0.07 ppm NO_3-N).

To ensure that small soil particles in and on the resin bag were not contaminating the extract, I opened the seam on 5 anion and 5 cation resin bags and rinsed and separated any small soil or plant fragments from the IER. I then extracted nutrients separately from the IER and from the resin bag plus any soil and plant particles. The resin bag and the residual soil and plant particles inside the resin bag contributed insignificant amounts of nutrients relative to the nutrients that were extracted from the IER (3.2% NH_4-N; 0% NO_3-N; 2.5% PO_4-P; n=2 for NO_3-N; n=5 for NH_4-N and PO_4-P). Consequently, nutrients were extracted from the resin bags without removing the IER from the resin bags, which greatly expedited processing time.

Nutrients were also extracted twice from the IER (after removal from the resin bag) to test the efficacy of the first extraction. Recovery rates for the first extraction [1st ext./(1st ext. + 2^{cd} ext.)] were high (97.6% NH_4-N; 99.8% NO_3-N; 97.7% PO_4-P; n=2 for NO_3-N; n=5 for NH_4-N and PO_4-P), and consequently only one extraction was done on all subsequent measurements. Coincidentally, this loss of nutrients by not extracting the IER twice is similar in magnitude and roughly compensated by the additional nutrients extracted by including the bag and fine soil particles.

All nutrient supply estimates are reported as mmol NH_4^+, NO_3^-, or PO_4^{3-} per bag. The time component was not included in the nutrient supply estimates because, while all deployment durations were similar, it is unknown whether nutrients accumulated on the IER as a linear or curvilinear function of time.

Statistical analyses

All statistical analyses were done using SYSTAT version 9.01 (SPSS Inc. 1998) on a PC with a Windows 2000 operating system. The exceptions were the 75th and 25th quartile calculations in Figure 2.13, which were done using Minitab version 12 (Minitab 2000).

RESULTS

Hydrochemical characterization of wetland and source waters

The hydrochemistry of the near-surface porewaters in these wetlands spanned a very broad range (Table 2.4). Specific conductance, a measure of the total dissolved ions in solution, varied by an order of magnitude from the more ionically poor bog waters to the more ionically rich fen and swamp waters. Most ionically rich waters were Ca-Mg-HCO_3 waters, which reflects the influence of the calcite and dolomite in the glacial till of this area. NO_3-N was either very low or below detection limits of ca. 0.01 mg NO_3-N/L ("0" values). NH_4-N, PO_4-P, and TDP were quite variable across wetlands. The pH of these porewaters was measured during a different sampling period in Aug 2003 (Table 2.5). pH values

Table 2.4: Hydrochemical characterization of the porewaters of 24 wetlands in southwest Michigan for three sampling periods during Oct 2000 – Sep 2001. Values represent the mean (m), minimum (min), and maximum (max) and are reported in µS/cm at 25°C (specific conductance), meq/L (alkalinity), µg/L (NH_4-N, PO_4-P, TDP), or mg/L. NH_4-N, PO_4-P, and TDP measurements were made on samples from Oct 2000 and May 2001 (most sites) or on one of those dates (denoted by *). PO_4-P and TDP data for porewaters were not available for two sites; PO_4-P and TDP data for surface waters (denoted by ^{s}) are reported instead. Si, NH_4-N, PO_4-P, and TDP values for all bog study sites may be over-estimated due to colorimetric interference by dissolved organic matter. NO_3-N values reported as “0” were below detection limits of ca. 0.01 mg NO_3-N/L.

site	sp. conductance			Ca^{2+}			Mg^{2+}			Na^{+}			K^{+}		
	m	min	max	m	min	max	m	min	max	m	min	max	m	min	max
Blachman Bog	74	64	82	1.7	1.3	2.3	0.52	0.34	0.65	0.39	0.32	0.48	0.72	0.61	0.88
Purdy Bog	47	31	57	2.0	1.4	2.6	0.57	0.27	0.77	0.43	0.19	0.76	1.0	0.47	1.4
Kidd Bog	86	55	107	1.7	0.73	2.8	0.62	0.48	0.81	0.50	0.35	0.68	1.4	0.55	2.4
Leatherleaf Bog	57	48	68	2.3	1.7	2.8	0.46	0.36	0.53	0.33	0.29	0.35	1.2	0.60	1.9
Chainfern Bog	86	45	116	2.7	2.3	3.6	0.48	0.36	0.74	0.17	0.06	0.24	0.20	0.05	0.49
Blueberry Bog	69	64	74	3.3	2.6	3.7	0.82	0.53	1.1	0.60	0.51	0.76	0.64	0.55	0.71
Longman Road Bog	49	26	61	5.5	2.5	7.4	0.87	0.09	1.4	0.34	0.11	0.52	1.5	0.72	2.0
Chokeberry Bog	86	46	109	5.5	3.1	7.6	1.2	0.79	1.6	1.4	0.81	1.7	3.0	1.8	4.6
Winterberry Fen	70	55	87	10	6.8	15	1.6	1.4	2.0	0.42	0.35	0.45	0.31	0.09	0.65
Lang Fen	314	224	363	59	43	76	11	6.2	13	4.2	3.5	4.8	1.3	0.08	3.8
Glasby Fen	348	302	425	56	47	73	12	9.4	16	5.2	2.0	8.3	1.7	0.01	4.5
Cemetery Fen	420	407	427	67	65	67	12	10	13	10	9.2	11	0.04	0.03	0.05
Butterfield Fen	331	176	425	67	57	75	13	11	16	2.0	1.8	2.2	0.33	0.18	0.59
Balker Lake Swamp	357	338	392	49	47	50	12	11	14	11	9.9	12	0.53	0.22	1.0
Otis Pond Swamp	112	99	124	19	16	22	4.3	3.9	5.0	1.0	0.92	1.1	0.17	0.15	0.19
Stafford Fen	409	362	434	61	53	65	14	13	16	6.4	5.5	7.1	1.3	0.50	1.7
Sherriff Fen	475	396	534	75	66	82	17	14	21	3.3	2.0	4.9	0.45	0.07	0.82
Mott Road Fen	479	370	540	86	81	93	18	16	20	2.5	2.1	3.1	0.68	0.58	0.83
Starflower Swamp	274	244	296	42	37	45	11	10	12	2.6	2.4	2.9	0.65	0.49	0.74
Serbin Swamp	359	340	379	53	52	54	16	13	18	1.8	1.7	1.9	0.31	0.12	0.49
Turner Creek Fen	279	256	308	44	39	51	12	12	12	2.2	2.0	2.5	0.29	0.06	0.59
Stafford Swamp	517	452	591	88	77	102	20	15	24	2.4	2.1	2.6	0.72	0.47	0.95
Prairieville Creek Fen	678	575	778	107	91	116	22	20	24	4.2	3.3	4.7	0.52	0.45	0.57
Kalamazoo River Swamp	458	427	503	72	68	77	17	14	20	3.4	3.2	3.5	0.91	0.52	1.2

Table 2.4

site	alkalinity			SO_4^{2-}			Cl^-			Si		
	m	min	max	m	min	max	m	min	max	m	min	max
Blachman Bog	0	0	0	0.11	0.08	0.17	0.92	0.60	1.2	4.5	2.3	8.7
Purdy Bog	0	0	0	0.23	0.07	0.39	0.71	0.18	1.3	0.96	0.39	1.4
Kidd Bog	0	0	0	0.28	0.09	0.47	0.72	0.61	0.81	1.8	1.2	2.4
Leatherleaf Bog	0.02	0	0.06	0.12	0.03	0.26	1.4	1.0	1.7	3.2	2.3	4.5
Chainfern Bog	0	0	0	0.21	0.03	0.55	0.65	0.23	1.3	2.3	0.51	4.3
Blueberry Bog	0	0	0	0.24	0.06	0.52	1.7	1.6	1.9	5.7	5.5	6.2
Longman Road Bog	0.15	0.03	0.32	1.6	0.03	3.5	0.93	0.37	1.2	2.5	1.6	4.0
Chokeberry Bog	0.03	0	0.09	2.3	0.14	6.7	1.7	0.38	2.9	6.4	0.94	13
Winterberry Fen	0.07	0	0.15	8.5	0.79	20	0.64	0.59	0.68	2.3	1.0	3.7
Lang Fen	3.0	1.5	3.8	11	0.05	33	9.2	5.3	13	4.7	1.1	8.5
Glasby Fen	3.5	2.8	4.6	0.74	0.58	0.91	8.6	0.89	16	6.1	1.4	10
Cemetery Fen	4.0	3.8	4.3	2.1	0.28	4.1	27	19	32	4.1	3.4	5.5
Butterfield Fen	4.1	3.6	4.5	8.0	1.7	16	2.0	1.5	2.3	4.8	2.7	6.6
Balker Lake Swamp	3.1	3.1	3.2	0.30	0.29	0.31	25	18	33	3.6	2.6	4.1
Otis Pond Swamp	1.1	0.91	1.2	0.42	0.36	0.46	0.66	0.45	1.0	6.2	4.9	7.5
Stafford Fen	4.1	3.5	4.4	0.88	0.73	0.96	20	10	31	5.3	5.0	5.7
Sherriff Fen	5.1	4.3	5.5	4.9	0.18	14	6.9	1.2	16	5.2	4.9	5.6
Mott Road Fen	5.4	4.9	5.8	25	9.2	36	7.5	4.9	9.4	5.2	4.6	5.6
Starflower Swamp	3.0	2.7	3.2	1.2	0.39	2.2	1.6	1.2	2.4	8.9	5.0	15
Serbin Swamp	3.5	3.1	3.7	10	3.0	20	2.2	1.8	2.7	4.1	3.8	4.3
Turner Creek Fen	3.1	2.8	3.5	0.8	0.68	0.95	1.5	0.67	2.2	4.9	3.1	6.6
Stafford Swamp	5.6	4.7	6.7	18	1.7	45	3.7	1.7	5.3	6.3	4.1	8.2
Prairieville Creek Fen	4.4	3.4	5.0	237	181	278	8.7	4.6	14	4.6	3.7	5.2
Kalamazoo River Swamp	5.1	4.9	5.6	2.5	0.09	5.8	4.4	3.4	5.7	7.8	7.1	8.5

Table 2.4 (cont'd).

site	NH_4-N	NO_3-N			PO_4-P	TDP
	m	m	min	max	m	m
Blachman Bog	111	0	0	0	25	28
Purdy Bog	11	0.04	0	0.13	4	9
Kidd Bog	20	0	0	0.01	7	30
Leatherleaf Bog	434	0	0	0	51^{s}	71^{s}
Chainfern Bog	26	0	0	0	18	51
Blueberry Bog	578	0.01	0	0.01	48	61
Longman Road Bog	734	0.03	0	0.07	83	79
Chokeberry Bog	331	0	0	0	13	39
Winterberry Fen	286	0.04	0	0.12	19	38
Lang Fen	92	0	0	0.01	5*	13*
Glasby Fen	13	0	0	0	34	42
Cemetery Fen	7	0	0	0.01	2	10
Butterfield Fen	59	0.02	0.01	0.02	3	10
Balker Lake Swamp	24	0	0	0	18	18
Otis Pond Swamp	895	0.01	0	0.02	132*	128*
Stafford Fen	90	0	0	0.01	43*	35*
Sherriff Fen	205	0	0	0	13^{*s}	20^{*s}
Mott Road Fen	38	0.04	0	0.11	10	20
Starflower Swamp	152	0.04	0	0.10	24*	22*
Serbin Swamp	10	0	0	0.01	3	7
Turner Creek Fen	29	0	0	0	17	37
Stafford Swamp	37	0.02	0	0.06	8	9
Prairieville Creek Fen	39	0.01	0	0.01	10	10
Kalamazoo River Swamp	107	0	0	0.01	4	8

Table 2.4 (cont'd).

site	pH
Blachman Bog	3.97
Purdy Bog	4.48
Kidd Bog	4.40
Leatherleaf Bog	4.08
Chainfern Bog	3.95
Blueberry Bog	4.14
Longman Road Bog	4.84
Chokeberry Bog	3.98
Winterberry Fen	5.50
Lang Fen	6.37
Glasby Fen	6.34
Cemetery Fen	6.82
Butterfield Fen	6.94
Balker Lake Swamp	6.50
Otis Pond Swamp	6.40
Stafford Fen	6.73
Sherriff Fen	6.72
Mott Road Fen	7.22
Starflower Swamp	6.74
Serbin Swamp	6.98
Turner Creek Fen	6.60
Stafford Swamp	6.80
Prairieville Creek Fen	6.99
Kalamazoo River Swamp	7.10

Table 2.5: pH of porewaters from 24 wetlands in southwest Michigan. Each value is the mean of three samples collected from different locations within each wetland in Aug 2003.

ranged from 3.95 to 7.22 (more than three orders of magnitude), indicating how markedly variable the acidity was in these wetland porewaters.

In terms of wetland source waters, local precipitation was hydrochemically quite distinct from local groundwaters (Table 2.6). The pH of local precipitation (24-year mean pH calculated based on $[H^+]$ = 4.41), as in many areas of the eastern U.S., is very low due to industrial pollution (Schwartz 1989). This acidity, which was nearly 10^3 times greater than that in local groundwaters, was an important hydrochemical difference between local precipitation and groundwaters.

Like the more ion-rich wetland waters, local groundwaters (springs and seeps) were generally Ca-Mg-HCO_3 waters. With the exception of Otis stream, groundwaters were hydrochemically similar. NO_3-N ranged from below detection limits to very high (Prairieville Creek mean = 8.3 mg NO_3-N/L) in groundwaters; NO_3-N was relatively low in precipitation (0.42 mg NO_3-N/L). NH_4-N, PO_4-P, and TDP were all relatively low in local groundwaters (ca. 1-10 μg/L), although local precipitation was quite high in NH_4-N (341 μg NH_4-N/L).

Water sources

Based on Mg dissolved in soil porewaters, seasonal variability in wetland water sources was relatively low (Table 2.7), although several sites appeared more variable than others (Figure 2.4). f_{gw} estimates were generally lower during the May 2001 sampling period – likely because precipitation was well above-

source water	sp. conductance			Ca^{2+}			Mg^{2+}			Na^{+}			K^{+}		
	m	min	max	m	min	max	m	min	max	m	min	max	m	min	max
KBS precipitation		24			0.22			0.05			0.09			0.02	
Prairieville spring	613	601	626	87	85	89	22	18	24	8.5	8.3	8.8	1.4	1.3	1.5
Smith spring	563	516	621	88	83	97	20	19	22	2.6	2.1	3.0	1.5	1.1	1.9
Turner spring	312	291	337	47	43	50	13	12	14	2.3	2.2	2.5	0.64	0.18	1.0
Cemetery seep	554	531	581	83	80	88	19	16	20	7.7	7.0	8.0	0.86	0.83	0.88
Serbin seep	410	401	422	59	58	60	17	15	19	2.0	1.8	2.1	0.61	0.54	0.73
Kalamazoo seep	436	393	493	72	70	74	18	16	20	3.2	2.8	4.1	1.1	0.91	1.2
Balker stream	496	458	545	77	72	86	19	16	23	3.4	3.2	3.5	0.56	0.37	0.91
Mott stream	572	560	580	88	85	90	23	20	25	5.4	5.0	5.7	1.1	1.0	1.1
Otis stream	155	129	189	25	21	28	6.2	5.4	7.4	1.2	1.1	1.4	0.34	0.23	0.41
Butterfield stream	387	356	410	45	40	50	20	17	23	7.8	6.5	8.7	1.2	1.1	1.3

Table 2.6: Hydrochemical characterization of local precipitation and groundwaters (springs, seeps, and streams). Groundwater values represent the mean (m), minimum (min), and maximum (max) for three samples during the period Oct 2000 – Sep 2001. Precipitation values are means of annual volume-weighted means for 1979-2002 (NADP/NTN 2003); PO_4-P, and TDP values represent the annual mean for two local weather stations during Oct 1986-87 (Rheaume 1990). Alkalinity and Si are negligible in precipitation. Values are reported with no units (pH) or in µS/cm at 25°C (specific conductance), meq/L (alkalinity), µg/L (NH_4-N, PO_4-P, TDP), or mg/L. NH_4-N, PO_4-P, and TDP measurements were generally made on samples from Oct 2000 and May 2001 or on only one sample (denoted by *). NO_3-N values reported as "0" were below detection limits of ca. 0.01 mg NO_3-N/L.

source water	pH			alkalinity			SO_4^{2-}			Cl^-			Si		
	m	min	max	m	min	max	m	min	max	m	min	max	m	min	max
KBS precipitation		4.41			~0			2.5			0.14			~0	
Prairieville spring	7.52	7.37	7.74	5.2	4.7	5.5	27	24	33	23	19	29	6.9	6.5	7.2
Smith spring	7.06	6.97	7.12	5.9	5.4	6.6	25	17	33	3.1	2.5	3.8	6.5	6.1	7.0
Turner spring	7.24	6.88	7.44	3.2	2.9	3.4	9.9	3.0	15	2.3	2.2	2.4	7.0	3.9	12
Cemetery seep	7.10	6.88	7.32	5.2	5.2	5.4	34	29	42	21	10	37	6.1	6.0	6.2
Serbin seep	7.33	7.04	7.55	3.9	3.7	4.0	33	23	40	2.3	1.8	2.6	4.6	4.5	4.8
Kalamazoo seep	7.28	7.00	7.68	4.7	3.7	5.2	17	9.6	26	7.0	4.6	8.4	6.0	5.7	6.3
Balker stream	7.19	6.74	7.55	5.4	5.1	5.9	4.4	3.2	5.4	4.7	4.3	5.0	7.0	5.4	9.0
Mott stream	7.71	7.57	7.92	5.2	5.0	5.3	58	49	72	16	13	22	6.5	6.0	6.8
Otis stream	6.90	6.85	6.97	1.7	1.4	2.0	4.5	3.3	6.8	0.87	0.77	0.97	4.0	1.8	5.7
Butterfield stream	7.91	7.77	8.02	3.5	3.1	3.8	22	19	24	13	7.4	21	4.2	3.2	6.2

source water	NH_4-N	NO_3-N			PO_4-P	TDP
	m	m	min	max	m	m
KBS precipitation	341		0.42		10	30
Prairieville spring	2	8.9	5.3	13	1	5
Smith spring	9	0.55	0	0.94	2	7
Turner spring	9	0	0	0	6*	15*
Cemetery seep	6	0.66	0.54	0.83	2	6
Serbin seep	3	0	0	0.01	3	7
Kalamazoo seep	3	0.21	0.12	0.26	3	9
Balker stream	9	0	0	0.01	7	11
Mott stream	4	1.7	1.4	2.2	2	6
Otis stream	16	0.34	0	1.0	2	11
Butterfield stream	32	0.04	0	0.09	1	6

Table 2.6 (cont'd).

site	Oct 2000	May 2001	Sep 2001	groundwater endmember
Blachman Bog	0.04	0.01	0.02	Balker stream
Purdy Bog	0.04	0.01	0.03	Smith spring
Kidd Bog	0.05	0.02	0.02	Balker stream
Leatherleaf Bog	0.04	0.02	0.03	Turner spring
Chainfern Bog	0.03	0.02	0.05	Turner spring
Blueberry Bog	0.06	0.02	0.03	Prairieville spring
Longman Road Bog	0.07	0.00	0.04	Mott stream
Chokeberry Bog	0.05	0.05	0.03	Prairieville spring
Winterberry Fen	0.35	0.16	0.20	Otis stream
Lang Fen	0.32	0.57	0.49	Smith spring
Glasby Fen	0.59	0.53	0.72	Balker stream
Cemetery Fen	0.65	0.66	0.57	Cemetery seep
Butterfield Fen	0.67	0.57	0.69	Butterfield stream
Balker Lake Swamp	0.69	0.68	0.55	Balker stream
Otis Pond Swamp	0.75	0.65	0.66	Otis stream
Stafford Fen	0.74	0.59	0.80	Smith spring
Sherriff Fen	0.75	0.61	0.88	Smith spring
Mott Road Fen	0.81	0.77	0.80	Mott stream
Starflower Swamp	0.89	0.82	0.80	Turner spring
Serbin Swamp	0.82	0.85	0.86	Serbin seep
Turner Creek Fen	0.99	0.84	0.83	Turner spring
Stafford Swamp	0.78	0.94	0.99	Smith spring
Prairieville Creek Fen	1.00	0.85	0.95	Prairieville spring
Kalamazoo River Swamp	0.87	0.94	0.99	Kalamazoo seep

Table 2.7: Seasonal variability in fraction groundwater (f_{gw}) for 24 wetlands in southwest Michigan. f_{gw} is an estimate of the relative importance of groundwater vs. precipitation as wetland water sources. f_{gw} values range from 0 (strongly precipitation-fed) to 1 (strongly groundwater-fed). The groundwater sample from Table 2.6 that was used as the endmember for calculating f_{gw} for each site is included for reference.

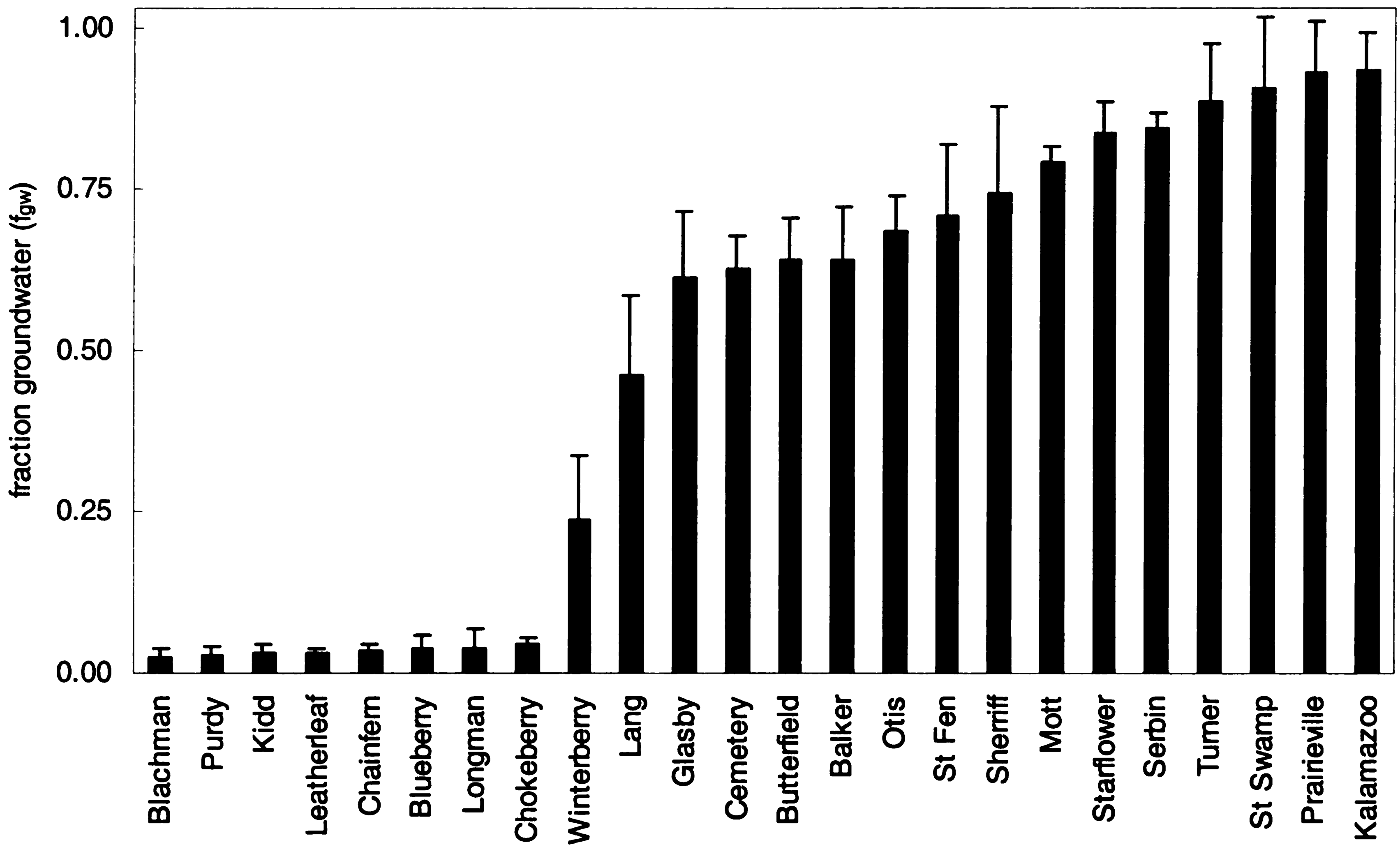


Figure 2.4: Fraction groundwater (f_{gw}) for 24 wetlands in southwest Michigan (mean + standard deviation). Means are calculated from three different sampling periods (Oct 2000, May 2001, and Sep 2001).

average (NADP/NTN 2003), when one might expect the greatest influence of precipitation vs. groundwater as source waters. The late summer samples that were collected in early Sep 2001 represent the time when wetlands were most dry. The Oct 2000 sampling period characterizes wetland porewaters during the more seasonally intermediate conditions in autumn. Taken together, these three f_{gw} estimates should be considered a robust test of the seasonal variability in wetland water sources for local wetlands.

Wetlands in this study exhibited a discrete transition from more precipitation-fed wetlands ($f_{gw} < 0.05$) to more groundwater-fed wetlands ($f_{gw} > 0.60$); only two sites (Winterberry Fen, Lang Fen) were in the f_{gw} range 0.05-0.60 (Figure 2.4). This abrupt change in water sources across wetlands is likely real and not a sampling artifact, especially given my attempts to include more intermediate sites when the second set of 12 sites were added (see METHODS, *Study sites* above). Note that while most fens and all swamps were predominantly groundwater-fed (mean $f_{gw} > 0.60$), the relative importance of groundwater varied substantially within these two wetland classes. The bog study sites exhibited much less within-class variability in f_{gw}, although this was likely an artifact of the calculations due to their dilute waters relative to their groundwater endmembers; even a two-fold increase in Mg^{2+} in bog porewaters would have had a negligible effect on their f_{gw} values.

In all tables and figures throughout this chapter, study sites are arranged in increasing order of mean f_{gw}, which provides a consistent sequence for comparisons across tables and figures.

Water level variability

Water levels varied seasonally with higher water levels occurring in the late spring and fall and the seasonal low occurring in the late summer (Figure 2.5). Water levels generally remained near or above the soil surface during the fall, winter, and spring, then decreased during the growing season, when rates of evapotranspiration were highest. However, some wetlands remained relatively wet throughout the year (e.g., Sherriff Fen), while others were only occasionally inundated (e.g., Stafford Swamp, Kalamazoo River Swamp).

Across the water source gradient, wetlands that were more groundwater-fed generally exhibited lower mean water levels (Figure 2.6A). Because the study wetlands represent the terrestrial end of the wetland continuum, from moist soils to standing water, it was not surprising that maximal water levels at any site during 2001 never exceeded 30 cm depth (Table 2.8). In fact, based on these limited data, almost 30% of the sites were never flooded above the soil surface during 2001. The range of water level variability was as small as 7.7 cm and as great as 40.5 cm with no consistent trend with respect to f_{gw} (Figure 2.6B).

Soil characterization

Soils from wetland study sites were organic with small or insignificant mineral components. Soil texture spanned the gradient of identifiable plant matter, from poorly decomposed peats, to more intermediate mucky peats and peaty mucks,

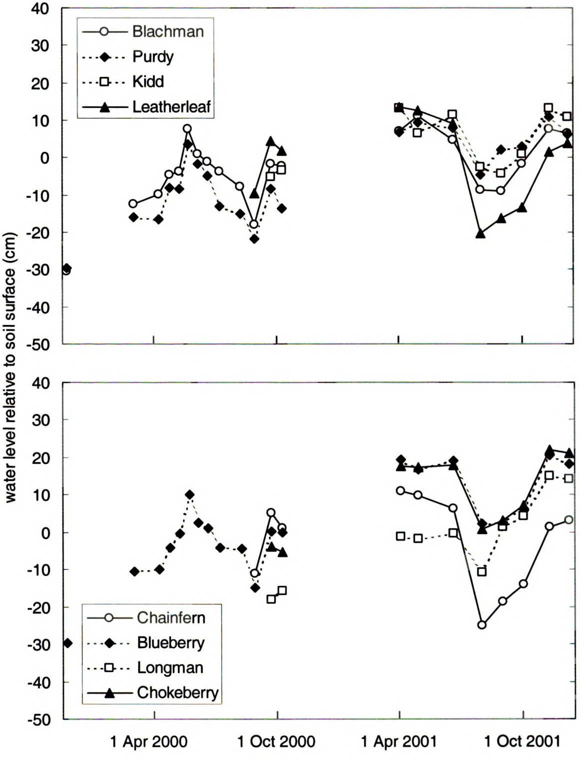
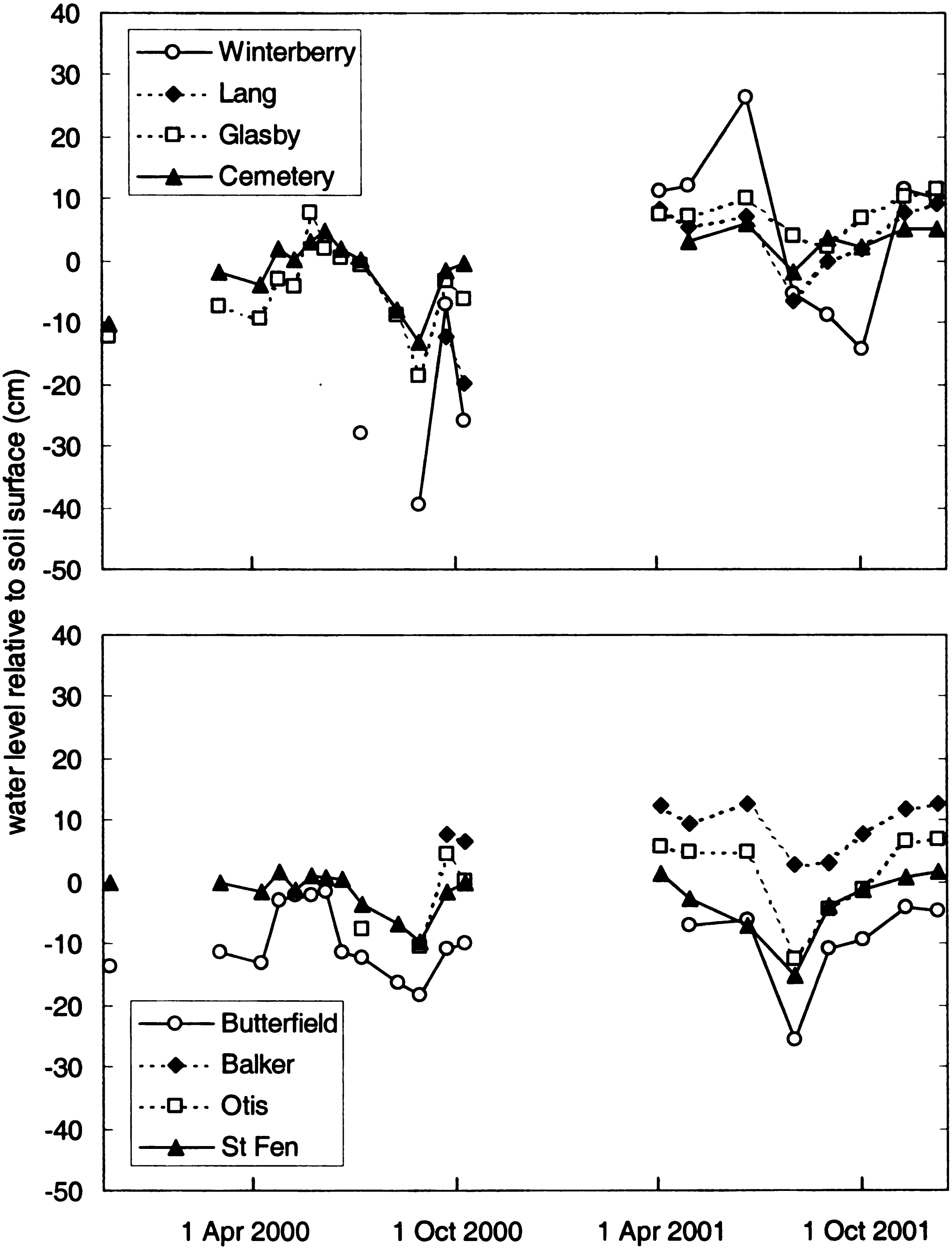


Figure 2.5: Mean wetland water levels during the period Dec 1999 – Dec 2001. Twelve sites were monitored the first season and an additional 12 were added for the second season.



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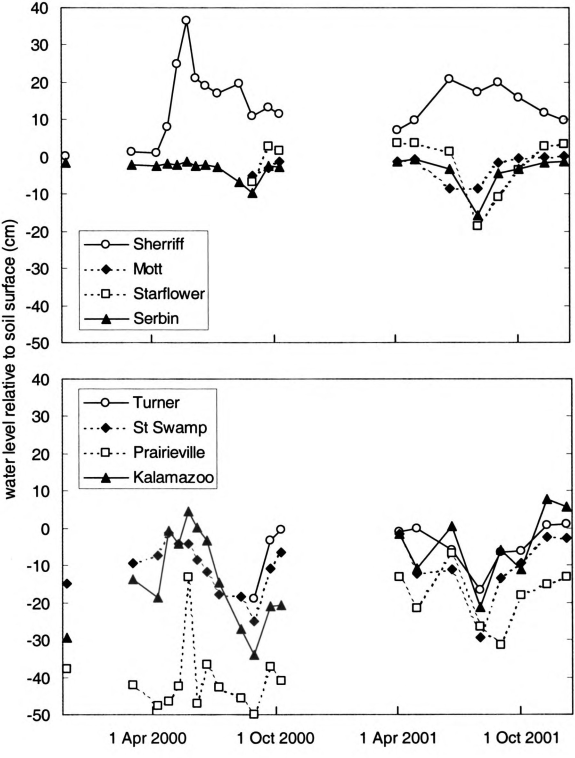

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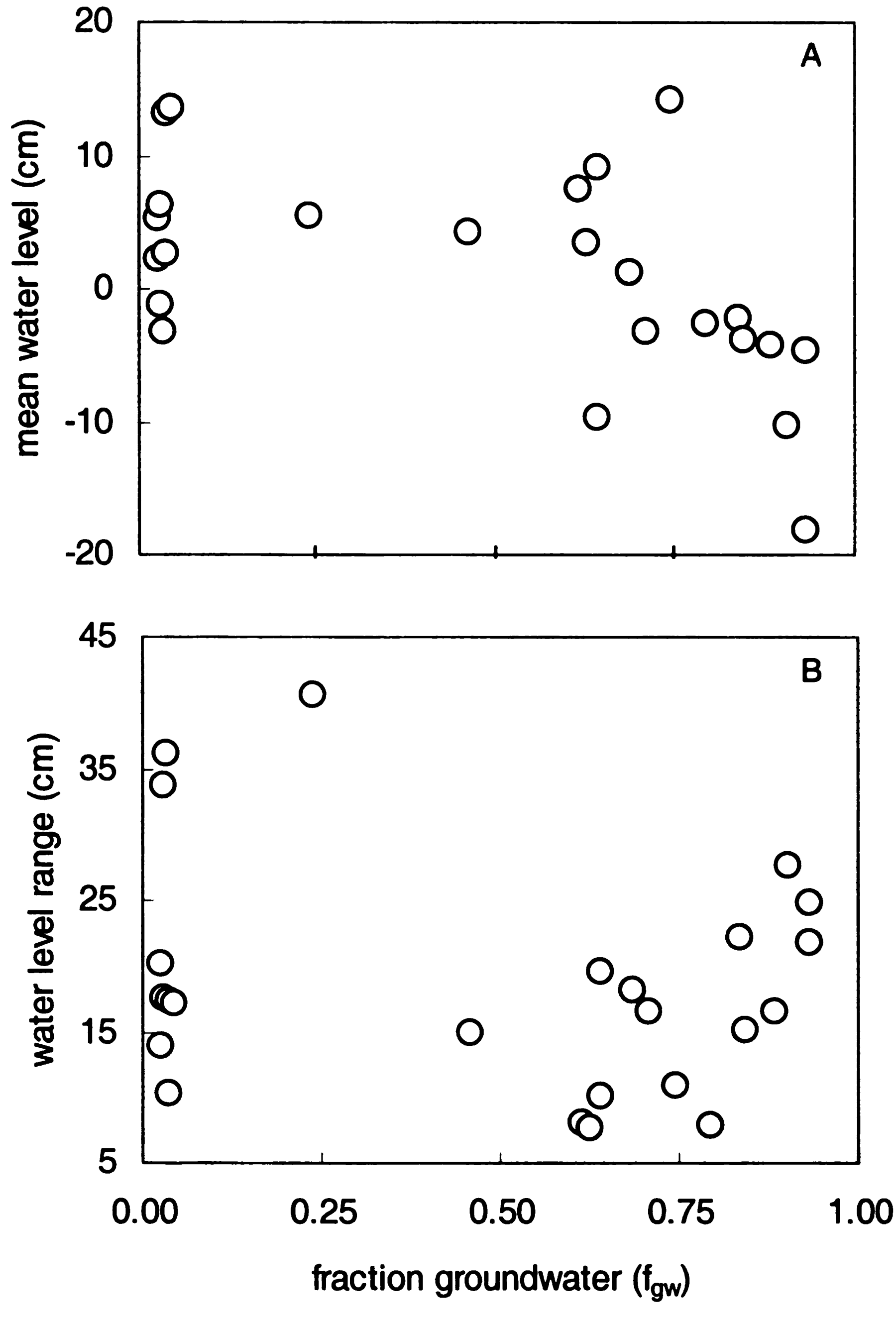

Figure 2.6: Relationships between fraction groundwater (f_{gw}) and two water level summary statistics for 24 wetlands in southwest Michigan. (A) The correlation between f_{gw} and mean water level is significant ($p = 0.011$, n=24); (B) the correlation between f_{gw} and water level range is not significant ($p = 0.300$, n=24). Water level data are for Apr – Dec 2001.

site	max	min	range	mean	median
Blachman Bog	11.2	-8.9	20.1	2.3	5.7
Purdy Bog	9.3	-4.6	14.0	5.2	6.5
Kidd Bog	13.3	-4.3	17.5	6.2	8.7
Leatherleaf Bog	13.4	-20.2	33.7	-1.1	2.7
Chainfern Bog	11.1	-25.1	36.2	-3.3	2.2
Blueberry Bog	19.4	2.2	17.3	13.2	17.5
Longman Road Bog	-0.5	-10.7	10.2	2.6	0.5
Chokeberry Bog	17.8	0.8	17.1	13.4	17.5
Winterberry Fen	26.3	-14.3	40.5	5.4	10.7
Lang Fen	8.3	-6.5	14.8	4.2	6.4
Glasby Fen	10.2	2.3	8.0	7.4	7.2
Cemetery Fen	5.9	-1.8	7.7	3.4	3.7
Butterfield Fen	-6.2	-25.7	19.5	-9.7	-7.0
Balker Lake Swamp	12.8	2.8	10.0	9.1	10.7
Otis Pond Swamp	5.6	-12.5	18.1	1.3	4.8
Stafford Fen	1.5	-15.0	16.5	-3.2	-2.0
Sherriff Fen	20.8	9.9	10.9	14.1	13.9
Mott Road Fen	-0.7	-8.5	7.7	-2.6	-1.0
Starflower Swamp	3.7	-18.5	22.3	-2.3	2.1
Serbin Swamp	-0.6	-15.7	15.1	-3.9	-2.3
Turner Creek Fen	-0.2	-16.7	16.5	-4.3	-3.5
Stafford Swamp	-1.6	-29.3	27.7	-10.3	-10.3
Prairieville Creek Fen	-6.6	-31.3	24.7	-18.2	-16.6
Kalamazoo River Swamp	0.4	-21.3	21.7	-4.6	-3.6

Table 2.8: Water level summary statistics for 24 wetlands in southwest Michigan for 8 different sampling dates during the period Apr-Dec 2001. Max = spring maximum; min = summer/fall minimum; range = difference between spring maximum and summer/fall minimum. All measurements are relative to the soil surface (cm).

to highly decomposed mucks (Table 2.9). In general, soils ranged from peaty in more precipitation-fed sites to mucky in more groundwater-fed sites. Muck soils were generally restricted to drier sites without standing water (Table 2.8). This is consistent with expectations given that plant decomposition proceeds further when standing water is absent (Gambrell et al. 1991), causing plant biomass to further decompose to muck.

Soil color, as determined using the Munsell Soil Color Charts (2000), generally covaried with soil texture. Peat colors ranged between dark yellowish brown (10 YR 4/4), dark brown (10 YR 3/3), very dark brown (10 YR 2/2), and black (10 YR 2/1). All mucky peats and peaty mucks were black (10 YR 2/1), and all muck soils were also black (10 YR 2/1, GLEY 1 2.5/N).

Soil pH ranged from 3.58 to 7.17, with low soil pH values (< 4.2) occurring in bog sites and higher soil pH values (> 5.9) occurring in all other sites (Table 2.9) except Winterberry Fen (soil pH = 4.34). Soil pH values were generally consistent with aqueous pH measurements (Table 2.5). However, I used aqueous pH values for all subsequent analyses and interpretations because aqueous measurements, which involve water collected from the wetland, are likely more representative of in situ conditions than soil pH measurements, which are derived from a slurry of soil and deionized water.

Soil chemistry patterns were somewhat consistent with the water source gradient (Table 2.10). N, P, Ca, Mg, S, Fe, Zn, and B were all generally higher in soils from more groundwater-fed sites. This pattern was somewhat apparent for

site	Munsell soil color	soil texture	soil pH
Blachman Bog	10 YR 4/4	P	3.58
Purdy Bog	10 YR 2/2	P	3.97
Kidd Bog	7.5 YR 3/3	P	3.85
Leatherleaf Bog	10 YR 3/3	P	3.84
Chainfern Bog	10 YR 3/3	P	3.93
Blueberry Bog	10 YR 4/4	P	4.04
Longman Road Bog	10 YR 4/4, 10 YR 2/1	P, PM	3.98
Chokeberry Bog	10 YR 2/2	P	4.17
Winterberry Fen	10 YR 2/1	PM	4.34
Lang Fen	10 YR 2/2	P	6.23
Glasby Fen	10 YR 2/1	MP	6.11
Cemetery Fen	10 YR 2/1	P	6.85
Butterfield Fen	GLEY 1 2.5/N	M	7.17
Balker Lake Swamp	10 YR 2/1	MP	6.64
Otis Pond Swamp	10 YR 2/1	M	5.98
Stafford Fen	10 YR 2/1	PM	6.76
Sherriff Fen	10 YR 2/1	MP	6.45
Mott Road Fen	10 YR 2/1	PM, MP	6.98
Starflower Swamp	10 YR 2/1	MP	6.59
Serbin Swamp	10 YR 2/1	PM	7.05
Turner Creek Fen	10 YR 2/1	PM	6.43
Stafford Swamp	GLEY 1 2.5/N	M	7.07
Prairieville Creek Fen	GLEY 1 2.5/N	M	6.67
Kalamazoo River Swamp	10 YR 2/1	M	6.59

Table 2.9: Characterization of 24 wetland soils from southwest Michigan. Soil color was determined using the Munsell soil color charts. All 24 wetland soils are organic and are further subdivided based on the fraction of identifiable plant material in the soil after gentle rubbing (soil texture): M = muck (<16.6% identifiable plant material); PM = peaty muck (16-45.8%); MP = mucky peat (45.8-75%); and P = peat (>75%) (Tiner 1999). Multiple soil color and texture measurements for Longman Road Bog are for the upper 5 cm of soil (first entry) and the 5-15 cm depth of soil (second entry). Multiple soil texture measurements for Mott Road Fen are for two different locations within the fen. Soil pH was determined by mixing fresh (undried) soil and deionized water in a 1:2 ratio and measuring the pH of the resulting soil slurry (Robertson et al. 1999); soil pH values represent the mean of three soil samples from each wetland.

site	N	P	Ca	Mg	K	Na	S	Fe	Al	Mn	Zn	Cu	B
Blachman Bog	1.51	0.05	0.16	0.04	0.04	0.01	0.16	0.20	0.11	20	45	4	2
Purdy Bog	1.53	0.05	0.20	0.05	0.01	0.01	0.27	0.18	0.14	36	41	6	3
Kidd Bog	1.59	0.06	0.21	0.05	0.03	0.01	0.19	0.14	0.09	184	35	5	3
Leatherleaf Bog	1.58	0.06	0.26	0.05	0.03	0.01	0.22	0.14	0.10	24	52	5	3
Chainfern Bog	1.86	0.09	0.33	0.06	0.03	0.02	0.22	0.15	0.12	152	42	7	4
Blueberry Bog	1.86	0.09	0.36	0.07	0.02	0.01	0.31	0.22	0.21	75	49	9	6
Longman Road Bog	1.99	0.10	0.27	0.05	0.04	0.01	0.26	0.21	0.21	65	48	8	4
Chokeberry Bog	2.25	0.09	0.25	0.05	0.04	0.01	0.30	0.17	0.12	79	38	6	3
Winterberry Fen	2.64	0.12	0.54	0.07	0.06	0.01	0.37	0.30	0.38	53	35	9	7
Lang Fen	2.88	0.13	1.71	0.17	0.03	0.02	0.45	0.88	0.19	300	54	8	13
Glasby Fen	2.49	0.11	2.20	0.20	0.02	0.01	0.79	1.07	0.20	115	47	11	21
Cemetery Fen	2.68	0.11	2.90	0.21	0.03	0.02	0.59	0.68	0.30	240	83	11	18
Butterfield Fen	2.87	0.16	3.29	0.31	0.04	0.01	0.52	3.89	0.46	876	75	12	27
Balker Lake Swamp	2.27	0.08	2.78	0.27	0.01	0.01	0.73	0.44	0.23	129	135	12	18
Otis Pond Swamp	2.64	0.12	2.15	0.21	0.02	0.01	0.84	0.57	0.39	85	103	18	13
Stafford Fen	2.40	0.16	2.08	0.27	0.06	0.02	0.49	4.70	0.48	2328	100	11	22
Sherriff Fen	2.91	0.16	1.88	0.18	0.03	0.01	0.70	1.82	0.15	300	46	7	21
Mott Road Fen	2.79	0.13	3.13	0.27	0.04	0.01	0.57	2.83	0.55	1746	78	11	20
Starflower Swamp	2.36	0.09	2.84	0.32	0.02	0.01	0.67	0.66	0.29	227	124	13	18
Serbin Swamp	2.02	0.13	2.84	0.34	0.05	0.01	0.50	1.94	0.22	435	82	8	20
Turner Creek Fen	1.92	0.13	1.79	0.40	0.14	0.01	0.37	1.74	1.41	600	128	21	13
Stafford Swamp	2.40	0.23	3.62	0.33	0.05	0.01	0.34	4.39	0.50	1307	145	13	22
Prairieville Creek Fen	2.85	0.14	3.19	0.28	0.06	0.01	0.49	0.57	0.27	586	66	11	25
Kalamazoo River Swamp	1.79	0.26	2.39	0.41	0.14	0.02	0.37	6.93	1.39	1939	348	62	28

Table 2.10: Chemical analysis of 24 wetland soils from southwest Michigan. Each measurement is a composite of three separate soil samples. Elements are expressed as % element/gram dry soil (N, P, Ca, Mg, K, Na, S, Fe, Al) or ppm (Mn, Zn, Cu, B).

Al, Mn, and Cu, although the pattern was less clear and more variable. K and Na exhibited no discernable pattern across sites.

Nutrient supply

Mean NH_4^+ supply estimates ranged from 0.02-13.42 mmol NH_4^+/bag across all sites, and the highest supply estimates were observed at sites with intermediate f_{gw} values (Figure 2.7). Mean NO_3^- supply estimates, ranging from below detection limits ("0") to 0.39 mmol NO_3^-/bag, were highly variable (Figure 2.8). PO_4^{3-} supply spanned 0.07-42.73 mmol PO_4^{3-}/bag (Figure 2.9). Mean NO_3^- and PO_4^{3-} supply estimates were generally higher at more groundwater-fed sites. The within-site variability for all nutrient supply estimates was very high.

NH_4^+ and PO_4^{3-} supply was more strongly associated with pH and soil moisture (Figures 2.10-2.11). Resin bags, which were incubated at 5 cm depth, were considered subject to "wet" conditions if the water table was above the resin bags at either the beginning or the end of the incubation. Soils with aqueous pH < 6 were defined as "acidic" while those with pH > 6 were considered "circumneutral." NH_4^+ accumulation on resin was lower in more acidic soils than in more circumneutral soils (t-test, data log-transformed; n=25,44; df=67; $p <$ 0.001). At circumneutral locations NH_4^+ accumulation on resin was higher in wet soils than in dry soils (t-test, data log-transformed; n=21,23; df=42; $p < 0.001$). These patterns were also evident in the PO_4^{3-} supply estimates. PO_4^{3-} accumulation on resin was lower in more acidic soils than in more circumneutral

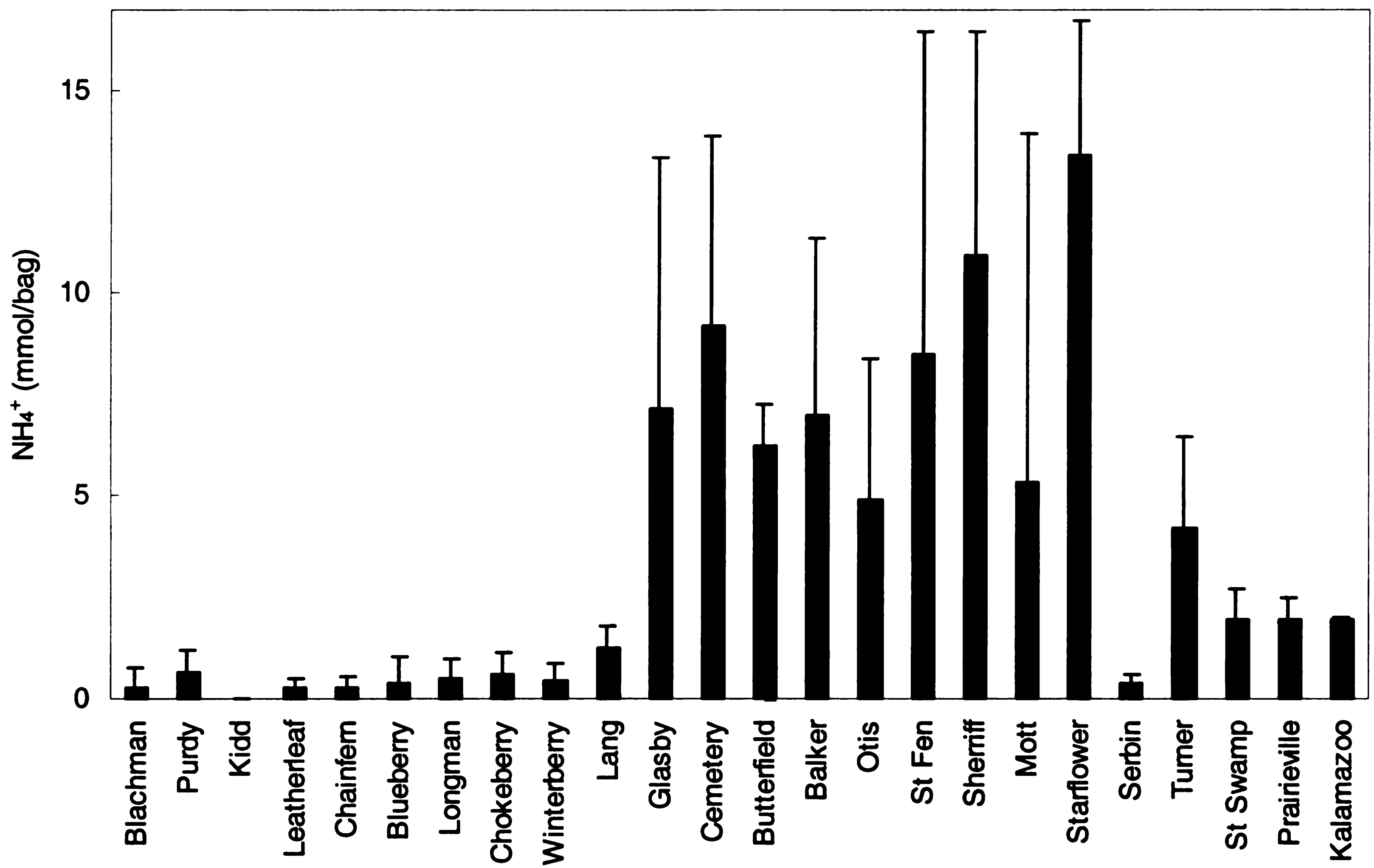

Figure 2.7: NH_4^+ accumulation on cation exchange resin during a 4-week incubation in 24 wetlands. Each bar represents the mean + standard deviation of 3 resin bags.

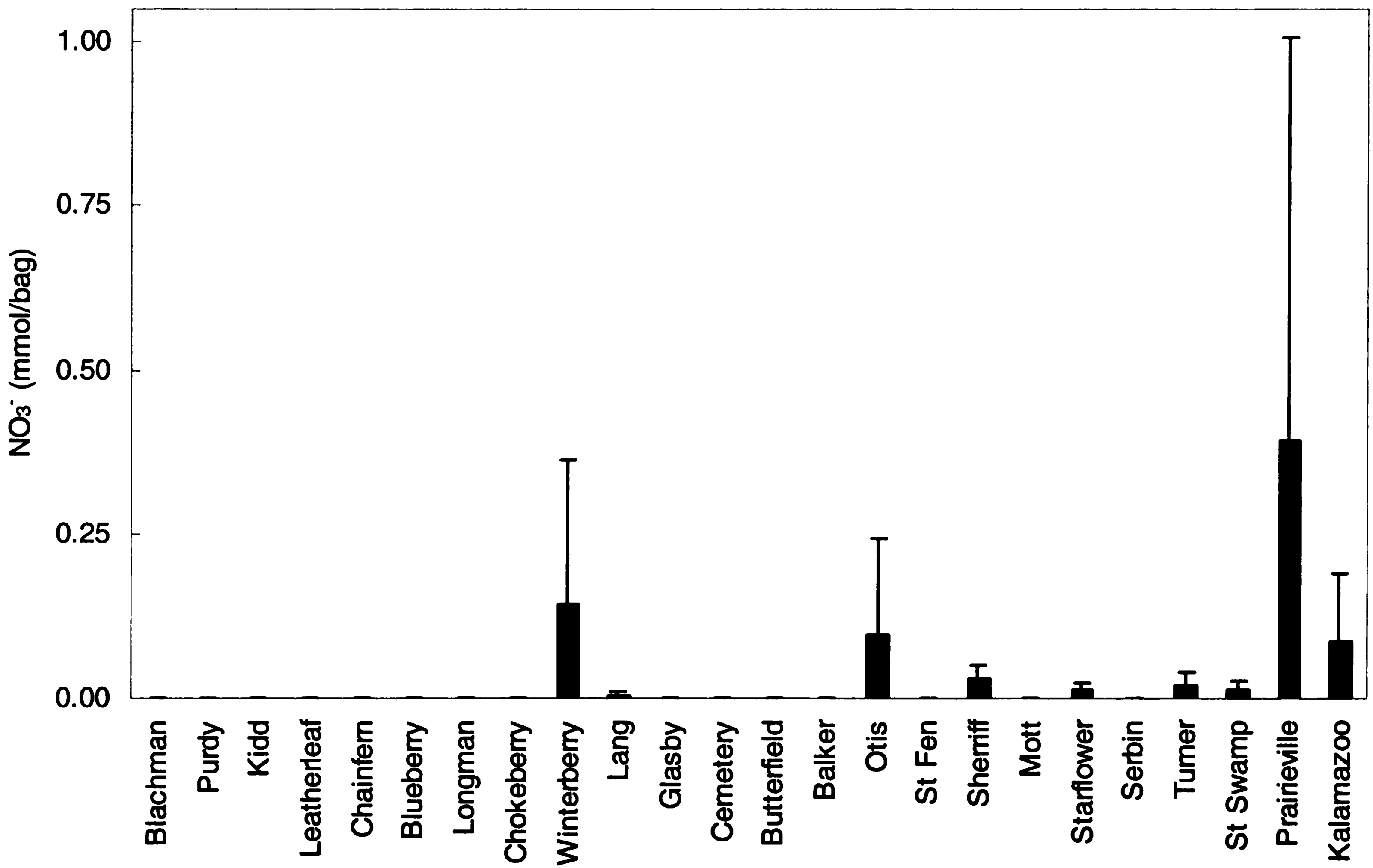

Figure 2.8: NO_3^- accumulation on anion exchange resin during a 4-week incubation in 24 wetlands. Each bar represents the mean + standard deviation of 3 resin bags.

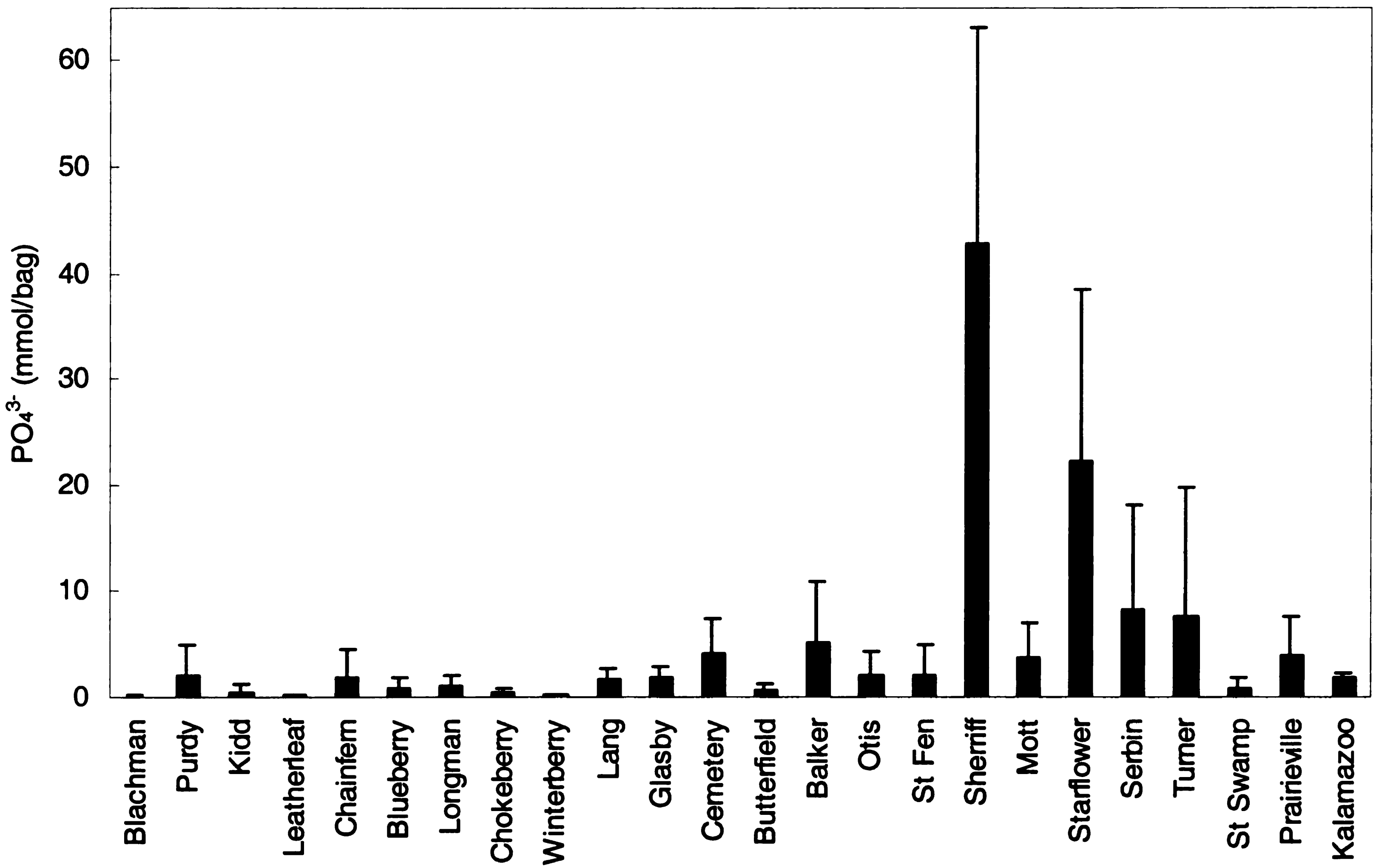

Figure 2.9: PO_4^{3-} accumulation on anion exchange resin during a 4-week incubation in 24 wetlands. Each bar represents the mean + standard deviation of 3 resin bags.

Figure 2.10: pH vs. NH_4^+ accumulation on cation exchange resin during a 4-week incubation in 24 wetlands. "Wet" points indicate locations where the water table was at or above 5 cm depth (the depth at which the resin bags were deployed) at either the beginning or the end of the incubation period. NH_4^+ accumulation on resin was lower in more acidic (pH < 6) soils than in more circumneutral (pH > 6) soils (t-test, data log-transformed; n=25,44; df=67; $p < 0.001$). At circumneutral (pH > 6) locations NH_4^+ accumulation on resin was higher in wet soils than in dry soils (t-test, data log-transformed; n=21,23; df=42; $p < 0.001$).

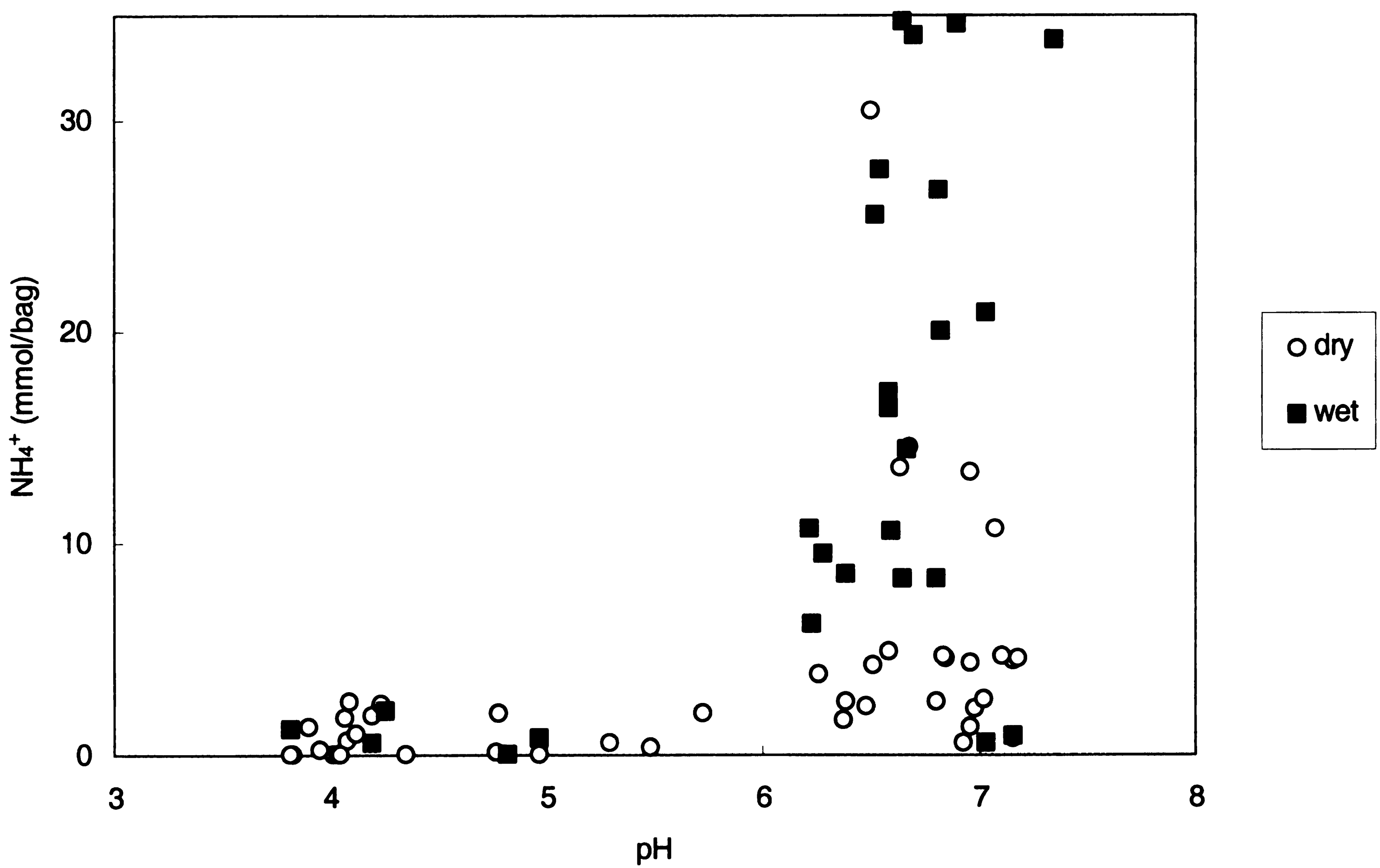

Figure 2.10

Figure 2.11: pH vs. PO_4^{3-} accumulation on anion exchange resin during a 4-week incubation in 24 wetlands. "Wet" points indicate locations where the water table was at or above 5 cm depth (the depth at which the resin bags were deployed) at either the beginning or the end of the incubation period. PO_4^{3-} accumulation on resin was lower in more acidic (pH < 6) soils than in more circumneutral (pH > 6) soils (t-test, data log-transformed; n=26,44; df=68; $p < 0.001$). At circumneutral (pH > 6) locations PO_4^{3-} accumulation on resin was higher in wet soils than in dry soils (t-test, data log-transformed; n=21,23; df=42; $p < 0.001$).

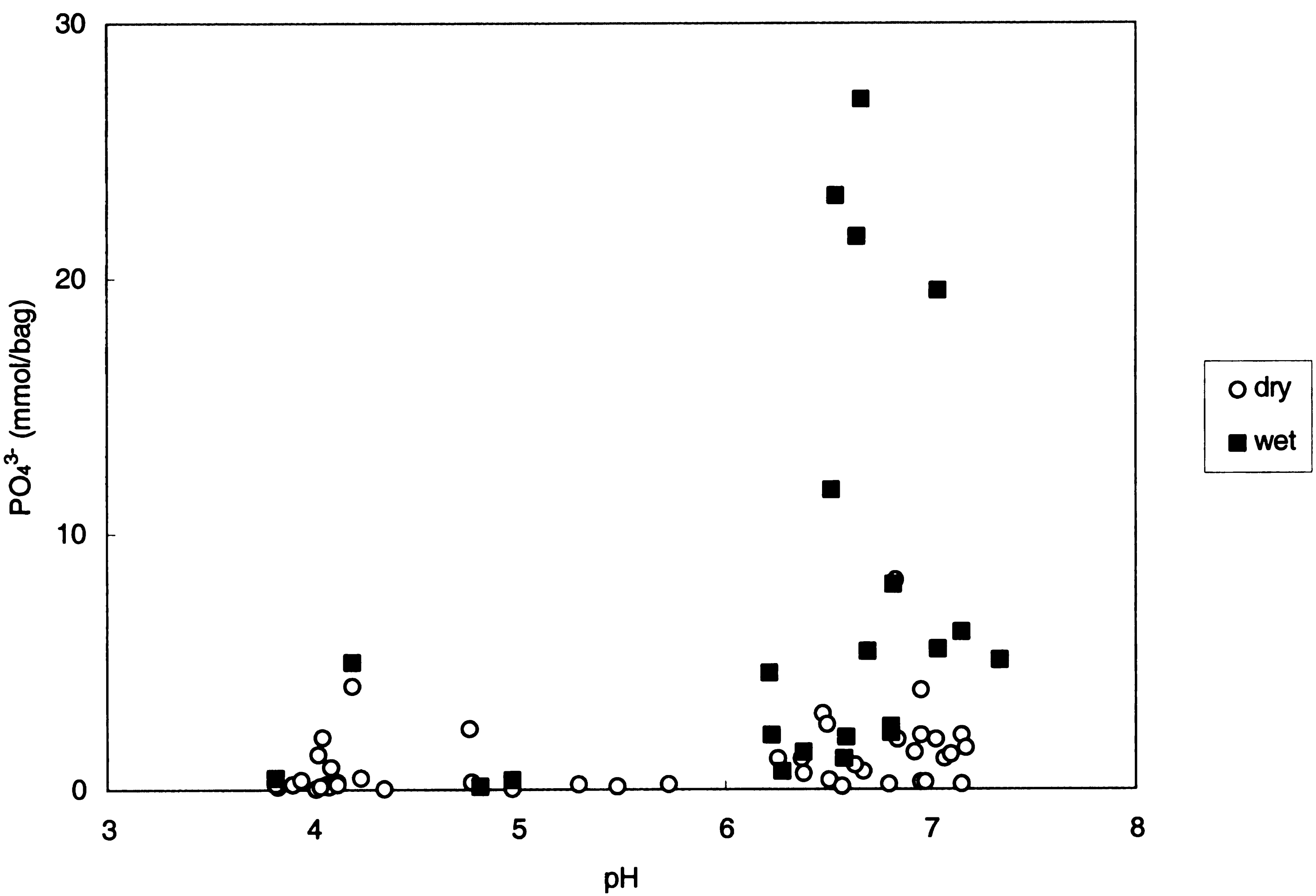

Figure 2.11

soils (t-test, data log-transformed; n=26,44; df=68; $p < 0.001$). At circumneutral locations PO_4^{3-} accumulation on resin was higher in wet soils than in dry soils (t-test, data log-transformed; n=21,23; df=42; $p < 0.001$).

DISCUSSION

Many detailed hydrologic studies have more rigorously quantified inflows and outflows (Richardson 1983, Siegel and Glaser 1987, Mitsch and Reeder 1992), groundwater flow via hydraulic head measurements (Siegel and Glaser 1987, Drexler et al. 1999), and water sources for wetlands (Glaser et al. 1990, Hunt et al. 1998). Those studies excel in elucidating with greater clarity more site-specific hydrogeologic influences. Yet, the time-intensive measurements that yield such insights frequently restrict the scope of such projects to one or only a few wetlands. As an alternative approach, this study encompasses a broad suite of wetlands. While each study site is understood less well, the comparative approach yields insights that are not available from detailed site-specific studies. The results of this study are applicable to southwest lower Michigan; they may also be applicable to other areas of glacial terrain in the northern U.S. and southern Canada that have ion-rich groundwaters and flow paths that are predominantly beneath the land surface (as opposed to overland runoff).

Wetlands are variable ecosystems, and studies that span short time periods often miss ecologically important events that only occur infrequently. While this study spanned several years, most measurements were restricted to one or two years. It is appropriate to question how representative the hydrologic conditions during this study were relative to more long-term hydrologic conditions.

Fortunately, we have a more long-term record of water levels in the study area that shows how my study period compares to the hydrologic conditions over the last several decades. Two citizens (Wendell Shafer, Terry Smith) in the KBS area have monitored water levels at Fair Lake, a local lake, over the last 47 years. This lake lies at the headwaters of the Augusta Creek system and has no channelized inflows (it sustains a small outflow stream except when water levels are low). The Fair Lake data provide insights into water level variability in local lakes and wetlands from 1956 to the present (Figure 2.12). The Fair Lake record shows how the dry period in 1998-99 pales in comparison to the more extended drawdown of lake levels in the early 1960s. Therefore, while the sites in this study experienced drier conditions in the earlier portion of this study, these conditions were not unprecedented. This is more apparent by comparison of monthly summary statistics for the 47-year Fair Lake record to the monthly mean stage at Fair Lake during this study (Figure 2.13). Except for the dry period during Oct 1999 – May 2000, Fair Lake stage generally remained within the 75th and 25th quartiles throughout this study. Thus, the hydrologic conditions during this study were similar to and representative of the average water level conditions over the last several decades.

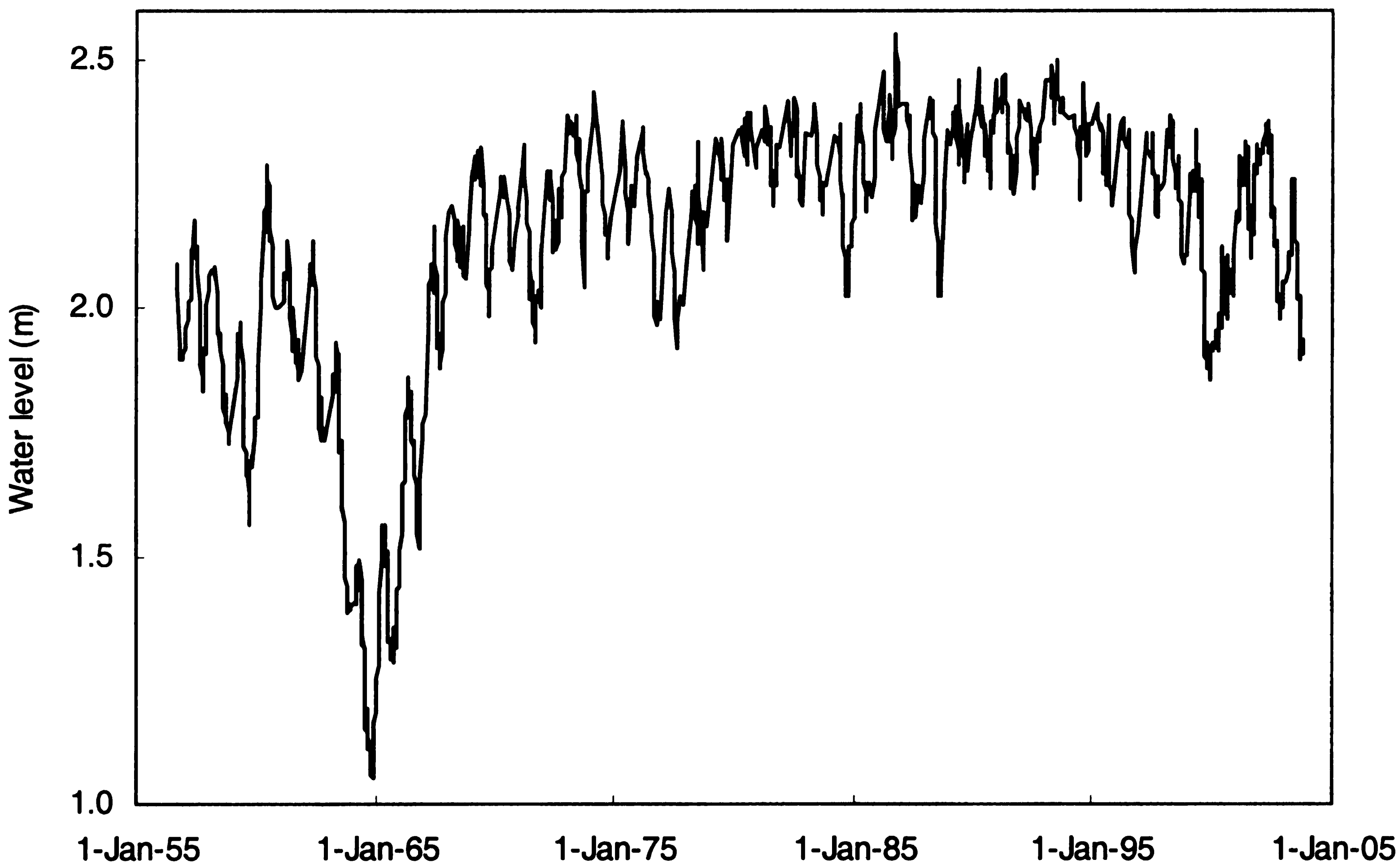

Figure 2.12: Fair Lake water level record for the period Sep 1955 – Oct 2003. Data graciously provided by the late Wendell Shafer and Terry Smith.

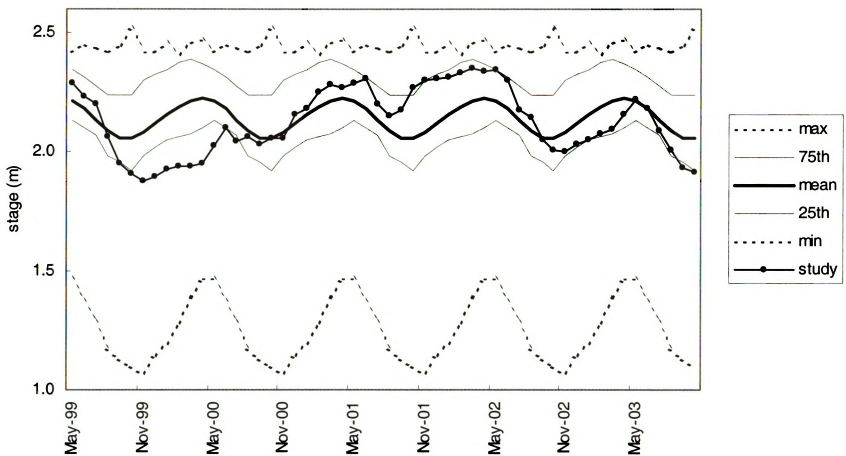

Figure 2.13: A comparison of monthly summary statistics (maximum, 75th quartile, mean, 25th quartile, and minimum) for Fair Lake stage during the period 1956-2003 vs. mean monthly stage during the course of this study. Note that except for the dry period during Oct 1999 – May 2000, Fair Lake stage generally remained within the 75th and 25th quartiles throughout this study.

Hydrochemical characterization of wetland waters

Wetland studies conducted in more northern peatlands have documented the hydrochemical variability that spans the ombrotrophic to minerotrophic gradient (Heinselman 1970, Vitt et al. 1995). What distinguishes the wetlands around KBS from more northern peatlands is that the groundwater is more ionically rich in the KBS vicinity. In contrast to minerotrophic swamps in northern Minnesota (range in specific conductance = 84-119 μS/cm; Heinselman 1970) and extreme-rich fens in Alberta (seasonal mean specific conductance = 184 μS/cm; Vitt et al. 1995), rich fens and swamps in this study are much more ion-rich (range in mean specific conductance = 279-678 μS/cm).

In this study, the most ionically rich waters are usually Ca-Mg-HCO_3 waters. Consequently, Ca^{2+}, Mg^{2+}, and alkalinity are all correlated with and largely create the bimodal conductivity distribution (Table 2.4). pH (Table 2.5) shows a bimodal distribution that parallels the distribution of specific conductance. Na^+, K^+, SO_4^{2-}, and Cl^- also increase with conductivity. Some of these hydrochemical parameters are higher at a few sites for reasons that are unknown or will not be discussed here, but none of these are as important as Ca^{2+}, Mg^{2+}, and HCO_3^- in driving the variation in conductance. Si shows the least variability across sites. The low NO_3-N values are likely due to denitrification, which rapidly removes nitrate from wetland waters (Whitmire 2003). NH_4-N, PO_4-P, and TDP are all highly variable with no discernable patterns across wetland types. NH_4-N is quite high at some sites (107-895 μg NH_4-N/L; n=10). If the plants are able to take up

NH_4^+ and maintain both internal cytoplasmic pH and the electrochemical potential gradient necessary for ion uptake (Raven and Smith 1976, Brix et al. 2002), it seems unlikely that N limitation would be an issue in some of these wetlands.

Water sources, acidity, and the evolution of bog systems

Because Mg^{2+} is correlated with conductivity, the bimodal distribution in wetland specific conductance values is paralleled in the water source calculations. A plot of f_{gw} vs. pH exemplifies these disparate distributions (Figure 2.14). Wetlands with low f_{gw} values (0.03-0.04) are generally acidic (pH range = 3.95-4.84) and discrete from wetlands with high f_{gw} values (0.46-0.93) that are circumneutral (pH range = 6.34-7.22). Winterberry Fen is the sole outlier in the middle of the distribution (f_{gw} = 0.24; pH = 5.50). Why are so few local wetlands intermediate in terms of water sources and acidity? I will address the issue of acidity first and then return to the topic of water sources.

In terms of acidity, the most probable explanation is due to the relationship between pH and alkalinity (Gorham et al. 1984). Like an alkalinity titration, as a circumneutral water containing carbonate alkalinity is acidified, there will be little change in pH until its buffering capacity starts to become exhausted near pH 6. Once the alkalinity is exhausted, pH drops rapidly and only slows as the pH approaches 4 (Drever 1997). A plot of pH vs. alkalinity for all 24 wetlands shows this pattern (Figure 2.15). Study sites are either circumneutral with relatively high alkalinity (alkalinity range = 1.08-5.56 meq/L) or more acidic with minimal or no

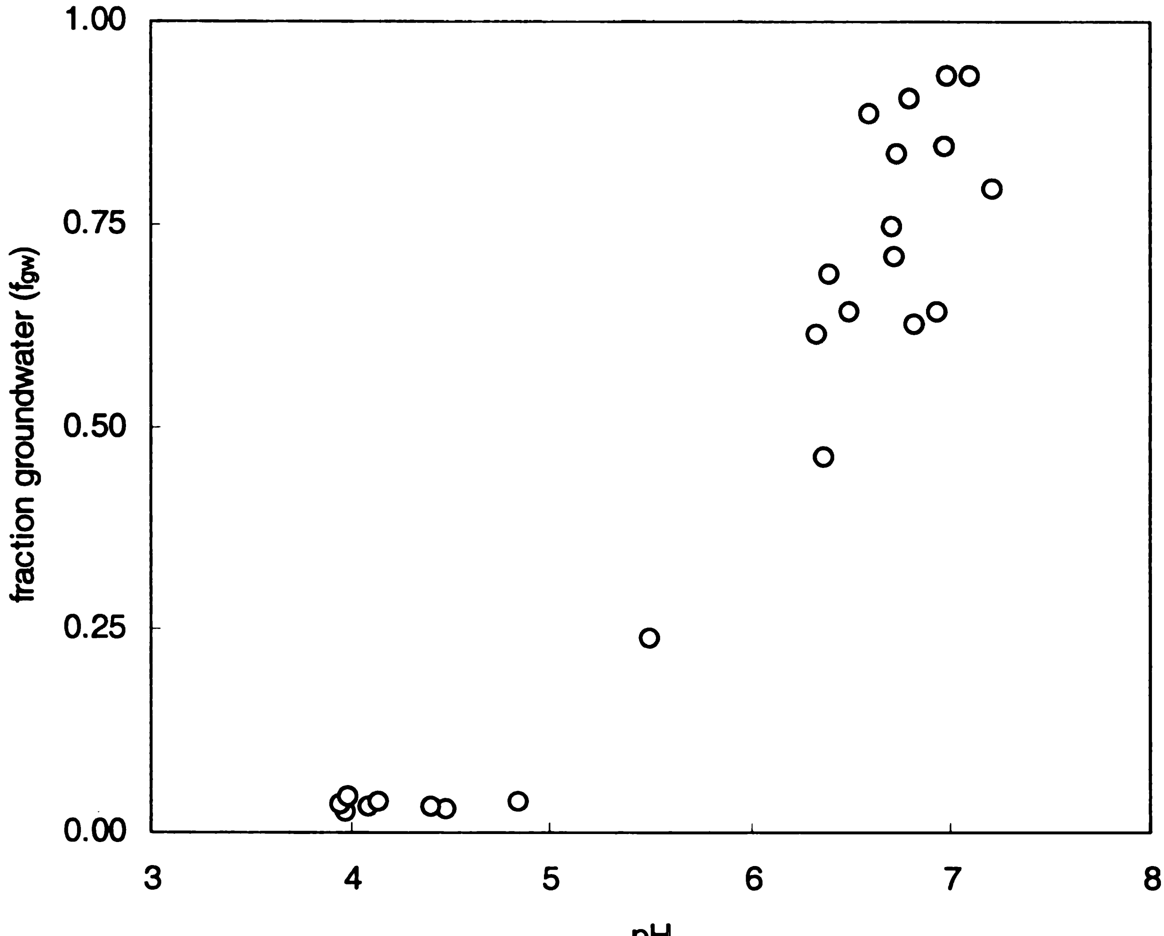

Figure 2.14: Fraction groundwater (f_{gw}) vs. pH for 24 wetlands in southwest Michigan. Note the paucity of wetlands that lie in the f_{gw} range 0.05-0.5 and the pH range 4.9-6.3.

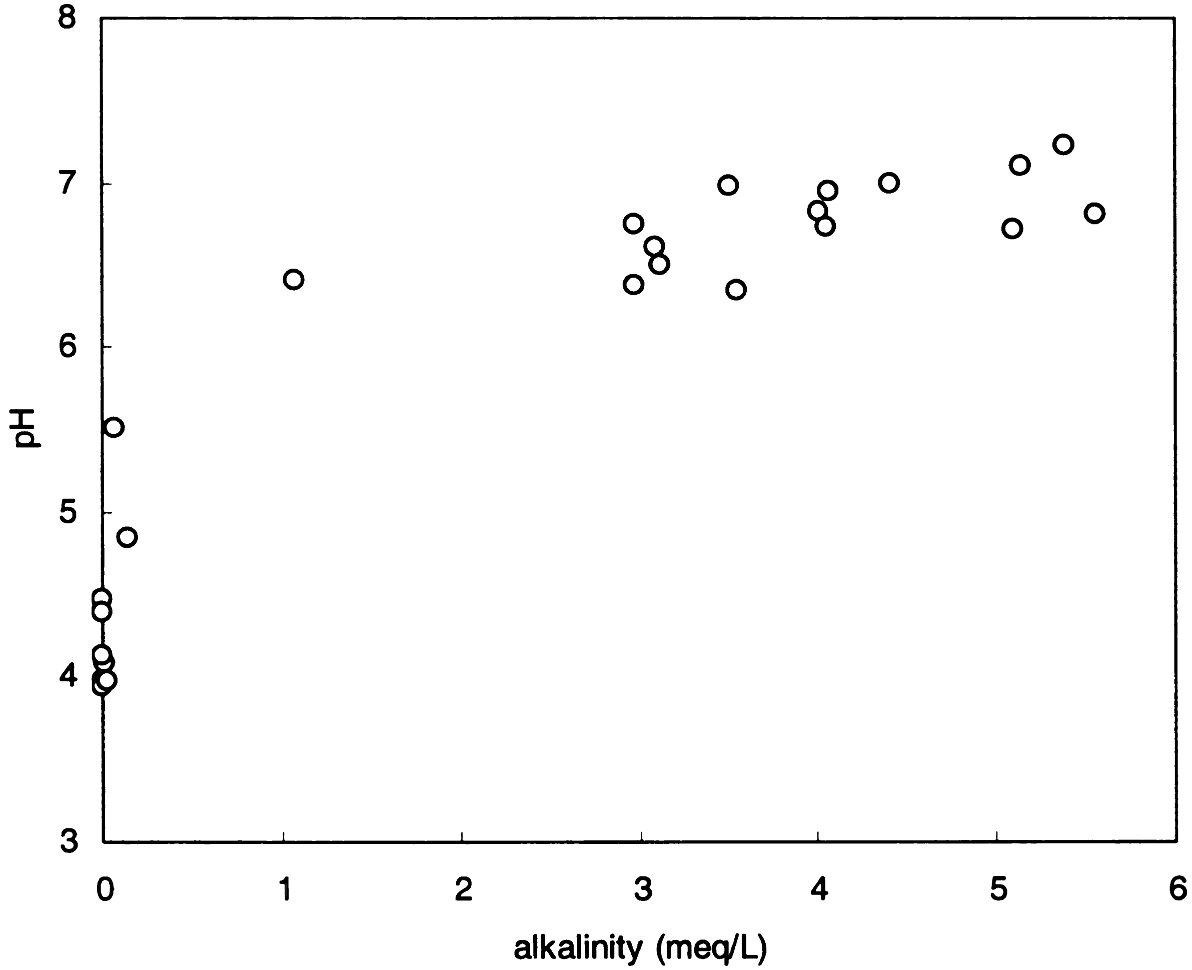

Figure 2.15: pH vs. alkalinity for 24 wetlands in southwest Michigan. Note that these hydrochemical parameters do not correspond to the same date of sample collection; pH values are means for each site in Aug 2003, while alkalinity measurements are means for three sampling periods in Oct 2000 – Sep 2001.

alkalinity (alkalinity range = 0-0.15 meq/L). It is important to note that these pH and alkalinity measurements do not correspond to the same water samples; pH measurements were made in Aug 2003 and represent the mean for each site, while alkalinity values are means for three sampling periods during Oct 2000 – Sep 2001. Therefore, these data may be affected by some minor hydrochemical variation between the sampling periods. However, in our experience sampling these and other similar wetlands, this seasonal and interannual hydrochemical variation is usually small.

A bryologist would grin at this alkalinity explanation, for while the acidity pattern is explainable via hydrochemistry, the main players that catalyze this ecosystem transition are the brown and *Sphagnum* mosses (Crum 1988). But in order to understand the importance of bryophytes, we must first consider the post-glacial landscape and wetland succession.

When the glaciers retreated ca. 10,000 years ago, they had scraped the local landscape and deposited up to 200 feet of glacial till and outwash containing carbonate minerals (calcite and dolomite) in this part of Michigan (Rheaume 1990). After ice blocks melted and mineral-rich lakes and ponds were formed, plant communities recolonized these limnetic habitats. In some depressions the plant communities likely transitioned along the following chronosequence: pond, marsh, fen, bog (Swinehart and Parker 2000). Local ponds and lakes began as mineral-rich systems that partially filled in due to sedimentation from both the local watershed and aquatic plant production. As shallow littoral zones developed, submersed aquatic vegetation and eventually emergent plants flourished. Following this marsh phase, a floating mat fen consisting of sedges and brown mosses advanced out over the pond. As the floating mat continued to thicken and become more hydrologically isolated from the mineral-rich pond waters, the brown mosses and eventually *Sphagnum* mosses acidified their local environments (Glime et al. 1982). The end result was a bog community perched above what was a mineral-rich pond or lake edge.

It is important to note that pH changes gradually during the fen mat phase, but then greatly accelerates after *Sphagnum* colonization (Gorham et al. 1984). *Sphagna* are not readily decomposed (Crum 1988), and decomposition rates are lower in acid habitats (Kittle et al. 1995); both of these factors lead to increased peat accumulation following *Sphagnum* colonization. This accelerated peat accumulation leads to greater hydrologic isolation from the underlying, more alkaline ground waters and, thus, a shift towards precipitation as the predominant water source.

This rapid transition from rich fen (brown moss peat) to bog (*Sphagnum* peat) is evident in the macrofossils of peatlands in northeast Indiana (Swinehart and Parker 2000). Kuhry et al. (1993), using linear interpolation of radiocarbon-dated peat samples, estimated that rich fens could shift to poor fens and then to bogs in only 50-350 years. They noted that this rapid transition would explain why the distribution of modern peatlands tends to be bimodal with peaks in the bog range (pH 3.0-5.0) and the rich fen range (pH 6.0-7.0), but with relatively few poor fens (pH 5.0-6.0). Thus, the paucity of wetlands in this study that lie in the pH range

4.9-6.3 is likely a result of the short duration over which these intermediate systems persist.

It is interesting to ponder which study sites are the most likely candidates, if any, to become more precipitation-fed *Sphagnum* peat bogs. If this process is necessarily preceded by the exhaustion of alkalinity, then Figure 2.15 may be a useful guide in this determination. Clearly Winterberry Fen, a poor fen with intermediate acidity (pH 5.50), is well on its way to becoming an acid bog. Yet, the high variability in water levels at Winterberry Fen (40.5 cm; Table 2.8) may provide drier conditions during the summer that facilitate decomposition and, therefore, impede peat accumulation and subsequent acidification. Otis Pond Swamp is another depression that has somewhat lower alkalinity (1.08 meq/L) and pH (6.40). In fact, *Chamaedaphne calyculata* (leatherleaf), a characteristic bog species, occurs in the portion of the swamp directly adjacent to Otis Pond. So perhaps the transition towards a bog system has already begun in Otis Pond Swamp.

Lastly, it is important to recognize that the topographic variability in certain wetlands may sufficiently perch microhabitats above the influences of groundwater. I have estimated the relative importance of water sources from one water sample collected on three separate dates from a hollow, or low point, in each wetland. Four study sites (Balker Lake Swamp, Otis Pond Swamp, Starflower Swamp, and Serbin Swamp) are perennially wet swamps with *Sphagnum* hummocks scattered throughout (see METHODS, *Study site descriptions*). These *Sphagnum* hummocks may actually act as precipitation-fed microhabitats (Glime et al. 1982), although I never sampled porewaters from these hummocks to verify this. Thus, on an areal basis, these wet swamps could be a mixture of groundwater-fed and precipitation-fed plant communities, depending on how abundant and well-developed the hummocks are in each swamp.

While these explanations may account for the variation in pH and water sources for local wetlands, another question remains: Why have some local wetland systems developed into bogs while others have not and show little indication of change in that direction?

Landscape position and landscape context

To answer this question, it is necessary to take a hydrogeomorphic approach and evaluate the wetland not as an isolated system, but as a basin with a certain landscape position and landscape context. One aspect of landscape context is surface water connectivity. The wetlands in this study vary in terms of surface water connectivity along the following gradient: depressions with no inlets or outlets; depressions with outflows only; depressions with marginal connection to an inflow/outflow system that are not strongly affected by that flow; and depressions that are strongly affected by an inflow/outflow system passing through them (Table 2.2). Surface water connectivity pertains to this study because streams in southwest Michigan are largely maintained by groundwater discharge (Rheaume 1990). Hence, wetlands associated with inflow/outflow systems are more likely to be groundwater-fed systems.

Landscape position reflects where the wetland occurs along the maximum hydrologic flow path in the wetland's watershed. To describe landscape position, I used the metric "relative elevation": the elevation of the wetland relative to its upper catchment boundary (1) and the topographic low in that wetland's watershed (0), which is either the Kalamazoo River or the Thornapple River (Table 2.3). Landscape position should be a good predictor of wetland water sources because the length of groundwater flow paths generally increases with decreasing elevation in a watershed (Figure 2.16; Webster et al. 1996). Thus, depressions located higher in the watershed should receive more of their water from precipitation (vs. groundwater). In contrast, groundwater should become increasingly more important as a water source in depressions that are positioned sequentially lower in the landscape.

Taken together, landscape position and surface water connectivity provide insights into the relative importance of wetland source waters (Figure 2.17). All sites that lack surface inlets and outlets are positioned relatively high in the landscape (relative elevation range = 0.65-0.94). In addition, most of these sites are strongly precipitation-fed ($f_{gw} < 0.05$), although two sites (Winterberry Fen, Lang Fen) are more intermediate in terms of water sources. The more groundwater-fed wetlands ($f_{gw} > 0.6$) span the spectrum of relative elevation, although two patterns emerge concerning these wetlands. First, groundwater-fed sites that occur high in the watershed (relative elevation range = 0.67-0.85) are

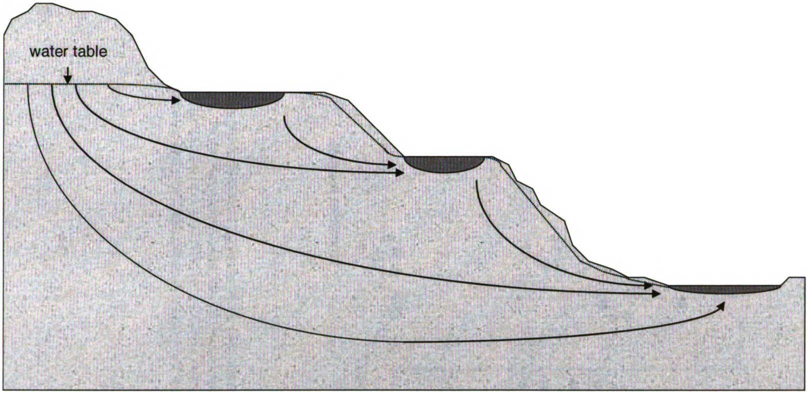

Figure 2.16: A simplified cross-section of a watershed showing groundwater flow paths. Note that depressions high in the watershed are predominantly precipitation-fed, while depressions located farther downgradient are more influenced by groundwater inflows.

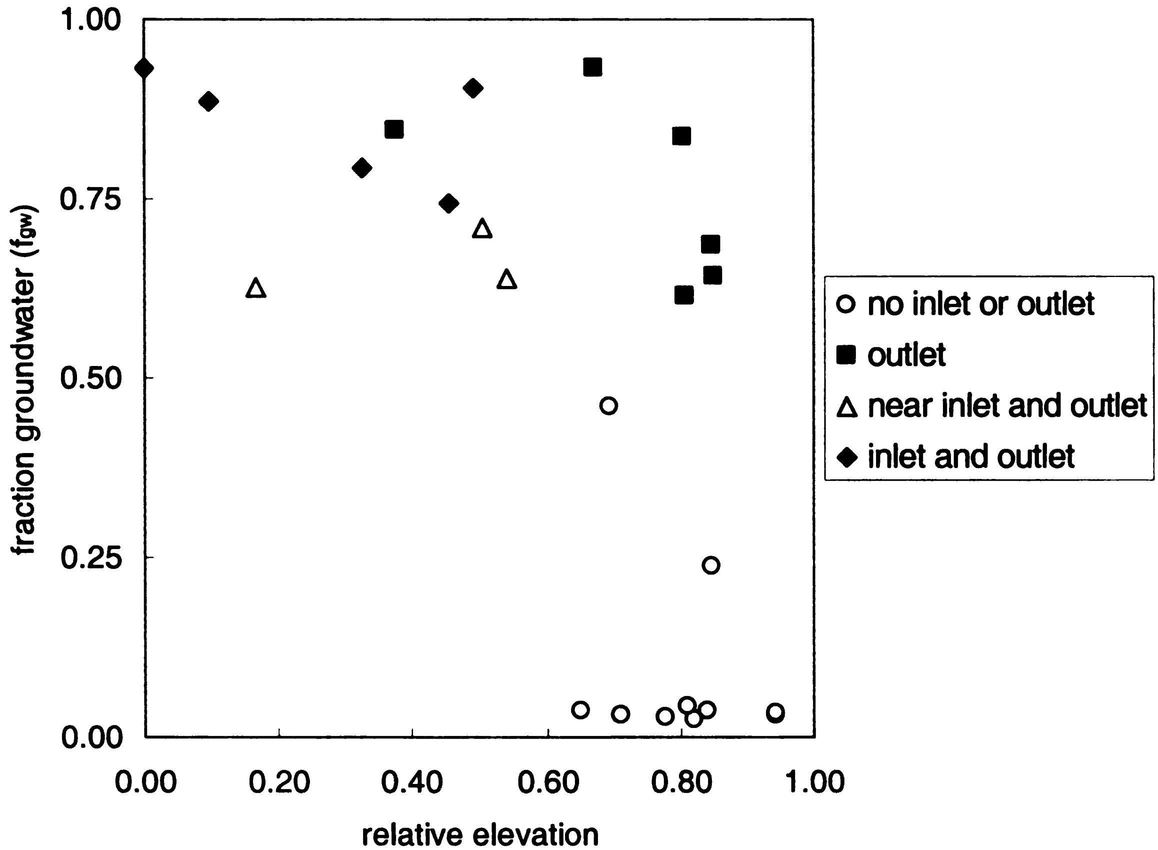

Figure 2.17: Fraction groundwater (f_{gw}) vs. relative elevation for 24 wetlands in southwest Michigan. Note that study wetlands located in isolated depressions generally have low f_{gw} values and are located relatively high in the watershed, while more groundwater-fed wetlands occur throughout the entire watershed.

generally headwater systems that only have a surface outflow. Second, of the remaining groundwater-fed sites that are associated with streams, wetlands that are only marginal to inflow/outflow systems tend to have lower f_{gw} values than systems that are bisected by streams. In summary, groundwater-fed wetlands, while occurring throughout the watershed, are hydrologically connected to surface waters in a predictable way based on their relative elevation. In contrast, precipitation-fed wetlands appear to be restricted to depressions with no inlets or outlets that only occur in the upper portions of their catchments.

The observation that there is an elevational threshold below which bogs do not occur is a novel finding, although one might predict it based on a simplified view of water flow across a watershed (Figure 2.16). However, with only 24 study sites, most of which span only one watershed, this hypothesis concerning a bog elevational threshold is put forth tentatively. A stronger test of this hypothesis would involve calculation of the relative elevation of many bogs using a geographic information system (GIS), a digital elevation model, and restricting the study to the PSS3 NWI class (which generally corresponds with *Chamaedaphne calyculata* (leatherleaf), a characteristic bog shrub). Finally, this bog threshold hypothesis is subject to several geographical constraints: inland depressional wetlands that lie in a glacial landscape with groundwater that is strongly influenced by underlying carbonate geology.

In a study of peatland palaeoecology in northeastern Indiana, Swinehart and Parker (2000) noted that fens lacking inflows and outflows eventually became bogs (i.e., precipitation-fed systems), while two of their three extant fen sites had surface outflows (they attempted to exclude riparian peatlands from their study). Thus, surface water connectivity may be a good predictor of the occurrence of bog systems (no inlets or outlets) vs. more ion-rich wetlands (outlets or inlets and outlets) in the southern Great Lakes region.

The opposite pattern evidently occurs for moderate and rich fens in New York State (Godwin et al. 2002). Based on my results, I would expect more ion-rich wetlands to be associated with inflow/outflow systems. However, Godwin et al. (2002) report that more ion-rich fens occurred almost exclusively in isolated depressions, while medium fens tended to be connected to local flow systems. The underlying geology of many rich fens in New York State consists of either calcareous bedrock or calcareous glacial deposits (Bedford and Godwin 2003), which is not dissimilar from the calcareous glacial deposits in this part of Michigan. The pattern in surface water connectivity reported in this study, thus, requires further testing in other glaciated regions.

Water level variability

The variability in water levels reported here was similar to that reported for a swamp in Ontario (Woo and Winter 1993) and Midwestern fens (Amon et al. 2002). The summers in southern lower Michigan are warm, and precipitation is sporadic but normally exceeded by evapotranspiration; local wetlands frequently dry down during the late summer. However, some wetlands dried down more than others (larger ranges; Table 2.8).

I expected that groundwater inflows would confer hydrologic stability to wetlands and that groundwater-fed wetlands would exhibit less water level decline throughout the growing season. However, there was no correlation between f_{gw} and the range of water level variability (Figure 2.5B). Instead, there was a significant negative correlation between f_{gw} and mean water levels for 2001 (Figure 2.5A). Thus, more groundwater-fed wetlands were, on average, drier during summer than more precipitation-fed wetlands.

However, this relationship is more likely a consequence of surface water connectivity. Because groundwater-fed wetlands tend to be associated with streams (Figure 2.17), drainage via surface outflows lowers water levels in more groundwater-fed wetlands. In contrast, more precipitation-fed wetlands with closed basins lack outflows and maintain higher mean water levels. In fact, mean water levels in 2001 were higher in wetlands with no inlets or outlets than in wetlands with surface outflows (t-test; n=10,14; df=22; $p = 0.043$).

It is important to note that precipitation in May 2001 was well above-average (NADP/NTN 2003). Substantial precipitation inputs to more precipitation-fed wetlands may have caused these wetlands to experience unusually high water levels. This could also explain the significant pattern in mean water levels. Water level data spanning several years would allow more conclusive determination of whether wetlands lacking surface outflows experience, on average, higher mean water levels.

Finally, I would like to point out the unusual nature of Sherriff Fen, the only floating mat fen in the study. The monitoring wells at this site were installed in

Oct 1999, when water levels were quite low (Figure 2.13); this set the zero mark relatively low. When water levels increased in May 2000 (Figure 2.6) relative to this zero mark, they remained relatively high for much of 2000 and 2001 – exceeding +35 cm on 29 May 2000! The water level pattern is real, but the plants rooted in the floating mat were not subject to 20-30 cm of inundation during these periods, as the hydrograph suggests (since the hydrograph is referenced to the zero mark at all sites for consistency). Instead, the floating mat and the plants rooted in it rose with the increasing water levels. Consequently, high water levels at Sherriff Fen do not reflect inundation per se. Yet, the site remained very wet overall relative to other sites (e.g., no shrubs were ever observed growing on the mat, which is indicative of how wet the conditions were at this site). Thus, while I leave the water level measurements uncorrected for Sherriff Fen, plants growing at this site did not experience the water level variability that Figure 2.6 suggests.

Soil characterization

Soil analyses were done in part to facilitate comparisons with other studies that did not make hydrochemical measurements. Several studies have data on %N and %P in soils across a gradient of wetland types. Vitt and Chee (1990) report mean %P values for soils in poor fens (0.13) and moderate fens (0.19) in Alberta that are similar to %P values for more intermediate wetland soils in this study (0.10-016; Table 2.10). Bridgham et al. (1998) report mean %N and %P for soils from several bogs (1.14, 0.05), acidic fens (1.51, 0.06), and intermediate fens (2.52, 0.08) in northern Minnesota. Bog and poor fen peat in this study spans 1.51-2.64 %N and 0.05-0.12 %P, which is generally consistent with the soil data for Minnesota peatlands. Bedford et al. (1999) reviewed the literature and summarized mean %N and %P for soils from a broad spectrum of wetland types: bogs (1.16, 0.05), poor fens (1.35, 0.07), moderate-rich fens (1.88, 0.08), rich fens (1.98, 0.09), marshes (1.41, 0.25), and swamps (1.28, 0.09). Mean %N and %P for wetland types in this study were as follows: bogs (1.77, 0.07; n=8), poor fen (2.64, 0.12; n=1), fens (2.64, 0.14; n=9), and swamps (2.25, 0.15; n=6). Note that my use of the term "fen" is broad relative to many definitions, which restrict its use to connote calcareous wetlands dominated by graminoids; definitions of "fen" vary considerably (Bedford and Godwin 2003). Compared to the data summarized by Bedford et al. (1999), wetland soils in this study generally have higher %N and %P.

However, interpretations from soil nutrient data are limited because soil nutrients only represent nutrient pools, not nutrient fluxes, which are more pertinent to understanding nutrient availability to the biota (Bedford et al. 1999).

Nutrient supply

Mean nutrient accumulation on IER and mean aqueous nutrient measurements were not consistent across sites (Table 2.4; Figures 2.7-2.9). This is not surprising because these two techniques measure nutrients in different ways, and nutrient availability is quite variable in space and time. While there are questions regarding what the accumulation of nutrients on IER actually represents, IER is conceptually a better measure of nutrient availability than porewater samples because IER incubations estimate nutrient supply, not absolute nutrient concentrations (Bedford et al. 1999). Additionally, unlike laboratory incubations of soil cores, IER bags are exposed to in situ conditions, which provides a measure of nutrient supply that reflects soil moisture conditions and the flow of water and nutrients through soils (Giblin et al. 1994).

NO_3^- supply was either below detection limits or very low relative to NH_4^+ supply. NO_3- is rapidly depleted in local wetland soils (Whitmire 2003), so this low NO_3^- supply is not unexpected. NO_3^- supply was highest at Prairieville Creek Fen, where nitrate-rich (5-13 mg NO_3-N/L) groundwaters emerge as springs throughout the wetland.

NH_4^+ and PO_4^{3-} accumulation on IER was variable within and among sites, but patterns were visible at smaller spatial scales. NH_4^+ and PO_4^{3-} supply varied as a function of acidity and moisture (Figures 2.10-2.11). NH_4^+ and PO_4^{3-} accumulation on IER was relatively low at acidic locations (pH 3.82-5.73) and circumneutral locations (pH 6.22-7.35) that were "dry" (i.e., where the IER was not exposed to saturated conditions at either the beginning or the end of the incubation). NH_4^+ and PO_4^{3-} supply was higher at "wet" circumneutral locations.

Acidic bogs are generally considered to be nutrient-poor habitats (Zoltai and Vitt 1995), and the nutrient supply estimates from this study are consistent with that concept. Because saturated conditions increase the contact surface on the

IER, it is not surprising that nutrient accumulation was higher in wet circumneutral locations than in dry circumneutral conditions. Yet, it is interesting that soil moisture only increased nutrient supply at circumneutral sites and not acidic sites. Thus, it appears that nutrient supply in these wetlands varies primarily as a function of acidity and secondarily as a function of soil moisture.

This is the first study to report nutrient accumulation on IER across such a broad suite of wetland hydrochemical conditions. Giblin et al. (1994) report nutrient availability in a variety of arctic wetland ecosystems, including moist tussock tundra, wet sedge tundra, a riverside willow community, and more acidic moist tussock sites. NH_4^+, NO_3^-, and PO_4^{3-} supply in Michigan wetlands was generally 10^2-10^4 times greater than that reported by Giblin et al. (1994). Bowman et al. (2003) report $NH_4^+ + NO_3^-$ and PO_4^{3-} supply estimates for alpine moist and wet meadows that are 10^2 and 10^4 times lower than in Michigan wetlands, respectively. Thus, while comparisons are limited, NH_4^+, NO_3^-, and PO_4^{3-} supply appear to be several orders of magnitude higher in Michigan wetlands than in tundra and alpine communities. These results are consistent with previous observations that nutrient availability in arctic ecosystems is very low relative to temperate wetlands (Nadelhoffer et al. 1992).

Kiernan et al. (2003) report NH_4^+ and NO_3^- supply estimates for shrub wetlands in the Adirondack Mountain region of New York State; these NY shrub wetlands have no, low, or high abundance of *Alnus incana* ssp. *rugosa* (speckled alder), a known nitrogen fixer. NH_4^+ supply to NY alder shrub wetlands is 10^2

times lower than shrub wetlands in Michigan, while NO_3^- supply to NY alder shrub wetlands is similar to NO_3^- supply to shrub wetlands in this study.

Finally, from the perspective of the plant community, these nutrient supply estimates only describe nutrient availability at 5 cm depth, and interpretations are limited to this depth. If NH_4^+ and PO_4^{3-} supply was low at circumneutral locations due to unsaturated conditions at 5 cm depth, these nutrients may be in greater supply at 15 or 30 cm depth if the soils are saturated at greater depth. Thus, "dry" circumneutral locations with low NH_4^+ and PO_4^{3-} supply could have either 1) low nutrient supply or 2) low nutrient supply at 5 cm depth, but higher nutrient supply at greater depth. If the latter were true, plant roots could acquire more nutrients by growing roots deeper and closer to the water table. Therefore, while my results suggest that acidic soils have low nutrient supply and saturated, circumneutral soils have relatively higher nutrient supply, sites with unsaturated circumneutral soils remain an open case. To resolve the issue of nutrient availability for plants in circumneutral wetlands that exhibit lower water levels, I suggest IER deployment throughout the rooting zone.

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CHAPTER 3

LINKAGES BETWEEN WETLAND PLANT COMMUNITIES AND ENVIRONMENTAL VARIABLES

INTRODUCTION

Understanding the abundance and distribution of species has fascinated ecologists for a century or more (Cowles 1899). Both biotic and abiotic factors are thought to control where and when species occur (Harley 2003). In particular, plants respond to a variety of abiotic conditions: soil moisture, light, the availability of soil nutrients, to name a few. Together, these abiotic conditions limit where a plant could grow. Within that abiotic context, species interactions such as competition and facilitation occur, which may further restrict whether a plant may persist at a given site. Thus, both biotic and abiotic factors contribute to the development and maintenance of different plant communities.

In wetlands, where abiotic forcings are strong, plant communities are thought to vary primarily as a function of hydrology and, in particular, water depth and the duration of soil saturation (Cronk and Fennessy 2001). The primary stress associated with increasing water depth is low oxygen in the rooting zone (Pezeshki 1994). Atmospheric oxygen diffuses 10^4 times slower through water-filled soil pores than through unsaturated sediments (Greenwood 1961). After flooding, the oxygen demand by heterotrophic microbes and plant root respiration quickly depletes any oxygen remaining in the soil solution (Ponnamperuma 1984). Insufficient oxygen results in the loss of root function, including water and nutrient uptake, which may cause leaf chlorosis, growth inhibition, and eventually death (Pezeshki 1994). Wetland plants possess many different adaptations that help them cope with anoxia in waterlogged soils. These include aerenchymous tissue for transporting oxygen from the leaves down the stem to the roots (Laan et al. 1989); hypertrophied stems and lenticels, which increase gas exchange between the plant and its environment (Kozlowski 1984); and shallow and adventitious roots, rooting systems that attempt to avoid hypoxic or anoxic conditions deeper in the soil (Visser et al. 1995).

In addition, there are other abiotic stresses often associated with anoxia that may adversely affect plant growth and survival. As oxygen disappears from wetland sediments, the redox potential declines. Under increasingly reduced conditions, a series of microbially mediated processes ensues, including denitrification, manganese reduction, iron reduction, sulfate reduction, and methanogenesis (Laanbroek 1990). Several of the reduced products of these reactions, including Mn^{2+}, Fe^{2+}, and S^{2-}, are readily subject to root uptake and toxic to plants at low levels (Ernst 1990). In addition to these reduced geochemical species, anaerobic decomposition of organic matter produces a wide range of differentially phytotoxic organic compounds, including acetic and butyric acids (Ponnamperuma 1984, Cronk and Fennessy 2001). To avoid these toxins that develop under anoxic conditions, plants that can transport oxygen to their roots exhibit radial oxygen loss, which oxidizes the surface of their roots (Koncalova 1990). In summary, waterlogged soils with little or no oxygen pose a complex set of physiological challenges to plant rooting systems.

Because root oxygen deficiency and soluble phytotoxins are associated with saturated soil conditions, and plant species likely vary in their tolerance of these stressors (e.g., Fe^{2+} toxicity; Snowden and Wheeler 1993), wetland plant ecologists are often interested in understanding water level variability at a site. A hydrograph describing seasonal and interannual water level variability should help elucidate why different plant communities occur in different hydrologic environments. The problem is that each hydrograph is unique, and it is difficult to summarize a hydrograph in a way that is relevant to plants. Hydroperiod, the number of days flooded during a year, is a summary variable that has been related to different plant communities (Duever 1982, Lockwood et al. 2003). Yet, hydroperiod is a very coarse summary variable, and it fails to account for any differences in water level variability below the soil surface. (Hunt et al. 1999) and (Cole and Brooks 2000) have calculated the proportion of time that the water level was in the rooting zone (i.e., above -30 cm depth) to generate a water level statistic with more relevance to the plant community. This "root-zone probability" is more biologically relevant than hydroperiod, but still suffers from the simplistic threshold concept that underlies the notion of hydroperiod. A summary of water levels above, below, and throughout the rooting zone of plants would be more biologically relevant to the plants. In fact, if soil moisture is more important than water levels per se in determining wetland plant communities, it may be necessary to shift towards measuring soil moisture in addition to or instead of water levels (Hunt et al. 1999). It remains a challenge to relate water level measurements quantitatively to wetland plant communities in a way that is both biologically relevant and not overly simplistic.

While water level variability is important, wetland plant communities also vary strongly across hydrochemical gradients, most notably acidity and nutrient availability (Heinselman 1970, Vitt and Chee 1990, Bedford et al. 1999). Acidity gradients that correlate with vegetation differences have been extensively studied in northern peatlands (Heinselman 1970, Karlin and Bliss 1984, Vitt and Bayley 1984, Vitt and Slack 1984, Vitt et al. 1995). Nutrient gradients have also been related to differences in wetland plant communities (Vitt and Chee 1990, Bedford et al. 1999). Vitt and Chee (1990) evaluated acidity and nutrient availability together with respect to different plant communities in Alberta fens. What remains is to evaluate many environmental factors together – the relative importance of acidity, nutrient availability, water level variability, and reduced geochemical phytotoxins – across different types of wetlands.

To further our understanding of which environmental factors are most strongly associated with different plant communities, it would also be helpful to consider which landscape- or system-level factors (e.g., landscape position, wetland water sources) may control the environmental variables most likely acting on wetland plants (e.g., pH, light, nutrient availability, water level variability, reduced phytotoxins). Water source is a commonly cited hydrologic variable of interest that may be important in structuring wetland ecosystems. To date, attempts to relate water sources to plants have generally focused on the water source endmembers (i.e., precipitation-fed bogs or groundwater-fed fens) or relied on qualitative, not quantitative, estimates of water source (Goslee et al. 1997). Landscape-level features show promise for predicting the occurrence of calcareous fens in glacial terrains (Godwin et al. 2002), and at a coarse level, landscape-level factors may be a good starting point in determining where different wetland hydrologic environments occur (Winter 1992).

In this chapter I evaluate a broad range of environmental variables and their relationship to the plant communities in a variety of wetlands in southwestern Michigan. The primary goal was to evaluate the relative importance of these environmental variables with respect to differences in the wetland plant communities. These comparisons are only possible in studies that both span a wide range of wetland environmental conditions and measure many of the potentially important environmental variables. In addition, the study wetlands are all located in a relatively small area. Consequently, the variations in underlying geology and climate that may confound comparisons across regions do not limit comparisons across wetland types in this study.

METHODS

Vegetation surveys

As noted in Chapter 2, the wetlands in this study represent the terrestrial end of the wetland gradient in this area, including bogs, fens, and swamps. Trees existed in many of my sites, but herbaceous plants and shrubs comprise most of the species in all cases. Wetlands with permanent or semi-permanent standing water (ponds, littoral zones of lakes) were purposely excluded to focus on emergent plant communities. To better span the gradient of wetlands, I selected six wetlands from each of four National Wetland Inventory (NWI) subclasses (PSS3, PEM, PSS1, and PFO; see Chapter 2, METHODS, for more information on NWI subclasses). 12 sites were selected in 1999 and an additional 12 sites were added in 2000 (for a total of 24 study sites); these years correspond with when the vegetation was surveyed at these sites (Appendix Table A1.1). In both years the vegetation surveys were conducted between 1 July and 20 Sep.

To characterize the dominant plant species in these wetlands, I used a line-intercept technique (Brower et al. 1990) along a 200 m transect oriented through the central portion of the wetland. To determine the transect starting point, I walked a random number of paces (using a random number table) into the wetland and defined the general direction that would orient the transect through the middle of the wetland. I then randomly chose a compass bearing restricted to that general direction (so that the transect did not exit the wetland). Specific information on the vegetation transects (LAT/LONG of starting point; compass bearing of transect) is listed in Appendix Table A1.1. Due to time limitations, a systematic subsampling approach was adopted where shrubs and herbaceous vascular plants were sampled from 5 m increments at 20 m intervals along the 200 m transect (Figure 3.1). Thus, shrubs and herbaceous vascular plants were sampled from 8 x 5 = 40 m total. Trees were sampled along the entire 200 m transect. I constructed a densitometer (using a piece of PVC, a small wooden

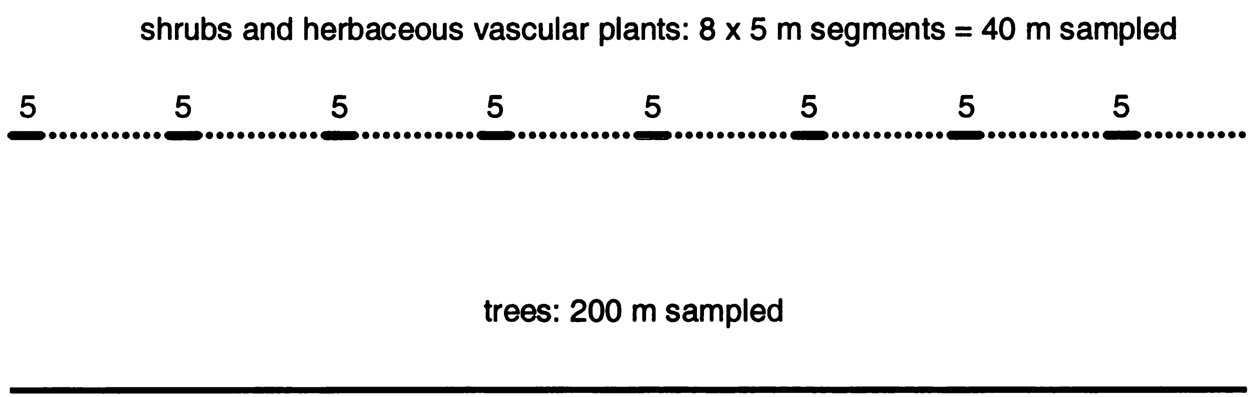


Figure 3.1: The systematic line-intercept method used to sample wetland vegetation in this study.

block cut at a 45° angle, a piece of mirror from a lipstick box, and the oil level from my toolset at home; $4 instead of $90!) to assist in estimating where the tree canopy intercepted the transect. Vegetation surveys generally required 12-15 hours of field work at each site, although some species-poor sites were completed in only 4 hours.

I opted for a line-intercept technique over quadrat sampling for several reasons. First, a line-intercept technique allowed me to estimate species cover more accurately (by estimating interception lengths to within 1 cm, or 10 cm for tree canopies) than could be accomplished by estimating aerial cover using six cover classes (the approach typically used for quadrat sampling). Second, because quadrat size should scale with the size of the plants being studied (Brower et al. 1990), including herbs, shrubs, and trees would require the use of several different quadrat sizes; a line-intercept technique requires only a single transect and is, therefore, more practical and time-efficient. Third, line-intercept sampling is well suited to characterize gradients, which are common in wetland environments (Carter et al. 1994). Lastly, the purpose of the vegetation surveys was to describe the dominant species at these sites, not to sample rare species or estimate plant diversity, both of which are better done using quadrat sampling.

Botanical nomenclature follows Voss (1972, 1985, 1996) except for the family Equisetaceae (horsetails) and the division Polypodiophyta (ferns), for which nomenclature follows Gleason and Cronquist (1991).

Cover value calculations

To calculate fraction cover for each species at each site, the interception lengths for each species were summed and divided by the total sampled transect length: 40 m (shrubs and herbaceous vascular plants) or 200 m (trees). This provided a fractional cover value between 0-1 for all species. The cover values for all species that occurred on transects are reported in Appendix Table A2.1.

Multivariate analyses

Ordination is both a data reduction technique and a pattern-seeking exercise. It is infeasible to simultaneously consider the correlation between each pair of different species across all sample units. Ordination reduces the myriad correlations in relative abundance for all species down to a few synthetic axes, which are much easier to interpret. Ordination also aids in visualizing differences in sample units. The distance between sample units in ordination space approximates the difference in species composition in the sample units. Thus, sample units with more similar communities plot closer together in the ordination. In addition, predefined groups of sample units may be designated using different symbols, which facilitates comparisons between and among groups.

Ordination also assists in relating the position of the sample units in ordination space to environmental variables. A common technique for accomplishing this is a joint plot. In a joint plot, lines radiate out from the centroid of the ordination.

The angle and length of a line indicate the direction and strength of the relationship between the environmental variable and the sample units. Additionally, the ordination may be rotated to maximize the correlation between an ordination axis and an environmental variable (usually the variable that relates most strongly to the position of the sample units in ordination space). Differences in sample units along that axis are then correlated with that environmental variable, which aids in interpreting the ordination.

All multivariate statistical analyses were performed using PC-ORD version 4 (McCune and Mefford 1999). Ordination of study sites was performed using nonmetric multidimensional scaling (NMS; Mather 1976). NMS is an ordination technique that uses an iterative optimization method in finding a solution with the least stress. Stress is the opposite of fit from regression. In regression, it is optimal to maximize goodness of fit; in NMS, it is optimal to minimize stress. NMS is an ideal ordination technique for ecological community data because it is robust to nonnormal or discontinuous data (McCune and Grace 2002). A Sorensen distance measure was used in all ordinations because this distance measure is an effective measure of sample similarity (McCune and Grace 2002). NMS ordination procedures followed this sequence: a random starting configuration; 50 runs with the real data; an assessment of dimensionality; 50 randomized runs; an assessment of stability of the solution (stability criterion: standard deviations in stress over the last 10 iterations ≤ 0.005).

NMS was chosen over other ordination techniques following the guidelines for technique selection given by McCune and Grace (2002). In the interests of brevity, I have only included the most salient problems with some of the alternative ordination techniques below. Principal components analysis (PCA) was deemed inappropriate because it forces a line through the ecological community data, which are often nonnormal and poorly described by a linear solution. Correspondence analysis (CA), which finds linear solutions based on chi-square distances, has several faults, the most important of which is its tendency to distort second and later ordination axes in a "horseshoe" pattern. Detrended correspondence analysis (DCA), which is based on CA, squashes the horseshoe pattern using a brute force rescaling procedure, but in so doing imposes assumptions about the sample units that are inappropriate in most instances. Canonical correspondence analysis (CCA), which is based on CA, ignores all patterns in the community data that are unrelated to the environmental variables included in the analysis – a kind of "multivariate myopia", if you will. Bray-Curtis (polar) ordination, which references all sample units to two endpoints (chosen subjectively or objectively), is only appropriate for community data that vary along a single environmental axis. Weighted averaging, which has been used to produce noteworthy documents such as the Federal Wetlands Manual (Federal Interagency Committee for Wetland Delineation 1989) and various Indices of Biotic Integrity (Karr 1991, Kerans and Karr 1994), forces ordination results along a single gradient and, thus, severely limits exploratory data analysis.

Ordination facilitates pattern detection. However, to optimize the ability to detect pattern, it is preferable to maximize the signal to noise ratio. Exclusion of rare species (for the purposes of this study, species with low cover values that occur at only one site) often improves the ability to detect relationships between the plant community data and environmental variables, but with minimal loss of information (McCune and Grace 2002). Deleting rare species is inappropriate if patterns in species diversity are of interest (Cao et al. 1998). However, the purpose of this study was not to evaluate diversity patterns, but to characterize the dominant vegetation across these wetlands.

To evaluate the optimal number of species to include in all multivariate analyses, I performed NMS ordinations on successively smaller plant community data sets; rotated the ordination so as to maximize the relationship between NMS Axis 1 and pH; and correlated NMS Axis 1 scores with pH, an environmental variable that is strongly related to differences at these sites. The optimal number of species to include is indicated by where the correlation is strongest between pH and NMS Axis 1 (McCune and Grace 2002). After performing 11 different ordinations using successively stricter criteria in determining which species to include (from 208 down to only 32 species), the ordination structure remained relatively unchanged; the correlation coefficient between pH and NMS Axis 1 only decreased from 0.950 to 0.944. I followed this procedure for the Canopy variable (described below) and NMS Axis 2 as well, and again the ordination structure remained relatively unchanged until the species pool was reduced below 39 species. Thus, this approach did not indicate an optimal number of species to include in the ordination, although it did confirm that inclusion of all species did not weaken the overall structure of the ordination.

Species that are both infrequent (i.e., occur at only one site) and rare (cover values < 0.01) are not well characterized by my sampling technique and may be erratic occurrences. For example, *Phytolacca americana* (pokeweed), a native species of rich, disturbed soils (Voss 1985), occurred once on a transect at one of the bog sites. Inclusion of rare, infrequent occurrences such as this example contributes little to our understanding of wetlands at the plant community level. Therefore, I have excluded species that only occur at one site and have cover values < 0.01; 163 species were retained for all subsequent multivariate analyses.

Three ordinations were performed to visualize patterns in the plant community data from this study: the first ordination included all 24 study sites (hereafter referred to as the "overall" ordination); the second included the 15 fen and swamp sites (the "alkaline" ordination); the third included the 8 bogs and 1 poor fen (the "acidic" ordination). The pattern in the overall ordination was dominated by the acidity gradient; the acidic and alkaline ordinations were performed in order to better detect patterns among the more acidic and alkaline study sites, respectively. Ordinations were rotated using Varimax rotation (Mather 1976) in order to maximize the correlation between one of the NMS axes and the variable most strongly related to differences in the plant communities: pH (overall ordination), Canopy (alkaline ordination), and H_2O Range (acidic ordination).

All abiotic variables included in the joint plots were detailed in Chapter 2 except for the variable Canopy. Canopy is a surrogate for shade (or the inverse of light):

Canopy = Σ cover values for all trees and shrubs that can reach 3 m in height

Barnes and Wagner (1981) and Gleason and Cronquist (1991) were used as the botanical authorities in determining maximum shrub height. Canopy values ranged from 0-2 and corresponded well with visible shade differences across sites.

It is preferable to relate environmental variables that are independent of the ordination to the ordination; otherwise one must address the issue of logical circularity. In the strictest sense, Canopy is not independent of the ordination because the 34 species that comprise the Canopy variable were included in the ordination. However, after removing these 34 species and rerunning the overall ordination, the general structure of the ordination remained relatively unchanged, as did the direction and strength of the relationship between Canopy and the study sites. Therefore, while Canopy is not strictly independent of the ordination, the fundamental interpretation of the ordination does not change by inclusion or exclusion of the species that comprise the Canopy variable. Consequently, all 163 species were retained in the overall ordination, and the Canopy variable was considered to be independent of the ordination for all practical purposes.

Due to the diversity of wetland study sites, I grouped sites with similar plant communities to aid interpretation of the ordinations. Study sites were grouped by hierarchical, polythetic, agglomerative cluster analysis using a Sorensen distance measure and a flexible beta (-0.25) linkage method, as suggested by McCune and Grace (2002). To identify where to prune the resulting dendrogram, I employed indicator species analysis (Dufrene and Legendre 1997), which identifies species that are both faithful and exclusive to predetermined groups; a randomization procedure was used to test the statistical significance of indicator values. The most appropriate number of groups both maximized the number of significant indicator species (α=0.01) and provided the lowest mean *p*-value for all species (McCune and Grace 2002). Indicator species analysis also generated indicator species for the resulting wetland groups. These groups were then used to interpret the NMS ordinations.

The multi-response permutation procedure (MRPP; Biondini et al. 1985) was used to test the statistical significance of identified groups. MRPP is a nonparametric method for testing the null hypothesis of no difference between groups. MRPP was performed using a Sorensen distance measure, the same distance measured used in the NMS ordinations. One of the groups identified by cluster analysis contained a single site: Winterberry Poor Fen. MRPP may not be performed when one of the groups contains only a single member. Consequently, Winterberry Poor Fen was excluded from the MRPP.

RESULTS

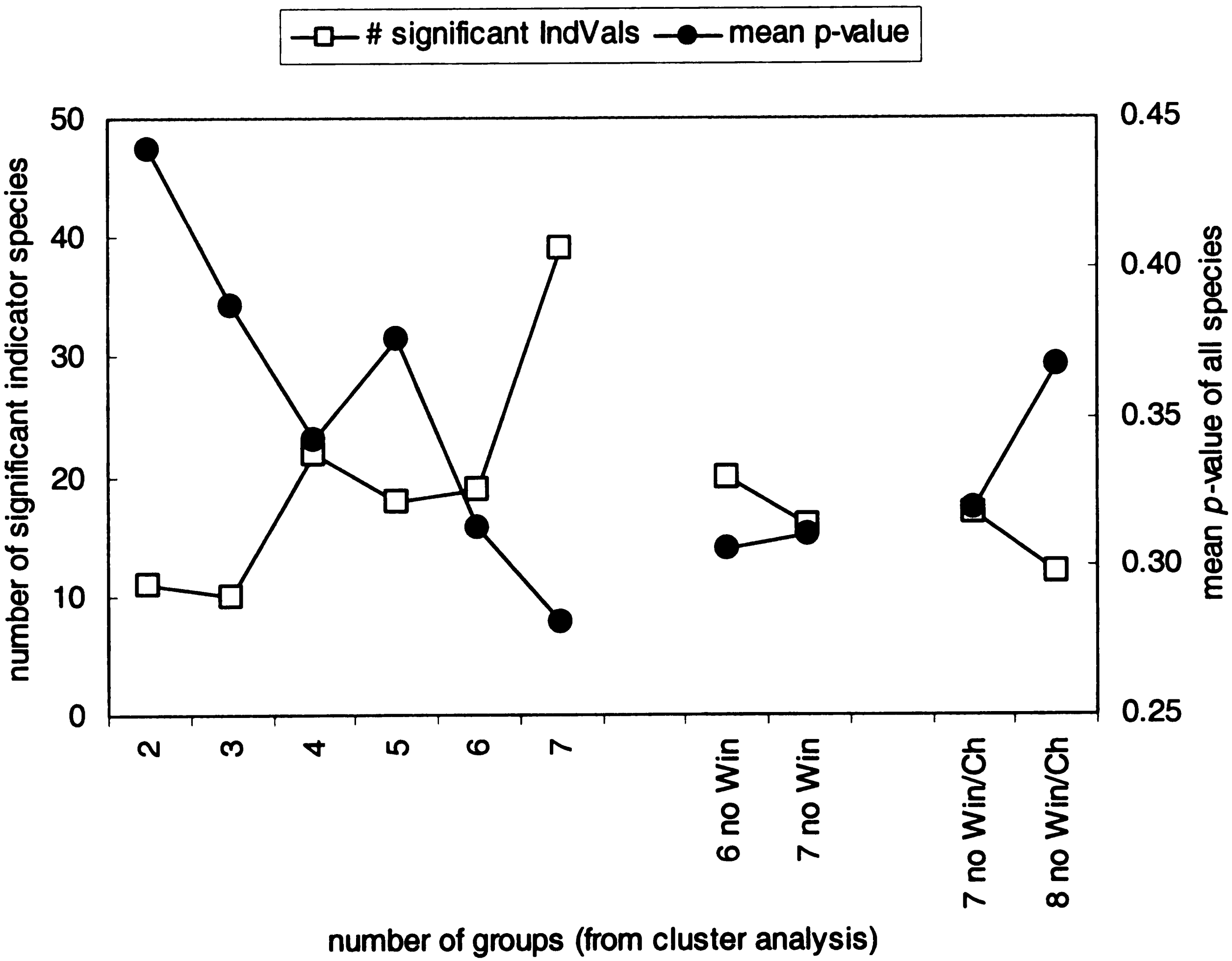
Wetland groups

Using indicator species analysis (Dufrene and Legendre 1997), I determined that the wetland plant communities in this study were characterized best by 7 groups (Figure 3.2). At 7 groups the number of significant indicator species is maximized, and the mean *p*-value of all species is minimized. MRPP confirmed that these groups were significantly different ($T = -10.9$, $A = 0.326$, $p = 0.0000$). The T statistic indicates group separation: more negative T values indicate stronger separation. The A statistic is a description of the effect size. If within-group heterogeneity is equal to that expected by chance, $A = 0$; if $A = 1$, all objects in a group are identical. In community ecology A values near 0.1 are common, and A values > 0.3 are relatively high (McCune and Grace 2002). All three MRPP summary statistics indicate strong differences between the 7 groups. The dendrogram from the cluster analysis was then pruned at 7 groups (Figure 3.3), and each group was named based on my gestalt of the local wetland flora. These group names (leatherleaf bogs, bogs, poor fen, fens, sedge meadow fens, wet swamps, and dry swamps) are used to facilitate discussion.

Indicator species

Several species in each wetland group had significant indicator values (α=0.01) and were considered representative of the plant communities in these wetland groups (Table 3.1). However, indicator species that occurred at only 1-2 study sites in a group are not adequately sampled in this study to be considered representative of that group. Nevertheless, these species are still useful in the broad sense and, for the botanically inclined, provide an indication of the overall plant community at the study sites.

Figure 3.2: The number of significant indicator species (α=0.01) and the mean *p*-value of all species from indicator species analysis of different numbers of groups from cluster analysis. Note that at 7 groups the number of significant indicator species is maximized, and the mean *p*-value of all species is minimized; this indicates that 7 groups characterize the plant communities best. Limitations on running indicator species analysis precluded a simple progression from 2 to 10 groups. However, by eliminating groups with only one site ("Win" = Winterberry Fen, the only site in group 7; "Ch" = Chainfern Bog, the only site in group 9) prior to performing indicator species analysis, the trend only worsens in terms of maximizing the number of significant indicator species or minimizing the mean *p*-value of all species. Thus, it is apparent that 8 or more groups do not explain the species distributions better than 7 groups.



significant IndVals
mean p-value
50
40
30
20
10
0
number of significant indicator species
0.45
0.40
0.35
0.30
0.25
mean p-value of all species
2
3
4
5
6
7
6 no Win
7 no Win
7 no Win/Ch
8 no Win/Ch
number of groups (from cluster analysis)

Figure 3.2

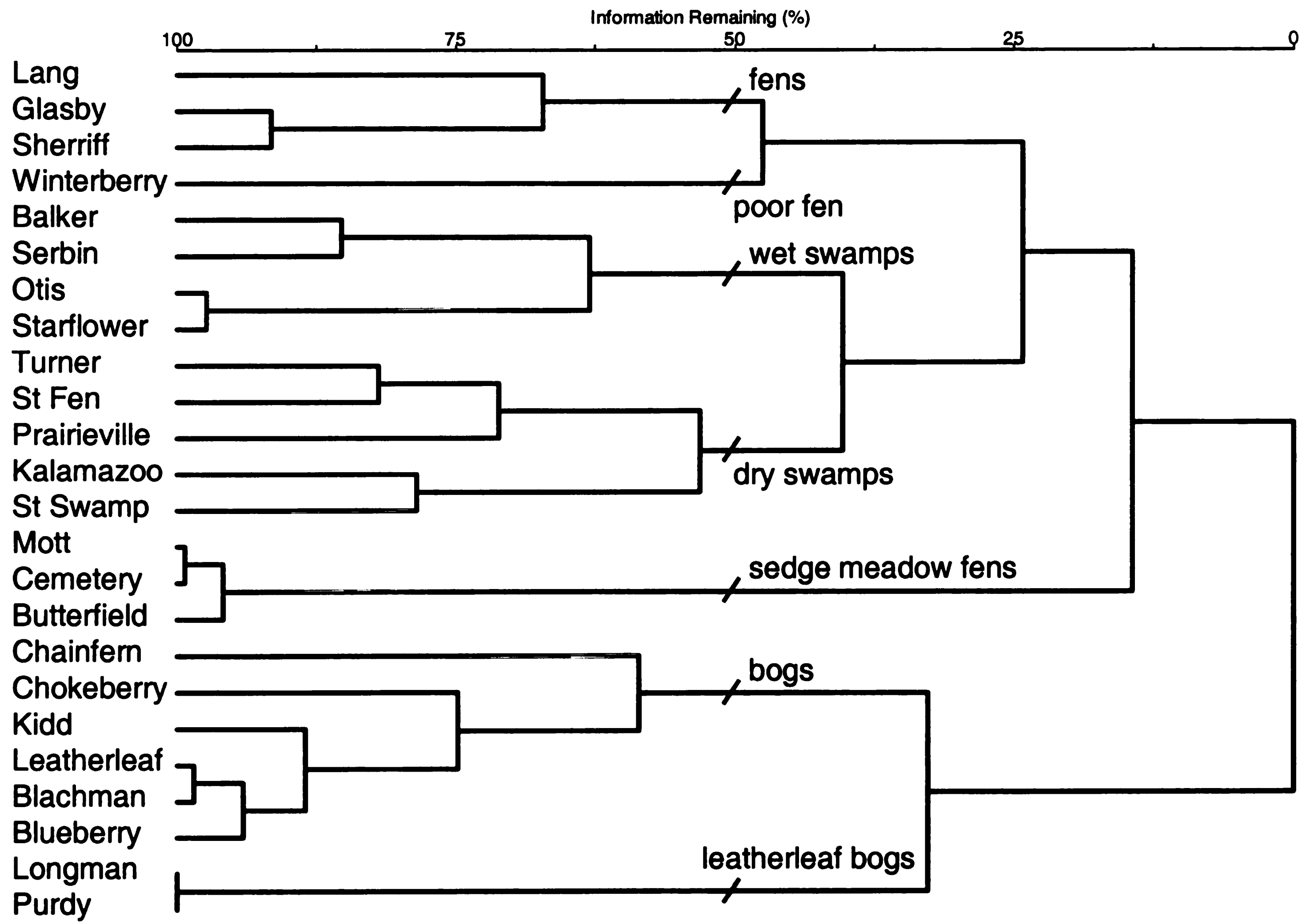


Figure 3.3: Cluster dendrogram that has been pruned based on indicator species analysis. The 7 groups of wetlands are labeled as in Table 3.1.

Table 3.1: Significant indicator species (α=0.01) for the 7 wetland groups in this study. Species with indicator species values (IndVals) approaching 100 are better indicators of wetland groups. Indicator species denoted by a * occur at only 1-2 sites in a group and are not adequately sampled in this study to be considered representative of that group. However, for persons familiar with wetland flora, these species generally characterize the plant communities in these wetland groups.

wetland group (# of sites)	species	IndVal (%)	*p*-value
leatherleaf bogs (2)	*Chamaedaphne calyculata**	75	0.002
	*Rhynchospora alba**	50	0.003
bogs (6)	*Aronia prunifolia*	94	0.001
	Woodwardia virginica	83	0.001
	Vaccinium corymbosum	66	0.003
poor fen (1)	*Scirpus cyperinus**	100	0.001
	*Calamagrostis canadensis**	85	0.005
	*Lysimachia thyrsiflora**	77	0.002
	*Triadenum fraseri**	75	0.001
	*Polygonum sagittatum**	69	0.006
fens (3)	*Epilobium leptophyllum*	92	0.001
	Pilea pumila	84	0.001
	*Bidens cernuus**	64	0.002
	*Rumex orbiculatus**	63	0.003
	*Carex comosa**	59	0.002
sedge meadow fens (3)	*Agalinis purpurea*	100	0.001
	Lythrum salicaria	93	0.001
	Mentha arvensis	88	0.001
	Carex stricta	82	0.001
	Aster puniceus	81	0.001
	Solidago canadensis	77	0.001
	Eupatorium maculatum	68	0.001
	*Pycnanthemum virginianum**	67	0.002
	*Potentilla fruticosa**	66	0.006
	Muhlenbergia mexicana	66	0.005
wet swamps (4)	*Osmunda cinnamomea*	97	0.001
	Maianthemum canadense	96	0.001
	Acer rubrum	85	0.001
	Ulmus americana	85	0.001
	Fraxinus nigra	75	0.001
	Viola cucullata	74	0.001
	Lindera benzoin	68	0.006
	Arisaema triphyllum	62	0.001
	Osmunda regalis	60	0.005
	Scutellaria lateriflora	60	0.001
dry swamps (5)	*Onoclea sensibilis*	86	0.001
	Senecio aureus	80	0.002
	Carex bromoides	70	0.001
	Solidago patula	63	0.001

Table 3.1

Ordinations

A 2-dimensional solution was considered best for all three ordinations. Increasing the dimensionality from one to two dimensions resulted in a sizable reduction in stress (10.5, 30.4, and 12.2 points) for the overall, alkaline, and acidic ordinations, respectively, while increasing the dimensionality from two to three dimensions only reduced the stress by 4.7, 2.1, and 2.0 points, respectively. A 2-dimensional solution was also preferable because 2 dimensions are much easier to visualize and interpret than 3 dimensions.

The final stress values for the overall, alkaline, and acidic ordinations were 15.043, 13.688, and 9.765, respectively, which are all satisfactory. A solution with a final stress < 10 is quite good; a stress between 10-20 is common for ecological community data and is satisfactory (with values approaching 20 becoming less satisfactory); a stress of 20+ is poor (McCune and Grace 2002). In all three ordinations, the probability of extracting stronger axes by chance was low ($p = 0.0196$). The final solutions for the overall, alkaline, and acidic ordinations required 39, 20, and 32 iterations, respectively. The total variance explained by the NMS axes from the 2-dimensional solutions is satisfactory for all three ordinations (Table 3.2). Note that unlike eigenvalue ordination methods such as PCA and CA, where the first axis explains the most variance and the second axis explains additional variance after taking into account the variance explained by the first axis, NMS axes are arbitrary (Legendre and Legendre 1998).

Ordination	Axis 1	Axis 2	Total
overall	47.3	16.3	63.7
alkaline	23.8	48.9	72.7
acidic	52.2	24.9	77.1

Table 3.2: Summary of the variance explained (%) by the 2-dimensional solution relative to the original *n*-dimensional space for all three ordinations.

Overall ordination

The 7 wetland groups identified via cluster analysis showed good separation in the overall ordination space (Figure 3.4). The correlations between each environmental variable and NMS Axes 1 and 2 indicate the strength of the relationship between the environmental variables and the arrangement of the study sites in ordination space (Table 3.3). The large number of environmental variables included in this study (n=40) precluded a single joint plot. Instead, I constructed three joint plots that included pH, Canopy, and either selected environmental variables (Figure 3.5), hydrochemical variables (Figure 3.6), or soil nutrient variables (Figure 3.7).

The distribution of study sites across Axis 1 was most strongly correlated with pH ($r = 0.95$; Table 3.2); more acidic sites were located on the left side of the ordination while more circumneutral sites were on the right. Other variables that were positively (e.g., f_{gw}) or negatively (e.g., Rel Elev) correlated with pH also showed strong relation to Axis 1. Canopy was the variable most strongly correlated with Axis 2 ($r = -0.84$; Table 3.2). More open sites (with less canopy)

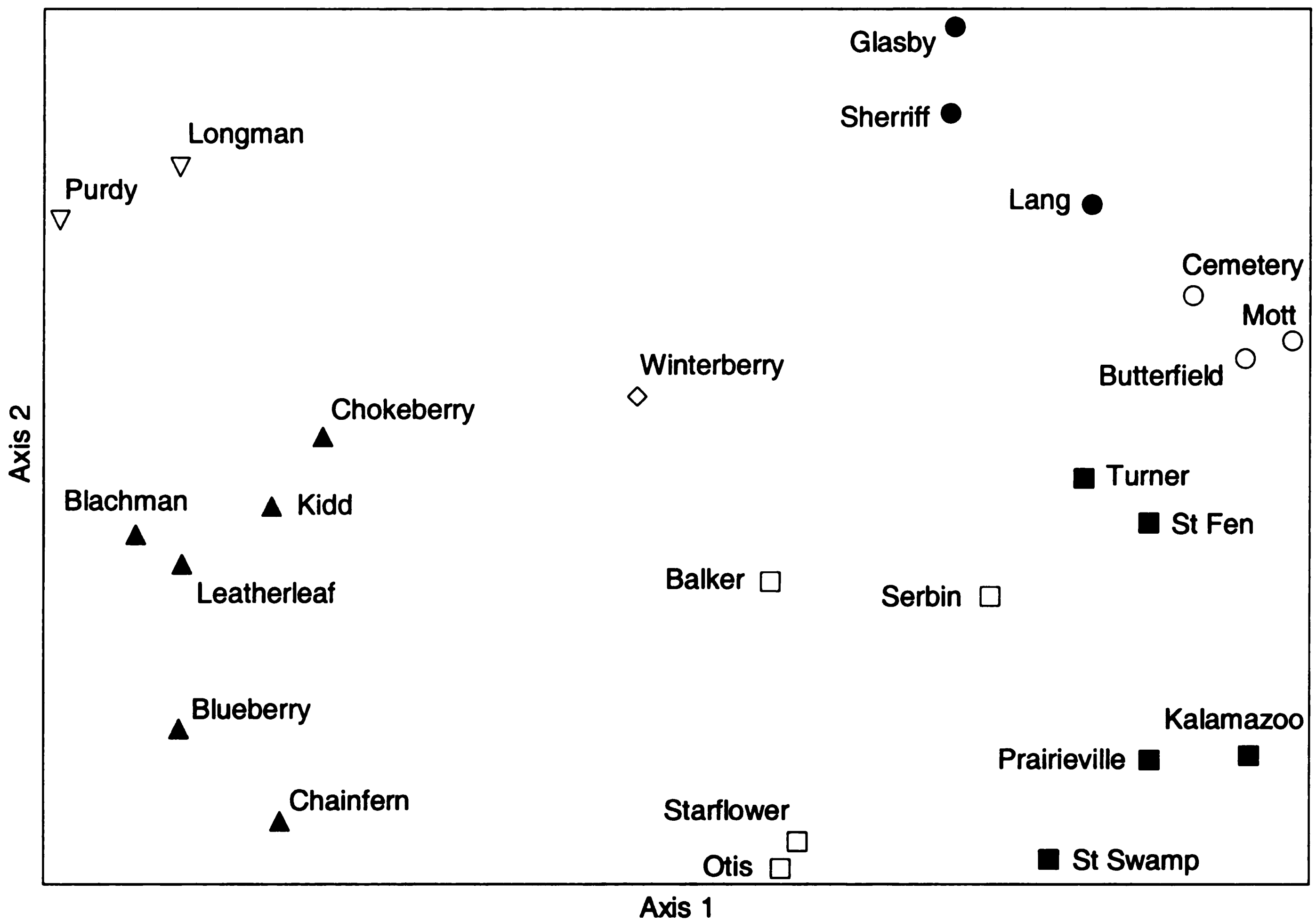


Figure 3.4: NMS ordination of 24 wetland plant communities in southwestern Michigan. Wetland groups are coded as leatherleaf bogs (▽), bogs (▲), poor fen (◇), fens (●), sedge meadow fens (○), wet swamps (□), and dry swamps (■).

category	abiotic variable	abbreviation	Axis 1	Axis 2
landscape	elevation	Elev	-0.26	0.37
	relative elevation	Rel Elev	-0.68	-0.10
light	canopy	Canopy	0.03	-0.84
water source	fraction groundwater	f_{gw}	0.91	-0.19
water level	maximum	H_2O Max	-0.55	0.20
	minimum	H_2O Min	-0.24	0.58
	range	H_2O Range	-0.25	-0.53
	mean	H_2O Mean	-0.47	0.45
	median	H_2O Med	-0.53	0.32
hydrochemical	pH	pH	0.95	0.00
	specific conductance	Cond	0.87	-0.04
	Ca^{2+}	Ca	0.91	0.01
	Mg^{2+}	Mg	0.90	-0.06
	Na^+	Na	0.56	0.16
	K^+	K	-0.33	0.31
	alkalinity	Alk	0.92	0.03
	SO_4^{2-}	SO_4	0.26	-0.21
	Cl^-	Cl	0.46	0.19
	Si	Si	0.49	-0.33
	NH_4-N	NH_4-N	-0.40	-0.13
	NO_3-N	NO_3-N	-0.05	0.06
	PO_4-P	PO_4-P	-0.29	-0.18
	TDP	TDP	-0.43	-0.17
soil	soil pH	soil pH	0.95	-0.06
	soil Ca	soil Ca	0.89	-0.17
	soil Mg	soil Mg	0.86	-0.27
	soil Na	soil Na	0.34	0.08
	soil K	soil K	0.38	-0.21
	soil S	soil S	0.61	0.10
	soil Fe	soil Fe	0.66	-0.15
	soil Al	soil Al	0.53	-0.20
	soil Mn	soil Mn	0.64	-0.17
	soil Zn	soil Zn	0.48	-0.42
	soil Cu	soil Cu	0.23	-0.03
	soil B	soil B	0.26	-0.04
	soil N	soil N	0.71	0.22
	soil P	soil P	0.74	-0.19
nutrient supply	NH_4-N supply	NH_4 Sup	0.53	0.13
	NO_3-N supply	NO_3 Sup	0.25	-0.29
	PO_4-P supply	PO_4 Sup	0.21	0.15

Table 3.3: Abiotic variables included in the overall ordination joint plots. Pearson correlation coefficients (*r*) between each variable and NMS Axes 1 and 2 are listed for the overall ordination following rotation.

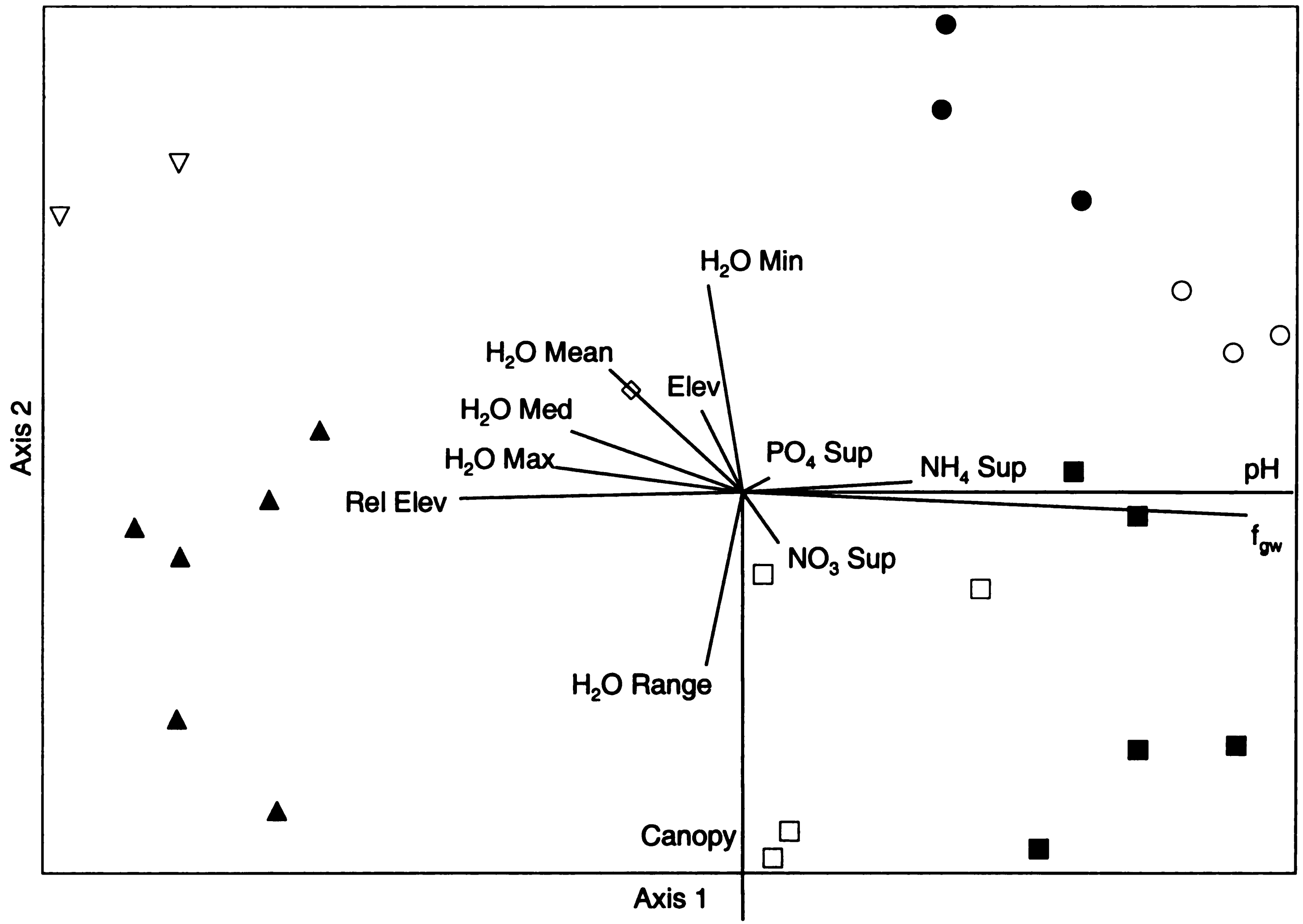


Figure 3.5: NMS ordination of 24 wetland plant communities with pH, Canopy, and selected environmental variables plotted over the ordination. Wetland group symbols are identical to Figure 3.4.

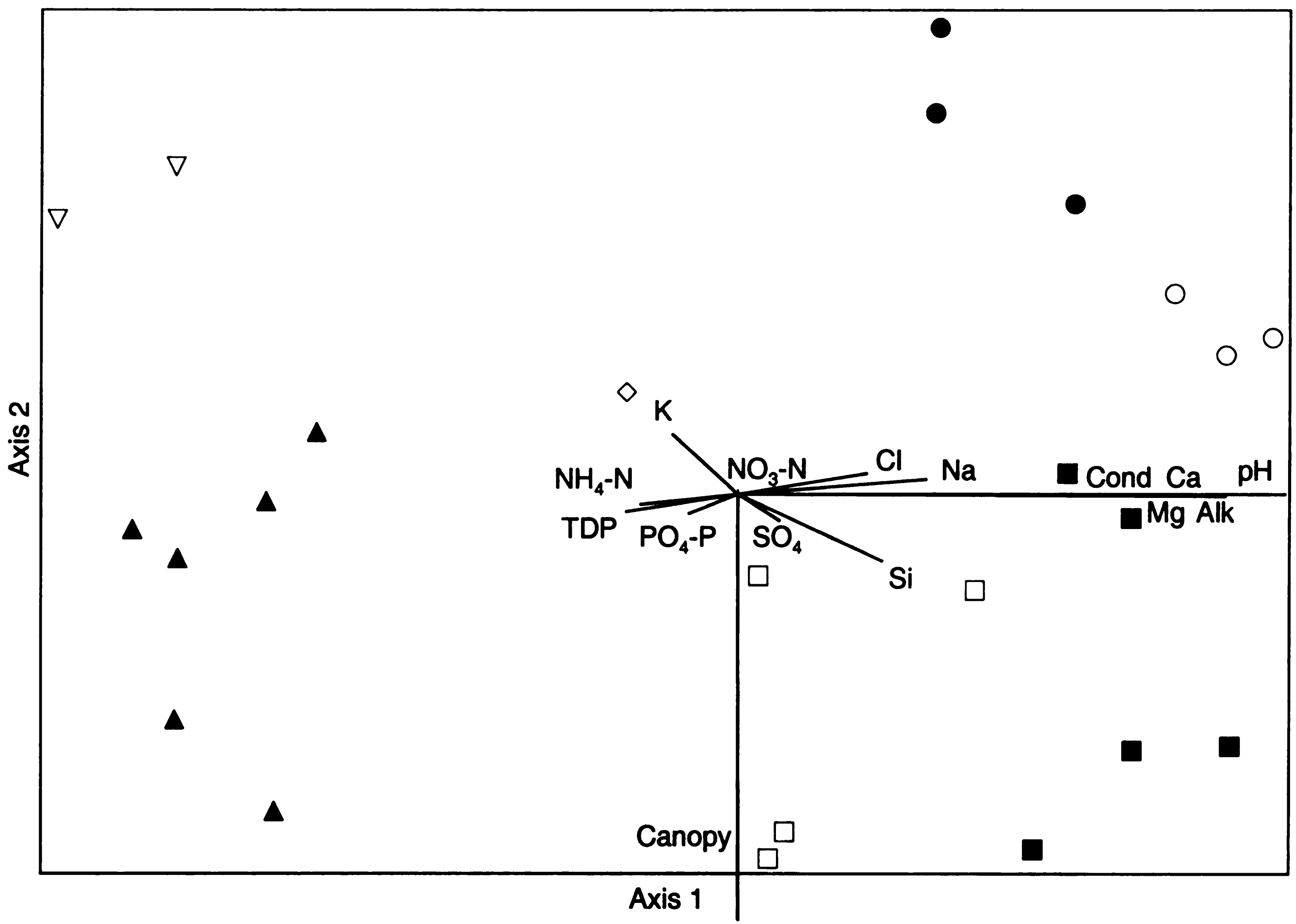


Figure 3.6: NMS ordination of 24 wetland plant communities with pH, Canopy, and hydrochemical variables plotted over the ordination. Wetland group symbols are identical to Figure 3.4.

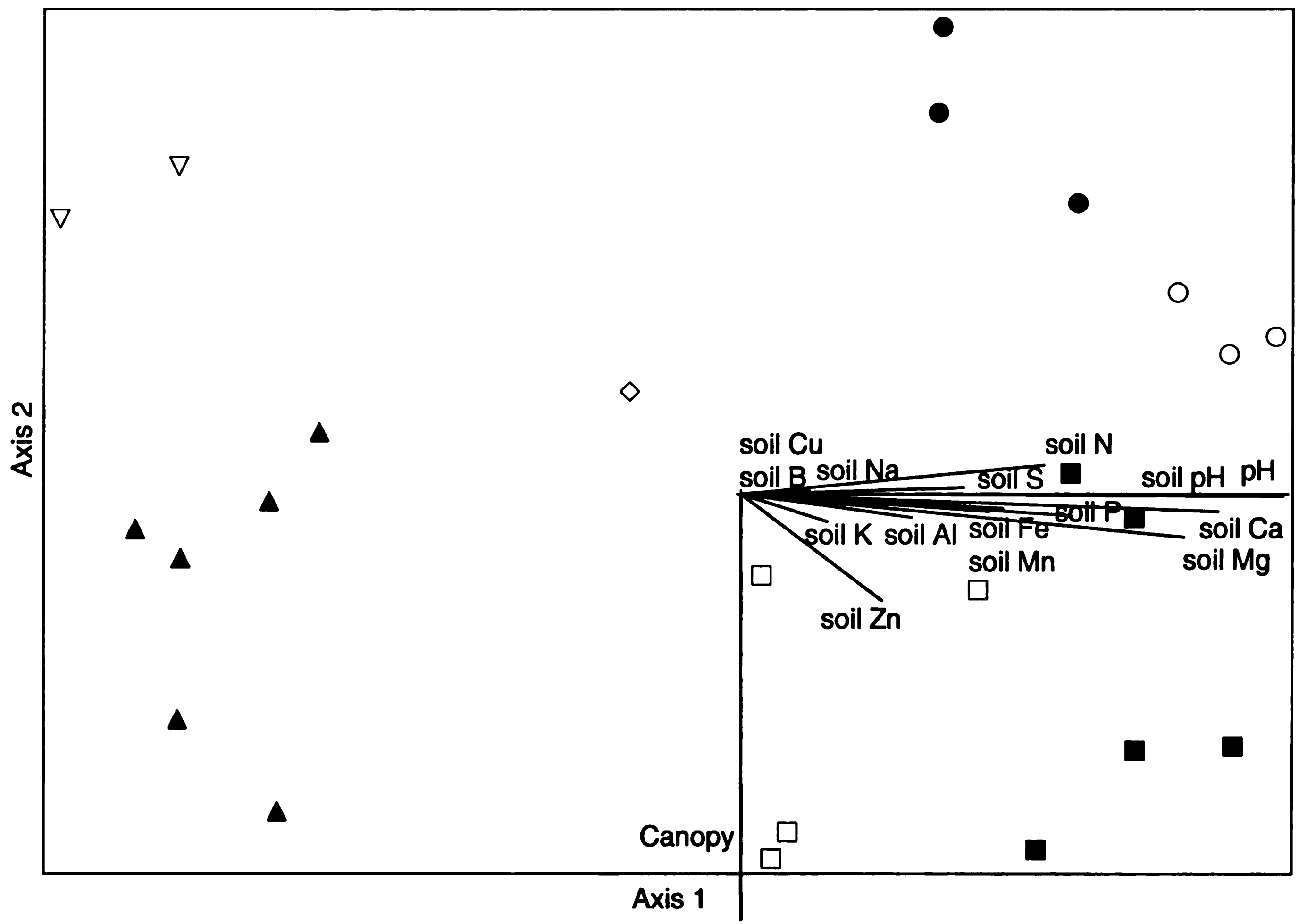


Figure 3.7: NMS ordination of 24 wetland plant communities with pH, Canopy, and soil nutrient variables plotted over the ordination. Wetland group symbols are identical to Figure 3.4.

generally were located toward the top of the ordination, while sites with more canopy cover are located toward the bottom. The strength of the relationship between the water level summary variables and the ordination was similar, although the direction varied somewhat, especially for H_2O Min and H_2O Range. Generally, sites with higher mean water levels are located towards the upper left area of the ordination, and sites with lower mean water levels are located in the lower right. Neither PO_4^{3-} nor NO_3^- supply showed strong correlation with either ordination axis, although NH_4^+ supply was positively correlated with Axis 1.

The pH and Canopy variables were retained in Figures 3.6 and 3.7 for comparison across joint plots and as a reminder that these variables showed the strongest relationship with Axis 1 and 2, respectively. In Figure 3.6, several hydrochemical variables (Alk, Ca, Mg, Cond) were strongly correlated with pH and, thus, Axis 1; this was expected due to the well-buffered Ca-Mg-HCO_3 waters that characterize local groundwater. The other hydrochemical variables were not as strongly correlated with the ordination. In Figure 3.7, nearly all of the soil nutrient variables were moderately to strongly correlated with Axis 1; soil pH, soil Ca, soil Mg, soil P, and soil N show the strongest correlation.

Alkaline ordination

The arrangement of the more alkaline wetland groups in the alkaline ordination space (Figure 3.8) remained generally unchanged relative to the overall ordination (Figure 3.4); the minor difference is the movement of the fens

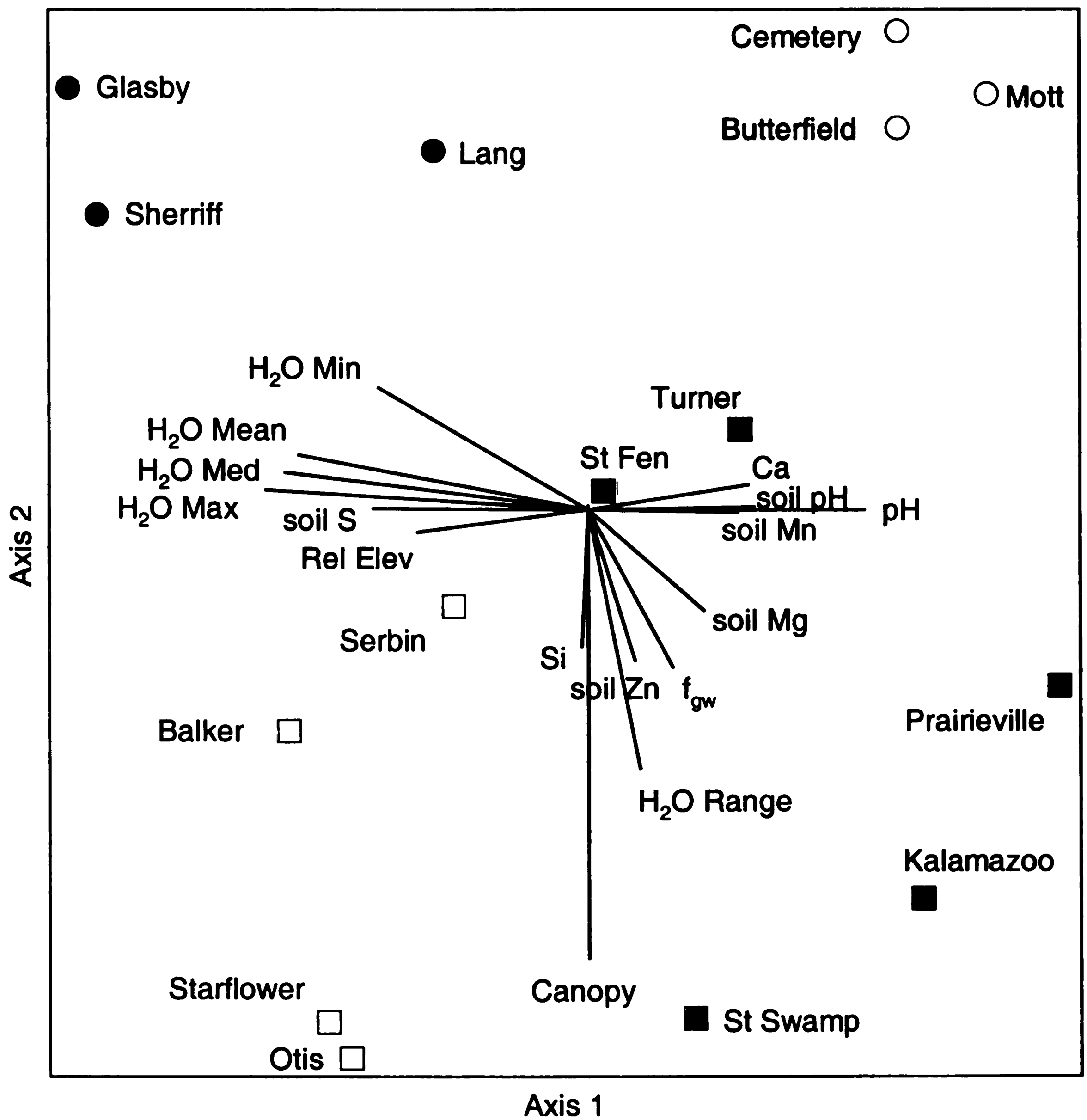


Figure 3.8: NMS ordination of 15 fen and swamp plant communities with selected environmental variables (those with an $r^2 > 0.25$ with either Axis 1 or Axis 2) plotted over the ordination. Wetland group symbols are identical to Figure 3.4.

to the upper left area of the alkaline ordination. The alkaline ordination did not require rotation because Canopy, the variable most strongly correlated with the ordination, was already well aligned with Axis 2 ($r = -0.94$). Hence, the upper portion of the alkaline ordination is associated with sites with little or no canopy cover, while sites with more canopy cover are located toward the bottom.

The water level variables were more strongly correlated with the alkaline ordination than they were with the overall ordination. For example, while the direction was similar, the correlation between H_2O Max and Axis 1 was greater in the alkaline ordination ($r = -0.79$) than in the overall ordination ($r = -0.55$; Table 3.2). pH was also correlated with Axis 1 in the alkaline ordination ($r = 0.73$), although the correlation was not as strong as it was in the overall ordination ($r = 0.95$; Table 3.2). Therefore, in the alkaline ordination, Axis 1 represents a pH-wetness gradient: wetter, less alkaline sites were generally located on the left side of the ordination, while drier, more alkaline sites were found on the right. Lastly, H_2O Range and, to a lesser degree, f_{gw} were more associated with the lower or lower right portion of the alkaline ordination.

Acidic ordination

The more acidic wetland groups showed strong separation in the acidic ordination space (Figure 3.9). Because H_2O Range was the variable most strongly related to the acidic ordination space, the ordination was rotated to maximize the correlation between H_2O Range and Axis 1 ($r = 0.87$). H_2O Max

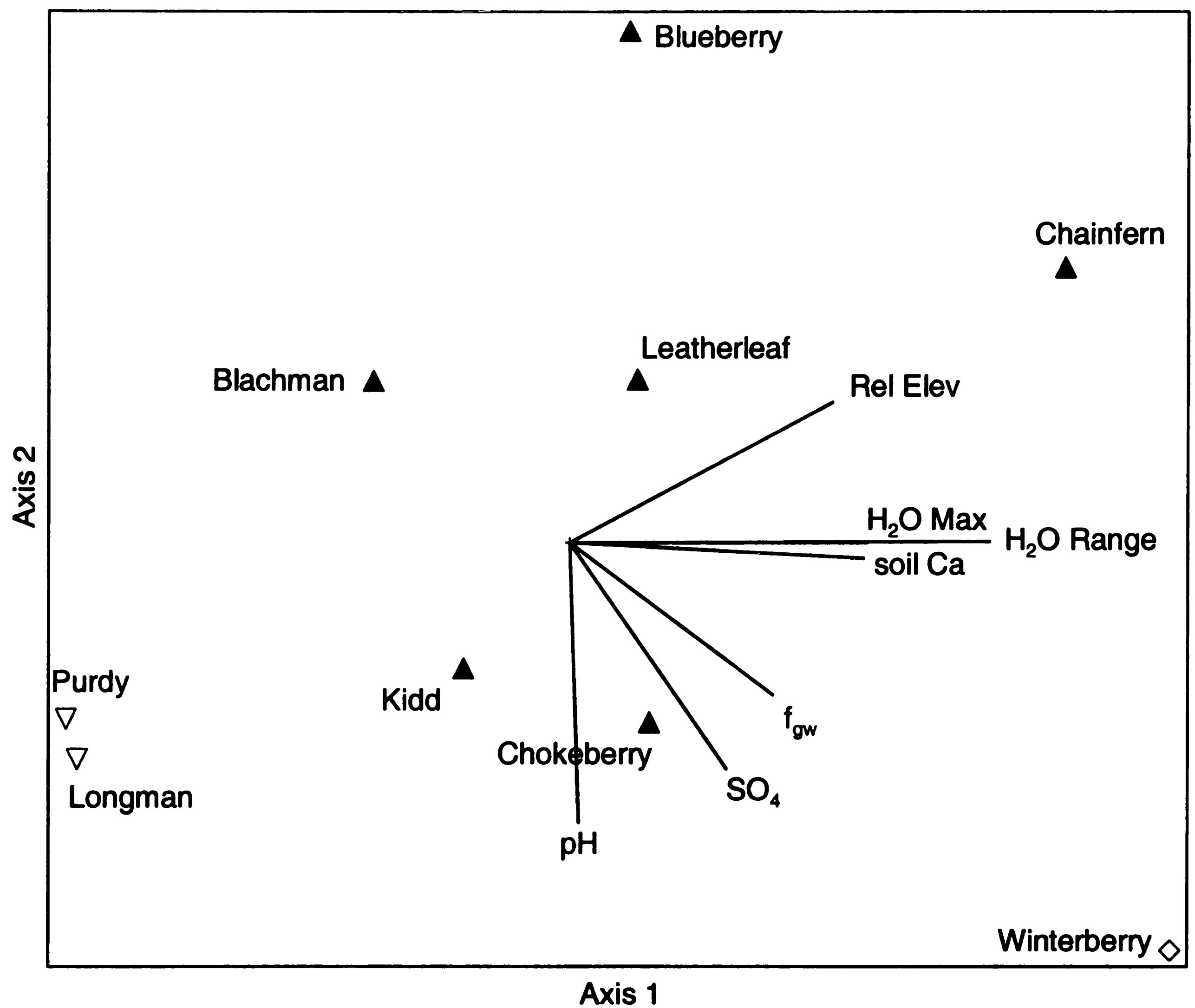


Figure 3.9: NMS ordination of 9 bog and poor fen plant communities with selected environmental variables (those with an $r^2 > 0.45$ with either Axis 1 or Axis 2) plotted over the ordination. Wetland group symbols are identical to Figure 3.4.

and soil Ca also showed a positive correlation with Axis 1. Relative elevation generally increased towards the upper right portion of the acidic ordination space.

Winterberry Fen, the only poor fen in this study, is hydrochemically very different from the bog sites included in the acidic ordination. As a result, the relationship between f_{gw}, SO_4, and, to a lesser extent, pH were all strongly affected by the position of Winterberry Fen in the acidic ordination. These variables should not be interpreted as representing patterns across the acidic ordination space.

DISCUSSION

Wetland groups and indicator species

The seven wetland plant community groups identified in this study (leatherleaf bogs, bogs, poor fen, fens, sedge meadow fens, wet swamps, and dry swamps) span much of the diversity of more terrestrial wetlands in southwest Michigan. Generally, these sites could be considered in terms of bogs, fens, and swamps, but that would belie the very different plant communities within these three broad wetland categories. I expected that the cluster analysis would distinguish many of these community types, but not all of them. For example, I usually lump all bogs into one category because the plant communities in bogs are so distinct from other local wetland plant communities. Yet, the community differences between leatherleaf bogs and bogs (that include taller shrubs) are quite pronounced and were distinguished in the cluster analysis. In this sense, cluster analysis is helpful because it provides a more objective means of distinguishing group membership. Finally, distinguishing groups and assigning names to these groups facilitates discussion, which was the primary purpose of grouping the study sites.

Because of the low sample size for each of the seven wetland plant community groups, I prefer to think of the indicator species in this study as generally descriptive as opposed to indicative of specific wetland types. The leatherleaf bogs were characterized by a carpet of *Chamaedaphne calyculata* (leatherleaf) with few other vascular plant species. In contrast, bogs contained leatherleaf as well as taller shrubs such as *Aronia prunifolia* (chokeberry) and *Vaccinium corymbosum* (highbush blueberry). The lone poor fen could not be satisfactorily characterized, but *Scirpus cyperinus* (wool-grass) and *Calamagrostis canadensis* (blue-joint) were prevalent throughout (*C. canadensis* very much so). Fens in this study represented three idiosyncratic sites, but all three shared the species *Epilobium leptophyllum* (narrow-leaved willow herb) and *Pilea pumila* (clearweed). In contrast, the sedge meadow fen plant communities were much more similar in composition, including community dominants such as *Carex stricta* (tussock sedge) and *Aster puniceus* (purple-stemmed aster), subdominants such as *Eupatorium maculatum* (Joe-pye-weed) and *Lythrum salicaria* (purple loosestrife), and *Agalinis purpurea* (purple agalinis). Wet swamps were those with wet hollows and *Sphagnum* hummocks scattered throughout. Common trees included *Acer rubrum* (red maple), *Ulmus americana* (American elm), and *Fraxinus nigra* (black ash), while *Lindera benzoin* (spicebush) was the characteristic shrub. The dominant understory species in wet swamps was *Osmunda cinnamomea* (cinnamon fern), although hummocks were also populated by *Maianthemum canadense* (Canada mayflower) and *Viola cucullata* (marsh violet). Dry swamps comprised five relatively heterogeneous sites and had understory communities that were commonly dominated by more shade-tolerant species, including *Onoclea sensibilis* (sensitive fern), and *Carex bromoides* (brome tussock sedge), and *Senecio aureus* (golden ragwort).

Abiotic drivers of plant community composition across bogs, fens, and swamps

In the overall ordination solution NMS Axis 1 explains three times as much variability (47%) as NMS Axis 2 (16%) relative to the original *n*-dimensional space; the dominant vegetation pattern in the overall ordination is thus reflected in NMS Axis 1. pH is highly correlated with NMS Axis 1 ($r = 0.95$; Table 3.3), and the sorting of plant communities along NMS Axis 1 separates the bog sites from the non-bog sites (Figure 3.5). Thus, the variable that most strongly distinguishes bog plant communities from non-bog plant communities is acidity. I will argue that acidity is the most plausible environmental constraint excluding plant species from bogs and, therefore, that acidity is the primary determinant of the differences between bog and non-bog plant communities.

In contrast to pH, two measures of nutrient availability, nutrient accumulation on ion exchange resin (NH_4 Sup, NO_3 Sup, or PO_4 Sup; Figure 3.5) and dissolved inorganic nutrients (NH_4-N, NO_3-N, or PO_4-P; Figure 3.6), were not highly correlated with the overall ordination. NH_4^+ supply, the measure of nutrient availability most strongly related to the overall ordination, is correlated with NMS Axis 1 ($r = 0.53$), but the relationship is much weaker than between pH and NMS Axis 1 ($r = 0.95$). Because the relationship between pH and NMS Axis 1 is much stronger, I conclude that the bog and non-bog environments are more different in terms of acidity than they are in terms of nutrient availability.

Bogs are the textbook example of nutrient poor habitats (Mitsch and Gosselink 2000, Cronk and Fennessy 2001). Differences in bog and fen plant communities are often ascribed to lower nutrient availability in bogs (Zoltai and Vitt 1995). However, while pH and alkalinity generally increase across the bog to fen gradient (Vitt et al. 1995, Zoltai and Vitt 1995), nutrient availability often does not increase, and sometimes decreases (Waughman 1980, Bridgham et al. 1996). Bogs have often been inferred to be nutrient poor habitats, perhaps because of the nutrient-acquiring or nutrient-conserving adaptations that many bog plant species possess, including carnivory (pitcher plants, sundew) and evergreen leaves (ericaceous shrubs). Based on these examples from the literature, I expected one of the measures of nutrient availability to be most highly correlated with the separation of bog and non-bog plant communities in the overall ordination. Instead, pH was most strongly associated with differences in plant communities along the bog to fen gradient. I then considered the possibility that acidity, not nutrient availability, might be excluding many plant species from bogs and thereby generating the very different plant communities in bog and non-bog wetlands.

A review of the plant physiology literature demonstrates that acidic conditions (pH < 4.5) can have adverse effects on plant root function and survival, although these adverse effects are tied to nitrogen (N) uptake by plant roots. Nitrogen is the primary nutrient thought to limit plant growth in bogs (Wassen et al. 1995). NH_4^+ is the dominant form of N in waterlogged, reduced soils (Armstrong 1982). In two midcontinental bogs NO_3^- in precipitation was rapidly taken up by *Sphagnum* moss and did not reach the waterlogged peat below (Urban and Eisenreich 1988). Thus, vascular plants that are rooted in bog peat must be able to take up NH_4^+ in order to meet their nitrogen demands. However, as the roots take up NH_4^+, the root cell membranes must excrete H^+ in order to maintain both internal cytoplasmic pH and the electrochemical potential gradient necessary for ion uptake (Raven and Smith 1976, Brix et al. 2002). In acidic soil solutions, like those found in bogs, the high H^+ activity in the soil medium inhibits the efflux of H^+ ions from root cells (Schubert et al. 1990). This has at least two detrimental effects on the plant. First, root growth may be inhibited by failure to properly regulate cytoplasmic pH (Yan et al. 1992). Second, NH_4^+ uptake is greatly reduced at low pH, resulting in N deficiency in the plant (Tolley-Henry and Raper 1986, Brix et al. 2002). Thus, plant species may be excluded from acidic wetland environments for physiological reasons related to acidity and its effects on root cell maintenance and/or N uptake, not reasons relating directly to nutrient concentrations in the rooting zone.

In community and ecosystem ecology, it is common to measure nutrient availability for plants in some indirect way (e.g., mineralization rates, nutrient accumulation on ion exchange resin, extracted soil nutrients, soil nutrient pools, or dissolved inorganic or organic nutrients). If these measures of apparent nutrient availability differ between two groups of plant communities, it is then inferred that these differences in nutrient availability may be the reason for the differences in the plant communities. But if a variable other than nutrient availability (e.g., acidity) is limiting biological nutrient uptake, then measures of nutrient availability become much less informative. There could be any level of NH_4^+ in the soil solution, but if pH < 4.5, then the plant may not be able to take up the NH_4^+. A measure of nutrient availability that does not directly measure N uptake by the plant may not accurately describe nutrient availability from the perspective of the plant. Furthermore, plant species likely differ in their tolerance of acidity. If the goal is to validate our measures of nutrient availability with respect to the plant community, then more physiological studies on wetland plants will be necessary in order to better understand the relationship between nutrients that are available vs. nutrients that may be taken up by various wetland plant species under different levels of acidity.

After pH, Canopy was the next variable most strongly associated with differences in wetland plant communities in the overall ordination (Figure 3.5). Canopy was highly correlated with NMS Axis 2 ($r = -0.84$; Table 3.3); thus, canopy values were higher in the lower portion of the overall ordination space. Most of the Canopy pattern was driven by differences along the swamp to fen gradient. If Canopy is a good estimate of the shade experienced by understory species, then these results suggest that light reduction by tall woody species is an important environmental variable associated with the differences in these plant communities.

Relative elevation and f_{gw}, both correlated with pH, also showed strong relationships with NMS Axis 1. The correlations between these variables were discussed in Ch. 2 (Figure 2.17); wetlands with low pH and low f_{gw} also tended to be located relatively high in their local watershed. These relationships will be developed more in Ch. 4, where I model the relations between landscape-level variables, environmental variables, and the wetland plant communities.

Differences in water levels are often used to define or distinguish wetland plant community studies (Murkin et al. 2000). However, among this set of wetlands water level measurements showed weaker correlation with the overall ordination than pH and Canopy (Figure 3.5). On one hand this might be expected because I restricted site selection to the more terrestrial end of the wetland gradient in southwest Michigan. By excluding more submersed aquatic plant communities from this study I effectively controlled for large differences in water levels. Still, water level differences remained between the study sites, and I expected water levels to be more strongly related to the overall ordination.

However, the interaction of environmental variables with the plant community can be complex and affect different types of plants over different time scales.

There could also be threshold responses that strongly altered the structure of these communities in the past and continue to affect them currently. For example, the drought in the early 1960s (Figure 2.12) could have allowed what were sedge meadow fen communities to be invaded by shrub species. After the shrubs were strongly established by the end of the five-year drought, water levels could have increased again sufficiently to prohibit continued colonization by shrubs, but not enough to kill the recent shrub colonizers. If the shrubs could persist, they could change the light levels below their canopies sufficiently to favor shade-tolerant understory species, which could then replace what was a sedge meadow fen community. Thus, water level conditions prior to the current study could have had very strong lag effects that greatly determined the current plant communities. Analysis of current environmental conditions only provides a snapshot of the conditions that may have generated the extant vegetation. Therefore, water levels likely remain important in determining these wetland plant communities over longer time scales, but do not appear to be as important as pH and Canopy as factors explaining the current differences in plant communities.

As pointed out earlier, measures of nutrient supply, which reflect nutrient accumulation on ion exchange resin, were not strongly related to the overall ordination (Figure 3.5), although NH_4^+ supply did tend to increase with increasing pH along NMS Axis 1 (i.e., along the bog to non-bog gradient). PO_4^{3-} supply showed virtually no relationship with the overall ordination. As these were my best estimates of nutrient availability in these wetlands, they suggest that differences in nutrient availability were not as strongly related to differences in plant communities as variables such as acidity, shade, and water levels. Other measures of nutrient availability, including dissolved inorganic nutrients (Figure 3.6) and soil N and P (Figure 3.7), showed either weak relationships with the overall ordination (dissolved nutrients) or relatively strong relation to NMS Axis 1 (soil N and P). However, these nutrient availability measures reflect nutrient pools more than nutrient supply and, thus, may not reflect the nutrients supplied to plants as well as the nutrients that accumulated on ion exchange resin (Bedford et al. 1999). Furthermore, as noted previously, if there are physiological limitations (e.g., acidity) that restrict plant nutrient uptake, then these estimates of nutrient availability may not actually represent what is available to the plants.

The hydrochemical variables (Figure 3.6) and soil nutrient variables (Figure 3.7) were closely associated with the bog to non-bog gradient along NMS Axis 1. The shift in hydrochemistry across these sites was largely a function of the change in source waters, from dilute precipitation to alkaline groundwaters. Similarly, all the soil nutrient variables increased along the gradient from bog peat to fen and swamp peat.

Abiotic drivers of plant community composition in circumneutral wetlands

Of the 72.7% of the variance explained by the two-dimensional solution in the alkaline ordination, 48.9% was explained by NMS Axis 2, while 23.8% was explained by NMS Axis 1; thus, the dominant vegetation pattern in the alkaline ordination was represented by NMS Axis 2. Canopy was most strongly correlated with NMS Axis 2 (*r* = -0.94; Figure 3.8), which suggests that the shade gradient from swamps to fens was the strongest pattern across the circumneutral wetlands. Therefore, differences in light availability may be the key environmental variable in distinguishing plant communities in circumneutral wetlands in southwest Michigan.

After Canopy, water levels and pH were the environmental variables most strongly associated with differences in circumneutral wetland plant communities. Water level variables (e.g., H_2O Mean) and pH were both correlated with NMS Axis 1. Sites changed from wetter, less alkaline wetlands to drier, more alkaline sites moving from left to right across the alkaline ordination. The wetness pattern was apparent in the shift from wet swamps (left) to dry swamps (right). The sedge meadow fens and dry swamps also tended to be more alkaline than the fens and wet swamps. Sedge meadow fens are often slightly alkaline (Amon et al. 2002), and some of the species in these wetlands, such as *Lobelia kalmii* (Kalm's lobelia), are commonly called calciphiles (Voss 1996), perhaps more because of their tendency to occur in relatively alkaline wetlands than an affinity for calcium per se.

Lastly, H_2O Range, which generally reflects the seasonal decline in water levels throughout the growing season, was greater in the swamps and somewhat more so in the dry swamps. Mean water levels may not be the only aspect of water level variability that is important in determining wetland plant communities. If water levels decline sufficiently during the growing season, tree species may be able to take advantage of the relatively drier late-summer conditions and exhibit greater growth during that period. This is a good example where specifying what aspect of hydrology may be linked to differences in plant communities is helpful in hypothesizing potential hydrologic forcings acting on the plants. By quantifying the concept of interest (in this case, the decline in water levels during the growing season), it is possible to test this relationship in other studies. In contrast, general categorization of sites using terminology such as short, medium, and long hydroperiods (periods of flooding) complicates attempts to evaluate hypotheses from one study in subsequent studies. Attempts to specify and quantify which hydrologic variables may be most important to plants will greatly aid hypothesis testing in wetland plant ecology.

Abiotic drivers of plant community composition in acidic wetlands

The acidic ordination included only nine study sites; consequently, interpretations from this ordination are somewhat limited. Of the 77.1% of the variance explained in the two-dimensional solution, most was represented in NMS Axis 1 (52.2%). The environmental variable most strongly correlated with NMS Axis 1 was H_2O Range ($r = 0.87$; Figure 3.9). Hence, the leatherleaf bogs tended to dry down less during the summer than the other bog sites. *Chamaedaphne calyculata* (leatherleaf) is often the pioneering shrub species that colonizes wetter bog habitats (Kratz and Dewitt 1986). Because taller shrubs such as *Vaccinium corymbosum* (highbush blueberry) and *Aronia prunifolia* (chokeberry) are taller and appear to shade out *C. calyculata* (personal observation), perhaps only in wetter bogs can *C. calyculata* dominate the shrub community. Because bog ecosystems do not extend much farther south than southern Michigan (Curtis 1959), the warm, dry summers in this area may promote conditions where bog water tables drop more than in more northern peatlands. This could explain why two of the bogs in this study are leatherleaf bogs and the other six bog sites are dominated by taller bog shrubs.

Winterberry Poor Fen is the only poor fen, or slightly acidic peatland, in this study; consequently, it is not possible to generalize about poor fens and their relation to the other types of wetlands in this study. Because acidity appears to act strongly in sorting wetland plant communities in southern Michigan, the unique plant community in Winterberry Poor Fen is likely a function of this site's intermediate levels of acidity (pH 5.5). As discussed in Chapter 2, poor fens appear to be relatively short-lived ecosystems, lasting perhaps only 50-350 years (Kuhry et al. 1993) until their alkalinity is exhausted and they shift over to become bog ecosystems (Swinehart and Parker 2000). Still, these transitional ecosystems are intriguing. It would be interesting to evaluate the distribution of extant poor fens and try to determine whether landscape-level controls may be good predictors of where such systems occur.

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CHAPTER 4

A PARTIAL LEAST SQUARES COMPOSITE VARIABLE MODEL FOR PREDICTING NORTH TEMPERATE WETLAND PLANT COMMUNITIES FROM ENVIRONMENTAL VARIABLES

INTRODUCTION

Ecologists are often interested in predicting the species that occur in different habitats. In wetlands, species occurrence is frequently limited by abiotic conditions (Mitsch and Gosselink 2000). These environmental variables are often a function of the landscape-scale hydrologic and geomorphological properties of wetland basins. Hence, a more comprehensive model of predicting species occurrence could include not only the environmental variables thought to act on the species of interest, but also the landscape-level variables that predicate these environmental variables.

Wetlands exemplify harsh habitats for plant growth. Water level fluctuation results in variable flooding and soil saturation conditions. This in turn creates conditions of low oxygen in the rooting zone that can reduce or halt root function (Pezeshki 1994) and, thus, limit the occurrence of plant species. Nutrient availability, which varies across different types of wetlands (Waughman 1980, Walbridge 1991, Vitt et al. 1995, Zoltai and Vitt 1995, Bridgham et al. 1996, Bedford et al. 1999), could also limit the occurrence of plant species. Acidity varies strongly across wetlands, the most salient example of which is the bog to fen gradient (Heinselman 1970, Vitt and Chee 1990). Acidic root environments may impede nutrient uptake (Tolley-Henry and Raper 1986, Brix et al. 2002) and acidify the cytoplasm of root cells (Yan et al. 1992), with detrimental effects on the plant. Finally, light reduction by tree and shrub canopies could alter the composition of understory species by restricting the occurrence of light-demanding species. Therefore, all these environmental variables could have profound effects in reducing the plant species pools in different types of wetlands.

Landscape-level factors likely give rise to environmental variables such as acidity and nutrient supply. Brinson's hydrogeomorphic wetland classification system (Brinson 1993) is founded on consideration of landscape-level variables such as hydrogeomorphic setting, water source, and hydrodynamics. One outstanding question concerns how well these landscape-level variables predict the proximate environmental variables thought to influence wetland plant species. If a strong correlation exists among landscape-level variables, other environmental variables, and plant community composition, then it may be possible to extract greater predictive power from landscape-level variables for predicting environmental variables and plant communities than is currently employed in wetland studies. Advantages of linking wetland plant communities to landscape variables include a better understanding of how certain kinds of wetlands can be created or restored in particular landscape settings; and the potential of using remote sensing and other landscape-scale spatial data to predict the occurrence and spatial distribution of wetland types, thereby facilitating wetland protection efforts (e.g., legal protection, conservation planning).

In this chapter I develop a partial least squares composite variable model, which is similar to a structural equation model, with the goal of predicting wetland plant communities from environmental variables. In addition, I seek to establish relationships between these proximate environmental variables and larger scale ecosystem- and landscape-level variables. The end product is a multivariate hypothesis that simultaneously considers the linear relationships between the landscape-level variables that give rise to the proximate environmental variables which, in turn, help explain the variance in plant communities in southwest Michigan. Like any hypothesis, this model could be tested in subsequent studies.

METHODS

Structural equation modeling

Structural equation modeling (SEM) represents a statistical model of the interrelationships among complex sets of variables. In the broadest sense, these variables can represent any idea or theoretical variable of interest. In a strict sense these theoretical variables are considered unobservable; thus, it is necessary to measure other variables that relate to these theoretical variables.

SEM is an emerging technique in ecology and evolution (Pugesek et al. 2003). SEM has been applied for decades in other fields, including economics, psychology, marketing, political science, and sociology (Falk and Miller 1992). Path analysis (Wright 1921), which is more familiar to ecologists and evolutionary biologists than SEM, can be considered a special case of SEM (McCune and Grace 2002). However, as with many new techniques, the first obstacle to learning about SEM is terminology. An overview of SEM terminology follows.

A structural equation model consists of two types of variables: latent variables (which I will refer to as composites; see below also), which are denoted by circles, and measurement variables (indicators), which are denoted by rectangles (Figure 4.1). *Composites* represent theoretical variables, including those that cannot be easily measured (e.g., attitude, intent, etc.). Each composite is associated with one or more *indicators*, which are measured variables that range from answers on opinion questionnaires to light measurements.

Composites are related to one another graphically by using unidirectional arrows (i.e., "arrows") or bidirectional arrows (i.e., "spans"). *Arrows* imply a causal or asymmetrical relationship between two composites, whereas *spans* represent a correlation between two composites (Figure 4.1). The entire set of composites and their interrelationships is known as the *structural model*. Composites with arrows directed into them from one or more composites are termed *endogenous*, while composites with no arrows directed into them from other composites are termed *exogenous* (Figure 4.1). The variance explained, or R^2, in endogenous variables is one of the parameters estimated by SEM.

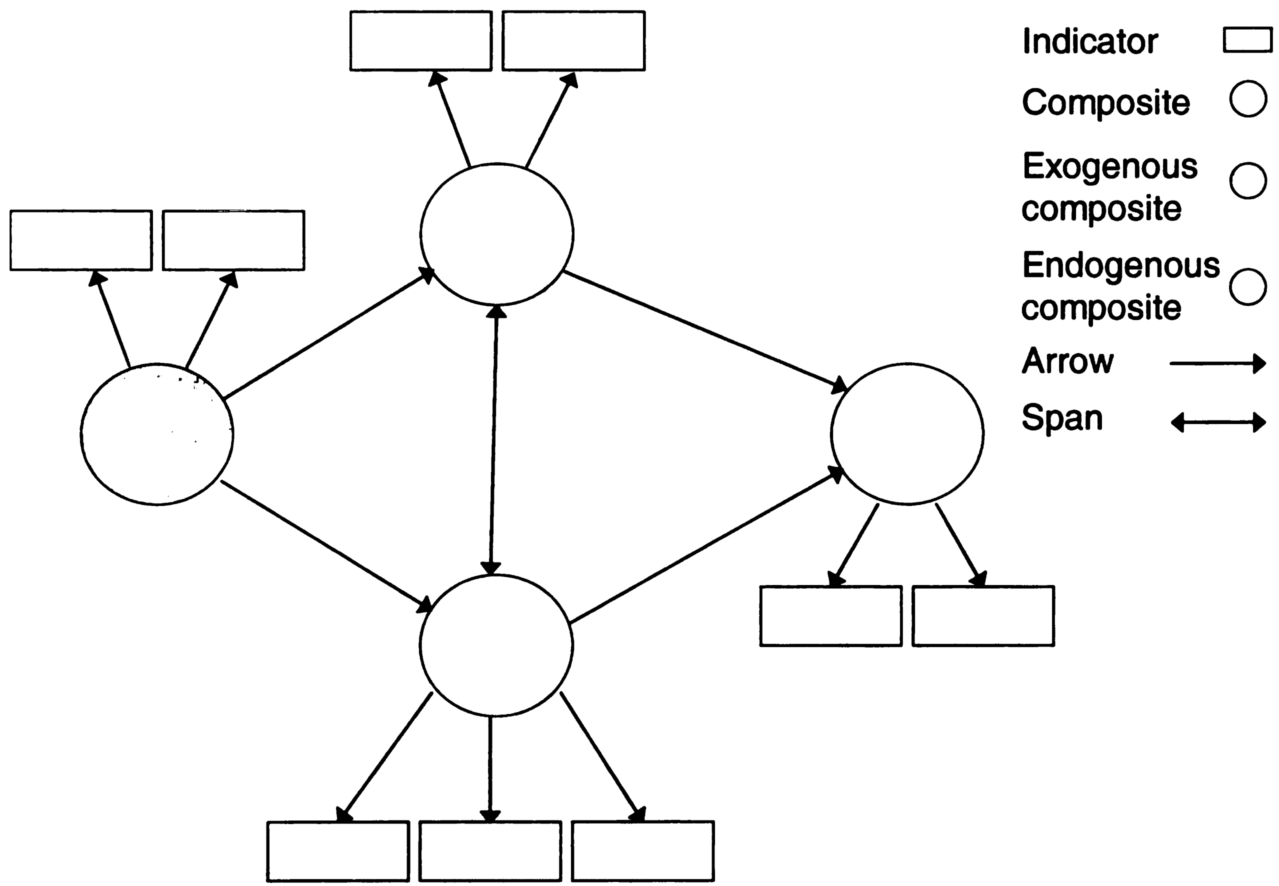

Figure 4.1: Symbols used in structural equation modeling. Circles represent theoretical variables (composites); rectangles represent measurement variables (indicators); unidirectional arrows (arrows) imply a causal or asymmetrical relationship between composites; bidirectional arrows (spans) represent a correlation between two composites. Endogenous composites have arrows directed into them, while exogenous composites have no arrows directed into them.

This provides a useful metric in determining how well the model predicts composites of interest.

Indicators connect the theoretical composites to real-world measurements. Arrows are used to denote relationships between a composite and its indicators. The arrows can be directed either from the composite to its indicators or from the indicators to their associated composite. Suffice to say that in most cases the arrows direct outward from the composite to its indicators. The set of composites and their relationships with their respective indicators is known as the *measurement model*. Each composite is associated with one or more indicators. When multiple indicators are used to estimate a composite, it is possible to estimate the measurement error associated with these indicators with respect to their composite (i.e., how well the composite is represented by the indicators). The advantages of estimating measurement error will be discussed later, but this is an important philosophical difference between SEM and multiple regression, which assumes that predictors (independent variables) are measured without error (McCune and Grace 2002).

The *structural equation model* represents the complete set of relationships between all variables and includes both the structural model and the measurement model. Path coefficients ranging from -1 to +1 are estimated along the arrows and spans in the structural equation model. Path coefficients near 0 imply very weak relationships between variables, while path coefficients approaching -1 and +1 imply very strong relationships (negative and positive, respectively). Weak paths are often removed from models because 1) they explain very little in terms of the total variance explained in endogenous composites, and 2) their removal improves the estimation of other model parameters (Falk and Miller 1992). The structural equation model may also be evaluated and refined in other ways, depending on the parameter estimation technique used.

The maximum likelihood and partial least squares methods

There are generally two categories of techniques used in estimating parameters in this kind of modeling. *Maximum likelihood* (ML) methods (Joreskog 1973), which simultaneously estimate the entire covariance matrix in the structural equation model, are by far more well known and more frequently employed. Software programs such as LISREL (Joreskog and Sorbom 1996) employ ML estimation. Because the entire covariance matrix is simultaneously estimated, ML methods require large sample sizes (at least 100-200 samples) in order to properly estimate path coefficients (McCune and Grace 2002). Composites are referred to as *latent variables* under ML techniques.

The *partial least squares* (PLS) approach (Wold 1980) was developed in large part by a demand in the social sciences to model systems under less restrictive distributional, measurement, and theoretical assumptions than those required by ML estimation techniques (Falk and Miller 1992). The PLS approach estimates parameters in the measurement model in blocks, where each composite and its indicators comprise one block. PLS estimates the path coefficients between composites and their indicators in the measurement model, then estimates the path coefficients between composites in the structural model, iterating back and forth between the measurement model and the structural model until a stability criterion has been reached (Chin 1998). In PLS a composite is estimated by its indicators much like a first principal component (Falk and Miller 1992). As functions of observed variables, composites are observable and, thus, not strictly latent (McDonald 1996), which is one of the distinctions between ML and PLS methods. Because PLS estimates parameters under more relaxed assumptions, it is more appropriate to interpret results from PLS estimation in the context of prediction rather than causation (Falk and Miller 1992). For an excellent introduction to the concept of causation as it pertains to non-experimental, observational data, see Shipley (2000).

Because the number of simultaneous independent regressions done at any one time is much lower using the PLS approach as opposed to the ML method, the sample size requirements for PLS are much reduced. Still, the robustness of path estimates in PLS is not without limits, and as a general rule the minimum number of samples in a model estimated using PLS should be ten times the maximum number of independent regressions done at any one time, or less if the effect size of component loadings is high (Chin 1998). Under such small sample sizes, it is still possible, or even likely, that PLS estimation will produce biased "parameter estimates, with (bootstrapped) standard errors that are rather wide" (Ed Rigdon, personal communication).

A partial least squares composite variable model for predicting wetland plant communities

The parameter estimates in the model that follows were estimated by PLS using the beta version (build 1060) of PLS-Graph 3.0 (Chin and Frye 2001). PLS was chosen over ML methods primarily because of the small sample size (n=24) of wetlands included in this study. McCune and Grace (2002) note that "In the initial phase where a field such as ecology begins to use SEM methods, early applications may rely on inadequate sample sizes due to a failure to anticipate or appreciate the need for larger sample sizes." This is certainly true in my case. My small sample size is also a result of the more ecosystem-level questions of interest. System-level variables are often time-consuming to estimate or measure, and ecological questions at the scale of square meters will usually be more tractable than questions at the ecosystem and landscape scales because it is easier to increase sample sizes at small spatial scales. McCune and Grace (2002) go on to suggest that "conclusions must be reasonable for the data that are available." Thus, the results of this model should be considered a tentative hypothesis, but nonetheless a first attempt at generating a multivariate hypothesis using landscape- and ecosystem-level variables to predict plant communities in Michigan wetlands.

The structural model (Figure 4.2) includes 8 composites; these composites represent theoretical variables that were introduced in one form or another in Chapters 2-3. Each path represents a relationship between composites that is

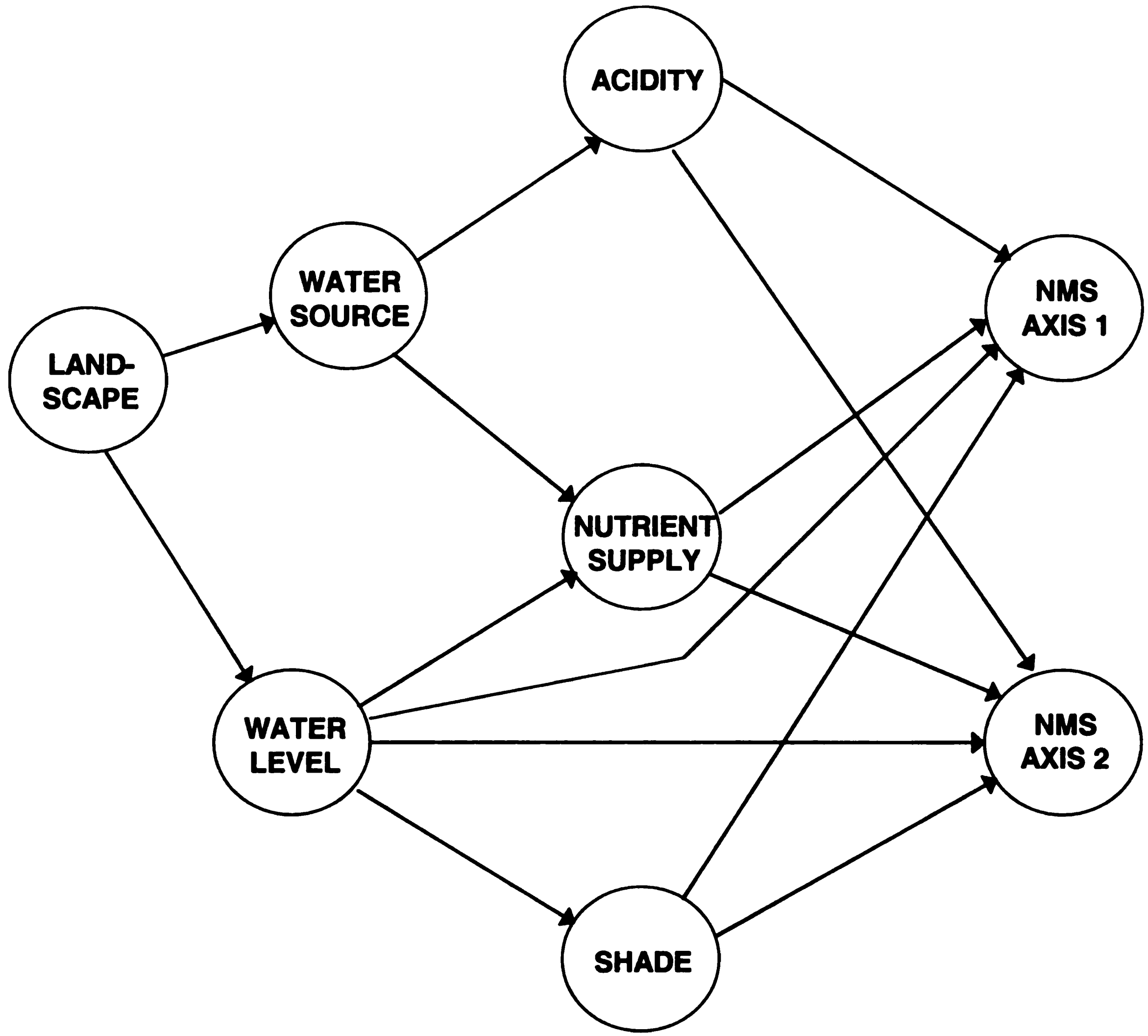

Figure 4.2: Structural model relating landscape variables, environmental variables, and plant community ordination axes from nonmetric multidimensional scaling.

supported by theory, prior research, or the current study. The variable Landscape is hypothesized as the cause of the ecosystem-level variables Water source and Water level. The first relationship is supported by this study: more precipitation-fed wetlands appear to be restricted to the upper portion of watersheds in the landscape (Chapter 2, Figure 2.17). The effect of Landscape on Water level could be due to the surface water connectivity of basins (Chapter 2), where basins with surface water outflows act to lower water levels in wetlands via drainage. Water source and Water level jointly act to determine Nutrient supply because groundwater is thought to supply nutrients more constantly through time, while higher water levels provide increased aqueous contact with, and thus greater nutrient supply to, root surfaces. Water source predicates the Acidity in wetlands because the alkaline groundwater typical of southern Michigan is well buffered and circumneutral, while precipitation-fed wetlands lack this acid neutralizing capacity and are characteristically acidic (pH ca. 4). As Water level increases, one would expect to find reduced cover by woody species, which in turn would reduce Shade cast by woody species on understory species; hence, the arrow from Water level to Shade. Finally, Acidity, Nutrient supply, Water level, and Shade are all thought to generate differences in wetland plant species abundance; all four of these composites have arrows directed toward the plant community ordination results from nonmetric multidimensional scaling (NMS): NMS Axis 1 and NMS Axis 2 (Chapter 3, Figure 3.4).

The measurement model (Figure 4.3) shows the relationship between indicators, or measured variables, and their associated composites.

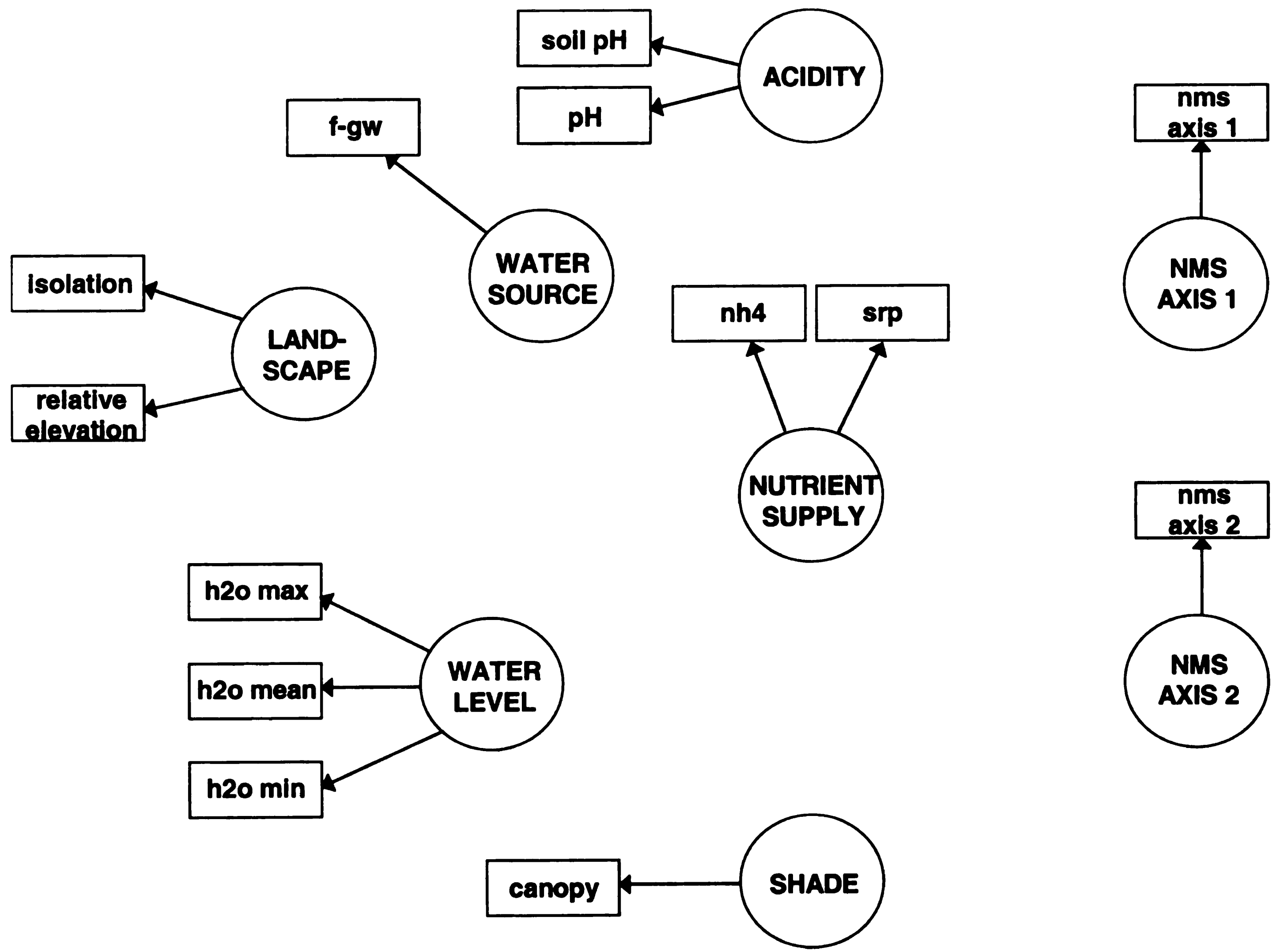

Figure 4.3: Measurement model relating composites to their indicators.

Two indicators, isolation and relative elevation, reflect the composite Landscape. Isolation is the opposite of surface water connectivity (Chapter 2, Table 2.2); isolation values vary along the following scale:

1 – depressions with no inlets or outlets;

0.66 – depressions with outflows only;

0.33 – depressions with marginal connection to an inflow/outflow system;

0 – depressions with an inflow/outflow system passing through them.

Relative elevation values also vary from 0–1; wetlands located higher in their watershed have relative elevation values that approach 1. Because isolated basins (isolation value = 1) tend to be located relatively high on the landscape (relative elevation value approaching 1), both these indicators will load on Landscape in a similar manner, which is preferable for interpretation of their path coefficients. Water source is associated with only one indicator: f-gw (identical to f_{gw} from Chapter 2, Figure 2.4). The composite Water level has three indicators, h20 max, h20 mean, and h20 min (Chapter 2, Table 2.8), all of which reflect water level in a wetland throughout the year in slightly different ways. Acidity is associated with the indicators pH and soil pH (Chapter 2, Tables 2.5 and 2.9, respectively). The indicators nh4 and srp, which are measures of nutrient accumulation on ion exchange resin (Chapter 2, Figures 2.7 and 2.9, respectively), reflect the composite Nutrient supply. Because NH_4^+ is the dominant form of N in reduced, waterlogged soils (Armstrong 1982) and in these wetlands (Chapter 2), NO_3^- is not included as an indicator of Nutrient supply. Shade is estimated by the indicator canopy, a measure of the amount of canopy cover by trees and tall shrubs at each wetland (Chapter 3, METHODS). Light measurements would be an excellent companion indicator of Shade, but were not made in this study. Finally, the NMS axis scores for each study site from the rotated ordination (Chapter 3, Figure 3.4) are the sole indicators of the composites NMS Axis 1 and NMS Axis 2.

Four of the eight composites (Water source, Shade, NMS Axis 1, and NMS Axis 2) only have a single indicator, which has two general disadvantages: the indicator is assumed to perfectly reflect the composite, and a single indicator does not allow the estimation of measurement error associated with the indicator. First, in PLS (and SEM in general) it is assumed that a single indicator perfectly reflects the theoretical composite of interest, and the path coefficient between the composite and the indicator is assigned a value of 1.0. However in ecology our measurements are often imperfect representations of the concepts that we are interested in studying. In such cases, multiple indicators that are all appropriate on theoretical grounds would better characterize the theoretical variable of interest.

Second, multiple indicators allow the estimation of measurement error associated with each indicator. Scientists rarely make measurements without error. If only one indicator is associated with a composite, it is assumed that the indicator is measured without error. The path coefficient from a composite to an indicator reflects how well the indicator correlates with other indicators loading on the same composite. Removing error variance associated with a composite and its indicators improves the parameter estimates in the model. Otherwise, the error variance that should be associated with a composite and its indicator remains as residual variance in the model, resulting in less accurate estimates of path coefficients and less explained variance (R^2 values) in endogenous composites (McCune and Grace 2002).

Of the four composites with only one indicator, two (NMS Axis 1 and NMS Axis 2) are certainly not a problem, as we know that the NMS axis scores reflect themselves exactly. Additional indicators of Water source and Shade would be desirable, especially as the estimation of water sources by [Mg^{2+}] and the estimation of shade from the cover values of tall woody species are imperfect measures of the theoretical variables of interest.

The initial model (Figure 4.4) includes both the structural model and the measurement model. It is helpful to evaluate this initial model and to remove any weak paths; this reduces unnecessary complexity in the model and thereby allows for more precise estimation of model parameters (Falk and Miller 1992). One model evaluation technique involves calculating the effect size f^2 of a composite that predicts an endogenous composite in the model (Chin 1998). This is done by deleting one of multiple paths from multiple composites that lead to an endogenous composite in the model, then evaluating the reduction in variance explained (R^2) in the endogenous composite due to the removal of that path. The effect size can be calculated as follows:

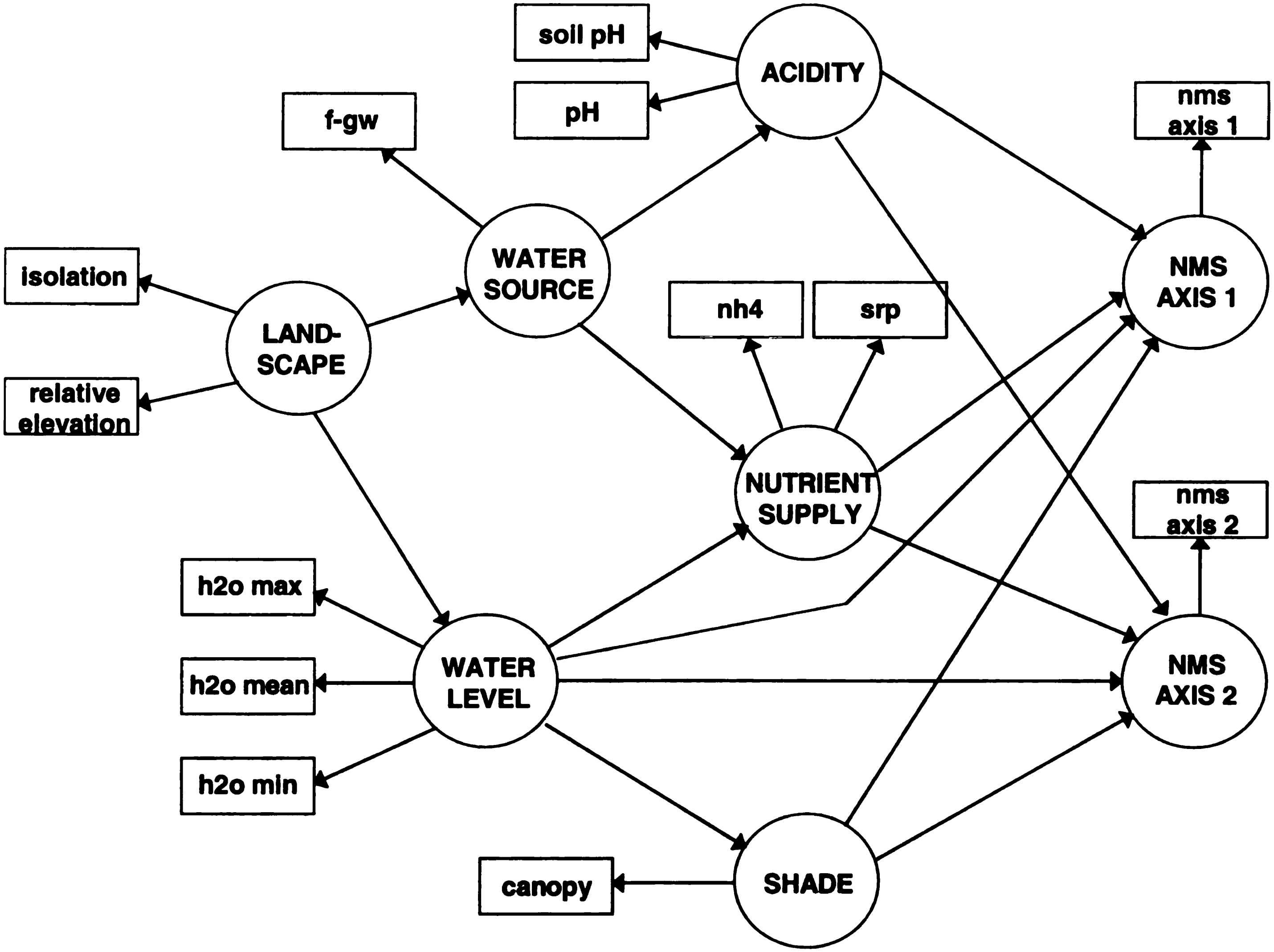

Figure 4.4: The initial model, including both the structural model and the measurement model.

$$f^2 = (R^2_{\text{included}} - R^2_{\text{excluded}}) / (1 - R^2_{\text{included}})$$

where R^2_{included} and R^2_{excluded} represent the variance explained with and without the path from the composite to the endogenous composite. As a general rule, f^2 values of 0.02, 0.15, and 0.35 represent small, medium, and large effect sizes (Chin 1998). Some paths were found to be very weak (i.e., small effect sizes), explaining little variance in the endogenous composites; these paths were deleted from the initial model. In addition, the paths from Landscape to Water level and Water level to Shade could not be evaluated using the calculation of effect sizes because removal of these paths changed Water level and Shade from endogenous to exogenous composites. These two paths were evaluated and subsequently deleted because the R^2 values for Water level (0.14) and Shade (0.06) were very low when these paths were included in the model. The final model (Figure 4.5) includes only those structural paths that had medium to large effect sizes.

Finally, to evaluate the stability of parameter estimates, a bootstrapping procedure in PLS-Graph was used to generate 100 subsamples of size n=24 (the same size as the original data set) in order to calculate standard errors for path coefficients in the structural model (Efron and Tibshirani 1993).

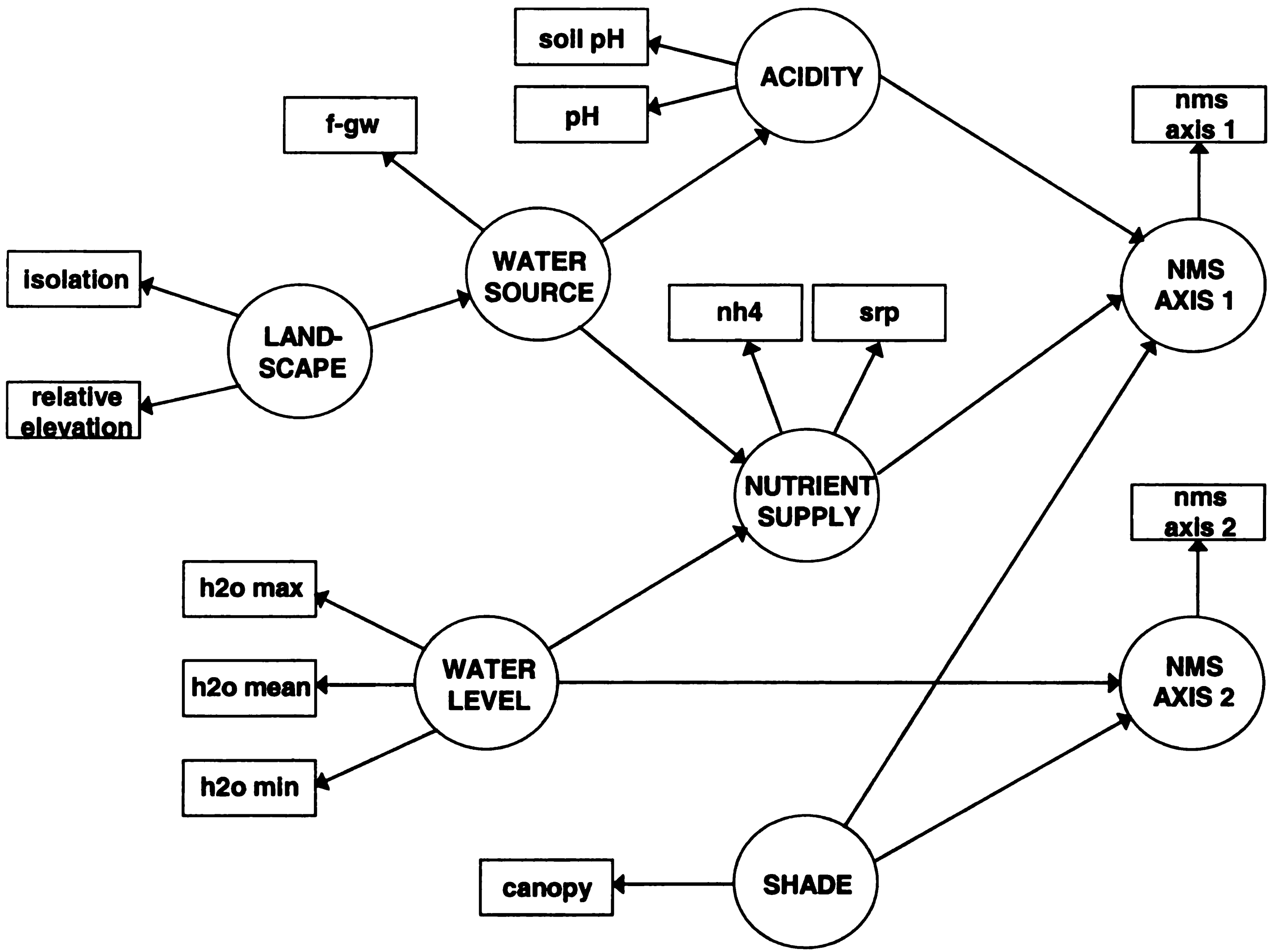

Figure 4.5: The final model includes only those structural paths that had medium to large effect sizes.

RESULTS

The final model (Figure 4.6) includes loadings between indicators and composites, the variance explained in endogenous composites, and path coefficients between composites. In the measurement model indicators showed strong relationships with their composites. Note that when a composite has a single indicator (e.g., Water source), the loading between the composite and the indicator is automatically set to 1.0, which assumes that the indicator perfectly reflects the composite and has 0 error variance. Of the four composites with multiple indicators (Landscape, Water level, Acidity, and Nutrient Supply), the loadings between each composite and its indicators were all very high (greater than 0.8, and generally greater than 0.93), which greatly exceed Falk and Miller's (1992) rule of thumb that they be greater than 0.55. The square of these loadings reflects the common shared variance between indicators via their composite; this is referred to as the indicator's communality (Falk and Miller 1992). Communality values were all relatively high (0.64 or greater, and generally 0.87 or greater; data not shown), demonstrating that the indicators in each block are loading onto their composites in similar ways with little residual variance that does not contribute to the composite.

The final model explained a very high percentage of the variance in NMS Axis 1 ($R^2 = 0.94$) and NMS Axis 2 ($R^2 = 0.80$), which together synthetically represent the wetland plant communities. Variance in Acidity was also explained well by the model ($R^2 = 0.92$), while variance in Water source ($R^2 = 0.60$) and Nutrient

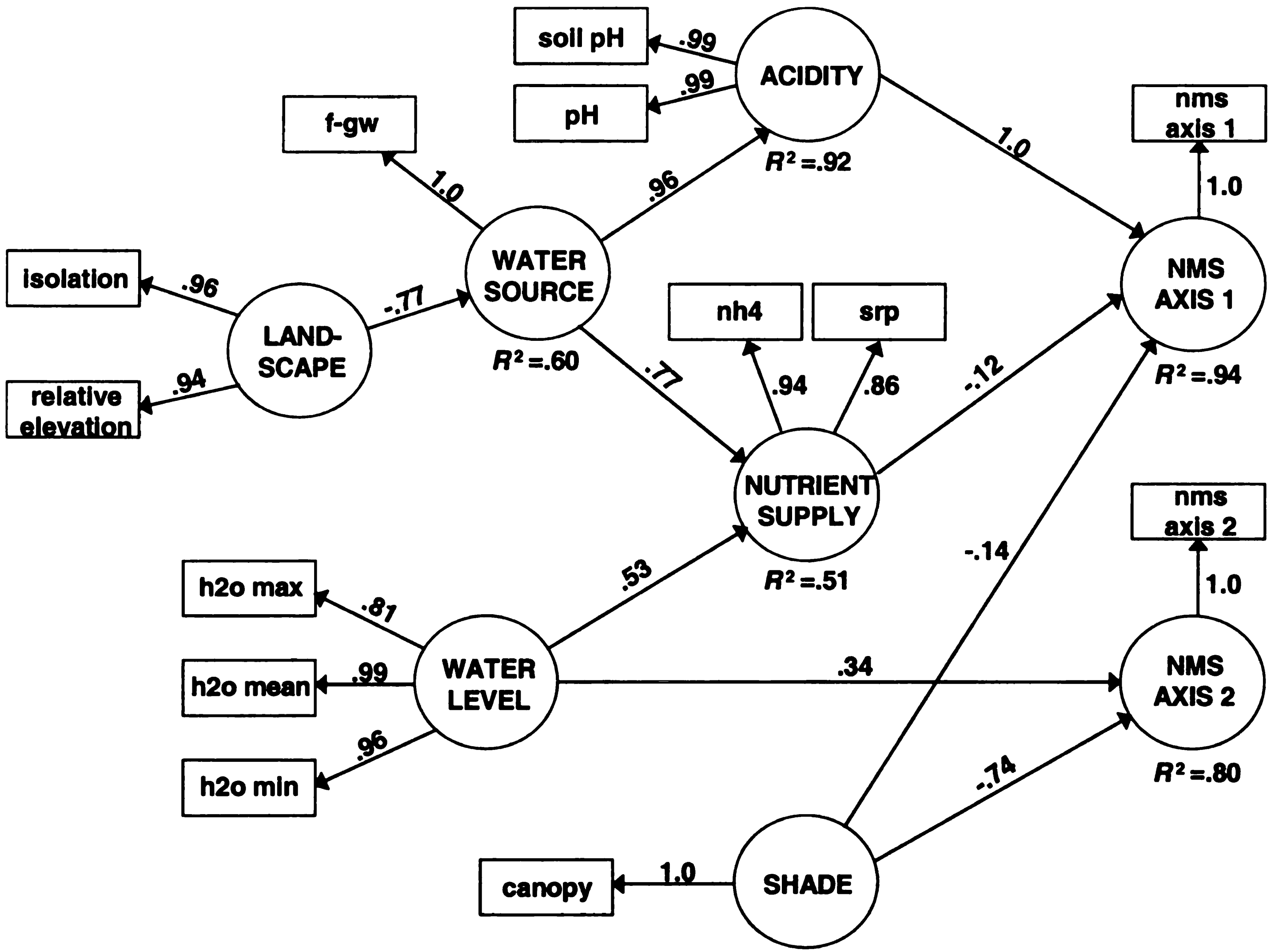

Figure 4.6: The final model with estimated path coefficients and variance explained (R^2) for endogenous composites.

supply (R^2 = 0.51) were explained moderately well. Overall, the model explains much of the variance in the five endogenous variables, indicating that the model has excellent predictive capability.

The path coefficients between composites are estimates of partial regression coefficients (Grace and Pugesek 1997). It is important to scrutinize the stability of path coefficients in a model with so few samples (n=24). Bootstrapped standard errors that are large indicate low parameter stability in the model. However, the bootstrapped standard errors for path coefficients were small in this model (0.09 or lower, and generally 0.05 or lower; Table 4.1), indicating relatively stable parameter estimates. Overall, while the model is very data-limited, it appears to perform well with regards to various model evaluation criteria.

predictor composite	predicted composite	path coefficient	standard error
Landscape	Water source	-.77	.01
Water source	Acidity	.96	.08
Water source	Nutrient supply	.77	.05
Water level	NMS Axis 2	.34	.03
Water level	Nutrient supply	.53	.04
Acidity	NMS Axis 1	1.0	.09
Shade	NMS Axis 1	-.14	.01
Shade	NMS Axis 2	-.74	.01
Nutrient supply	NMS Axis 1	-.12	.01

Table 4.1: Path coefficients (with bootstrapped standard errors) for the structural model.

DISCUSSION

The wetlands included in this partial least squares composite variable model span much of the diversity of more terrestrial wetlands in southwest Michigan. Therefore, this model can tentatively be considered a general model for predicting wetland plant communities in lower Michigan, with potential generality to other glacial terrain in the northern U.S. and southern Canada with ion-rich groundwaters and wetlands that vary across the hydrologic spectrum from largely precipitation-fed to largely groundwater-fed. The 161 vascular plant species, including trees, shrubs, forbs, graminoids, vines, and ferns, that were included in the ordination are represented synthetically by the two NMS ordination axes. The variance explained by the 2-dimensional ordination solution relative to the original *n*-dimensional space was 47.3% (NMS Axis 1) and 16.3% (NMS Axis 2) for a total of 63.7% variance explained. Note that three quarters of the explained variation in wetland plant communities was represented by NMS Axis 1. Consequently, the ability of the model to predict NMS Axis 1 is of greater importance than the model's ability to predict NMS Axis 2.

In the structural equation model, the variance explained in NMS Axis 1 (R^2 = 0.94) and NMS Axis 2 (R^2 = 0.80) by other composites was excellent. Based on the large path coefficients from Acidity to NMS Axis 1 and from Shade to NMS Axis 2, acidity and shade (i.e., light) appear to be the best predictors of different wetland plant communities in Michigan. Water level and Nutrient supply are also important in a predictive sense, but less so than acidity and shade. Tentatively, I conclude that these four environmental variables can explain much of the variance in wetland plant communities in glacial terrains like southern Michigan, although this hypothetical model requires subsequent independent testing.

If one takes the "causal leap" from prediction to causation, which should be done with caution, these paths from environmental variables to synthetic plant community variables suggest that acidity and shade are the strongest environmental variables generating the differences in wetland plant communities in Michigan. Based on what we know about plant physiology, these two variables are expected to influence plant community composition, so causality is certainly plausible. There may be other environmental variables that are important but were not included in this model, but I cannot evaluate their importance (although there is little unexplained variance remaining in NMS Axis 1 and NMS Axis 2, so additional environmental variables may not contribute much in terms of explaining additional variance). Still, it is possible to evaluate the relative importance of acidity, shade, nutrient supply, and water levels in terms of predicting and, tentatively speaking, causing differences in wetland plant communities in Michigan.

Based on the path coefficients in this model, acidity is much more important than nutrient supply in determining NMS Axis 1. Note that the plant communities along NMS Axis 1 span the bog to non-bog (i.e., fen and swamp) gradient (Chapter 3, Figure 3.5). Therefore, based on this model, I hypothesize that the differences in plant communities along the bog to non-bog gradient are due primarily to differences in species' abilities to tolerate acidic wetland habitats and much less so due to differences in nutrient availability in bog vs. non-bog habitats. Similarly, shade appears to be a more important controlling variable than water levels in determining wetland plant communities in this study. The relative importance of environmental variables in determining ecological outcomes (i.e., community composition) will remain a challenge for ecologists to disentangle, but structural equation modeling offers an interesting alternative for generating and subsequently testing multivariate hypotheses using observational data (Shipley 2000).

Acidity was very well predicted by Water sources in the final model (R^2 = 0.92). This was to be expected because [Mg^{2+}], which was used to estimate f-gw (and, hence, the composite Water source), is highly negatively correlated with pH, the indicator of the composite Acidity (Chapter 2, Tables 2.4-2.5); this is likely because dolomite weathering is the major source of both Mg^{2+} and alkalinity in groundwater. Because of this strong correlation between [Mg^{2+}] and pH, it is incorrect to consider these model results as confirmation that water sources are the primary determinant of differences in acidity in Michigan wetlands. Instead, this hypothesized relationship between water sources and acidity should, if possible, be corroborated by subsequent studies that attempt to estimate wetland water sources using other techniques that are not, for geochemical reasons, highly correlated with pH, the predicted variable of interest. However, because predicting the wetland plant communities was the primary goal of this model, an inability to independently predict acidity from water sources is not a major shortcoming of the model.

The Water source and Water level composites explained a moderate amount of the variance in the composite Nutrient supply ($R^2 = 0.51$). Based on the path coefficients to Nutrient supply from Water source (0.77) and Water level (0.53), the source of a wetland's water is more important than the water level in the wetland in terms of predicting the availability of nutrients in the wetland. In addition, because each of the path coefficients is positive, nutrient availability shows a positive relationship with water source and water level; thus, more groundwater-fed wetlands and wetlands with higher water levels are more likely to have greater nutrient availability.

Nutrient availability in wetlands has been a research topic of great interest for both biogeochemists and plant ecologists (Waughman 1980, Vitt et al. 1995, Bridgham et al. 1996, Bedford et al. 1999). While this model combines the availability of nitrogen (N) and phosphorus (P) into a single theoretical composite, N and P are usually treated separately in terms of nutrient limitation in plants. However, in the interests of simplicity, the model combines both N and P supply into a single composite. Note that other measures of nutrient availability could have been used in the model (aqueous nutrient concentrations, total N and P in peat), but nutrient accumulation on ion exchange resin was deemed the most appropriate estimate of nutrient supply to plants in this study.

The composite Landscape explained a substantial amount of the variance ($R^2 = 0.60$) in Water source. The path coefficient between Landscape and Water source was negative (-0.77), indicating a negative relationship between these two composites. Because high Landscape values reflect high isolation and high relative elevation, and high Water source values represent high f_{gw} estimates, this path reflects the shift from more groundwater-fed to precipitation-fed wetlands as wetlands become more isolated and positioned higher in their catchment. It is interesting that in this set of southern Michigan wetlands more than half the variation in wetland water sources can be explained by an understanding of the wetland's position in and association with its local landscape. This confirms some of the basic principles on which Brinson's (1993) hydrogeomorphic approach to wetland classification is based.

Finally, this model is a multivariate hypothesis of the landscape-level controls on ecosystem-level parameters and their subsequent determination of wetland plant communities. Few hypothetical models have been put forth to determine the relative importance of environmental variables in determining wetland plant communities across such a broad range of wetland types. To my knowledge, no statistical models have attempted to explain how landscape-level controls could act on these hypothesized environmental drivers of plant community composition. Yet, without such models that span different types of wetlands and bridge the scale from the landscape to communities, it will be difficult to advance theory in terms of the strength of abiotic controls on the distribution of different plant species, as well as what information landscape-level factors provide for ecologists. Structural equation modeling offers a very general template by which to first hypothesize and then subsequently test theoretical relationships in ecology; I expect that it will become a more commonly used technique in the ecologist's toolbox. Furthermore, the partial least squares approach offers a viable alternative to SEM in situations where sample size limitations, a very real issue in ecosystem ecology, prevent the use of the more common maximum likelihood estimation techniques.

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CHAPTER 5

CONCLUSIONS

As a comparative study, one of the strengths of this research was the diverse set of wetlands under study using the same methods across all sites. Because the study sites were situated in close proximity (within 50 km), comparisons across sites were not confounded by differences in climate or underlying geology. In addition, few studies have attempted to describe plant and environmental conditions across such different types of wetland ecosystems. Attempts at explaining the abundance and distribution of species in nature will always rely on studies that span broad environmental gradients. This kind of descriptive research remains a strong approach for generating testable hypotheses for future research.

The wetlands in this study included bogs, a poor fen, a diverse set of fens, and several different kinds of swamps located in southern Michigan. Over 200 vascular plant species were encountered in these wetlands, and 161 were included in the plant community analyses. The results of this study are applicable to southwestern lower Michigan; they may apply to other wetlands that 1) vary across the hydrologic spectrum from largely precipitation-fed to largely groundwater-fed; and 2) are located in glaciated landscapes where the underlying geology is comprised mainly of carbonate-rich glacial drift that determines the chemical composition of groundwater.

The water sources for the wetlands in this study spanned the gradient from precipitation-fed wetlands to highly groundwater-fed basins. Precipitation-fed wetlands were all acidic peatlands, or bogs, which were dominated by *Sphagnum* moss and included characteristic shrub species, including *Chamaedaphne calyculata* (leatherleaf) and *Vaccinium corymbosum* (highbush blueberry). The vegetation analyses helped distinguish two types of bog communities: leatherleaf bogs, which were dominated by *C. calyculata*, and bogs that contained taller shrubs. These precipitation-fed ecosystems appear to be restricted to the upper portions of their watersheds, where hydrologic flow paths have likely not been in contact with the underlying carbonate-rich glacial till. A perched water table above the alkaline groundwater, which has resulted from extensive peat accumulation, or the lack of inflowing, alkaline groundwater because of the formation of an aquiclude are probably both responsible for these systems having evolved along the pond-marsh-fen-bog trajectory since the last glaciation (Swinehart and Parker 2000). Plant communities in acidic peatlands remain distinct from most other types of local wetland plant communities. Although many plant species are thought to be excluded from bog habitats due to a paucity of nutrients, based on the results of this study, a more likely hypothesis is that most species that do not occur in bogs cannot tolerate the acidic conditions in the bog rooting zone. However, that lack of tolerance may involve the effect of acidity on root function and nutrient uptake, as discussed below.

Moving across the water source gradient, only one poor fen was included in this study. This was likely due to the rarity of such ecosystems. Poor fens are transitional between more circumneutral fens and bogs. Because of the rapid decrease in pH when a water's alkalinity is exhausted, the shift from fen to poor fen to bog may take only 50-350 years (Kuhry et al. 1993). The plant community in the poor fen included in this study was a mixture of species from fens and bogs. It would be interesting to include other poor fens in subsequent studies to better evaluate if the plant communities of poor fens are consistently transitional between the more prevalent bog and fen ecosystems.

Fens, while considered primarily groundwater-fed ecosystems, received as little as half their water from groundwater (vs. precipitation) and sometimes most of their water from groundwater. Hence, fens, while generally groundwater-fed, are not all strongly groundwater-driven ecosystems. The vegetation analyses distinguished two types of fens: sedge meadow fens and a more heterogeneous group of fens. Sedge meadow fens were slightly more alkaline and exhibited lower water levels than the other fens. Sedge meadow fens were characterized by species such as *Carex stricta* (tussock sedge) and *Aster puniceus* (purple-stemmed aster), while *Epilobium leptophyllum* (narrow-leaved willow herb) and *Pilea pumila* (clearweed) were more typical of the heterogeneous fens. All fen basins except one were associated with stream outflows or occurred along a small stream. Because small streams in this landscape tend to occur in areas of groundwater discharge, the hydrogeologic setting for fens in southern Michigan is generally associated with areas where groundwater discharges to the land surface (Winter et al. 2001, Amon et al. 2002).

Within the broad category of fens, species-rich fens, or "rich fens" ("rich" due to alkalinity, not species diversity), have received much attention from both conservation organizations and scientists (Amon et al. 2002, Godwin et al. 2002, Bedford and Godwin 2003). Several areas in this study that include characteristic species such as *Potentilla fruticosa* (shrubby cinquefoil), *Lobelia kalmii* (Kalm's lobelia), and *Parnassia glauca* (grass of Parnassus) might qualify as rich fens. The northern portion of Prairieville Creek, which was not included in the vegetation surveys, includes a small rich fen area. Likewise, portions of Mott Road Fen that are near the wetland-upland border (and not immediately adjacent to the small stream passing through the fen) are rich fen or wet prairie habitats (Legge et al. 1995). And while portions of Cemetery Fen include areas dominated by *Typha latifolia* (wide-leaved cattail), *Lythrum salicaria* (purple loosestrife), and various shrubs, rich fen areas remain. Future studies in the KBS area with an interest in rich fens could include these study sites. It would also be interesting to evaluate whether *T. latifolia* and *L. salicaria*, which are present nearby but do not currently persist in these rich fen habitats, invade these areas.

Swamps were moderately to highly groundwater-fed. In this study I encountered two broad types of swamps: wet swamps and a heterogeneous group of dry swamps. The microtopography in wet swamps varied between wet hollows and drier *Sphagnum* hummocks. Trees typical of wet swamps included *Acer rubrum* (red maple), *Ulmus americana* (American elm), and *Fraxinus nigra* (black ash), while *Osmunda cinnamomea* (cinnamon fern), *Maianthemum* *canadense* (Canada mayflower) and *Viola cucullata* (marsh violet) characterized the understory species. Overall, wet swamps tended to occur relatively high in their local watersheds and were areas of groundwater discharge where stream headwaters were borne. The widely distributed hummocks provided sufficiently drier, raised microsites in which trees and shrubs were rooted. The canopies of the trees and shrubs decreased light penetration and, together with the dichotomous moisture environment provided by hummocks and hollows, set the conditions in which a diverse herbaceous understory developed. Species such as *Vaccinium corymbosum* (highbush blueberry), *Nemopanthus mucronatus* (mountain holly), and *Ilex verticillata* (winterberry), which all occurred in several bog study sites, were also present in several wet swamps. (I even found *C. calyculata* (leatherleaf) growing on a few hummocks in one of the wet swamps!) This suggests that the hummocks in wet swamps may represent a unique wetland habitat type that is intermediate between acidic bogs and more alkaline swamps and fens, which has also been deduced by analysis of bryophytes on hummocks in a local fen (Glime et al. 1982).

The heterogeneous group of dry swamps included a floodplain swamp, a stream swamp, two treed fens, and a site that transitioned from swamp to fen to sedge meadow fen; thus, this was a diverse group of ecosystems. These sites included the driest and most groundwater-fed wetlands under study. While similar to wet swamps in terms of shade, dry swamps generally exhibited lower water levels and, as a likely consequence, had understory communities that were quite different from wet swamps. Species characteristic of dry swamps included

Onoclea sensibilis (sensitive fern), *Carex bromoides* (brome tussock sedge), and *Senecio aureus* (golden ragwort). Dry swamps, like fens, were strongly associated with streams and rivers, and this increased association with riverine inflows and outflows may have promoted greater drainage and decreases in water levels during the growing season. This short period of tension-saturated (vs. saturated) conditions in the rooting zone may provide the necessary temporal window in which trees are most photosynthetically active and can persist in these wetlands as opposed to others.

Statistically modeling the relations between landscape-level variables, environmental variables, and variance in wetland plant communities showed great promise in terms of predictive power. Landscape-level variables such as basin isolation and relative elevation in the watershed were strong predictors of a wetland's water sources. Wetlands that received more groundwater and exhibited higher water levels generally received greater nutrient supply. More groundwater-fed wetlands also tended towards circumneutrality, although this may have been an artifact of how water sources were estimated in this study. Acidity and shade were more important than nutrient supply and water levels in terms of predicting wetland plant communities in southern Michigan.

Based on results from this and other studies (Godwin et al. 2002), a landscape-level, hydrogeomorphic classification of wetlands (Brinson 1993) is an informative, hierarchical approach to classifying wetlands. One interesting result from this study was that bogs were restricted to the upper portions of their local watersheds. While this has been hypothesized before (Walbridge 1994), this is the first study to document a relative elevational threshold restricting bog occurrence. A strong test of this hypothesis would involve calculation of the relative elevation of many bogs using a geographic information system (GIS), a digital elevation model, and restricting the study to the PSS3 NWI class (which generally corresponds with *Chamaedaphne calyculata* (leatherleaf), a characteristic bog shrub). It is important to note that this bog threshold hypothesis is subject to several geographical restrictions: inland depressional wetlands that lie in a glacial landscape with groundwater that is strongly influenced by underlying carbonate geology.

Another interesting hypothesis that follows from this research is that wetland species are excluded from bog habitats due to acidity more than any measure of nutrient availability. Nitrogen limitation could still be acting to exclude most wetland species from bogs, but cytoplasmic acidosis as a result of high proton activity in the rooting zone could be the fundamental restriction on plant nutrient uptake. The largest consequence of this result is that it may be inappropriate to scale up measures of nutrient availability to the overall plant community in ecological studies that include acidic peatlands. The next step in evaluating this pattern should entail plant physiology experiments in which species performance is evaluated under rooting zone conditions that vary across gradients of acidity and nutrient availability. Only by studying both bog and non-bog species in a controlled experiment may it be possible to distinguish whether acidity or nutrient availability is the fundamental limitation on wetland plant occurrence in acidic peatlands.

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APPENDICES

APPENDIX A

LOCATION OF STUDY SITES

site	year	starting point		bearing	length
		LAT	LONG	(°)	(m)
Blachman Bog	1999	29.969'	22.445'	206	330
Purdy Bog	1999	25.880'	19.530'	281	100
transect 2		25.908'	19.745'	21	100
Kidd Bog	2000	27.312'	20.362'	221	100
transect 2		27.258'	20.400'	221	100
Leatherleaf Bog	2000	37.703'	30.687'	190	90
transect 2		37.675'	30.715'	217	110
Chainfern Bog	2000	37.507'	30.651'	34	100
transect 2		37.554'	30.617'	332	100
Blueberry Bog	1999	26.216'	27.090'	116	200
Longman Road Bog	2000	17.019'	18.862'	230	200
Chokeberry Bog	2000	24.418'	26.766'	245	200
Winterberry Bog	2000	35.970'	25.211'	80	100
transect 2		36.031'	25.207'	202	100
Lang Fen	2000	25.174'	19.182'	185	100
transect 2		25.141'	19.200'	236	100
Glasby Fen	1999	28.292'	23.977'	342	200
Cemetery Fen	1999	20.084'	19.603'	340	150
transect 2		20.104'	19.682'	340	50
Butterfield Fen	1999	21.586'	24.608'	216	200
Balker Lake Swamp	2000	29.401'	21.043'	90	200
Otis Pond Swamp	2000	36.159'	25.260'	110	200
Stafford Fen	1999	24.996'	20.426'	268	200
Sherriff Fen	1999	24.178'	19.796'	270	30
transect 2		24.218'	19.875'	243	20
transect 3		24.235'	19.985'	210	20
transect 4		24.297'	20.055'	256	20
Mott Road Fen	2000	17.937'	19.445'	9	100
transect 2		17.987'	19.400'	180	100
Starflower Swamp	2000	37.687'	30.223'	287	200
Serbin Swamp	1999	35.918'	29.769'	180	350
Turner Creek Fen	2000	39.159'	28.522'	175	80
transect 2		39.112'	28.528'	221	10
transect 3		39.110'	28.533'	193	110
Stafford Swamp	1999	24.176'	19.451'	309	100
transect 2		24.147'	19.240'	178	100
Prairieville Creek Fen	1999	26.255'	25.836'	340	285
Kalamazoo River Swamp	1999	19.241'	21.635'	297	200

Table A1.1: Locations of vegetation transects at 24 wetland study sites. All LAT coordinates are at N 42° and all LONG coordinates are at W 85°. Vegetation surveys were conducted in either 1999 or 2000.

site	well 1		well 2		well 3	
	LAT	LONG	LAT	LONG	LAT	LONG
Blachman Bog	29.939'	22.457'	29.894'	22.489'	29.851'	22.516'
Purdy Bog	25.880'	19.530'	25.891'	19.605'	25.899'	19.681'
Kidd Bog	27.271'	20.349'	27.273'	20.384'	27.224'	20.442'
Leatherleaf Bog	37.703'	30.687'	37.660'	30.736'	37.630'	30.775'
Chainfern Bog	37.507'	30.651'	37.554'	30.620'	37.589'	30.647'
Blueberry Bog	26.205'	27.066'	26.178'	27.002'	26.180'	26.928'
Longman Road Bog	17.019'	18.862'	16.982'	18.918'	16.951'	18.963'
Chokeberry Bog	24.418'	26.766'	24.392'	26.832'	24.354'	26.824'
Winterberry Bog	35.979'	25.206'	35.998'	25.210'	35.021'	25.206'
Lang Fen	25.174'	19.182'	25.129'	19.184'	25.108'	19.230'
Glasby Fen	28.295'	23.978'	28.328'	23.996'	28.389'	24.026'
Cemetery Fen	20.107'	19.613'	20.140'	19.634'	20.092'	19.675'
Butterfield Fen	21.586'	24.608'	21.546'	24.645'	21.498'	24.679'
Balker Lake Swamp	29.402'	21.033'	29.405'	20.964'	29.411'	20.911'
Otis Pond Swamp	36.159'	25.260'	36.137'	25.193'	36.127'	25.124'
Stafford Fen	24.996'	20.426'	24.990'	20.499'	24.992'	25.572'
Sherriff Fen	24.178'	19.796'	24.174'	19.815'	24.170'	19.833'
Mott Road Fen	17.937'	19.445'	17.993'	19.433'	17.978'	19.399'
Starflower Swamp	37.687'	30.223'	37.696'	30.294'	37.711'	30.372'
Serbin Swamp	35.918'	29.769'	35.837'	29.767'	35.783'	29.765'
well 4	35.733'	29.764'				
Turner Creek Fen	39.148'	28.520'	39.100'	28.537'	39.062'	28.553'
Stafford Swamp	24.176'	19.451'	24.202'	19.487'	24.248'	19.497'
Prairieville Creek Fen	26.266'	25.851'	26.312'	25.910'	26.347'	25.965'
Kalamazoo River Swamp	19.241'	21.635'	19.255'	21.667'	19.263'	21.705'
wells 4-5	19.280'	21.737'	19.278'	21.668'		

Table A1.2: Locations of water level monitoring wells at 24 wetland study sites. All LAT coordinates are at N 42° and all LONG coordinates are at W 85°.

APPENDIX B

VEGETATION DATA

site	Ace rub	Ace sac	Bet all	Fag gra	Fra ame	Fra nig	Fra pen	Gle tri
Blachman Bog	0.001	0	0	0	0	0	0	0
Purdy Bog	0	0	0	0	0	0	0	0
Kidd Bog	0.005	0	0	0	0	0	0	0
Leatherleaf Bog	0	0	0	0	0	0	0	0
Chainfern Bog	0.045	0	0	0	0	0	0	0
Blueberry Bog	0.002	0	0	0	0	0	0	0
Longman Road Bog	0	0	0	0	0	0	0	0
Chokeberry Bog	0	0	0	0	0	0	0	0
Winterberry Bog	0	0	0	0	0	0	0	0
Lang Fen	0	0	0	0	0	0	0	0
Glasby Fen	0	0	0	0	0	0	0	0
Cemetery Fen	0	0	0	0	0	0	0.001	0
Butterfield Fen	0	0	0	0	0	0	0	0
Balker Lake Swamp	0.196	0	0.041	0	0	0.025	0	0
Otis Pond Swamp	0.430	0	0.076	0	0	0.162	0	0
Stafford Fen	0	0	0	0	0	0.055	0	0
Sherriff Fen	0	0	0	0	0	0	0	0
Mott Road Fen	0	0	0	0	0	0	0	0
Starflower Swamp	0.376	0	0.046	0.0315	0.044	0.059	0.014	0
Serbin Swamp	0.020	0	0	0	0	0.308	0	0
Turner Creek Fen	0.104	0	0	0	0	0	0	0
Stafford Swamp	0.067	0	0.221	0	0.001	0.118	0	0
Prairieville Creek Fen	0.004	0	0	0	0	0	0	0
Kalamazoo River Swamp	0	0.4385	0	0	0.059	0.057	0.295	0.0245

Table A2.1: Fraction cover values for all 208 plant species that occurred on the vegetation transects. Each species is abbreviated by the first three letters of its genus and specific epithet. Botanical nomenclature follows Voss (1972, 1985, 1996) except for the family Equisetaceae (horsetails) and the division Polypodiophyta (ferns), for which nomenclature follows Gleason and Cronquist (1991). Species are alphabetized by plant category: tree; shrub; forb, vine, and fern; graminoid. “Unk” = unknown.

site	Lar lar	Lir tul	Pin str	Pla occ	Pop tre	Pru ser	Pru vir	Que bic
Blachman Bog	0	0	0.015	0	0	0	0	0
Purdy Bog	0	0	0	0	0	0	0	0
Kidd Bog	0.259	0	0	0	0	0	0	0
Leatherleaf Bog	0	0	0	0	0	0	0	0
Chainfern Bog	0	0	0	0	0	0	0	0
Blueberry Bog	0	0	0	0	0	0	0	0
Longman Road Bog	0	0	0	0	0	0	0	0
Chokeberry Bog	0	0	0	0	0	0	0	0
Winterberry Bog	0	0	0	0	0	0	0	0
Lang Fen	0	0	0	0	0	0	0	0
Glasby Fen	0	0	0	0	0	0	0	0
Cemetery Fen	0	0	0	0	0	0.0175	0	0
Butterfield Fen	0	0	0	0	0	0	0	0
Balker Lake Swamp	0.030	0	0	0	0	0	0	0
Otis Pond Swamp	0	0	0	0	0	0	0	0
Stafford Fen	0	0	0	0	0	0	0	0
Sherriff Fen	0	0	0	0	0	0	0	0
Mott Road Fen	0	0	0	0	0	0	0	0
Starflower Swamp	0	0	0.203	0	0	0	0.009	0
Serbin Swamp	0.185	0.0175	0.036	0	0	0	0	0
Turner Creek Fen	0.046	0	0	0	0	0	0	0
Stafford Swamp	0	0	0	0	0	0	0	0
Prairieville Creek Fen	0	0	0	0	0.008	0	0	0
Kalamazoo River Swamp	0	0	0	0.062	0	0	0	0.1505

Table A2.1 (cont'd).

site	Sal nig	Til ame	Ulm ame	Aln rug	And gla	Aro pru	Bet pum	Car arb
Blachman Bog	0	0	0	0	0	0.15	0	0
Purdy Bog	0	0	0	0	0	0	0	0
Kidd Bog	0	0	0	0	0.0002	0.002	0.01	0
Leatherleaf Bog	0	0	0	0	0	0.1995	0	0
Chainfern Bog	0	0	0	0	0	0.1533	0	0
Blueberry Bog	0	0	0	0	0	0.147	0	0
Longman Road Bog	0	0	0	0	0	0	0	0
Chokeberry Bog	0	0	0	0	0	0.3768	0	0
Winterberry Bog	0	0	0	0	0	0.006	0	0
Lang Fen	0	0	0	0	0	0	0	0
Glasby Fen	0	0	0	0	0	0	0	0
Cemetery Fen	0	0	0	0	0	0	0	0
Butterfield Fen	0	0	0.017	0	0	0	0	0
Balker Lake Swamp	0	0	0.097	0	0	0.0215	0	0
Otis Pond Swamp	0	0	0.511	0.0705	0	0	0	0
Stafford Fen	0	0	0.027	0	0	0	0	0
Sherriff Fen	0	0	0	0	0	0	0	0
Mott Road Fen	0	0	0	0	0	0	0	0
Starflower Swamp	0	0	0.316	0	0	0	0	0
Serbin Swamp	0	0	0.038	0	0	0	0	0
Turner Creek Fen	0	0	0	0	0	0	0	0.017
Stafford Swamp	0	0.071	0.112	0	0	0	0	0
Prairieville Creek Fen	0	0	0	0	0	0	0.0017	0
Kalamazoo River Swamp	0.061	0	0.045	0	0	0	0	0

Table A2.1 (cont'd).

site	Car car	Cep occ	Cha cal	Cor foe	Cor sto	Ile ver	Lin ben	Lon mor
Blachman Bog	0	0	0.605	0	0	0	0	0
Purdy Bog	0	0	0.8998	0	0	0	0	0
Kidd Bog	0	0	0.2653	0	0	0.0655	0	0
Leatherleaf Bog	0	0	0.3795	0	0	0.1005	0	0
Chainfern Bog	0	0	0.0295	0	0	0.0085	0	0
Blueberry Bog	0	0	0.0573	0	0	0	0	0
Longman Road Bog	0	0	0.955	0	0	0	0	0
Chokeberry Bog	0	0	0.446	0	0	0.3523	0	0
Winterberry Bog	0	0.0057	0.0053	0	0	0.1303	0	0
Lang Fen	0	0	0	0	0	0	0	0
Glasby Fen	0	0	0	0	0.0065	0	0	0
Cemetery Fen	0	0	0	0.1073	0.0183	0.0368	0	0.0318
Butterfield Fen	0	0	0	0.0052	0.0928	0	0	0
Balker Lake Swamp	0	0	0.002	0.1005	0.0043	0.3412	0	0
Otis Pond Swamp	0	0	0	0.1038	0	0.11	0.0168	0
Stafford Fen	0.0363	0	0	0.153	0.1968	0	0	0
Sherriff Fen	0	0	0	0	0	0	0	0
Mott Road Fen	0	0	0	0.1765	0.0168	0	0	0
Starflower Swamp	0	0	0	0.0685	0	0.1853	0.3223	0
Serbin Swamp	0	0	0	0	0.1375	0.0775	0.24	0
Turner Creek Fen	0	0	0	0	0	0	0.0202	0
Stafford Swamp	0.475	0	0	0.0205	0	0.0098	0.016	0
Prairieville Creek Fen	0	0	0	0.0683	0.0005	0	0	0
Kalamazoo River Swamp	0	0	0	0.0295	0	0	0.039	0

Table A2.1 (cont'd).

site	Nem muc	Pot fru	Rha fra	Rib ame	Rib hir	Ros pal	Rub set	Rub str
Blachman Bog	0.0145	0	0	0	0	0	0	0
Purdy Bog	0	0	0	0	0	0	0	0
Kidd Bog	0.0403	0	0.0012	0	0	0	0	0
Leatherleaf Bog	0.0023	0	0	0	0	0	0	0
Chainfern Bog	0	0	0	0	0	0	0	0
Blueberry Bog	0	0	0	0	0	0	0	0
Longman Road Bog	0	0	0.0137	0	0	0	0	0
Chokeberry Bog	0	0	0.108	0	0	0	0	0
Winterberry Bog	0	0	0	0	0	0	0	0
Lang Fen	0	0	0	0	0	0.0012	0	0
Glasby Fen	0	0	0.0658	0	0	0	0	0
Cemetery Fen	0	0.0172	0.0225	0	0	0	0.0308	0.0188
Butterfield Fen	0	0	0	0	0	0.049	0	0
Balker Lake Swamp	0	0	0.0025	0	0.0038	0.0635	0	0
Otis Pond Swamp	0.0593	0	0	0	0	0.0243	0	0
Stafford Fen	0	0	0.0477	0.008	0.0188	0	0	0
Sherriff Fen	0	0	0	0	0	0	0	0
Mott Road Fen	0	0.107	0	0	0.0015	0	0	0
Starflower Swamp	0.1348	0	0	0	0	0.0017	0	0
Serbin Swamp	0	0	0	0	0.0147	0	0	0
Turner Creek Fen	0	0	0	0	0	0	0	0
Stafford Swamp	0	0	0	0.0045	0.008	0	0	0.0015
Prairieville Creek Fen	0	0.0032	0.7393	0	0	0.002	0	0
Kalamazoo River Swamp	0	0	0	0	0	0	0	0

Table A2.1 (cont'd).

site	Unk	Sal dis	Spi alb	Tox ver	Vac cor	Vac oxy	Vib den	Vib len
Blachman Bog	0	0	0	0	0.6035	0.1227	0	0
Purdy Bog	0	0	0	0	0	0.1933	0	0
Kidd Bog	0	0	0	0.0035	0.3752	0.126	0	0
Leatherleaf Bog	0	0	0	0	0.5235	0	0	0
Chainfern Bog	0	0	0	0	0.109	0	0	0
Blueberry Bog	0	0	0	0	0.9533	0	0	0
Longman Road Bog	0	0	0	0	0	0	0	0
Chokeberry Bog	0	0	0	0	0.1083	0	0	0
Winterberry Bog	0	0	0	0	0.15	0	0	0
Lang Fen	0	0.1618	0.0828	0	0	0	0	0
Glasby Fen	0	0	0	0	0	0	0	0
Cemetery Fen	0	0	0.096	0	0	0	0.0878	0.0155
Butterfield Fen	0	0	0	0.0585	0	0	0	0
Balker Lake Swamp	0	0	0	0.0825	0.1685	0	0	0
Otis Pond Swamp	0	0	0	0.0065	0.0823	0	0	0
Stafford Fen	0	0.037	0	0.1075	0	0	0	0
Sherriff Fen	0	0	0	0	0	0	0	0
Mott Road Fen	0	0	0	0	0	0	0	0
Starflower Swamp	0	0	0	0.0555	0.0787	0	0	0
Serbin Swamp	0.0092	0	0	0.12	0	0	0	0
Turner Creek Fen	0	0	0	0.2488	0	0	0	0
Stafford Swamp	0	0	0	0	0	0	0	0
Prairieville Creek Fen	0	0.135	0	0.079	0	0	0	0.0813
Kalamazoo River Swamp	0	0	0	0	0	0	0	0.0633

Table A2.1 (cont'd).

site	Aga pur	Agr pub	Ali pla	Amp bra	Ang atr	Api ame	Ari tri	Asc inc
Blachman Bog	0	0	0	0	0	0	0	0
Purdy Bog	0	0	0	0	0	0	0	0
Kidd Bog	0	0	0	0	0	0	0	0
Leatherleaf Bog	0	0	0	0	0	0	0	0
Chainfern Bog	0	0	0	0	0	0	0	0
Blueberry Bog	0	0	0	0	0	0	0	0
Longman Road Bog	0	0	0	0	0	0	0	0
Chokeberry Bog	0	0	0	0	0	0	0	0
Winterberry Bog	0	0	0	0	0	0	0	0
Lang Fen	0	0	0	0	0	0	0	0
Glasby Fen	0	0	0	0	0	0	0	0
Cemetery Fen	0.01	0	0	0.0025	0	0	0	0
Butterfield Fen	0.0043	0	0	0.0045	0	0	0	0
Balker Lake Swamp	0	0	0	0	0	0	0	0
Otis Pond Swamp	0	0	0	0	0	0	0.0037	0
Stafford Fen	0	0	0	0.07	0	0	0	0
Sherriff Fen	0	0	0	0	0	0	0	0
Mott Road Fen	0.0035	0	0	0	0	0	0	0
Starflower Swamp	0	0	0	0.0317	0	0	0.0038	0
Serbin Swamp	0	0	0.0002	0.0355	0	0.0142	0.007	0
Turner Creek Fen	0	0	0.0017	0.018	0.019	0	0	0
Stafford Swamp	0	0	0	0.0877	0	0	0.0002	0
Prairieville Creek Fen	0	0.0108	0	0.0008	0	0	0.0035	0.0073
Kalamazoo River Swamp	0	0.003	0	0	0	0	0	0

Table A2.1 (cont'd).

site	Ast bor	Ast lan	Ast lat	Ast pun	Ast umb	Ath fil	Bid cer	Bid con
Blachman Bog	0	0	0	0	0	0	0	0
Purdy Bog	0	0	0	0	0	0	0	0
Kidd Bog	0	0	0	0	0	0	0	0
Leatherleaf Bog	0	0	0	0	0	0	0	0
Chainfern Bog	0	0	0	0	0	0	0	0
Blueberry Bog	0	0	0	0	0	0	0	0
Longman Road Bog	0	0	0	0	0	0	0	0
Chokeberry Bog	0	0	0	0	0	0	0	0
Winterberry Bog	0	0	0	0	0	0	0	0
Lang Fen	0	0	0	0.0033	0	0	0	0
Glasby Fen	0	0	0	0	0	0	0.0295	0.002
Cemetery Fen	0.003	0	0	0.23	0.0212	0	0	0
Butterfield Fen	0	0	0.0087	0.1748	0	0	0	0
Balker Lake Swamp	0	0.0155	0.0015	0	0	0	0	0.01
Otis Pond Swamp	0	0	0.007	0.0153	0	0.0292	0	0
Stafford Fen	0	0.0068	0	0.0883	0	0	0	0.0078
Sherriff Fen	0	0	0	0	0	0	0.1003	0
Mott Road Fen	0	0	0.058	0.0988	0	0	0	0
Starflower Swamp	0	0.0015	0	0.0282	0	0.0012	0.0075	0.0023
Serbin Swamp	0	0	0.012	0.007	0	0.012	0	0
Turner Creek Fen	0	0	0	0.0182	0	0	0	0
Stafford Swamp	0	0	0.0495	0	0	0.0185	0	0
Prairieville Creek Fen	0	0	0	0.018	0	0	0	0
Kalamazoo River Swamp	0	0	0.0237	0	0	0	0	0

Table A2.1 (cont'd).

site	Bid cor	Boe cyl	Calla pal	Calt pal	Cam apa	Che gla	Cic bul	Cic mac
Blachman Bog	0	0	0	0	0	0	0	0
Purdy Bog	0	0	0	0	0	0	0	0
Kidd Bog	0	0	0	0	0	0	0	0
Leatherleaf Bog	0	0	0	0	0	0	0	0
Chainfern Bog	0	0	0	0	0	0	0	0
Blueberry Bog	0	0	0.053	0	0	0	0	0
Longman Road Bog	0	0	0	0	0	0	0	0
Chokeberry Bog	0	0	0	0	0	0	0	0
Winterberry Bog	0	0	0	0	0	0	0.0003	0
Lang Fen	0.0003	0	0	0	0.002	0	0.0018	0
Glasby Fen	0.0135	0	0	0	0	0	0.004	0
Cemetery Fen	0.0027	0	0	0	0	0	0	0
Butterfield Fen	0	0.0155	0	0	0.0057	0	0	0
Balker Lake Swamp	0.0005	0.0195	0	0	0	0	0.0178	0
Otis Pond Swamp	0	0.0415	0	0	0	0	0	0
Stafford Fen	0.0015	0	0	0	0.0133	0	0	0
Sherriff Fen	0	0.0007	0	0	0.0098	0	0.013	0
Mott Road Fen	0	0	0	0	0.001	0.012	0	0
Starflower Swamp	0	0.0095	0	0	0	0	0	0
Serbin Swamp	0	0.0192	0	0.0077	0.0038	0	0	0
Turner Creek Fen	0	0.059	0	0	0.002	0	0	0
Stafford Swamp	0	0.0418	0	0	0	0	0	0
Prairieville Creek Fen	0	0.0022	0	0	0	0	0	0.0072
Kalamazoo River Swamp	0	0.026	0	0.003	0	0.005	0	0

Table A2.1 (cont'd).

site	Cir mut	Cli bor	Cop tri	Cyp aca	Cyp cal	Dec ver	Dio vil	Dro rot
Blachman Bog	0	0	0	0	0	0	0	0
Purdy Bog	0	0	0	0	0	0	0	0.0045
Kidd Bog	0	0	0	0.003	0	0.0498	0	0.0067
Leatherleaf Bog	0	0	0	0	0	0.0183	0	0
Chainfern Bog	0	0	0	0	0	0.0695	0	0
Blueberry Bog	0	0	0	0	0	0	0	0
Longman Road Bog	0.0043	0	0	0	0	0	0	0
Chokeberry Bog	0	0	0	0	0	0.1958	0	0
Winterberry Bog	0	0	0	0	0	0.096	0	0
Lang Fen	0	0	0	0	0	0	0	0
Glasby Fen	0	0	0	0	0	0.017	0	0
Cemetery Fen	0	0	0	0	0	0	0	0
Butterfield Fen	0	0	0	0	0	0	0	0
Balker Lake Swamp	0	0	0	0	0	0	0	0
Otis Pond Swamp	0	0	0.0217	0	0	0	0	0
Stafford Fen	0.0095	0	0	0	0	0	0	0
Sherriff Fen	0	0	0	0	0	0.1148	0	0
Mott Road Fen	0.0033	0	0	0	0	0	0	0
Starflower Swamp	0	0	0.0173	0	0.0063	0	0	0
Serbin Swamp	0	0.004	0	0	0	0	0	0
Turner Creek Fen	0	0	0	0	0	0	0	0
Stafford Swamp	0	0	0	0	0	0	0.0008	0
Prairieville Creek Fen	0.0047	0	0	0	0	0	0	0
Kalamazoo River Swamp	0	0	0	0	0	0	0.0135	0

Table A2.1 (cont'd).

site	Dry car	Dry cri	Epi cil	Epi lep	Euo obo	Eup mac	Eup per	Eup rug
Blachman Bog	0	0	0	0	0	0	0	0
Purdy Bog	0	0	0	0	0	0	0	0
Kidd Bog	0	0	0	0	0	0	0	0
Leatherleaf Bog	0	0	0	0	0	0	0	0
Chainfern Bog	0	0	0	0	0	0	0	0
Blueberry Bog	0	0	0	0	0	0	0	0
Longman Road Bog	0	0	0	0.004	0	0	0	0
Chokeberry Bog	0	0	0	0	0	0	0	0
Winterberry Bog	0	0	0	0	0	0	0.0023	0
Lang Fen	0	0	0	0.0165	0	0.0085	0.0403	0
Glasby Fen	0	0	0.0135	0.021	0	0	0	0
Cemetery Fen	0	0.0115	0	0	0	0.048	0.0018	0.0028
Butterfield Fen	0	0	0	0	0	0.0638	0.0292	0
Balker Lake Swamp	0	0	0	0	0	0	0	0
Otis Pond Swamp	0	0.0048	0	0	0	0	0	0
Stafford Fen	0	0.0045	0	0	0	0.0163	0.0015	0
Sherriff Fen	0	0	0	0.032	0	0.0023	0	0
Mott Road Fen	0	0.0025	0	0	0	0.03	0.0017	0.0003
Starflower Swamp	0	0	0.0023	0	0	0	0	0
Serbin Swamp	0	0	0	0	0	0.0103	0.004	0
Turner Creek Fen	0	0.0042	0	0	0	0.0553	0	0
Stafford Swamp	0.0015	0.0025	0	0	0	0	0	0
Prairieville Creek Fen	0	0	0	0	0	0.0085	0.0035	0
Kalamazoo River Swamp	0	0	0	0	0.0178	0	0	0.0018

Table A2.1 (cont'd).

site	Fra ves	Fra vir	Gal asp	Gal trifid	Gal triflor	Gen cri	Geu can	Hab cla
Blachman Bog	0	0	0	0	0	0	0	0
Purdy Bog	0	0	0	0	0	0	0	0
Kidd Bog	0	0	0	0	0	0	0	0
Leatherleaf Bog	0	0	0	0	0	0	0	0
Chainfern Bog	0	0	0	0	0	0	0	0
Blueberry Bog	0	0	0	0	0	0	0	0
Longman Road Bog	0	0	0	0	0	0	0	0
Chokeberry Bog	0	0	0	0	0	0	0	0
Winterberry Bog	0	0	0	0.011	0	0	0	0
Lang Fen	0	0	0	0.0577	0	0	0	0
Glasby Fen	0	0	0	0	0	0	0	0
Cemetery Fen	0	0	0	0	0	0	0	0
Butterfield Fen	0	0	0	0.008	0	0	0	0
Balker Lake Swamp	0	0	0	0	0	0	0	0
Otis Pond Swamp	0	0	0	0	0.0037	0	0	0.0013
Stafford Fen	0	0	0	0	0.012	0	0	0
Sherriff Fen	0	0	0	0.0545	0	0	0	0
Mott Road Fen	0	0	0	0	0.0018	0.0015	0	0
Starflower Swamp	0	0.0017	0	0	0.0035	0	0.0017	0
Serbin Swamp	0	0.002	0	0	0.0178	0	0	0
Turner Creek Fen	0.0035	0	0.0253	0	0	0	0	0
Stafford Swamp	0	0	0.0045	0	0	0	0.023	0
Prairieville Creek Fen	0	0	0	0	0.0115	0	0	0
Kalamazoo River Swamp	0	0	0	0	0.0017	0	0	0

Table A2.1 (cont'd).

site	Hyd umb	Imp cap	Iri vir	Lap can	Lat pal	Lem min	Lyc ame	Lyc uni
Blachman Bog	0	0	0	0	0	0	0	0
Purdy Bog	0	0	0	0	0	0	0	0
Kidd Bog	0	0	0	0	0	0	0	0
Leatherleaf Bog	0	0	0	0	0	0	0	0
Chainfern Bog	0	0	0	0	0	0	0	0
Blueberry Bog	0	0	0	0	0	0	0	0
Longman Road Bog	0	0	0	0	0	0	0	0.0057
Chokeberry Bog	0	0	0	0	0	0	0	0
Winterberry Bog	0	0	0	0	0	0	0	0.0735
Lang Fen	0	0.3023	0	0	0	0	0	0.114
Glasby Fen	0	0.0015	0	0	0	0	0	0.027
Cemetery Fen	0	0.002	0	0	0.0032	0	0.001	0.0235
Butterfield Fen	0.0018	0.0465	0.015	0	0.0007	0	0	0.0108
Balker Lake Swamp	0	0.0135	0	0	0	0	0	0.0053
Otis Pond Swamp	0	0.0057	0	0	0	0	0	0.0028
Stafford Fen	0	0.0013	0	0	0	0	0.0025	0.0093
Sherriff Fen	0	0	0	0	0	0.0992	0	0.0158
Mott Road Fen	0	0	0	0	0	0	0	0.0132
Starflower Swamp	0	0.0142	0	0	0	0	0	0
Serbin Swamp	0	0.0685	0	0.009	0	0.0133	0	0
Turner Creek Fen	0	0.015	0	0	0.006	0.002	0	0.0093
Stafford Swamp	0	0.013	0	0.195	0	0	0	0
Prairieville Creek Fen	0	0.0718	0	0	0.003	0	0	0.0008
Kalamazoo River Swamp	0	0.005	0	0.2465	0	0	0	0

Table A2.1 (cont'd).

site	Lys cil	Lys num	Lys thy	Lyt sal	Mai can	Men arv	Mit rep	Mon fis
Blachman Bog	0	0	0	0	0	0	0	0
Purdy Bog	0	0	0	0	0	0	0	0
Kidd Bog	0	0	0	0	0	0	0	0
Leatherleaf Bog	0	0	0	0	0	0	0	0
Chainfern Bog	0	0	0	0	0	0	0	0
Blueberry Bog	0	0	0	0	0	0	0	0
Longman Road Bog	0	0	0	0	0	0	0	0
Chokeberry Bog	0	0	0	0	0	0	0	0
Winterberry Bog	0	0	0.0385	0	0	0	0	0
Lang Fen	0	0	0.005	0.0195	0	0	0	0
Glasby Fen	0	0	0.0065	0	0	0	0	0
Cemetery Fen	0	0	0	0.062	0	0.0137	0	0
Butterfield Fen	0	0	0	0.361	0	0.0093	0	0
Balker Lake Swamp	0	0.001	0.0015	0	0.0063	0	0	0
Otis Pond Swamp	0	0	0.006	0	0.022	0	0.0088	0
Stafford Fen	0.0092	0	0	0	0	0.0063	0	0
Sherriff Fen	0	0.0018	0.0115	0.015	0	0	0	0
Mott Road Fen	0	0	0	0.0207	0	0.0055	0	0.0118
Starflower Swamp	0	0	0	0	0.011	0	0.0153	0
Serbin Swamp	0	0	0.0065	0	0.016	0	0	0
Turner Creek Fen	0	0.0053	0	0	0	0	0	0
Stafford Swamp	0	0	0.002	0	0.0027	0	0	0
Prairieville Creek Fen	0	0	0	0	0	0	0	0
Kalamazoo River Swamp	0	0.005	0	0	0	0	0	0

Table A2.1 (cont'd).

site	Myo sco	Ono sen	Osm cin	Osm reg	Oxy rig	Par qui	Ped lan	Pel vir
Blachman Bog	0	0	0	0	0	0	0	0
Purdy Bog	0	0	0	0	0	0	0	0
Kidd Bog	0	0	0	0	0	0	0	0
Leatherleaf Bog	0	0	0	0	0	0	0	0
Chainfern Bog	0	0	0	0	0	0	0	0
Blueberry Bog	0	0	0	0	0	0	0	0
Longman Road Bog	0	0	0	0	0	0	0	0
Chokeberry Bog	0	0	0	0	0	0.0015	0	0
Winterberry Bog	0	0	0.0015	0	0	0	0	0
Lang Fen	0	0.03	0	0	0	0.0008	0	0
Glasby Fen	0	0.0015	0	0.0435	0	0	0	0
Cemetery Fen	0	0.0035	0	0	0.0015	0	0	0
Butterfield Fen	0	0	0	0	0.002	0	0	0
Balker Lake Swamp	0	0.004	0.034	0.1542	0	0	0	0
Otis Pond Swamp	0	0.073	0.6838	0.077	0	0.0548	0	0
Stafford Fen	0	0.1535	0	0	0.0102	0.003	0.0148	0
Sherriff Fen	0	0	0	0	0	0	0	0
Mott Road Fen	0	0.0012	0	0	0	0	0	0
Starflower Swamp	0	0	0.4158	0.0023	0	0.004	0	0
Serbin Swamp	0	0	0.129	0	0	0.007	0.0055	0.0165
Turner Creek Fen	0	0.3338	0	0	0	0.0028	0	0
Stafford Swamp	0	0.054	0.0358	0	0	0.027	0	0
Prairieville Creek Fen	0	0.386	0	0	0	0.0212	0	0
Kalamazoo River Swamp	0.0035	0.0455	0	0	0	0.0033	0	0

Table A2.1 (cont'd).

site	Phy ame	Pil pum	Pol amp	Pol ari	Pol pun	Pol sag	Pol vir	Pot pal
Blachman Bog	0	0	0	0	0	0	0	0
Purdy Bog	0	0	0	0	0	0	0	0
Kidd Bog	0	0	0	0	0	0	0	0
Leatherleaf Bog	0	0	0	0	0	0	0	0
Chainfern Bog	0	0	0	0	0	0	0	0
Blueberry Bog	0	0	0	0	0	0	0	0
Longman Road Bog	0.0033	0	0	0	0	0.0015	0	0
Chokeberry Bog	0	0	0	0	0	0	0	0
Winterberry Bog	0	0	0.0118	0.0118	0	0.071	0	0
Lang Fen	0	0.226	0.0058	0	0.033	0.073	0	0.0198
Glasby Fen	0	0.3523	0.0003	0	0	0	0	0
Cemetery Fen	0	0	0.0153	0	0	0	0	0
Butterfield Fen	0	0.0103	0.0078	0	0	0	0	0
Balker Lake Swamp	0	0.0045	0	0	0	0	0	0
Otis Pond Swamp	0	0	0	0.007	0	0	0	0
Stafford Fen	0	0.0443	0	0	0	0.006	0	0
Sherriff Fen	0	0.3978	0	0	0	0.0065	0	0
Mott Road Fen	0	0	0	0	0	0	0	0
Starflower Swamp	0	0.0002	0	0	0.0018	0	0	0
Serbin Swamp	0	0.0115	0	0.0047	0	0	0	0.069
Turner Creek Fen	0	0.1148	0	0	0.009	0.0168	0	0
Stafford Swamp	0	0.0513	0	0.0313	0	0	0.0002	0
Prairieville Creek Fen	0	0	0.0045	0	0	0.0015	0	0
Kalamazoo River Swamp	0	0.0548	0	0	0	0	0.0058	0

Table A2.1 (cont'd).

site	Pru vul	Pyc vir	Ran rec	Ror pal	Rub pen	Rub pub	Rud lac	Rum orb
Blachman Bog	0	0	0	0	0	0	0	0
Purdy Bog	0	0	0	0	0	0	0	0
Kidd Bog	0	0	0	0	0	0	0	0
Leatherleaf Bog	0	0	0	0	0	0	0	0
Chainfern Bog	0	0	0	0	0	0	0	0
Blueberry Bog	0	0	0	0	0	0	0	0
Longman Road Bog	0	0	0	0	0.001	0	0	0
Chokeberry Bog	0	0	0	0	0	0	0	0
Winterberry Bog	0	0	0	0	0	0	0	0
Lang Fen	0	0	0	0.0055	0	0	0	0.004
Glasby Fen	0	0	0	0	0	0	0	0
Cemetery Fen	0	0.06	0	0	0	0	0	0
Butterfield Fen	0	0	0	0	0	0.0013	0	0
Balker Lake Swamp	0	0	0	0	0	0.031	0	0
Otis Pond Swamp	0	0	0	0	0	0.0125	0	0
Stafford Fen	0	0	0	0	0	0.0115	0	0
Sherriff Fen	0	0	0	0	0	0	0	0.0153
Mott Road Fen	0.0588	0.0312	0	0	0	0	0	0
Starflower Swamp	0	0	0.0095	0	0	0.0052	0	0
Serbin Swamp	0.0032	0	0	0	0	0	0	0.0015
Turner Creek Fen	0	0	0	0	0	0	0	0
Stafford Swamp	0.0028	0	0.0015	0	0	0.001	0	0
Prairieville Creek Fen	0	0	0	0	0	0	0	0
Kalamazoo River Swamp	0	0	0	0	0	0	0.0677	0

Table A2.1 (cont'd).

site	Sag lat	Sag rig	Sar pur	Scu gal	Scu lat	Sen aur	Unk	Unk
Blachman Bog	0	0	0	0	0	0	0	0
Purdy Bog	0	0	0.001	0	0	0	0	0
Kidd Bog	0	0	0.0118	0	0	0	0	0
Leatherleaf Bog	0	0	0	0	0	0	0	0
Chainfern Bog	0	0	0	0	0	0	0	0
Blueberry Bog	0	0	0	0	0	0	0	0
Longman Road Bog	0	0	0	0	0	0	0	0
Chokeberry Bog	0	0	0	0	0	0	0	0
Winterberry Bog	0	0	0	0	0	0	0	0
Lang Fen	0.0068	0	0	0.0392	0	0	0	0
Glasby Fen	0	0	0	0.006	0	0	0	0
Cemetery Fen	0	0	0	0	0	0	0	0
Butterfield Fen	0.004	0	0	0	0.002	0	0	0
Balker Lake Swamp	0	0	0	0	0.0005	0	0	0
Otis Pond Swamp	0	0	0	0	0.006	0	0	0
Stafford Fen	0	0	0	0	0	0.0003	0	0
Sherriff Fen	0.16	0.0002	0	0	0	0	0	0
Mott Road Fen	0	0	0	0	0	0	0	0
Starflower Swamp	0	0	0	0	0.011	0	0	0
Serbin Swamp	0.0235	0	0	0.0032	0	0	0.0015	0.009
Turner Creek Fen	0	0	0	0.0045	0	0.0003	0	0
Stafford Swamp	0	0	0	0	0.0022	0.0495	0	0
Prairieville Creek Fen	0	0	0	0	0	0.0825	0	0
Kalamazoo River Swamp	0.0325	0	0	0	0	0	0	0

Table A2.1 (cont'd).

site	Unk	Unk	Unk	Unk	Siu sua	Smi sp	Smi ste	Sol can
Blachman Bog	0	0	0	0	0	0	0	0
Purdy Bog	0	0	0	0	0	0	0	0
Kidd Bog	0	0	0	0	0	0	0	0
Leatherleaf Bog	0	0	0	0	0	0	0	0
Chainfern Bog	0	0	0	0	0	0	0	0
Blueberry Bog	0	0	0	0	0	0	0	0
Longman Road Bog	0	0	0	0	0	0	0	0
Chokeberry Bog	0	0	0	0	0	0	0	0
Winterberry Bog	0	0	0	0	0	0	0	0
Lang Fen	0	0	0	0	0	0	0	0
Glasby Fen	0	0	0	0	0	0	0	0
Cemetery Fen	0	0	0	0	0	0	0	0.0488
Butterfield Fen	0	0	0	0	0	0	0	0.0082
Balker Lake Swamp	0	0	0	0	0	0	0	0
Otis Pond Swamp	0	0	0	0	0	0	0	0
Stafford Fen	0	0	0	0	0	0	0.0012	0.013
Sherriff Fen	0	0	0	0	0	0	0	0
Mott Road Fen	0	0	0	0	0	0	0.0078	0.0163
Starflower Swamp	0	0	0	0	0	0	0	0
Serbin Swamp	0.0023	0.01	0.0018	0.002	0.005	0.0065	0	0
Turner Creek Fen	0	0	0	0	0	0	0	0.016
Stafford Swamp	0	0	0	0	0	0	0	0
Prairieville Creek Fen	0	0	0	0	0	0	0	0
Kalamazoo River Swamp	0	0	0	0	0	0	0.0258	0.0085

Table A2.1 (cont'd).

site	Sol dul	Sol gig	Sol ohi	Sol pat	Sol rug	Spa chl	Sym foe	Tha das
Blachman Bog	0	0	0	0	0	0	0	0
Purdy Bog	0	0	0	0	0	0	0	0
Kidd Bog	0	0	0	0	0	0	0	0
Leatherleaf Bog	0	0	0	0	0	0	0	0
Chainfern Bog	0	0	0	0	0	0	0	0
Blueberry Bog	0	0	0	0	0	0	0	0
Longman Road Bog	0.002	0	0	0	0	0	0	0
Chokeberry Bog	0	0	0	0	0	0	0	0
Winterberry Bog	0	0	0	0	0	0.0058	0	0
Lang Fen	0	0	0	0	0	0	0	0
Glasby Fen	0.0042	0	0	0	0	0	0	0
Cemetery Fen	0	0	0	0.0105	0.1005	0	0	0
Butterfield Fen	0	0	0	0.01	0	0	0	0
Balker Lake Swamp	0.0013	0	0	0	0.0135	0	0	0
Otis Pond Swamp	0.001	0	0	0	0.0222	0	0.038	0
Stafford Fen	0	0	0	0.0483	0.0225	0	0.0015	0
Sherriff Fen	0	0	0	0	0	0.038	0	0
Mott Road Fen	0	0	0.0035	0.0123	0.0203	0	0	0
Starflower Swamp	0	0	0	0.0187	0.0095	0	0.0023	0
Serbin Swamp	0	0	0	0.0237	0.0335	0.006	0.0922	0
Turner Creek Fen	0	0.0145	0	0.046	0.0322	0.0117	0	0
Stafford Swamp	0	0	0	0.041	0.002	0	0.0038	0
Prairieville Creek Fen	0	0	0	0.02	0.0585	0	0.151	0.0008
Kalamazoo River Swamp	0	0	0	0.0275	0	0.061	0.0912	0.024

Table A2.1 (cont'd).

site	The pal	Tia cor	Tox rad	Tri bor	Tri fra	Typ ang	Typ lat	Urt dio
Blachman Bog	0	0	0	0	0	0	0	0
Purdy Bog	0	0	0	0	0	0	0	0
Kidd Bog	0	0	0	0	0	0	0	0
Leatherleaf Bog	0	0	0	0	0	0	0	0
Chainfern Bog	0	0	0	0	0	0	0	0
Blueberry Bog	0	0	0	0	0	0	0	0
Longman Road Bog	0	0	0	0	0	0	0	0
Chokeberry Bog	0	0	0	0	0.001	0	0	0
Winterberry Bog	0	0	0	0	0.0005	0	0	0
Lang Fen	0.011	0	0	0	0	0	0	0
Glasby Fen	0.182	0	0	0	0	0	0.7657	0
Cemetery Fen	0.1605	0	0	0	0	0	0.0477	0
Butterfield Fen	0.0285	0	0	0	0	0	0.0035	0
Balker Lake Swamp	0.0223	0	0	0.0012	0	0	0.0022	0
Otis Pond Swamp	0	0	0	0	0	0	0	0
Stafford Fen	0.03	0	0	0	0	0	0.2188	0
Sherriff Fen	0.0805	0	0	0	0	0	0.279	0
Mott Road Fen	0.0702	0	0	0	0	0	0	0
Starflower Swamp	0	0	0	0.002	0	0	0	0
Serbin Swamp	0.1065	0.0067	0.0103	0	0	0.018	0.157	0
Turner Creek Fen	0.0028	0	0	0	0	0	0	0
Stafford Swamp	0.0588	0	0.0182	0	0	0	0	0
Prairieville Creek Fen	0.0262	0	0	0	0	0	0.0155	0
Kalamazoo River Swamp	0	0	0.0308	0	0	0	0	0.0058

Table A2.1 (cont'd).

site	Vio cuc	Vit rip	Woo vir	And ger	Bro cil	Cal can	Car beb	Car bro
Blachman Bog	0	0	0.0365	0	0	0	0	0
Purdy Bog	0	0	0	0	0	0	0	0
Kidd Bog	0	0	0.0718	0	0	0	0	0
Leatherleaf Bog	0	0	0.4843	0	0	0	0	0
Chainfern Bog	0	0	0.746	0	0	0	0	0
Blueberry Bog	0	0	0	0	0	0	0	0
Longman Road Bog	0	0	0	0	0	0	0	0
Chokeberry Bog	0	0	0.0125	0	0	0	0	0
Winterberry Bog	0	0	0	0	0	0.7378	0	0
Lang Fen	0	0	0	0	0	0.0973	0.002	0
Glasby Fen	0	0	0	0	0	0	0	0
Cemetery Fen	0	0	0	0	0	0.094	0	0
Butterfield Fen	0	0	0	0	0	0.0672	0	0
Balker Lake Swamp	0.0005	0	0	0	0	0.0347	0.002	0
Otis Pond Swamp	0.0553	0	0	0	0	0.0042	0	0.022
Stafford Fen	0.0128	0	0	0	0	0	0	0.2558
Sherriff Fen	0	0	0	0	0	0	0	0
Mott Road Fen	0	0	0	0.0002	0.0027	0.114	0	0
Starflower Swamp	0.0077	0	0	0	0	0	0	0.0687
Serbin Swamp	0.0233	0	0	0	0	0.0005	0	0
Turner Creek Fen	0.0013	0	0	0	0	0	0	0
Stafford Swamp	0.008	0	0	0	0	0	0	0.1675
Prairieville Creek Fen	0	0	0	0	0	0	0	0.2237
Kalamazoo River Swamp	0.0163	0.0092	0	0	0	0	0	0.1765

Table A2.1 (cont'd).

site	Car com	Car hys	Car int	Car lac	Car lep	Car oli	Car ret	Car ros
Blachman Bog	0	0	0	0	0	0	0	0
Purdy Bog	0	0	0	0	0	0.1293	0	0
Kidd Bog	0	0	0	0	0	0.3728	0	0
Leatherleaf Bog	0	0	0	0	0	0	0	0
Chainfern Bog	0	0	0	0	0	0	0	0
Blueberry Bog	0	0	0	0	0	0	0	0.0275
Longman Road Bog	0	0	0	0	0	0	0	0.004
Chokeberry Bog	0	0	0	0	0	0	0	0
Winterberry Bog	0	0	0	0.053	0	0	0	0.0243
Lang Fen	0	0	0	0.2288	0	0	0.0735	0.1103
Glasby Fen	0.03	0	0	0	0	0	0	0
Cemetery Fen	0	0	0	0	0	0	0	0
Butterfield Fen	0	0	0	0.0597	0	0	0.0043	0
Balker Lake Swamp	0.0085	0	0	0.3652	0	0	0	0
Otis Pond Swamp	0	0	0	0	0.0005	0	0	0
Stafford Fen	0	0	0	0.0563	0	0	0.3398	0
Sherriff Fen	0.02	0	0	0.319	0	0	0	0
Mott Road Fen	0	0.0003	0	0	0	0	0	0
Starflower Swamp	0	0	0.0145	0	0	0	0	0
Serbin Swamp	0	0	0	0.2935	0	0	0	0
Turner Creek Fen	0	0	0	0	0	0	0.0065	0
Stafford Swamp	0	0	0	0	0	0	0.0225	0
Prairieville Creek Fen	0	0	0	0	0	0	0	0
Kalamazoo River Swamp	0	0	0	0.0353	0	0	0	0

Table A2.1 (cont'd).

site	Car sti	Car str	Cin aru	Dul aru	Ele ery	Ele int	Ely rip	Ely vir
Blachman Bog	0	0	0	0	0	0	0	0
Purdy Bog	0	0	0	0	0	0	0	0
Kidd Bog	0	0	0	0	0	0	0	0
Leatherleaf Bog	0	0	0	0	0	0	0	0
Chainfern Bog	0	0	0	0	0	0	0	0
Blueberry Bog	0	0	0	0.0215	0	0	0	0
Longman Road Bog	0	0	0	0	0	0	0	0
Chokeberry Bog	0	0	0	0	0	0	0	0
Winterberry Bog	0	0	0	0.0012	0	0	0	0
Lang Fen	0	0.1518	0	0	0.209	0	0	0
Glasby Fen	0	0	0	0	0	0	0	0
Cemetery Fen	0	0.8693	0	0	0	0	0	0
Butterfield Fen	0	0.7855	0	0	0	0	0	0
Balker Lake Swamp	0	0	0	0.0035	0.099	0	0	0
Otis Pond Swamp	0	0	0.006	0	0	0	0	0
Stafford Fen	0	0	0	0	0.0425	0	0	0
Sherriff Fen	0	0.021	0	0	0.4208	0	0	0
Mott Road Fen	0	0.9175	0	0	0.0293	0	0	0
Starflower Swamp	0	0	0	0	0	0	0	0
Serbin Swamp	0	0.0833	0	0	0.0615	0	0	0
Turner Creek Fen	0.0002	0.3908	0	0	0	0.091	0	0.001
Stafford Swamp	0	0	0	0	0	0	0.0005	0
Prairieville Creek Fen	0	0.052	0	0	0	0	0	0
Kalamazoo River Swamp	0	0.0983	0	0	0	0	0.016	0

Table A2.1 (cont'd).

site	Equ arv	Equ flu	Eri vir	Gly sep	Gly str	Hys pat	Lee ory	Muh mex
Blachman Bog	0	0	0	0	0	0	0	0
Purdy Bog	0	0	0.0032	0	0	0	0	0
Kidd Bog	0	0	0	0	0	0	0	0
Leatherleaf Bog	0	0	0	0	0	0	0	0
Chainfern Bog	0	0	0	0	0	0	0	0
Blueberry Bog	0	0	0	0	0	0	0	0
Longman Road Bog	0	0	0	0	0	0	0	0
Chokeberry Bog	0	0	0	0	0	0	0	0
Winterberry Bog	0	0	0	0.0035	0	0	0.0983	0
Lang Fen	0	0	0	0	0.0255	0	0.105	0
Glasby Fen	0	0	0	0	0	0	0.0365	0
Cemetery Fen	0	0	0	0	0	0	0.001	0.009
Butterfield Fen	0	0	0	0	0	0	0.0318	0.002
Balker Lake Swamp	0.0068	0	0	0	0.009	0	0.1857	0
Otis Pond Swamp	0	0	0	0	0.039	0	0	0
Stafford Fen	0	0.0393	0	0	0.0083	0	0.2413	0.0025
Sherriff Fen	0	0	0	0	0	0	0.3268	0
Mott Road Fen	0	0	0	0	0	0	0	0.0022
Starflower Swamp	0	0	0	0	0.0025	0	0.0493	0.0065
Serbin Swamp	0	0	0	0	0.0158	0	0.0528	0
Turner Creek Fen	0	0	0	0	0.0102	0	0.2393	0.001
Stafford Swamp	0	0	0	0	0.039	0.001	0.0185	0
Prairieville Creek Fen	0	0	0	0	0	0	0	0
Kalamazoo River Swamp	0	0	0	0	0	0	0.0335	0

Table A2.1 (cont'd).

site	Pha aru	Phr aus	Poa pal	Rhy alb	Sci atr	Sci cyp	Sci val	Spa pec
Blachman Bog	0	0	0	0	0	0	0	0
Purdy Bog	0	0	0	0.079	0	0	0	0
Kidd Bog	0	0	0	0	0	0	0	0
Leatherleaf Bog	0	0	0	0	0	0	0	0
Chainfern Bog	0	0	0	0	0	0	0	0
Blueberry Bog	0	0	0	0	0	0	0	0
Longman Road Bog	0	0	0	0	0	0	0	0
Chokeberry Bog	0	0	0	0	0	0	0	0
Winterberry Bog	0.0393	0	0	0	0	0.0393	0	0
Lang Fen	0.0793	0	0	0	0	0	0	0
Glasby Fen	0.0747	0	0	0	0	0	0	0
Cemetery Fen	0	0	0	0	0	0	0	0
Butterfield Fen	0	0	0	0	0.0003	0	0.0168	0
Balker Lake Swamp	0	0	0	0	0	0	0	0
Otis Pond Swamp	0	0	0	0	0	0	0	0
Stafford Fen	0.0138	0	0	0	0	0	0	0
Sherriff Fen	0	0.0828	0	0	0	0	0.0308	0
Mott Road Fen	0	0	0	0	0	0	0	0
Starflower Swamp	0	0	0	0	0	0	0	0
Serbin Swamp	0.0252	0	0.0265	0	0	0	0	0
Turner Creek Fen	0.1255	0	0	0	0	0	0	0.01
Stafford Swamp	0.0205	0	0	0	0	0	0	0
Prairieville Creek Fen	0	0	0	0	0	0	0	0
Kalamazoo River Swamp	0.0758	0	0	0	0	0	0	0

Table A2.1 (cont'd).